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The Coastal and Pelagic Foraging Behaviour of Grey Seals and Southern Elephant Seals: A Stable Isotope Approach

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University of Durham

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- 3 DEC 2004

ABSTRACT

Whisker samples were collected from grey seals from North Rona and from Isle of May in 1997-1999, from southern elephant seals from Pensinsular Valdés, Patagonia, from 1998 and 1999 and from South American sea lions also from Pensinsular Valdés in 1999. The whiskers were sub-sampled along their length and analysed for stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

There were significant differences between the two populations of grey seal and between years for each of the populations. Isotopic variations seen along the length of some of the whiskers were greater than could be attributed to background variation, indicating some seasonal variation. Possible prey items were herring, sandeels, some species of flat fish and gadoids. A strong temporal shift in apparent prey choice was seen only for the Isle of May, and the shift over a period of three years diminished the difference between the two populations. This could reflect changing prey choice or prey abundance in the North Sea over this time period.

Male and female southern elephant seals showed significant differences in their isotopic values, with the male seals showing three different isotopic clusters that were distinct from one another and from the female seals. Two of these groups showed higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than those of the females and the third group. South American sea lions showed significantly higher values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than female and most male southern elephant seals, suggesting that they were feeding at a higher trophic level. The South American sea lions and the group of male southern elephant seals with the highest values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were possibly eating similar prey species which could include various fish and elasmobranch species. The female seals were feeding on prey with an isotopic signature similar to that of krill.

To my parents who made this possible, Holly Megan and Beth

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Declaration

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Chapter 1 : Introduction

CHAPTER 1

Introduction

1.1. General Introduction

This chapter is concerned with outlining the need for a quantitative method of dietary assessment that can be successfully used in pinniped species to give a better understanding of feeding behaviour in this group of animals than existing methods have done thus far. It is proposed in this study that the stable isotope analysis of ^{13}C and ^{15}N would be able to provide the quantitative assessment required for further dietary studies. Furthermore, the use of this analysis of seal vibrissae should give a better indication of seal diet than that obtained by other methods. Due to the slow vibrissa growth (0.35mm/day for harbour seals (*Phoca vitulina*) (Hirons *et al.*, 2001) over a period of time (about one year)) the data from the analysis of sections of the vibrissae should give an indication of any seasonal variation present in the study animal's diet. It is this data that is lacking in many pinniped dietary studies. In order to establish the need for the use of this method, the life histories of the chosen study species, (the grey seal (*Halicohoerus grypus*) and the southern elephant seal (*Mirounga leonina*)) will be discussed, followed by a discussion of the current methodologies used to study pinniped feeding behaviour and where these methods fail to provide sufficient data. The use of stable isotope analysis in dietary studies will be examined and reasons given as to why stable isotope analysis is an appropriate method to use in a study of this kind.

Research into pinniped feeding biology is important to both enable a better understanding of the interactions between pinnipeds and their prey species and to understand how these interactions may affect or be affected by commercial fisheries or other human activities.

Pinnipeds are known to include in their diet some species of fish that are commercially important to fisheries (Rae, 1973; Murie & Lavigne; 1992, Hammond *et al.*, 1994 a and b), but the quantities of fish that are needed by the seals are estimated from energy requirements of the seals in indirect studies (Hammond *et al.*, 1994 b), and the species of fish making up the seal diet are gained from studies examining the stomach contents or scats of the seal (Rae, 1960 and 1973; Green & Williams, 1986; Rodhouse *et al.*, 1992; Green & Burton, 1993; Hammond *et al.*, 1994 a and b; Slip, 1995; Brown & Pierce, 1998; Kalges & Bester, 1998; Lawson *et al.*, 1998). It is not conclusively known from these studies whether some species of seals take sufficient fish from the commercial stocks to cause a significant decline. Around the world many fisheries are in decline (Hutchings, 1996; Mohon & Bowen, 1996; Fu *et al.* 2001; ICES, current website, 25th January 2003). Of particular importance are the cod (*Gadus spp.*) fisheries in the North Sea and Atlantic Ocean, whose decline is probably due to the over-fishing. The North Sea cod stocks are currently (as of 2002) considered to be outside biological safe limits for the species (ICES, 2002a) and other species are showing lower than normal spawning numbers. Other factors, apart from the potential effect on the fish stocks by commercial fisheries do need to be considered as potential causes of the observed declines, including environmental factors and the possibility of an impact from pinniped predation where populations of seals overlap with commercial fisheries (Hammond *et al.*, 1994 a and b; Lawson, 1995).

Harp seals (*Phoca groenlandica*) breed in large numbers off the east of Canada on ice floes (Lawson, 1995) and have been blamed by Canadian fishermen, the press and government (Hutchings, 1996; Myers *et al.*, 1996; Lambert & Dutil, 1997; Fu *et al.*, 2001) for taking a significant proportion of the Atlantic fishing industry's stocks of cod and capelin, leading to the slow recovery of these fish stocks after their collapse in the 1990s. For example, in 1992 six of the Canadian north-west Atlantic cod (*Gadus morhua*) stocks were closed to commercial fisheries to allow for their recovery after a huge decline in stock biomass (Hutchings & Myers, 1994) and were subsequently

reopened in 1994. The collapse has been attributed to over-fishing by the commercial fishing fleet. The slow recovery has been attributed to subsequent high mortality levels of juvenile and adult cod, low recruitment of commercial sized fish to the stocks and poor environmental conditions, in addition to seal predation (Myers *et al.* 1996; Lambert & Dutil, 1997; Fu *et al.*, 2001).

Despite the closure of the cod stocks to the commercial fleet, the stock has not yet recovered sufficiently to support the fishing effort of the Canadian fishing fleet (Myers *et al.*, 1996; Lambert & Dutil, 1997; Fu *et al.*, 2001). The fishing grounds overlap with the foraging areas of large numbers of harp and grey seals (Lawson, 1995). The industry claims that the large numbers of harp and grey seals have hampered the recovery to some extent. Harp seals are known to exhibit a preference for both cod and the probable principal prey of the adult cod, capelin (*Mallotus villosus*). However, there appears to be no significant change in the recruitment of five year old fish (allegedly taken by seals) to the stocks after the culls of large numbers of harp seals and smaller numbers of grey seals (Murie & Lavigne, 1992; Hutchings, 1996). To give evidence of this seal behaviour, fishermen have videotaped footage (Fu *et al.*, 2001) of seals eating only the bellies of adult cod. Since the presence of a species of fish in the diet of a seal is detected by the presence of the fish otoliths (earbones) in either the stomach or in the scats of the seal, this behaviour would lead to the presence of cod in the seals diet being underestimated. In 1994, with the reopening of the fish stock, a cull on harp and some grey seals during their breeding season was authorised and still continues in the hope that a decreased seal population would lead to a faster recovery for the fishery, although up to the present this has not been the case.

The North Sea fisheries are not the only fisheries that have seen a decline in fish stocks. With the increased fishing effort in the Antarctic Ocean, for example, the commercial harvest of Antarctic krill (*Euphausia superba*) coincides with the peak periods of demand for this prey item by several species of penguin and by Antarctic fur seals (*Arctocephalus gazella*) (Croll & Tershy, 1998). With the possibility of an

increased demand on this resource by the fisheries, the potential for conflict between marine animals and humans could increase. At present the commercial harvest is taking only 12% of the estimated krill consumption of terrestrially breeding marine predators (Croll & Tershy, 1998).

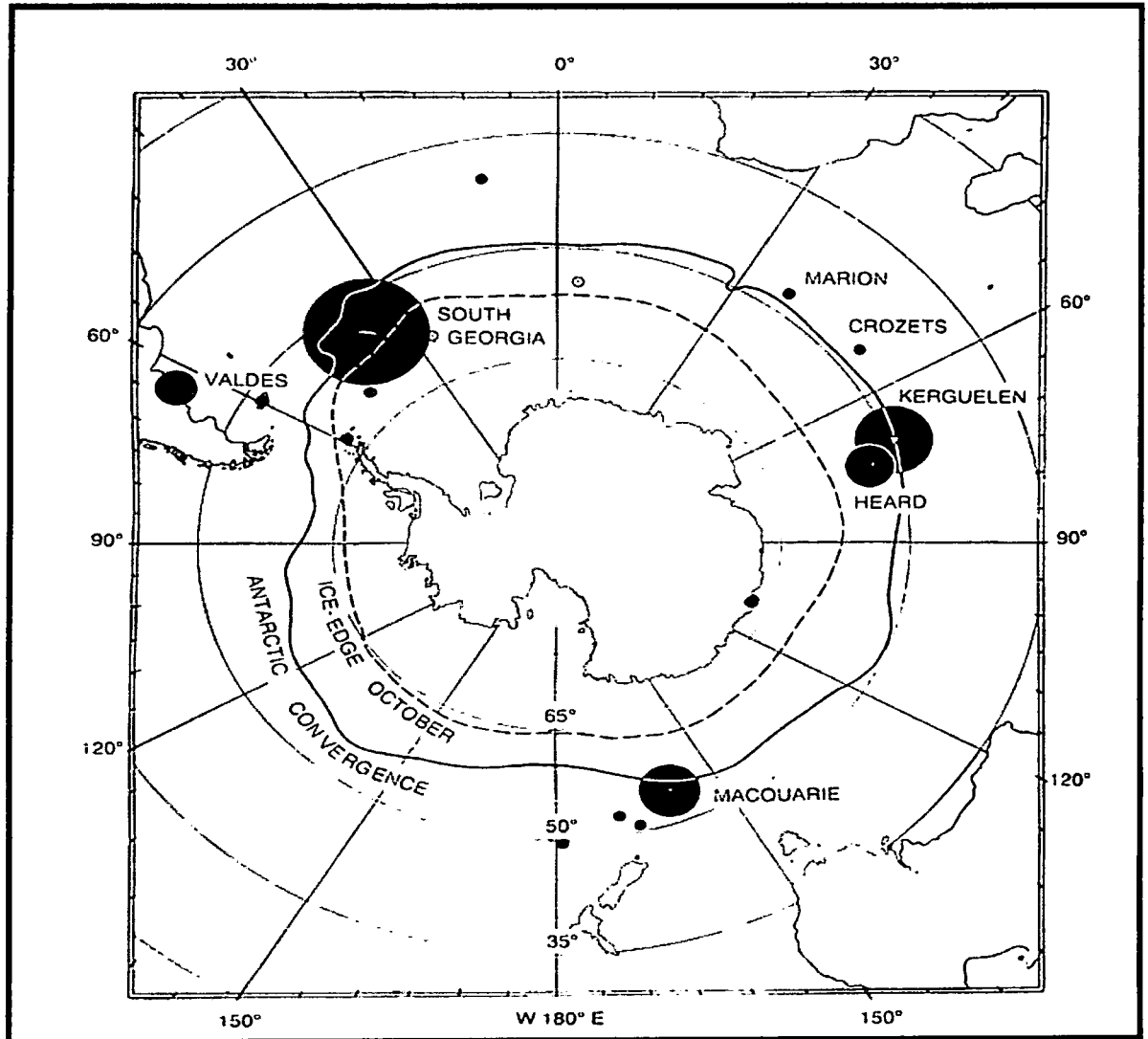


Figure 1.1 Map showing breeding locations of southern elephant seals (Le Boeuf & Laws, 1994).

An estimate of the dietary proportions of commercial and non-commercial species for several marine predators breeding on Heard Island (an island within the Antarctic

Convergence, see Figure 1.1 above) showed that while the proportions of species with commercial interest varied in the diets, non-commercial species appeared to be the preferred prey items. However, Green *et al.* (1998) believe that an increase in the fisheries for Patagonian toothfish (*Dissostichus eleginoides*) might impact heavily upon the diet of the Southern elephant seal (for whom the Patagonian toothfish may make up a significant proportion of the diet), and may have contributed to the possible decline in the southern elephant seal populations seen in recent years (Green *et al.*, 1998). The commercial fishery utilising the productive margins of the Patagonian shelf is increasing and may begin to impinge upon the feeding areas of the Patagonian population of southern elephant seals if this increase continues (Campagna *et al.*, 1999).

In Great Britain many of the fish stocks of the North Sea and other areas are in decline. This decline is linked by some, primarily by fishermen, to the increase in seal populations and their spread around the coast (Cornish Seals & Fisheries report, 2000; Orcadian, 30th November 2000; Guardian, November 7th and 8th 2002; BBC news, 17th July 2001; NFU Countryside News, 25th February 2002). Although it is not known to ^{actually} what extent the seals do take commercially important fish, it has been estimated that grey seals may take 76,000 tonnes of fish from the North Sea, including 28,000 tonnes of gadoid species (McConnell *et al.*, 1999). The results from studies based on scat analyses have shown that their favoured prey item is the sandeel (*Ammodytes spp.*) (of which there are several species) (Hammond *et al.*, 1994 a and b; McConnell *et al.*, 1999). While sandeels are not harvested for human consumption, they are taken for animal feed in amounts that may have an effect upon the sea birds and seals which prey upon them (Furness, 1990).

Culls of grey seals have been undertaken, with the most recent in Scotland from 1967 to 1978, when it was halted due to public outcry. Seals are known to tear the nets surrounding salmon (*Salmo salar*) farms (Mammal Society web site, 2001), causing damage to the nets and allowing farmed fish to escape into the wild. They also appear to damage fishing nets, causing financial loss to fishermen (Cornish Seals and Fisheries

Report, 2000). Grey seals causing such damage are allowed to be shot outside of the closed (breeding) season - 31st December to 1st September. Due to the increase in the grey seal population around Britain, together with the current decline in the numbers of gadoid fish species in the North Sea, there have been further calls for a seal cull by fishermen and some members of the government (McConnell *et al.*, 1999; BBC news, 17th July 2001; NFU countryside news, 25th February 2002). With the recently partial ban, on Atlantic cod and possibly white fish fishing in the North Sea (Guardian, November 7th and 8th 2002), there are likely to be further calls for a cull from both fishermen and politicians.

In these areas an understanding of pinniped feeding behaviour is useful in order to be able to better predict and understand their effect on fisheries. This is particularly important for species like the grey seal, which have large and expanding populations and whose feeding grounds and prey preferences of which overlap to a large extent with commercial fisheries interests, leading to a possible conflict between the seals and the fisheries.

1.2. The Grey Seal (*Halichoerus grypus*)

The grey seal was selected for this study for several reasons. It is the more common of the two native species to Great Britain (the other being the harbour or common seal). With its greater numbers, it is more likely to affect the fish stocks. It also breeds on sites that are generally more accessible than those favoured by the harbour seal, making sampling easier. In addition to this, the grey seal is less timid and easier to approach than the harbour seal, as it generally remains on land close to its pup at the approach of researchers. For a study that relies on sample collection directly from the animals, this is an advantage.

Grey seals are found on both sides of the Atlantic Ocean, in both sub-Arctic and more temperate waters (King, 1983). In Britain, where they are the largest carnivore, numbers were estimated at 111,400 for animals one year and older at the start of the 1997 breeding season (SMRU scientific report, 1995-1998). They account for about 35% of the world's population of grey seals. Of these, 85% of pups are born on traditional breeding grounds in the Inner and Outer Hebrides, Orkney, the coast of north and north-eastern Scotland, the Isle of May, South Wales, the Farne Islands and Shetland, with the rest breeding in smaller numbers on other sites around the British coast. The grey seal population of Britain is increasing at a current rate of about 7% per year (McConnell *et al.*, 1999; Pomeroy *et al.*, 2000) and is estimated to take approximately 76,000 tonnes of fish from the North Sea, including about 28,000 tonnes of gadoid species per annum (McConnell *et al.*, 1999) (figures based on data for 1994).

1.2. a. Life history

Female seals reach sexual maturity between the ages of three and five years. They may breed for 25 years or more and are on average 1.8m long (Pomeroy *et al.*, 1999). Males reach sexual maturity at about eight years old and breed for about 15 years. They are larger than the females, reaching an average length of about 2.3m. Both males and females show a high degree of site fidelity between breeding seasons, with females often returning to the site and area where they were pupped (Pomeroy *et al.*, 1994; Twiss *et al.*, 1994; Pomeroy *et al.*, 1999).

Male grey seals arrive at the British breeding sites from late August to the middle of September to establish territory. The older, more experienced males take the best sites closer to the water and thus areas more favoured by the females, leaving the younger males on the edges and on poorer parts of the territories less favoured by the females. Females arrive later, from September onwards, and spend 18 to 20 days

ashore, during which time they usually give birth to a single white-coated pup of about 15kg. The pup is suckled for between 16-21 days, during which it puts on weight mainly as blubber, increasing to about 50kg at weaning.

Female grey seals come into oestrus about 14 days after the pups are born and will mate with at least one male and sometimes up to seven (King, 1983). The female weans the pup soon after mating, by abandoning it to return to the water. After weaning their pups the females return to the water to forage, in order to build up lost fat stores in preparation for the moult. The pup remains on land during this period of rapid growth, and moults its white coat to grey, before it makes its way to the sea. Both male and female seals fast throughout the breeding season, although the females spend a shorter time on land and, thus, a shorter time fasting than the males. Both expend considerable energy: the males in defending territories and in mating and the females in giving birth and in subsequent lactation (King, 1983).

A successful mating results in a fertilised egg, which develops into a blastocyst. This remains free in the uterus for three and a half months before it is implanted into the uterus and development of the embryo can continue. Gestation lasts 240 days from implantation of the blastocyst to the birth of the pup. This strategy enables the female to regain weight and condition after the breeding fast before pregnancy begins again. It also limits the time required for mating on land by allowing the females to pup and mate in the same onshore period (King, 1983)

British grey seals come ashore again between January and March for the moult period. During this time the seal will completely shed its fur and replace it with a new coat, in order to provide itself with the best possible insulation. The females arrive first, followed later in the period by the males. As during the breeding period, the seals fast, since they are unable to return to sea while their new fur is growing in (King, 1983).

1.2. b. Foraging behaviour

When not hauled out for moulting or breeding periods, grey seals spend their time on long or short foraging trips (Thompson *et al.*, 1990; McConnell *et al.*, 1999). A study on grey seals from the Farne Islands showed that during long periods of travel the seals move distances of 75–100km per day. Long foraging trips are generally between regularly used foraging sites and may take the seals to 2,100km away from their breeding beaches (McConnell *et al.*, 1999). For the short trips (88% of total trips) the seals will travel for an average of 2.33 days and return to the same haul-out site from which they departed (McConnell *et al.*, 1999). Short trips are generally to areas with sandy or gravel sea beds - the preferred habitat of sandeels - and a mean of 39.8km from the haulout sites. Other studies on grey seals from the Moray Firth, North East Scotland, have also found this pattern of long and local foraging trips (Thompson *et al.*, 1996).

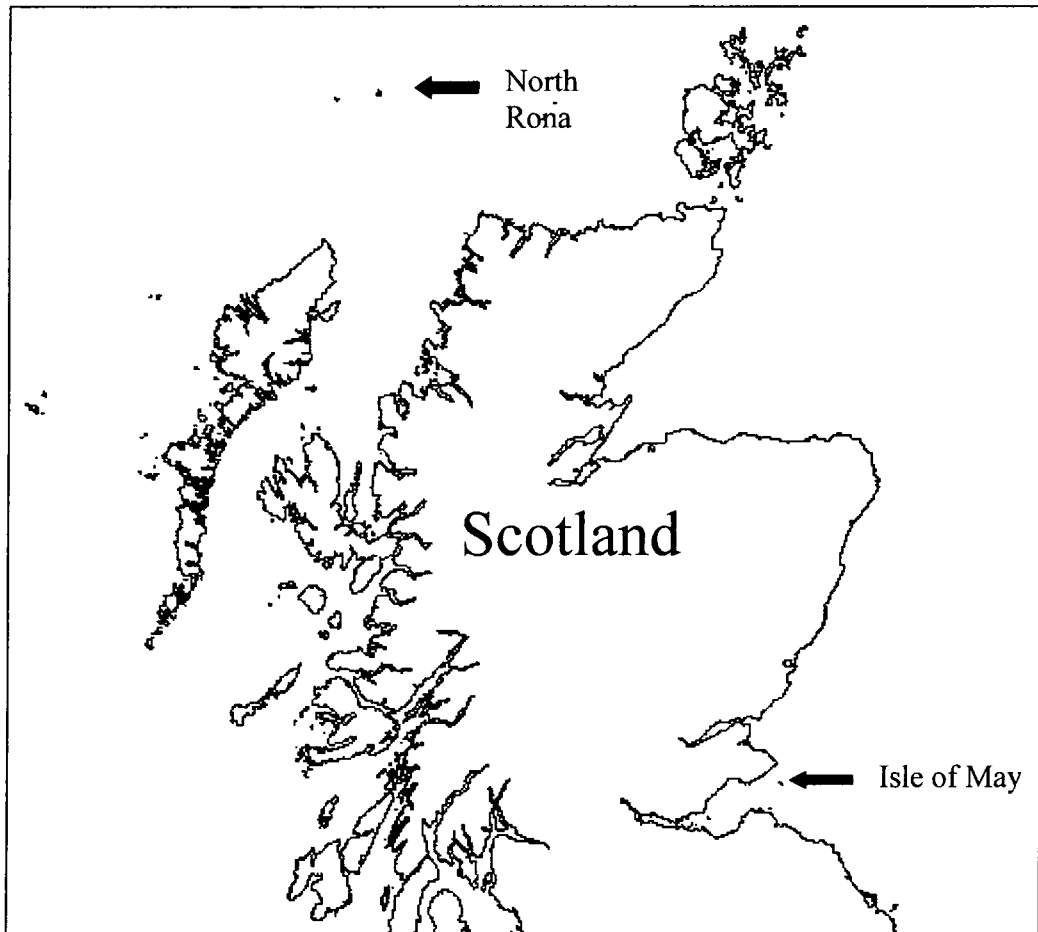
1.2. c. Study sites

Figure 1.2 Map of Scotland with the study sites of North Rona and the Isle of May marked.

North Rona, 65km north of the Butt of Lewis, Northern Scotland, has been used as a breeding site by grey seals since at least the 1880s (Pomeroy *et al.*, 2000). Grey seals have been tagged and branded on the island as pups since 1960 and as adults since 1985, as part of a long-term study of reproductive behaviour (Boyd & Laws, 1962). The main breeding colony lies on the Northern peninsula and measures approximately 1 x 0.3 km; the remaining area of the island is largely unsuitable for breeding (Boyd & Laws, 1962). The breeding season lasts for approximately 10 weeks, with 96% of pups born between 19th September and 29th October (Pomeroy *et al.*, 2000). Sampling of the

seals generally takes place during the breeding season, when the seals are hauled out in large numbers.

The Isle of May, lying 8km offshore in the mouth of the Firth of Forth, on the East coast of Scotland, has been studied as part of the same programme as North Rona, and during the study more pups have been born there than on any other island. Pups were first tagged for the study in the 1980s; branding of breeding adults began in 1987, and by 1997, 75 females and 16 males had been branded. The main breeding area lies to the north end of the island, on a flat peninsula; smaller groups breed around the coast on smaller beaches, and in gullies where the cliffs allow. The island has been used as a breeding site since the 1970s, with pup production increasing from 30 pups in 1977 to 1770 pups in 1997 (Pomeroy *et al.*, 2000). The breeding season lasts from the middle of October to early December with most pups being born later than on North Rona, in the first week of November (Pomeroy *et al.*, 2000). Pup numbers have been stable since 1995 (Pomeroy *et al.*, 2000).

1.3. The Southern Elephant Seal (*Mirounga leonina*)

The southern elephant seal, the second study species, is the largest of the pinniped species, and shows the greatest degree of sexual dimorphism in mammals, of up to ten times the mass of the female seals (Le Boeuf & Laws, 1994). The male southern elephant seal is the larger of the two sexes, with weights of 1.5 to 3 tonnes; some may reach 3.7 tonnes. The male has an average body length of 4.72m, with a maximum length of around 6m (Le Boeuf & Laws, 1994). Females weigh between 350-800kg and are 3m long. Females reach sexual maturity at three to six years of age (the majority at four years), and will begin to breed at this age generally producing a single pup each year. The males can reach sexual maturity at four to five years of age but they do not

reach full adult size until eight years of age and so are unlikely to breed successfully before this. The majority of male southern elephant seals breed at nine to twelve years of age, when they are of a larger size (Le Boeuf & Laws, 1994). The maximum life span seen is 20 years for both the male and the female seals (Deutsch *et al.*, 1994; Le Boeuf & Laws, 1994).

As well as its extreme size, the male southern elephant seal shows other secondary sexual characteristics - a large proboscis that can be inflated during territorial displays and thickened skin on the underside of its neck that gives some protection from the teeth of an opponent during territory fights during the breeding season (Le Boeuf & Laws, 1994).

The Southern elephant seal breeds largely on sub-Antarctic islands close to the Antarctic Polar front. There are three main breeding populations, the largest being South Georgia (including the Falkland Islands and Argentina) with a breeding stock of 340,000 in 1985-86 (Harwood & Croxall, 1988), 60% of the total southern elephant seal population (Laws, 1994). This population is stable, with the Argentinean colony the only one to show any increase between 1949 and 1990 (Hindell *et al.* 1991; Laws, 1994; Slip & Burton, 1994; Campagna *et al.*, 1999). The second population, Kerguelen and Heard Islands, was estimated at 264,000 in 1985 (Pascal, 1985) but has been decreasing in size over the last several decades (Hindell, Slip & Burton, 1994; Van Den Hoff *et al.*, 2002). Finally, the Macquarie population (see Figure 1.1) is estimated at 100,000 (Laws, 1979), and is also declining by approximately 2% per year.

The decline in these populations and the increase in the Argentinean one are not currently understood. One cause is thought to be juvenile mortality at sea, possibly due to changes in prey availability (Van Den Hoff *et al.*, 2002). In addition to these populations, there have been reports of animals giving birth in New Zealand, Australia and South Africa; however, these numbers are negligible (Laws, 1994). The total southern elephant seal population has been estimated at 664000 (Laws, 1994).

1.3. a. Life history

The southern elephant seal breeds in the austral spring, from early September to the middle of November (Le Boeuf & Laws, 1994). Both males and females show a high incidence of site fidelity (greater in the females than the males), with both sexes generally returning to the same traditional beaches to breed each year (Le Boeuf & Laws, 1994).

The breeding season starts with the arrival of the largest adult males on the beaches at the end of August. They fight to hold the best territories, with the winner of these fights becoming dominant over the beach. The females begin coming ashore in September and form harems with a dominant male in attendance. Females may join the harem to which they belonged in the previous year or may join up with a different set of females. Harem size varies, with the smaller harems having less than 100 females being dominated by one male. With a larger number of females, the dominant male is unable to protect his females from all other males; less dominant males will, therefore, take up position at the edges of the harem group and attempt to mate with as many of the females as possible (Le Boeuf & Laws, 1994).

A successful dominant male will prevent the attentions of subordinate males towards his females and may attempt to herd newly arrived females into his harem. The time spent on the breeding beach by the male varies from 60-90 days, during which period the male fasts in order to keep control of the females in this harem; such a male may lose up to 40% of his body weight. When not actively fighting to keep the females or mating, the male seal spends as much time as possible sleeping to conserve energy (Laws, 1994). The females spend a shorter time on the breeding beaches, but will also fast during this period.

The female seal gives birth to a single pup between the end of September and the middle of November, with the majority pupping in October. A female will give birth

within five days of arriving on the beach and will fast until weaning her pup. The pups are suckled for about 23 days before weaning, with the pup rapidly gaining weight (Le Boeuf & Laws, 1994). Mating occurs three to five days before the pup is weaned. The females wean their pups by leaving them to return to the sea (Le Boeuf & Laws, 1994), while the males remain on the beaches until the last of the females have left. The pups remain on the beach for an average of 37 days until their moult is complete. They reach about 70% of their weaned mass before leaving the beaches to enter the sea (Wilkinson & Bester, 1990). As in the grey seal female, the fertilised egg develops into a blastocyst, the implantation of which is delayed for four months after mating (Le Boeuf & Laws, 1994)

Moulting for both sexes also takes place at traditional sites, often the same as for breeding. It takes place for females during January to February, reaching a peak at the end of January. Juveniles moult earlier, from mid-November, peaking in mid-December and ending by late January. The adult males' moult lasts for 30-40 days, during the period from February to May, with most individuals ashore for moulting in the middle of March (Le Boeuf & Laws, 1994). The moult for the southern elephant seal is dramatic, with the fur being shed still attached by the follicles to sheets of epidermis (Worthy *et al.*, 1992; Le Boeuf & Laws, 1994). During this period both sexes fast until their fur is replaced.

1.3. b. Foraging behaviour

Squid and fish prey items are believed to be important in the diet of the southern elephant seal. A study by Green & Burton (1993) found that 77.2% of the seals eat fish of 11 taxa, including both benthic and pelagic species. Their study indicates that southern elephant seals from Heard Island spend more time in Antarctic waters than southern elephant seals from Macquarie Island. Slip (1995) found that 86% of southern

elephant seal stomachs from the Heard Island population contained cephalopods of 17 species. 66% of the stomachs contained fish and a few contained crustaceans. Slip (1995) found differences between the adult and juvenile seal diet and also found that smaller seals ate smaller prey items. No differences between the diets of the male and female seals were found in this study.

With the extreme sexual dimorphism seen in the southern elephant seal, it is likely that any differences found in foraging behaviour will reflect the greater energy requirements of the larger male seals (Le Boeuf *et al.*, 1993). Sexual differences in foraging behaviour in both the northern elephant seal (*Mirounga angustirostris*) (Le Boeuf *et al.*, 1993) and in the northern elephant seal have been described (McConnell & Fedak, 1996; Campagna *et al.*, 1998). The studies on the southern elephant seal have shown that the male seals tend to forage over the continental shelf or at the break between it and deep water, while the female seals make long trips away from the shelf to forage in mid to deep water. (McConnell & Fedak., 1996; Campagna *et al.*, 1998). The differences seen may be due to the increased energy requirements of the male seals or to competition with other species (Slip, 1995).

In the northern elephant seal species the male seals require up to three times the energy that the smaller females do (Le Boeuf *et al.*, 1993). In other pinniped species where a degree of sexual dimorphism is also seen, such as the stellar sea lion, (*Eumetopias jubatus*) the male supplements its diet by taking warm-blooded prey items, such as birds, in addition to the fish prey items taken by the females (Alonso *et al.*, 2000).

Both male and female seals make two foraging trips a year. The females leave the breeding beaches after mating and spend an average of 73 days at sea, before returning to the beaches to spend a month ashore moulting. This is followed by an eight month foraging trip several thousands of kilometres from land (Le Boeuf & Laws, 1994; Campagna *et al.*, 1998). At the start of the second foraging period the fertilised blastocyst will implant in the uterus, so the female will spend the whole of the trip

gestating. The adult male seal will also make the two foraging trips but spends only eight months in total at sea, as opposed to the females who spend ten months in total. This is due to the greater amount of time spent on land by the males during the breeding season (Le Boeuf & Laws, 1994).

1.3. c. The Study Site

The Pensínsular Valdés breeding colony of southern elephant seals, from which samples were taken for this study, belongs to the South Georgia southern elephant seal breeding stock (see Figure 1.1). It is the most northerly colony and is the only population of southern elephant seals to breed on the mainland and in temperate waters (see Figure 1.1) rather than Antarctic or sub-Antarctic waters (Campagna *et al.*, 1992). It lies 550km from the deeper water where elephant seals normally forage (Campagna *et al.*, 1992). The rest of the South Georgia stock, together with the other populations, breed on sub-Antarctic islands further to the south. The Patagonia shelf at this point is large, extending about 300km east from the land. It is shallow, at about 100m deep, and is considered to be productive (Campagna *et al.*, 1999). The population produces 12,000 pups in a year and has increased in size by 3.4% a year since 1982 (Campagna & Lewis, 1992). The southern elephant seals of Patagonia breed at lower densities than the other populations, since the beaches do not restrict the females to small proportions of the coast (Campagna & Lewis, 1992; Baldi *et al.*, 1996).

Female southern elephant seals leaving the beaches on foraging trips cross the continental shelf in less than a week and forage in open water in the south-western Atlantic, between 36°–50° S, and at distances of up to 1,200km from the shore (Campagna *et al.*, 1999). Further distances are travelled by females in the post-moult period, with distances of 2,300km being recorded by satellite tracking. The longest migration recorded from Pensínsular Valdés was that of a post-moult female which travelled 11,600 km (Campagna *et al.*, 1998). The females appear to be mid-water

feeders, making infrequent dives to the sea bed, with most of the dives (recorded by depth/time recorders) to depths between 200m and 1000m (Campagna *et al.*, 1995). They show similar dive patterns to female southern elephant seals from the other populations, but they do not appear to forage as far as the Antarctic polar front (Hindell *et al.*, 1991; Campagna *et al.*, 1995 & 1998). The range of the female seal does overlap somewhat with that of the males in the areas closer to the continental shelf (Campagna *et al.*, 1998).

Since the larger males require greater amounts of energy than the smaller females (Le Boeuf *et al.*, 1993; Boyd *et al.*, 1994) they are, therefore, likely to forage in areas with high prey abundance. Satellite tracking data (Campagna *et al.*, 1999) showed that five males in the study swam in a short period of time (three to eleven days) to the edge of the continental shelf where they stayed, probably foraging. The other two males in the study remained over the shelf. All of the males made frequent dives. Those that were over the shelf tended to dive to the sea bed, whilst the males foraging on the shelf edge made most dives to mid-water depths, with a few to the seabed. Deeper dives were made during daylight hours, possibly to take advantage of prey movements in the water column. This suggests that the male seals prey on benthic species and on those that are found in the water column during daylight (Campagna *et al.*, 1999).

1.4. Current methods of pinniped dietary assessment

Seals spend a large proportion of their life cycle at sea, returning to the land twice a year: once to give birth to their pups and to mate and once for a moult period (King, 1983; Le Boeuf & Laws, 1994). The rest of the life cycle is spent on feeding trips of varying lengths, with the seals spending from a few days to several months at sea (Hindell *et al.* 1991; Campagna *et al.*, 1998) and then resting at traditional haul-out sites, which may be in remote regions and potentially far from land. For example, the

southern elephant seal female hauls out on ice floes far from shore (Fedak *et al.*, 1994). This makes their feeding behaviour and diet composition difficult to study accurately over the entire year. Direct observations are impractical or even impossible during most of the year, since seals hunt some distance away from shore and often consume their prey while at sea. Mark-recapture studies conducted rely on a tagged seal being spotted or found and are unreliable and are used infrequently in pinniped studies (Bester, 1989; Bester & Pansegrouw, 1992).

Although seals spend time on land for the breeding and moult periods, they fast during this time, producing little or no faeces. This means that little or no food items will be found in their stomachs or scats after they have been on land for a while, making dietary sampling potentially inaccurate (Da Silva & Neilson, 1985; Harvey, 1989).

Methods for dietary scat studies that avoid the need for direct observations of the animals for a long period of time have been used. These methods are able to give an indication of the animals' diet during some, but not all seasons of the year. These include stomach content analysis (Rae, 1960 & 1973; Rodhouse *et al.*, 1992; Green & Burton, 1993; Antonelis *et al.*, 1994; Slip, 1995; Tollit *et al.*, 1997; Lawson *et al.*, 1998), scat analysis (Green & Williams, 1986; Thompson *et al.*, 1991; Bowen & Harrison, 1994; Hammond *et al.*, 1994 a and b; Brown & Pierce, 1998; Kalges & Bester, 1998), satellite tracking and other remote recording devices to record dive depths, water temperatures and dive profiles (Hindell *et al.*, 1991; Thompson *et al.*, 1991; McConnell *et al.*, 1992; Le Boeuf *et al.*, 1993; Jonker & Bester, 1994; McConnell & Fedak, 1996; Thompson *et al.*, 1996; Campagna *et al.*, 1998; Campagna *et al.*, 1999; McConnell *et al.*, 1999; Field *et al.*, 2001) and stable isotope analysis (Lawson *et al.*, 1995; Hobson *et al.*, 1997; Burton & Koch, 1999; Hirons *et al.*, 2001; Clementz & Koch, 2001; Van Den Hoff *et al.*, 2002). These methods will now be reviewed in the following sections of this chapter.

1.4. a. Stomach content analysis

This method involves the examination of an animal's stomach contents for recognisable and identifiable prey remains. In seal species the remains are generally fish otoliths or cephalopod beaks and these can be identified using keys developed for this purpose. Seals are normally sampled during the breeding or moulting period when the animals are on shore for an extended period of time, or from haul out sites out of the breeding/moulting seasons (Green & Williams, 1986; Hammond *et al.*, 1994 a and b; Brown & Pierce, 1998; Kalges & Bester, 1998). Samples may be obtained by the dissection of the stomach from dead seals (Rae, 1960 & 1973; Murie & Lavigne, 1992; Lawson *et al.*, 1998; Lindstrom *et al.*, 1998) or by stomach lavage of seals that have first been sedated for the purpose (Rodhouse *et al.*, 1992; Green & Burton, 1993; Slip, 1995). Stomach lavage involves pumping the stomach of the sedated animal full of water and then collecting the contents. The procedure is repeated until the water runs clear from the stomach. Both of these methods allow data on the age, sex and condition of the seal to be collected at the same time as the dietary data.

In Rae's studies (1960 & 1973), both dead harbour and grey seals were collected over a period of several years, largely from fishermen who had either shot the seals (both at sea or on land) or found them entangled in fishing nets. The 1960 samples were collected from around the east coast of Scotland during the salmon fishing season. They showed a high proportion of salmon (80%) and cod (18%) in the stomachs of the grey seals, leading to the conclusion in this paper that the grey seals exhibit a preference for these species, at least in the area in which the seals were collected.

In Lawson's study (1998), Canadian harp seals were shot offshore during research trips or near-shore by seal hunters over a two-year period. Their stomachs were dissected out and the contents analysed. These data, along with those obtained from research trawls throughout the area where the seals were collected, concluded that the harp seals were preferentially selecting capelin over other prey species that may or may

not have been more abundant in the area. Arctic cod (*Borogadus saidar*) was also selected preferentially in near-shore areas but not in offshore ones. Data of this kind are useful in looking at the effect that seals may have on fisheries, and in the area where this study was conducted it is relevant to the current crisis in the north-western Canadian cod fisheries.

Grey seal stomachs were collected from 82 dead Canadian grey seals which had been collected during a hunt season in 1983 (Murie & Lavigne, 1992). It was discovered that most of the stomachs contained cod, herring (*Clupea harengus*) and capelin. The herring and capelin were of sizes of commercial interest, while most of the cod was of smaller sizes. The study did not investigate the potential overlap between seal foraging grounds and commercial fisheries.

The diet of the southern elephant seal has also been studied by collecting stomach samples from sedated animals (Rodhouse *et al.*, 1992; Green & Burton, 1993; Slip, 1995). Slip (1995) examined the contents of 76 southern elephant seals from Heard Island during the breeding and moulting seasons from July 1992 to March 1993. It was discovered that 86% of stomachs contained cephalopods, with 17 different species of fish occurring less often and with less diversity than the cephalopods. Differences were seen in the species of cephalopod taken by adults and juveniles, while there were no sex differences in the diet apart from the tendency of the adult males to take larger prey than the smaller females.

Green & Burton (1993) collected stomach lavages from adult southern elephant seals from two of the three major breeding colonies, Macquarie and Kerguelen-Heard Islands, during the moulting period. The food remains found consisted of cephalopod beaks, fish otoliths and fish eye lenses. Differences were found between the proportions of Antarctic and non-Antarctic squid and the proportions of fish, with more fish being found in the stomachs of the animals from Heard Island than those from Macquarie. This is likely to be accounted for by the different foraging patterns of the seals from the two populations or, if the seals do forage in similar areas, from the differences in prey

availability on the return trips from the foraging areas back to the haulout beaches. At Macquarie Island differences were found between summer and winter sampling periods in the amounts of squid found in the diets of the adult male seals, although no differences in the proportions of the squid from Antarctic and non-Antarctic species were found. In another study no differences were found from the Heard Island samples comparing samples when collected in different seasons and from different age classes (Slip, 1995).

The stomach contents of southern elephant seals were sampled on South Georgia in November 1986 (the breeding season), and from November 1988 to February 1989, during breeding and moulting haulouts (Rodhouse *et al.*, 1992). Cephalopod beaks, but not fish remains, were collected and identified. They show that the species taken in the two years of sampling were largely similar but that different proportions of squid species made up the diet in each year. The diversity of cephalopods taken as prey by each seal was shown to increase with the size of the seal, with the greatest species diversities being taken by the largest male seals; however, no increase in numbers of prey items was found.

The data collected in these studies do show actual prey taken by the seals, but the methods are subject to known sources of bias (Boyd *et al.*, 1994; Slip, 1995). Due to the short length of time that the prey species remain in the stomach before they are digested, the studies that collect samples from seals that are on shore during the moult and breeding period show bias. It has been estimated that, in southern elephant seals, items may remain in the stomach for between 18 hours to three days (Krockenberger & Bryden, 1994). Cephalopod beaks may become caught in the stomach lining and remain undigested (Rodhouse *et al.*, 1992), while fish bones and other remains are either digested faster or pass through the stomach more rapidly. There is, therefore, a possibility that the amount of the cephalopods may be overestimated and the fish component of the diet underestimated. As this method gives an indication only of what the seal has been eating in the short term prior to its capture or death, data gained by

sampling seals during the moult and breeding fast periods may be misleading, as the seals may not have fed for several days prior to sampling (Green & Burton, 1993; Rodhouse *et al.*, 1992). If the species of seal sampled forages at distances greater than three days' travel from shore, in different foraging habitats than those close to the haul-out site (as has been observed in southern elephant seals (McConnell & Fedak, 1996)), then data obtained by stomach lavage will not show this potential for dietary variation on a seasonal basis.

Other species, such as the grey seal, spend shorter times on foraging trips before returning to a haul-out site (McConnell *et al.*, 1999), which may make the data obtained by this method more accurate. As shown in the discussion of their life history, female and male southern elephant seals are known to forage in different locations (females travelling considerable distances from the breeding sites (Campagna *et al.*, 1998), males remaining in closer proximity to the coast throughout the year (McConnell & Fedak, 1996). During the females' return to the haul-out sites, the diets of the two sexes are likely to overlap, leading to the similarities in male and female diet seen in studies using stomach lavage (Slip, 1995), with the female diet shown by these studies potentially differing from the diet consumed by the females at their primary foraging area.

In addition, since samples can only be collected from most seal species during their two periods on shore, this method will not be able to show the potential for dietary variation throughout the year but only for the few days preceding each of the two land-based periods. This increases the possibility that data obtained from such samples may not be representative of the diet at a seasonal level.

Studies where stomach analysis (by dissection) is conducted upon dead animals may show less bias, since animals may be taken throughout the year (Rae, 1973) and results are, therefore, likely to give a better indication of the diet. This method, however, is only suitable for species which are not endangered or protected: sample size would diminish hugely if no animals were shot and the study, therefore, relied upon animals killed by natural causes or by accident (for example, by entanglement in fishing

equipment). While shooting animals for purposes of sampling is possible if the seal species is not endangered, not all animals that are shot will contain food in their stomachs (Kalges & Bester, 1998). Stomach lavage of live animals is likewise suited only to small sample sizes, being expensive due to the equipment, sedatives and labour required, as well as stressful and potentially dangerous for the animal as it requires a full sedation.

1.4. b. Scat analysis

This has been a popular method of studying the diet of many species of pinnipeds, as it is non-invasive and relatively undistruptive to the animal (Green & Williams, 1986; Antonelis *et al.*, 1992; Daneri, 1992; Hammond *et al.*, 1994 a and b; Brown & Pierce, 1998; Kalges & Bester, 1998; Daneri *et al.*, 1999).

Scat samples are collected from known haul-out sites for the study species and may be stored frozen until they can be analysed. The scats are then sieved with water to remove any hard undigested material; generally otoliths or cephalopod beaks which are removed and subsequently identified and measured. From the otoliths it is possible both to identify the fish prey and to estimate its length and weight. Similar data can be obtained from cephalopod beaks. It is possible to collect samples throughout the year from haul-out sites, making the study of seasonal data possible in cases where a study species hauls out in sufficient numbers at an accessible site.

This method has the benefit of not relying upon shooting or collecting dead seals; nor does it cause stress to live animals by sedating them to examine stomach contents (Harkonen, 1987; Thompson *et al.*, 1991; Hammond *et al.*, 1994 a and b; Thompson *et al.*, 1996). However, sampling can only take place where one species of seal is hauled out (Thompson *et al.*, 1996), in order to avoid confusion with the samples. This is a

particular problem in Britain where grey seals and harbour seals sometimes share haul-out sites (Thompson *et al.*, 1996).

In one study, scat analysis was used to look at differences in both seasonal and regional feeding in harbour seals from two populations in different habitats off the coast of Sweden (Harkonen, 1987). This study shows that the prey items taken depend on the habitat and the seasonal availability of prey species. The seals did not appear to be taking some of the more abundant commercial species, such as mackerel (*Scomber scombrus*) though other commercial species (including herring and hake (*Merluccius merluccius*)) were found in the scats. About 50% of the diet was made up of members of the cod family. Seasonal variation in harbour seals was also studied using this method for seals from south-east Shetland (Brown & Pierce, 1998), and in a similar study (Kalges & Bester 1998) on two species of Antarctic fur seals, which also showed some seasonal variation.

Studies on grey seals were conducted around the Inner and Outer Hebrides and around Orkney (Hammond *et al.*, 1994 a and b). The studies showed that the diet of the Orkney animals was 50% sandeels. In the scats from Orkney, sandeels were found in greater numbers in samples collected during February and the summer months than in those collected in November. Greater numbers of sandeels were found in the Orkney scats than in samples from the Hebridian animals. The difference seen may be explained by the sandeels' habitat preferences: the area around the Orkneys is sandy and provides a better habitat for sandeels than the rocky sea bed around the Hebrides. The studies showed that some species that were important in the grey seal diet were also important for commercial fisheries: cod, for example, was important in all seasons. Other commercial species, such as herring and mackerel, were not found in the scats.

Daneri (1996) collected 34 scats from Antarctic fur seals (*Arctocephalus gazella*) it was found that fish made up 90% of the prey remains found in the scats. The remains were identified as pelagic fish species associated with krill. These data were supported by the dive patterns that the fur seals show (Croxall *et al.*, 1985).

Further scat samples from Antarctic fur seals (Daneri *et al.*, 1999) showed an increase in the numbers of squid in the fur seal diet in the autumn, a period when the squid are more common. Despite this, it was possible to conclude that cephalopods were not an important component of the diet, as the depths at which they are found are deeper than the Antarctic fur seal generally dives.

Scat analysis is a useful tool. It allows a good analysis of a species' diet to be built up and allows for comparison with other populations (Hammond *et al.*, 1994 a and b) and other species (Thompson *et al.*, 1996). However, there are several problems associated with this method which can lead to inaccurate or biased results. Scat analysis generally only considers the fish otoliths or cephalopod beaks; prey items that have neither or that are not eaten whole will not be taken into account during the analysis (Hammond *et al.*, 1994a). Rae (1973) noted that although grey seals do not take large amounts of salmon they do not appear to eat the heads. Therefore, if salmon did feature in the diet of the seals in this study, it may not have been detected as the otoliths would not have been consumed. Grey seals eat the bellies of cod (Fu *et al.*, 2001) and such behaviour may be present in other pinniped species. A further problem with this method is presented again by the larger cephalopod beaks being often retained in the stomach of the seal (Rodhouse *et al.*, 1992) and not excreted in the scats. Cephalopods may, therefore, be underestimated by scat analysis and overestimated in a stomach content study. There is also the problem of remains appearing in the scats only from prey items taken close to the haulout sites, and so scats are unrepresentative of the diet of long foraging trips of longer than several days.

In a study on a captive harbour seal (Da Silva & Neilson, 1985), herrings of varying sizes were fed to the seal. The results showed that only otoliths from the largest class of herring were recovered, and of these only 4% were recovered. The study predicted that other prey species would likewise be underestimated by this method. After passing through the animal's digestive tract, the otoliths were found to have been reduced in

size. It was also found that the annuli that are used to estimate fish age were similarly eroded, leading to the possibility of underestimating both prey size and age.

Correction factors derived from feeding seals otoliths of known sizes and retrieving them after their passage through the digestive tract of the seal have been developed to allow for these factors (Harvey, 1989; Tollit *et al.*, 1997). However, despite these precautions, inaccuracies are likely to occur if identifiable otoliths or cephalopod beaks are not found in the scats. Despite these problems, a much better understanding of seal diet can be obtained from studies using this method than from stomach content analysis, when a larger sample size is obtained.

Scat analysis, however, is to a great extent unsuitable for use in species such as southern elephant seal, the haul-out areas of which are often far from land, on ice floes that are difficult to reach, and where distribution is over a very wide area (Campagna *et al.*, 1998). In such cases, samples are not able to be collected in sufficient numbers for significant results to be obtained. This means that in such situations scat collection is impractical as a method of studying diet and does not give a good indication of overall dietary intake. Where scats are collected from such populations or species they are likely to be biased towards feeding areas that are close to shore. Data obtained from analysis of such scats may not be representative of the seals' overall feeding patterns. This is particularly likely if the animal generally forages offshore and in deeper water and potentially on very different prey species than those found in near-shore areas, so this method gives no data from extended foraging excursions.

1.4. c. Other methods of study

Where direct dietary information is difficult to obtain, diving data (dive times, depths and water temperatures) and data from satellite tracking of seal movements can be used to infer feeding behaviour. When used in combination with either scat or

stomach content analysis, a better indication of foraging behaviour can be gained (Hindell *et al.*, 1991; Thompson *et al.*, 1991; McConnell *et al.*, 1992; Le Boeuf *et al.*, 1993; Thompson *et al.*, 1996; McConnell & Fedak, 1996; Campagna *et al.*, 1998; Campagna *et al.*, 1999; McConnell *et al.*, 1999).

Satellite tracking studies have shown that male and female southern elephant seals forage in different areas (McConnell & Fedak, 1996). The tracking of three adult seals over more than one season showed that from one season to the next they were consistent in their direction of travel away from their South Georgia breeding site. Similar data have been collected from southern elephant seals from different populations (Campagna *et al.*, 1998), showing that, although the foraging areas may not overlap for animals from different populations, differences are seen between the males and females.

Southern elephant seal males from Pensínsular Valdés forage over the continental shelf, while the females forage several thousand kilometres off shore in their two foraging trips a year (Campagna *et al.*, 1998). The females have fewer stationary periods than the male seals (McConnell & Fedak, 1996). The post-breeding trip lasts around 70 days, and the post-moult feeding trip lasts around eight months, covering the gestation period (McConnell & Fedak, 1996). Data from tags collecting dive data have shown that females generally forage in water of about 200m, while males tend to remain in the shallower water over the continental shelf (Campagna *et al.*, 1998).

Data from a northern elephant seal study (Le Boeuf *et al.*, 1993) used time-depth recorders in a study to show that there are also foraging differences between the males and females of this species. The male northern elephant seals migrated along the coastal margins from their breeding beaches, making pelagic and flat-bottomed dives. This second kind of dive is likely to be to the sea floor, indicating prey such as skate, ray and shark, species found at the edge of the continental shelf. The females moved off shore and showed mainly pelagic foraging throughout the trip. The differences seen in the foraging behaviour of the two species are likely to be due to the extreme sexual dimorphism seen in both species and, thus, the greater energy requirements of the male

seals. They may also indicate differences in prey selection, although this was not part of the study (Le Boeuf *et al.*, 1993).

It was discovered by radio tracking harbour seals that these seals moved an average of 6-10km between their foraging grounds and haul-out sites, while grey seals moved up to 145km (Thompson *et al.*, 1996). This suggests that scat analysis for grey seals may provide a more biased indication of prey than for harbour seals. Satellite tags have been used to track grey seals from the Farne islands (McConnell *et al.*, 1999); data from these showed that while seals travelled over both long and short distances, most trips were made to areas which were over a sandy seabed. Such areas are preferred by sandeels, thought to be an important prey item of the grey seal (Hammond *et al.*, 1994 a and b).

Data retrieved from satellite or radio tags is most useful when linked with data from another source, such as stomach or scat analysis. For example, data satellite-linked time depth recorders from harp seals were linked to stomach content analysis from dead harp seals (Lawson *et al.*, 1998). Samples of the seals were taken from both near and offshore locations, in order to examine whether harp seals preferentially foraged for any particular species of fish. It was discovered by combining these data that the seals preferred capelin, regardless of variations of the abundance of the species in the areas in which the seals were foraging.

Antonelis *et al.*, 1990, showed from telemetry data that the foraging areas of the northern fur seal (*Callorhinus ursinus*) and Californian sea lions (*Zalopus californianus*) were similar. However, the fur seals spent twice as long at sea as the sea lions while on foraging trips; they also spent less time on shore. The scat samples showed that the diets of the two species were similar, although each species of pinniped ate different proportions of given prey species.

Although these methods cannot give data on prey species or quantities consumed, data recorded by remote tags on diving and foraging data are a useful addition to information on seal foraging behaviour. This is particularly the case in species which are difficult to study, like the southern elephant seal. Problems with these methods arise

due to the high cost of each tag so that it is only possible to track a few individuals. This gives small sample sizes that may not be representative of the population as a whole. Data from some tags can only be retrieved upon recapturing the animal; if this does not happen, due to the animal failing to return or losing the tag, both data and the tag itself are lost. This also means that only data from animals that survive the year at sea and return to the same breeding beach as the year before to breed. Data from this kind of tag would not be obtained for unsuccessful animals who fail to return to the beach. This means that it is not possible to make dietary comparisons in order to examine possible causes of an animal failing to return to its traditional breeding and moulting site. However, this method does enable periodic data uplinks to the satellite, giving more seasonal data than other methods are able to give.

Data on prey species cannot be collected by using dive recorders or satellite tags. However, data on water temperature (Campagna *et al.*, 2000) and dive depths can be used to infer the areas of the ocean where seals are foraging and species of prey that are likely to be taken by a seal (Hindell *et al.*, 1991; Campagna *et al.*, 1998). It is also possible to look at the dive profiles of the animals from data obtained from dive recordings and to deduce from these if the animal is making bottom dives or is foraging in mid- or deep water. This would indicate whether the pinniped is preying on bottom-feeding prey items or free-swimming ones (Campagna *et al.*, 1998; Daneri *et al.*, 1999).

Radio telemetry is appropriate for use in species of pinnipeds that remain comparatively close to land, but not for species (like the southern elephant seal) that travel over large distances to feed (Le Boeuf *et al.*, 1993, McConnell & Fedak, 1996; Campagna *et al.*, 1998).

From the bias and possible inaccuracies in all these study methods, it becomes obvious that there is a need for the development of a method of dietary analysis that is able to avoid the bias caused by the short land-based periods of the pinniped life cycle. Such a method should also be able to offer more information on the diet throughout the year, with the potential for showing variation due to seasonality or other factors.

1.5 Stable Isotope Analysis

Analysis of the stable carbon and nitrogen isotopic values has been used to study trophic relationships and nutrient sources in many species. In both marine and terrestrial food webs (e.g. Minagawa & Wada 1984; Hobson, 1986 and 1990; Hobson & Welch, 1992; Mitzutani *et al.*, 1992; Hobson *et al.*, 1994; Thompson *et al.*, 1995; Abend & Smith, 1997; Frazer *et al.*, 1997; Macko *et al.*, 1999 a and b; Jennings *et al.*, 2001; Pinnegar & Polunin, 2001), where more traditional methods are considered to be inaccurate or inappropriate or where further data are required for clarification of diet.

1.5. a. Principles behind the method

The method utilises the fact that ratios of the stable isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) of carbon and nitrogen do not change over time, or change to a predictable extent, during metabolic processes (DeNiro & Epstein, 1978; DeNiro & Epstein, 1980; Kelly, 2000).

The isotopes of nitrogen reflect the dietary protein source. Proteins in the body's tissues are generally enriched by 3‰ per trophic level (although they can vary from 2.4‰ to 4‰) (DeNiro *et al.*, 1980; DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Schoeninger, & DeNiro, 1984; Peterson & Fry, 1987; Schwarz & Schoeninger, 1991; Kelly, 2000). The source of this enrichment is not completely understood but is thought to be due to isotopic fractionation during amino acid deamination, where the lighter ^{14}N isotope is preferentially excreted as urea and the heavier ^{15}N isotope is retained by the body and incorporated into tissues, largely as proteins (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Schoeninger, & DeNiro, 1984; Macko *et al.*, 1986; Peterson & Fry, 1987; Schwarz & Schoeninger, 1991; Kelly, 2000).

Carbon isotopes are related to the $^{13}/^{12}\text{C}$ ratios of primary photosynthesising plants (or algae), and appear in the tissues of the animals that feed on them, enriched by about

1-5‰ in relation to the isotopic value of the plant (DeNiro & Epstein, 1978). The enrichment values for some tissues are not well documented, but in vibrissa keratin from harbour seals $\delta^{13}\text{C}$ enrichment was found to be 3-3.4 ‰ over diet (Hobson *et al.*, 1996). Keratin is normally found to be enriched by 1 to 3‰ over diet and about 5‰ over collagen (DeNiro & Epstein, 1978; Tieszen *et al.*, 1983; Ambrose & Norr, 1993). Carbon isotopes can be used to separate C_3 (e.g. wheat, rice, root crops, legumes, vegetables, nuts, honey and fruit), C_4 (e.g. maize, sugar cane and tropical pasture grasses) and Crassulacean acid metabolism (CAM) (e.g. cacti) plants. These differences are also seen in marine plants and algae.

C_4 plants fix atmospheric carbon dioxide using enzymes which function at their optimum in full sunlight and temperatures of 30-40°C and stop when temperatures increase. This allows CO_2 fixing with smaller stomatal openings to allow less water loss than C_3 plants; such plants are, thus, well adapted to hot, dry sunny conditions. C_3 plants operate best at up to 25% of full sun and at lower temperatures. This places them in shadier, wetter and colder environments. CAM plants operate both C_3 and C_4 pathways, depending on environmental conditions. The carbon dioxide containing the heavier isotope is discriminated against to different extents in the different systems, with C_3 plants discriminating against the heavier isotope to a greater extent than the C_4 , due to diffusion and enzymatic reactions. This means that the plants provide different isotopic signatures, with C_4 and CAM plants showing lower carbon isotopic fractionation than C_3 plants (Kelly, 2000) which can be used to identify which plant source is taken in as an animal's diet.

The ^{13}C enrichment of the body in relation to the diet is balanced by a depletion of ^{13}C in respired CO_2 (DeNiro & Epstein, 1978; Tieszen *et al.*, 1979), although the $^{13}\text{C}/^{12}\text{C}$ ratio of the diet in the tissues depends on the tissue type and the diet. The relationships between the major fractions - lipids, carbohydrates and proteins - are qualitatively preserved as carbon is incorporated into the animal. The results from both of these studies looking at $^{13}/^{12}\text{C}$ fractionation would indicate that carbon isotopic

analysis would be a useful tool in differentiation between terrestrial and aquatic diets, or C₃ and C₄ plants (DeNiro & Epstein, 1978; Tieszen *et al.*, 1979).

Together the two isotopes have been used in many ecological and archaeological studies, including studies on the diet of mammals and fish and birds in a variety of habitats (Hobson, 1986 and 1990; Hobson & Welch, 1992; Mitzutani *et al.*, 1992; Hobson *et al.*, 1994; Thompson *et al.*, 1995; Frazer *et al.*, 1997; Macko *et al.*, 1999 a and b; Jennings *et al.*, 2001; Pinnegar & Polunin, 2001). Stable isotope analysis is not able to give information on exact diet, but gives an average of dietary input over the time the protein was synthesised.

1.5.b. Applications of stable isotope analysis in dietary and ecological studies

Stable isotope analysis has been used in many dietary studies, often to look at the diets of animals where it is difficult to make direct observations; for example, in marine or aquatic environments. The understanding of the diet of a species will improve the understanding of an organism's place in the food web and, thus, its ecology.

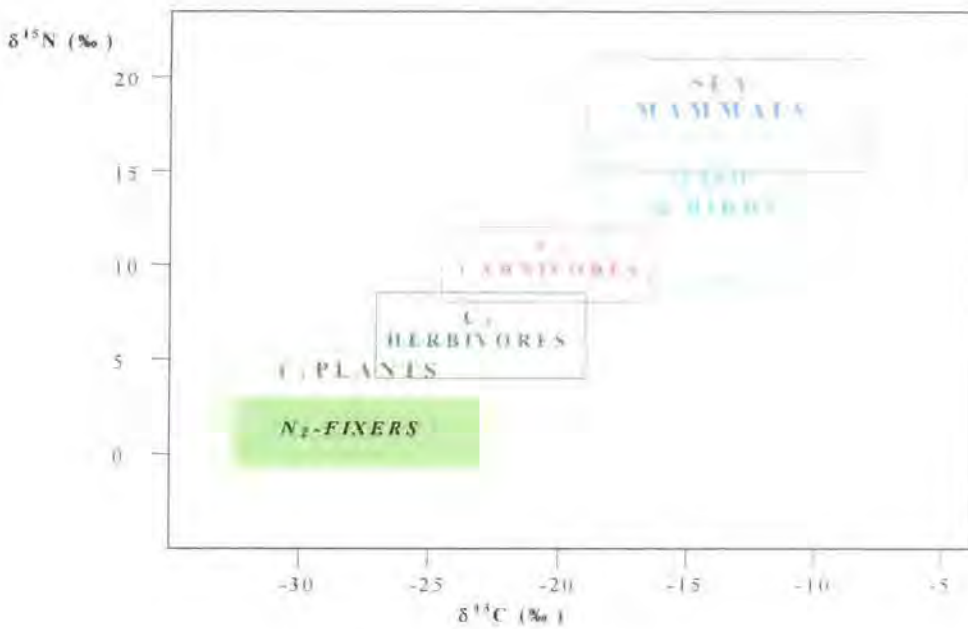


Figure 1.3 Graph showing relative values of marine and terrestrial $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for groups of organisms (O'Connell, Personal communication, January 2002)

DeNiro & Schoeninger (1983) looked at the ratio of N^{14} : N^{15} ($\delta^{15}\text{N}$) of a total of 66 species (100 individuals) of birds, fish and mammals. It was found that animals feeding on a marine diet were on average 9‰ greater than those on a terrestrial one, with the marine and terrestrial ranges overlapping by only 1‰. Those animals that feed on a mixture of both showed $\delta^{15}\text{N}$ values that were intermediate between the two. There was shown to be an enrichment of an average of 3‰ of $\delta^{15}\text{N}$ for each trophic level between animals that feed on different trophic levels. This indicates that nitrogen isotopic analysis is a useful tool for predicting an organism's place in the food web. It is particularly of use for marine food webs that are difficult to study and where relationships and placing of an animal are not known.

Minagawa & Wada (1984) looked at isotopic values of nitrogen of plankton and fish from surface water, the intertidal zone, tidal pools and surrounding water. A stepwise increase of an average of 3.4‰ per trophic level was found, independent of

what habitat the animal was taken from. The study also looked at mussels of different ages and found that the values were near to constant. From this it was concluded that age has little affect and that there is no accumulation of N^{15} over an individual's lifetime. The stepwise increase of nitrogen is seen in all animals in about the same magnitude, regardless of their age or method of nitrogen excretion.

1.5 c. The use of stable isotope analysis in pinniped studies

The diet of harp seals has been studied using this method (Lawson *et al.*, 1995). Samples of muscle from culled seals were compared to that from potential prey items. The method showed that there are age-related, seasonal and location differences in the diet of harp seals. Stomach content analysis (Lawson *et al.*, 1995) has also shown that Arctic cod, a species thought to be an important dietary component in some months was not a major component of the diet (Lawson *et al.*, 1995). The study also showed that the seals appeared to be feeding at a lower trophic level than expected if their diet was composed of a majority of Atlantic cod and Greenland halibut (*Reinhardtius hippoglossoides*).

The feeding and foraging behaviour of pregnant and migrating adult female and migrating juvenile male Northern fur seals was studied using the stable isotope analysis of skin (Kurle & Worthy, 2001). It was found that the pregnant females showed $\delta^{13}C$ and $\delta^{15}N$ values significantly higher than those of the juvenile males. The pregnant females were compared to two migrating nulliparous females, and were found to also show significantly higher $\delta^{13}C$ values than them; however no differences were found in $\delta^{15}N$ values. The results indicate different foraging areas for the fur seals, and that the females are likely to be feeding at a higher trophic level than the juvenile males.

In another study, analysis of hair from harbour seals was used to determine whether a population of Canadian harbour seals living in fresh water with access to salt water

was feeding on a largely freshwater diet (Smith *et al.*, 1996). It was also used to determine if this population could be distinguished both from a population of seals from the same species who lived in a marine environment and from a third population which had access to both marine and freshwater habitats. The results showed that the diet of the population was largely a freshwater one, with $\delta^{13}\text{C}$ values that were less enriched than those of the seals from marine food webs. The population that was feeding in an entirely marine environment showed the most enriched values, while the population feeding in both showed an intermediate value. Analysis of $\delta^{15}\text{N}$ showed that the freshwater feeding seals shared a similar trophic level with the seals feeding on a mixed diet, with the marine seals feeding approximately two trophic levels higher.

Samples of tissue from northern fur seals, harbour seals, Californian sea lions and northern elephant seals were analysed for carbon and nitrogen stable isotopes in order to look at the potential differences between near- and off-shore foraging (Burton & Koch, 1999). While the results showed that nitrogen values varied little between the species sampled, the $\delta^{13}\text{C}$ values varied to a greater extent than would be expected from the small differences in nitrogen and, thus, in trophic level. The differences in $\delta^{13}\text{C}$ were attributed to variations in the species of macro algal primary protein production between near- and off-shore areas.

Stable isotope analysis of the prey remains from the scats of Weddell seals (*Leptonychotes weddelli*) were compared to the isotopic values from seal blood samples and to values from potential prey items identified in previous studies (Burns *et al.*, 1998). It was found that, despite the bias generally associated with the scat analysis method, there was a good match between the prey remains and seal samples.

The failing of these studies, and of many others using this method to study diet and trophic level in ecology, is that samples that are able to show long-term diet (such as muscle and collagen) are generally only removed from dead animals, as the removal of these samples is surgically intrusive for live animals. While blood sampling is less invasive, it still necessitates the restraint and often sedation of the animal, and the blood

sample will give only a short term indication of the diet. This necessitates the capture of animals several times in a year to collect repeat samples if seasonality in the diet is to be studied.

Although different tissues do show a different turnover of isotopes (Kelly, 2000), sampling tissues such as bone or liver is an invasive procedure and can only be carried out on dead animals. It is, therefore, not suitable for the study of populations where a cull is not already in place or of endangered populations. In order to study the potential seasonal variation in the diet of seals, it is necessary to take samples that are non-invasive to collect and which are able to show variability over a time-period of a year or more.

1.5 d. The use of hair in stable isotope analysis

Hair has been used to study both modern and ancient diets of both humans (Schoeller, 1986; White, 1993; Yoshinaga, 1996; Witt *et al.*, 1998; O'Connell & Hedges 1999a and b; Macko *et al.*, 1999a and b) and some animals (Steele & Daniel, 1978; Jones *et al.*, 1981; Hobson *et al.*, 1997; Schoeninger *et al.*, 1997; Schoeninger *et al.*, 1998), since the ratio of the stable isotopes are not affected over time or by environmental factors (Yoshinaga *et al.*, 1996; O'Connell & Hedges, 1999a). Data suggest that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of keratin, the principal protein of both hair and vibrissae, closely reflects the animal's diet (Jones *et al.*, 1981; Tieszen & Fagre, 1993; O'Connell & Hedges, 1999a).

Wool staples (untreated wool fibres) both from modern Merino sheep in Australia and from historical samples from South African sheep (Witt *et al.*, 1999) were cut into 2mm sections (each section containing many wool fibres), and were analysed for $\delta^{13}\text{C}$. The values gave a profile of diet variation along the length of the staple for a period of about three years. This variation correlated with recorded changes in the vegetation

(and so the sheep's diet), which were in turn linked to changes in rainfall levels. It was concluded that the wool samples showed sufficient resolution for this to be developed as a method to examine changes in vegetation over time for both modern and historical studies.

Vibrissae (whiskers) are keratinous structures similar to animal fur and human hair with the same protein composition (Ling, 1966). They have a much greater diameter than hair or fur (but not necessarily a greater length), and grow from a proportionally larger follicle which has a complex nervous system and large blood sinuses. The vibrissae's movement is controlled by voluntary muscles (Ling, 1966). Dehnhardt & Kaminski (1995) showed that harbour seals could find diameter differences in disks using their vibrissae, and it is thought that the pinniped is able to use its vibrissae to locate prey items, possibly by feeling vibrations made in the water by the fish.

The vibrissae of the phocids have a beaded surface and appear flattened (King, 1983). Otariid vibrissae are smooth along their length and round in cross-section (King, 1983). In both phocids and otariids, the vibrissa tapers towards the tip end. The length of vibrissae varies, with otariids having longer vibrissae than most of the phocid species (Hirons *et al.*, 2001).

The vibrissa is a good material to sample since, unlike most tissue samples, its removal is non-invasive and relatively unstressful for the animal and may not require sedation. As with hair samples several samples representing different stages of growth and diet can be taken from one vibrissa, removing the need for repeated captures of animals over the year for more samples (Jones *et al.*, 1981; Tieszen & Fagre, 1993; O'Connell & Hedges, 1999a; Hirons *et al.*, 2001). A vibrissa is long enough and thick enough that only one need be taken from the seal to give a number of sections for sampling, unlike seal hair which is generally short and fine, making sample preparation more difficult. In addition to this, seals moult their fur once a year, meaning that the isotopic signature of a hair sample would only be representative of the diet in the period before the moult and hair growth. Vibrissae do not appear to be moulted along with the

rest of the pelage but are instead replaced gradually over time as they become damaged (Ling, 1966). Vibrissa turnover is thought to be about two years in southern elephant seals (Ling, 1966) and about a year in harbour seals (Hirons *et al.*, 2001). Hirons *et al.* (2001) observed that broken or cut vibrissae on the Stellar sea lion were rapidly replaced.

Vibrissae can be used in the same way as hair or fur to study the diet of seals. This not only gives results as a mean for the period of vibrissa growth but also enables the potential diet change over time to be studied as long as the vibrissa is growing. Hirons *et al.* (2001) used stable isotope analysis to estimate the growth rate of vibrissae for captive harbour seal and Stellar sea lions. Growth rate was estimated by injecting the animals with glycine enriched with ^{13}C and ^{15}N . Vibrissae were collected at five months and then ten months after the dose of glycine was administered to the animals. The vibrissae were analysed along their length, and the growth rate was calculated from the distance that the peaks had moved along the length of the vibrissa in the time period. The growth rate was calculated to be 0.10-0.17mm/day for captive Stellar sea lions, and an average of 0.33mm per day for captive harbour seals.

The following chapter will discuss the methodology and materials used to analyse seal vibrissae for dietary trends in this study and to compare the isotopic variation between the two populations of the grey seals over the three years of this study, and to look at potential dietary differences between male and female seals that previous studies have suggested might be found.

Chapter 2 : Materials and methods

CHAPTER 2

Materials and Methods

2.1. Wild caught vibrissae samples

2.1. a. Sample collection from grey seals

Grey seal samples were taken from breeding populations at two study sites: North Rona (59° 06' N, 05° 50' W), a small island of about 1.2km² in area in the outer Hebrides, 65 km north of the Butt of Lewis, Scotland, and the Isle of May (56° 11' N, 2° 3' W) which lies 8 km offshore in the mouth of the Firth of Forth, Scotland, and is 2.5 x 0.5km in area (Figure 1.1). Southern elephant seal and South American sea lion (*Otaria flavescens*) samples were collected from breeding populations at Pensínsula Valdés, Southern Argentina (42° 45' S, 63° 38' W). For maps showing locations of the study sites please see Chapter One, pages 5 and 11).

Vibrissae samples from 57 different grey seals were collected from the Isle of May, Scotland, and from 39 individuals from North Rona, Scotland, during the breeding seasons of 1997-1999 (mid-September to early December). The animals sampled were those that were being caught and sedated as part of the ongoing research on the populations conducted by the Sea Mammal Research Unit (SMRU) based in St Andrews, Scotland). In total 99 vibrissae samples from Isle of May and 114 samples from North Rona were taken over the four year study period. Samples from 30 individual southern elephant seals were collected during the breeding seasons of 1998 and 1999 at Pensínsula Valdés in September and October 1998 and 1999, totalling 62 samples in the two years. Southern elephant seal samples were taken from animals that were being sampled for other research. Male samples were taken from any animal that was easy and safe to approach. Samples were taken from six captive grey seals from the Gweek Seal Sanctuary in Cornwall (August 8th 2000) and two from captive study

animals from SMRU kept at St Andrews, Scotland. All the vibrissae were removed from three dead seals found on North Rona in 1998 and from a dead male southern elephant seal in 1999.

Of the grey seals that were sampled, 38 were adult females which were part of the SMRU seal study program. These animals had been hot-iron branded on their sides (while sedated) for identification purposes, in 1985 and 1988 (Pomeroy *et al.*, 2000) on North Rona and on the Isle of May in the years since 1987 and where possible were caught twice more for sampling during each breeding season. Six branded females were caught on North Rona in 1997, and 15 on the Isle of May (ten branded and three tagged) and their whiskers sampled. In 1998, 28 animals from North Rona, and 33 animals from the Isle of May of which 17 were branded from North Rona and seven were tagged, and 25 branded from Isle of May and eight tagged were sampled. In 1999 15 branded animals were sampled and four tagged on North Rona and 26 branded and two tagged on the Isle of May. The seven males were sampled having been caught and sedated in order to be branded for future research conducted by SMRU, during the breeding season of 1999 on the Isle of May.

During the study period two females from North Rona and four female seals from Isle of May were sampled in every year of the study. Eighteen females from North Rona were sampled in at least two years of the study, and 25 females from Isle of May were sampled in at least two years. Seven males were sampled from Isle of May in 1999. One dead seal from North Rona had all its whiskers collected in 1998 and three dead females were similarly sampled in 1999. Three of these seals were un-tagged or un-branded animals and were thus of unknown ages, one sampled in 1999 was a branded seal 'A5'. In total 213 whiskers were collected from grey seals over the four year period. Although whiskers were collected in 2000, and subsequently prepared, due to time constraints the whiskers were not analysed as part of this study.

The adult grey seals were sedated using a mixture of ketamine hydrochloride ((2-chlorophenyl)-2-methylaminocyclohexane hydrochloride) and diazepam (7-chloro-1, 3,

dihydro-1-methyl 1-5-phenyl-2H-14, benzodiazepine-2-one) (Pomeroy *et al.*, 2000) injected into a rear muscle by using a blowpipe (personal observations). Care was taken during this procedure that the seals were not too close to the sea, so they would not be likely to enter it during the period when the sedative was taking effect. The seal was left for ten minutes after administration of the sedative for it to take effect. The seal was then further restrained by a net, which was also used to raise it from the ground to weigh it using a balance suspended from a tripod. Blood, urine and whisker samples were collected and measurements of mass, length and girth recorded for other ongoing SMRU studies (personal observations from assisting with SMRU field work). In 1997 whisker samples were cut from the face of the seal; in the other years (1998, 1999) they were pulled out of the face of the seal. While the female was sedated, similar samples and measurements were taken from her pup, which was not sedated, but restrained in a specially designed pup bag out of the mother's line of sight to try to avoid additional stress to her. After sample collection the seals were released from the nets and left to recover from the sedative (the field work and seal handling was carried out by collaborators at SMRU under a Home Office license).

One whisker was taken from each animal, except for two animals from North Rona in 1997, three animals from Isle of May in 1998, and three in 1999, where two whiskers were taken from each animal. Whisker samples were stored at room temperature in individual glass or plastic tubes labelled with the date, animal's sex and its identity, until they were prepared for analysis.

2.1. B. Sample collection of southern elephant seal whiskers

In total 62 vibrissae were collected from 30 southern elephant seals (18 females and 11 males) during the breeding seasons of 1998 and 1999. Samples were collected from conscious adult females and sub-adult males. In addition, in 1998, three whiskers were collected off a dead adult female seal, and in 1999, 11 whiskers were collected from a

dead male seal. Three whiskers from one male and varying numbers of whiskers from seven females were collected. In 1999 whiskers were collected from ten males of varying age class and from 11 females. Also in 1999 whiskers were collected from five adult South American sea lion (one male animal and four females). Whiskers from both species were stored in individual glass tubes or plastic bags labelled with details of the seal's age class (if male) and sex as well as date of collection and tag numbers if available.

One male southern elephant seal sample was collected from a population on the Falkland Islands in 1998 and five samples (two female, one male) were collected in 2000, but were not analysed as part of this study.

Southern elephant seal and South American sea lion samples were cut off as close to the face as possible. One or more whiskers were taken from each individual (up to six whiskers from one live animal). Where seals were found dead the whiskers were pulled out from the face. Samples were sent to England for analysis at the end of the breeding season.

2.2. Samples from captive seals

2.2. a. Samples from the National Seal Sanctuary, Gweek, Cornwall

Samples were taken from six captive seals from the National Seal Sanctuary in Gweek, Cornwall, four were female and two were male, one male was a sub-adult. All were resident at the seal sanctuary due to various health problems (e.g. blindness, thyroid problems) that prevented their return to the wild. Whiskers were cut off from the faces of the seals by their handler at feeding time, while the seals were hand-fed fish. The seals had all been fed a constant diet of herring (sizes not documented) with small numbers of other commercial species of fish subject to availability that were not documented. All these seals had been in captivity for at least two years.

2.2. b. Samples from captive animals from SMRU, St Andrews's

Samples from two captive animals, “Gloria” (brand 9L) and “Heidi” (unbranded) at the SMRU facility in St Andrews were collected during routine sedation for sample collection for another project (Carol Sparling, SMRU, personal communication). One whisker was cut from each animal, from Gloria on 6th June 2001 and from Heidi on 27th June 2001. Both seals were adult females. Gloria was tagged in 1991 when she had a pup and so is at least 15 years old; Heidi is an adult female. The seals were both captured on the 9th March 2001 from the Isle of May. The seals had been fed a constant diet of herring since their capture.

In both cases whiskers from captive seals were dried and stored in labelled plastic bags until their preparation.

2.3. Sample Pre-treatment

All vibrissae (whisker) samples were pre-treated using the same method. They were cleaned individually for 20 minutes in an ultrasonic bath in a beaker covered with aluminium foil containing 150ml of distilled water, then in 150ml of a solution of 2:1 methanol: chloroform for 20 minutes and then in 150ml of distilled water for a further 20 minutes (O'Connell & Hedges, 1999). The samples were then rinsed three times in distilled water, and examined under a dissecting microscope for any remaining dirt or skin still attached to the vibrissae, particularly around the vibrissae follicle. Any dirt particles found were scraped off with a scalpel blade and the whisker was rinsed in distilled water. The vibrissae were dried and the length measured and recorded. Any

pigmentation was recorded at the distance it presented along the vibrissae from the distal end (closest to the seal's face). It was also noted whether the vibrissae had been cut from the seal or pulled out.

The vibrissae were cut into sections (starting from the face end) using small mammal toe nail clippers. The sections weighed 2-3mg and were typically of 2.0mm to 20.0mm long. As the vibrissae tapered towards the tip end the sections increased in length. Every third sample was weighed on a balance accurate to 0.00mg to check that the samples were of weights between 2-3mg and the mass was recorded. Each section's length was measured to 0.5mm using a metal ruler with 0.5mm divisions and recorded. The sections were wrapped in cleaned tin capsules (6 x 4mm, pressed tin capsules, standard weight, Elemental Microanalysis Ltd). Using forceps, the tin capsule was rolled around the sample into as small a ball as possible and stored in an individual Eppendorf tube labelled with the seal's identity, vibrissae section number, and the year of sample collection.

Preparation of the majority both the grey seal and southern elephant seal samples was conducted by the author in Durham (Biological and Biomedical Science Department), a few vibrissae were prepared in Oxford.

Tin capsules were cleaned by soaking them for 20 minutes in 50 ml of methanol and then rinsing them three times with distilled water after which they were dried in a fume hood overnight. They were stored before use in glass petri dishes.

For grey seal samples from North Rona in 1998 and 1999, and from the Isle of May in 1997, 1998 and 1999, alternate sections along each whisker were analysed isotopically. All samples from North Rona in 1997 were analysed isotopically. For the southern elephant seal samples, all samples along the vibrissae were analysed for the 1998 samples and alternate ones for the samples collected in 1999. This was due to constraints of both time and money. Repeat samples were run for those individuals where more than one whisker was collected, to ensure consistency between whiskers.

Note on Labelling: Throughout this study the following identification symbols were used. For grey seal identification, the code on their brand or tag was used, e.g. A5, G45. These symbols are used for grey seals sampled in 1997. However, since multiple whiskers were removed from some animals, a code followed by a * would indicate a second whisker that was analysed. For example, A5* would indicate this was the second whisker analysed from animal A5 in 1997. ‘!’ indicates a whisker sampled from an animal in 1998; ‘A5!’ would therefore be a whisker from animal A5 collected in 1998, and a prefix of * indicates a whisker collected in 1999, e.g. *A5.

To identify southern elephant seal and South American sea lion samples the codes for the samples were kept the same as those on the tag of the animal from which they were collected. In 1999, the whiskers from the southern elephant seals and South American sea lion did not come from tagged or marked animals, so a code was derived from the age class/ other information that was sent with the samples, for example SA34 would indicate a sub-adult male of age class three to four years.

2.4. Fish samples

British fish were selected based on published findings from scat and stomach content analysis of grey seals (Rae, 1973; Thompson *et al.* 1991; Hammond *et al.*, 1994 a and b; Mohan & Bowen, 1996; Thompson *et al.*, 1996). Where samples could not be obtained, published data were used where possible. For most British fish species the discards were collected, since these generally include the head, spine, ribs and tails of the fish and enough white muscle to analyse isotopically. They are also free of charge and so avoided the financial outlay of buying whole fish samples. Samples of six herring heads and one large cod head that were reported to have been caught between Edinburgh and the Farne islands in July 1999 were collected from a fish shop in Leith (Edinburgh, Scotland). Samples of discards from cod, mackerel, plaice (*Pleuronectes*

platessa), haddock (*Melanogrammus aeglefinus*), pollock (*Theragra finnmarchica*), herring and witch (*Glyptocephalus cynoglossus*) from Hartlepool fishing port were collected from three different fishing vessels which had been fishing offshore in the North Sea in an area where grey seals from the Isle of May have been found to forage (Hammond *et al.*, 1996) (collected 20th September 1999). Six of each species were collected and samples were stored frozen in labelled bags. Samples of discards of haddock, monkfish (*Squatina squatina*), whiting (*Micromesistius poutassou*), hake, sprats (*Sprattus sprattus*) (whole fish), witch and cod were collected by the Mallaig (Scotland) fisheries inspector on 6th November 2000 from fishing vessels that had been fishing to the north and west of Scotland in areas where seals from North Rona are thought to feed (Hammond *et al.*, 1994, a and b). Six of each species were collected and samples were stored frozen at -20°C before preparation. All fish had been stored on ice whilst on the fishing vessels.

Samples of fish from Argentina were collected from a private vessel 'Harengus S.A.' that fished off the Argentine continental shelf (organised by Dr. M. Lewis, Argentina). One animal from each species was taken from each fishing net. Twenty one species of fish and two species of cephalopod were taken. In total, samples were taken from 200 individuals. Muscle samples were taken from each animal and these were oven dried at a temperature of $80-90^{\circ}\text{C}$ for 48 hours. The samples were wrapped individually in tin foil, labelled and sent by airmail to England where they were stored at -20°C until preparation.

Four species of fish (salmon, hake, tuna (of unknown species) and one other unknown fish species) and one unknown cephalopod species were also collected from a fish market in Argentina by Ana Topf (University of Durham) in 2001. These samples were oven dried (unspecified temperature) for 12 hours and wrapped in tin foil. Upon arrival in the England the samples were stored frozen.

Samples from Argentina were collected largely based on availability rather than on any previous dietary analysis, but results from previous studies were considered during

the collection of fish samples. Samples were collected in areas where southern elephant seals are known to forage and attempts were made to collect items of known dietary interest for the seals (Green & Williams, 1986; Rodhouse *et al.*, 1992; Green & Burton, 1993; Slip, 1995).

Table 2.1: Species of fish collected from Patagonia

Sample Number	Species	Common Name	Number sampled
2	<i>Sebastes oculatus</i>	Patagonian redfish	4
3	<i>Seriorella puntaca</i>	Silver warehound	4
4	<i>Illuocoetes fimbriatus</i>	Eelpout	5
5	<i>Austrophycis marginata</i>	Dwarf codling	2
6	<i>Cottoperca gobio</i>	Thornfish	6
7	<i>Congeopodus peruvianus</i>	Racehorse/pigfish	5
8	<i>Congeopodus peruvianus</i>	Racehorse/pigfish	6
9	<i>Congeopodus peruvianus</i>	Racehorse/pigfish	5
10	<i>Merluccius hubbsi</i>	Argentine Hake	4
11	<i>Merluccius hubbsi</i>	Argentine Hake	8
12	<i>Brama brama</i>	Atlantic pomfrey	7
13	<i>Bathyraja brachyurops</i>	Broadnosed skate	2
14	<i>Bathyraja macloviana</i>	Patagonian skate	3
16	<i>Dipturus flavirrostris</i>	Skate	5
17	<i>Bathyraja scaphiops</i>	Cuphead skate	2
18	<i>Bathyraja scaphiops</i>	Cuphead skate	1
19	<i>Psammobatis scobina</i>	Raspthorn sandskate	1
20	<i>Psammobatis scobina</i>	Raspthorn sandskate	2
21	<i>Bathyraja albomaculata</i>	White-dotted Skate	4
22	<i>Stromateus maculatus o brasiliensis</i>	Butterfly fish	3
23	<i>Stromateus maculatus o brasiliensis</i>	Butterfly fish	7
24	<i>Coelorhynchus fasciatus</i>	Banded whiptail	10
25	<i>Coelorhynchus fasciatus</i>	Banded whiptail	6
26	<i>Patagonotothen ramsayi</i>	Cod ice fish	6
28	<i>Macroronus maguellanicus</i>	Patagonan grenadier	3
29	<i>Macroronus maguellanicus</i>	Patagonian grenadier	2
30	<i>Genypterus blacodes</i>	Pink cask-eel	5
31	<i>Genypterus blacodes</i>	Pink cask-eel	1
32	<i>Squalus acanthias</i>	Piked dog fish	8
33	<i>Squalus acanthias</i>	Piked dog fish	7

34	<i>Schroederichthys biviuis</i>	Narrow-mouthed cat shark	5
35	<i>Illex argentinus</i>	Argentine short fin squid	11
37	<i>Illex argentinus</i>	Argentine short fin squid	12
39	<i>Morotheuthis ingens</i>	Greater hooked squid	1
40	<i>Bassanago albescens</i>	Conger eel	15
41	<i>Merluccius australis</i>	Southern hake	5
42	<i>Micromesistius australis</i>	Southern blue whiting	3
45	<i>Salilota australis</i>	Tadpole codling	1
46	<i>Salilota australis</i>	Tadpole codling	1
47	<i>Cottunculus granulosis</i>	Fathead	1
48	<i>Nemadactylus bergui</i>	Morwong	1
49	<i>Paralichthys patagonicus</i>	Patagonian flounder	1
50	<i>Mancopsetta maculata</i>	Southern flounder	3
51	<i>Mancopsetta maculata</i>	Southern flounder	4
52	<i>Parona signata</i>	Parona leather jacket	1
54	<i>Dissostichus eleginoides</i>	Patagonian toothfish	1

Frozen fish samples were thawed overnight in a fume hood. Muscle, skin and bone samples were then cut off the fish heads and stored separately frozen in labelled containers. The samples were then freeze dried, and 3-5mg of each sample was weighed and wrapped into a cleaned tin cap (6 x 4mm). Three samples of both skin and bone were taken from each fish, and where possible three to six fish of each species were used. Any remaining samples were frozen in case repeat samples were necessary. Three samples of skin and muscle were analysed for the samples collected in 1999 using the same methods used for the vibrissae analysis. Samples from Argentina were prepared and run in the same way. Preparation of all of the fish samples was carried out by the author in the Oxford Radiocarbon Laboratory.

2.5. Isotopic Analysis

All isotopic analysis was carried out in the Research Laboratory for Archaeology and the History of Art at the University of Oxford. The majority of the samples were analysed by Dr. T O'Connell and research assistants at the radiocarbon research facility in Oxford, although the author did assist in loading some of the runs.

Samples were run with two standards of cleaned nylon for every six samples in runs totalling 99 samples. Standards were made of 2.0-3.2 mg of clean ground nylon, weighed using a electronic balance accurate to 0.00mg and wrapped in a 6 x 4mm tin cap that was folded into a small ball and then stored in a Eppendorf tube with other standards of the same mass. Nylon standards were prepared by the author either in Oxford or in the Archeoscience Laboratory at the University of Durham Archaeology Department. During this study approximately 4800 samples were run, with about 1600 nylon standards in about 50 runs.

All isotopic analyses were performed using an automated carbon and nitrogen analyser and a continuous-flow isotope-ratio-monitoring mass-spectrometer (Carlo Erba carbon and nitrogen elemental analyser automated Dumas preparation system coupled to a Europa Geo 20/20 mass spectrometer). Typical replicate measurement errors were of the order of $\pm 0.2\%$ (Standard deviation) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Samples are dropped into a furnace at 1000°C whilst in an atmosphere of oxygen. The tin sample container ignites and burns exothermically, and the temperature rises to about 1,800°C, oxidizing the sample. After combustion, the atmosphere is switched from oxygen to helium, and helium is used as the carrier gas throughout the rest of the system. The combustion products are passed through a bed of chromium trioxide, followed by a layer of copper oxide then a layer of silver wool at 1000°C to complete

the oxidation and remove any sulphur. The products then pass through a second copper-containing reduction furnace at 600°C where excess oxygen is removed and nitrogen oxides are reduced to elemental nitrogen. Water is then removed in a trap containing anhydrous magnesium perchlorate. The elemental nitrogen gas and carbon dioxide are separated using a molecular sieve: the gas stream is passed through a column of Carbosieve 60-80 mesh. This slows down the larger carbon dioxide molecules sufficiently to separate the two gases completely. Thus the nitrogen is analysed first, followed immediately by the carbon dioxide. The stream of gas passes first through a thermal conductivity detector (TCD) to quantify the mass of the gas of interest, then 1% is bled into the mass-spectrometer for isotopic analysis.

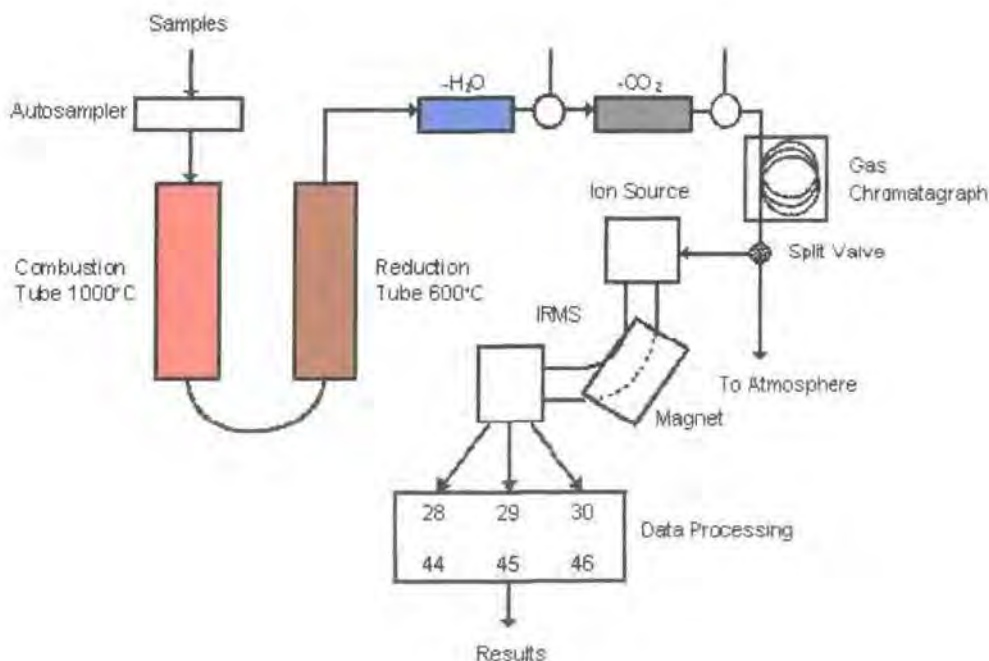
The mass spectrometer used was an Europa Geo 20/20 isotope-ratio-monitoring mass-spectrometer. The mass-spectrometer consists of a 120° extended geometry magnetic sector analyser with a triple Faraday cup ion collector. The analytical mass range is 27 to 47 atomic mass unit (amu). Detection of both carbon and nitrogen isotopes is achieved by switching the source conditions from those suitable for nitrogen to those suitable for carbon after the nitrogen has passed through the mass-spectrometer. For nitrogen, the high tension accelerator voltage is first set to 4000V, which permits the Faraday cups to detect the amu masses 28, 29 and 30 ($^{14}\text{N}_2$, $^{14}\text{N}^{15}\text{N}$ and $^{15}\text{N}_2$ respectively). When the nitrogen peak is finished, and just before the carbon dioxide enters the mass-spectrometer, the HT voltage is switched to 2,500V, which allows the Faraday cups to detect the amu masses 44, 45 and 46 ($^{12}\text{C}^{16}\text{O}^{16}\text{O}$, then $^{13}\text{C}^{16}\text{O}^{16}\text{O}$, then $^{12}\text{C}^{16}\text{O}^{18}\text{O}$ respectively).

The mass spectrometer can accurately analyse samples within the mass range of 200µg to 800µg of nitrogen or 800 to 1500µg carbon. Within this range, a comparison

of the measured carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values with sample mass has demonstrated that isotopic analysis is not mass dependent.

Results are reported in units of parts per thousand (permil, ‰) with $\delta^{13}\text{C}$ relative to Vienna-PDB (fossil carbonate from Belemnite of Pee Dee Formation), and with $\delta^{15}\text{N}$ relative to Air (Gonfiantini, 1984; Mariotti, 1983; Gonfiantini *et al.*, 1990).

Figure 2.1 Schematic of continuous flow isotope ratio mass spectrometer



2.6. Amino-acid analysis - hydrolysates

Eight 2.0-3.2mg vibrissae samples, from two grey seals and two southern elephant seals, were analysed using the method below. Two samples, one from each species, were pigmented with black pigment for part of their length, while the remaining two were from whiskers that were un-pigmented in order to compare amino acid

composition between pigmented and unpigmented whiskers. From each whisker two samples were taken, one from the face end and one from the far end of the whisker in order to compare amino acid composition between the two ends of the whiskers.

Method of analysis – conducted by and credited to: Tony Willis, MRC

Immunochemistry Unit, University of Oxford, for the amino acid analyses (Heinrikson, R.L. & Meredith, S.C, 1984).

Samples were dried in a centrifugal concentrator (Savant SpeedVac), 2.0 nanomoles of nor-leucine added as an internal standard and the samples were dried down again. They were then hydrolysed in gas-phase constant-boiling (5.7N) hydrochloric acid at 110°C for 24 hours. Phenol was added as a competitive inhibitor to facilitate maximum tyrosine recovery.

After hydrolysis the samples were redissolved in 50µl of 0.5 mg/ml potassium EDTA and 10µl of this were applied to the sample frit of an ABI 420A derivatiser/analyser (PE Applied Biosystems, Warrington, UK). The 420A utilises pre-column derivatisation with phenylisothiocyanate (PITC) to form phenylthiocarbamyl amino acids (PTC-aa). These are then automatically sampled into a narrow-bore HPLC system (Applied Biosystems 130A) for analysis. Data handling is performed using Gynkotek Chromeleon software (version 4.10 from Gynkotek UK Ltd, Macclesfield UK). The internal standard value is used to calculate amino-acid content of the whole of the original sample.

Standard amino-acid mixtures at 100picomole/10µl were used to calibrate the HPLC system before each series of analyses.

HPLC conditions

Column	Applied Biosystems PTC C-18 (220x2.1mm)(from PE Applied Biosystems, Warrington, UK)
Buffer A	150mM sodium acetate pH5.5 in water
Buffer B	70% acetonitrile in water
Column temp.	34°C
gradient	7-32 over 10', 33-62 over 10' and then 62-100% over 5' (as % of A).

2.7. Statistical analysis

Results from isotopic analysis and the amino acid analysis were stored in Microsoft Excel version 2000. This was used to plot graphs of isotopic variation, $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ variation against length (mm) of vibrissae for each vibrissa that was analysed. All graphs showing $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ plotted against whisker length were plotted with the cut (distal) end of the whisker as zero.

For the samples that were analysed for amino acid composition, graphs showing the percentage amino acid composition per sample were plotted (also in Excel). This enabled a visual comparison of potential isotopic variation along the whisker length, between whiskers, populations and sexes; between the four years of sampling for grey seals and two years for southern elephant seals; and for amino acid variation since sample numbers were too small to carry out any statistical analysis.

Comparisons between the data sets were carried out using Mann-Whitney U-tests (SPSS version 10.0) to look for differences in grey seals between the three years of the

study (comparing all sample results in 1997:1998, 1998:1999 and 1997:1999) for each of the two populations. Statistical comparisons (Mann-Whitney U-test) were then carried out to examine differences between the two populations. These were carried out for 1997, 1998 and 1999. Mann-Whitney U-tests were used due to non-normal distributions and the lack of independence.

To look at possible variation trends along the whisker length between the two populations and between the years, the beginning, the middle and the end of each whisker were compared to each other for each group using the Mann-Whitney U-test. This was carried out for the grey seal samples from both populations, between the populations, and also for the southern elephant seal and South American sea lion data.

The southern elephant seals results were statistically analysed (Mann-Whitney U-test) to look for differences between the two years and between males and females. To do this, the males were divided into three groups on a visual basis from the isotopic variation graph.

Using Mann-Whitney U-tests each of these groups was compared to the others and to the female animals and the South American sea lions.

The significance of these tests was usually taken at a 95% level, except where Bonferroni corrections were applied. Such instances are stated in the text.

2.8 Correction factor

For $\delta^{13}\text{C}$ values of fish where the C: N ratio was found to be greater than 4.0 a correction factor was calculated using the following formula:

$$\delta^{13}\text{C} = \delta^{13}\text{C} + 6\{-0.207 + 3.9 / [(1 + 287(1 + 1 / (0.246\text{C}/\text{N} - 0.775))) / 93]\} \quad (\text{Rau } et al. 1992)$$

Chapter 3 : Calibration data for diet analyses

CHAPTER 3

Calibration data for diet analyses

3.1 Introduction

The research reviewed in Chapter One showed that stable isotope analysis has been used in many ecological studies of diet. However, despite the large number of studies, few have been carried out using hair or vibrissae as the sample material (e.g. Scholler *et al.*, 1986; White, 1993; Yoshinga *et al.*, 1996; Witt *et al.* 1998; Macko *et al.*, 1999 a and b; O'Connell & Hedges, 1999 a and b; Hirons *et al.*, 2001) along the sample length (Jones *et al.* 1981; Witt *et al.*, 1998; Hirons *et al.*, 2001). Most of these studies use hair samples for analysis (Scholler *et al.*, 1986; White, 1993; Yoshinaga *et al.*, 1996; Witt *et al.*, 1998; Macko *et al.*, 1999 a and b; O'Connell & Hedges, 1999 a and b) which, due to the small diameter of the hair, requires the analysis of a bundle of multiple hairs to give enough sample weight for analysis. Such studies need to make the assumption that the isotope value of hair samples is similar at similar lengths along the hair.

In this study, and in Hirons *et al.* (2001), seal vibrissae are used. These have a sufficient diameter that analysis of a section from only one vibrissa provides a sufficient sample mass for accurate results. However, it was considered appropriate to analyse several vibrissae from a few individuals from both study species in order to ensure that different vibrissae from an individual do show similar isotopic values.

It is probable that there will be some background variations in isotopic composition along the length of a vibrissa, due to slight variations in isotope incorporation both from the diet and metabolic processes and to machine errors during the analysis of the vibrissae. This variation has been demonstrated in harbour seals during a constant diet feeding experiment on captive seals that had been fed herring for at least two years (Hobson *et al.*, 1996). The isotopic range of the vibrissae was found to be from 0.21 to

0.57‰ for $\delta^{13}\text{C}$, and from 0.27‰ to 0.45‰ for $\delta^{15}\text{N}$. Their study found no differences in either isotope for seals of different ages or sexes.

For this study it is necessary to quantify the variation along vibrissa lengths of seals fed a constant diet of a single species of fish, in order to consider whether variations seen along the profiles of vibrissae from the wild study seals (discussed in Chapters 4 and 5) are large enough to be due to seasonal dietary changes or are merely due to background isotopic variation. The results from the analysis of the vibrissae from six captive grey seals from the National Seal Sanctuary in Cornwall, which were fed a constant herring diet, were analysed and compared to the study conducted on harbour seals (Hobson *et al.*, 1996), the results of which are shown below.

Furthermore, in order to properly interpret any seasonal dietary changes in wild seals, it is necessary to have some assessment of the likely growth rate for pinniped vibrissae. Few data are available on vibrissa growth rates for pinnipeds as it is understandably difficult to measure in a wild seal, where the animal spends the majority of its time in the water and is unlikely to cooperate with the process required when on land. From observations, Ling (1966) estimated that southern elephant seal vibrissae grow for up to two years before their replacement, which occurs gradually and not during the main moulting period for the seal. However, it is not clear what methods were used to reach this conclusion in Ling's study, nor are the data on sample size or on the age or the sex of the seals available. As such, this estimate of growth rate should be used with caution.

The growth rate of harbour seals was calculated to be 0.33mm/day for seals (Hirons *et al.*, 2001). This rate was determined by injecting glycine enriched with ^{13}C and ^{15}N into two captive harbour seals. One seal received two doses 147 days apart and the second received a single dose. The positions of the isotope peaks after the analysis of the vibrissae showed that the vibrissae appear to grow from the autumn through to June, when the growth of the vibrissae appeared to cease.

As a part of the same study (Hirons *et al.*, 2001), three tagged adult wild harbour seals were sampled twice, at seven month intervals. Vibrissae from these seals were analysed and the vibrissae from one of the seals showed similar trends in both the vibrissae analysed from it. From the distance that the trend had moved along the vibrissa over the seven months, a growth rate of 0.08mm/day was calculated for this individual. The initial vibrissae collected from the other two wild harbour seals showed no trends that could be recognised in the vibrissae collected after the seven month period.

The discrepancy in the growth rate between wild and captive harbour seals is attributed in the Hirons *et al.*, (2001) paper to differences in habitat, feeding and energetics. As some differences are seen on the plot shown in the paper, it is possible that the trends seen in both the vibrissae used for the calculation are not actually due to the same period of dietary change and that the vibrissae are actually growing faster than calculated. Since the vibrissae are short (three to four centimetres), it would not take long for observed trends to be replaced by new growth at the faster growth rate demonstrated in the captive animals.

Also in the same study (Hirons *et al.*, 2001), two captive stellar sea lions both received two doses of isotopically enriched glycine, and it was found that the growth rate of their vibrissae was 0.05-0.07mm/day. The study also sampled 30 wild Stellar sea lions, which showed regular oscillations along the vibrissae. This led to the assumption made by the authors that these were of an annual nature, giving a growth rate of between 0.05 and 0.18 mm/day. However the paper is unclear as to the cause of these oscillations, which were not seen in the captive animals

It is hypothesised that the change in isotopic values seen when the diet of wild seals is changed to a constant diet of a single species of fish would cause a sufficient and noticeable difference in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the seal vibrissae to make it possible to measure the growth rate from the point of change of diet. To test this,

vibrissae from two captive seals were collected at a known time after the seal's capture from the Isle of May and were then analysed (see Chapter 2 for methods).

Finally, this chapter looks at the results from the amino acid analysis of two samples from each of four vibrissae, two from each species of seal. One sample was taken from the beginning and one from the end of the vibrissae from each animal. Of these, one sample was taken from a pigmented vibrissa and one from an un-pigmented one, in order to examine any possible changes in the amino acid composition along the length of the vibrissa and to determine whether any changes could be related to differences in pigmentation along the vibrissa's length. Different amino acids are known to have different isotopic values. Therefore, a change in amino acid composition could alter the bulk keratin isotopic value (Jones *et al.*, 1981; White, 1993; O'Connell & Hedges, 1999b; O'Connell *et al.*, 2001).

Four hypotheses will be examined in this chapter.

1. That the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation along the length of a seal vibrissa is similar to the variation seen in other vibrissae collected from the same seal at the same time.
2. That the isotopic variation along a vibrissa from a seal fed a single species of fish in captivity is less than the variation that would be seen from a seal eating a variable diet in the wild. Variation is expected to be $\pm 0.7\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ based on feeding trial with constant diet in captivity (Hobson *et al.* 1996).
3. That vibrissa growth rate can be calibrated based on diet transition data.
4. That any $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations seen along the vibrissa are not correlated to amino acid changes.

3.2. Results.

3.2. a. Replicate vibrissae

3.2. a.i. Grey seals

1. Replicate vibrissae from dead grey seals

Analysis (for methodology please see Chapter 2, sections, 2.1. a. and 2.3.) of multiple vibrissae collected from four dead female grey seals from North Rona in 1998 and 2000 showed that different vibrissae from the same animal had strong isotopic correlation with each other for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

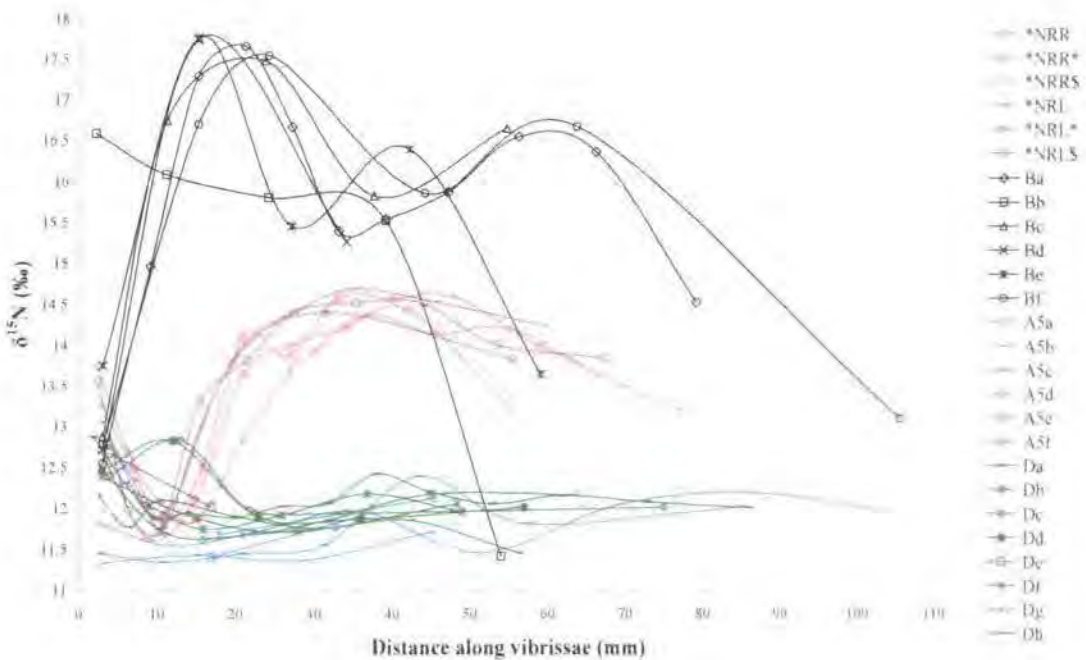


Figure 3.1: $\delta^{15}\text{N}$ of vibrissae against vibrissae length for sets of vibrissae from four dead seals from North Rona. For 'NR' plot shows vibrissae from left side of face 'L' and the right side 'R'. The vibrissae from each seal are shown as the same colour; for 'NR' the vibrissae from the left and right sides of the face are shown in different colours and are labelled to indicate left or right side, i.e. 'NRR' denotes vibrissae from the right side of the face and 'NRL' those from the left.

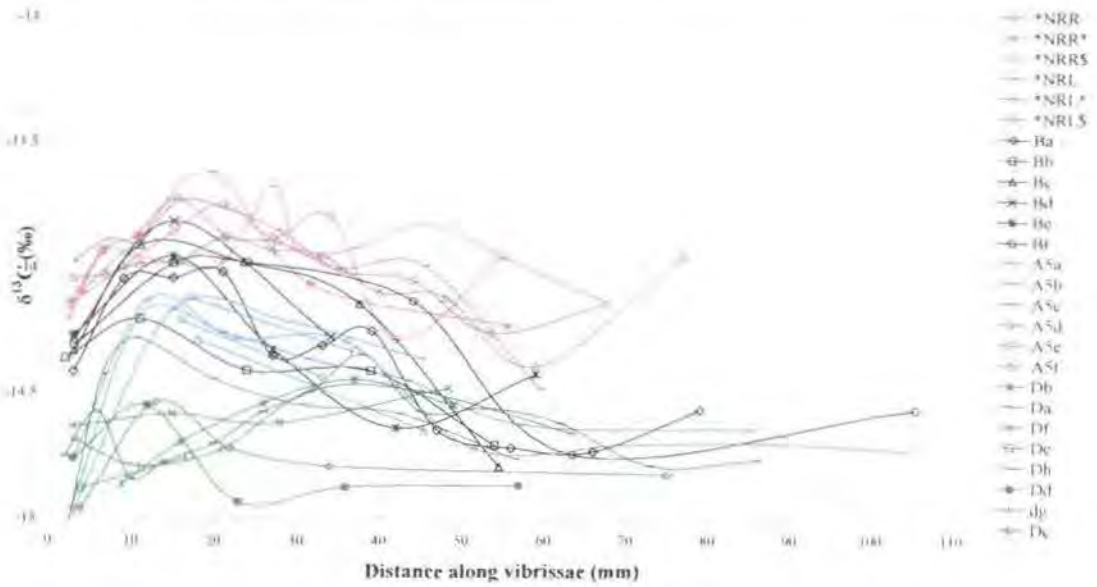


Figure 3.2: $\delta^{13}\text{C}$ of vibrissae against vibrissae length for sets of vibrissae from four dead seals from North Rona. For ‘NR’ plot shows vibrissae from left side of face ‘L’ and the right side ‘R’. The vibrissae from each seal are shown as the same colour; for ‘NR’ the vibrissae from the left and right sides of the face are shown in different colours and are labelled to indicate left or right side, i.e. ‘NRR’ denotes vibrissae from the right side of the face and ‘NRL’ those from the left. Colours are the same as those shown in Figure 3.1.

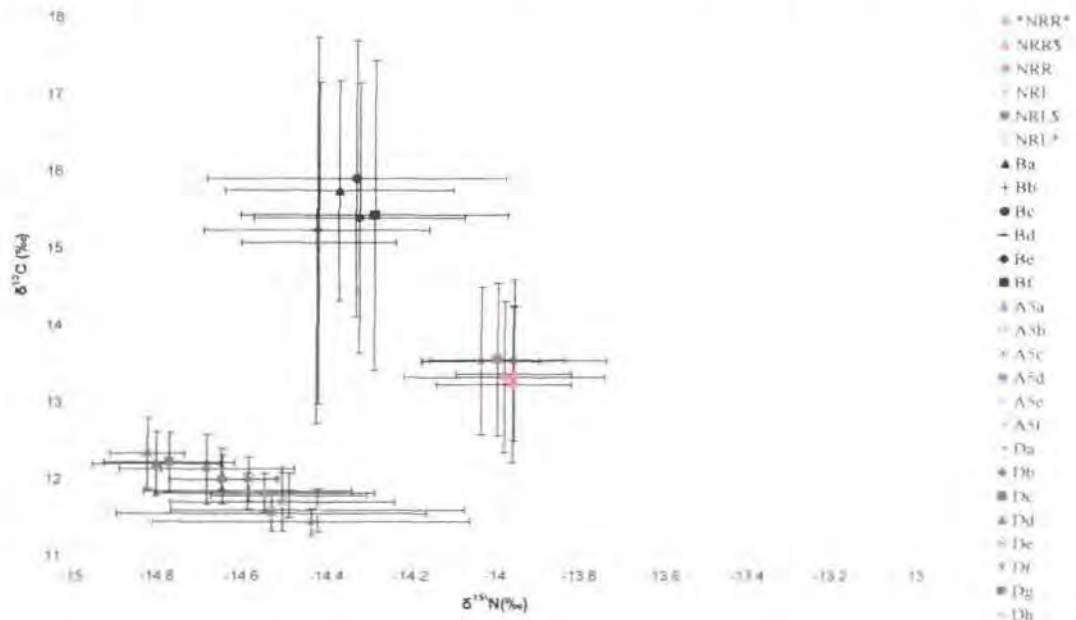


Figure 3.3: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with standard deviation bars for the sets of vibrissae from four dead seals from North Rona. The vibrissae from each seal are shown as the same colour; for ‘NR’ the vibrissae from the left and right sides of the face are shown in different colours and are labelled to indicate left or right side, i.e. ‘NRR’ denotes vibrissae from the right side of the face and ‘NRL’ those from the left.

Figure 3.1 shows the $\delta^{15}\text{N}$ profiles for the vibrissae taken from each of the four dead female grey seals

The traces from animals 'A5' and 'D' showed a small variation of 1‰ along their lengths (minimum 11.4‰ and maximum 12.4‰ for $\delta^{15}\text{N}$ for both sets). The vibrissae from both these animals showed similarity in the $\delta^{15}\text{N}$ trends to the other vibrissae in the set. The vibrissae from the right and left side of the face of 'NR' show a similar pattern to all the other vibrissae within their set, but these show greater variation along the vibrissa length than 'A5' and 'D', with a minimum $\delta^{15}\text{N}$ value of 11.6‰ and a maximum value of 14.7‰. The vibrissae from 'B' showed the greatest overall $\delta^{15}\text{N}$ variation, with a 5‰ for $\delta^{15}\text{N}$ change over their length (from 11.4‰ to 17.8‰). They also appeared to show the most variation amongst the vibrissa set. The vibrissae from each seal show similar $\delta^{15}\text{N}$ values to the other vibrissae taken from the same animal, although some variations are seen in all the vibrissa sets.

The $\delta^{13}\text{C}$ data (Figure 3.2) vary over a total of 1.5‰, and thus showed less variation than for $\delta^{15}\text{N}$. The plots for 'NR' (minimum $\delta^{13}\text{C}$ -14.5‰ and maximum -13.6‰) and 'B' (minimum $\delta^{13}\text{C}$ value -14.8‰ and maximum -13.6‰) show similar trends both to series within the sets and to each other, and show more variation than the other two vibrissa sets. The vibrissae from 'A5' and 'D' also show similar patterns to the other vibrissae from the seal and show lower $\delta^{13}\text{C}$ values than vibrissae from the other two seals ('D' has a minimum $\delta^{13}\text{C}$ value of -15‰ and a maximum of -14.5‰ and 'A5' has a minimum of -15‰ and a maximum of -14.1‰). The minimum and maximum standard deviations for $\delta^{13}\text{C}$ were ± 0.00 and ± 0.32 (Table 3.1).

The greatest $\delta^{13}\text{C}$ difference between the vibrissae in a set is 0.24‰, seen in the vibrissae from animal 'D', and the greatest $\delta^{15}\text{N}$ difference is seen in the vibrissae from 'B' and is 0.1‰.

Table 3.1: Mean values and standard deviations for each vibrissa plot from each of the dead grey seals sampled from North Rona.

Vibrissa	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	Mean / ‰	Standard deviation	Mean / ‰	Standard deviation
NRR	-13.96	±0.18	13.24	±1.02
NRR*	-13.98	±0.24	13.33	±0.98
NRR\$	-13.95	±0.14	13.37	±0.87
NRL	-13.95	±0.22	13.55	±1.05
NRL*	-14.03	±0.14	13.54	±0.96
NRL\$	-13.99	±0.16	13.56	±0.99
Ba	-14.37	±0.27	15.76	±1.43
Bb	-14.42	±0.18	15.08	±2.09
Bc	-14.33	±0.35	15.91	±1.79
Bd	-14.42	±0.27	15.24	±2.50
Be	-14.32	±0.25	15.20	±1.76
Bf	-14.29	±0.32	15.45	±2.01
A5a	-14.54	±0.26	11.82	±0.25
A5b	-14.43	±0.37	11.44	±0.17
A5c	-14.50	±0.26	11.70	±0.38
A5d	-14.53	±0.37	11.56	±0.23
A5e	-14.42	±0.35	11.59	±0.28
A5f	-14.49	±0.18	11.79	±0.29
Da	-14.65	±0.14	12.13	±0.27
Db	-14.69	±0.21	12.13	±0.46
Dc	-14.77	±0.15	12.22	±0.38
Dd	-14.80	±0.15	12.20	±0.42
De	-14.82	±0.09	12.33	±0.46
Df	-14.58	±0.07	12.00	±0.29
Dg	-14.59	±0.12	11.99	±0.32
Dh	-14.59	±0.25	11.84	±0.24

2. Replicate vibrissae from live grey seals.

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation plots for replicate whiskers collected from live grey seals over the course of this study are shown in this section.

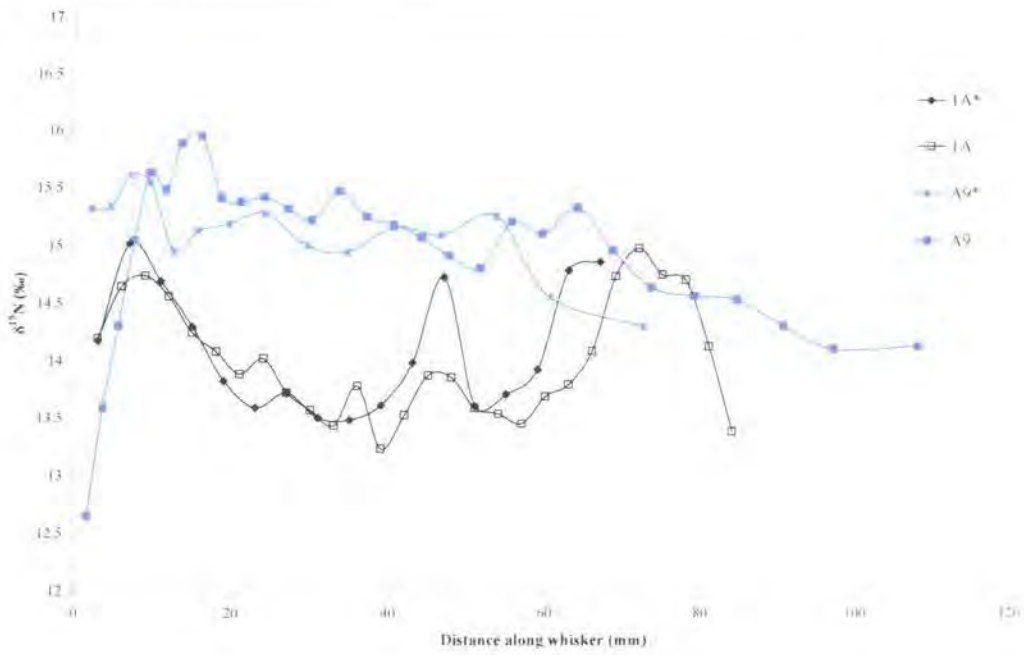


Figure 3.4: $\delta^{15}\text{N}$ variation along vibrissae length for replicate whiskers taken from two grey seals from North Rona in 1997.

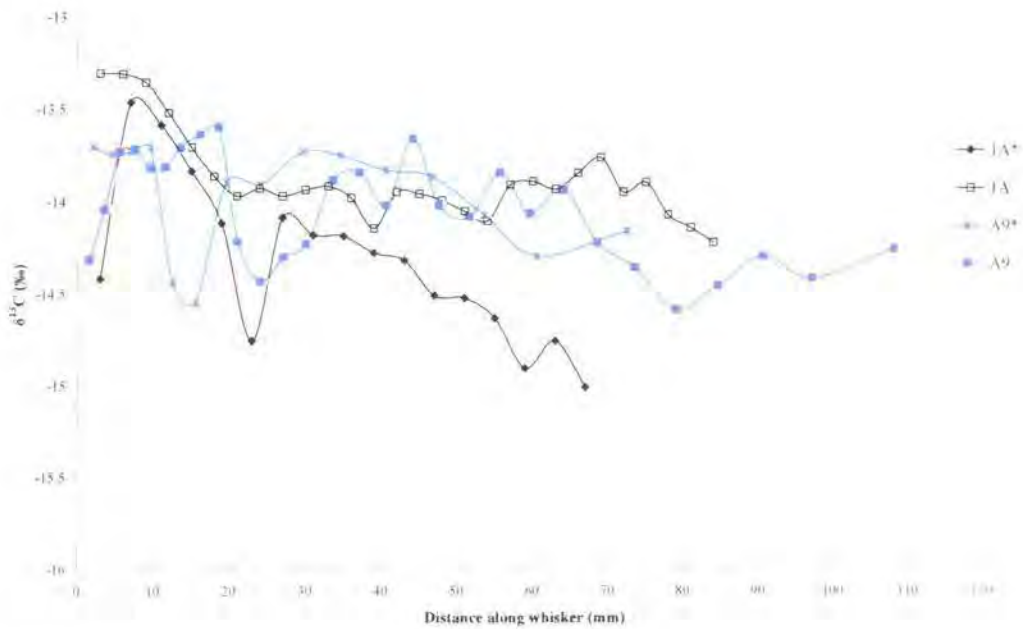


Figure 3.5: $\delta^{13}\text{C}$ variation along vibrissae length for replicate whiskers taken from two grey seals from North Rona in 1997.

The plots for 'A9' and '1A' (Figures 3.4 and 3.5) show similarity between the two vibrissae collected from each animal. The plots for $\delta^{13}\text{C}$ show greater variation between

the vibrissae from '1A' than were seen for 'A9' or for either animal on the $\delta^{15}\text{N}$ plot. 'A9' shows a difference between the average isotopic values of 0.28‰ for $\delta^{13}\text{C}$ and 0.06‰ for $\delta^{15}\text{N}$. For '1A' a mean difference of 0.19‰ for $\delta^{13}\text{C}$ and 0.2‰ for $\delta^{15}\text{N}$ is seen. The average isotopic values for each vibrissa plotted are shown below in Table 3.3, along with their standard deviation values.



Figure 3.6: $\delta^{15}\text{N}$ variation long vibrissae length for two whiskers from five grey seals sampled on the Isle of May. The vibrissae from each animal are plotted in different colours.

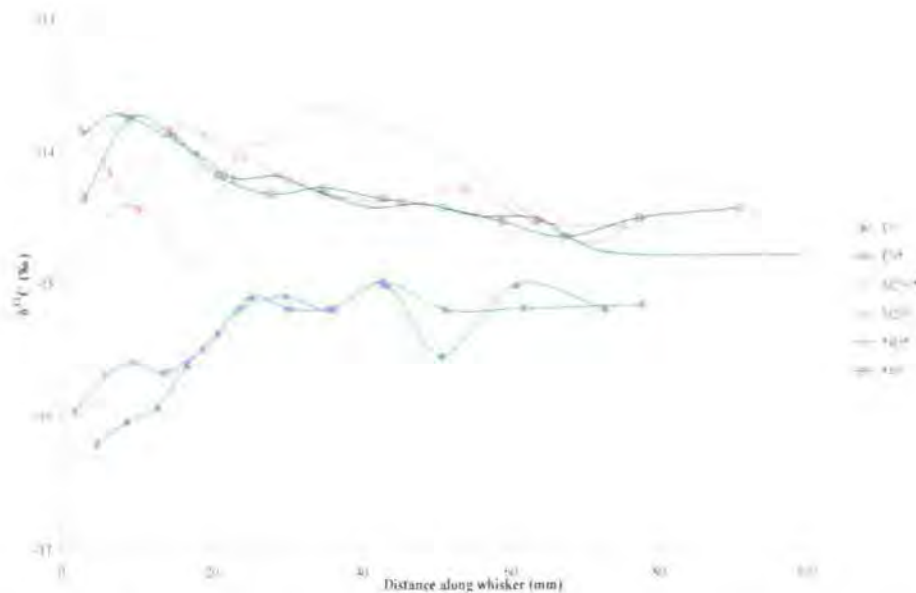


Figure 3.7: $\delta^{13}\text{C}$ variation long vibrissae length for two whiskers from five grey seals sampled on the Isle of May. The vibrissae from each animal are plotted in different colours.

As with the vibrissae from the two live grey seals from North Rona (Figures 3.4 and 3.5), the plots of isotopic variation along vibrissa length for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shown in Figures 3.6 and 3.7 for the live seals from the Isle of May all show some similarity within the vibrissa pairs taken from the same animals. The vibrissae taken from '6B' show the greatest difference of about 1‰ for $\delta^{13}\text{C}$ along all of the length of the two vibrissae and show a similar difference between the two vibrissae for $\delta^{15}\text{N}$. The trends seen along the two vibrissae are similar for $\delta^{13}\text{C}$, but show a greater variation between the vibrissae for $\delta^{15}\text{N}$.

The mean isotopic values for each vibrissa with its standard deviations are shown below in Table 3.2. Mann-Whitney comparisons between each set of replicate whiskers are shown in Table 3.3.

Table 3.2: Mean values and standard deviations for all replicate vibrissae from animals from North Rona and Isle of May.

Vibrissa	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	Mean / ‰	Standard deviation	Mean / ‰	Standard deviation
A9	-14.33	±0.43	14.09	±0.53
A9*	-14.05	±0.28	14.03	±0.50
1A	-13.76	±0.54	14.79	±0.57
1A*	-13.85	±0.28	15.01	±0.34
D	-16.57	±0.39	14.07	±0.47
D*	-16.60	±0.54	14.08	±0.27
4H	-14.30	±0.26	14.41	±0.68
4H*	-14.30	±0.33	14.42	±0.78
C9	-15.44	±0.42	15.00	±0.66
C9*	-15.37	±0.31	15.01	±0.60
M291	-14.21	±0.26	15.00	±0.86
M291*	-14.28	±0.42	15.14	±0.80
6B	-14.84	±0.30	14.99	±1.54
6B*	-15.08	±0.21	15.11	±1.20

Table 3.3: Mann-Whitney U-tests comparisons between replicate whiskers from seals sampled on the Isle of May.

Animal	Population	$\delta^{15}\text{N} / \delta^{13}\text{C}$	n₁, n₂	U statistic	P
C9	Isle of May	$\delta^{15}\text{N}$	12,12	73.5	0.9774
		$\delta^{13}\text{C}$	12,12	73.0	0.9774
D	Isle of May	$\delta^{15}\text{N}$	18,15	147.5	0.6512
		$\delta^{13}\text{C}$	18,15	131	0.8850
A9	North Rona	$\delta^{15}\text{N}$	17,15	199	0.0069
		$\delta^{13}\text{C}$	17,15	194	0.0120
1A	North Rona	$\delta^{15}\text{N}$	28,29	294	0.0738
		$\delta^{13}\text{C}$	28,29	294	0.0738
6B	Isle of May	$\delta^{15}\text{N}$	15,10	30	0.0115
		$\delta^{13}\text{C}$	15,10	55	0.2852
4H	Isle of May	$\delta^{15}\text{N}$	12,11	60	0.7399
		$\delta^{13}\text{C}$	12,11	74	0.6505
M291	Isle of May	$\delta^{15}\text{N}$	14,13	50	0.0482
		$\delta^{13}\text{C}$	14,13	103	0.5826

Table 3.3 shows that none of the Mann-Whitney comparisons between the replicate whiskers showed significant differences.

3.2. a. ii. Replicate vibrissae from southern elephant seals and south American sea lions

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plots for replicate vibrissae for some of the animals where duplicate whiskers were sampled from these two species are shown in the following figures. The mean values from set of replicate vibrissa with their standard deviations are shown in Table 3.4 below. Results for Mann-Whitney U-test comparisons between whiskers where two whiskers were sampled from an animal are shown below in Table 3.5. For animals where more than two whiskers were samples the comparisons were made using Kruskal-Wallis tests. These results are below shown in Table 3.6.

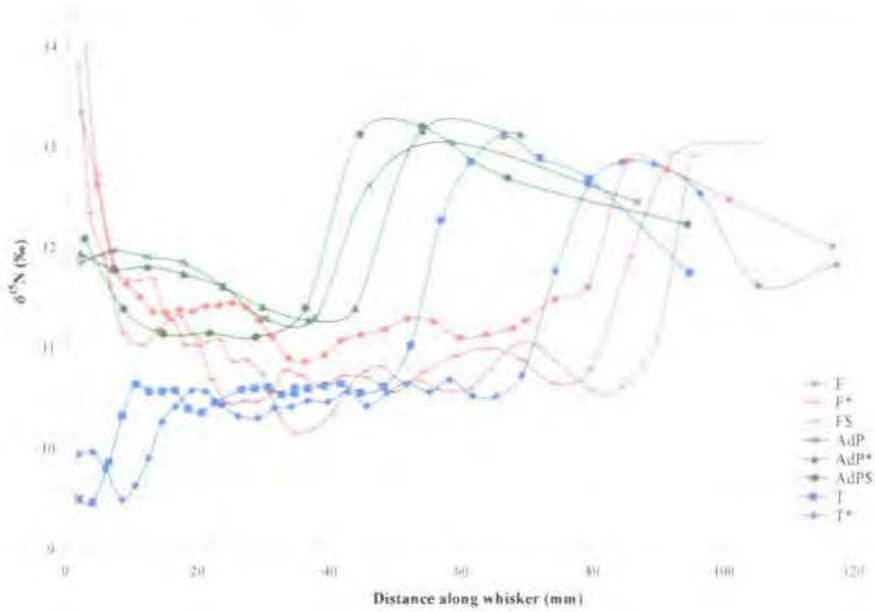


Figure 3.8: $\delta^{15}\text{N}$ variation along vibrissa length for the vibrissae taken from three female southern elephant seals. Vibrissae from the same animal are plotted in the same colour.

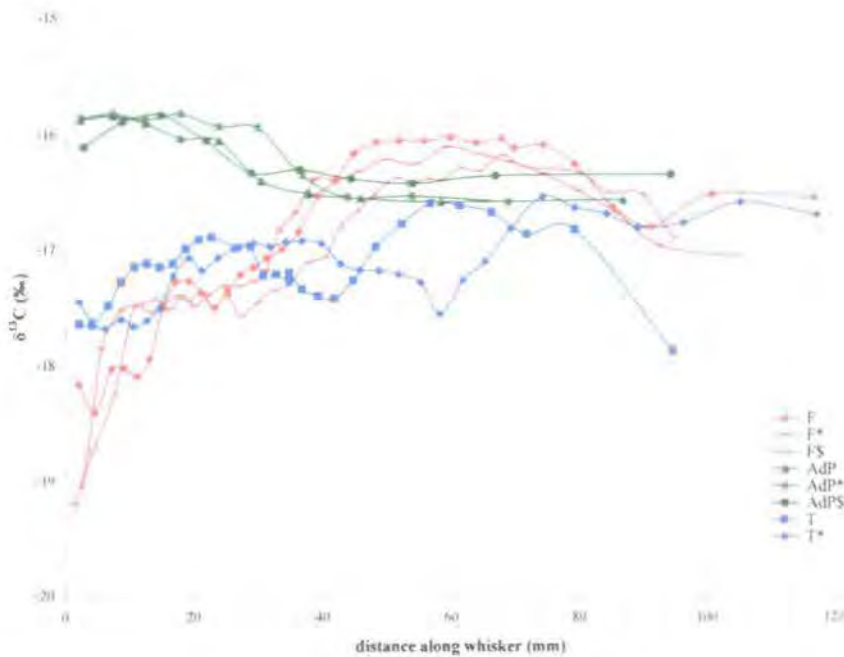


Figure 3.9: $\delta^{13}\text{C}$ variation along vibrissa length for the vibrissae taken from three female southern elephant seals. Vibrissae from the same animal are plotted in the same colour.

The plots in Figure 3.8 show that the trends along the replicate vibrissae from each of the three animals are similar to each other. The two vibrissae from animal 'T' show

the same trend along their lengths, although the trend is seen at a shorter distance along the whisker 'T' than in 'T*'.

The $\delta^{13}\text{C}$ plots (Figure 3.9) shows that the trends between the duplicate vibrissae for all three seals shown on the plot are similar to each other.

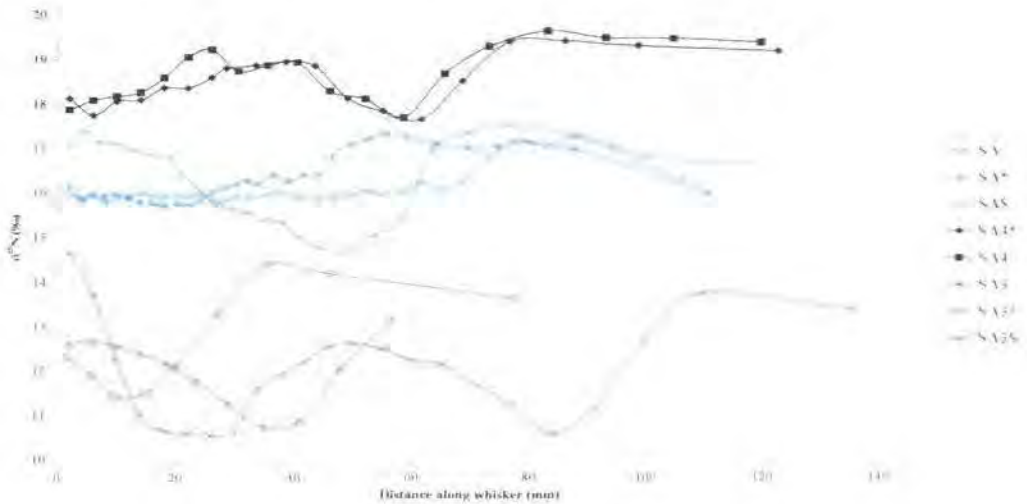


Figure 3.10: $\delta^{15}\text{N}$ variation for vibrissa sets for three male southern elephant seals. Vibrissae from the same animal is plotted in the same colours.

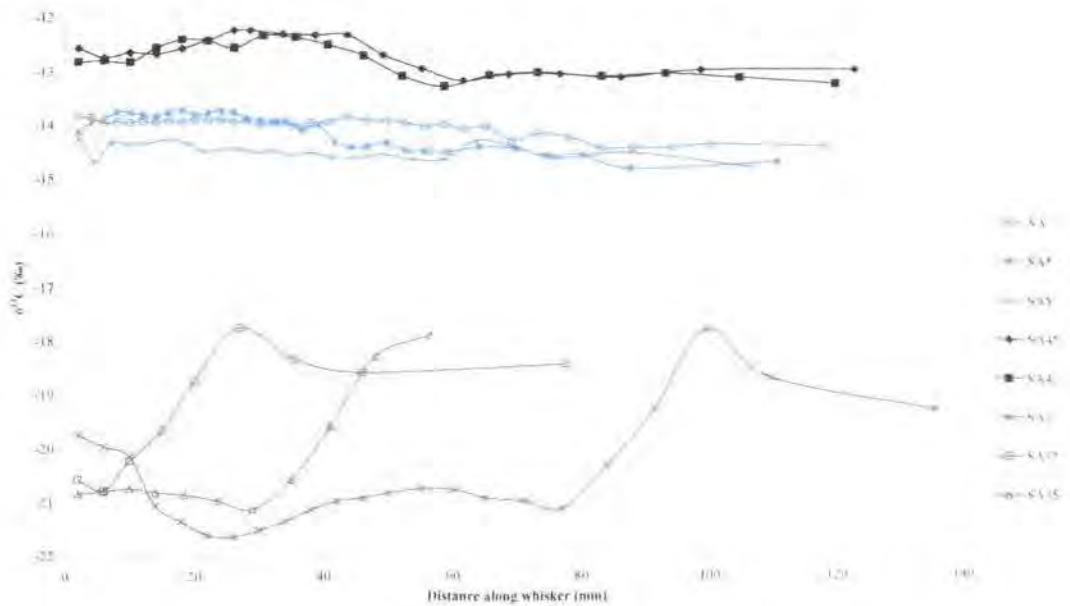


Figure 3.11: $\delta^{13}\text{C}$ variation for vibrissa sets for three male southern elephants. Vibrissae from the same animal is plotted in the same colours.

Figures 3.10 and 3.11 show that the vibrissae from animals 'SA' and 'SA4' show similar $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation along the lengths for all the replicate whiskers taken

from them. The three vibrissae from 'SA3' also show similarity in the trends for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, but the trends appear with a 40-65mm shift seen between the position of the trends along the vibrissae.

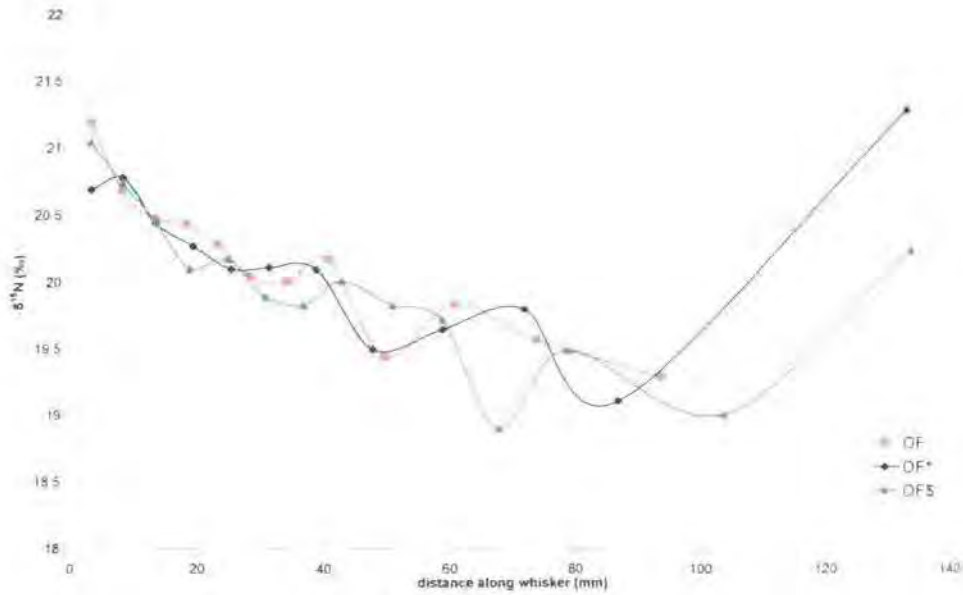


Figure 3.12: $\delta^{15}\text{N}$ variation along the length of three vibrissae taken from an adult female South American sea lion in 1999. The vibrissae are plotted in different colours.

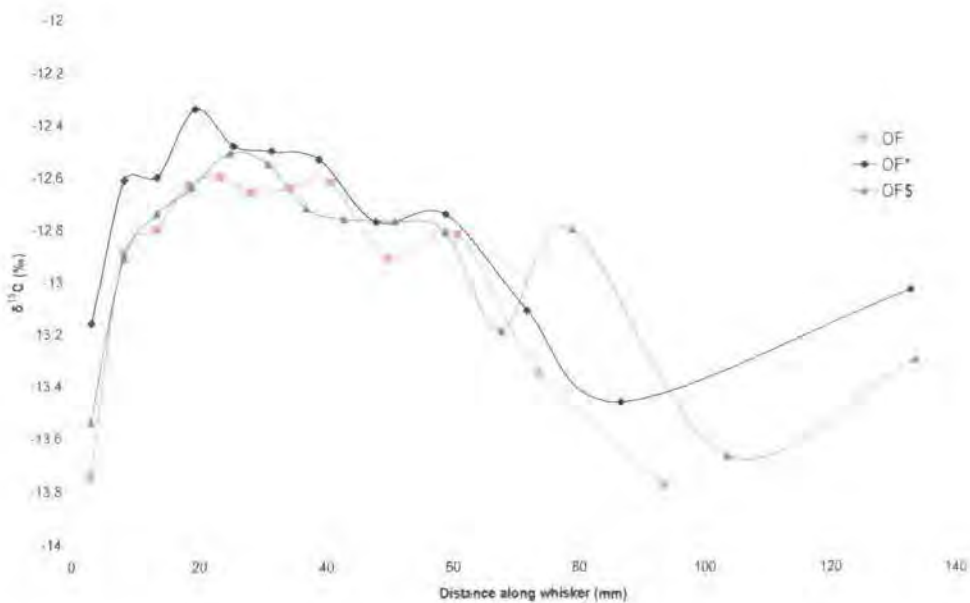


Figure 3.13: $\delta^{13}\text{C}$ variation along the length of three vibrissae taken from an adult female South American sea lion in 1999, using the same colours as in Figure 3.12

Figures 3.12 and 3.13 show the plots for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the three vibrissae collected from a female South American sea lion in 1999. While the vibrissae show different lengths, the plots show some similarity between all the vibrissae sampled, with little overall variation for either isotope along the vibrissa length. Periods of isotopic values are seen in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots. Mean values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are shown below in Table 3.4, a Kurskal-Wallis comparison between the whiskers are shown in Table 3.6.

Table 3.4: Mean values with standard deviations for male and female southern elephant seals collected in 1998 and 1999 and for one South American sea lion female collected in 1999.

Vibrissa	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	Mean / ‰	Standard deviation	Mean / ‰	Standard deviation
M17	-17.09	±0.15	11.74	±0.41
M17*	-16.91	±0.29	11.24	±0.75
F	-16.92	±0.75	11.55	±0.61
F*	-17.04	±0.75	11.19	±0.86
F\$	-17.06	±0.72	11.09	±0.82
S	-16.67	±0.21	10.65	±0.84
S*	-16.62	±0.19	11.09	±0.97
T	-17.31	±0.31	10.89	±0.97
T*	-17.11	±0.34	10.75	±0.89
N	-16.98	±0.47	11.34	±0.65
N*	-17.05	±0.61	10.63	±0.51
N\$	-17.09	±0.76	10.01	±1.32
M16£	-16.88	±0.45	11.41	±1.09
M16\$	-16.96	±0.47	11.16	±1.02
SX	-15.99	±0.19	11.77	±0.46
SX*	-16.26	±0.25	11.65	±0.70
FI*	-17.00	±0.37	11.02	±0.55
FI	-16.92	±0.38	11.16	±0.58
Q	-16.5	±0.37	11.47	±0.53

Q*	-16.71	±0.16	11.01	±0.52
SA34	-14.55	±0.47	15.06	±0.76
SA34\$	-14.53	±0.50	15.32	±0.68
SA34*	-14.86	±0.51	14.15	±1.22
SA34£	-14.85	±0.51	14.70	±1.07
SA4	-12.82	±0.32	18.72	±0.43
SA4*	-12.70	±0.32	18.53	±0.56
SAY	-16.12	±0.16	12.85	±0.60
SAY*	-16.13	±0.18	13.23	±0.74
SA2	-13.35	±0.34	19.32	±0.90
SA2*	-13.69	±0.50	18.95	±0.92
SA2\$	-13.29	±0.29	19.68	±0.82
SA4A	-21.19	±0.37	13.19	±0.40
SA4A*	-21.17	±0.36	13.13	±0.36
SA23	-13.64	±0.33	19.31	±0.65
SA23*	-13.53	±0.52	19.45	±1.11
SA3	-20.54	±0.99	12.02	±0.89
SA3*	-19.84	±1.09	12.75	±1.15
SA3\$	-20.24	±1.13	12.02	±0.79
SA	-14.04	±0.18	16.16	±0.44
SA*	-14.13	±0.34	16.36	±0.55
SA\$	-14.49	±0.14	16.25	±0.94
AdP	-16.23	±0.32	11.99	±0.56
AdP*	-16.12	±0.33	11.93	±0.68
AdP\$	-16.20	±0.21	11.96	±0.83
AdF	-17.51	±0.64	10.97	±0.68
AdF\$	-17.53	±0.67	10.80	±0.95
AdF*	-17.82	±0.79	10.52	±0.86
AdT	-16.98	±0.34	11.61	±0.98
AdT*	-16.93	±0.24	11.82	±0.91
Ad2	-16.46	±0.19	11.89	±0.86
Ad2*	-16.59	±0.19	12.55	±1.09

AdM	-17.53	±0.49	10.42	±0.97
AdM*	-14.47	±0.38	10.15	±0.82
OF	-12.95	±0.43	20.12	±0.54
OF*	-12.78	±0.34	20.24	±0.81
OF\$	-12.92	±0.36	19.96	±0.59

Table 3.5: Results from Mann-Whitney U-test comparisons between duplicate whiskers collected from southern elephant seals.

Animal	Male/ Female	$\delta^{15}\text{N} / \delta^{13}\text{C}$	n_1, n_2	U statistic	P
AdP	Female	$\delta^{15}\text{N}$	10,10	0.29	0.8629
		$\delta^{13}\text{C}$	10,10	1.04	0.5959
M16	Female	$\delta^{15}\text{N}$	6,6	14	0.5887
		$\delta^{13}\text{C}$	6,6	15.5	0.8182
SX	Female	$\delta^{15}\text{N}$	9,15	37	0.0732
		$\delta^{13}\text{C}$	9,15	46	0.2152
M17	Female	$\delta^{15}\text{N}$	25,16	117	0.0265
		$\delta^{13}\text{C}$	25,16	280	0.0325
AdT	Female	$\delta^{15}\text{N}$	10,12	55.5	0.8212
		$\delta^{13}\text{C}$	10,12	57.5	0.9229
AdM	Female	$\delta^{15}\text{N}$	10,10	46	0.7959
		$\delta^{13}\text{C}$	10,10	53.5	0.8534
Ad2	Female	$\delta^{15}\text{N}$	5,7	9	0.2020
		$\delta^{13}\text{C}$	5,7	28	0.1061
S	Female	$\delta^{15}\text{N}$	13,28	97	0.020
		$\delta^{13}\text{C}$	13,28	212	0.4006
SA4A	Male	$\delta^{15}\text{N}$	13,14	106	0.4879
		$\delta^{13}\text{C}$	13,14	82.5	0.7203
SA23	Male	$\delta^{15}\text{N}$	8,8	30.5	0.9591
		$\delta^{13}\text{C}$	8,8	20	0.2345
SA4	Male	$\delta^{15}\text{N}$	19,19	215.5	0.3068
		$\delta^{13}\text{C}$	19,19	137	0.2039
SAY	Male	$\delta^{15}\text{N}$	15,13	90	0.7510
		$\delta^{13}\text{C}$	15,13	129	0.1555
SA2	Male	$\delta^{15}\text{N}$	11,15	102.5	0.3302
		$\delta^{13}\text{C}$	11,15	118	0.0687

Table 3.6: Kruskal-Wallis comparisons between whiskers from southern elephant seals and from south American sea lions where three whiskers were sampled from each animal.

Animal	male/female	$\delta^{15}\text{N} / \delta^{13}\text{C}$	n₁, n₂, n₃	K-W statistic	P
AdF	Female	$\delta^{15}\text{N}$	19,12, 11	4.25	0.1196
		$\delta^{13}\text{C}$	19,12,11	2.31	0.3150
SA3	Male	$\delta^{15}\text{N}$	9,23,11	2.06	0.3574
		$\delta^{13}\text{C}$	9,23,11	4.22	0.11211
OF	otaria	$\delta^{15}\text{N}$	12,12,14	0.77	0.6788
		$\delta^{13}\text{C}$	12,12,14	2.43	0.2966
F	Female	$\delta^{15}\text{N}$	31,29,33	2.07	0.3558
		$\delta^{13}\text{C}$	31,29,33	0.96	0.6198

The comparisons shown in Tables 3.5 and 3.6 show that no significant differences were found between replicate whiskers.

3. 2. b: Captive animals from the National Seal Sanctuary, Gweek, Cornwall.

Vibrissae were collected from six resident captive seals from the Cornish National Seal Sanctuary, Gweek, Cornwall. The seals had all been fed a constant diet of herring since their arrival at the seal sanctuary. All had been in residence for at least two years. One seal 'G3' was a juvenile showing kidney and thyroid disorders (personal communication: Gweek Seal Sanctuary Staff).

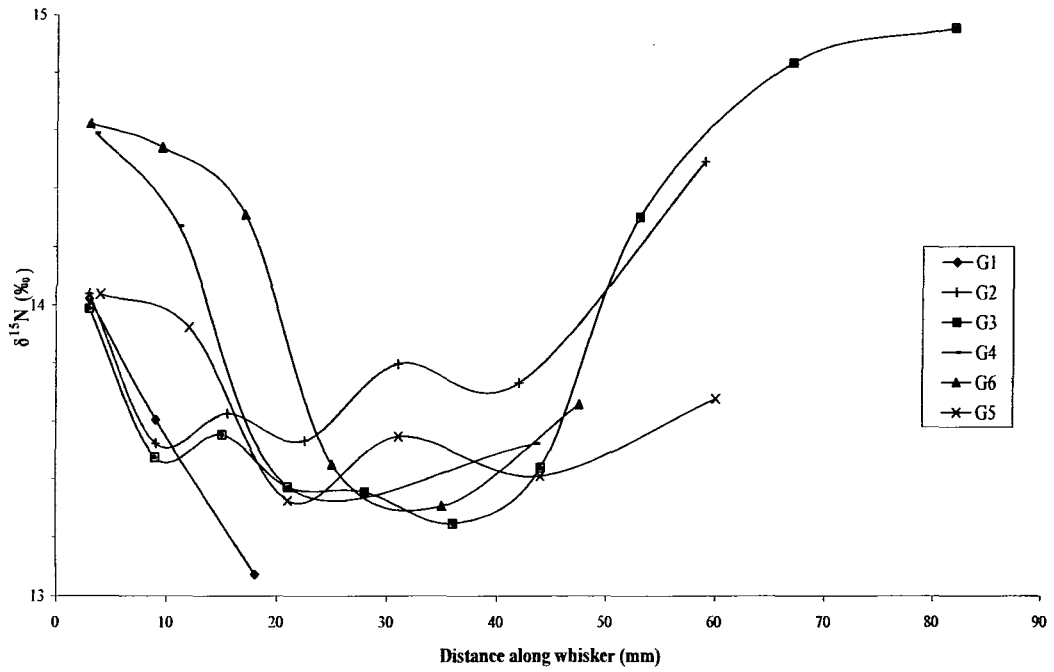


Figure 3.14: $\delta^{15}\text{N}$ variation along vibrissae length for vibrissae from six captive grey seals from Gweek.

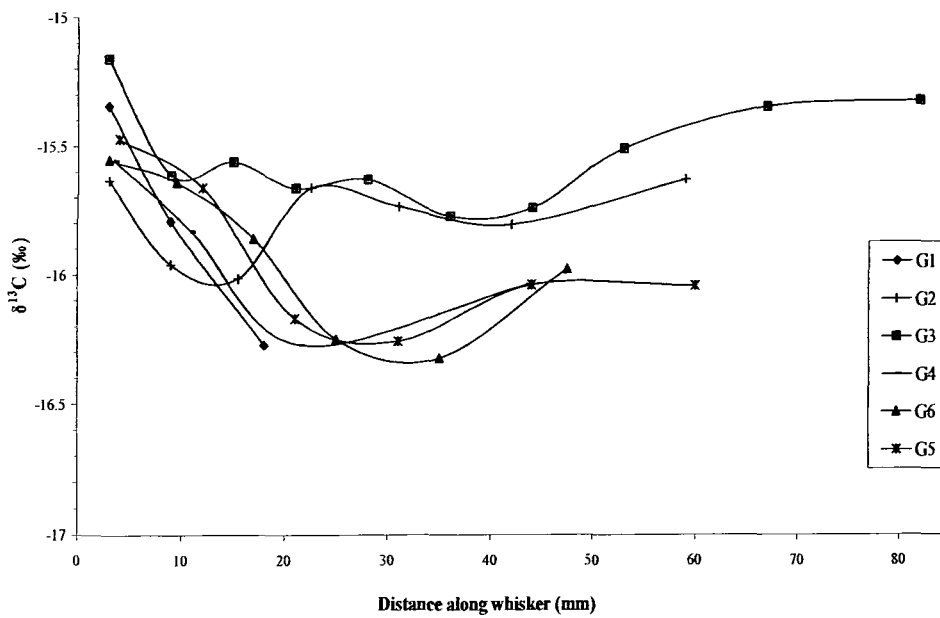


Figure 3.15: $\delta^{13}\text{C}$ variation along vibrissae length for vibrissae from six captive grey seals from Gweek.

The plots for $\delta^{15}\text{N}$ (Figure 3.14) for the captive seals shows that all the vibrissae except that taken from 'G3' (taken from the juvenile animal) and G2, show a similar pattern: an initial decrease in $\delta^{15}\text{N}$ and then an increase towards the end of the vibrissa. 'G3' shows only three data points and has a decrease in $\delta^{15}\text{N}$ over its whole length. The vibrissae show a variation of 1.9‰ at the greatest.

The series for $\delta^{13}\text{C}$ (Figure 3.15) show a greater difference in the $\delta^{13}\text{C}$ trends than those shown by $\delta^{15}\text{N}$. Two general trends are shown by the vibrissae, the first, shown by 'G2' and 'G3', shows little overall $\delta^{13}\text{C}$ change along the vibrissae. The second shown by the other vibrissae show an overall decline along their length. The overall $\delta^{13}\text{C}$ variation over the plot is at the greatest 0.7‰

3.2. c. Growth rate of grey seal vibrissae

A vibrissa was collected from each of two adult female grey seals, 'G' and 'H', captured on the Isle of May, Scotland on the 9th March 2001 and kept in the captive seal facility at SMRU, St Andrew's. Whilst in captivity the seals were fed a constant diet of herring. (Note: the herring that these two seals were fed on were not available for analysis as a part of this study) A vibrissa was clipped from 'G' on the 6th of June 2001 (90 days in captivity) and from 'H' on the 27th June 2001 (111 days in captivity).

Analysis of the vibrissae from animals 'H' and 'G' showed a decline in both isotopes for animal 'G' and a small increase along the vibrissae length in $\delta^{15}\text{N}$ for animal 'H', while $\delta^{13}\text{C}$ shows a small decrease. For the vibrissa from 'G', the isotopic values showed a decline from 16.53‰ ($\delta^{15}\text{N}$) and -13.79‰ ($\delta^{13}\text{C}$) at 39.5mm from the cut end of the vibrissae to 13.79‰ ($\delta^{15}\text{N}$) and -15.58‰ ($\delta^{13}\text{C}$) at 24 mm, giving a change of 2.74‰ for $\delta^{15}\text{N}$ and of 1.78‰ for $\delta^{13}\text{C}$. For the vibrissa from 'H', the decline was from 15.84‰ ($\delta^{15}\text{N}$) and -14.34‰ ($\delta^{13}\text{C}$) at 43.5mm to 14.16‰ ($\delta^{15}\text{N}$) and -16.02‰ ($\delta^{13}\text{C}$) at 22.5mm, giving a change of 1.68‰ for $\delta^{15}\text{N}$ and of 1.68‰ for $\delta^{13}\text{C}$.

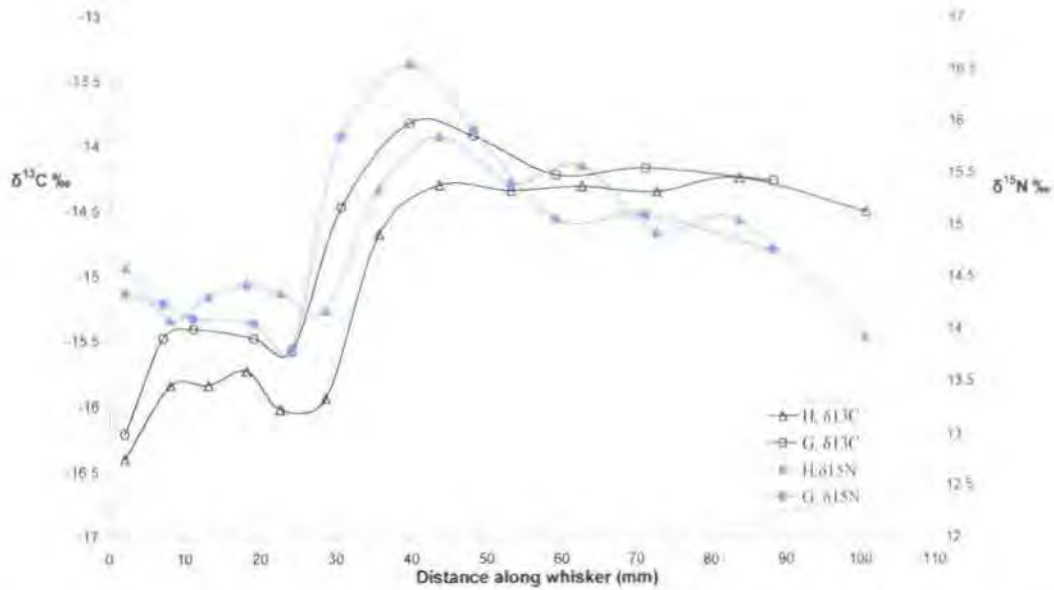


Figure 3.16: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots along the length of the vibrissae from seals captured on 9th March 2001. Vibrissae were collected from seal 'G' on 6th on June and from 'H' on 27th of June 2001. Both seals were kept during their captivity at the SMRU facility in St Andrews.

The point of dietary change was interpreted to be at the start of the large isotopic decline seen in the plots for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each vibrissa. It is possible that the change in diet occurred some time after this point; the exact point is not known, and a fixed point needed to be chosen for the following calculations. Growth rates were calculated using the length of captivity in days minus ten days to allow for the different isotopic signature of the captive diet to be incorporated into the vibrissa keratin (Hirons *et al.*, 2001).

Table 3.7: Results from growth rate calculations using total length of vibrissa after the isotopic decline and time in captivity minus ten days.

Animal	Time in captivity (days)-10	Distance along vibrissa (mm)	Growth rate (mm/day)
G	(90) 80	39.5	0.49
H	(111) 101	43.5	0.43
Mean growth rate			0.46

Further calculations on growth rate were made using the lag between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots from 'H' and 'G'. Since the vibrissae were not collected at the same time the lag represents the 21 days between sampling. Since (from Figure 3.24) the gradient of the two lines is not equal, values were taken from the top, middle and bottom of the gradient. The results from the calculations are shown in Table 3.8.

Table 3.8: Results from growth rate calculations using the distance between the isotopic plots for the vibrissae from animals 'H' and 'G' and a constant time period of 21 days (time between the sampling of the two vibrissae)

	Distance measured (mm)	Time (days)	Growth rate (mm/day)
Top of decline	39.0-30.5	21.0	0.42
Middle of decline	35.0-26.0	21.0	0.43
End of decline	29.0-24.0	21.0	0.23
Mean growth rate			0.36

The mean growth rate from combining these two methods gives a mean vibrissa growth rate of 0.41mm/day.

Both carbon and nitrogen isotopes show a trend in their decline towards, although not equivalent to the isotopic values for herring (the only food item of the captive seals) taken from various studies, values for herring range from -22.1‰ to -17.94‰ for $\delta^{13}\text{C}$ and from 6.57‰ to 13.8‰ for $\delta^{15}\text{N}$ (Fry, 1998, Hobson, 1994, my data).

3.2. d. Amino acid analysis

Samples from two southern elephant seal vibrissae and from two grey seal vibrissae were analysed for amino acid content. One sample was taken from the beginning and one from the end of each of the vibrissae. In addition to this, one vibrissa from each species was pigmented and one showed no pigment, and one sample from each species was from a male seal and one from a female.

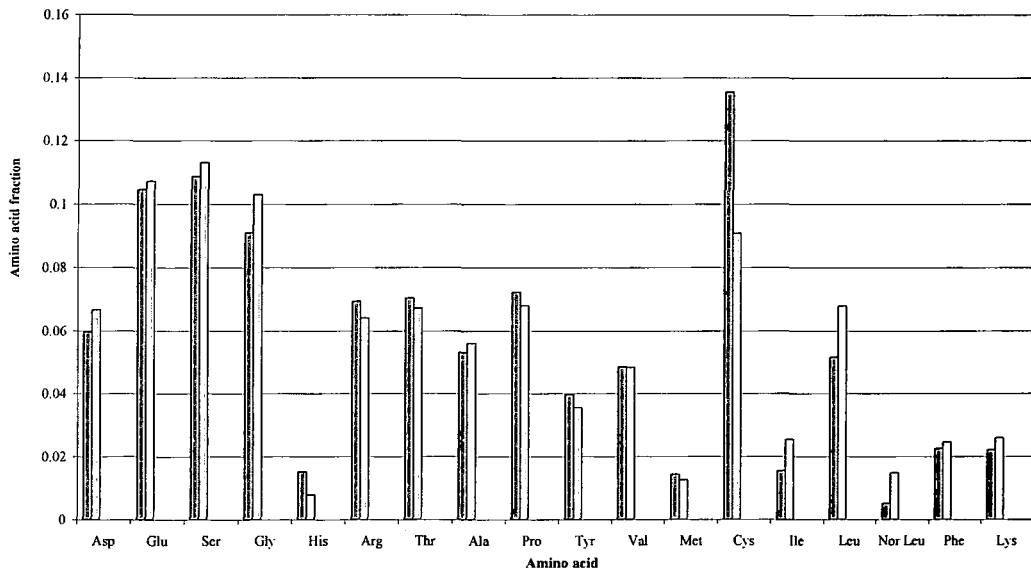


Figure 3.17: Amino acid analysis from one sample taken from the beginning and one from the end of a vibrissa from 'AdM', a female southern elephant seal (pigmented).

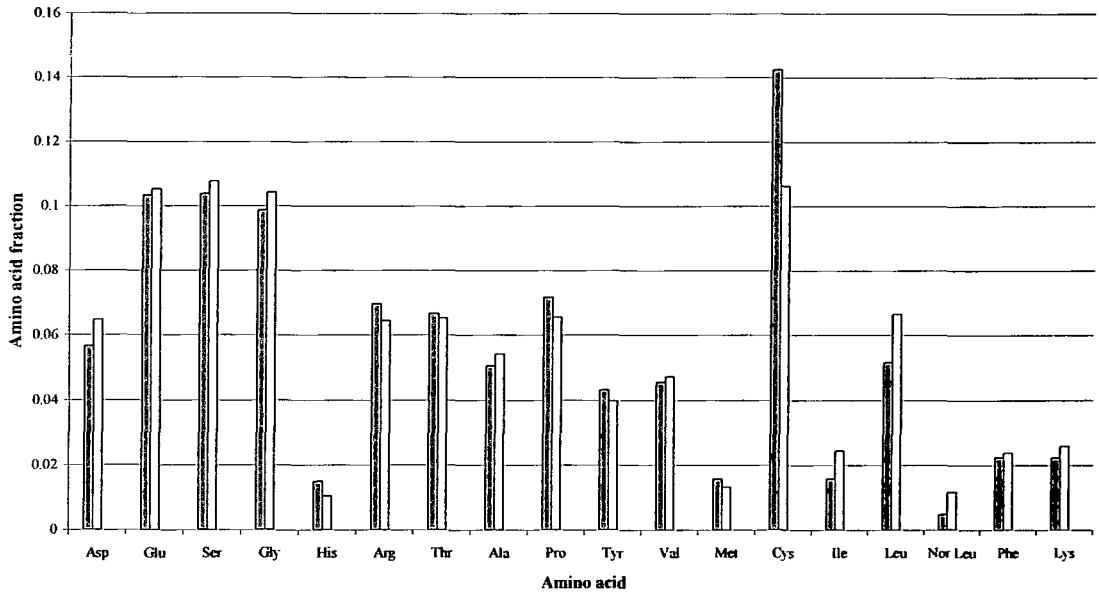


Figure 3.18: Amino acid analysis from one sample taken from the beginning and one from the end of a vibrissa from 'SA34b', a male southern elephant seal (un-pigmented).

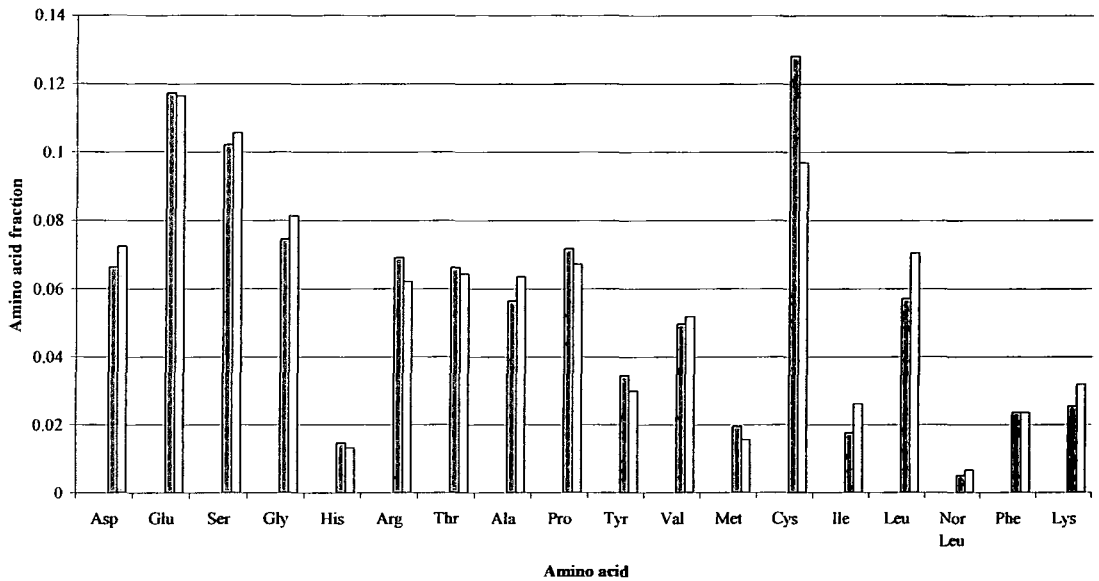


Figure 3.19: Amino acid analysis from one sample taken from the beginning and one from the end of a vibrissa from 'W7,' a female grey seal (pigmented).

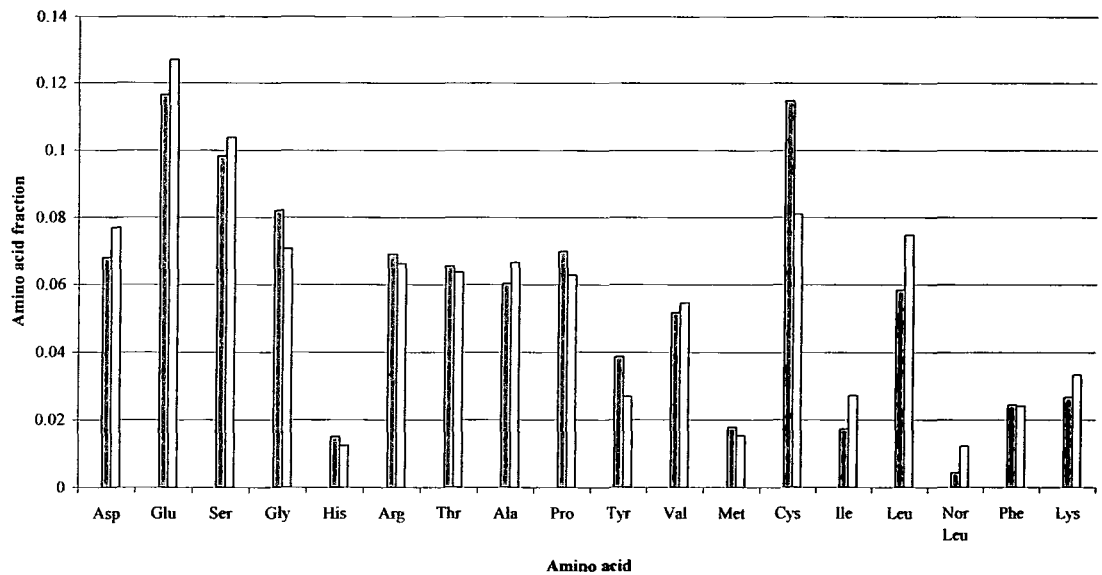


Figure 3.20: Amino acid analysis from one sample taken from the beginning and one from the end of a vibrissa from 'M392', a male grey seal (un-pigmented).

The samples from all the vibrissae analysed show some changes in all the amino acids between the first and last sample. Most of these changes are small and are not consistent between the vibrissae. Seven amino acids - aspartic acid, serine, histadine, Methionone, cysteine, isoleucine, leucine and lysine - do show consistent changes from the first to last sample. Of these, most are small changes. Cysteine shows the largest, most noticeable change of 2-3%. No further correlations in amino acids are seen between the species, sexes or pigmentations.

3.3. Discussion

From the results from the vibrissae from all three species analysed, there appear to be little differences between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within sets of vibrissae taken from the same animal. This is consistent with the findings from similar studies (Hirons *et al.*, 2001, Hobson *et al.*, 1996) which also found little variations between the vibrissae of harbour seals. The vibrissa plots from the vibrissae taken from the same

seal show similar patterns and trends along their lengths for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with small amounts of isotopic variation between each vibrissa and the point at which the trends appear. These differences seen are likely to be due to the method of vibrissa sampling. The vibrissae sampled from the dead animals were pulled from the face of the seal rather than cut from it, and are so more likely to show similar isotopic values at the base of all of the vibrissae. The vibrissae taken from the live grey seals were cut in 1997 and pulled or cut in 1998 and 1999, thus leading to discrepancies in the position of changes in isotopes along the vibrissae. Differences in the positioning of isotopic trends among the vibrissae of an individual seal could also be due to differing growth rates of the vibrissae of the seal. Although it is unknown if vibrissae do grow at different rates on an individual, it has been noted (Hirons *et al.*, 2001) that a broken vibrissa on a Stellar sea lion appears to be replaced more rapidly than the usual vibrissa growth rate. The vibrissae taken from the southern elephant seals also show similarities between vibrissae taken from the same animals. However, since most of these vibrissae (except 'F') were collected from live and un-sedated animals, the vibrissae were cut from the face at an unknown distance. Vibrissae from the same animal may, therefore, be of widely differing lengths, with variations of up to 80mm seen between the lengths of vibrissae from one animal. The similar trends that appear at different lengths along the vibrissae are likely to be due to this problem with the sampling method. Comparisons of the magnitude of the mean values for each whisker, however, showed good consistency for multiple whiskers collected from the same animals (Tables 3.5 & 3.6).

In humans a hair may remain in the scalp for up to six weeks after the hair has stopped growing and died (Valkovic, 1977), thus leading to discrepancies seen in the isotopic variation along the hair's length. It is unknown whether this also occurs in pinnipeds, but this is an alternative explanation for differences seen between trends in both the grey seal and the southern elephant seal vibrissae.

From these results, it will be assumed that a single vibrissa from either species of seal is representative of the rest of the vibrissae on the face of the seal and that one

vibrissa per seal will be used for the rest of the study. Where two vibrissae were analysed from each seal the longer of the vibrissae will be used, since this gives the most data points.

The vibrissae analysed from the captive seals from Gweek, Cornwall, showed less variation than has been seen in some of the plots for wild caught grey seals. However, a 1.9‰ difference is seen within the $\delta^{15}\text{N}$ and 0.7‰ in the $\delta^{13}\text{C}$. The values for this group of seals is greater than that seen in the Hobson *et al.* study (1996) where the greatest isotopic variation for $\delta^{15}\text{N}$ was seen to be 0.57‰ and for $\delta^{13}\text{C}$, 0.45‰. It should be noted that, although the seals had been fed only herring in their diet, the size of herring varied according to availability. The isotopic values of fish are not consistent throughout the size range of the species, possibly due to the differences in diets that can be seen in different age classes of the fish. It is possible that this has led to the range of values seen in the captive seals. Published data provides a range of -22.1 to -17.94‰ for $\delta^{13}\text{C}$ and from 6.57 to 13.8‰ for $\delta^{15}\text{N}$ for herring (Fry, 1998, Hobson, 1994, this study). This range of isotopic values for herring could account for the greater variation seen in the captive seals in this study for both of the isotopes. From this data and for the purpose of this study, variations of $\delta^{13}\text{C}$ along a vibrissa greater than 0.7‰ will be taken to be greater than that due to background isotopic variation. For $\delta^{15}\text{N}$ the variation found in these seals could be due to both background variation and/or differing $\delta^{15}\text{N}$ values of the herring. Given the size of the variation seen (amounting to two thirds of a trophic level) it is likely that the differing sizes of the herring diet have had some effect on the enrichment of the vibrissa $\delta^{15}\text{N}$ values, and that this value is not a true estimate of the background variation in vibrissae. Thus this value will not be used in this study to discount any $\delta^{15}\text{N}$ variations seen in vibrissae up to this level as owing to background variation. A value of 0.7‰ for $\delta^{15}\text{N}$ will also be used. This is based on the Hobson *et al.* (1996) paper, but given the values found in this study it is more conservative. Since a similar study could not be carried out on southern elephant seals, the same values will

be used for this species as for the grey seals as a first estimation of the variation seen in this species.

It would appear from the data collected in this study that the measurement of vibrissa growth rate can be measured using a dietary change as a marker, rather than the introduction into the study animal of isotopically enriched compounds as in Hirons *et al.* (2001). The growth rate of the grey seal vibrissae calculated in this study show a more rapid rate, with an average of 0.41mm/day, than that demonstrated in the harbour seal (Hirons *et al.* 2001) where the rate is given as 0.33mm/day for captive seals and a value of 0.08mm/day for a wild caught harbour seal. The rate of human hair growth is given as 0.35mm/day (Saitoh, 1969).

The value calculated by Hirons *et al.* (2001) for wild harbour seals is very different from the values calculated both for captive harbour seals and for that of the grey seals in this study. The grey seals in this study had both spent their lives up until their time of capture in the wild and it seems unlikely that they would show such a large change in vibrissa growth rate. It seems more likely that the value of 0.08mm/day found in Hirons *et al.* (2001) study may have arisen from incorrectly matching patterns in the vibrissae sampled at the two separate times. The similarity of these patterns could be coincidental, particularly as no matches were found in the vibrissae of the other two harbour seals used in the samples to support the data. In addition to this, the values calculated in the Hirons *et al.* (2001) paper show similar values for wild and captive Stellar sea lions, indicating that a similar difference in the growth rate is not seen in this species, although it may have been predicted from the discrepancy found between wild and captive harbour seals.

While a similar method to that used in this study was used in the afore mentioned study (i.e. the use of dietary trends in the vibrissa to calculate the growth rate), the Hirons *et al.* (2001) study required the sampling of the seals twice at seven monthly intervals - which would not be practical in the southern elephant seal populations and difficult in grey seals. The other two seals that were sampled at the same time (Hirons

et al. 2001) showed no repeated patterns in the vibrissa collected from the second capture and so no calculations could be made.

The method used in this study does require the captivity of a seal over a period of at least 80 days, to allow the effect of a dietary change to be reflected in the isotopic composition of the animal's vibrissae, and the dietary change needs to be to a fish species that is as isotopically distinct as possible from the seal's wild diet. In an ideal situation, the seals would have remained in captivity for at least a year to study the potential effect that seasonal changes in the seals' life cycle could have on growth rate – for example, the effect of the periods of fasting during the moult and breeding seasons – and to establish if, like the harbour seal, the vibrissae show periods of slow/zero growth.

The differences seen in the growth rates of the two species could be due to a number of factors. Primarily, different species of seal are likely to show different growth rates. The seals sampled in the two studies come from different areas, with different climates: the harbour seals in Hirons *et al.* (2001) were sampled in Connecticut, USA, and the grey seal samples in this study were collected from the Isle of May and North Rona, Scotland.

Given a growth rate of 0.23-0.49mm/day for the grey seals in this study, a year's growth of 84-149mm would be seen. For many of the grey seals sampled the length analysed in this study falls inside of these values, i.e. most of the vibrissa plots seen show a year's growth.

Since it was not possible to measure the growth rate of the southern elephant seal vibrissae, for the purpose of this study it will be assumed that the growth rate of the southern elephant seal is similar to that for the grey seal and harbour seals, thus giving each vibrissa about a year's growth rate. Obviously to better interpret results from southern elephant seal vibrissae the vibrissa growth rate would need to be calculated by a method similar to that used in this study or by the use of isotopically enriched glycine as in Hirons *et al.* (2001). Further work to study the potential for possible seasonal variations in the vibrissae of grey seals would also better aid data interpretation.

Amino acid analysis shows that the pigmented or un-pigmented vibrissae show no amino acid differences from each other, nor are there any consistent differences between the vibrissae from the two species or from the two sexes. There is, however, a consistent change seen between the ends of the vibrissa in seven amino acids. Six of these amino acids show very small changes. The changes fall within the range of variations that might be expected for different hair samples (O'Connell *et al.*, 2001). The amino acid cysteine shows a greater change than the others, a decline of about 1 to 2% between the samples from the vibrissa's base to the one from the vibrissa's tip. Cysteine is known to be a labile amino acid, i.e. it breaks down over time to cystaic acid (Dr. T. O'Connell, personal communication). It is possible that the difference in cysteine composition between the two ends of the vibrissae is due to the breakdown of a small amount of this amino acid. Variations greater than seen in these vibrissae were found in the amount of cystine in both human hair and nail keratin have been found in samples from two test subjects (O'Connell *et al.*, 2001), thus the difference in the cysteine content may be due to natural variation between the vibrissae. The analysis of more vibrissae would be required to study if this trend is common to all, or only a few.

It is possible that a change in the amino acid composition could change the isotopic composition of the vibrissae. If this is the case, however, it would be likely that the change seen would be consistent among all the vibrissae sampled, which it is not. It is unknown how an amino acid change would affect the isotopic composition. Plots of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation along vibrissa length for the four vibrissae from which samples were analysed for amino acids are shown below.

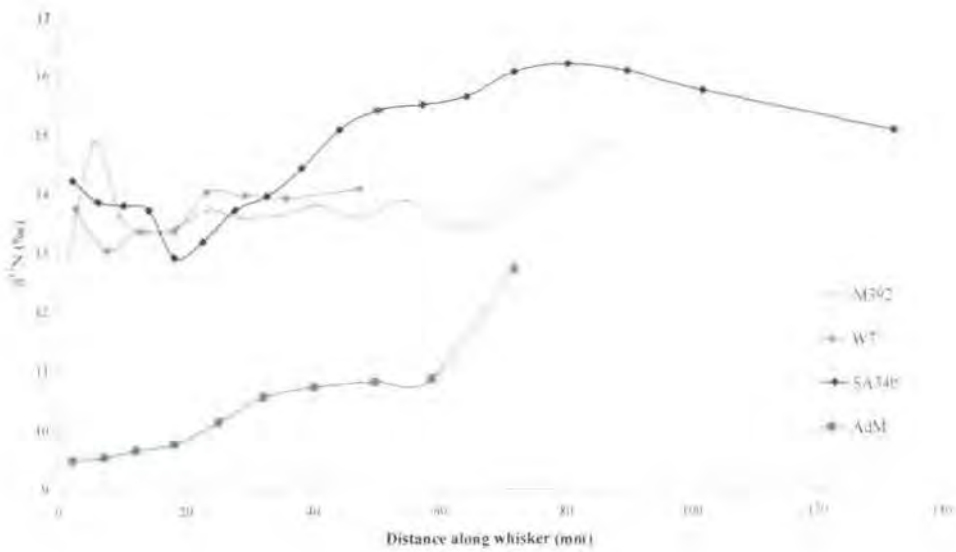


Figure 3.21: $\delta^{15}\text{N}$ variation along vibrissa length for ‘M392’, ‘W7!’, ‘SA34b’ and ‘AdM’, all of which had samples analysed for amino acid content. Plots are from base to tip, with each series in a different colour.

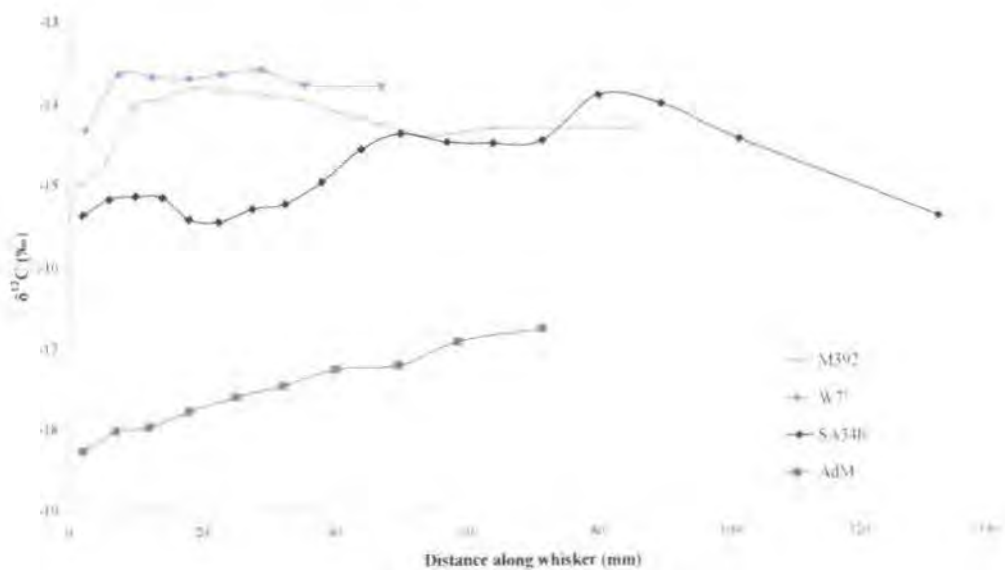


Figure 3.22: $\delta^{13}\text{C}$ variation along vibrissa length for ‘M392’, ‘W7!’, ‘SA34b’ and ‘AdM’, all of which had samples analysed for amino acid content. Plots are from base to tip, with each series the same colours as for Figure 3.21.

The $\delta^{15}\text{N}$ of the two vibrissae showed (‘M392’ and ‘AdM’) increasing trends (Figure 3.21). ‘W7!’ shows little variation along its length, and ‘SA34b’ tends down at

its tip end, though shows an overall increase. Figure 3.22 shows that 'AdM' shows an increase in $\delta^{13}\text{C}$ over its whole length, while the three remaining vibrissae show little change. The vibrissae do not show the consistent change along their length which would be expected if the change in cysteine content was sufficient to effect an isotopic change. It will, therefore, be assumed that any amino acid changes along the vibrissae do not change the isotopic composition of them and that changes seen are due to other factors.

3.4. Summary

1. The vibrissae collected at the same time from one seal show similar $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to the other vibrissae from the same animal. Thus, it is appropriate to sample a single vibrissa from each animal for the rest of this study.
2. Grey seals fed a constant species of fish showed a 1.9 ‰ difference in $\delta^{15}\text{N}$ and 0.7 ‰ difference in $\delta^{13}\text{C}$. It should be noted that, while the species of fish fed were constant, the size of fish varied so these values are not necessarily a true representation of background isotopic variation in seal vibrissae.
3. The growth rate of grey seal vibrissae was calculated to be an average of 0.41mm/day. Thus a seal's vibrissa represents approximately a year's growth. A similar growth rate will be assumed for southern elephant seals.
4. Amino acid composition was found not to be affected by species, pigmentation or sex. However, a consistent change in several amino acids, with the greatest seen in cysteine, was found between the base and tip of all vibrissae, though these changes do not appear to be sufficient to affect the isotopic variation of the vibrissae.

Chapter 4 : Grey Seal Data

CHAPTER 4

Grey Seal Data

4.1 Introduction

The data examined in this chapter are taken from 106 adult grey seals from two populations, North Rona (46 adult females) and the Isle of May (54 adult females and six adult males). The samples were collected during the breeding season of October-December for each of the study years - 1997, 1998 and 1999.

The grey seal is Britain's largest predator, and it forages exclusively at sea. As the foraging areas and prey species of the grey seal are likely to overlap with the grounds of commercial fisheries, competition between humans and seals is likely. With the impending ban on white fish fishing in the North Sea (Guardian, November 2002) it is likely that the take of commercial fish species by the seals will once more become a political issue. In order to properly assess the impact of grey seals on fisheries it is necessary to study the species of prey that the seals feed on i.e. their foraging behaviour. The methods commonly used to study pinniped diet have been reviewed in Chapter One, and so will not be discussed further here except where relevant to the grey seal foraging around the coast of Britain.

Much of the research carried out on grey seal diet and foraging behaviour has involved stomach content analysis (Rae, 1967 and 1973), scat analysis (Thompson *et. al.*, 1996; Hammond *et. al.*, 1994 a and b), inferred from satellite or radio tracking (Thompson *et. al.*, 1991; McConnell *et. al.*, 1999) or direct observations, (Carter *et. al.*, 2001).

The stomach contents of 241 grey seals from around the Scottish coast (Rae, 1973) were examined over a four year period. The stomachs were found to contain predominantly salmonids, cod and whiting (*Theragra chalcogramma*). However, since a

large number of the seals sampled (119) during the study were found drowned in salmon nets these results, may not be representative of the over all diet of the species.

Scat analysis has been used to study the diets of grey seals from the Inner and Outer Hebrides (Hammond *et. al.*, 1994 a), from Orkney and sites from North-eastern Scotland (Hammond *et. al.*, 1994 b) and from the Moray Firth, Scotland (Thompson *et. al.*, 1996).

Scats from grey seals from the 22 locations in the Inner and Outer Hebrides were collected in January, June, August and November 1985 and fish otoliths and cephalopod beaks were identified from them (Hammond *et al.*, 1994, a). Relative proportions showed that overall gadoid species e.g. cod were the most important dietary group making up 40% of the diet in total. The gadoid species which showed the greatest dietary importance varied depending on the year and the location. Flat fish were also found to be important dietary components, again with the species varying between season and location. Sandeels were found to be important in the Outer Hebrides but not in the Inner Hebrides. Cephalopods were found to be present in low proportions as were herring and horse mackerel (*Sarda sarda*).

Scats collected from 18 haulout sites around the Orkneys and mainland North East Scotland (1985) showed that sandeels were the most important prey item around the Orkneys, but are more frequent in February and in the summer samples (Hammond *et .al.* 1994, b). The seals appeared to feed on the smaller sandeel species during November and February. Cod was found to be the most important gadoid species in all locations and during all seasons. Ling (*Urophycis tenuis*), was found to be of importance in the northerly and westerly locations, since this is a typically open water species it is possible that seals from these areas may have been feeding at greater distances from the islands.

Fourteen grey seals from the Farne Islands and Abertay were tracked from their haulout sites using satellite tags (McConnell *et .al.*, 1999) between August 1991 and July 1993. The seals showed two kinds of movements: short local trips from the haulout sites

and long trips of up to 2100km away. 43% of the study animal's time was spent within 10km of their haulout sites and out of 88% of the trips the seals returned to the same haulout site that they had left. The average duration of the trips were 2.33 days and were generally to locations with a gravel/sand seabed, sites favoured by sandeels. The dives in these areas were found to be to the seabed, indicating that these trips were likely to be for foraging. The long distance trips i.e. those greater than 100km were generally to known grey seal haulout sites in the Orkneys, Shetland, Faroes or offshore to the East Atlantic and the North Sea implying that the grey seal populations may not be isolated from each other.

Three sub-adult males from the Farne islands were fitted with radio tags (Thompson *et al.*, 1999) which were then tracked from a boat. Their behaviour was shown to fall into three types while at sea: travel between haulout sites, short trips and resting close to haulout sites. It was suggested that the short trips observed from the data were foraging trips, since these included dives to the seabed in locations associated with species taken by grey seals as prey e.g. sandeels, cod and whiting (Thompson *et al.* 1999).

From these data above it was suggested that it was likely that grey seals in the study areas will favour sandeels and gadoid species of fish and that seasonal changes in abundance of these fish may affect the prey preferences of the seals (Thompson *et al.* 1999). Since many of these fish are also commercial species the scat analysis data suggest there is likely to be some overlap between the seals and human fishing activities (Thompson *et al.* 1999).

This chapter aims to examine the results of the data collected from grey seal vibrissae from each of the two study populations, the Isle of May and North Rona and to elucidate from the data a better understanding of grey seal diet than is currently known. Furthermore the chapter will discuss the relevance of the data shown to the current state of the commercial fisheries surrounding the United Kingdom. The data shown in Chapter three will be used in addition to the data in this chapter to further the discussion.

It is hypothesised that:

1. There will be both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ changes along the vibrissae of the seals sampled from each population and in each year.
2. That both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences will be found between the vibrissae sampled from the same population in different years.
3. That there will be isotopic differences found between the two sexes sampled from the Isle of May.
4. That isotopic differences will be seen between the vibrissae analysed from each of the two populations.
5. That the comparison of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the vibrissae of the grey seals with isotopic values from fish sampled from areas where the seals are likely to feed will enable a better understanding of the likely prey species of these seals

4.2 Results

4.2. a. Differences along vibrissae

This section examines the isotopic variations along individual whisker plots taken from each year and from each of the two populations. Due to the volume of data collected in this section, not all the data will be displayed, overall trends have been identified and these will be displayed graphically in this section as representative plots of selected whisker profiles for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. A complete set of the graphic profiles of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all the whiskers analysed are shown in Appendix 1, with the data for the plots in Appendix 2. This section will then show the results from the statistical analysis of the whiskers will

be shown to examine if any of the isotopic variations along the length of the whiskers are significant.

4.2. a. i. Trends seen in the whiskers collected from Isle of May and North Rona from 1997-1999

Three major trends can be identified in the isotopic plots for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. These trends are identified in Figures 4.1 - 4.6 shown below:

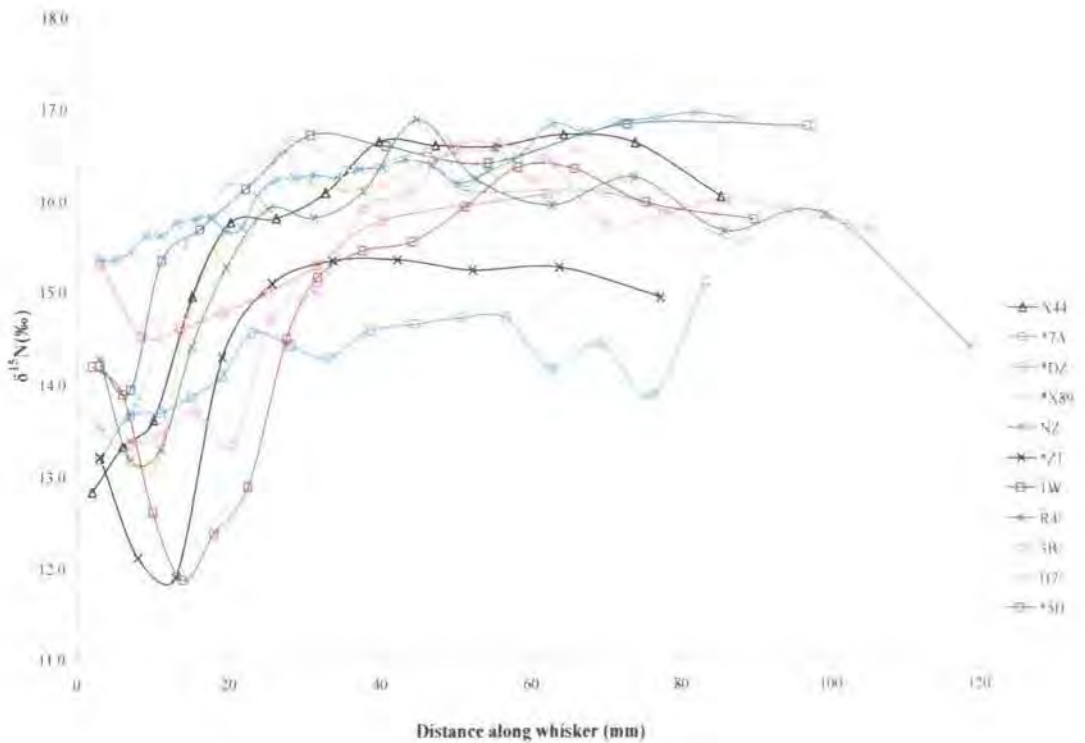


Figure 4.1: Whiskers that show an increase in $\delta^{15}\text{N}$ from their proximal to their distal ends. Each whisker is plotted in a different colour, Isle of May plots are marked with a square and North Rona animals with a cross.

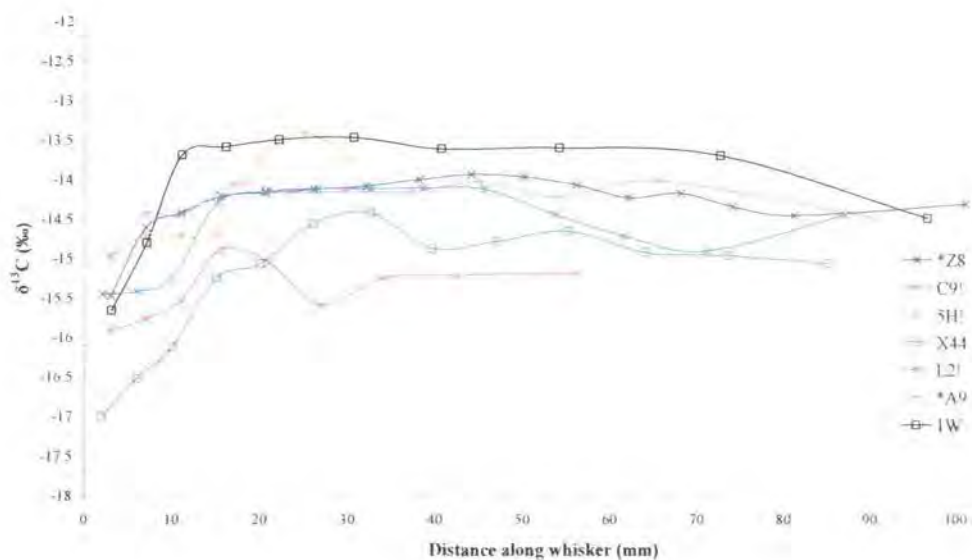


Figure 4.2: Whiskers that show an increase in $\delta^{13}\text{C}$ from their proximal to their distal ends. Each whisker is plotted in a different colour, Isle of May plots are marked with a square and North Rona animals with a cross.

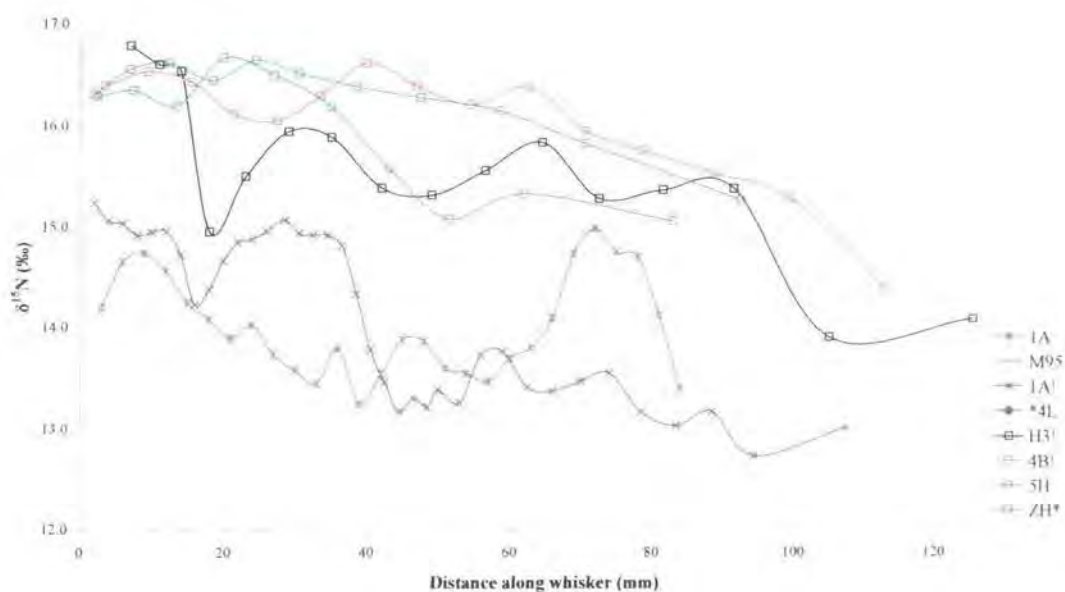


Figure 4.3: Whiskers that show a decrease in $\delta^{15}\text{N}$ from their proximal to their distal ends. Each whisker is plotted in a different colour, Isle of May plots are marked with a square and North Rona animals with a cross.

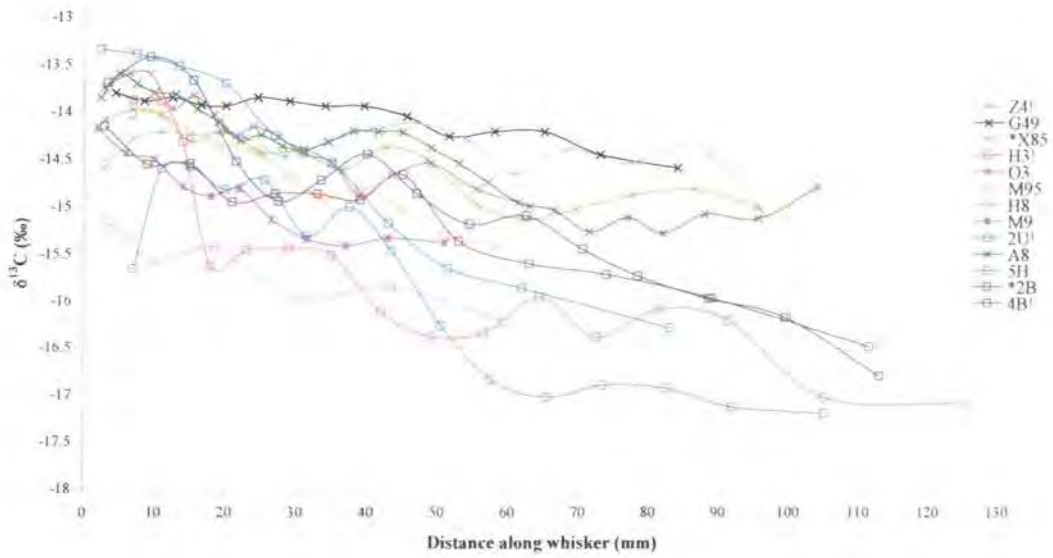


Figure 4.4: Whiskers that show a decrease in $\delta^{13}\text{C}$ from their proximal to their distal ends. Each whisker is plotted in a different colour, Isle of May plots are marked with a square and North Rona animals with a cross.

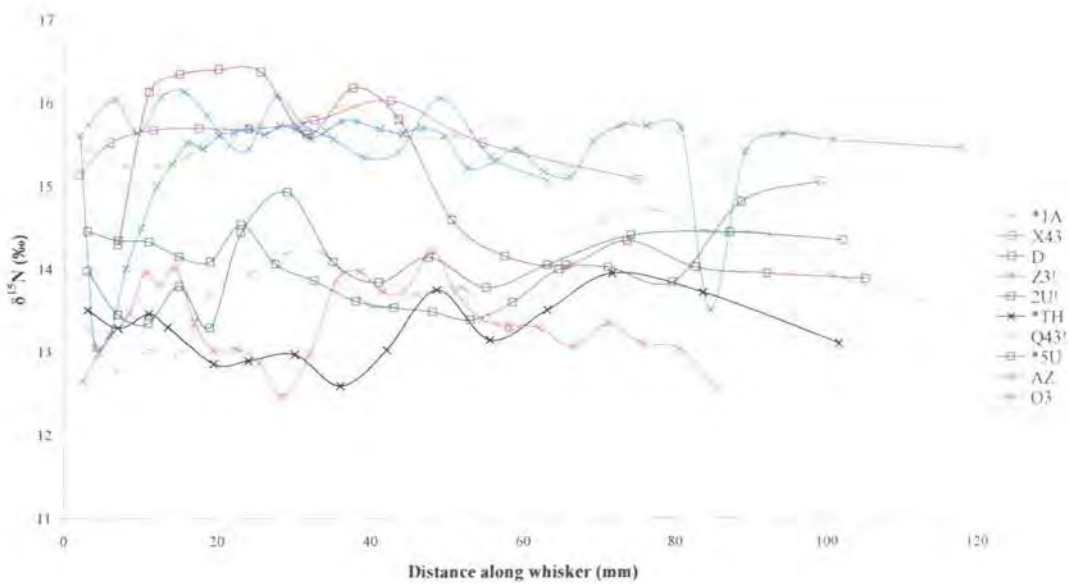


Figure 4.5: Whiskers that show little variation in $\delta^{15}\text{N}$ from their proximal to their distal ends. Each whisker is plotted in a different colour, Isle of May plots are marked with a square and North Rona animals with a cross.

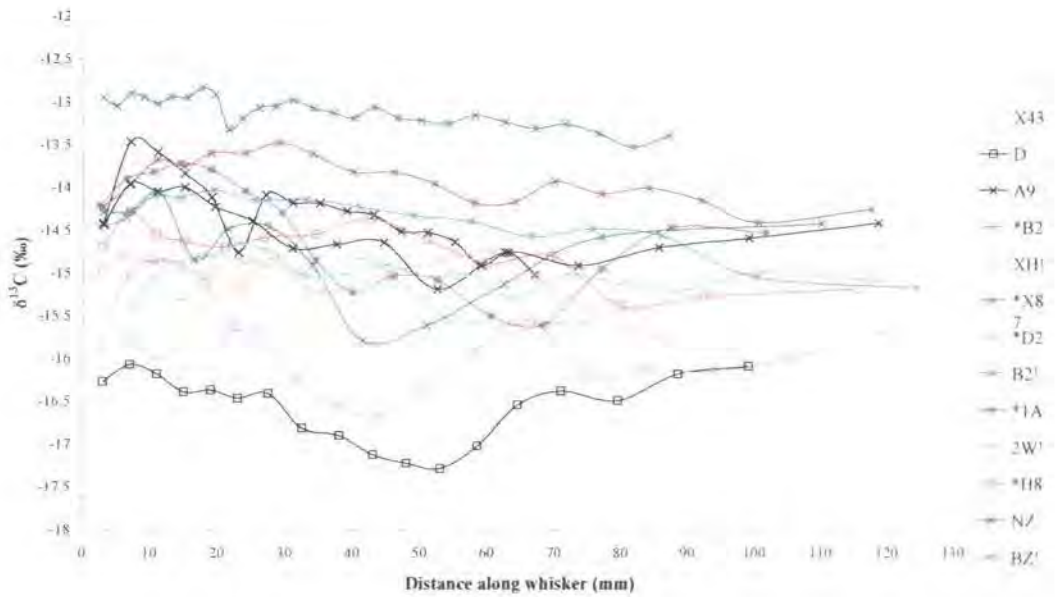


Figure 4.6: Whiskers that show little variation in $\delta^{13}\text{C}$ from their proximal to their distal ends. Each whisker is plotted in a different colour, Isle of May plots are marked with a square and North Rona animals with a cross.

The first trend, shown in Figures 4.1 and 4.2 is an upwards trend, the isotope shows an increase in enrichment along the whisker from the proximal to the distal end. For $\delta^{15}\text{N}$ this increase is of 1 to 3‰ and is seen in whiskers from the Isle of May and North Rona for all the years samples where collected for. For the $\delta^{13}\text{C}$ an increase is seen of 0.7 to 2‰ and is seen in animals from Isle of May in 1997 and 1998 and in animals from North Rona in 1998 and 1999.

Figures 4.3 and 4.4 show the second trend, i.e. that of a depletion in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ from the proximal to the distal end of the whisker. For $\delta^{15}\text{N}$ the decrease seen is 1 to 2‰ and is seen in animals from North Rona in 1997 and 1998 and from Isle of May in all three years. The decrease in $\delta^{13}\text{C}$ seen is 1 to 3‰ and is seen in animals from North Rona in 1997 and 1998 and Isle of May in 1997, 1998 and 1999.

The third trend seen is that shown by Figures 4.5 and 4.6. These figures show plots that have little change (less than 0.70‰) in the overall isotopic variation from one end of the plot to the other. Some of the whiskers plotted e.g. 'Z3!' for $\delta^{15}\text{N}$ and '*DZ' for $\delta^{13}\text{C}$ show variation of 1 to 2‰ along their lengths but return to a similar value at the distal end that they showed at the proximal, other whiskers e.g. 'Q43!' for $\delta^{15}\text{N}$ and 'NZ' for $\delta^{13}\text{C}$ show little variation along the whole plot. Whiskers from both population and three years of sampling show this trend.

Table 4.1: Proximal and distal values of each whisker analysed from North Rona and Isle of May from 1997-1999. Trends are classified as upwards or downwards if the isotopic difference seen between the two ends is greater than 0.70‰, if the difference seen is less than this value the trend is classified as none. (Chapter 3, discussion section)

Animal	Population/ year	$\delta^{13}\text{C}$ whisker beginning	$\delta^{13}\text{C}$ whisker end	Trend	$\delta^{15}\text{N}$ whisker beginning	$\delta^{15}\text{N}$ whisker end	Trend
A9	North Rona/1997	-14.42	-15.01	None	14.17	14.86	None
1A	North Rona/1997	-13.31	-14.22	Down	14.19	13.38	Down
O3	North Rona,1997	-13.76	-15.00	Down	15.73	15.07	None
NZ	North Rona,1997	-12.96	-13.39	None	15.34	16.91	Up
A8	North Rona,1997	-13.85	-14.80	Down	15.70	15.72	None
AZ	North Rona,1997	-14.02	-14.79	Down	12.65	12.55	None

1A!	North Rona,1998	-14.16	-14.47	None	15.23	13.00	Down
A9!	North Rona,1998	-14.55	-14.19	None	12.15	13.83	Up
Z3!	North Rona, 1998	-14.34	-14.16	None	15.60	15.46	None
Z4!	North Rona,1998	-14.09	-15.01	Down	13.38	11.94	Down
G49!	North Rona,1998	-13.80	-14.49	None	12.58	11.61	Down
G48!	North Rona,1998	-13.93	-14.52	None	12.47	13.21	Up
Z8!	North Rona, 1998	-14.86	-14.66	None	13.27	12.27	Down
Z1!	North Rona,1998	-13.58	-13.76	None	13.49	14.59	Up
HR!	North Rona,1998	-14.26	-14.89	None	14.89	13.96	Down
B2!	North Rona,1998	-14.22	-14.53	None	15.43	14.51	Down
Q43!	North Rona, 1998	-14.22	-13.77	None	15.45	15.53	None
G44!	North Rona,1998	-14.16	-14.81	None	14.08	14.37	None
W7!	North Rona,1998	-14.31	-13.78	None	13.74	14.08	None
X2!	North Rona,1998	-16.22	-15.95	None	14.30	14.67	None
BZ!	North Rona, 1998	-14.47	-15.17	None	14.38	15.34	Up



R4!	North Rona,1998	-14.43	-14.41	None	14.27	14.41	None
G45!	North Rona,1998	-14.36	-14.41	None	12.98	13.80	Up
L7!	North Rona,1998	-14.87	-14.64	None	13.46	12.42	Down
V7!	North Rona, 1998	-13.80	-14.23	None	15.97	15.83	None
AZ!	North Rona,1998	-14.79	-14.37	None	10.67	12.66	Up
Z2!	North Rona,1998	-14.20	-14.69	None	12.72	12.48	None
L2!	North Rona,1998	-15.45	-14.44	Up	13.48	15.68	Up
X6!	North Rona, 1998	-13.89	-14.05	None	15.12	16.49	Up
A5!	North Rona,1998	-14.12	-14.43	None	12.17	12.40	None
*X87	North Rona,1999	-14.30	-14.42	None	13.24	13.60	None
*X47	North Rona,1999	-13.80	-14.02	None	12.44	13.11	None
*Z8	North Rona, 1999	-15.47	-14.31	Up	12.84	12.70	None
*X89	North Rona,1999	-14.09	-13.87	None	13.57	16.24	Up
*A9	North Rona,1999	-15.00	-14.48	None	11.59	14.33	Up
*Z1	North Rona,1999	-14.52	-13.88	None	13.22	14.95	Up

*X85	North Rona, 1999	-14.60	-16.39	Down	11.61	11.98	None
*1A	North Rona,1999	-14.23	-14.25	None	13.28	13.51	None
*TH	North Rona,1999	-14.26	-14.11	None	13.51	13.11	None
*Z7	North Rona,1999	-13.69	-14.28	None	12.84	13.74	Up
*TL	North Rona, 1999	-14.63	-14.29	None	11.71	13.29	Up
*TB	North Rona,1999	-14.55	-15.39	Down	13.30	14.18	Up
*7A	North Rona,1999	-14.31	-14.62	None	13.19	15.11	Up
D	Isle of May,1997	-16.27	-16.09	None	14.46	15.07	None
Z4	Isle of May,1997	-14.09	-15.01	Down	13.38	11.94	Down
6C	Isle of May,1997	-16.94	-15.83	Up	14.62	15.79	Up
X43	Isle of May,1997	-15.02	-15.59	None	15.13	15.08	None
4H	Isle of May,1997	-17.55	-15.14	Up	13.44	15.64	Up
DZ	Isle of May,1997	-17.13	-15.83	Up	13.46	14.79	Up
5B	Isle of May,1997	-15.23	-15.64	None	14.61	15.46	Up
X44	Isle of May,1997	-17.01	-15.06	Up	12.84	16.05	Up

D2	Isle of May,1997	-17.21	-15.33	Up	12.68	16.30	Up
5H	Isle of May,1997	-13.35	-16.29	Down	16.28	15.05	Down
ZH*	Isle of May,1997	-15.58	-15.71	None	16.30	15.26	Down
3B	Isle of May,1997	-16.19	-15.90	None	13.66	16.68	Up
C9	Isle of May,1997	-16.20	-15.18	Up	13.85	15.80	Up
1W	Isle of May,1997	-15.65	-14.48	Up	14.20	16.82	UP
H8	Isle of May,1997	-15.17	-16.23	Down	15.83	14.91	Down
D8!	Isle of May,1998	-15.54	-16.34	Down	13.07	14.82	Up
1W!	Isle of May,1998	-14.76	-13.60	Up	14.38	16.53	Up
6L!	Isle of May,1998	-15.60	-16.44	Up	13.93	14.96	Up
4B!	Isle of May,1998	-13.70	-16.80	Down	16.38	14.39	Down
D1!	Isle of May,1998	-15.16	-15.97	Down	13.58	14.64	Up
2W!	Isle of May,1998	-15.16	-15.09	None	15.87	17.90	Up
7J!	Isle of May,1998	-16.36	-16.60	None	13.05	14.70	Up
F2!	Isle of May,1998	-14.56	-14.49	None	14.33	16.06	Up

6C!	Isle of May,1998	-15.30	-16.89	Down	13.28	14.87	Up
2U!	Isle of May,1998	-15.98	-17.20	Down	15.03	13.89	Down
XH!	Isle of May,1998	-15.67	-15.93	None	14.04	15.46	Up
H3!	Isle of May,1998	-14.57	-17.10	Down	16.30	14.08	Down
3B!	Isle of May,1998	-15.71	-15.87	None	14.54	15.68	Up
H8!	Isle of May,1998	-15.35	-16.62	Down	13.90	14.24	None
H7!	Isle of May,1998	-16.14	-16.11	None	13.48	15.52	Up
DZ!	Isle of May,1998	-13.70	-15.43	Down	15.96	15.47	None
C9!	Isle of May,1998	-15.92	-15.18	Up	13.42	14.94	Up
6J!	Isle of May,1998	-15.23	-16.51	Down	13.65	15.05	Up
5H!	Isle of May,1998	-14.97	-13.73	Up	15.37	16.92	Up
3H!	Isle of May,1998	-14.16	-16.49	Down	16.04	15.48	Up
M392	Isle of May,1999	-15.00	-14.31	None	12.99	14.82	Up
M94	Isle of May,1999	-13.98	-14.89	Down	14.87	16.24	Up
M90	Isle of May,1999	-14.94	-14.84	None	16.30	16.43	None

M95	Isle of May,1999	-14.56	-15.43	Down	16.19	14.44	Down
M291	Isle of May,1999	-14.42	-13.82	None	15.98	15.23	Down
M9	Isle of May,1999	-14.18	-15.39	Down	13.14	14.99	Up
*6B	Isle of May,1999	-14.63	-14.21	None	12.94	16.43	Up
*6J	Isle of May,1999	-14.35	-15.04	Down	13.80	14.16	None
*HT	Isle of May,1999	-14.33	-14.02	None	14.14	14.84	Up
*4L	Isle of May,1999	-14.12	-15.06	Down	16.85	16.45	None
*ZH	Isle of May,1999	-14.58	-14.55	None	14.23	15.38	Up
*H7	Isle of May,1999	-14.55	-14.52	None	13.84	17.03	Up
*3H	Isle of May,1999	-13.82	-14.64	Down	15.15	15.49	None
*H8	Isle of May,1999	-14.69	-15.19	None	14.22	15.07	Up
*DZ	Isle of May,1999	-13.67	-13.79	None	15.30	16.07	Up
*D1	Isle of May,1999	-14.33	-14.41	None	13.54	15.46	Up
*4H	Isle of May,1999	-14.36	-14.42	None	13.97	14.92	Up
*5B	Isle of May,1999	-14.95	-15.20	None	14.60	14.10	None

*6L	Isle of May,1999	-14.37	-15.93	Down	13.76	12.84	Down
*D2	Isle of May,1999	-15.86	-15.68	None	15.15	14.85	None
*D8	Isle of May,1999	-15.13	-16.74	Down	11.65	12.83	Up
*5H	Isle of May,1999	-15.08	-14.83	None	14.20	15.80	Up
*5U	Isle of May,1999	-14.82	-15.18	None	13.98	14.36	None
*1H	Isle of May,1999	-16.16	-16.21	None	13.62	14.73	Up
*2B	Isle of May,1999	-14.39	-14.39	None	14.37	15.72	Up

Table 4.2: Summary of the numbers of each whisker from each population following each of the three major trends as identified in Table 4.1 above.

Population / Year	$\delta^{13}\text{C}$ trends			$\delta^{15}\text{N}$ trends		
	None	Up	Down	No	Up	Down
North Rona, 1997	2	0	4	4	1	1
North Rona 1998	22	1	1	9	8	7
North Rona 1999	10	1	2	6	7	0
Isle of May 1997	5	7	3	2	9	4
Isle of May 1998	6	4	11	3	15	3
Isle of May 1999	18	0	8	7	16	3

Tables 4.1 and 4.2 show that for $\delta^{13}\text{C}$ most of the whiskers show no overall variation along their lengths, i.e. the values at the base and tip of the whiskers fall within 0.7‰ of

each other, however some of the whiskers do show variation between the two ends of values greater than 0.7‰. For $\delta^{15}\text{N}$ most of the whiskers show an upwards trend along their length, with the tip value being 0.7‰ or greater than the value seen at the base of the whisker.

4.2. a. iii. Statistical analysis of whiskers to examine potential differences seen along their lengths

The whisker series were divided into three sections, containing equal (or near equal numbers of points), in order to examine if the differences seen along the whisker lengths were significant, each section was compared to the others using Mann-Whitney U-tests.

Table 4.3: Results from Mann-Whitney U-test comparing the points from the proximal (1), third of the whisker, to the middle (2), 2nd third of the whisker and to the distal (3), third of all whiskers from each year and each population. $\alpha = 0.013$ after Bonferroni correction.

Population	Year	Comparison	$\delta^{13}\text{C}/\delta^{15}\text{N}$	N1, N2	U	P
Isle of May	1997	1:2	$\delta^{13}\text{C}$	46,47	796.500	0.082
			$\delta^{15}\text{N}$	46,47	731.000	0.023
Isle of May	1997	1:3	$\delta^{13}\text{C}$	46,47	903.500	0.233
			$\delta^{15}\text{N}$	46,47	623.500	0.001
Isle of May	1997	2:3	$\delta^{13}\text{C}$	47,47	986.000	0.372
			$\delta^{15}\text{N}$	47,47	943.500	0.225
Isle of May	1998	1:2	$\delta^{13}\text{C}$	96,95	4226.000	0.382
			$\delta^{15}\text{N}$	96,95	2642.000	<0.001
Isle of May	1998	1:3	$\delta^{13}\text{C}$	96,97	2568.500	<0.001
			$\delta^{15}\text{N}$	96,97	3086.000	<0.001
Isle of May	1998	2:3	$\delta^{13}\text{C}$	96,96	2867.500	<0.001
			$\delta^{15}\text{N}$	96,96	3949.500	0.087

Isle of May	1999	1:2	$\delta^{13}\text{C}$	126,126	6414.000	0.008
			$\delta^{15}\text{N}$	126,126	5467.500	<0.001
Isle of May	1999	1:3	$\delta^{13}\text{C}$	127,128	4897.500	<0.001
			$\delta^{15}\text{N}$	127,128	3432.500	<0.001
Isle of May	1999	2:3	$\delta^{13}\text{C}$	126,128	6529.500	0.004
			$\delta^{15}\text{N}$	126,128	5611.500	<0.001
North Rona	1997	1:2	$\delta^{13}\text{C}$	45,46	409.500	<0.001
			$\delta^{15}\text{N}$	45,46	834.000	0.307
North Rona	1997	1:3	$\delta^{13}\text{C}$	45,46	398.000	<0.001
			$\delta^{15}\text{N}$	45,46	862.000	0.175
North Rona	1997	2:3	$\delta^{13}\text{C}$	46,46	776.500	<0.001
			$\delta^{15}\text{N}$	46,46	1239.000	0.690
North Rona	1998	1:2	$\delta^{13}\text{C}$	139,140	8329.000	0.110
			$\delta^{15}\text{N}$	139,140	7383.500	0.002
North Rona	1998	1:3	$\delta^{13}\text{C}$	139,141	5575.500	<0.001
			$\delta^{15}\text{N}$	139,141	8986.00	0.106
North Rona	1998	2:3	$\delta^{13}\text{C}$	140,141	7082.500	<0.001
			$\delta^{15}\text{N}$	140,141	9645.000	0.139
North Rona	1999	1:2	$\delta^{13}\text{C}$	60,60	1682.000	0.537
			$\delta^{15}\text{N}$	60,60	802.000	<0.001
North Rona	1999	1:3	$\delta^{13}\text{C}$	60,61	1760.500	0.072
			$\delta^{15}\text{N}$	60,61	574.000	<0.001
North Rona	1999	2:3	$\delta^{13}\text{C}$	60,61	2001.000	0.314
			$\delta^{15}\text{N}$	60,61	1821.500	0.070

Statistical analysis of the results shows that the whiskers from the 1997 Isle of May samples show a significant difference only in $\delta^{15}\text{N}$ between the proximal end and distal end

of the whisker, no other differences were found (Table 4.3). For the 1998 Isle of May whiskers a significant difference was found in the proximal and middle comparison for $\delta^{15}\text{N}$, for the proximal and distal comparison in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and in the middle and distal comparison in $\delta^{13}\text{C}$ only, other comparisons showed no significant differences. All the comparisons for whiskers from the Isle of May in 1999 showed significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

For the North Rona comparisons significant differences were found in all three comparisons of $\delta^{13}\text{C}$ for 1997, but not for $\delta^{15}\text{N}$. For 1998 significant differences were found in $\delta^{15}\text{N}$ for the proximal and middle comparison and for $\delta^{13}\text{C}$ in the proximal and distal and middle and distal comparison. For 1999 no significant differences in $\delta^{13}\text{C}$ were found, but $\delta^{15}\text{N}$ showed significant differences in both the proximal and middle and proximal and distal comparisons.

4.2. b. Results from animals sampled in more than one year.

The figures shown in the following section show $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plots for the whiskers sampled from every seal that was sampled in more than one year. Mean isotopic values with standard deviation values and whisker trends, as identified in section 4.2.c, are shown below in Table 4.4

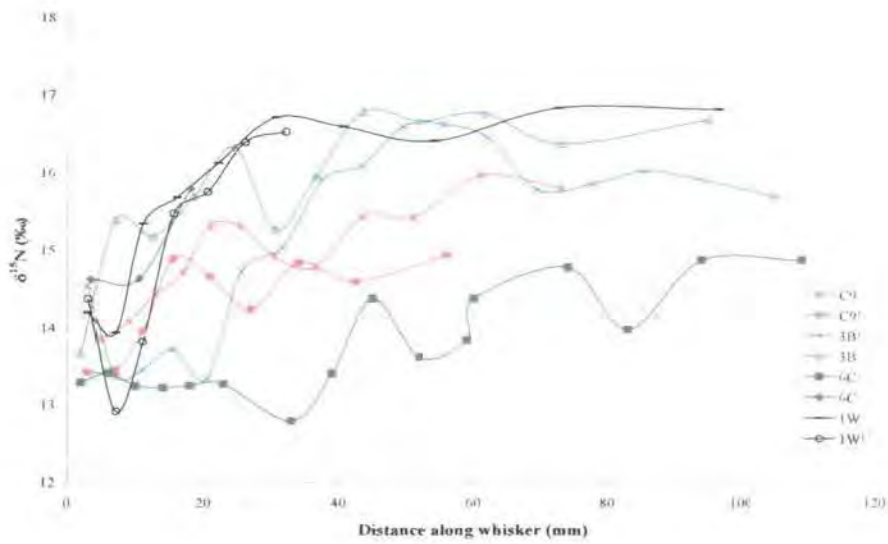


Figure 4.7: $\delta^{15}\text{N}$ for whiskers collected in 1997 and 1998 from 'C9', '3B', '6C' and '1W', four adult female seals from the Isle of May.

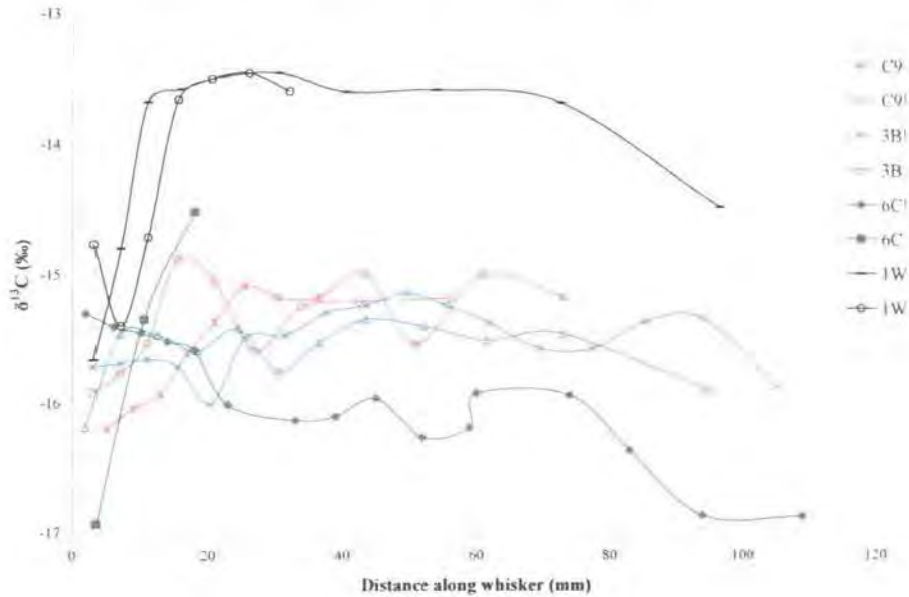


Figure 4.8: $\delta^{13}\text{C}$ for whiskers collected in 1997 and 1998 from 'C9', '3B', '6C' and '1W', four adult female seals from the Isle of May.

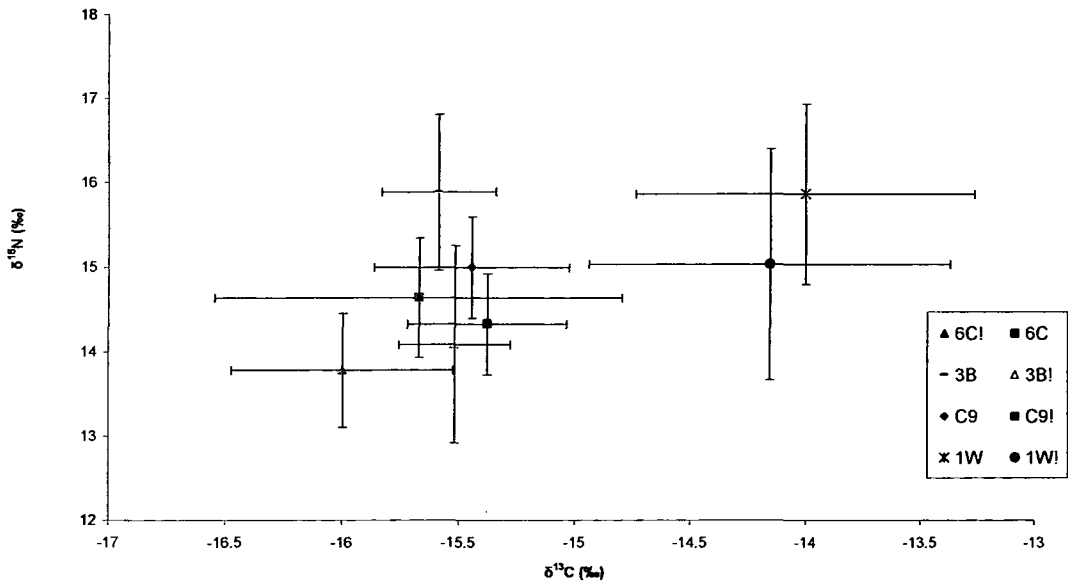


Figure 4.9: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with standard deviation bars for whiskers collected in 1997 and 1998 from 'C9', '3B', '6C' and '1W', four adult female seals from the Isle of May.

Figures 4.7 and 4.8 show plots of whiskers for four animals from consecutive years, the plots for three of the animals, show similar trends to each other i.e. an increased enrichment in the two isotopes is seen in the plots. Greater variation between the plots for the two whiskers taken from 'C9' is seen than for those from '1W'.

Figure 4.9 shows the mean isotopic variation values for the seals. The values for the vibrissae 'C9' and '1W' are most similar to each other, the two vibrissae taken from '3B' shows similar average $\delta^{13}\text{C}$ values but show greater $\delta^{15}\text{N}$ values in the 1997 vibrissa than in the one from 1998. '6C' also shows greater $\delta^{15}\text{N}$ values in 1997 than 1998 along with similarly larger values in $\delta^{13}\text{C}$.

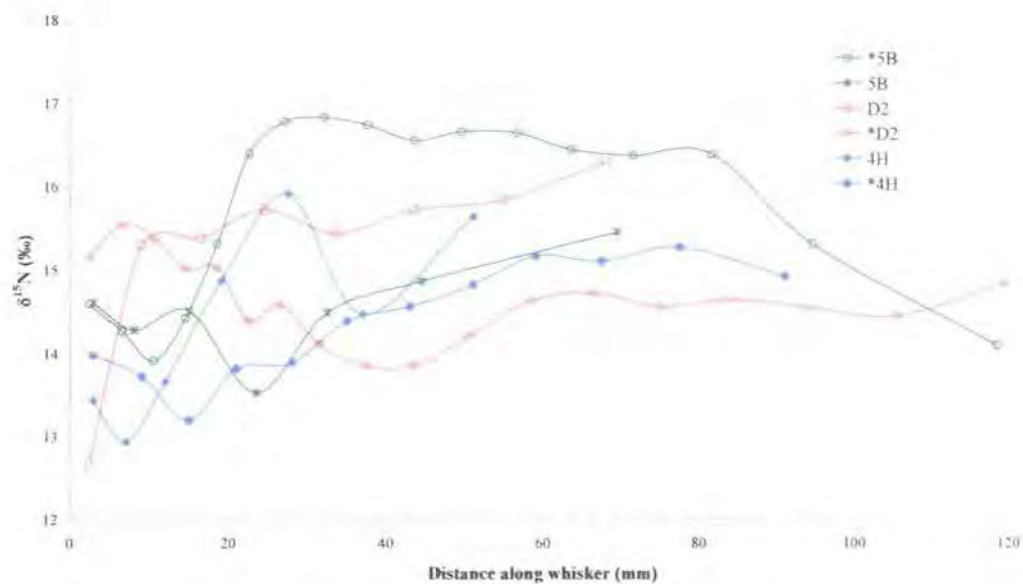


Figure 4.10: $\delta^{15}\text{N}$ for whiskers collected in 1997 and 1999 from '5B', 'D2', '4H', three adult female seals from the Isle of May.

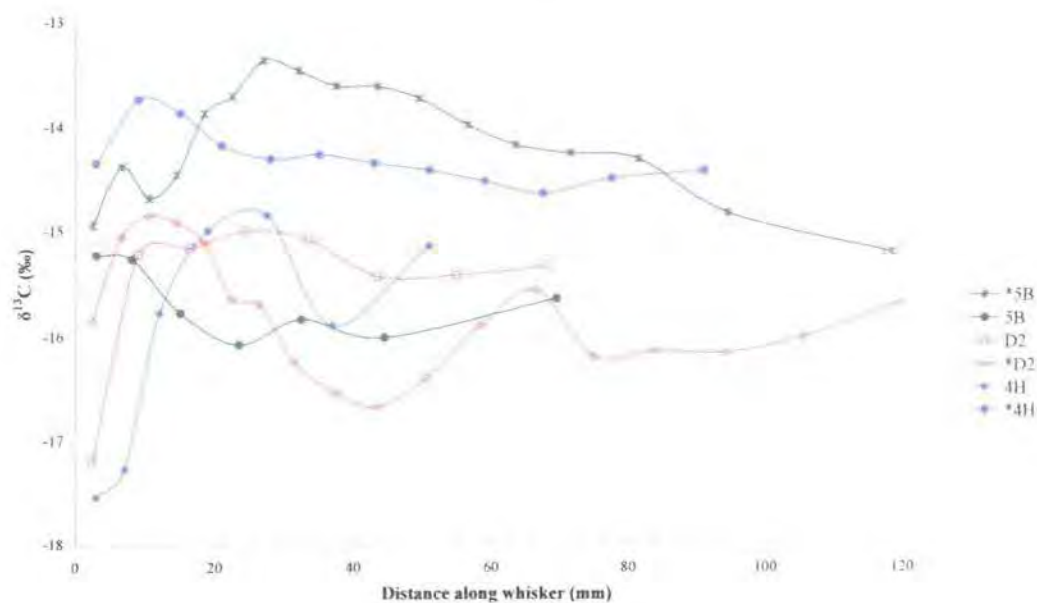


Figure 4.11: $\delta^{13}\text{C}$ for whiskers collected in 1997 and 1999 from '5B', 'D2', '4H', three adult female seals from the Isle of May.

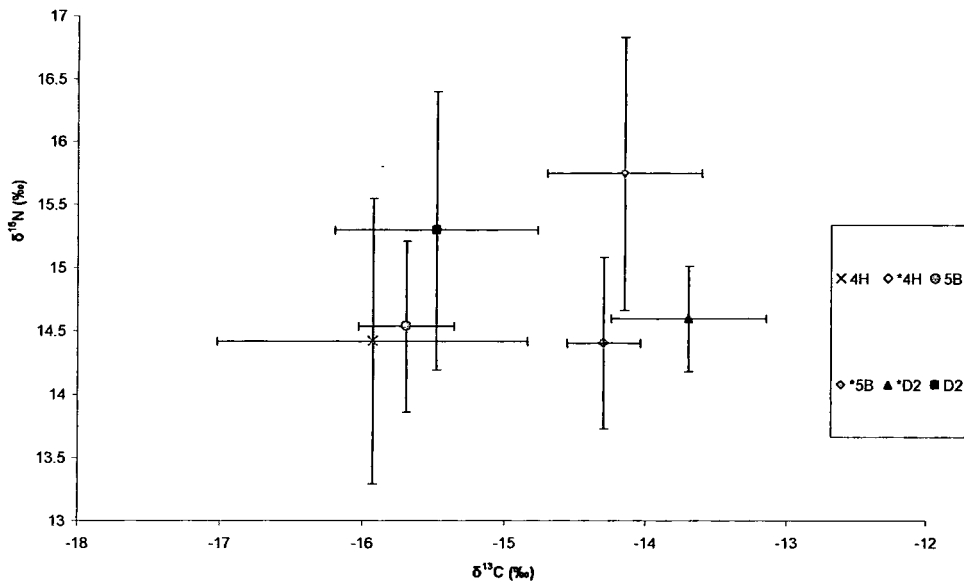


Figure 4.12: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with standard deviation bars for whiskers collected in 1997 and 1999 from '5B', 'D2', '4H', three adult female seals from the Isle of May.

The three sets of whiskers taken from animals in 1997 and then in 1999 (Figures 4.10 and 4.11) show little similarities in the plots for $\delta^{13}\text{C}$, the whiskers from '4H' show similar trends for $\delta^{15}\text{N}$, none of the whiskers from the other animals show strong similarities.

The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the whiskers (Figure 4.12), show that there are some differences in these values in all of the vibrissae, although little difference in $\delta^{15}\text{N}$ is seen between the vibrissae from '4H'. The mean values of $\delta^{13}\text{C}$ for all the vibrissae sampled in 1997 are less enriched than for the 1999 samples.

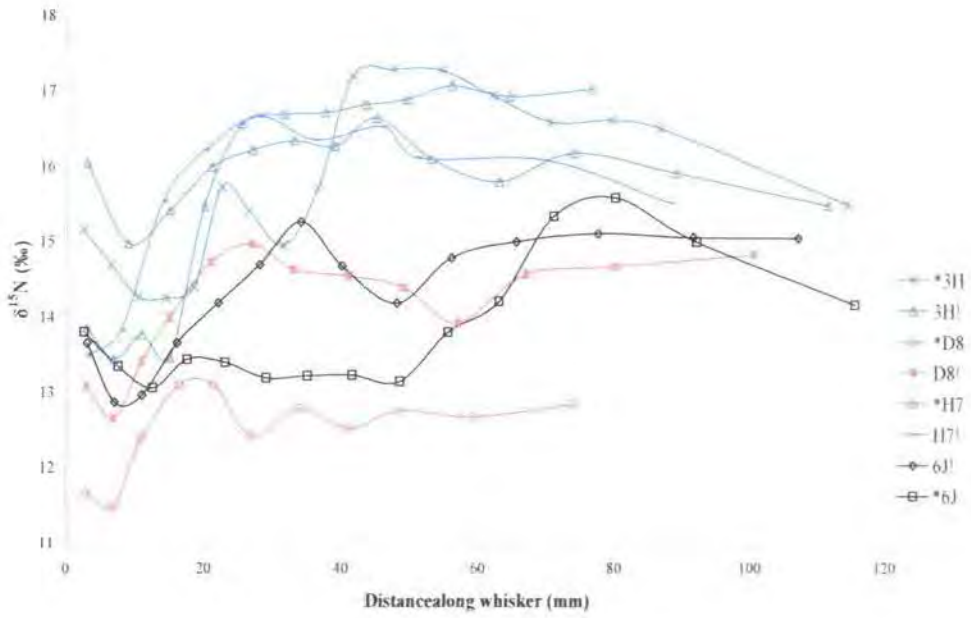


Figure 4.13: $\delta^{15}\text{N}$ plots of whiskers collected in 1998 and 1999 from '3H', 'H7', '6J', and 'D8' four adult female seals from the Isle of May.

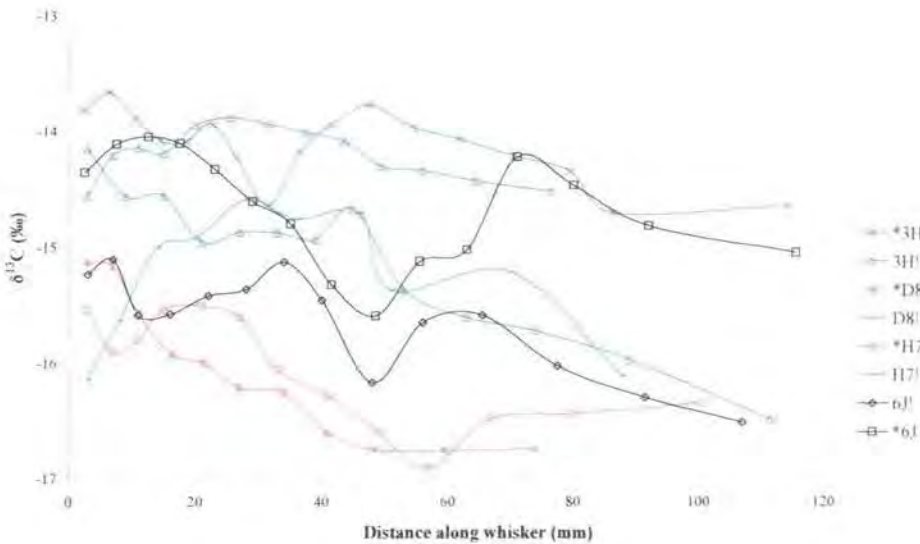


Figure 4.14: $\delta^{13}\text{C}$ plots of whiskers collected in 1998 and 1999 from '3H', 'H7', '6J', and 'D8', four adult female seals from the Isle of May.

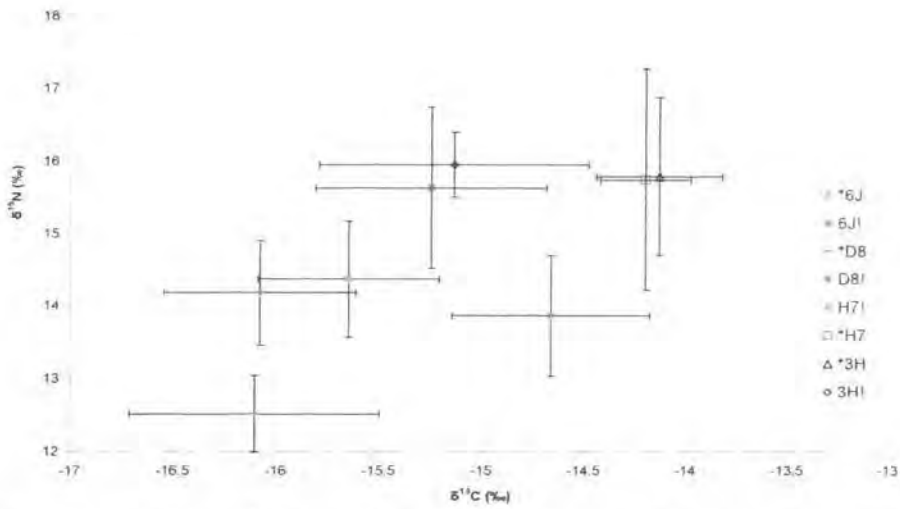


Figure 4.15: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation bars for whiskers collected in 1998 and 1999 from ‘3H’, ‘H7’, ‘6J’, and ‘D8’, four adult female seals from the Isle of May.

The three pairs of whiskers (Figures 4.13, 4.14 and 4.15) show similar overall trends in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, although variations between the whiskers collected in the two years are seen.

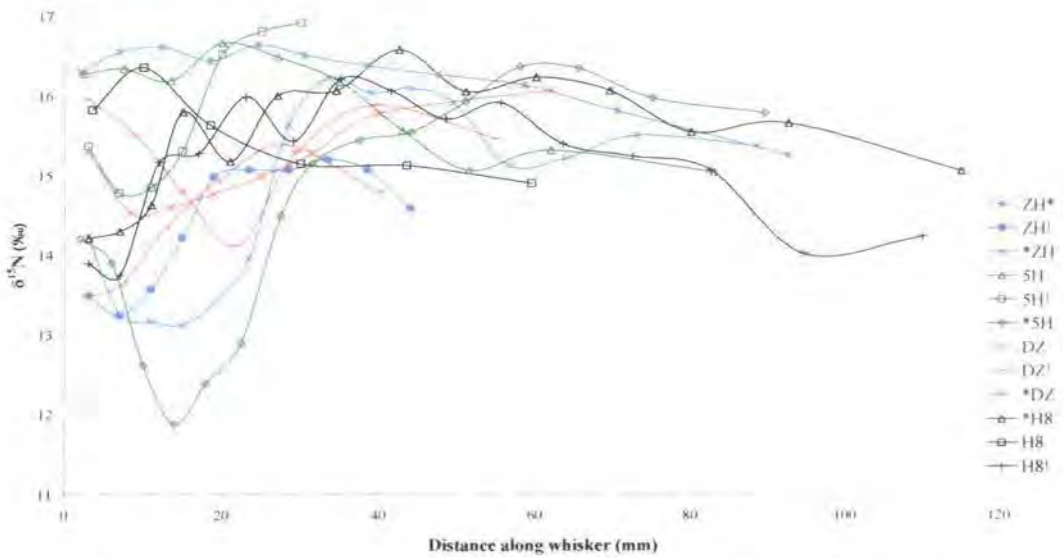


Figure 4.16: $\delta^{15}\text{N}$ plots of whiskers collected in 1997, 1998 and 1999 from ‘5H’, ‘DZ’, ‘H8’ and ‘ZH’, four adult female seals from the Isle of May.

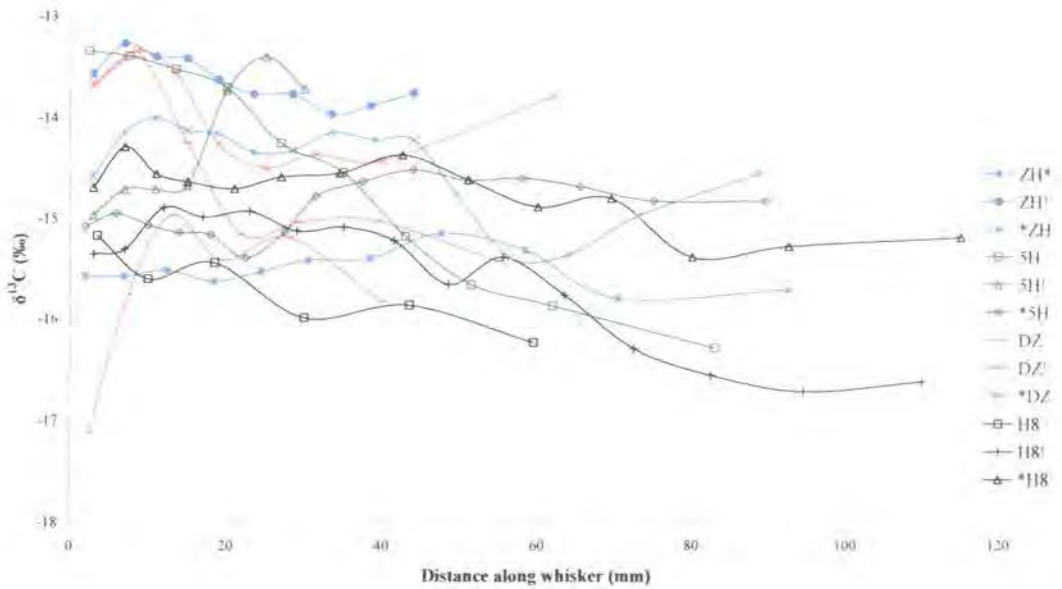


Figure 4.17: $\delta^{13}\text{C}$ plots of whiskers collected in 1997, 1998 and 1999 from '5H', 'DZ', 'H8' and 'ZH' four adult female seals from the Isle of May.

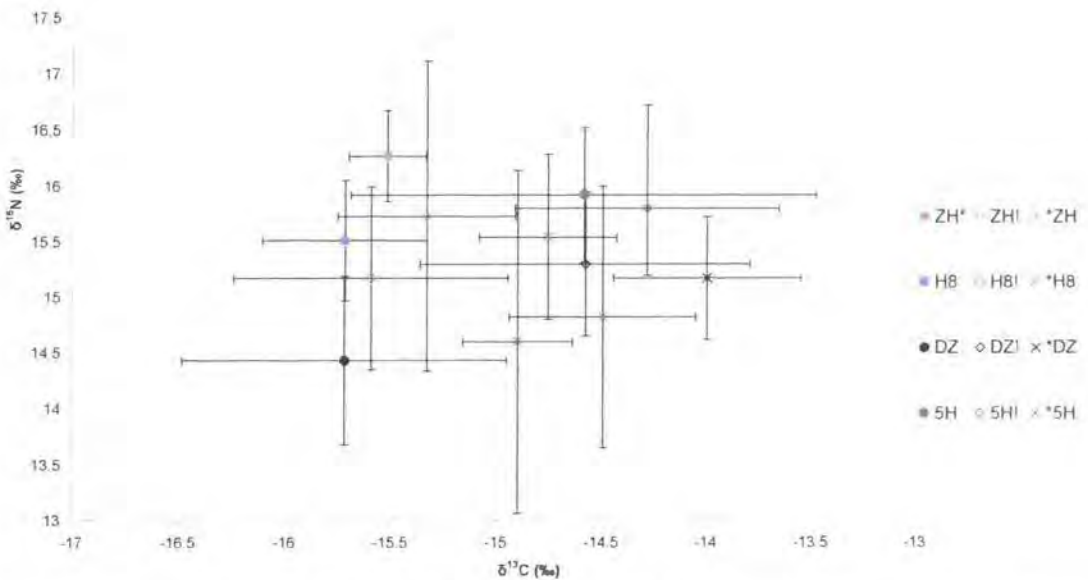


Figure 4.18: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation bars for whiskers collected in 1997, 1998 and 1999 from '5H', 'DZ', 'H8' and 'ZH' four adult female seals from the Isle of May.

The plots for $\delta^{15}\text{N}$ (Figure 4.16), show that the three whisker plot for 'H8' and 'DZ' show similar trends between the three whiskers taken from each animal in each year, the whiskers from 5H show greater variation between the whiskers, although its whiskers all show an increase. The $\delta^{13}\text{C}$ plots (Figure 4.17), show that the whiskers from 'H8' show similar trends to each other, while the whiskers from the other two animals do not. Figure 4.18 shows that the mean isotopic values are not consistent over the three years of the study.

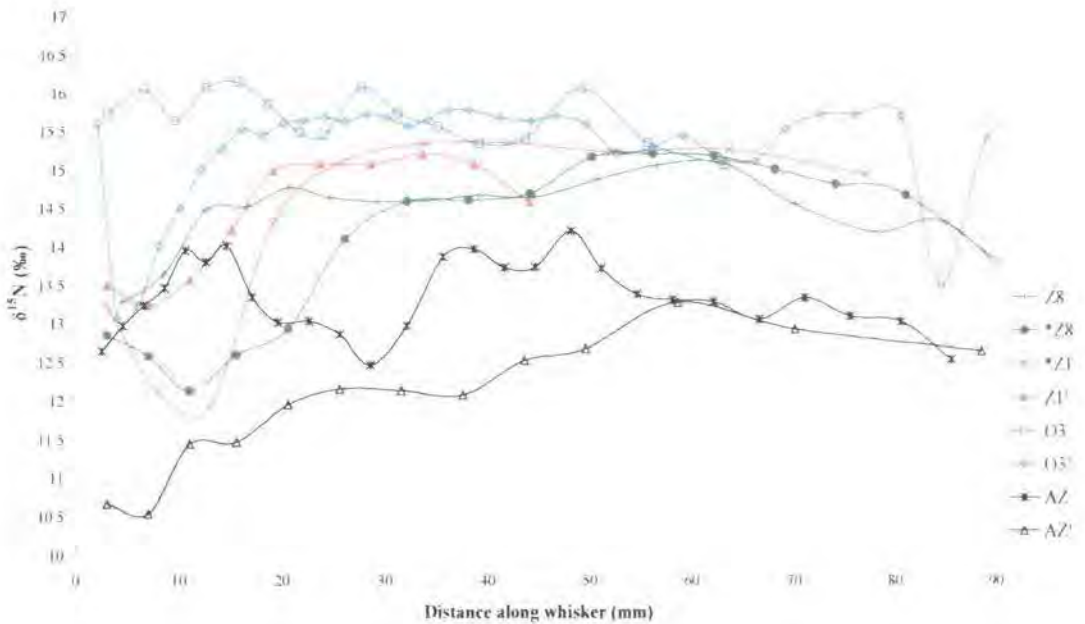


Figure 4.19: $\delta^{15}\text{N}$ plots of whiskers collected in 1997 and 1998 from 'O3', 'Z8', 'Z1', and 'AZ', four adult female seals from North Rona.

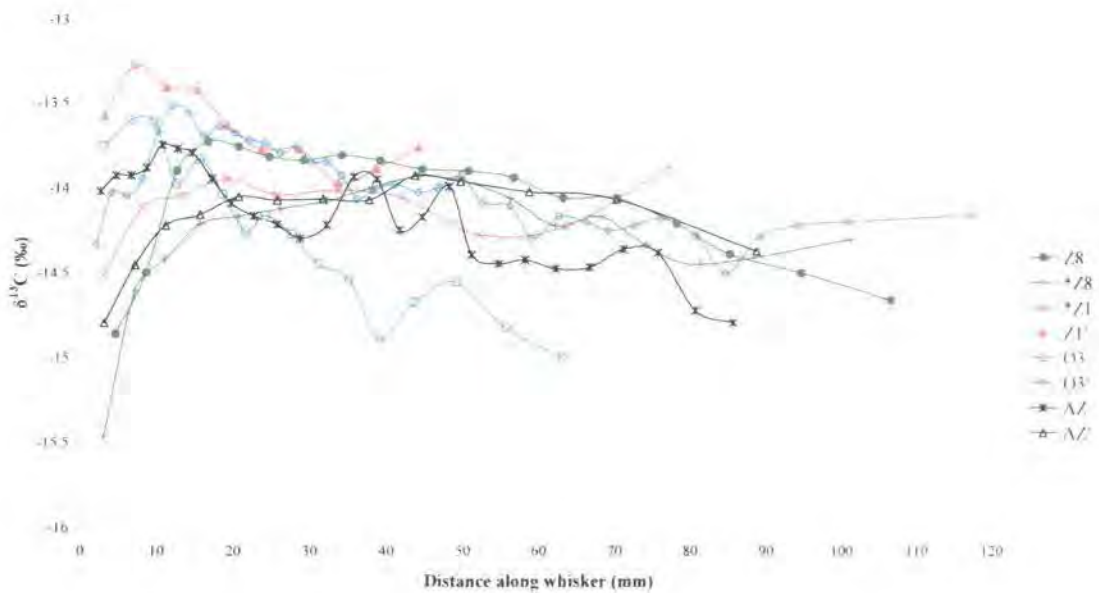


Figure 4.20: $\delta^{13}\text{C}$ plots of whiskers collected in 1997 and 1998 from 'O3', 'Z8', 'Z1' and 'AZ', four adult female seals from North Rona.

The plots for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Figures 4.19 and 4.20) show that the whiskers from each of the seals show similar trends in each isotope to the whisker taken from the same animal in a different year. The plots for $\delta^{13}\text{C}$ tend to show greater similarities between the whiskers than for $\delta^{15}\text{N}$.

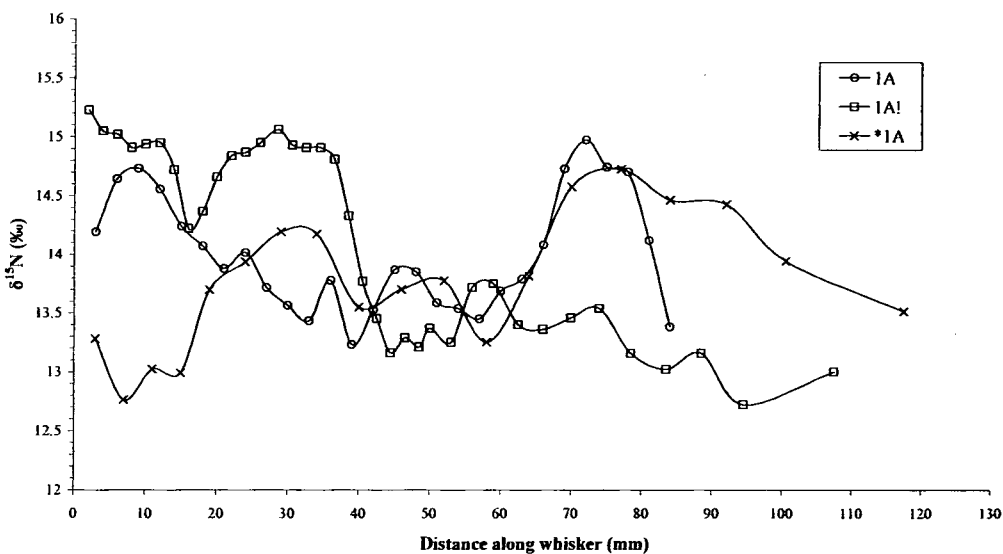


Figure 4.21: $\delta^{15}\text{N}$ plots of whiskers collected in 1997, 1998, 1999 from '1A' an adult female seal from North Rona

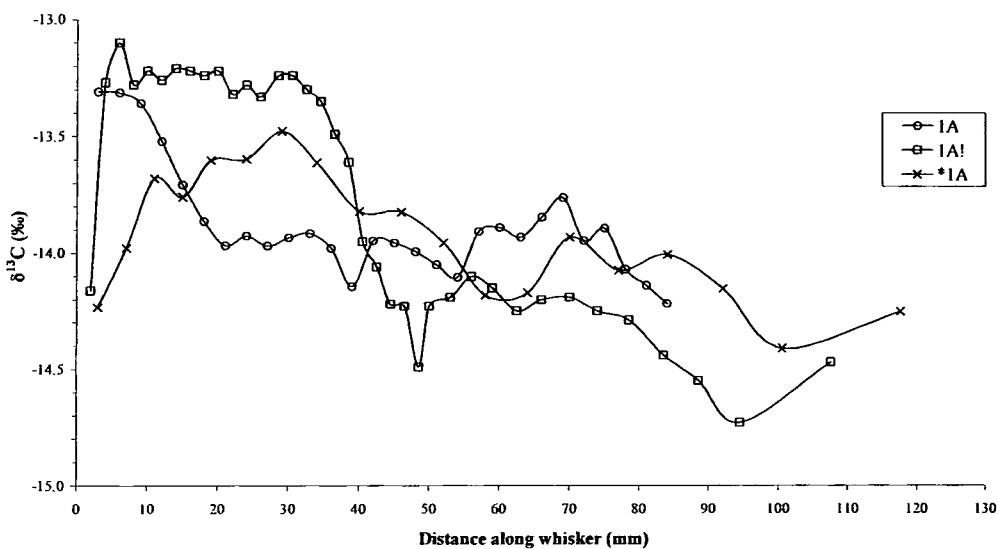


Figure 4.22: $\delta^{13}\text{C}$ plots of whiskers collected in 1997, 1998, 1999 from '1A' an adult female seal from North Rona.

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plots (Figures 4.21 and 4.22) for the whiskers from '1A' show that the whiskers collected from this animal show similar trends to each other in each of the three years. The $\delta^{15}\text{N}$ plots show greater variation than the $\delta^{13}\text{C}$ plots.

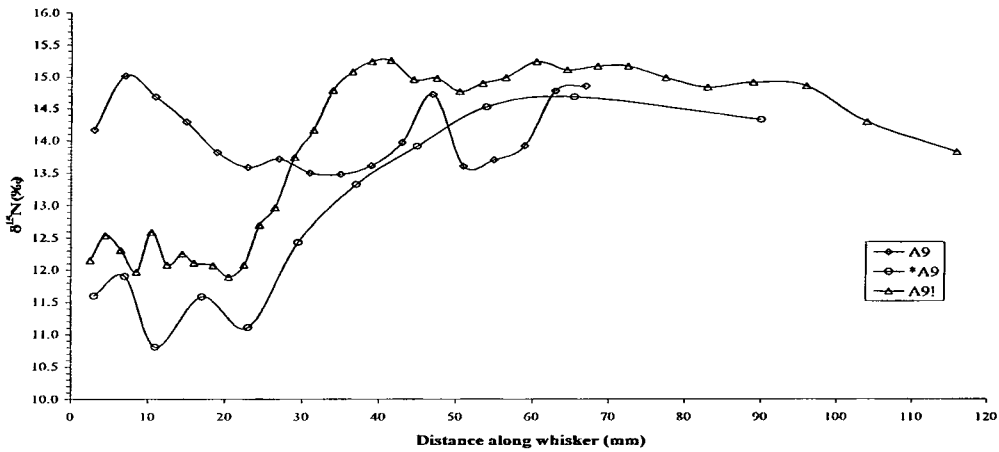


Figure 4.23: $\delta^{15}\text{N}$ plots of whiskers collected in 1997, 1998, 1999 from 'A9' an adult female seal from North Rona.

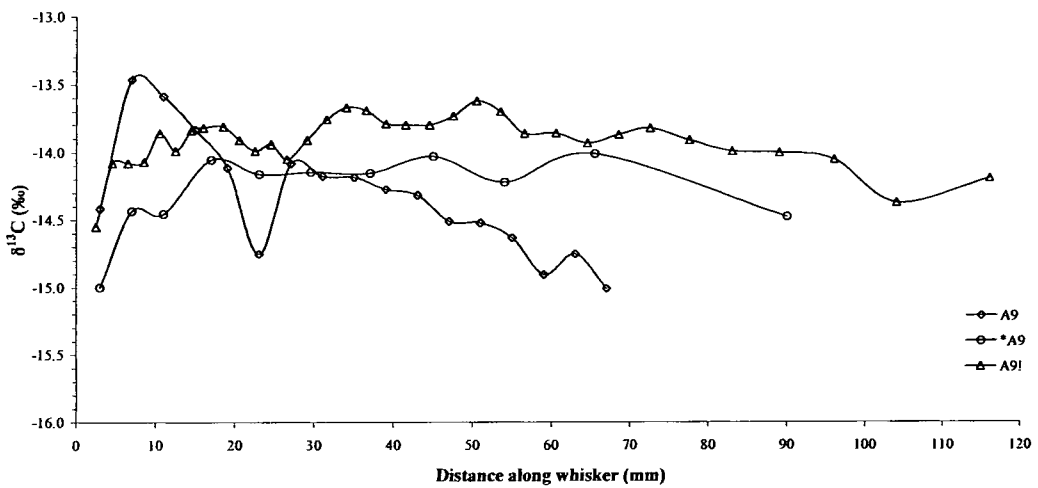


Figure 4.24: $\delta^{13}\text{C}$ plots of whiskers collected in 1997, 1998, 1999 from 'A9' an adult female seal from North Rona.

The plots for 'A9' (Figures 4.23 and 4.24) show similar trends to each other, with greater variations seen in the $\delta^{15}\text{N}$ plots than for the $\delta^{13}\text{C}$. The $\delta^{15}\text{N}$ plot shows that the values for the distal of the whiskers show a 2‰ difference, although the plots show similar values at the proximal ends of the whiskers. The $\delta^{13}\text{C}$ (Figure 4.20) show a similar trend with little overall variation.

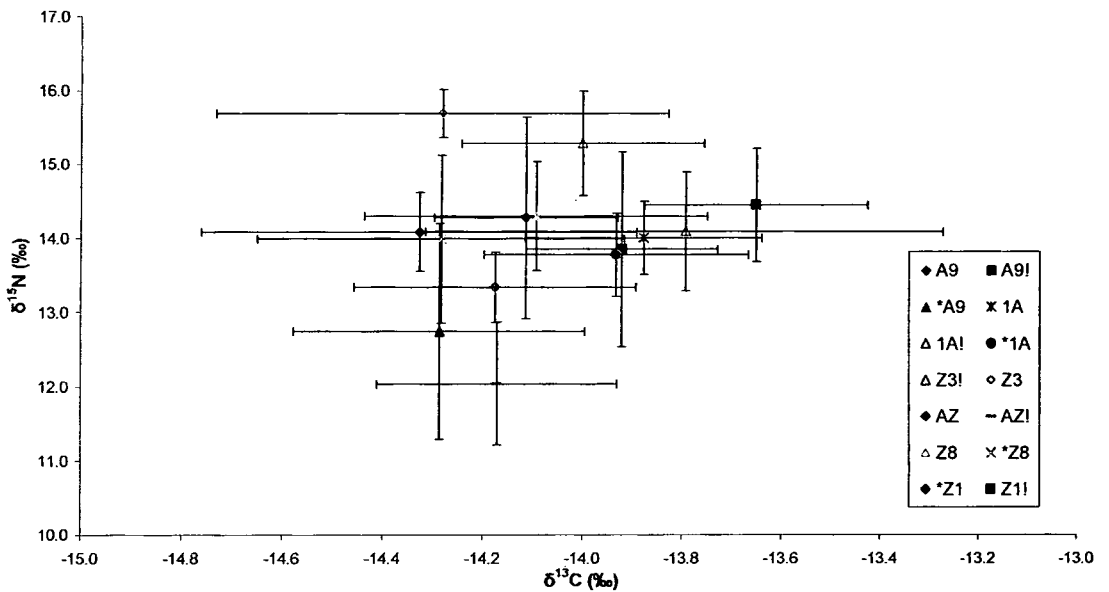


Figure 4.25: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation bars for whiskers collected from grey seals sampled on North Rona in more than one year

Table 4.4: Mean isotopic values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, with relevant standard deviation values, for the vibrissae from seals from the Isle of May and North Rona which were sampled in more than one year of the study. Included in the table are the trends identified for each vibrissa in the previous section for comparison.

Individual	Year	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		Mean	Standard deviation	Vibrissa trend	Mean	Standard deviation	Vibrissa trend
C9	1997	-15.44	± 0.42	Up	15.00	± 0.66	Up
C9!	1998	-15.38	± 0.34	Up	14.33	± 0.60	Up
3B	1997	-15.59	± 0.25	None	15.89	± 0.92	Up
3B!	1998	-15.52	± 0.24	None	15.23	± 1.17	Up
6C	1997	-15.67	± 0.86	Up	14.64	± 0.70	Up
6C!	1998	-16.00	± 0.48	Down	13.78	± 0.68	Up
1W	1997	-14.00	± 0.74	Up	15.87	± 1.07	Up
1W!	1998	-14.15	± 0.78	Up	15.04	± 1.37	Up
5B	1997	-15.69	± 0.34	None	15.75	± 0.69	Up
*5B	1999	-14.15	± 0.55	None	15.89	± 1.09	None
D2	1997	-15.48	± 0.72	Up	15.30	± 1.10	Up
*D2	1999	-14.00	± 1.00	None	14.60	± 0.42	None
4H	1997	-15.93	± 1.90	Up	14.41	± 1.13	Up
*4H	1999	-14.30	± 0.26	None	14.54	± 0.68	Up
3H!	1998	-15.13	± 0.69	Down	15.95	± 0.45	Up
*3H	1999	-14.12	± 0.31	Down	15.79	± 1.09	None
D8!	1998	-16.08	± 0.46	Down	14.18	± 0.73	Up
*D8	1999	-16.10	± 0.61	Down	12.51	± 0.52	Up

H7!	1998	-15.25	±0.56	None	15.63	±1.11	Up
*H7	1999	-14.20	±0.22	None	15.74	±1.53	Up
6J!	1998	-15.65	±0.44	Down	14.37	±0.80	Up
*6J	1999	-14.66	±0.48	Down	13.86	±0.83	None
ZH*	1997	-15.51	±0.18	None	16.27	±0.41	Down
ZH!	1998	-15.33	±0.42	None	15.72	±1.39	Up
*ZH	1999	-14.49	±0.44	None	14.82	±1.18	Up
5H	1997	-14.58	±1.10	Down	15.92	±0.60	Down
5H!	1998	-14.28	±0.63	Up	15.80	±0.93	Up
*5H	1999	-14.90	±0.26	None	14.60	±1.54	Up
DZ	1997	-15.72	±0.77	Up	14.42	±0.76	Up
DZ!	1998	-14.57	±0.78	Down	15.29	±0.65	Down
*DZ	1999	-13.99	±0.45	None	15.17	±0.55	Up
H8	1997	-15.71	±0.39	Down	15.51	±0.54	Down
H8!	1998	-15.59	±0.65	Down	15.17	±0.82	Up
*H8	1999	-14.75	±0.33	None	15.54	±0.74	Up
Z8!	1998	-14.09	±0.34	None	14.30	±0.74	Down
*Z8	1999	-14.28	±0.37	Up	13.99	±1.14	None
Z1!	1998	-13.65	±0.23	None	14.45	±0.77	Up
*Z1	1999	-14.11	±0.18	None	14.28	±1.36	Up
O3	1997	-14.28	±0.45	Down	15.69	±0.71	None
O3!	1998	-14.00	±0.24	None	15.28	±0.33	None
AZ	1997	-14.17	±0.28	Down	13.34	±0.47	None
AZ!	1998	-14.17	±0.24	None	12.04	±0.83	Up

1A	1997	-13.88	±0.24	Down	14.00	±0.50	Down
1A!	1998	-13.79	±0.52	None	14.09	±0.81	Down
*1A	1999	-13.93	±0.27	None	13.78	±0.56	None
A9	1997	-14.33	±0.43	None	14.09	±0.53	None
A9!	1998	-13.92	±0.19	None	13.85	±1.31	Up
*A9	1999	-14.29	±0.29	None	12.75	±1.45	Up

From North Rona, none of the seals sampled in only two years showed similar trends for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in both of the years of sampling, and none sampled in three years showed similar trends over all three of the years. 'A9' showed similar trends in 1998 and 1999: a trend to show no overall change in $\delta^{13}\text{C}$ values and a trend to show an increase in $\delta^{15}\text{N}$ along the length of the vibrissae. Six seals from the Isle of May, including one that was sampled in three years showed similar trends, in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in two consecutive years of sampling. No animals showed one trend for both isotopes in all three years of sampling. One animal, 'H8', showed a different trend in each of the three years.

4.2. c. Differences between the years.

Data have been collected over a three year period from both North Rona and for the Isle of May giving results from 106 vibrissae. All data-points for each year were used to analyse the potential differences in isotopic value between the years for each population.

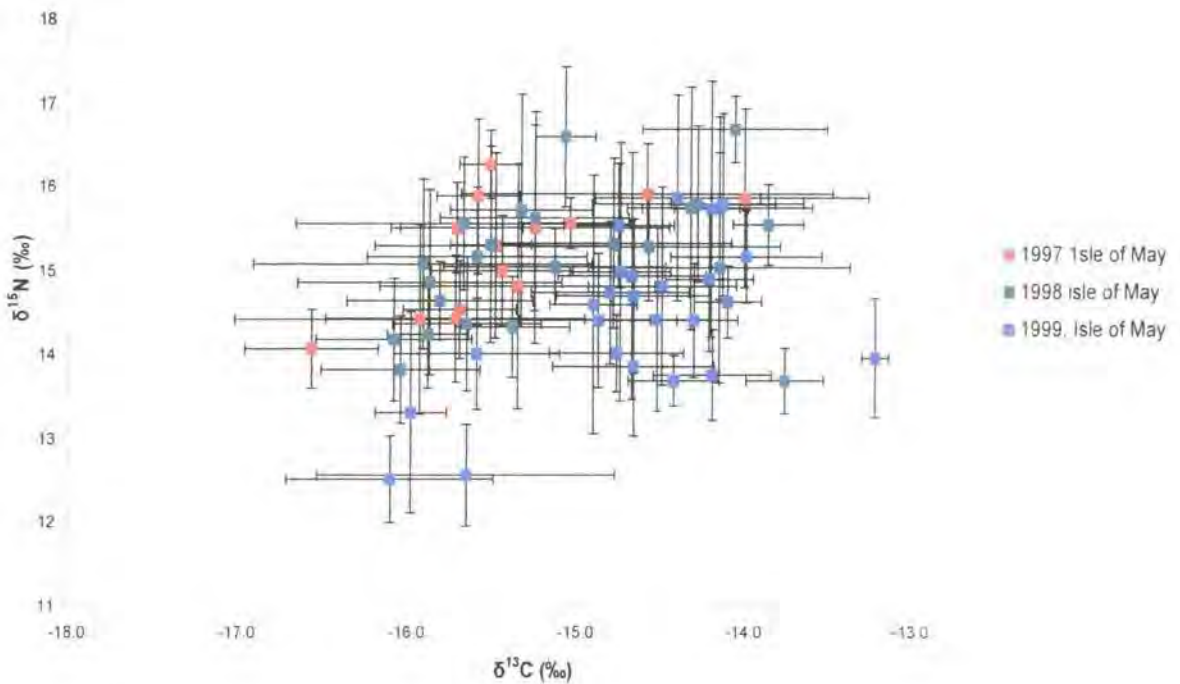


Figure 4.26: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each vibrissa from the Isle of May for 1997-1999, with standard deviation bars for each vibrissa. Where replicate vibrissae from one animal were sampled data for the longest were used).

The data points (Figure 4.26) show a spread of -17.22‰ to -14.00‰ for $\delta^{13}\text{C}$ and 16.27‰ to 12.10‰ for $\delta^{15}\text{N}$ in 1997. For 1998 a spread of -16.08‰ to -13.76‰ for $\delta^{13}\text{C}$ and 16.69‰ - 13.69‰ for $\delta^{15}\text{N}$ is seen. In 1999 a spread of -16.01‰ to -13.22‰ for $\delta^{13}\text{C}$ and 15.87‰ to 12.51‰ for $\delta^{15}\text{N}$ is shown. Mean values for each year and each isotope are shown below in Table 4.5. The results for Mann-Whitney U-test comparisons between the data from each year are shown in Table 4.6 below.

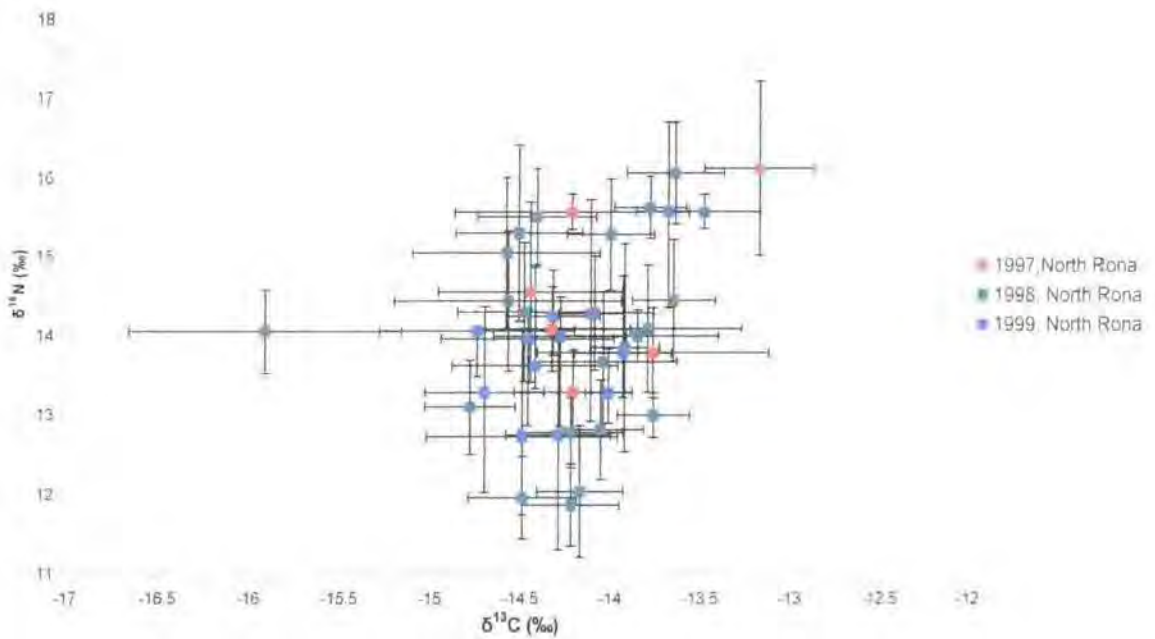


Figure 4.27: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each vibrissa analysed for North Rona for 1997-1999, with standard deviation bars for each vibrissa. Where repeat vibrissae from one animal were sampled the data from the longest were used).

The data points for North Rona (Figure 4.27) show a spread for 1997 of -14.45‰ to -13.00‰ for $\delta^{13}\text{C}$ and from 13.29‰ to 16.00‰ for $\delta^{15}\text{N}$. The data points for 1998 show a spread of -15.91‰ to 13.48‰ for $\delta^{13}\text{C}$ and 11.87‰ to 16.07‰ for $\delta^{15}\text{N}$. The data from 1999 shows values from -14.74‰ to -13.68‰ for $\delta^{13}\text{C}$ and 12.73‰ to 15.58‰ for $\delta^{15}\text{N}$. Mean values for each year and each isotope are shown in Table 4.5 below. The results for Mann-Whitney U-test comparisons between the data from each year are shown in Table 4.6 below.

Table 4.5: Mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratio with standard deviations for 1997, 1998 and 1999 for both the Isle of May and North Rona.

Population	Year	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	Mean C:N ratio
Isle of May	1997	-15.57 ± 1.09	14.36 ± 1.70	3.52 ± 0.61
Isle of May	1998	-15.34 ± 1.85	14.89 ± 1.42	3.46 ± 0.59
Isle of May	1999	-14.69 ± 0.97	14.51 ± 2.51	3.47 ± 0.48
North Rona	1997	-14.00 ± 0.53	14.68 ± 1.12	3.51 ± 0.05
North Rona	1998	-14.14 ± 0.57	14.02 ± 1.33	3.44 ± 0.04
North Rona	1999	-14.27 ± 0.48	13.77 ± 1.23	3.43 ± 0.05

Statistical comparisons of the results of the isotopic analysis for each population and between each year were made using Mann-Whitney U-tests to examine if the differences seen in Figures 4.26 and 4.27 are significant.

Table 4.6: Results of the statistical comparison of the data from each year for the Isle of May and North Rona. $\alpha = 0.017$ after Bonferroni correction.

Population	Comparison	$\delta^{13}\text{C} / \delta^{15}\text{N}$	n_1, n_2	U	P
Isle of May	1997:1998	$\delta^{13}\text{C}$	178,318	23268.5	0.001
		$\delta^{15}\text{N}$	178,318	26955	0.379
Isle of May	1998:1999	$\delta^{13}\text{C}$	318,445	46685.5	<0.001
		$\delta^{15}\text{N}$	318,445	51506	<0.001
Isle of May	1997:1999	$\delta^{13}\text{C}$	178,445	18186.5	<0.001
		$\delta^{15}\text{N}$	178,445	29655.5	<0.001
North Rona	1997:1998	$\delta^{13}\text{C}$	187,406	31874	0.002
		$\delta^{15}\text{N}$	187,406	27878	<0.001
North Rona	1998:1999	$\delta^{13}\text{C}$	406,147	27704	0.198
		$\delta^{15}\text{N}$	406,147	26095.5	0.024
North Rona	1997:1999	$\delta^{13}\text{C}$	147,187	10522	<0.001
		$\delta^{15}\text{N}$	147,187	7859.5	<0.001

As can be seen from Table 4.6, significant differences were found for all comparisons of $\delta^{13}\text{C}$ for vibrissae from the Isle of May, and for all comparisons of $\delta^{15}\text{N}$ apart from the 1997:1998 comparison, where no significant difference was found. An increase in $\delta^{13}\text{C}$ is seen from 1997 to 1999. The data points for 1997 tend to fall at the lower $\delta^{13}\text{C}$ values seen and the 1999 values tend to fall at the higher values, with values from 1998 falling between the two.

For North Rona significant differences were found in all comparisons for $\delta^{15}\text{N}$, apart from the 1998:1999 comparison. $\delta^{15}\text{N}$ tends to show a decrease from 1997 to 1999. Significant differences were found for all comparisons for $\delta^{13}\text{C}$, except for the comparison between 1998 and 1999 where no difference was seen. The data points for 1997 tend to show higher $\delta^{15}\text{N}$ values than the points for 1999, which tend to show lower $\delta^{15}\text{N}$ values.

4.2. d. Sex differences in grey seals

Male grey seals were only sampled in 1999, from the Isle of May. Comparisons between them and the female seals from the same year were made, since differences have been found between the different years.

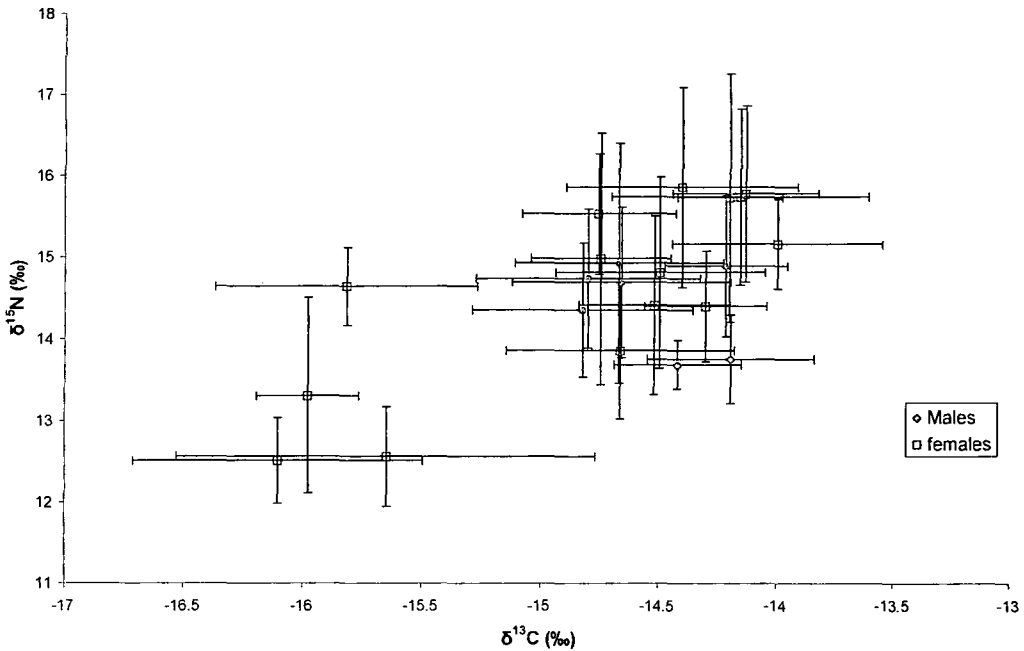


Figure 4.28: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for whiskers collected from male and female grey seals from the Isle of May in 1999.

Figure 4.28 shows that the isotopic variation for the male seals are similar to those of most of the female seals collected in 1999. Four of the values for the female seals show lower $\delta^{13}\text{C}$ values than the rest and as such show no overlap with any of the values for the male seals.

Table 4.7: Results of the statistical comparison of the data from the male and female grey seal vibrissa results collected in 1999. Analyses were conducted using Mann-Whitney U-tests.

Isotope	n ₁ , n ₂	U	P
$\delta^{13}\text{C}$	105,216	9538.000	0.021
$\delta^{15}\text{N}$	105,216	10775.000	0.469

From the results shown in Table 4.7 a significant difference in $\delta^{13}\text{C}$ between male and female seals is seen, but no significant difference is seen in $\delta^{15}\text{N}$, but the $\delta^{13}\text{C}$ difference is small (Figure 4.28)

4.2. e. Comparison of North Rona and Isle of May

The data from the two populations were compared, in order to investigate for any significant differences or trends that the two populations might show. Data from all three years were examined, using one vibrissa from each animal sampled. Where duplicate vibrissae were collected from an animal the longest vibrissa was used, since vibrissae taken from the same animal show similar isotopic values (see Chapter 3).

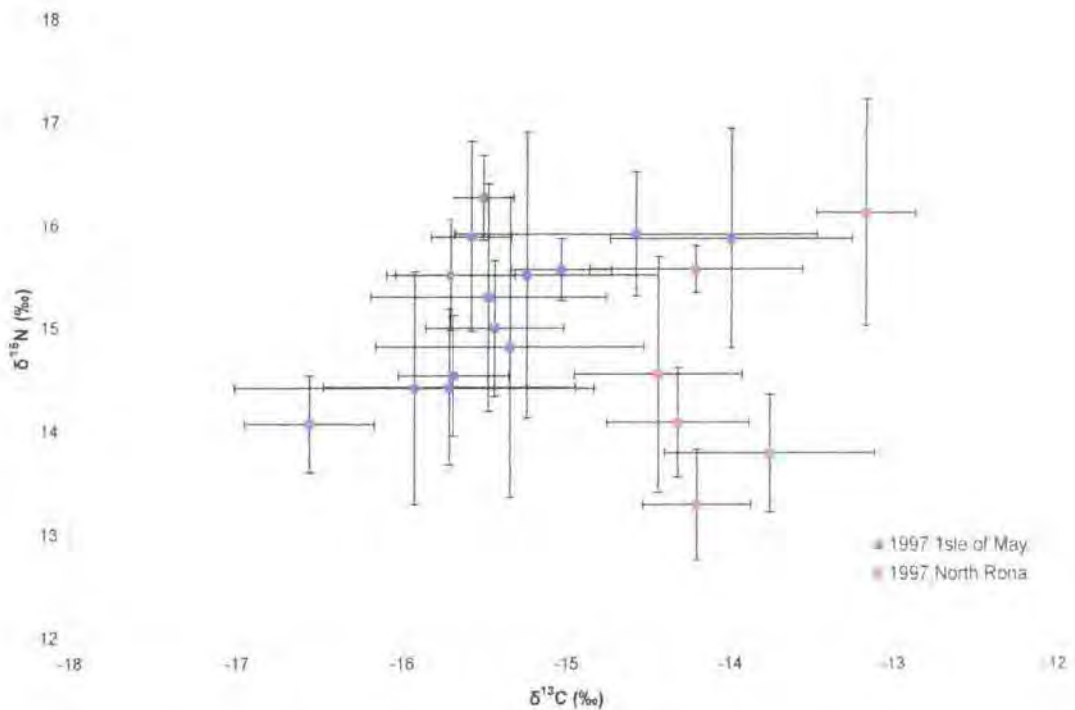


Figure 4.29: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation bars for each grey seal sampled in 1997 from the Isle of May and North Rona

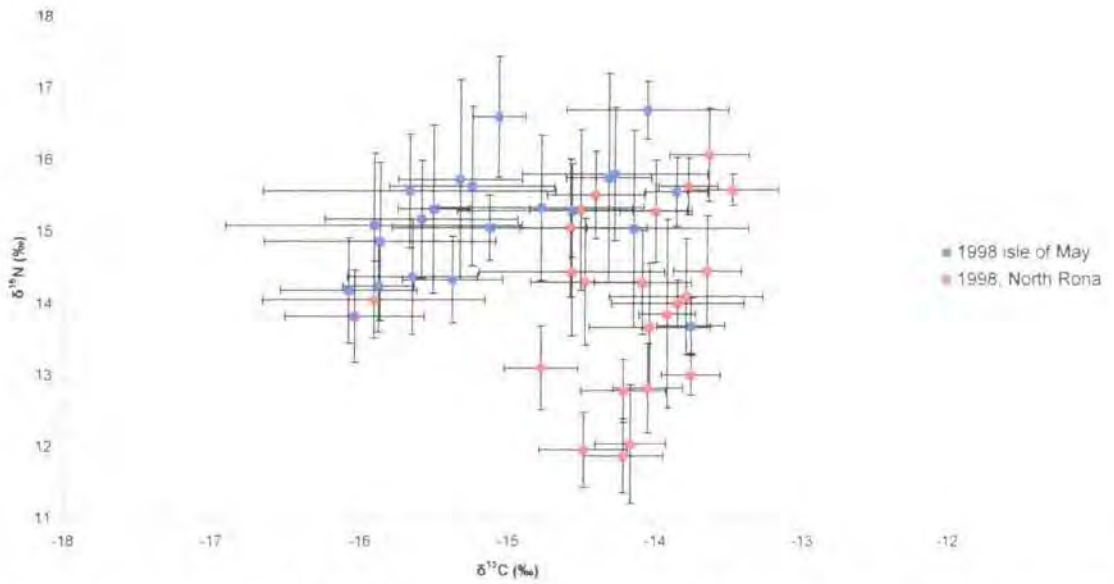


Figure 4.30: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation bars for each grey seal sampled in 1998 from the Isle of May and North Rona

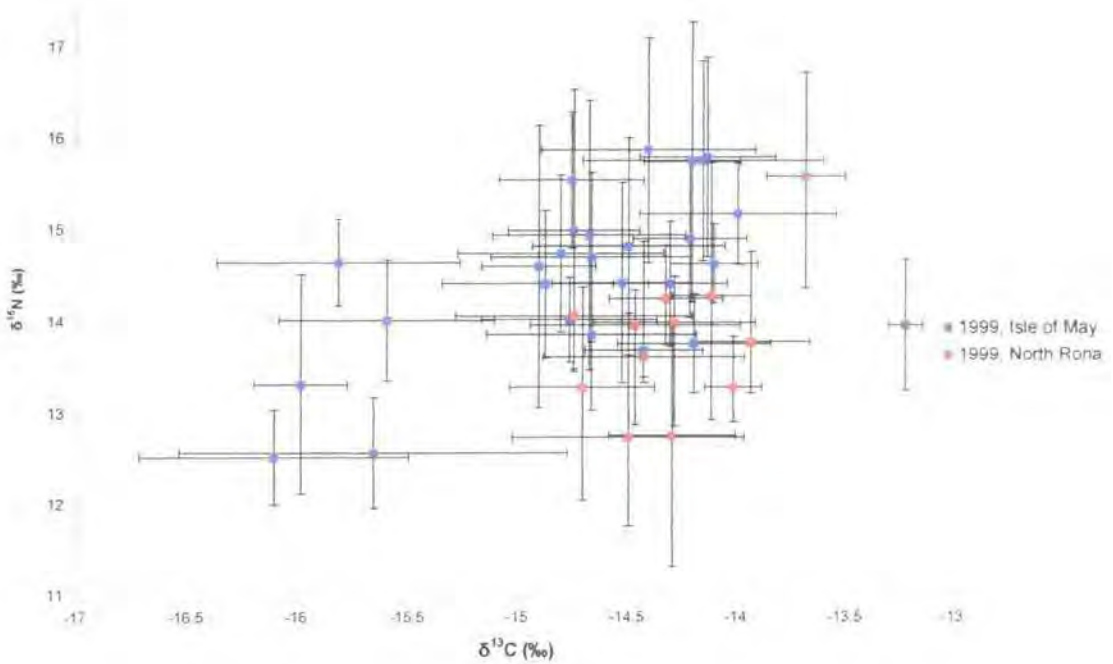


Figure 4.31: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation bars for each grey seal sampled in 1999 from the Isle of May and North Rona

Figure 4.29 shows the plots from 14 vibrissae from seals from the Isle of May and 6 seals from North Rona, the points are spread over ranges of 3.57 ‰ of $\delta^{13}\text{C}$ and 2.98 ‰ of $\delta^{15}\text{N}$. The data from the Isle of May vibrissae fall to the left of the graph and show lower $\delta^{13}\text{C}$ values than those from North Rona. No apparent differences are seen in $\delta^{15}\text{N}$.

The results from 1998 (Figure 4.30) the two populations, show a spread 2.60‰ for $\delta^{13}\text{C}$ and 4.82‰ for $\delta^{15}\text{N}$. The points for Isle of May still seem to show a lower $\delta^{13}\text{C}$ value than the North Rona points.

The mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the Isle of May and North Rona in 1999 (Figure 4.31) show a spread of 2.88‰ for $\delta^{13}\text{C}$ and 3.36‰ for $\delta^{15}\text{N}$. Some points from the Isle of May have lower $\delta^{13}\text{C}$ values than those from North Rona.

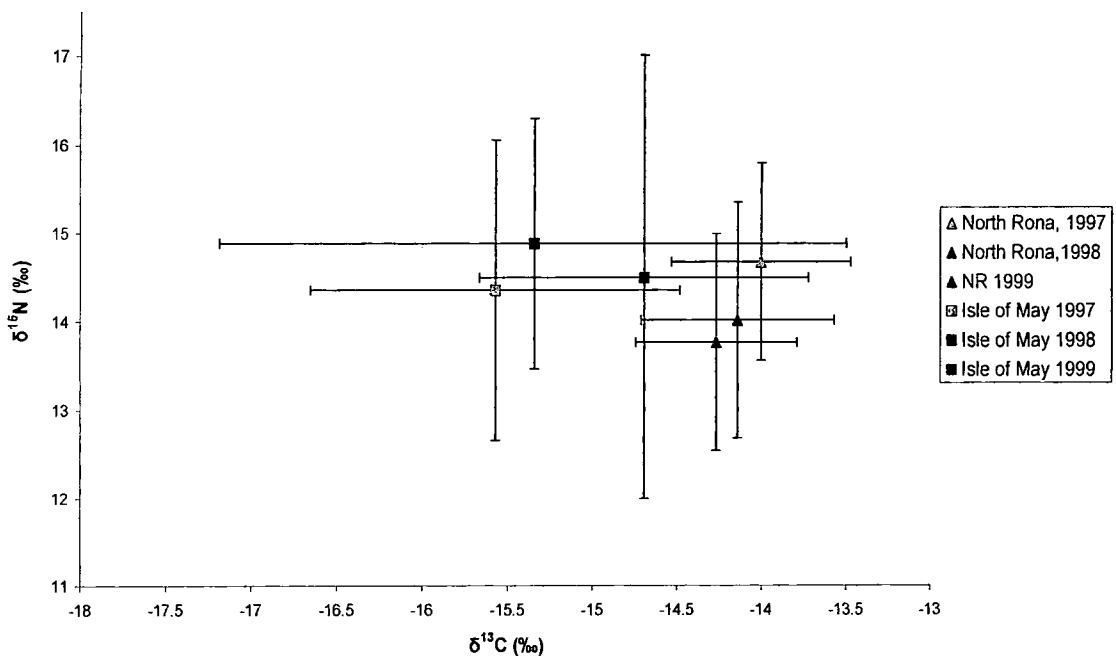


Figure 4.32: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with standard deviation values for 1997, 1998 and 1999 for both the Isle of May and North Rona.

Figure 4.32 shows that the points for the Isle of May values appear to show lower $\delta^{13}\text{C}$ values than for those of North Rona. They also appear to show higher $\delta^{15}\text{N}$ values than the North Rona points for 1998 and 1999, and to share a comparable value to that of 1997.

The results from this section were compared to each other statistically using Mann-Whitney U-tests. The results are shown in Table 4.8 below.

Table 4.8: Results from the statistical comparison (Mann-Whitney U-test) of the data from the Isle of May to that from North Rona by year. $\alpha = 0.013$ after Bonferroni correction.

Population	Year	Isotope	n_1, n_2	U	P
Isle of May : North Rona	All years	$\delta^{13}\text{C}$	593,496	50166	<0.001
		$\delta^{15}\text{N}$	593,496	96219.5	<0.001
Isle of May : North Rona	1997	$\delta^{13}\text{C}$	187,178	3333	<0.001
		$\delta^{15}\text{N}$	187,178	13828	0.005
Isle of May : North Rona	1998	$\delta^{13}\text{C}$	406,318	27245.5	<0.001
		$\delta^{15}\text{N}$	406,318	37169	<0.0001
Isle of May : North Rona	1999	$\delta^{13}\text{C}$	147,445	19832	<0.001
		$\delta^{15}\text{N}$	147,445	22259	<0.001

Statistical comparison showed that the populations are significantly different from each other in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ when all data was used for the analysis. When comparisons were made between the populations on a yearly basis, significant differences were found for all three years for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

4.2. d. Grey seals and their potential fish prey.

The figure below show the data for the fish (Figure 4.33) overlaid by boxes outlining the giving the range of values seen for seals from the Isle of May and North Rona. The next figure, 4.34, shows the same plots for the fish samples with the Isle of May seal values adjusted by $\delta^{15}\text{N} -3$ and $\delta^{13}\text{C} -1$, and then by $\delta^{15}\text{N} -3$ and $\delta^{13}\text{C} -3.4$, to account for the lowest and highest likely $\delta^{13}\text{C}$ enrichment of vibrissa keratin over diet (Hobson *et al.* 1996). The same plot is shown in Figures 4.34 with data from North Rona .

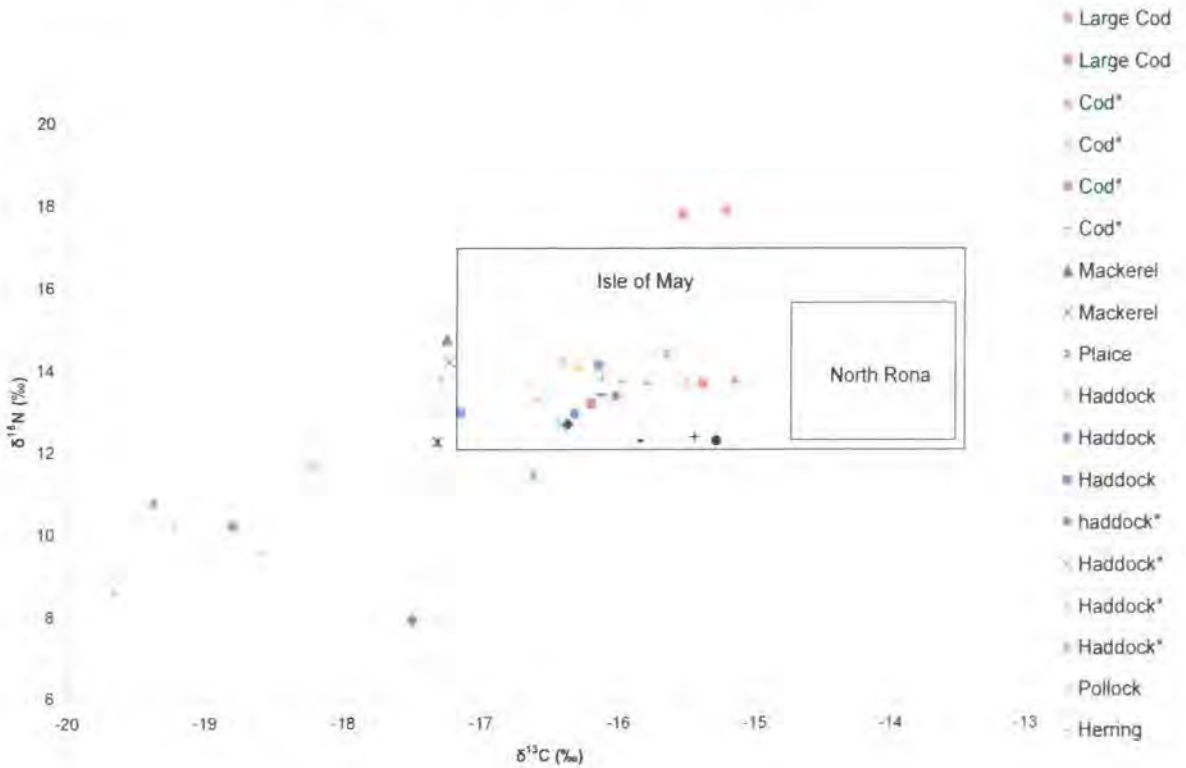


Figure 4.33: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish collected from Mallaig and Hartlepool with values of seals from Isle of May and North Rona overlaid, as boxes.

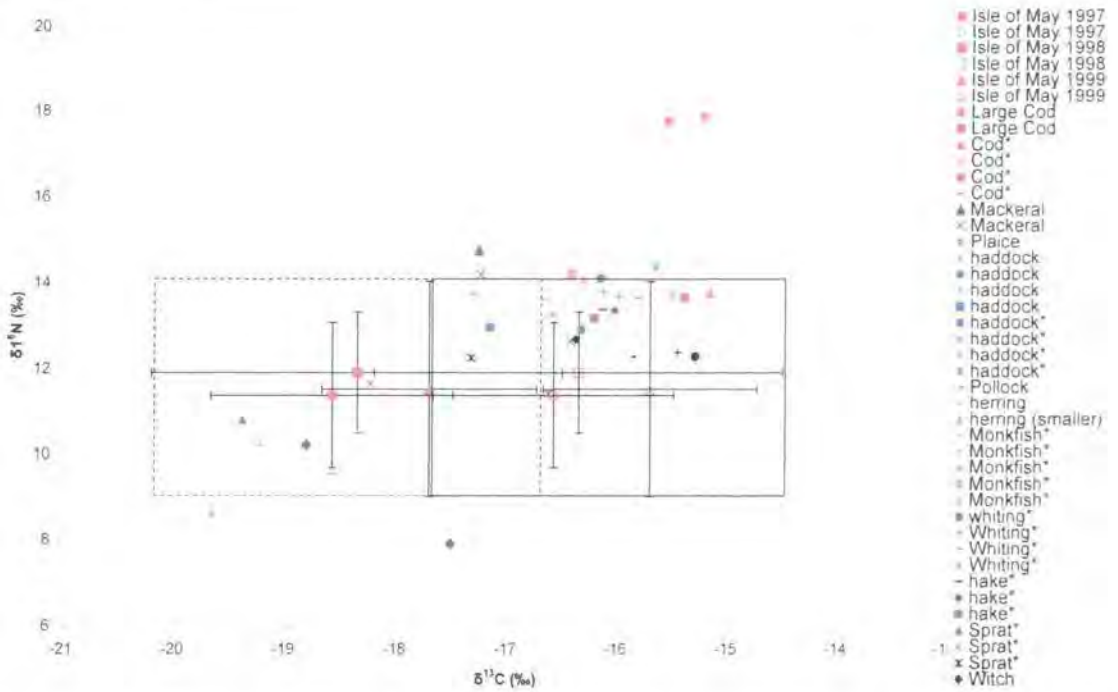


Figure 4.34: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of fish collected from Mallaig and Hartlepool with values of seals from Isle of May plotted as $\delta^{15}\text{N}$ -3 and as $\delta^{13}\text{C}$ -1 (solid box) and $\delta^{15}\text{N}$ -3 and $\delta^{13}\text{C}$ -3.4 (dashed box).

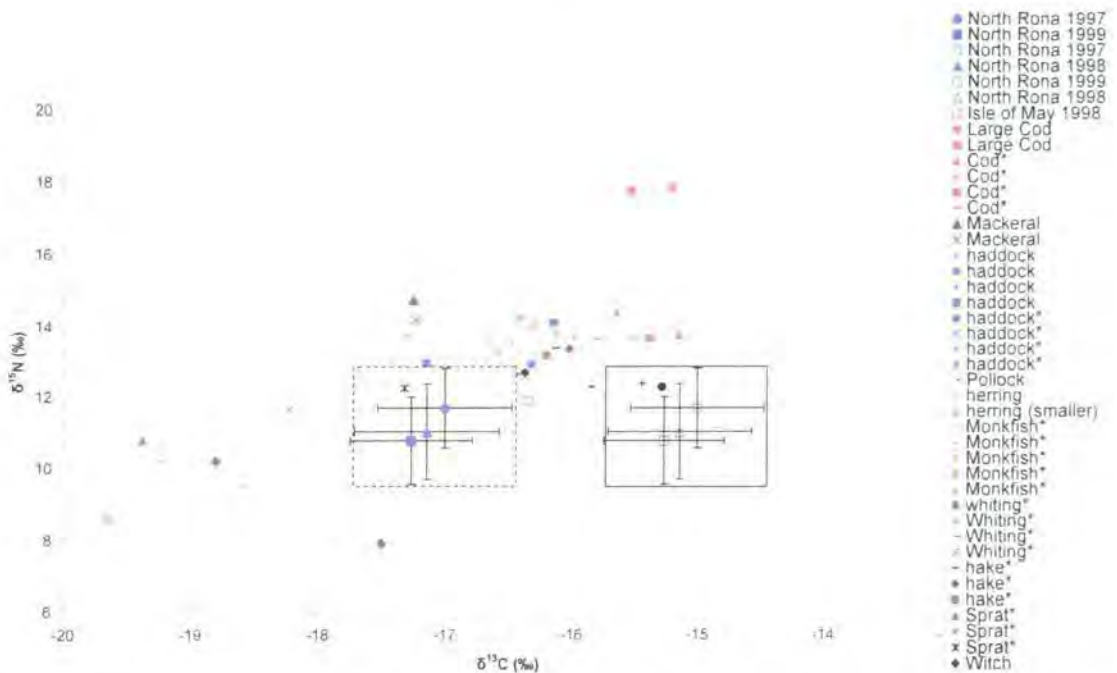


Figure 4.35: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of fish collected from Mallaig and Hartlepool with values of seals from North Rona plotted as $\delta^{15}\text{N}$ -3 and as $\delta^{13}\text{C}$ -1 (solid box) and $\delta^{15}\text{N}$ -3 and $\delta^{13}\text{C}$ -3.4 (dashed box).

The fish data range from -23.0‰ to -13.5‰ for $\delta^{13}\text{C}$ and from 6.6‰ to 18.0‰ for $\delta^{15}\text{N}$. The largest cluster of fish species is found between -17.5‰ and -14.2‰ for $\delta^{13}\text{C}$ and 12.1‰ and 14.8‰ for $\delta^{15}\text{N}$. Herring had the lowest carbon and nitrogen range from -17.5‰ to -14.22‰ for $\delta^{13}\text{C}$ and from 12.1‰ to 14.8‰ for $\delta^{15}\text{N}$ (published values for herring are -22.1‰ for $\delta^{13}\text{C}$ and 11.2‰ for $\delta^{15}\text{N}$ (Fry, 1998)). The published data for sandeels, -18.80 to -17.50‰ for $\delta^{13}\text{C}$ and 7.9 to 10.2‰ for $\delta^{15}\text{N}$ (Fry 1998), fell within the range shown for herring.

The boxes outlining the range of variation for each population of seals (Figure 4.33) show that the seals from the Isle of May and some of the fish samples overlap, indicating that they are feeding at a similar trophic level. The North Rona values do not overlap with any of the fish sampled. The values for the large cod sampled fall at the edges of the box for the Isle of May, and above that for North Rona, indicating that the cod of the size sampled in this study fed at a trophic level higher than the seals.

Isle of May seals with values adjusted by $\delta^{15}\text{N}-3$ and $\delta^{13}\text{C}-1$ showed some overlap with most of the species of fish sampled (Figure 4.34 (solid box)). However, most of the data points for the herring, sprat (*Sprattus novaehollandiae*) and pollock sampled do not fall within the range of the seals. None of the data from the two large cod sampled or from the sandeel values taken from published data (Fry, 1998) fall within the range of the Isle of May seals' isotopic values. The least overlap with the fish species is seen from the 1997 and 1998 Isle of May data, which show lower $\delta^{13}\text{C}$ values. Most of the overlap with the fish species occurs with the higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values shown by the 1999 data. The values adjusted by $\delta^{15}\text{N}-3$ and $\delta^{13}\text{C}-3.4$ (dashed box) also show overlap with haddock, plaice, mackerel and monkfish. The values of the seals have moved away from those of the smaller cod and many of the other species. Overlap is seen between the seals and values for the herring, sprat and sandeels that was not seen for $\delta^{15}\text{N}-3$ and $\delta^{13}\text{C}-1$.

The data from the North Rona population, overlaying the fish in Figure 4.35 show that these seals overlap fewer fish species than those from the Isle of May population for $\delta^{15}\text{N}-3$ and $\delta^{13}\text{C}-1$. Only witch falls within the marked range. The values for the small cod (30-40mm) are seen to be higher than the values for the seals. Most of the fish sampled show lower $\delta^{13}\text{C}$ values than the seals from North Rona; $\delta^{15}\text{N}$ values show a range both higher and lower than that of the seals. The greatest overlap with the fish occurs with the seals showing the lowest values for $\delta^{13}\text{C}$, which tend to be the 1997 samples. When the seal values are shifted by $\delta^{15}\text{N} -3$ and $\delta^{13}\text{C} -3.4$

4.3. Discussion.

The results will be discussed in terms of differences along the vibrissa length, in relation to the possibility of seasonal differences or differences in feeding behaviours seen within the populations. Differences in isotopic values seen between the years will be discussed in terms of the possibilities of a shift in feeding behaviour or prey selection over the years of the studies; this will be linked to the isotopic differences seen between the two populations for each year of the study. The comparison of the isotopic values for the seals will be compared to the values from the fish sampled during the study and from values for fish drawn from published data, in order to discuss the likely composition of the seal diet as inferred by stable isotopic analysis and to consider the accuracy of other methods of dietary analysis. It is impossible to discuss these points separately since differences seen in the isotopic variations in each section of the results are linked together.

From Chapter Three the vibrissa growth rate is taken to be 0.41mm/day. The vibrissa lengths for grey seals tended to fall within the range of 70 to 135mm. Given this, the vibrissae collected in this study represent 270 to 355 days of growth: i.e. up to a year of

growth, assuming a constant growth rate throughout the year. Thus any changes over the length of the vibrissa plots shown in this chapter are representative of the dietary changes for a grey seal over approximately one year.

Section 2 of this chapter displays the results of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of five to 45 points along a vibrissa taken from each animal sampled. Three trends were seen in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that can be identified from the vibrissa profiles and data. It should be noted that the trends identified could be further broken down. For example, those vibrissae which show a large isotopic decrease and then increase in the middle of the vibrissa but similar isotopic values at the ends of the vibrissa could be divided from those vibrissae that show little variation along the entire vibrissa length. This was avoided to simplify this section. The first of the trends is that of an increase in enrichment of $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ along the vibrissa length. It is seen in both populations in all years, except for $\delta^{13}\text{C}$ in North Rona, 1997 and also for $\delta^{13}\text{C}$ in Isle of May 1999. The second trend that of a decrease in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ along the length of the vibrissa, is seen in the Isle of May for all years of the study for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. For North Rona it is seen in all years of the study for both isotopes, except for $\delta^{13}\text{C}$ in 1999. The third trend observed is seen in both populations in all three years of the study and includes all those vibrissae that do not show an increase or decrease in their isotopic variation greater than 0.7‰ between the base and tip ends.

The trends in isotopic variation along the lengths of the vibrissae may be due to dietary changes of prey species or prey size. These changes may be due to seasonal changes in prey availability which may affect the dietary choices of the seals.

The most common trend in the vibrissae from North Rona is to show little or no differences between the base and tip for either isotope. This is also the most common trend in $\delta^{13}\text{C}$ for the Isle of May vibrissae; however, for $\delta^{15}\text{N}$ an increase in enrichment along the vibrissa length is the trend seen in most of the vibrissa plots.

The increase in $\delta^{15}\text{N}$ enrichment along vibrissa length, would indicate that the most recent diet that the seal had been eating was of a lower trophic level, and thus possibly prey size, than the diet eaten earlier in the year. In some of the vibrissae showing this trend the base end of the vibrissae shows a small decrease over the first few points of the plot before the typical increase is seen. In some, a small decrease is then seen at the tip end over the last few points. Given that the vibrissa grows for approximately one year this may indicate that the seals showing this pattern have a yearly foraging cycle of prey items that gives increases and decreases in isotopic variation over the year.

Depletion in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ along the vibrissa length would indicate the opposite of the above: that the seal has most recently been feeding on prey of with a higher isotopic signature but fed on prey with lower values earlier in the year.

Many of the plots for the $\delta^{15}\text{N}$ variation show changes over the length of the vibrissa of 3‰ or greater. This indicates that the seals are showing a dietary change of one trophic level over the length of the vibrissa and thus a one trophic level change over a year (DeNiro & Epstein, 1980). This enrichment of $\delta^{15}\text{N}$ in vibrissa keratin by about 3‰ over diet is well documented (DeNiro & Epstein, 1980; Kelly, 2000), and enrichment or depletion of this isotope along vibrissa length is likely to be due to changes in the trophic level of the prey taken by the seals over a year.

$\delta^{13}\text{C}$ is an indicator of the primary producers in a diet, and as such can give an indication of prey changes in an animal's diet (DeNiro & Epstein, 1978; Kelly, 2000). However, it is also linked to trophic level. The enrichment of $\delta^{13}\text{C}$ in vibrissa keratin over diet is less well-documented than for $\delta^{15}\text{N}$, and it has been found to vary between 1-3.4‰ over the diet (Hobson *et al.*, 1996; O'Connell *et al.* 2001). Thus a change in $\delta^{13}\text{C}$ in the vibrissae may also be linked to trophic level. If this were the case in the samples from this study, a similar, corresponding change in the $\delta^{15}\text{N}$ isotopes should be seen, and this is not always the case. In some vibrissae an increase in $\delta^{15}\text{N}$ is seen coupled with a decrease in

$\delta^{13}\text{C}$, and vice versa. In some of the vibrissae there a change of 1 to 3‰ in the $\delta^{13}\text{C}$ plot, but a threefold increase in the corresponding $\delta^{15}\text{N}$ plot was not seen, indicating that the change in $\delta^{13}\text{C}$ may not be purely due to trophic level changes but is potentially due to a shift in the source of the primary protein producer(s) of the prey items selected by the seals. It may thus indicate a change in the species of prey selected by the seal and not in the trophic level of the prey.

Since these differences are not consistent and different isotopic trends have been identified in the data, it is possible that groups of grey seals show different foraging specialisations within a population. Differing strategies could include differences in prey choice or differences in foraging locations, and it is likely that the seals from the two populations would show different trends.

However, if foraging specialisation is seen in the grey seals from Isle of May and North Rona, it might be expected that the same seal would exhibit the same strategy every year. This is not the case. The seals appear to be opportunistic feeders. From the data collected from seals sampled in more than one year of the study it would appear that the seals are not necessarily consistent to one foraging trend. While some of the seals showed the same trend in two consecutive years, none of the six seals sampled in all three years showed the same trend in all the years. This data indicates that the seals may switch foraging trends, potentially as prey abundance varies, and there appears to be little evidence in this data for foraging specialization.

Other studies on the foraging behaviour of grey seals have had insufficient data to draw any conclusions about a population's foraging strategies. Studies using satellite tracking of small numbers of grey seals from the Farne Islands (McConnell *et al.*, 1999) have shown that grey seals do not all follow the same foraging patterns, but insufficient numbers of seals were used to examine if any seal follows the same pattern.

Satellite tracking data have shown that grey seals from the Farne Islands travel large distances, to areas used by seals from other populations, including one seal that travelled from the Farnes to the Irish Sea (McConnell *et al.* 1999). It is likely that the seals in each of the study populations do not show one single foraging pattern which is common to that population, and that the individual seals exhibit a range of behaviour, and possibly foraging areas, which are likely to be linked to prey availability.

The statistical analysis shows that some significant differences are seen along some of the vibrissa lengths for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, indicating that dietary changes occur during the vibrissa growth. Since the vibrissa's growth is likely to be for a year, the difference seen could be due to seasonal variations in the diet, possibly prompted by the availability of prey items. Seasonal variations in diet of grey seals have been found in scats sampled from the Orkneys and the Inner and Outer Hebrides where scats were sampled over several seasons of a year and were attributed to availability of the fish species (Hammond *et al.*, 1994 a and b), and it is likely that this is the cause of the variations seen along the vibrissa profiles in this study.

The statistical analysis of the data comparing the three years of the study showed that there are significant differences between all years for $\delta^{13}\text{C}$ for the Isle of May and for all years for $\delta^{15}\text{N}$ with the exception of 1997. This indicates that over the three years of the study the grey seals from the Isle of May have shown a significant diet shift, which is, shown in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figures 4.26 and 4.27). Although the changes seen in the isotopes are not large, there is a trend throughout the three years of the study for $\delta^{15}\text{N}$ to decrease and for $\delta^{13}\text{C}$ to increase. The changes seen in this study are small for both isotopes, being on average not greater than 1‰. The North Rona data do show significant changes between all years (except for 1998: 1999 $\delta^{13}\text{C}$) but the amount of isotopic variation between each year is smaller than for the Isle of May data. Over the three years of the

study, the North Rona population's diet would appear to be more stable than that of the Isle of May population.

The change in $\delta^{13}\text{C}$ seen over the three year period could indicate that the seals are feeding on fish in 1999 that, since size is inferred by trophic level, are still of a similar size to those that made up the diet in 1997 which, due to the shift in $\delta^{13}\text{C}$, could be of different species. Although differences between Isle of May and North Rona are seen in all years, it can be seen from Figure 4.32 that the mean isotopic variation data points from the Isle of May populations become closer to those of North Rona from 1997 to 1999, with little overlap seen in 1997 and a much larger amount seen in 1999.

It was only possible to sample male grey seals during one year of the study and from one population, the Isle of May. Given the significant differences seen between the comparisons of the different years, the data from these males were compared to females collected in the same year (1999) and from the same population. Sex differences in foraging behaviour have been identified in both northern and southern elephant seals, and in some species of sea lions (Le Boeuf *et al.*, 1993; Campagna *et al.*, 1995; McConnell & Fedak, 1996; Campagna *et al.*, 1998; 1999). These differences are attributed for the greater energy requirements of the larger male animals, and males of these species are thought to prey on different, and possibly larger, species of prey than the smaller females (Le Boeuf *et al.*, 1993; McConnell & Fedak, 1996).

The male grey seal is up to 100kg heavier on average than the females (King, 1983). It might therefore be expected that it would forage on larger prey species, and this would cause a difference in $\delta^{15}\text{N}$ (Le Boeuf *et al.*, 1993). This is not the case: no significant difference was found in $\delta^{15}\text{N}$, and graphically (Figure 4.28) the $\delta^{15}\text{N}$ values for the male and female seals are very similar. The $\delta^{13}\text{C}$ comparison showed a significant difference. Although the males seem to be close to the $\delta^{13}\text{C}$ values of many of the female seals, the females show a greater spread of $\delta^{13}\text{C}$ than the males, and some of the females showed

values that tend to be lower than the $\delta^{13}\text{C}$ values of the males. The sample number of the males was also smaller than that of the females. The difference in $\delta^{13}\text{C}$ is not linked to a corresponding difference in $\delta^{15}\text{N}$, which might indicate a difference in trophic level and is likely to be due to a difference in the primary producer(s) in the food chain - that is the two sexes are likely to be feeding on different species of prey. This could be due to different prey preferences or to different foraging strategies or areas. Further conclusions cannot be at present drawn due to the lack of data from other years or populations. It is also unknown if the male grey seals would exhibit the same changes over time that have been seen in the female seals also from the Isle of May.

Since the vibrissae show up to a year's isotopic variation along their length, it cannot be assumed that the significant differences seen from year to year are part of the seal's normal feeding variations, relating to prey abundance throughout the year. It is likely that there is an external force, such as commercial or industrial fishing or environmental factors acting to change the abundance of traditional fish prey available.

The changes seen in the data over the three years could be due to natural dietary variations of the seals that cycle on a time scale greater than that taken in by this study. A study of greater length might possibly highlight any longer term changes. The sandeel stock in the North Sea is historically known to show dramatic fluctuations in biomass (Furness, 1990; Pomeroy *et al.*, 2001). Since the sandeel species are believed to be an important prey item for the grey seal (Hammond *et al.*, 1994, a and b; Pomeroy *et al.*, 2001) it is possible that this change may affect the seals' dietary choices.

In the light of the current problems in the North Sea fishing industry (Hutchings, 1996; Mohan & Bowen, 1996; Fu *et al.* 2001; ICES current website, January 2003), it is interesting to examine the data from the two populations of seals along with trends in stock biomass of commercial fish over the years of the study, since this is the main foraging area

for the seals from Isle of May, the population which has shown the largest changes over time in this study.

In the North Sea there are two types of fishery: those that target fish for human consumption - largely fishing for demersal species such as cod, haddock, whiting, plaice and sole, while pelagic fisheries catch herring, mackerel and horse mackerel. These fish may also be used for industrial purposes. The second fishery is the industrial fishery. This fleet largely targets sandeel, Norway pout (*Trisopterus esmarkii*) and sprat, but will also use by-catch of other species (ICES report, 2002). Both the fisheries impinge upon the likely fish prey of the grey seals foraging from North Rona. For example, grey seals are known to forage for sandeels on the 'Wee Bankie' area of the North Sea (Pomeroy *et al.*, 2001), where there is also a large catch of sandeels for the North Sea fishery. Other species, such as herring, and cod, are also likely species of grey seal prey, both from data in this study and from scat analysis (Hammond *et al.*, 1994 a and b), and are also fished in similar areas to where the greys seals from the Isle of May forage.

In the North Sea all fish stocks are highly exploited. Stock assessments indicate that the stocks of whiting and saithe (*Pollachius virens*) have been fished less in the last three years, and saithe is considered to have returned to safe limits; but while the whiting stock does appear to be showing an increase in size, it is believed that this stock is outside biological safe limits (ICES, 2002c). The haddock, plaice and sole stocks are all over-exploited by commercial fishing, and there are concerns over the sustainability of the stocks as they are also outside biological safe limits. The stocks of sandeel and Norway pout, both fished by the industrial fleets, show large variations in stock biomass as part of their life history, but are believed to be sustainable (ICES, 2002 b, Impress, 2001).

The herring, mackerel and cod stocks are a different story. In the mid 1970s the North Sea herring stock collapsed (autumn spawning herring) and as a result the fisheries were closed between 1977 and 1981. The stock recovered, but declined again in the mid 1990s.

In 1996 measures to reduce the fishing of this species were introduced, leading to a decrease in the fishing mortality. This, coupled with a high recruitment and a high spawning stock biomass, has led to the partial recovery of the stock (ICES 2001/2 b). The North Sea mackerel stock, part of the North-East Atlantic stock, also collapsed in the 1970s, but unlike the herring has not yet showed signs of a recovery, and commercial catches of this species in the North Sea are thought to be due to fish migrating from the western stock areas of the Atlantic.

The North Sea cod stock spawning biomass (Figure 4.36) is also outside safe biological limits. Recruitment to the stock has been lower than average since 1985, and fishing mortality remains high.

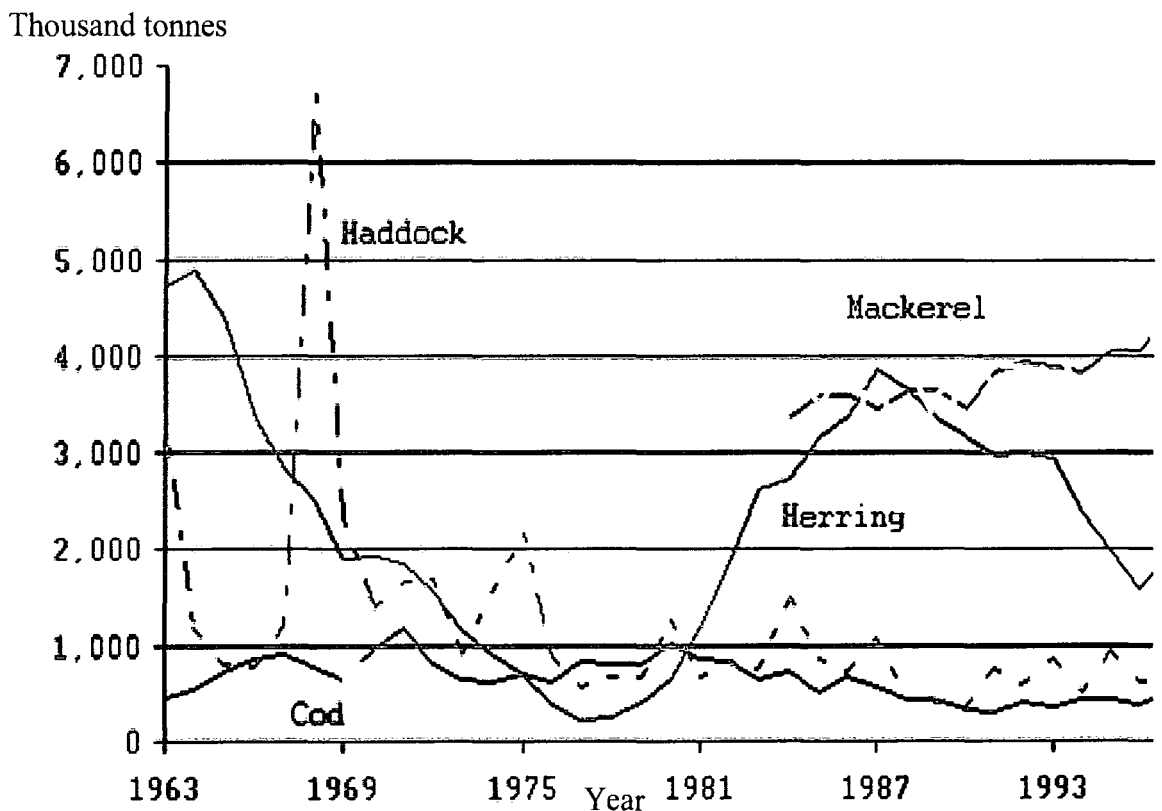


Figure 4.36: Spawning stock biomass of North Sea fish species (Centre for Environment, Fisheries and Aquaculture Science; International Council for the Exploration of the Sea)

While the quantities of commercial fish taken by grey seals is not known, and only estimates can be given, it is likely that the seals do take a proportion of commercial fish, including those species that are in decline. Given the decline seen in previous years in many of the species, and that the decline was seen in the years preceding the study, it is likely that the activities of the human fishing industries have had an impact on the diet and prey choice of the grey seal.

Since seals from the Isle of May are known to forage in the North Sea (Thompson *et al.*, 1991; McConnell *et al.*, 1999), and given that over the three years of this study a significant change has been seen in the isotopic composition of the vibrissae, (and thus the diets of the seals), it is likely that this change can be attributed, at least in part to the changes in the fish stocks in the North Sea. A study used sandeel CPUE (catch per unit effort) to look at a possible link between food supply and grey seal pup production on the Isle of May (Pomeroy *et al.*, 2001). Weak statistical correlations were found between pup production and the availability of sandeels, although the wide prey preferences of the seals were thought to be able to overcome any fluctuations in sandeel availability. The results from the study indicate that grey seals are likely (and, moreover, able) to switch prey species if availability changes, and that these changes are likely to show as isotopic changes in their vibrissae and are likely to be linked to changes in the availability due to over-fishing of species that are also of commercial interest ((Pomeroy *et al.*, 2001)).

Significant changes in the diets of the seals from North Rona were also found in this thesis. However, there are fewer concerns raised about the fish stocks in the areas where these seals are likely to forage. For example the herring stocks of the North-East Atlantic are considered stable, as are the mackerel stocks, and the Shetland sandeel fisheries are believed to be fishing at levels below those of natural mortalities (ICES 2002, b and c). Changes in the North-East Atlantic fisheries appear to be lagging behind those seen in the North Sea, since they do not support as much commercial fishing as the North Sea.

Differences in the North Rona isotopic values could be due to the smaller changes seen in this stock - for example concerns have been raised (Furness, 1990) over the effect of the sandeel fishery on the diets of both seabirds and seals. In addition to this, the seal populations of Britain are not isolated from each other. Studies have shown movement from Isle of May to the North of Scotland (McConnell *et al.*, 1999), making it likely that there is also movement in the other direction. Thus seals from the North Rona population that forage in similar areas to those from the Isle of May population may also have made dietary shifts on a smaller scale than those from the Isle of May.

Throughout the years of the study, differences have been seen between the two populations. Differences in the diet of two populations of seals that forage in different areas are not unexpected, and could be due to differences in prey choice and foraging behaviour. If the differences seen were consistent throughout the three years of this study, then this would be the conclusion drawn from the data. However, over the three year period the difference in isotopic variation is not consistent, making this explanation unlikely to be the sole cause of the differences seen between the two populations. It is likely that other factors are causing the differences seen.

Looking at the figures comparing the Isle of May to North Rona, it can be seen that the values for the Isle of May from 1997 to 1999 shift over the study period to values closer to those of North Rona. This could indicate either that the seals from Isle of May are travelling further distances from their traditional foraging grounds and are sharing a greater overlap between foraging areas with the animals from the more northerly North Rona population, or that while the seals from the Isle of May are still foraging in their traditional areas, their prey items may have changed to prey that are isotopically more similar to those taken by North Rona animals. Obviously, without further studies to examine the foraging patterns of these animals no definite conclusions can be drawn, but it would appear likely that in the course of the study a dietary shift that is very possibly linked to prey availability

in prey species is seen, which is in turn affected by fishing pressures exerted on the stocks by the human fishing industry.

From the isotopic data collected from the fish species in this study and compared to the seal isotopic variations it can not be concluded that one species of fish appears to be more prevalent in the diet of the grey seal. From the plots showing the fish data it can be seen that many of the fish species show little isotopic variation from each other, although the samples from the large cod and data from herring, sprat and sandeel samples do show a greater spread away from the central cluster made up of the majority of the fish.

While the $\delta^{15}\text{N}$ values of the fish and the seals seem to show that the seals could be eating many of the fish analysed, the $\delta^{13}\text{C}$ is open to wider debate, since the enrichment of keratin over diet is not well quantified. Taking the enrichment as $\delta^{13}\text{C} + 1$, the seal's diet appears to include many of the white fish (cod, mackerel, hake, and haddock) and flatfish (plaice and witch). If $\delta^{13}\text{C} + 3$ is used, then the diet of the seals appears to be more similar to the values for herring, sprat and sandeel. Since dietary studies using scat analysis (Hammond *et al.*, 1994 a and b) show that the diet of seals from the Orkneys and Hebrides include a large amount of sandeels, the enrichment $\delta^{13}\text{C} + 3$ over diet would appear to give a representation of diet that is closer to that predicted by other studies. Although there are known biases associated with scat analysis (see Chapter 1), since the data from studies using these methods are supported by data from satellite and radio telemetry studies showing that grey seals forage in the North Sea and make dives to the seabed in areas where the habitat is suitable for sandeels, it is likely that these studies are able to give a fair indication of the grey seal's diet and that the enrichment of vibrissa keratin over diet is closer to $\delta^{13}\text{C} + 3$ than $\delta^{13}\text{C} + 1$. This is further supported by the findings of Hobson *et al.* (1996) where $\delta^{13}\text{C}$ in vibrissa keratin was found to be 3.4‰ over diet.

No definite prey preference can be identified from the data collected, since none of the fish show an isotopic signature that is sufficiently distinct to be linked to those of the seals.

While it is likely that the seals take prey similar to that suggested by scat analysis (Hammond *et al.*, 1994, a and b), and the isotopic variations support this, there is a problem with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of this nature in that the isotopes reflect the average prey taken by the seals. In the most extreme case the seals could be eating both large cod and small herring, which combined would give isotopic values similar to those shown by the seals in this study. This is an extreme case, and it is more likely, when other data are considered that the seals' diet is composed largely of herring and sandeels with varying amounts of species like cod, haddock and plaice depending on the availability over the seasons.

4.4. Summary.

To summarise this chapter briefly:

1. Some significant differences in isotopic variation were found along the lengths of the vibrissae from both populations and for most years. The differences indicate changes in diet during the year, possibly linked to prey availability.
2. Significant differences were seen between the years for each population, indicating possible long term variability due to prey availability. Alternatively, differences could be related to changes in the fish stocks and the effect on said fish stocks by the commercial/industrial fishing fleets.
3. Significant differences were found between the two populations, possibly due either to differences in the prey preferences of the two populations, or to the changes in the fish

-
- stocks putting a greater pressure on the seals from the Isle of May and causing them to switch to a diet that is more similar to that of the animals from North Rona.
4. Few conclusions can be drawn about the fish prey eaten by the seals, as the method leaves a great degree of uncertainty since values are dietary averages only. However, the results do seem to support the data from studies using other methods.
 5. Overall, stable isotope analysis is a useful tool for the study of grey seal diet, particularly on a population level, and can be used to monitor dietary changes over time. With more data on the isotopic values of fish it may be possible to obtain further resolution and to use this method to study seasonal changes in diet. The method is useful when used in combination with other methods of dietary study.

Chapter 5: Southern Elephant Seal Data

CHAPTER 5

Southern elephant seal data

5.1: Introduction

This chapter examines the data collected from one male and 12 female southern elephant seals sampled in 1998, from ten males and six females in 1999 from Pensínsular Valdés, Argentina, and from one sub-adult male from the Falkland Islands. Five South American sea lions, four females and one male were also sampled in 1999, and are included in this chapter for comparison with the southern elephant seal data.

The Pensínsular Valdés population is the only group of southern elephant seals that do not feed in sub-Antarctic or Antarctic waters and whose pup production has shown an increase in the last 20 years (Campagna & Lewis, 1992). Animals from the South Georgia population forage in areas that lie closer to that of the animals from Pensínsular Valdés than those of the other breeding populations of southern elephant seals. A female from the South Georgia population reported in McConnell & Fedak, (1996) reached an area 1,500km to the east of a female seal from Pensínsular Valdés that was reported in Campagna *et al.* (1998).

Satellite tracking studies on both male and female southern elephant seals from Pensínsular Valdés have shown that the male and female seals display different foraging behaviour (Campagna *et al.*, 1995 and 1998).

Female southern elephant seals leaving the beaches on foraging trips cross the continental shelf in less than a week and forage in open water in the South-Western Atlantic, around 36°–50°S, and at distances of up to 1,200km from the shore (Campagna *et al.*, 1999). Females travel further distances in the post-moult period, with distances of 2,300km being recorded by satellite tracking. The longest migration recorded from Pensínsular Valdés was that of a post-moult female which travelled 11,600km

(Campagna *et al.*, 1998). The females appear to be mid-water feeders, making infrequent dives to the seabed, with most of the dives (recorded by depth/time recorders) to depths greater than 200m and in the first 1000m of the water column (Campagna *et al.*, 1995). They show similar dive patterns to female southern elephant seals from the other populations, but they do not appear to forage as far as the Antarctic polar front (Hindell *et al.*, 1991, Campagna *et al.*, 1995, 1998). The range of the female seals does overlap with that of the males in the areas closer to the continental shelf (Campagna *et al.*, 1998).

The larger males require at least three times more energy than the smaller females and are, therefore, likely to forage in areas with higher prey abundance (Boyd *et al.*, 1994, Le Boeuf *et al.*, 1993) or to use different foraging strategies, or to take larger prey items. Satellite tracking data (Campagna *et al.*, 1999) showed that five males swam in 3-11 days to the edge of the continental shelf where they stayed, another two males in the study remaining over the shelf. All of the males made frequent dives. Those that were over the shelf tended to dive to the sea bed, whilst the males foraging on the shelf edge made most dives to mid-water, with a few to the sea bed. Deeper dives were made during daylight hours. This suggests that the male seals prey on benthic species and on those that are found in the water column during daylight (Campagna *et al.*, 1999).

Sex differences have been found in the foraging behaviour of southern elephant seals from other populations, for example South Georgia (McConnell & Fedak, 1996), and have been observed in the foraging and diving behaviour of the northern elephant seal (Le Bouf *et al.*, 1993). In addition to this, some sex differences in $\delta^{13}\text{C}$ isotopic data have been shown in the northern elephant seal (Burton & Koch, 1999). Female northern elephant seals foraging offshore showed a mean $\delta^{13}\text{C}$ value 1‰ higher than that of the male seals foraging in inshore areas. The study found no differences in the $\delta^{15}\text{N}$ values between males and females of the species.

Studies on the prey choices of the southern elephant seal from other populations, using scat and stomach content analysis (Green & Burton, 1993; Slip, 1995; Rodhouse, 1997) have not shown any significant differences in prey choice between males and females. However, the data in these studies have only been collected during the seals' haulout periods and so may be biased away from the longer sea-based periods of their life cycle.

The South American sea lion (*Otaria flavescens*) is one of the most common marine mammals in the South-Western Atlantic and is found along the coasts of South America from Peru to South-Eastern Brazil and in both the Pacific and Atlantic Oceans (Alonso *et al.*, 2000). This species also shares similar breeding areas of the southern elephant seals, and is also likely to forage in similar areas.

A study was conducted on the South American sea lion using stomach content analysis of animals either found dead on beaches or accidentally drowned in fishing nets in central and northern Patagonia (Alonso *et al.*, 2000). The study found 37 prey species in the stomachs, mainly fish and cephalopods. The most important species were Argentine hake, red octopus (*Octopus (Octopus) rubescens*), Argentine shortfin squid Patagonian squid (*Loligo gahi*) and Argentine anchovy (*Engraulis anchoita*). Some of these species are also of commercial interest.

There were differences between the diet of the male and female animals, with the females feeding mostly on benthic species and the males on demersal-pelagic species, but no geographical differences were found (Alonso *et al.*, 2000). The sex differences seen may be due to differences in feeding behaviour that may be related to different energetic requirements - the South American sea lion also shows sexual dimorphism and the males appear to move further offshore than the females. This species does not fast during the breeding season so the females must return regularly to feed their pups, but this does not constrain the males (Alonso *et al.*, 2000).

Twenty female and two male South American sea lions from Patagonia were tagged and tracked by satellite (Campagna *et al.*, 2001). The study showed that both sexes

remained in the temperate waters over the Patagonian coastal shelf. The male sea lions travelled further than the females and come close to the continental shelf edge. The female's foraging trips lasted an average of 3.4 days, with an average distance of 117 km. Sixty-five percent of the dives recorded were of 2-30m deep. The males' foraging trips lasted an average of 5.7 days, with an average distance of 591km. It was found that the foraging areas of the sea lions overlap with the fishing areas of commercial fisheries.

The data collected in this study are intended to examine the possibility of seasonal changes over a period of about one year (assuming for the purpose of this study that southern elephant seal whiskers grow at a similar rate to those of the grey seals in Chapter 3) and will thus include periods that the male and female seals spend in different foraging areas and may highlight differences in prey species selected by the two sexes, both in seasonal variation and in the overall isotopic variations. Along with this data, samples from South American sea lions, from a population geographically close to the southern elephant seals, were collected. The results from the analysis of these will be compared to the elephant seal results in order to examine whether there is any evidence for competition for prey existing between the two species, and whether this could be a likely reason for the sex differences seen in the elephant seal foraging patterns.

The final section in this chapter will examine the isotopic values from different species of fish collected and analysed for this study, together with the data from relevant species taken from published data, which may potentially be prey items for the southern elephant seals. These results will be compared to the isotopic values from the seals in order to attempt to identify any likely prey species in the diet of the southern elephant seal.

Hypotheses

1. That the vibrissae from male and female southern elephant seals will have different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from each other due to differences in foraging strategies.
2. That the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the male southern elephant seal will be similar to those of the South American sea lions since they share similar foraging areas, but that the female southern elephant seal will be distinct from the sea lions, since their foraging grounds only overlap by a small extent.
3. That differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ will be seen between the two ends of the vibrissae analysed that may relate to seasonal variation in diet.
4. That the comparison of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the vibrissae from southern elephant seal with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from fish sampled within the seals known foraging areas will help to elucidate the prey species of the southern elephant seal.

5.2 Results

5.2. a. Sex differences in southern elephant seals

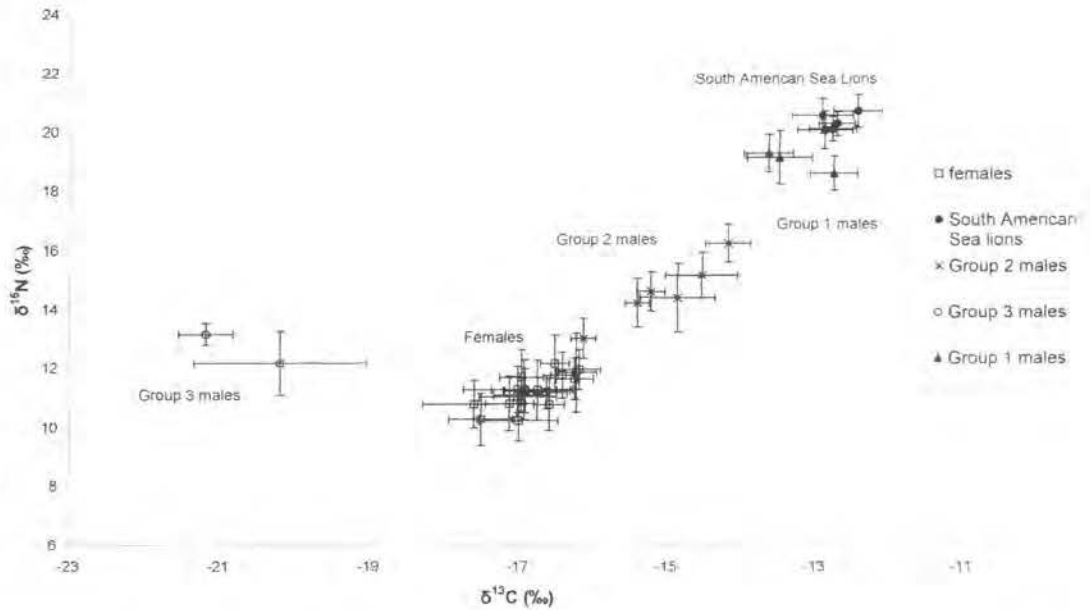


Figure 5.1 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation with standard deviation bars for male and female southern elephant seals and South American sea lions. The groups that have been visually assigned to the male and female southern elephant seals and South American sea lions are shown on the figure.

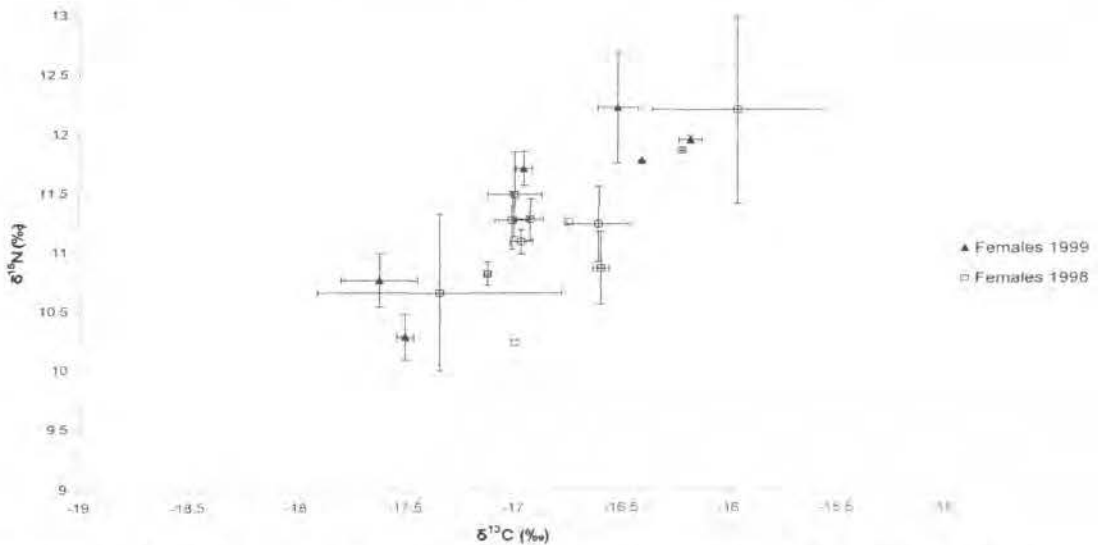


Figure 5.2: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation with standard deviation bars for the female southern elephant seals.

The isotopic variations of the animals sampled are spread over a large range: from -12.43 to -21.19‰ of $\delta^{13}\text{C}$ and from 20.75 to 10.01‰ of $\delta^{15}\text{N}$. The results fall into distinct groups, which have been identified as follows: males on Figure 5.1 are divided into three distinct groups, designated on Figure 5.1; groups one, two and three. The isotopic ratios and standard deviation bars shown by these groups do not intersect with each other. Two of these groups, one and three, contain few individuals. The female southern elephant seals and South American sea lions are assigned groups separate from those of the males, despite overlapping values with them.

Figure 5.2, a close-up part of Figure 5.1, shows that there appears to be little difference in the isotopic values among female seals collected in 1998 and those collected in 1999.

The relationships shown in Figures 5.1 and 5.2 were statistically tested and the results shown in Table 5.3.

Table 5.1: The animals assigned to each group shown in Figure 5.1.

Group 1	Group 2	Group 3	Females			South American sea lion
			1998		1999	
SA2	SA34a	SA3	M17	V	AdL	OF
SA23	SA34b	SA4A	M16	OI	AdT	OA (male)
SA4	SA4T		T	F	AdF	OB
	OSA4		S	N	Ad2	OC
	SA		SX	FO	AdM	OFa
	SAY		Q	FI	AdP	

Table 5.2: Mean values with standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each group of male and female southern elephant seals and South American sea lions.

Group	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		Mean	Standard deviation	Mean	Standard deviation
1	3	-13.20	± 0.52	19.04	± 0.91
2	6	-14.74	± 0.73	15.14	± 1.35
3	2	-20.57	± 1.04	12.55	± 1.00
Females	18	-16.92	± 0.64	11.19	± 0.97
Sea Lions	5	-12.77	± 0.36	20.29	± 0.59

Group 1 contained three males of ages 'sub-adult 2' to 'sub adult-adult 4' (sampled in 1999). Two whisker samples were analysed for each seal in this group with $\delta^{13}\text{C}$ ranges from -13.69‰ to -12.7‰ and $\delta^{15}\text{N}$ ranging from 18.5‰ to 19.68‰. Group 1 shared some overlap with the South American sea lions sampled.

Isotopic values for the South American sea lions range from -13.78‰ to -11.81‰ for $\delta^{13}\text{C}$ and 18.9‰ to 22.29‰ for $\delta^{15}\text{N}$. The South American sea lions show the highest values for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Group 2 contains six males. Five were sampled in 1999 and one in 1998 (SA). They have $\delta^{13}\text{C}$ values from -16.13‰ to -14.04‰ and $\delta^{15}\text{N}$ values from 12.84‰ to 16.3‰. This group shares some overlap with the group of females in both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the animals showing the lower isotopic values in this group.

Group 3 contains two males, one of which is sub-adult three and one sub-adult four to adult. These show $\delta^{13}\text{C}$ values between -21.19‰ and -19.23‰ and $\delta^{15}\text{N}$ values of 12.01‰ to 13.19‰. This group show the lowest values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for any of the groups shown in Figure 5.1.

The females (six from 1999 and 12 from 1998) from one group on Figure 5.1 and are also shown in Figure 5.2. $\delta^{13}\text{C}$ values were between -17.99‰ and -15.68‰ and $\delta^{15}\text{N}$ values between 10.01‰ and 12.77‰. From Figure 5.2 there seems to be little difference between the isotopic values for the females collected in 1998 and 1999.

Statistical analysis to examine the apparent differences between the groups was conducted using Mann-Whitney U-tests. This analysis was conducted for all possible comparisons between the groups and the results are presented in Table 5.3 below.

Table 5.3: Results from the statistical comparisons (Mann-Whitney U-test) of isotopic data between each group. Since the data were used for more than one comparison, $\alpha = 0.00125$ after Bonferroni corrections.

Comparison	Isotope	N ₁ ,N ₂	U	P
Males 1 : Males 2	$\delta^{13}\text{C}$	23,140	470.5	<0.001
	$\delta^{15}\text{N}$	23,140	125.5	<0.001
Males 1 : Males 3	$\delta^{13}\text{C}$	23,37	0.000	<0.001
	$\delta^{15}\text{N}$	23,37	0.000	<0.001
Males 1 : Females	$\delta^{13}\text{C}$	23,294	0.000	<0.001
	$\delta^{15}\text{N}$	23,294	0.000	<0.001
Males 1 : South American sea lions	$\delta^{13}\text{C}$	23,294	0.000	<0.001
	$\delta^{15}\text{N}$	23,294	0.000	<0.001
Males 2 : Males 3	$\delta^{13}\text{C}$	140,37	0.000	<0.001
	$\delta^{15}\text{N}$	140,37	309.5	<0.001
Males 2 : Females	$\delta^{13}\text{C}$	280, 294	1136.0	<0.0001
	$\delta^{15}\text{N}$	280, 294	997.0	<0.001
Males 2 : South American sea lion	$\delta^{13}\text{C}$	280, 68	1084.0	<0.001
	$\delta^{15}\text{N}$	280, 68	26.0	<0.001
Males 3 : Females	$\delta^{13}\text{C}$	74, 294	38.000	<0.001
	$\delta^{15}\text{N}$	74, 294	4835.0	<0.001
Males 3 : South American sea lion	$\delta^{13}\text{C}$	74, 68	0.000	<0.001
	$\delta^{15}\text{N}$	74, 68	0.00	<0.001
Females : South American sea lion	$\delta^{13}\text{C}$	294, 68	0.000	<0.001
	$\delta^{15}\text{N}$	294, 68	0.000	<0.001
Females 1998 : 1999	$\delta^{13}\text{C}$	226, 68	6660.500	0.096
	$\delta^{15}\text{N}$	226, 68	7411.000	0.657

5.2. b. Differences along whisker length

A $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ profile of each whisker was plotted against the sections distance along the whisker and represented graphically. The figures below show $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

profiles for a whisker collected from each southern elephant seal sampled during this study and from the five South American sea lions also sampled (included here for comparison with the southern elephant seals since they share similar breeding and foraging locations). The whiskers for the female seals are plotted with whiskers from other female seals, which share a similar trend to them along the whisker profile. Whiskers may not share the same trend for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Due to the wide range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values seen among the male southern elephant seal the whisker profiles are shown plotted for the animals in each group.

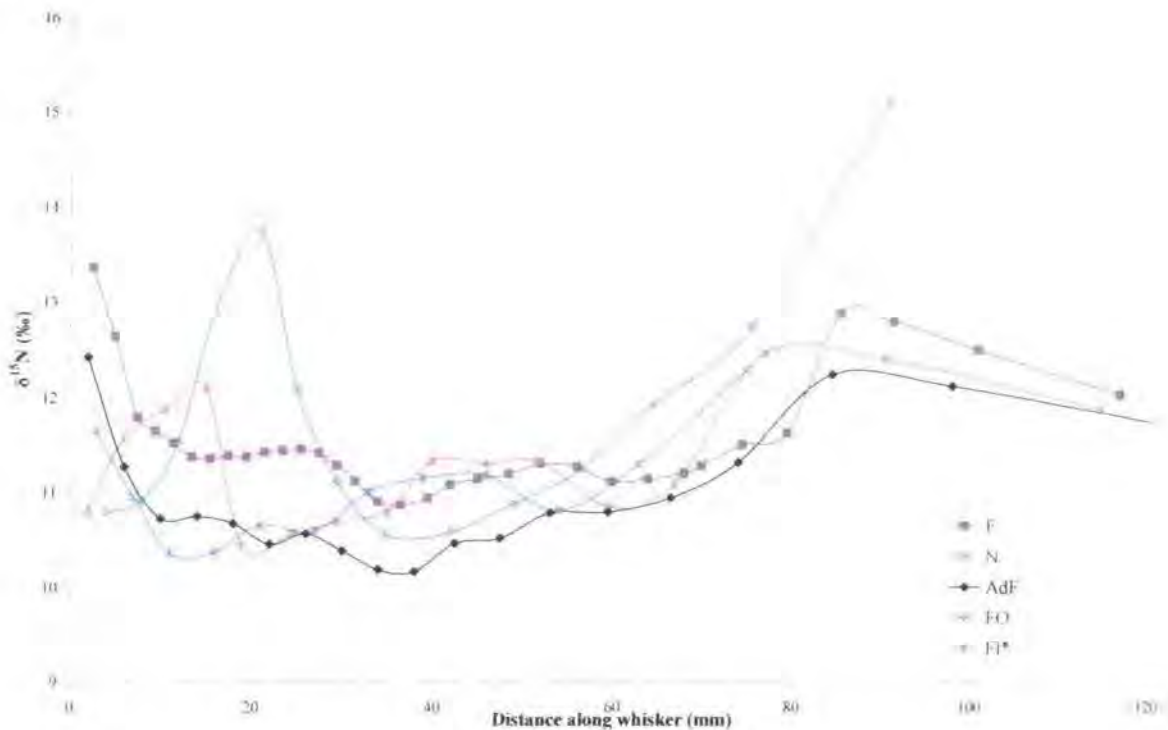


Figure 5.3: $\delta^{15}\text{N}$ variation along vibrissae length for vibrissae from five female southern elephant seals, which share a similar trend. Each individual is plotted in a different colour

The plots shown in Figure 5.3 show the $\delta^{15}\text{N}$ isotopic variation for five whiskers, three of which ('FI*', 'F' and 'AdF') show similar trends, a decrease in $\delta^{15}\text{N}$, followed by a period of little $\delta^{15}\text{N}$ variation and then an increase in $\delta^{15}\text{N}$ enrichment towards the tip end of the whisker. The whiskers from 'N' and 'FO' show an increase in $\delta^{15}\text{N}$ of 1 to 3‰ before they show the same trend as the other two whiskers on the graph and 'F'.

to 3‰ before they show the same trend as the other two whiskers on the graph and 'F'. As with one of the whiskers from 'F', a small decrease in $\delta^{15}\text{N}$ over the last two points of the whiskers is seen in the whiskers from 'N' and 'AdF'.

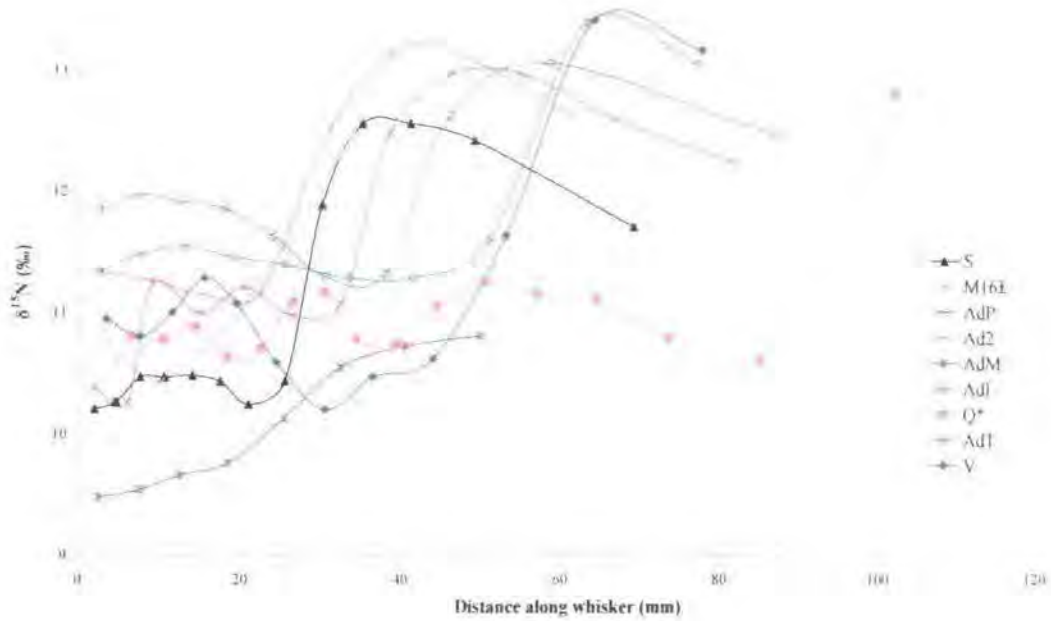


Figure 5.4: $\delta^{15}\text{N}$ variation along vibrissae length for the vibrissae from nine female southern elephant seals which show an increase in $\delta^{15}\text{N}$ at their distal ends. Each individual is plotted in a different colour.

Whiskers from female southern elephant seals demonstrated a period of lesser $\delta^{15}\text{N}$ variation for the first quarter of the whisker, followed by an increase at the distal ends of the whiskers of about 1 to 3‰ (Figure 5.4). All of the whiskers greater 50mm also show a small decline over the more distal sections of the whiskers (Figure 5.4).

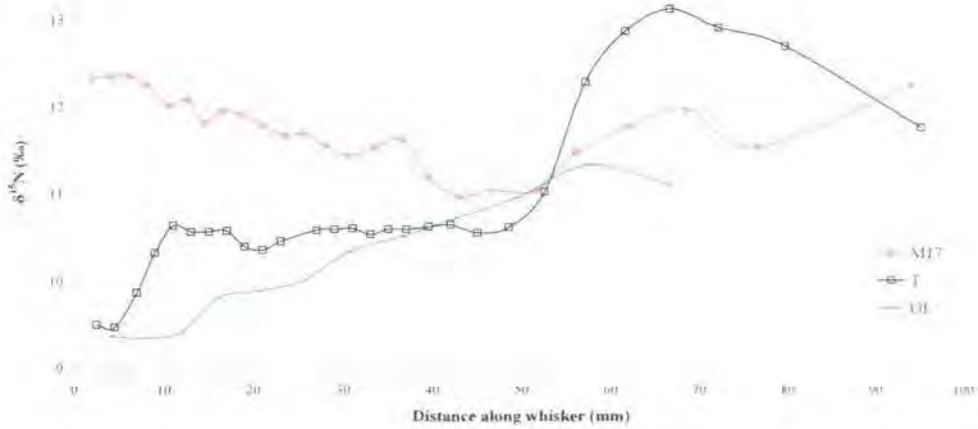


Figure 5.5: $\delta^{15}\text{N}$ variation along vibrissae length for vibrissae from three female southern elephant seals which share no consistent trends with the other animals sampled. Each vibrissae is plotted in a different colour.

The whiskers from three animals (Figure 5.5) show no trends or similarities to those shown in Figures 5.3 or 5.4 or to each other, although an increase in $\delta^{15}\text{N}$ towards the distal end of the whisker is seen in them all.

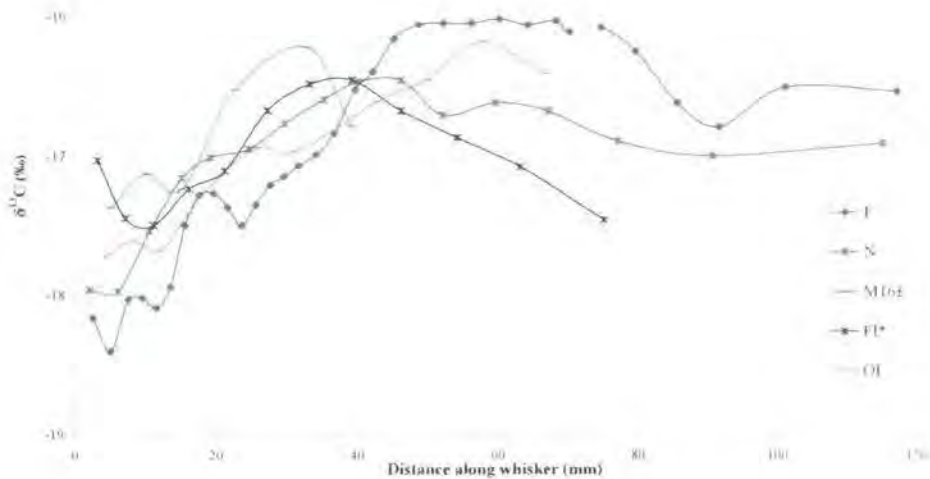


Figure 5.6: $\delta^{13}\text{C}$ variation for vibrissae from five female southern elephant seals that show a similar trend to each other.

The whiskers shown in Figure 5.6 show plots that show a similar trend in $\delta^{13}\text{C}$ to: an increase in the isotope from the base of the whisker of 1 to 2‰ and then a slight decline of 0.2 to 1‰ at the distal end of the whisker.

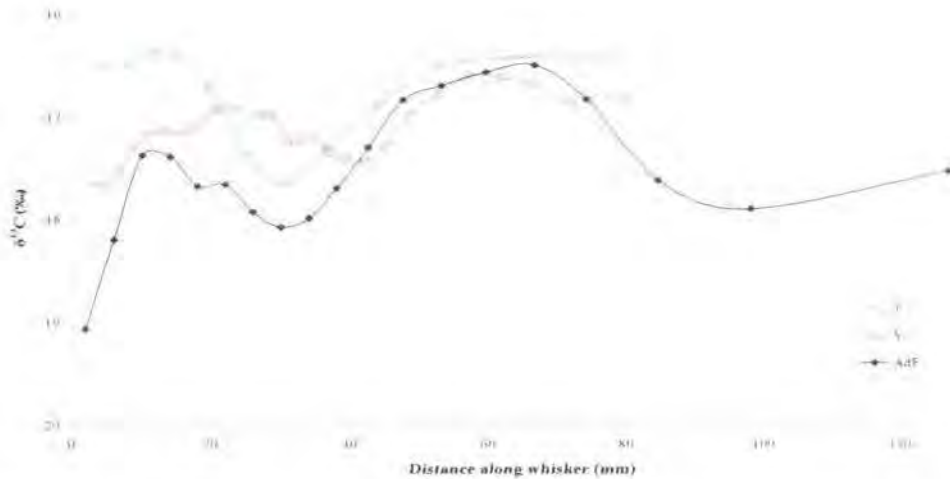


Figure 5.7: $\delta^{13}\text{C}$ variation for vibrissae from three female southern elephant seals which show similar trends to each other.

The whiskers shown in Figure 5.7 show a similar trend to one another. They show a small increase in $\delta^{13}\text{C}$, which is followed by a decline, a pattern that is then repeated in the second half of the whisker.

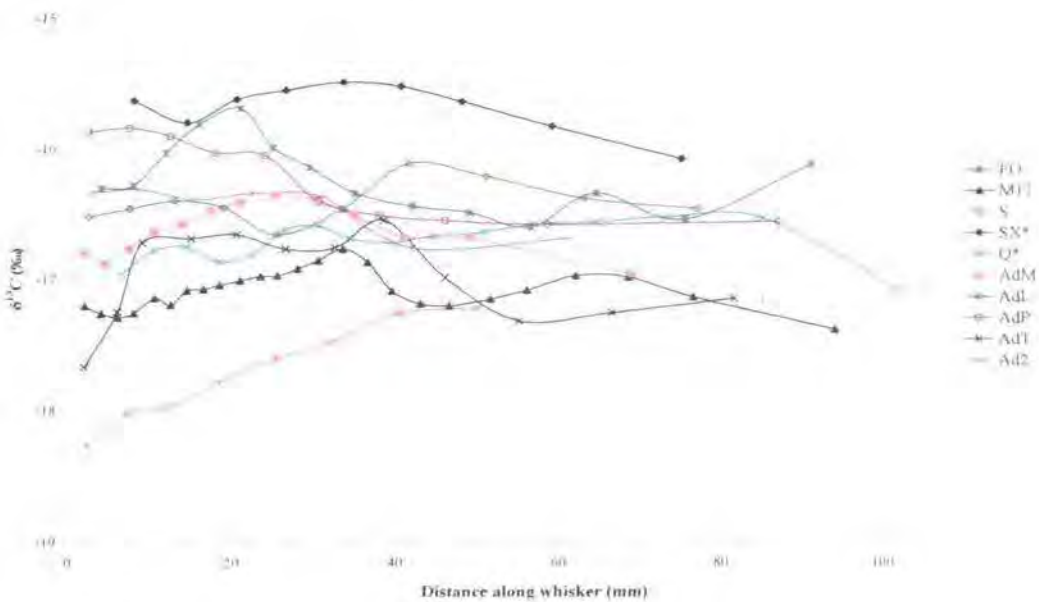


Figure 5.8: $\delta^{13}\text{C}$ variation for vibrissae from ten female southern elephant seals, which show no trends in common.

Figure 5.8 shows that $\delta^{13}\text{C}$ of the female southern elephant seals from both 1998 and 1999 varied little between the proximal and distal ends of the whiskers. 'AdM' shows the greatest change in $\delta^{13}\text{C}$, an increase of 1‰ along its length. Whiskers from 'FO', 'AdL' and 'AdT' also show a small increase along their lengths. The remaining whiskers all show small decreases in $\delta^{13}\text{C}$ from their base to tip ends.

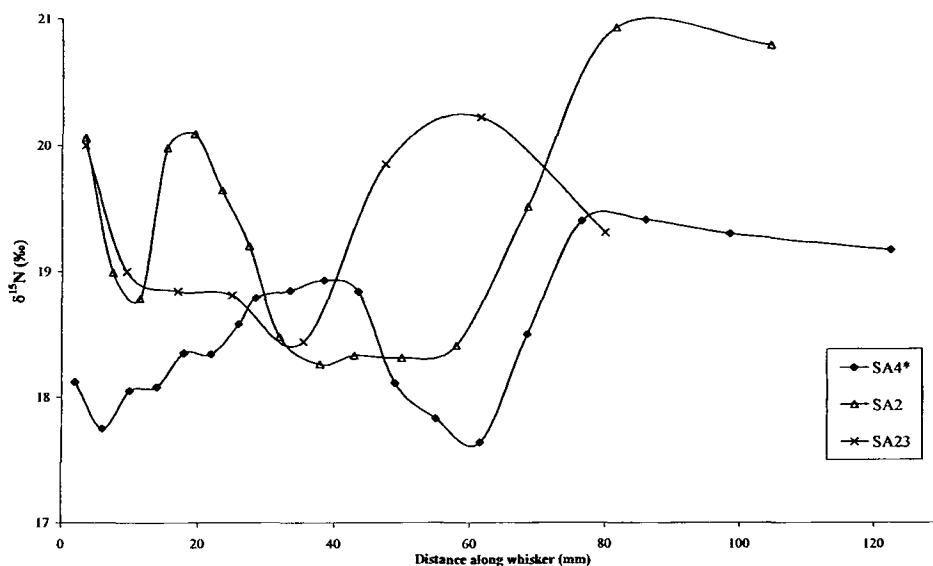


Figure 5.9: $\delta^{15}\text{N}$ variation for vibrissae from Group one male southern elephant seals

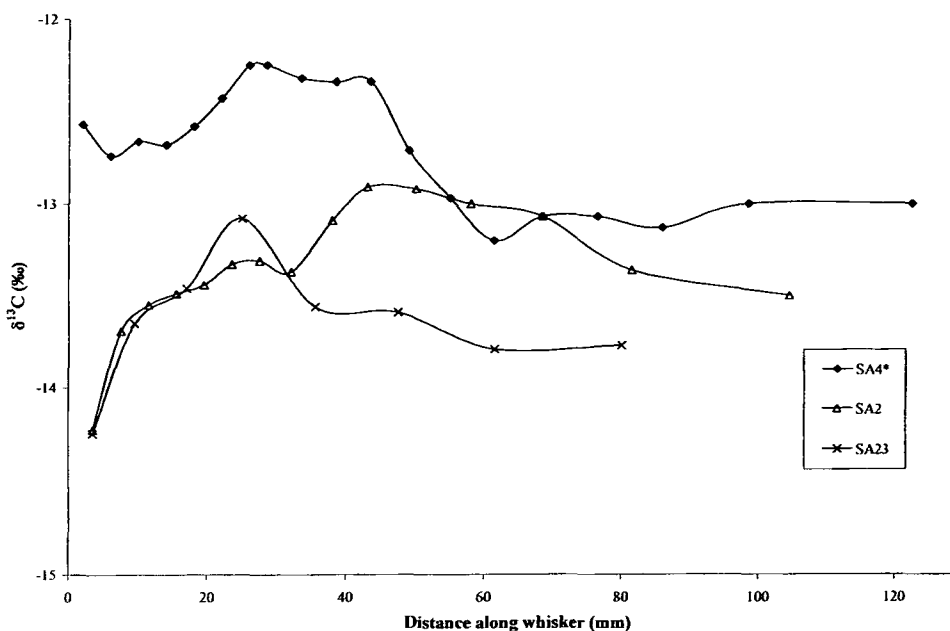


Figure 5.10: $\delta^{13}\text{C}$ variation for vibrissae from Group one male southern elephant seal.

One whisker from each animal assigned to Group 1 is plotted in Figures 5.9 and 5.10. Repeat whiskers were taken from all the animals in this group but have not been plotted since little isotopic variation was found in any of the whiskers from the same animal (Chapter 3).

The whisker plots shown in Figure 5.9 do not show similar trends to each other in the first half of the whiskers. In the second a similar trend is seen namely: an increase in $\delta^{15}\text{N}$ of 2 to 3‰. $\delta^{13}\text{C}$ plots were similar in 'SA2' and 'SA23', where an increase of 1‰ is seen followed by a period of little variation (Figure 5.10). The plot for the third whisker in this group shows a different trend.

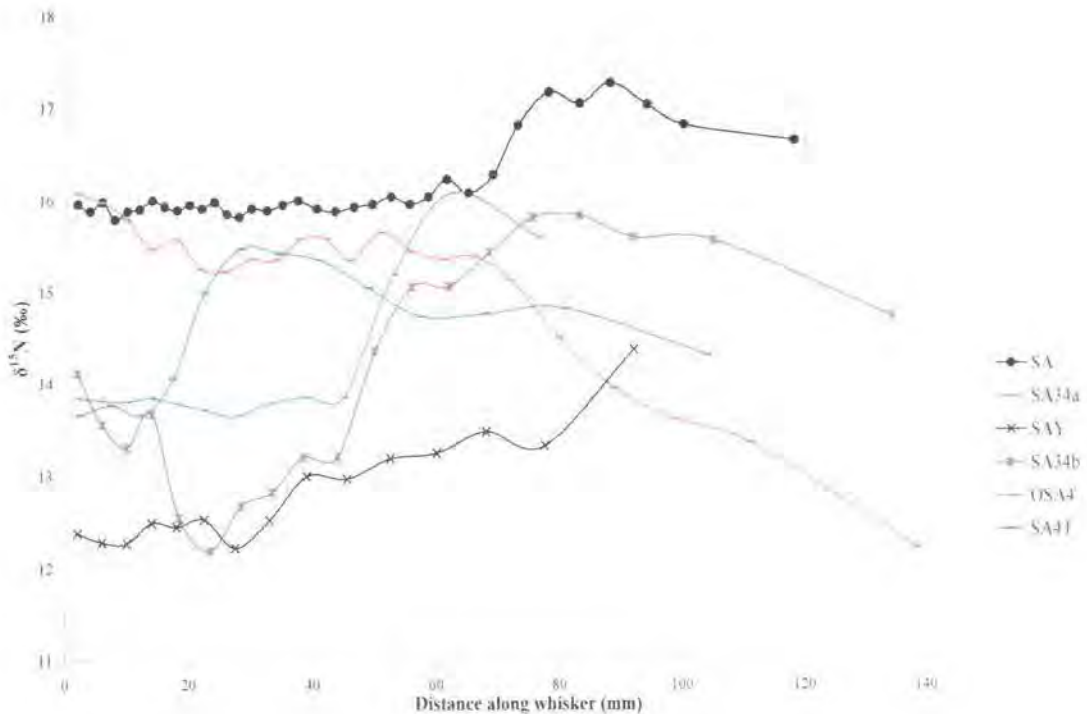


Figure 5.11: $\delta^{15}\text{N}$ variation for vibrissae for the male southern elephant seals in Group 2.

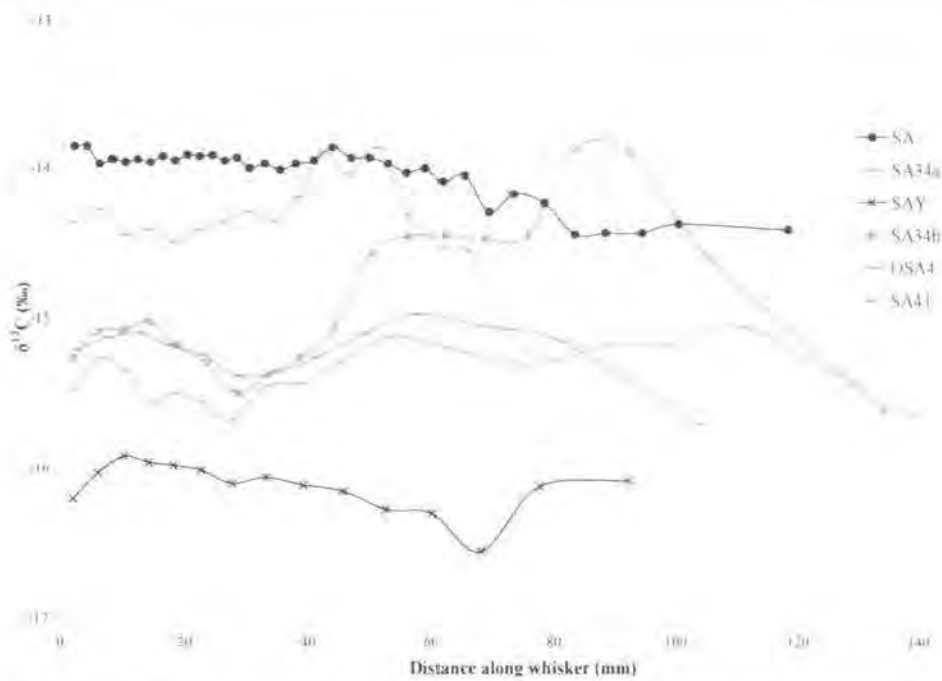


Figure 5.12: $\delta^{13}\text{C}$ variation for vibrissae for the male southern elephant seals in Group 2.

Four of the whiskers in Figure 5.11, 'SA4T', 'SA34b', 'SA' and 'OSA4' show a similar trend: a period of little isotopic variation followed by an increase in $\delta^{15}\text{N}$ towards the tip. The other two whiskers in this group show no trends similar to the rest of the group. 'SA34a' shows a decline over its length, while 'SAY' shows an increase in $\delta^{15}\text{N}$.

Three whiskers from 'OSA4', 'SA4T', and 'SA34b' show a small decrease, at about their midpoints (Figure 5.12). This is similar to the trend shown by the whisker from 'SA2' in Figure 5.10. 'SA34a' shows a similar decrease in $\delta^{13}\text{C}$ to 'SA4*' (also Figure 5.12). The plots for the remaining two whiskers, 'SAY' and 'SA', show little $\delta^{13}\text{C}$ variation along their lengths.



Figure 5.13: $\delta^{15}\text{N}$ variation for vibrissae from male southern elephant seals in Group 3

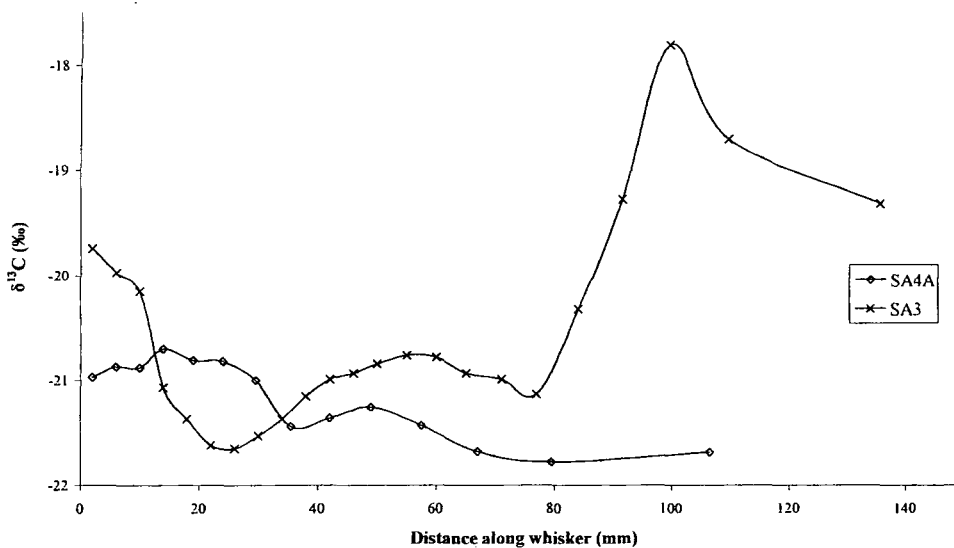


Figure 5.14: $\delta^{13}\text{C}$ variation for vibrissae from male southern elephant seals in Group 3

The plots for the two whiskers in Figures 5.13 and 5.14 show little similarity to each other. The $\delta^{15}\text{N}$ plots in Figure 5.13 also do not show a trend similar to any of the whiskers plotted on previous figures. The $\delta^{13}\text{C}$ plot for 'SA4A' in Figure 5.14 shows a small decrease in $\delta^{13}\text{C}$ over its length that is similar to the trend identified in some of

the whiskers, for example 'SA34b' and 'SA4*' from Figures 5.12 and 5.10. 'SA3' shows no similarity to any of the other whiskers plotted.

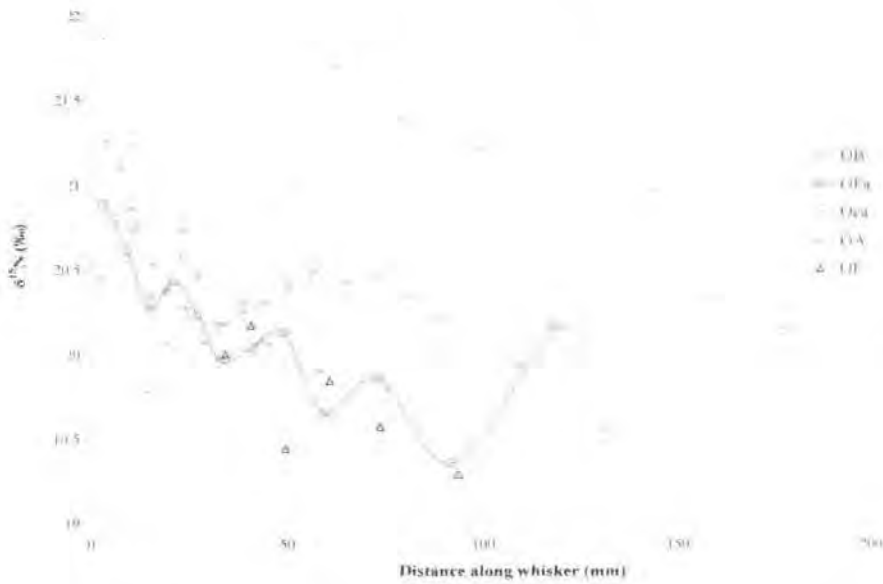


Figure 5.15: $\delta^{15}\text{N}$ variation for vibrissae from five South American sea lions. Animal 'OA' is a male; the others are females

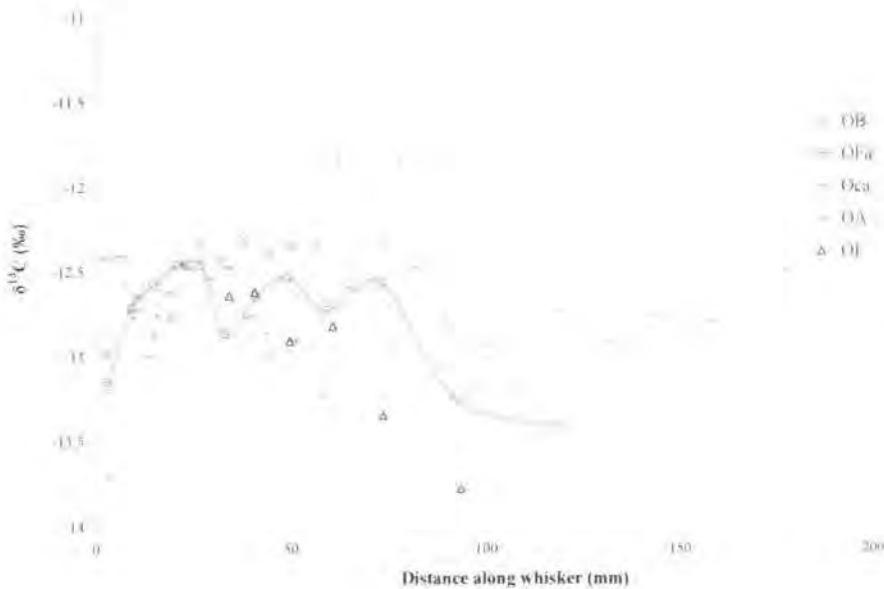


Figure 5.16: $\delta^{13}\text{C}$ variation for vibrissae from five South American sea lions. Animal 'OA' is a male; the others are females.

The isotopic data for the whiskers of the South American sea lions in 1999, show that the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plots for all but one of the animals are very similar (Figures 5.15 and 5.16). The plots for 'Oca' show an increase in $\delta^{13}\text{C}$ and a decrease in $\delta^{15}\text{N}$. The other four whiskers all show a degree of apparent periodicity along their length in both isotopes. This is most clearly seen in the plots for 'OA', the longest whisker, which shows three cycles about 40mm apart in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

In order to better examine the whisker profiles for possible trends over the length of the whiskers, graphs for the average value for each position were plotted. The series of these plots are shown in Figures 5.17 - 20 with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ series plotted on the same graph.

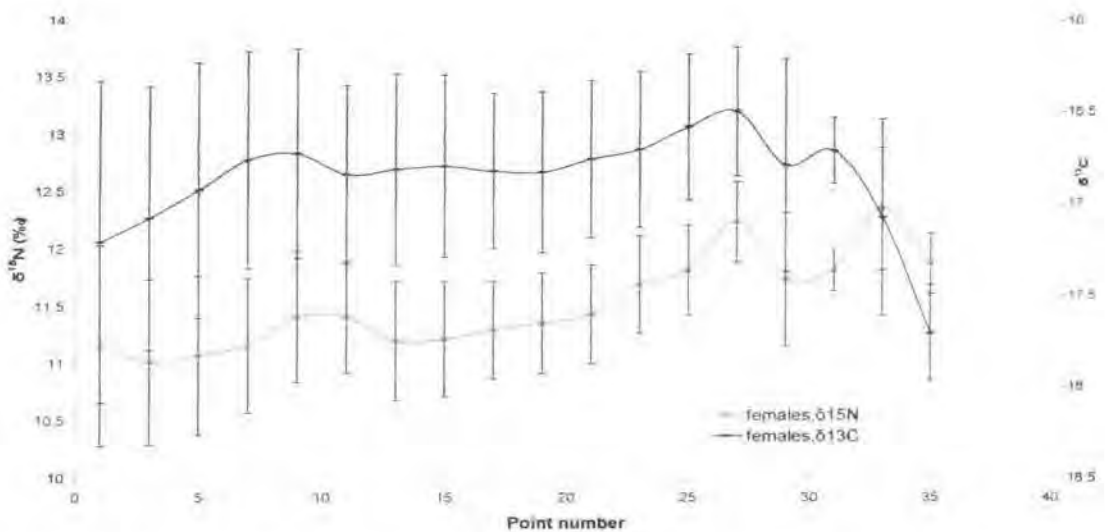


Figure 5.17: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation for each point for vibrissae from all female southern elephant seals sampled. Points were plotted with the proximal end of the vibrissae as zero.

The two series shown in Figure 5.17 show the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each point. They show a similar trend to each other: that is, an increase over the majority of the plot length. The $\delta^{13}\text{C}$ shows a greater decline than the $\delta^{15}\text{N}$ plot towards the end of the series and ends at a lower value than is seen at the start. The $\delta^{15}\text{N}$ series remains higher at the end. The two periods of alternating decreases and increases are seen in both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plot and at a similar place in each series.

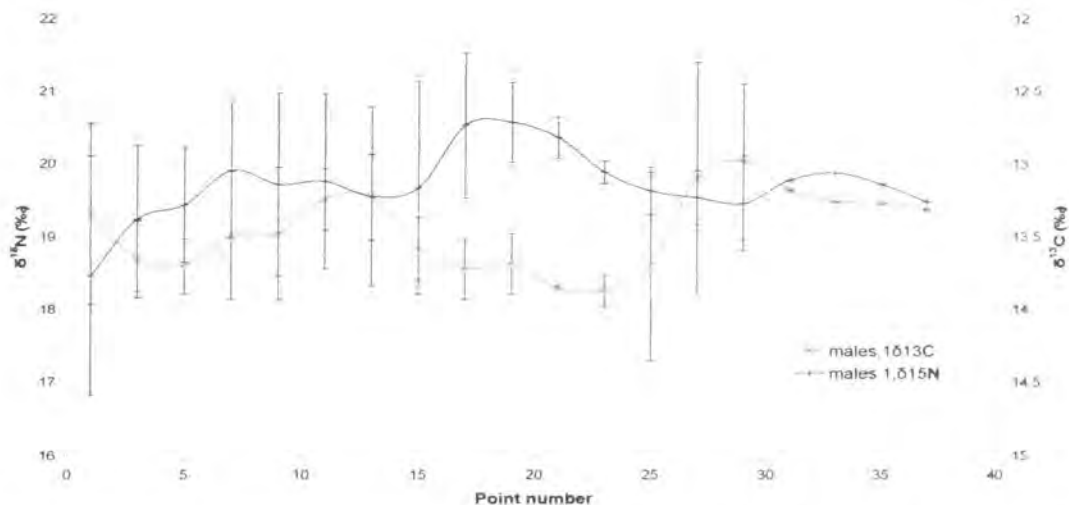


Figure 5.18: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation for each point for vibrissae from Group 1 male southern elephant seals. Points were plotted with the proximal end of the vibrissae as zero.

The series for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for Group 1, shown in Figure 5.18, shows that the two isotopes do not show similar trends to each other or to trends seen in the series for other groups. Both plots show an overall increase from the start to end of the series, with a variation along the length of about 1‰ for both isotopes.

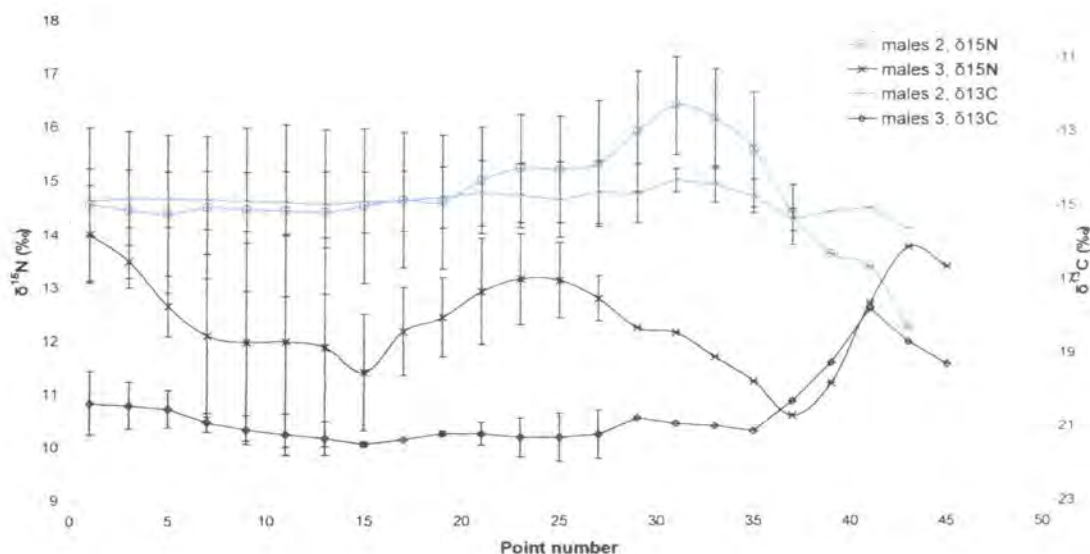


Figure 5.19 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation for each point for vibrissae from Group 2 and 3 male southern elephant seals. Points were plotted with the proximal end of the vibrissae as zero.

Figure 5.19 shows the series for Groups 2 and 3 of male southern elephant seals. The series for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shown for Group 2 are similar to each other, although the $\delta^{15}\text{N}$ shows greater variation in the last third of the plot and a subsequent greater decline at the end than is seen in the $\delta^{13}\text{C}$ plot. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots for Group 3 are neither similar to each other nor to other series plotted in previous graphs. It should be noted that for both these groups the sample size is small, resulting in the last third of the plot for Group 3 including data from only one whisker (thus standard deviation = 0).

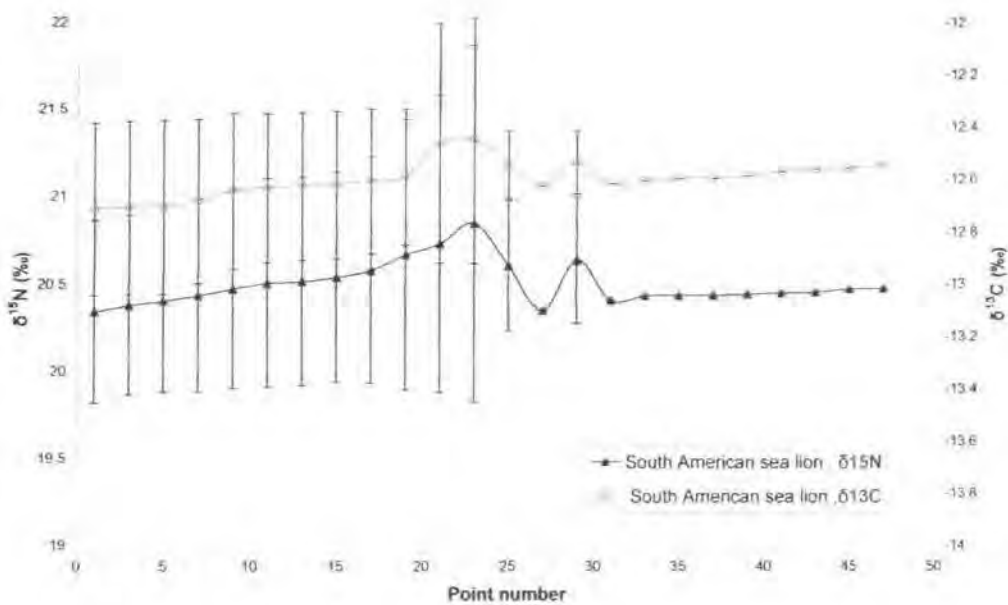


Figure 5.20: Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variation for each point for vibrissae from South American sea lions. Points were plotted with the proximal end of the vibrissae as zero.

The South American sea lion $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data were very similar (Figure 5.20). Both show a slight upward trend from the start to the end of the series, and both show the same alternating increase and decrease at the same point along the length of the plots.

The plots for the whiskers shown in the figures above show that three basic trends can be identified, an increase along whisker length, a decrease along whisker length or no overall change. The trend for the longest whisker from each southern elephant seal

and South American sea lion was identified and is shown in table 5.4 below with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the base and tips of it.

Table 5.4: Proximal and distal values of each whisker analysed from southern elephant seals and South American sea lions. Trends are classified as upwards or downwards if the isotopic difference seen between the two ends is greater than 0.70‰. If the difference seen is less than this value the trend is classified as 'None' (see Chapter 3).

Animal	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	Base	Tip	Trend	Base	Tip	Trend
Female southern elephant seals						
M17	-17.20	-17.39	None	12.32	12.26	None
S	-16.51	-16.57	None	10.60	11.76	Up
T	-17.64	-17.87	None	9.50	11.76	Up
F	-18.16	-16.54	Up	13.35	12.02	Down
N	-17.96	-16.91	Up	10.79	11.86	Up
M16	-17.37	-16.79	None	10.64	13.14	Up
FO	-16.30	-16.12	None	10.79	15.15	Up
SX	-15.63	-16.08	None	12.52	12.56	None
V	-16.50	-16.41	None	10.94	13.16	Up
OI	-17.73	-16.41	Up	9.37	11.12	Up
AdP	-15.87	-16.56	None	11.85	12.46	None
AdF	-19.06	-17.52	Up	12.42	11.63	Down
AdL	-16.52	-16.46	None	11.34	13.05	Up
Ad2	-16.33	-16.69	None	11.33	12.65	Up
AdT	-17.67	-17.15	None	10.38	12.24	Up
AdM	-18.27	-16.77	Up	9.48	12.72	Up
FI	-16.78	-17.50	Down	10.89	12.37	Up
Q	-16.44	-17.19	Down	11.82	12.81	Up
Male southern elephant seals						
SA23	-14.25	-13.77	None	20.00	19.31	None
SA2	-14.23	-13.50	Up	20.06	20.79	Up
SA4	-12.82	-13.26	None	17.87	19.37	Up
SA34b	-14.44	-15.56	Down	16.01	13.61	Down
SAY	-16.20	-16.08	None	12.38	14.38	Up
OSA4	-15.49	-15.32	None	13.85	15.61	Up
SA4T	-15.21	-15.71	None	13.66	14.33	None
SA	-13.85	-14.41	None	15.96	16.66	Up
SA34a	-15.26	-15.61	None	14.12	14.26	None
SA4A	-20.97	-21.69	Down	13.36	13.09	None
SA3	-19.74	-19.31	None	14.66	13.39	Down
MS3	-17.42	-17.46	None	13.24	14.59	Up

South American sea lions						
OF	-13.75	-13.78	None	21.18	19.29	Down
Oca	-13.70	-12.97	Up	21.27	19.79	Down
OA	-12.42	-12.84	None	20.45	20.08	None
OB	-12.98	-11.84	Up	21.89	21.39	None
OFa	-13.17	-13.41	None	20.89	20.17	Down

Table 5.5: Summarising the numbers of each whisker from each Group following each of the three trends as shown in Table 5.4 above.

Group	$\delta^{13}\text{C}$ trends			$\delta^{15}\text{N}$ trends		
	None	Up	Down	No	Up	Down
Females	11	5	2	3	13	2
Group 1	2	1	0	1	2	0
Group 2	5	0	1	5	0	1
Group 3	1	0	1	1	0	1
Falkland island male	1	0	0	0	1	0
South American sea lions	3	2	0	2	0	3

Most of the whiskers show no overall increases or decreases along their length (Table 5.4 and 5.5). However, an upward trend for $\delta^{15}\text{N}$ is shown in more of the whiskers from the female southern elephant seals than in whiskers from any other group. Although no overall upwards or downwards trends are seen in most of the whiskers, some of the whiskers do show large variations along their lengths (Table 5.4).

Table 5.6: Results from statistical (Mann-Whitney U-test) analysis along whisker length, comparing the proximal end (1), the middle (2) and, the distal end (3) for each whisker from females, Groups 1, 2, 3 male southern elephant seals and South American sea lions. $\alpha = 0.025$ after Bonferoni correction.

Group	Comparison	Isotope	n_1, n_2	U	P
Females	1:2	$\delta^{13}\text{C}$	93,93	3648.000	0.065
		$\delta^{15}\text{N}$	93,93	3788.500	0.144
Females	1:3	$\delta^{13}\text{C}$	93,93	3142.000	0.001
		$\delta^{15}\text{N}$	93,93	2406.000	<0.001

17	Cuphead skate
18	White-dotted skate
19	Narrow mouthed cat-shark
20	Conger eel
21	Patagonian grenadier
22	Thornfish*
23	Southern flounder
24	Patagonian toothfish*
25	Banded whiptail
26	Southern blue flounder
27	Argentine short finned squid
28	Dwarf codling
29	eelpout

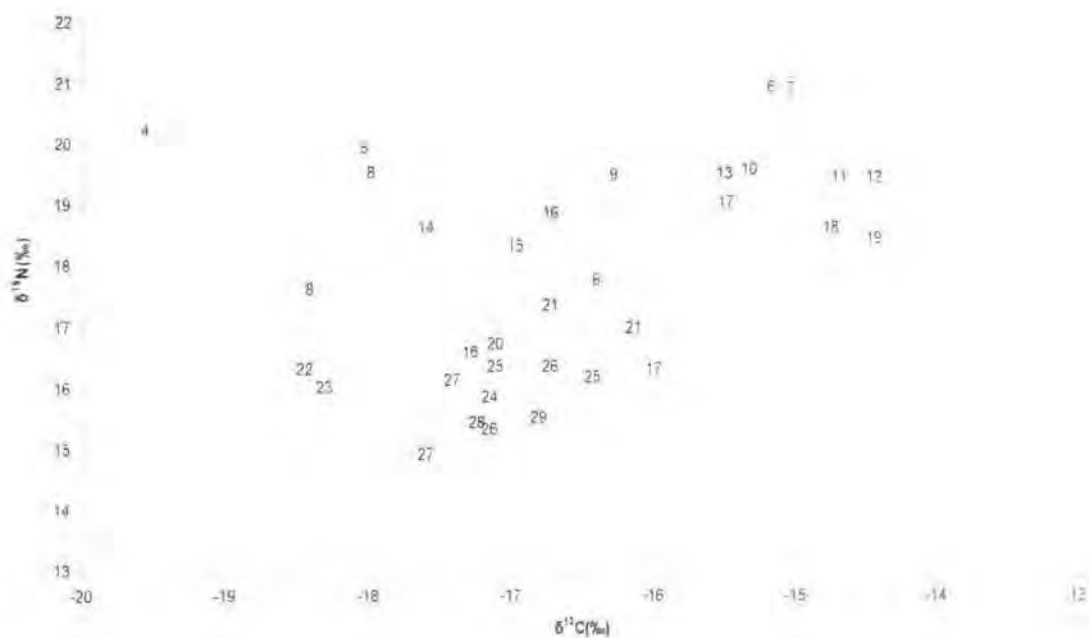


Figure 5.21: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all the fish and squid species sampled during the course of this study, after the application of a correction factor to those samples where the C:N ratio is greater than 4.0

The fish and squid isotopic data ranged from -20.4‰ to -14.0‰ for $\delta^{13}\text{C}$ and from 14.2‰ to 21.7‰ for $\delta^{15}\text{N}$ (Figure 5.21). The mean value from the Argentine short finned squid sampled (*Illex argentinus*) is -17.59‰ for $\delta^{13}\text{C}$ (SD = 0.08) and 14.90‰

(SD = 0.23) for $\delta^{15}\text{N}$. A second squid species, *Martialia hyadesia* has values given as -16.50 for $\delta^{13}\text{C}$ and 11.80 for $\delta^{15}\text{N}$ (Takai *et al.* 2000). Published data show euphausiids (krill) with $\delta^{13}\text{C}$ values of -23.5‰ and of $\delta^{15}\text{N}$ 7.1‰. The values for calanoid copepods are 20.7‰ for $\delta^{13}\text{C}$ and for $\delta^{15}\text{N}$, 10.6‰ (Schell *et al.*, 2000).

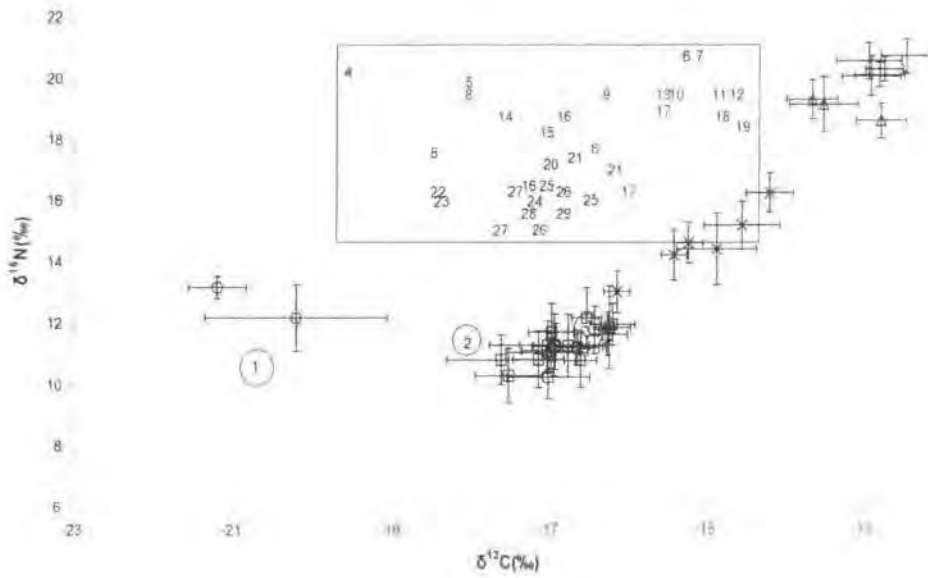


Figure 5.22: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish species with southern elephant seal and South American sea lion data. The prey species are marked with a box. Graph includes data from published sources for krill, squid and calanoid copepods (Shell *et al.* 2000, Takai *et al.*, 2000).

Figure 5.22 shows the values plotted for the southern elephant seals and South American sea lions and for the prey species (sampled for this study) outlined by a box. The points from Group 2 males fall inside of the box for the potential prey species, while the points for the female animals and those from Group 3 fall at lower $\delta^{15}\text{N}$ values than for the prey species.

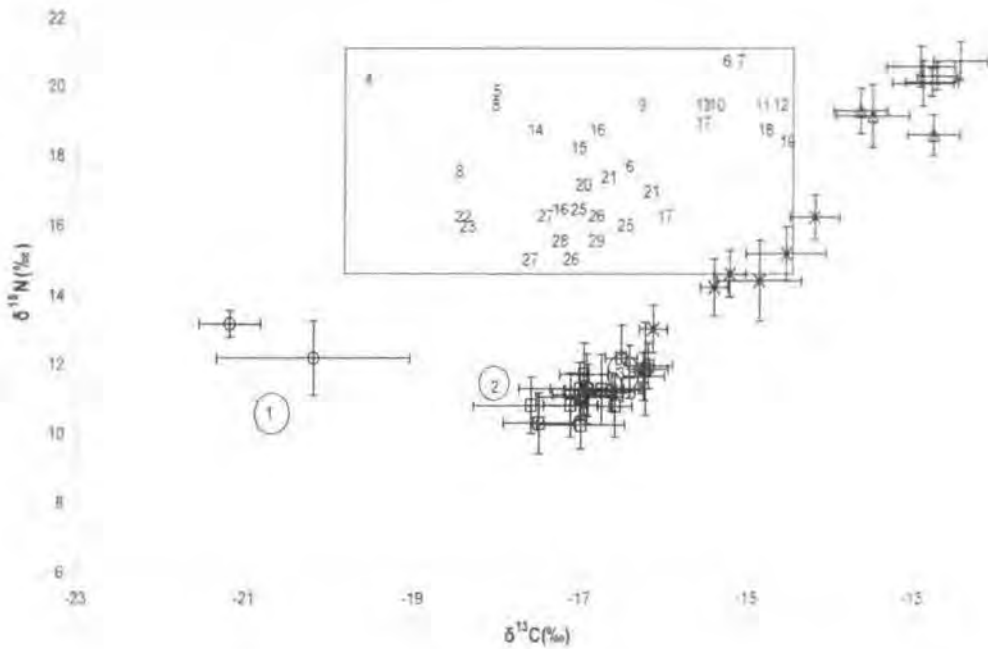


Figure 5.23: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish species with southern elephant seal and South American sea lion data plotted as $\delta^{13}\text{C} - 1$ and $\delta^{15}\text{N} - 3$. The prey species analysed in this study are marked with a box. Graph includes data from published sources for krill, squid and calanoid copepods (Shell *et al.* 2000, Takai *et al.*, 2000).

Figure 5.23 shows the values of the seals shifted by $\delta^{15}\text{N} - 3$ and $\delta^{13}\text{C} - 1$, to account for the expected level of $\delta^{15}\text{N}$ enrichment of the whisker keratin over the potential diet. $\delta^{13}\text{C}$ is plotted to account for the minimum expected level of $\delta^{13}\text{C}$ enrichment in whisker keratin over diet. When these values of enrichment are used few points from the seal values fall close to those of the prey species. Group 1 males show some overlap with part of the box, as do the standard deviation bars for some of the South American sea lion points. The value given for *Martialia hyadesia* (Takai *et al.* 2000) falls close to the values plotted for Group 2 males and the values for krill close to the isotopic variation for the Falkland Island southern elephant seal. The values for the females show lower $\delta^{15}\text{N}$ values, though similar $\delta^{13}\text{C}$ values than for the prey species, and Group 3 males show values most similar to those of the calanoid copepods.

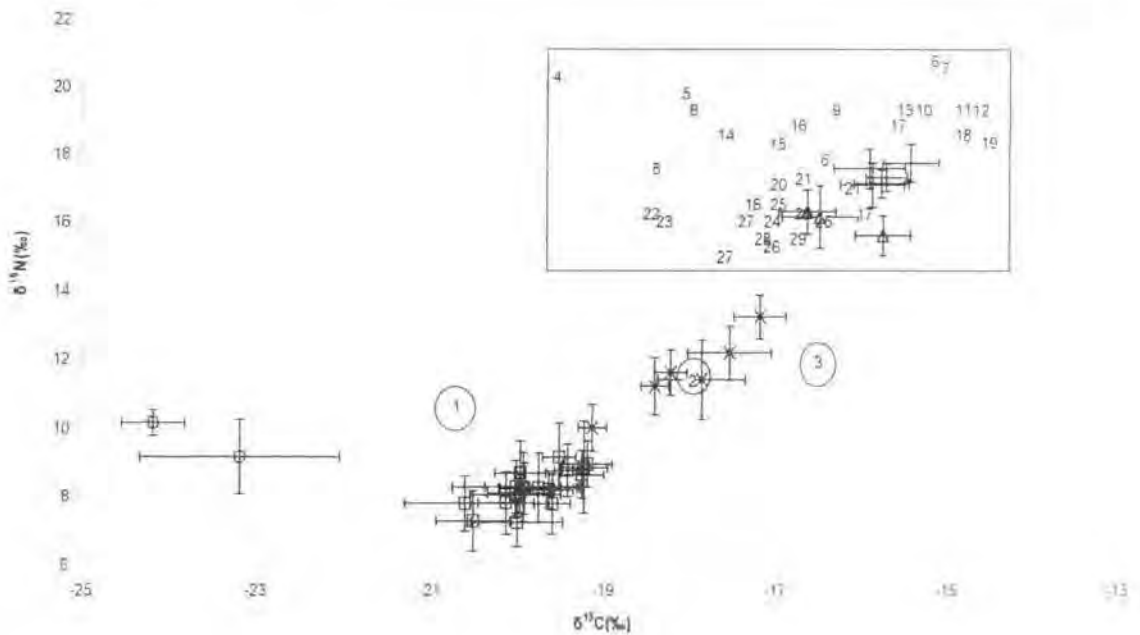


Figure 5.24: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish species with southern elephant seal and South American sea lion data plotted as $\delta^{13}\text{C} - 3.4$ and $\delta^{15}\text{N} - 3$. The prey species analysed in this study are marked with a box. Graph includes data from published sources for krill, squid and calanoid copepods (Shell *et al.* 2000, Takai *et al.*, 2000).

Figure 5.24 shows the same $\delta^{15}\text{N}$ values plotted for the seals. Here, however, the $\delta^{13}\text{C}$ values for the seals are plotted as $\delta^{13}\text{C} - 3$, to take in to account the maximum likely enrichment of whisker keratin over diet. Using these enrichment values, it can be seen that the isotopic values for Group 1 males and the South American sea lions fall within the range for the fish prey items and show similar values to several species: Piked dogfish, banded whiptail, southern flounder, cuphead skate, southern blue whiting, Patagonian grenadier and conger eel. The values for the krill (Shell *et al.*, 2000) fall within the range shown for Group 2 males, and the values for the calanoid copepods (Shell *et al.*, 2000) fall close to the value for the Falkland Island male. However, the isotopic values for the females and Group 3 males fall at lower $\delta^{15}\text{N}$ values than shown by any of the potential prey species and Group 3 shows lower $\delta^{13}\text{C}$ values than the possible prey species.

5.3. Discussion

In this study there were to be significant differences in the isotopic values between all groups of male and the female adult southern elephant seals from Pensinsular Valdés. This indicates that the two sexes are taking different prey items in their diet. In addition to this, the males in this study were found to fall into three groups each significantly distinct from one another and from the females in the study. No such differences were found in the group of females sampled. The female seals from 1998 and 1999 showed isotopic values that lay in a tight group. These differences will first be discussed in terms of the difference between the two sexes, and then the differences seen in the male seal isotopic values will be considered.

Differences in foraging behaviour of the male and female seals have been observed in southern elephant seals from both South Georgia and Pensinsular Valdés (McConnell *et al.*, 1996, Campagna *et al.*, 1998, 1999). The male seals tend to forage over, or close to the edge of, the continental shelf, while the female seals make biannual foraging trips away from the continental shelf, with distances recorded by satellite tags of 2300km (Campagna *et al.*, 1998, Campagna *et al.*, 1999).

Both foraging and dietary differences between the sexes in the northern elephant seal have been observed (Le Boeuf *et al.*, 1993, Burton & Koch, 1999). Differences in the prey species taken by the two sexes of the southern elephant seal are to be expected, although none have been observed in the scat or stomach content analysis of southern elephant seals' diet (Green & Burton, 1993, Rodhouse *et al.*, 1997, Slip, 1995). These methods, however, are subject to known bias (as discussed in Chapter One, Boyd *et al.*, 1994, Slip, 1995) and thus may not give a true representation of the diet of the southern elephant seal.

Since the southern elephant seal spends a large proportion of its life cycle at sea (Le Boeuf & Laws, 1994), it is likely that previous methods of dietary study are unable to give an entirely accurate indication of the composition of its diet since all current methods of direct dietary study require the animal to be studied on the land. Stable isotope analysis of whiskers in this study has shown that there is a large difference in the diet of the two sexes of the southern elephant seal. $\delta^{15}\text{N}$ data indicate that the smaller females feed at a lower trophic level than some of the males, which may be indicative of the size of the prey items that are being taken by each sex (larger prey being taken by the larger males, while the smaller females take smaller prey of the same or different species), however some males are also shown to be feeding at a lower trophic level than the females. While this difference may be predicted from the differences found in the foraging behaviour of the male and female seals, it indicates that the methods used to study southern elephant seals' diet in previous studies (i.e. stomach content and scat analysis) have failed to show these differences and that the methods are more biased than expected for this species.

The prey items (17 species of fish, cephalopods and crustaceans) identified in previous studies (Green & Burton, 1993, Rodhouse, 1997, Slip, 1995) have been eaten by the southern elephant seals and so must represent least a small part of the diet of this species. However, it would appear from the isotopic values that the data from previous studies may not be representative of the majority of the diet for all of the species and are most likely less accurate for the female southern elephant seals than the males, since the female seals spend longer at sea than the male seals (Le Boeuf & Laws, 1994)

Since the southern elephant seals females must travel to the breeding beaches from their foraging grounds over the continental shelf, where the male seals are believed to forage for most of their time at sea (McConnell & Fedak, 1996; Campagna *et al.*, 1999), it is possible that for a short period of time the female seals share the same or a similar diet to the male seals. Since the seals retain food in their stomachs for up to three days, (Krockenberger & Bryden 1994) it is likely to be this food that is sampled in scat and

stomach content analysis but is only representative of the prey that the female seals eat for a short period of their life, a few days.

This is a potential reason for the failure of traditional methods of dietary analysis to show any sex differences between the male and female southern elephant seals, then the whiskers collected from the female seals should show $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ values that are more similar to those of the male seals in the portion of the whisker showing the most recent period of growth (i.e. the base of the whisker) than they do in older parts of the whisker, which would correspond to the period of time that the female seal would spend crossing the continental shelf on her way to the breeding beaches. One of the assumptions made in this study (due to lack of data on this subject) is that a southern elephant seal's whisker grows at a similar rate to that of a grey seal and a harbour seal; if this is so, then a whisker corresponds to the diet over the period of about a year. The initial decline seen at the base end of some of the whiskers from female seals corresponds to the period immediately before the seal lands at the breeding beach and is sampled. Many of the whiskers show a similar increase at the tip end of the whisker, which could correspond to the period of travel back over the continental shelf during the preceding year. The higher values of $\delta^{15}\text{N}$ seen at the beginning of the whisker are likely to be due the animals feeding on prey species of higher trophic levels than for the majority of their diet and which are more similar to the values seen by the male seals, many of whom show higher $\delta^{15}\text{N}$ values than the females. The majority of the whiskers from the female seals do not show the decrease in $\delta^{15}\text{N}$ at the base end, while they do show the increase in $\delta^{15}\text{N}$ at the tip. Only the whiskers from one female seal, 'F', were complete, since she was dead when sampled. The whiskers from the other female seals were all from live animals and were thus cut from the face rather than pulled. They are therefore, not complete but are missing the portion of the whisker closest to the face; the part showing the most recent whisker growth rate and the period relating to the time the animal spent crossing the continental shelf. It should be noted that this is speculation.

The $\delta^{15}\text{N}$ values seen at the proximal end of the whiskers of the female seals are still lower than the $\delta^{15}\text{N}$ values shown by many of the male seals. Even if the two sexes were feeding on prey of similar species, the isotopes in the whiskers of the female seals would take a period of about 70 days to completely show the isotopic values of the new diet (Jones *et al.*, 1981). The female does not spend this amount of time foraging in the same area as the male seals, so the isotopes would be unlikely to reach values similar to those seen in the whiskers of the male seals but would instead show a value between that of the new and older diets. It would appear from some of the plots for whiskers from female seals that this could be the case.

The whiskers from some of the South American sea lions appear to show periodicity of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the lengths of the vibrissae. Similar periodicity is seen in the whiskers of wild stellar sea lions in Hirons *et al.* (2001) where each cycle was attributed to a year's whisker growth. In this study the growth rate of South American sea lion whiskers is unknown, so it is uncertain if the periodicity is due to annual changes in the diet of these animals, shorter seasonal dietary changes or the animals metabolism. Since not all of the South American sea lion whiskers sampled show this periodicity, it maybe indicative of differing feeding trends in this species, or may be due to another aspect of the life cycle. More samples would be required before any conclusions can be made.

The reasons for the sex differences seen in southern elephant seal foraging behaviour are not known. It is seen in all of the populations of southern elephant seals (Hindell *et al.*, 1991; Campagna *et al.*, 1995; McConnell & Fedak, 1996; Jonker & Bester, 1998; Campagna *et al.*, 1998 & 1999) as well as in the similar northern elephant seal species (Le Boeuf *et al.*, 1993). The southern elephant seals shows greater sexual dimorphism than any other mammal and so it is not surprising that the species also shows foraging and prey selection differences. It is probable that the larger males are able to prey on larger species than the much smaller females. This is demonstrated by

the $\delta^{15}\text{N}$ values from this study, the females showing lower values than those seen in the majority of the male seals.

The differences seen in the use of the foraging areas (Campagna *et al.*, 1995, McConnell & Fedak, 1996, Campagna *et al.*, 1999) and the isotopic differences between the two sexes could have developed due to competition pressures between the sexes within the southern elephant seal species, leading to a division in the foraging strategies of the species, with the smaller females foraging at greater distances from the shore than the males and preying upon different species.

In addition to the differences between the male and female seals, the isotopic values of the male seals were divided into three distinct groups. Two groups show higher $\delta^{15}\text{N}$ values than those of the female, which is anticipated due to the size difference and thus greater energy requirements, of the males. However, two males appear to be feeding at a similar trophic level to the females and at a more depleted $\delta^{13}\text{C}$ value than the females (and any of the other males). The values for $\delta^{15}\text{N}$ indicate trophic level (DeNiro & Epstein, 1980, Kelly, 2000) and an average increase of 3‰ per trophic level is expected. From this, it can be seen that Group 1 are on average 4‰ higher than Group 2, i.e. one trophic level higher. Group 1 are on average 7‰ higher than the average $\delta^{15}\text{N}$ value for the female, giving a difference of two trophic levels between them. It is possible that the male southern elephant seal shows three separate feeding strategies, or that there are two main strategies: one to take large prey of higher trophic levels, as shown by Group 1, and the second to take smaller prey of a lower trophic level, as shown by Group 3. It may be that the seals shown in Group 2 use a combination of these strategies, resulting in an isotopic signature that is between the two. Samples from more male seals would show if the feeding strategies shown by the males in this study were in reality distinct from one another or if they are points on a spectrum of strategies.

The differences in the feeding behaviour, inferred from isotopic data, between the males do not appear to be related to age and size. The largest male, 'SA4A', a sub-adult

– adult male is feeding in Group 3 at lower trophic levels than the smaller males found in Groups 1 and 2.

The potential difference in male foraging behaviour or diet has not been noted in any other southern elephant seal study. However, in Campagna *et al.* (1999), (as discussed in Chapter one), it was shown that out of seven males in the study two foraging behaviours could be identified: either to remain over the shelf making dives to the sea bed, or to forage over the shelf break and make some dives to the seabed. The authors make no indication that this difference seen in the few animals of the study could reflect a different prey choice (and so foraging strategy) thus further dividing the population. Due to the small sample size in the study it would be unlikely that any such conclusion would be drawn. However, in view of the isotopic data from this study, this observation shown by the above-mentioned study could be indicative of differences in prey choice between the male seals.

The isotopic values of the South American sea lions sampled are significantly different from Group 1 males in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, leading to the conclusion that the South American sea lions and Group 1 males are feeding at different trophic levels and, potentially, on different species of prey. Despite the differences seen between the two species, the values for them do lie close together (Figure 5.1). The values for these two groups are closer than for the other groups of males or for the females. It is interesting to note that, despite their smaller size, the South American sea lions have higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than the Group 1 males, indicating that they are feeding at a slightly higher trophic level than the males.

From the data the male southern elephant seals and the South American sea lions share prey that is more similar than the prey that is taken by the other groups of male southern elephant seals or by the females. Thus it is possible that they also share more similar foraging areas. This could lead to competition between the two species over foraging areas and prey species. If this were so then the pressure of competition with another species may have led the southern elephant seal to develop sex differences in

the foraging behaviour, since the food resource may be insufficient to support both the South American sea lions and the entire southern elephant seal population in the foraging areas most local to the haulout sites. This may have led to the division in foraging behaviour seen in the southern elephant seal populations, with the smaller females travelling considerable distances away from the breeding sites to distant foraging areas, and different prey species, while the larger males remain closer to shore in order to expend less energy, and to be close to the best breeding sites (Hindell *et al.*, 1991, Campagna *et al.*, 1992; McConnell & Fedak, 1996; Campagna *et al.* 1998 & 1999). If competition were a factor then it would appear also that this could have led to the development of different foraging strategies within the male southern elephant seal population.

Alternatively, since the female southern elephant seals and the South American Sea lions have a similar body size, competition over foraging sites and prey species could have developed between them, leading to the female southern elephant seals developing a different foraging strategy.

It is possible that competition between the two species has caused the differences in foraging behaviour seen within the southern elephant seal species, then the mechanism causing the differences is character displacement, whereby in a situation where two similar species are in direct competition for similar resources (i.e. prey) selection favours individuals who are able to exploit an alternative food source. If this is the case in the southern elephant seal, then it is possible that this mechanism has caused the division both between the male and female foraging behaviour and prey selection and the difference in prey selection amongst the male seals in this study.

Additional pressure may be put on the southern elephant seal population by internal competition, i.e. that between the male and female seals. The Patagonian shelf is fertile and supports other predatory species along with the male southern elephant seals and it is believed that it could also support the female seals as well (Campagna *et al.*, 1999). However, the male and female seals of this species do not show overlap within their

foraging areas (Campagna *et al.*, 1999). Although the female seals are more numerous than the males, a male seal requires a much larger energy source than a female due to its larger size and it is possible that the continental shelf could not support as many individuals as supposed.

Interspecific competition has been suggested (Slip, 1995) as a reason for the decline in the other populations of southern elephant seals. Slip (1995) hypothesised that species of Ziphiid odontocete (whales) may cause competition in some of these populations, since they feed on the same squid species as southern elephant seals do in Antarctic waters.

Due to the lack of data on the growth rate of southern elephant seal whiskers, it is impossible to make any definite conclusions as to the potential for seasonal variation along the lengths of the whiskers plotted. It would appear that many of the whiskers from the female seals show a similar trend. Depending on the length of the whisker and how far from the face of the seal it was cut, the whiskers show a decline from the base, a flat period and then an increase at the distal tip of the whisker. The shorter whiskers show no initial decline but otherwise, follow the same trend as the longer whiskers. This indicates that the seals must feed on prey of a higher trophic level during the periods of time corresponding to the base and tips of the whiskers and feed on prey of lower trophic levels in the middle of the whisker. As suggested above, the periods of greater $\delta^{15}\text{N}$ enrichment could correspond to periods when the female is foraging in similar areas to the male seals. The trend to show an increase in $\delta^{15}\text{N}$ greater than 0.7‰ is shown by the majority of the female seals which indicates that the diet eaten by the female seals was of a higher trophic level about a year before the whisker was sampled.

$\delta^{13}\text{C}$ variation can also be linked to changes in trophic level. The $\delta^{13}\text{C}$ in keratin can be enriched by 1-3.4‰ over diet (DeNiro & Epstein, 1978; Tieszen *et al.*, 1983; Ambrose & Norr, 1993; Hobson *et al.*, 1996). However, $\delta^{13}\text{C}$ variations along whisker length for the whiskers from the southern elephant seals do not show the same pattern of changes along the whisker as they do for $\delta^{15}\text{N}$ (Figures 5.3 – 5.14). It is therefore

probable that the variation in the $\delta^{13}\text{C}$ along whisker length seen in many of the elephant seal whiskers is not caused by the same changes such as changes in trophic level that produce the variations seen in $\delta^{15}\text{N}$. It is more likely that the changes seen in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are due to both trophic level changes and changes in prey species. In contrast the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots for the south American sea lions show similar changes in both plots (Figures 5.15 and 5.16) indicating that the same dietary changes, such as an increase or decrease in trophic level and potentially prey size, are causing the variations seen.

No single trend was found for any of the whiskers taken from the male seals and they did not show any significant differences in the statistical comparisons made between the proximal, middle or distal of the whiskers. This indicates that while the groups of males feed on prey items with similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, they do not show any seasonal patterns within the groups.

The South American sea lions show periodicity along their whisker length. This is similar to the patterns found in the whiskers of Stellar sea lions (Hirons *et al.*, 2001). In the Stellar sea lion each cycle corresponds to a year's whisker growth rate. It would appear that the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are linked in the Stellar sea lion since the changes in isotopic variation for both isotopes appear at the same position along the whiskers. Although it is not possible to infer from the data what dietary changes the South American sea lion makes throughout the year to cause the cycling pattern seen, it is likely that the animals sampled show a distinct foraging pattern that may be linked to seasonal changes in prey availability.

Figure 5.22 shows that Group 1 and 2 males and the South American sea lions are feeding at a similar $\delta^{15}\text{N}$ value and thus trophic level to those of the majority of the prey species sampled in this study. The females and Group 3 males have lower $\delta^{15}\text{N}$ values than the fish species and so are feeding at lower trophic levels than the fish. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data drawn from published data for *Martialia hyadesia* (Takai *et al.*, 2000) falls within the group of isotopic data for the female seals while the values for krill (Schell *et*

al., 2000) fall close to them, indicating that these species may share a diet of a similar trophic level. The $\delta^{13}\text{C}$ values for the fish are similar to those of Group 2 and 3 males and the females, but are more depleted than the values for Group 1 and for the South American sea lions.

The plot in Figure 5.23 shows the $\delta^{15}\text{N}$ values shifted by -3 and the $\delta^{13}\text{C}$ values by -1, in order to more easily look at likely prey species of the seals. As is seen on the Figure, only some of the values for Group 1 and the South American sea lions fall within the range of the fish species sampled, and these only fall at the edge of the box. Since the previous figure established that the other groups of seals on the plot were feeding at a lower trophic level than for the prey species sampled, it is unlikely that they are taking any of the sampled species as prey. However, the published values for *M. hyadesia* (Takai *et al.* 2000) fall close to the values for Group 2, indicating that this is a potential prey species for the male southern elephant seals in this group. The value for the krill, however, shows a higher $\delta^{15}\text{N}$ value than that for the female seals.

When the $\delta^{13}\text{C}$ enrichment of whisker keratin over diet is taken to be 3.4‰ as plotted in Figure 5.24, then it can be seen that Group 1 and the South American sea lions show similar values to those of the prey species sampled. These could be likely prey species for these animals. This further shift in $\delta^{13}\text{C}$ values makes little difference to the other groups, except that the value for krill is now similar to that of Group 2.

The fish species that were collected and analysed in this study were more random than would be ideal. In a future study sampling of prey species that are known to appear in stomach or scat analyses would be better. From the prey species data, it would appear that at least some of the prey species are likely to be taken by the males making up Group 1 and by the South American sea lions. No conclusions can be drawn from the data as to what prey the remaining animals are eating, except that they are not eating the species that were sampled during this study. It is possible that Group 2 is feeding largely on squid, if the enrichment of $\delta^{13}\text{C}$ is closer to 1‰. If other species of squid share similar isotopic values to that of *M. hyadesia*, this would be supported by

the data on the stomach content analysis of southern elephant seals from other populations, where a high proportion of squid was found (Rodhouse, 1997).

The prey whose isotopic value makes it most likely to be eaten by the female seal is the krill. However, the foraging locations of the female southern elephant seals make krill an unlikely dietary component. (Dr. M. Lewis, Centro Nacional Patagonico, Argentina, e-mail communication). It has been suggested that the female seals forage in the same area as large concentrations of a species of shrimp are found (Dr. M. Lewis, Centro Nacional Patagonico, Argentina, e-mail communication, 2002) and it is possible that these may account for the relatively low trophic level shown by the females.

For Group 3 males the closest values are for calonid copepods. These are an unlikely dietary component for such a large mammal so it is likely that the prey species of this group of males has not been sampled in this study.

5.4. Summary

1. Significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were found between the male and female southern elephant seals and between the southern elephant seals and the South American sea lions sampled in this study.
2. The male southern elephant seals appear to be split into 3 groups that are significantly different from one another in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.
3. The differences between groups may be due to competition within the species or with species that share similar habitats, prey or foraging areas, for example the South American sea lion, but conclusions cannot be further drawn in this area.
4. Seasonal differences appear to be found in the female southern elephant seals sampled and in some of the South American sea lions, but not in the male southern elephant seals. These differences would be further elucidated with the addition of accurate whisker growth rate data for both of these species.

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5. The fish species sampled are potential prey of Group 1 males and the South American sea lions, more fish species would need to be sampled for conclusions to be drawn on diet.
 6. Group 2 males are potentially eating squid as a major dietary component, although further samples of different squid species would be required for comparison.
 7. The female seals appear to be eating prey with similar isotopic values to krill, although this is not thought to be a likely dietary component. Prey of a similar size is a possibility, for example a species of shrimp.
 8. Group 3 male's diet is unknown. They show unusually low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for a predator of their size. More prey species are required to further elucidate this point, possibly including species of fish and crustaceans that feed close to the seabed on food of low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Chapter 6: Conclusions

CHAPTER 6

Conclusions

6.1. Summary

This study was carried out in order to study the feeding behaviour of two species of seal, the grey seal and the southern elephant seal. The objectives of the study were, for the grey seal, to examine the feeding behaviour of two populations of grey seal over a period of three years, to look for any differences between the populations or changes in diet over the period of the study, and to study the potential for seasonal variation in their diet. For the southern elephant seal the study aimed to examine any potential dietary differences between the male and female seals (Hindell *et al.*, 1991; Campagna *et al.*, 1995; 1998; 1999; McConnell & Fedak, 1996). For both the species of seal the study aimed to examine whether stable isotope analysis was feasible to be used to study dietary change over the period of whisker growth (i.e. seasonal variation) and to identify species of prey that may be a major dietary component for the seals.

In order to achieve these objectives it was necessary to first ensure that a single whisker taken from a seal would be isotopically representative of the rest of the whiskers on the animal. Whiskers from six seals from a captive seal facility, fed a single species of fish, were analysed to attempt to establish the amount of background variation that might be expected in wild seals. However, while the seals were fed the same species of fish, the sizes of the fish varied, leading to greater background variation than was expected, and than predicted by the similar study on harbour seals which used fish of a single species and size (Hobson *et al.*, 1996)

Two female grey seals, caught on the Isle of May were fed a diet of herring, all of similar sizes. A whisker was sampled from each of them after a period in captivity. The analysis of the whiskers showed a large decrease at the same point for both $\delta^{13}\text{C}$

and $\delta^{15}\text{N}$. This point was assumed to be the point at which the seals' diet changed from their wild diet to the herring fed to them in captivity. The growth rate calculated for the grey seals is an average of 0.41mm/day. Values for the growth rate of whiskers from Harbour seals is 0.33mm/day (Hirons *et al.*, 2001) and for human hair, 0.35mm/day (Saitoh, 1969).

Samples from four animals were analysed for amino acid content, to determine that pigmentation, sex or species of seal does not affect the amino acid content of the whiskers. The samples taken from the beginning and end of all the whiskers sampled showed a small decrease in cystine between the first and last sample. The change, however, is within the range of variation found between samples from two human subjects (O'Connell *et al.*, 2001).

The analysis of whiskers from grey seals from the two populations of the Isle of May and North Rona for 1997, 1998 and 1999 showed three general trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the whiskers: an increase from base to tip, a decrease from base to tip, and no overall change along the whisker length. Since the six seals sampled in all three years did not show the same trends in each of the years of the study, this is unlikely to indicate different foraging strategies shown by different groups of seals within a population. It is more likely that the grey seals all show various strategies, possibly depending upon prey abundance.

The two populations showed significant differences between each other, overall and for each year of the study, indicating that the two populations show dietary differences that may relate to prey availability. Over the years of the study the difference in $\delta^{13}\text{C}$ between the populations decreases, indicating that the diets of the populations are becoming more similar over time.

The populations also showed significant differences in both isotopes between years, indicating that grey seals from both populations have shown dietary changes over the years of the study. The differences seen in the Isle of May populations are greater than those seen in the North Rona population. One possible cause of the differences seen is

over-fishing by the commercial and industrial fleets in the North Sea. Due to the over-fishing causing a change in the availability of the prey of the grey seals and so causing the foraging differences that have been found in this study. The areas around the North and West of Scotland are less heavily fished by the commercial fleets, so the seals from North Rona show less change than those from the Isle of May.

The fish species on which the grey seals seem likely to be feeding on are similar to those found in scat and stomach content analysis (Hammond *et al.*, 1994 a & b). Previous studies (Hammond *et al.*, 1994 a and b) indicate that sandeels are a popular prey species of the grey seal, the isotopic data from this study seem to support these findings.

The whiskers collected from the southern elephant seals during the study showed that the male and female seals differed isotopically, with the females showing less enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than most of the male seals, indicating that the females prey on different species from the males. The differences seen are supported by the differences found in the foraging areas of the two sexes of southern elephant seals by studies that have tagged and satellite tracked male and female southern elephant seals from different populations (Hindell *et al.*, 1991; Campagna *et al.*, 1995; 1998; 1999; McConnell & Fedak, 1996)

In addition to the isotopic differences seen between the male and female seals, the male seals show three groups, each significantly different from the others. Two of these show higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the female seals and one shows lower values. This indicates that the male southern elephant seals show different foraging strategies that have not been previously observed in either tracking studies or through studies analysing stomach contents or scats.

The comparisons made with the isotopic values of the southern elephant seals and fish sampled during this study show that Group 1 males seem to be feeding on some of the species of fish collected during the study, or on species similar to them. Group 2 males appear to be feeding on the squid *M. hyadesia* or on species of fish or squid with

values isotopically similar to it. Both the female seals and Group 3 males show $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values lower than the other two groups of males and thus feed at lower trophic levels than them. The isotopic values shown by the female seals are similar to that found by a species of krill. Although this is not thought to be a likely to be a prey species of the female seals, it is likely that they are feeding on a species in a similar position in the food chain, and possibly of a similar size. A species of shrimp is found in high concentrations in the female seals foraging areas, and may be a possible prey species for the seals (Dr. M. Lewis, Centro Nacional Patagonico, Argentina, email communication, 2001), although there is as yet no evidence that this is the case and more species of fish, squid, krill and other possible prey species are needed to enable conclusions regarding the prey species of these seals to be made.

The male southern elephant seal whiskers show little overall trends along their length, whilst most of the female seals' whiskers show an increased enrichment in $\delta^{15}\text{N}$ towards the tip end of the whiskers in both years that the southern elephant seals were sampled. This shows that the female seals show a consistent foraging trend, which the males do not share.

6.2. Comparison of stable isotope analysis with more traditional methods of isotopic analysis

The data from stable isotopic analysis is unable to give exact data on prey species taken by an animal. The data that is gained from such analysis can only give an average value for the total diet eaten by an animal. As such, this is a constraint of the methodology. However a large amount of information can be gained despite this problem, as demonstrated by this study, and has included data not accessible by more traditional methods of dietary analysis.

Analysis of the whiskers showed that the diet of the grey seals differs between the two populations of the Isle of May and North Rona and the diets have changed over time. Previous studies have collected data from scats over several seasons, but have not shown these changes. Comparative studies on the two populations have not been previously carried out. Scat analyses have shown that the grey seals from the Inner and Outer Hebrides do show seasonal changes. This is supported by the data showing greater isotopic variations along the length of whiskers than that can be accounted for by background isotopic variations. The comparison of the isotopic variations of the grey seal to the fish samples shows that the prey which the seals are likely to be feeding on is similar to the prey found in the scat and stomach content analysis of grey seals (Rae, 1960 & 1973; Green & Williams, 1986; Thompson *et al.*, 1991; Rodhouse *et al.*, 1992; Green & Burton, 1993; Antonelis *et al.*, 1994; Bowen & Harrison, 1994; Hammond *et al.*, 1994; Slip, 1995; Tollit *et al.*, 1997; Brown & Pierce, 1998; Kalges & Bester, 1998; Lawson *et al.*, 1998). Tracking studies on grey seals at the Farne islands (close to the Isle of May) show that the grey seals do not appear to show a distinct foraging trend (McConnell *et al.*, 1999). In general, the isotopic data and data from traditional methods of dietary analysis show good agreement. While traditional methods tend to show bias (Boyd *et al.*, 1994; Slip, 1995), the foraging trips made by the grey seal are insufficiently long to overly bias the data away from the prey species taken by the seals for the majority of their time foraging.

The data from the southern elephant seals, however, show behaviour not previously discovered by traditional methods: the sex differences data and male groups of isotopic data. While differences in foraging strategies between the two sexes have been well documented in this species, the methods used to collect this information (tracking by radio or satellite) are unable to collect data on the species of prey on which the animals are feeding. The biases that are known to act in both stomach and scat analysis appear to skew the data from these studies away from the actual diet of the female southern elephant seals. The traditional methods have failed to show any sex differences found

in the prey selection of the southern elephant seals, leading to the conclusion that the results in the above-mentioned studies may show only the diet of the female seals in the few days during which they are making their return trips over the continental shelf and thus foraging in a similar habitat to the male seals, and probably eating a similar diet to them. The studies, if this is the case, are biased to a few days of the female southern elephant seals' foraging cycle, and give a false indication of the diet of these animals. While stable isotope analysis, as used in this study, cannot provide details of which prey species the female seals are in fact eating, it appears that they are eating different or smaller prey than that previously supposed.

Traditional studies have failed to demonstrate an apparent division in male southern elephant seals' foraging strategies, possibly since studies which have been conducted on male southern elephant seals' foraging behaviour have only included small sample numbers (e.g. five in Campagna *et al.*, 1999). It is also possible that the differing male foraging strategies have not been previously noted since the males forage in similar areas with similar foraging patterns whilst evidently taking different prey species.

It would appear that traditional methods are more accurate for the study of grey seal diet than for that of the southern elephant seals. The method of stable isotope analysis has an advantage over the traditional methods in that samples can be collected once yearly and used to study possible seasonal trends, and can be compared to samples from previous years to look for changes in feeding behaviour.

6.3. Further work.

1. As with any study on the behaviour of a species of animal a long term study would be desirable! For both species, sample collection on a yearly basis would elucidate any feeding trends that have not been demonstrated in this study, and would exhibit if the seals show patterns longer than a year in their foraging

- behaviour. A longer study period would also examine whether the changes seen in the Isle of May and North Rona populations over the three years of this study are part of a long term cycle shown by the grey seals or if are due to external pressures such as over fishing.
2. The expansion of the study to include other grey seal and also harbour seal populations around Britain would make it possible to examine whether changes in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are also seen in these populations, particularly if the changes seen are due to fishing pressures.
 3. The study of samples from other populations of southern elephant seals would show whether the same sex differences are shown in these populations where foraging differences have also been identified, and would also show whether the male seals in other populations also show different foraging behaviours. Since the Pensinsular Valdés population is the only population of southern elephant seals that is showing an increase in numbers, the data from such a study could show whether the feeding behaviour or prey species used by the other populations differ from those used by the Pensinsular Valdés population and are thus affecting the fitness of the other populations.
 4. The sampling of the same individuals in each year would determine whether some individuals follow set foraging patterns each year, or whether no overall patterns are shown. This would be particularly useful in the further study of the differences in the male southern elephant seals diet, where it could show whether the males feeding behaviour remains the same from year to year, or whether their behaviour changes.
 5. A greater sample size for the southern elephant seals, in particular more male seals, with a wider range of age classes would show if there were more than the three groups of males as shown in this study, and how these trends were distributed in the population.

6. The isotopic analysis of a greater variety of fish and other prey item species to build a data base, and make the identification of fish species in the diet of the seals more accurate, and would be advantageous in further examination of the seals' diet. The identification of fish species would be largely based on the analysis of scats and stomach contents, but would also include species that are found in large concentrations in foraging areas similar to those of the seals, identified by tracking studies.
7. To further study the accuracy of traditional methods of dietary study in pinnipeds, the prey remains from scats and stomach contents could also be isotopically analysed, and compared to the isotopic content of the seals. This would give an indication of whether scat/stomach content analysis is an accurate indication of the diet of the seals, or whether the majority of the diet is underrepresented by traditional methods.
8. The isotopic analysis of historical and archaeological samples (obtained from museum skins or bones from archaeological sites) would show if the diet of pinnipeds has shown changes throughout history. If changes were seen, this could be an indication of the impact of human activity on pinnipeds: Alternatively, changes could be due to environmental changes.
9. The determination of the growth rate of southern elephant seals whiskers would aid interpretation of results from this and further studies. The growth rate can be successfully calculated by using the same method as in this study, or by injections containing a compound enriched with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Both methods require the captivity of at least one and ideally more individuals. In an ideal situation the seals should be kept in captivity for at least one year, to study any possible seasonal effects on whisker growth rate. In addition to this, the growth rate from both male and female seals should be calculated to better interpret possible seasonal variations in diet.

10. The $\delta^{13}\text{C}$ enrichment of whisker keratin over diet is not well documented in any species. In order that better use can be made of data from this study and further studies this needs to be better quantified. Feeding experiments on captive seals where both the food and whisker keratin are both analysed and enrichment levels calculated should be conducted.
11. The rate of incorporation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the diet into the whisker keratin would also be useful. This could be studied in a similar way to that of the whisker growth rates, by injecting enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ into captive seals and then sampling whiskers on a regular basis, possibly every 2 days, until a peak in isotopic variation is detected in the whisker analysis.

6.4. In Conclusion

This research has shown that stable isotope analysis has huge potential for further use in the study of pinniped feeding behaviour. The combination of this method with more traditional methods of dietary studies can provide information on the behaviour of seals that has hitherto not been observed by the sole use of traditional methods, and it is believed that the continuation of this study could provide more data still. The better understanding of pinniped foraging behaviour will become more important, both in Britain and in the areas where the southern elephant seals forage, particularly if human exploitation of the oceans continues to increase as it has done in recent years. Since the feeding behaviour of pinnipeds and their possible impact on the fisheries are always of political interest as well as scientific interest, a better understanding of pinniped prey selection is of considerable importance.

Appendix 1 : Grey Seal Data

Appendix 1

Sample	Length	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C/N ratio	Sample	Length	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C/N ratio
A9_1	3.0	943	-14.42	307	14.17	3.59	A9*-1	2.5	909	-13.70	309	15.32	3.43
A9_2	7.0	1014	-13.46	340	15.02	3.48	A9*-2	5.0	899	-13.74	306	15.34	3.43
A9_3	11.0	892	-13.59	299	14.69	3.48	A9*-3	7.5	798	-13.72	271	15.60	3.43
A9_4	15.0	945	-13.84	316	14.29	3.49	A9*-4	10.0	708	-13.70	242	15.55	3.41
A9_5	19.0	917	-14.11	305	13.82	3.51	A9*-5	13.0	726	-14.44	243	14.95	3.49
A9_6	23.0	852	-14.75	276	13.59	3.60	A9*-6	16.0	693	-14.55	234	15.13	3.46
A9_7	27.0	1235	-14.08	407	13.72	3.54	A9*-7	20.0	810	-13.89	273	15.19	3.46
A9_8	31.0	1109	-14.18	360	13.50	3.60	A9*-8	24.5	962	-13.90	323	15.28	3.47
A9_9	35.0	1112	-14.18	362	13.48	3.59	A9*-9	30.0	979	-13.73	329	15.00	3.47
A9_10	39.0	1010	-14.28	333	13.61	3.53	A9*-10	35.0	665	-13.75	222	14.95	3.49
A9_11	43.0	995	-14.32	328	13.98	3.54	A9*-11	41.0	1056	-13.83	356	15.16	3.46
A9_12	47.0	855	-14.51	281	14.72	3.55	A9*-12	47.0	676	-13.86	227	15.09	3.47
A9_13	51.0	964	-14.52	315	13.61	3.58	A9*-13	54.0	969	-14.07	325	15.25	3.47
A9_14	55.0	891	-14.63	291	13.71	3.57	A9*-14	61.0	650	-14.29	219	14.56	3.46
A9_15	59.0	785	-14.90	255	13.92	3.60	A9*-15	73.0	725	-14.15	245	14.30	3.45
A9_16	63.0	942	-14.75	305	14.78	3.61	1a*1	2	982	-14.31	334	12.65	3.43
A9_17	67.0	834	-15.01	268	14.86	3.63	1A*2	4	972	-14.04	329	13.59	3.44
1A_1	3.0	1066	-13.31	354	14.19	3.51	1A*3	6	1125	-13.73	383	14.30	3.43
1A_2	6.0	1002	-13.31	336	14.64	3.48	1A*4	8	973	-13.72	330	15.05	3.44
1A_3	9.0	1072	-13.36	359	14.73	3.48	1A*5	10	1102	-13.81	373	15.63	3.45
1A_4	12.0	1161	-13.52	389	14.56	3.48	1A*6	12	960	-13.81	325	15.48	3.45
1A_5	15.0	1065	-13.71	357	14.24	3.48	1A*7	14	932	-13.70	316	15.88	3.44
1A_6	18.0	1075	-13.86	361	14.07	3.48	1A*8	16.5	1112	-13.63	375	15.95	3.46
1A_7	21.0	1150	-13.97	383	13.88	3.50	1A*9	19	1030	-13.59	346	15.41	3.48
1A_8	24.0	1084	-13.93	363	14.02	3.48	1A*10	21.5	949	-14.21	321	15.37	3.45
1A_9	27.0	1060	-13.97	352	13.72	3.51	1A*11	24.5	974	-14.43	328	15.42	3.46
1A_10	30.0	1115	-13.93	371	13.57	3.51	1A*12	27.5	928	-14.30	313	15.32	3.46

1A_11	33.0	930	-13.92	312	13.43	3.48	1A*13	30.5	1005	-14.23	340	15.22	3.45
1A_12	36.0	968	-13.98	322	13.78	3.51	1A*14	34	1161	-13.88	391	15.47	3.46
1A_13	39.0	892	-14.14	294	13.23	3.54	1A*15	37.5	1177	-13.84	395	15.25	3.47
1A_14	42.0	1039	-13.95	346	13.53	3.50	1A*16	41	1007	-14.02	339	15.18	3.46
1A_15	45.0	998	-13.96	332	13.87	3.51	1A*17	44.5	950	-13.66	320	15.07	3.47
1A_16	48.0	1014	-13.99	340	13.85	3.48	1A*18	48	916	-14.02	308	14.92	3.47
1A_17	51.0	994	-14.05	332	13.59	3.50	1A*19	52	964	-14.08	325	14.81	3.46
1A_18	54.0	877	-14.10	288	13.54	3.55	1A*20	56	1006	-13.84	338	15.20	3.47
1A_19	57.0	996	-13.91	331	13.45	3.51	1A*21	60	954	-14.06	323	15.11	3.45
1A_20	60.0	953	-13.89	318	13.69	3.50	1A*22	64.5	920	-13.93	310	15.33	3.47
1A_21	63.0	986	-13.93	329	13.79	3.50	1A*23	69	932	-14.22	316	14.96	3.44
1A_22	66.0	893	-13.85	299	14.08	3.49	1A*24	74	906	-14.35	307	14.64	3.44
1A_23	69.0	889	-13.76	298	14.73	3.48	1A*25	79.5	961	-14.58	322	14.57	3.48
1A_24	72.0	853	-13.95	284	14.98	3.50	1A*26	85	875	-14.45	295	14.53	3.46
1A_25	75.0	1015	-13.89	338	14.75	3.50	1A*27	91	823	-14.29	276	14.30	3.47
1A_26	78.0	946	-14.07	316	14.70	3.49	1A*28	97.5	680	-14.41	229	14.10	3.46
1A_27	81.0	979	-14.14	327	14.12	3.49	1A*29	108.5	574	-14.25	194	14.13	3.45
1A_28	84.0	1113	-14.22	372	13.38	3.49	AZ_1	2.5	1444	-14.02	483	12.65	3.49
O3_1	3.0	1121	-13.76	378	15.73	3.46	AZ_2	4.5	1214	-13.92	407	12.97	3.48
O3_2	6.5	1093	-13.60	370	16.04	3.45	AZ_3	6.5	970	-13.93	326	13.24	3.47
O3_3	9.5	1038	-13.61	350	15.63	3.46	AZ_4	8.5	1159	-13.88	391	13.46	3.46
O3_4	12.5	890	-13.98	298	16.07	3.48	AZ_5	10.5	1182	-13.74	395	13.96	3.49
O3_5	15.5	941	-13.83	317	16.14	3.47	AZ_6	12.5	1142	-13.77	383	13.80	3.48
O3_6	18.5	904	-14.04	303	15.85	3.48	AZ_7	14.5	1156	-13.79	387	14.02	3.49
O3_7	21.5	889	-14.26	296	15.49	3.50	AZ_8	17.0	1164	-13.95	390	13.35	3.48
O3_8	24.0	864	-14.17	290	15.45	3.48	AZ_9	19.5	1090	-14.09	365	13.02	3.48
O3_9	27.5	884	-14.28	296	16.08	3.49	AZ_10	22.5	1250	-14.16	418	13.03	3.49
O3_10	31.0	861	-14.45	289	15.74	3.48	AZ_11	25.5	1215	-14.21	403	12.86	3.52
O3_11	35.0	883	-14.54	294	15.56	3.51	AZ_12	28.5	1181	-14.29	393	12.47	3.51
O3_12	39.0	796	-14.90	266	15.34	3.48	AZ_13	32.0	1258	-14.22	418	12.97	3.51
O3_13	43.5	754	-14.67	249	15.41	3.54	AZ_14	35.5	1257	-13.93	416	13.87	3.52
O3_14	49.0	947	-14.56	313	16.06	3.53	AZ_15	38.5	1047	-13.95	347	13.97	3.52

O3_15	55.5	1037	-14.82	335	15.36	3.61	AZ_16	41.5	1038	-14.25	345	13.73	3.51
O3_16	63.0	894	-15.00	291	15.07	3.59	AZ_17	44.5	1056	-14.17	356	13.74	3.46
NZ_1	3.0	1613	-12.96	538	15.34	3.50	AZ_18	48.0	1180	-13.99	398	14.22	3.46
NZ_2	5.0	1084	-13.05	362	15.35	3.49	AZ_19	51.0	971	-14.39	328	13.72	3.45
NZ_3	7.0	1103	-12.91	367	15.44	3.50	AZ_20	54.5	991	-14.44	335	13.39	3.45
NZ_4	9.0	1156	-12.95	387	15.61	3.49	AZ_21	58.0	867	-14.42	294	13.32	3.44
NZ_5	11.0	1282	-13.03	425	15.61	3.52	AZ_22	62.0	940	-14.47	318	13.29	3.45
NZ_6	13.0	1107	-12.94	369	15.75	3.50	AZ_23	66.5	1021	-14.47	343	13.06	3.48
NZ_7	15.5	1296	-12.95	432	15.80	3.50	AZ_24	71.0	827	-14.36	277	13.34	3.48
NZ_8	17.5	1173	-12.84	392	15.81	3.49	AZ_25	75.5	772	-14.38	256	13.10	3.51
NZ_9	19.5	1108	-12.92	370	15.66	3.50	AZ_26	80.5	741	-14.72	248	13.04	3.49
NZ_10	21.5	1189	-13.33	394	15.70	3.52	AZ_27	85.5	951	-14.79	317	12.55	3.49
NZ_11	23.5	1117	-13.20	373	16.05	3.50	AZ_28		628	-15.12	210	11.94	3.49
NZ_12	26.0	1253	-13.07	416	16.23	3.51	A8_1	2.5	1181	-13.85	392	15.70	3.51
NZ_13	28.5	1233	-13.05	403	16.24	3.57	A8_2	5.0	1091	-13.60	365	15.83	3.49
NZ_14	31.0	1161	-12.98	385	16.28	3.52	A8_3	7.5	1048	-13.71	351	15.85	3.49
NZ_15	34.0	1089	-13.08	361	16.25	3.52	A8_4	10.0	867	-13.81	290	15.88	3.48
NZ_16	37.0	1082	-13.13	359	16.34	3.52	A8_5	13.0	1081	-13.82	357	15.58	3.53
NZ_17	40.0	1140	-13.19	376	16.36	3.54	A8_6	16.0	979	-13.98	325	15.26	3.51
NZ_18	43.0	978	-13.07	325	16.44	3.51	A8_7	19.0	1086	-14.12	358	14.39	3.54
NZ_19	46.5	963	-13.19	320	16.39	3.51	A8_8	22.0	1028	-14.31	338	14.67	3.55
NZ_20	50.0	953	-13.22	317	16.19	3.51	A8_9	25.0	949	-14.25	316	14.45	3.51
NZ_21	54.0	936	-13.25	311	16.32	3.51	A8_10	28.0	1055	-14.37	349	14.49	3.52
NZ_22	58.0	881	-13.16	292	16.48	3.52	A8_11	31.0	932	-14.41	309	14.90	3.52
NZ_23	62.5	872	-13.23	290	16.84	3.52	A8_12	34.5	1026	-14.33	340	15.25	3.51
NZ_24	67.0	948	-13.31	315	16.75	3.52	A8_13	38.0	1020	-14.21	333	15.11	3.57
NZ_25	71.5	813	-13.26	270	16.86	3.51	A8_14	41.5	1012	-14.22	330	15.24	3.58
NZ_26	76.5	856	-13.37	284	16.91	3.51	A8_15	45.0	981	-14.22	319	14.98	3.59
NZ_27	81.5	738	-13.52	243	16.97	3.54	A8_16	49.0	1014	-14.39	325	14.37	3.64
NZ_28	87.0	681	-13.39	226	16.91	3.51	A8_17	53.0	979	-14.55	314	13.90	3.63
A8_24	88.0	751	-15.08	242	14.76	3.62	A8_18	57.0	948	-14.75	302	12.58	3.66
A8_25	95.5	1002	-15.13	319	15.18	3.66	A8_19	61.5	873	-14.97	276	11.98	3.70

A8_26	104.0	599	-14.80	194	15.72	3.59	A8_20	66.5	906	-15.04	287	12.52	3.68
							A8_21	71.5	862	-15.27	274	12.39	3.67
							A8_22	77.0	772	-15.12	247	13.41	3.64
							A8_23	82.0	741	-15.29	237	14.00	3.65
1A!_1	2	0.51	-14.16	0.159	15.23	3.75	G44!_1	2.5	1006	-14.1601	329.3	14.0848	3.56
1A!_2	4	0.142	-13.27	0.383	15.05	3.48	G44!_3	6.5	1689	-13.2483	581.4	13.7732	3.39
1A!_3	6	0.165	-13.1	0.393	15.02	3.46	G44!_5	10.5	1513	-13.1416	522.7	13.6134	3.38
1A!_4	8	0.983	-13.28	0.329	14.91	3.49	G44!_7	14.5	1369	-13.4957	471.8	13.8477	3.39
1A!_5	10	0.022	-13.22	0.344	14.94	3.46	G44!_9	18.5	1049	-13.4362	357.9	13.9008	3.42
1A!_6	12	0.288	-13.26	0.438	14.95	3.43	G44!_11	22.5	1263	-13.3051	433.7	13.8587	3.40
1A!_7	14	0.363	-13.21	0.465	14.72	3.42	G44!_13	26.5	1152	-13.4251	393.2	14.0453	3.42
1A!_8	16	0.296	-13.22	0.44	14.22	3.44	G44!_15	30.5	1153	-13.4557	392.1	14.1065	3.43
1A!_9	18	0.167	-13.24	0.396	14.37	3.43	G44!_17	34.5	1010	-13.801	342	14.1006	3.45
1A!_10	20	0.016	-13.22	0.344	14.66	3.44	G44!_19	39.5	1179	-14.0185	400.4	13.6532	3.44
1A!_11	22	0.941	-13.32	0.319	14.84	3.44	G44!_21	45.0	1279	-14.1825	434.7	13.4171	3.43
1A!_12	24	0.083	-13.28	0.37	14.87	3.42	G44!_23	51.0	1240	-14.1274	420.1	13.5138	3.44
1A!_13	26	0.951	-13.33	0.322	14.95	3.44	G44!_25	57.0	1045	-14.0272	351.3	14.4227	3.47
1A!_14	28.5	0.202	-13.24	0.411	15.06	3.41	G44!_27	64.0	976.8	-14.0248	325.8	14.6791	3.50
1A!_15	30.5	0.035	-13.24	0.348	14.93	3.47	G44!_29	71.0	1025	-14.2735	342.2	14.2615	3.49
1A!_16	32.5	0.093	-13.3	0.371	14.91	3.44	G44!_31	79.5	967.3	-14.2222	321.5	14.0273	3.51
1A!_17	34.5	0.113	-13.35	0.379	14.91	3.43	G44!_33	89.0	992.2	-14.1889	330.2	14.2406	3.51
1A!_18	36.5	0.968	-13.49	0.327	14.81	3.45	G44!_35	107.0	511.1	-14.8054	164.1	14.3695	3.63
1A!_19	38.5	0.173	-13.61	0.4	14.33	3.42	W7!_1	3.0	918.1	-14.3129	293.3	13.7396	3.65
1A!_20	40.5	0.984	-13.95	0.332	13.77	3.46	W7!_3	8.0	1325	-13.6312	454.7	13.0351	3.40
1A!_21	42.5	0.033	-14.06	0.35	13.45	3.44	W7!_5	13.0	1239	-13.6658	424.3	13.3625	3.41
1A!_22	44.5	0.942	-14.22	0.315	13.16	3.48	W7!_7	18.5	1217	-13.6904	416.2	13.3599	3.41
1A!_23	46.5	0.827	-14.23	0.278	13.29	3.47	W7!_9	23.5	1020	-13.6277	346.3	14.0295	3.44
1A!_24	48.5	0.844	-14.49	0.28	13.21	3.52	W7!_11	29.5	1232	-13.5885	421.2	13.9677	3.41
1A!_25	50	0.013	-14.23	0.345	13.37	3.43	W7!_13	36.0	1157	-13.7676	390	13.9253	3.46
1A!_26	53	0.025	-14.19	0.349	13.25	3.43	W7!_15	47.5	1296	-13.781	434.1	14.0792	3.48
1A!_27	56	0.074	-14.1	0.365	13.72	3.43	X2!_1	2.5	990.8	-16.2152	322.1	14.3023	3.59
1A!_28	59	0.102	-14.15	0.375	13.75	3.43	X2!_3	6.5	1205	-15.3709	408.3	14.8514	3.44

1A!_29	62.5	0.11	-14.25	0.378	13.4	3.43	X2!_5	10.5	1113	-15.598	377.6	14.1123	3.44
1A!_30	66	0.002	-14.2	0.338	13.36	3.46	X2!_7	15.0	1193	-15.5395	406.4	14.0785	3.42
1A!_31	70	0.162	-14.19	0.396	13.46	3.43	X2!_9	21.0	1335	-14.7595	457.1	14.3339	3.41
1A!_32	74	0.014	-14.25	0.343	13.54	3.44	X2!_11	27.5	1823	-14.7214	630.6	13.0052	3.37
1A!_33	78.5	0.089	-14.29	0.372	13.16	3.42	X2!_13	34.5	1238	-15.6298	419.1	13.9246	3.45
1A!_34	83.5	0.155	-14.44	0.394	13.02	3.42	X2!_15	42.0	1365	-15.8914	463.8	14.5778	3.43
1A!_35	88.5	0.067	-14.55	0.361	13.16	3.45	X2!_17	49.5	1168	-16.6454	392.8	13.9003	3.47
1A!_36	94.5	0.055	-14.73	0.355	12.72	3.46	X2!_19	58.0	1306	-16.912	439.3	13.5584	3.47
1A!_37	107.5	0.132	-14.47	0.382	13	3.45	X2!_21	67.5	1007	-17.1799	335.9	13.2893	3.50
A9!_1	2.5	0.253	-14.55	0.409	12.15	3.57	X2!_23	77.5	925.1	-16.3797	306.9	14.0526	3.52
A9!_2	4.5	0.145	-14.08	0.384	12.54	3.48	X2!_25	94.5	1469	-15.9545	491	14.6717	3.49
A9!_3	6.5	0.171	-14.08	0.396	12.31	3.45	BZ!_1	2.5	1139	-14.4703	376.3	14.3761	3.53
A9!_4	8.5	0.22	-14.07	0.413	11.97	3.45	BZ!_3	6.5	1488	-14.3661	509.8	13.4009	3.41
A9!_5	10.5	0.162	-13.86	0.393	12.59	3.45	BZ!_5	10.5	1266	-14.1044	432	14.6645	3.42
A9!_6	12.5	0.262	-13.99	0.428	12.08	3.44	BZ!_7	14.5	1119	-14.1236	379.3	15.307	3.44
A9!_7	14.5	0.285	-13.84	0.434	12.25	3.45	BZ!_9	19.5	1314	-14.0393	449.4	15.1427	3.41
A9!_8	16	0.154	-13.82	0.388	12.11	3.47	BZ!_11	25.5	1294	-14.1553	440.8	15.4245	3.42
A9!_9	18.5	0.138	-13.81	0.386	12.07	3.44	BZ!_13	33.0	1445	-14.1495	494.2	15.265	3.41
A9!_10	20.5	0.245	-13.91	0.424	11.89	3.43	BZ!_15	41.0	1247	-14.2327	422	15.3722	3.45
A9!_11	22.5	0.115	-13.99	0.378	12.08	3.44	BZ!_17	49.0	1112	-14.3326	374	15.5927	3.47
A9!_12	24.5	0.155	-13.94	0.393	12.7	3.43	BZ!_19	57.5	1177	-14.3988	397.7	15.584	3.45
A9!_13	26.5	0.049	-14.05	0.355	12.97	3.45	BZ!_21	66.5	1057	-14.5769	353.3	15.0411	3.49
A9!_14	29	0.15	-13.91	0.391	13.74	3.43	BZ!_23	75.5	1001	-14.4828	333.8	15.5224	3.50
A9!_15	31.5	0.219	-13.76	0.413	14.17	3.44	BZ!_25	86.0	928.3	-14.5637	307.6	15.8335	3.52
A9!_16	34	0.215	-13.67	0.413	14.79	3.43	BZ!_27	100.0	664.1	-15.0454	217.1	15.4507	3.57
A9!_17	36.5	0.119	-13.69	0.379	15.08	3.45	BZ!_29	124.5	909.4	-15.17	299.3	15.3378	3.54
A9!_18	39	0.897	-13.79	0.301	15.24	3.48	R4!_1	3.0	1211	-14.4319	407.5	14.2716	3.47
A9!_19	41.5	0.916	-13.8	0.309	15.26	3.46	R4!_3	7.0	1463	-13.9519	505	13.1734	3.38
A9!_20	44.5	0.249	-13.8	0.426	14.96	3.42	R4!_5	11.0	1049	-14.0462	359.7	13.2984	3.40
A9!_21	47.5	0.099	-13.73	0.371	14.98	3.45	R4!_7	15.0	1043	-13.9974	358.8	14.4051	3.39
A9!_22	50.5	0.053	-13.62	0.354	14.77	3.47	R4!_9	19.5	1081	-14.2249	371.5	15.2644	3.39
A9!_23	53.5	0.038	-13.7	0.35	14.9	3.46	R4!_11	25.0	1074	-14.3895	368.2	15.9142	3.40

A9!_24	56.5	0.104	-13.86	0.373	14.99	3.45	R4!_13	31.0	1009	-14.7064	340.9	15.8068	3.45
A9!_25	60.5	0.102	-13.86	0.372	15.24	3.45	R4!_15	37.5	953.9	-14.6604	322.4	16.0979	3.45
A9!_26	64.5	0.003	-13.93	0.338	15.11	3.46	R4!_17	44.5	784.4	-14.6392	262.9	16.8853	3.48
A9!_27	68.5	0.058	-13.87	0.358	15.17	3.45	R4!_19	52.5	746.8	-15.1855	245.1	16.2309	3.55
A9!_28	72.5	0.936	-13.82	0.316	15.17	3.45	R4!_21	62.5	1201	-14.7525	405.1	15.9543	3.46
A9!_29	77.5	0.019	-13.91	0.345	14.99	3.44	R4!_23	73.5	912.8	-14.9074	303.9	16.2591	3.50
A9!_30	83	0.07	-13.99	0.36	14.84	3.47	R4!_25	85.5	912	-14.6971	303.4	15.672	3.51
A9!_31	89	0.107	-14	0.374	14.92	3.45	R4!_27	99.0	952	-14.5861	316.7	15.854	3.51
A9!_32	96	0.372	-14.05	0.469	14.86	3.41	R4!_29	118.5	1330	-14.4109	447	14.4083	3.47
A9!_33	104	0.965	-14.37	0.324	14.3	3.47	G45!_1	2.5	1027	-14.3639	335.1	12.9813	3.58
A9!_34	116	0.126	-14.19	0.381	13.83	3.45	G45!_3	6.5	1320	-14.0359	449.2	12.4828	3.43
G49!_2	4.5	0.441	-13.8	1.291	12.58	3.41	G45!_5	10.5	1301	-13.6495	445.1	13.875	3.41
G49!_4	8.5	0.473	-13.89	1.383	12.38	3.41	G45!_7	14.5	1211	-13.5781	412.3	14.429	3.43
G49!_6	12.5	0.454	-13.85	1.327	12.4	3.41	G45!_9	18.5	1143	-13.7095	389.7	13.7548	3.42
G49!_8	16.5	0.498	-13.93	1.448	12.78	3.39	G45!_11	23.0	835.3	-13.8987	281.7	13.9192	3.46
G49!_10	20	0.393	-13.94	1.151	13.11	3.42	G45!_13	28.0	988.9	-13.8859	335.3	13.6949	3.44
G49!_12	24.5	0.4	-13.85	1.173	13.45	3.42	G45!_15	33.5	1234	-13.8541	421.9	14.379	3.41
G49!_14	29	0.396	-13.89	1.164	13.62	3.43	G45!_17	39.5	962.5	-13.7724	324.9	14.6288	3.46
G49!_16	34	0.459	-13.94	1.347	13.67	3.42	G45!_19	46.0	1220	-13.7218	415.5	14.813	3.43
G49!_18	39.5	0.542	-13.94	1.581	13.72	3.4	G45!_21	53.0	1144	-13.7267	388.3	14.7703	3.44
G49!_20	45.5	0.568	-14.05	1.655	13.13	3.4	G45!_23	60.5	1172	-14.0044	398.2	13.5397	3.43
G49!_22	51.5	0.465	-14.26	1.369	12.85	3.44	G45!_25	68.5	1047	-14.3347	352.9	13.6239	3.46
G49!_24	58	0.453	-14.21	1.335	12.53	3.44	G45!_27	78.0	1007	-14.807	338.2	12.2476	3.47
G49!_26	65	0.542	-14.21	1.59	12.22	3.42	G45!_29	89.5	1071	-14.9409	359.6	11.8409	3.47
G49!_28	73	0.439	-14.45	1.301	12.21	3.46	G45!_31	104.5	1138	-14.4143	380.7	13.7965	3.49
G49!_30	84	0.454	-14.59	1.349	11.61	3.47	AZ!_1	3.0	1261	-14.7931	422.2	10.6688	3.48
G48!_2	4	0.643	-13.93	1.856	12.47	3.37	AZ!_3	7.0	1712	-14.4542	588.4	10.5401	3.39
G48!_4	8	0.679	-13.74	1.944	12.58	3.34	AZ!_5	11.0	1513	-14.2183	519.3	11.4417	3.40
G48!_6	11.5	0.751	-13.8	2.141	12.69	3.33	AZ!_7	15.5	1522	-14.1557	521.4	11.4682	3.41
G48!_8	15.5	0.679	-14.01	1.946	12.98	3.34	AZ!_9	20.5	1240	-14.0509	422.1	11.9526	3.43
G48!_10	20	0.716	-14	2.048	13.41	3.34	AZ!_11	25.5	1458	-14.0715	498.9	12.1609	3.41
G48!_12	24.5	0.575	-14.01	1.66	12.94	3.37	AZ!_13	31.5	1575	-14.0626	540.7	12.1387	3.40

G48!_14	28.5	0.285	-14.27	0.847	12.26	3.46	AZ!_15	37.5	1459	-14.0697	498.4	12.0828	3.42
G48!_16	33	0.268	-14.27	0.797	13.02	3.47	AZ!_17	43.5	1206	-13.9263	409.1	12.5299	3.44
G48!_18	38	0.323	-14.31	0.958	12.8	3.46	AZ!_19	49.5	961.8	-13.9606	323.9	12.6826	3.46
G48!_20	44	0.297	-14.21	0.884	13.57	3.47	AZ!_21	58.5	975.9	-14.0209	326.7	13.2845	3.49
G48!_22	51	0.304	-14.32	0.903	13.04	3.47	AZ!_23	70	934.5	-14.0652	312.2	12.9371	3.49
G48!_24	58.5	0.418	-14.28	1.23	12.6	3.44	AZ!_25	88.5	1221	-14.3715	407.5	12.6595	3.50
G48!_26	66.5	0.359	-14.41	1.06	12.27	3.45	Z2!*_1	3	1038	-14.1956	341.6	12.7221	3.55
G48!_28	77	0.419	-14.75	1.237	11.93	3.44	Z2!*_3	7	1498	-13.7659	513.7	12.7068	3.40
G48!_30	89.5	0.352	-14.67	1.046	12.64	3.47	Z2!*_5	11	1390	-13.9915	476.3	11.7955	3.40
G48!_32	97.5	0.435	-14.52	1.289	13.21	3.46	Z2!*_7	13	1387	-14.1996	476.2	11.2018	3.40
Z8!_2	4.5	1.395	-14.86	0.478	13.27	3.40	Z2!*_9	17.5	1104	-14.3676	376.2	11.125	3.42
Z8!_4	8.5	1.173	-14.5	0.4	13.64	3.42	Z2!*_11	22.5	1197	-14.4497	409	11.365	3.41
Z8!_6	12.5	1.292	-14.09	0.444	14.16	3.39	Z2!*_13	27.5	1277	-14.7728	437.2	11.8378	3.41
Z8!_8	16.5	1.186	-13.9	0.406	14.48	3.41	Z2!*_15	33.5	1428	-14.7277	487.2	12.238	3.42
Z8!_10	20.5	1.221	-13.73	0.419	14.52	3.40	Z2!*_17	39.5	1174	-14.4328	399.6	11.9982	3.43
Z8!_12	24.5	0.98	-13.76	0.334	14.77	3.42	Z2!*_19	45.5	1234	-14.7504	420.4	11.8545	3.42
Z8!_14	29.0	1.26	-13.82	0.43	14.64	3.42	Z2!*_21	51.5	1135	-14.5632	385	11.9935	3.44
Z8!_16	34.0	1.432	-13.84	0.491	14.59	3.40	Z2!*_23	59.5	1417	-14.6022	484.1	12.607	3.41
Z8!_18	39.0	1.377	-13.81	0.472	14.6	3.40	Z2!*_25	67.5	1106	-14.6458	374.2	11.5574	3.45
Z8!_20	44.5	1.087	-13.84	0.369	14.67	3.44	Z2!*_27	76.5	1235	-14.7008	418.3	11.6275	3.44
Z8!_22	50.5	1.158	-13.89	0.394	14.65	3.43	Z2!*_29	87	1259	-14.7732	425.5	11.7006	3.45
Z8!_24	56.5	1.088	-13.9	0.369	14.88	3.44	Z2!*_33	124	1737	-14.687	591.2	12.4767	3.43
Z8!_26	63.0	1.228	-13.94	0.417	15.07	3.44	V7!_1	3	1082	-13.9467	362.1	15.7509	3.49
Z8!_28	70.0	0.984	-14.06	0.332	15.09	3.46	V7!_3	7	1664	-13.7907	575.8	15.1456	3.37
Z8!_30	78.0	1.218	-14.06	0.413	14.56	3.44	V7!_5	11	1661	-13.6965	574.1	15.4117	3.38
Z8!_32	85.0	1.16	-14.21	0.393	14.2	3.44	V7!_7	15	1507	-13.7449	520.1	15.3749	3.38
Z8!_34	94.5	1.124	-14.39	0.378	14.32	3.47	V7!_9	19	1448	-13.6835	498.6	15.6082	3.39
Z8!_36	106.5	1.312	-14.5	0.444	13.21	3.45	V7!_11	23	1176	-13.7517	399.4	15.731	3.44
Z8!_38	128.5	1.521	-14.66	0.514	12.27	3.45	V7!_13	27	1412	-13.5982	484.3	15.988	3.40
Z1!_1	3.0	1240	-13.5771	415	13.493	3.49	V7!_15	31.5	1238	-13.5069	421.5	16.1983	3.43
Z1!_3	7.0	1326	-13.2779	454.8	13.2343	3.40	V7!_17	36.5	1062	-13.5941	358.8	16.0265	3.45
Z1!_5	11.0	1319	-13.4085	453.6	13.5638	3.39	V7!_19	41.5	1258	-13.5614	429.8	15.9881	3.41

Z1!_7	15.0	1225	-13.4272	419.2	14.2162	3.41	V7!_21	47.5	1491	-13.8091	510.9	15.9059	3.40
Z1!_9	19.0	1412	-13.6358	482.9	14.9847	3.41	V7!_23	54.5	1459	-13.9957	497.3	15.476	3.42
Z1!_11	23.5	1558	-13.7763	532.7	15.0722	3.41	V7!_25	65.5	1501	-14.1822	510.6	14.71	3.43
Z1!_13	28.5	1407	-13.777	480.5	15.0724	3.42	V7!_27	81.5	1511	-14.0796	516.4	15.567	3.41
Z1!_15	33.5	1304	-13.9745	443.3	15.2038	3.43	A5!_1	3	1674	-14.1241	566.4	12.1749	3.45
Z1!_17	38.5	1289	-13.8883	434.5	15.0792	3.46	A5!_3	7	1809	-13.7624	626.9	11.5913	3.37
Z1!_19	44.0	1212	-13.763	407	14.5855	3.47	A5!_5	11	1604	-13.7308	556	11.4687	3.37
HR!_1	3.0	1264	-14.2598	422.7	14.8945	3.49	A5!_7	15	1314	-14.1342	450.4	11.2853	3.40
HR!_3	7.5	1325	-13.9929	452.1	14.9408	3.42	A5!_9	19	1275	-14.2045	436.7	11.5052	3.41
HR!_5	11.5	1147	-14.0002	390.9	14.9908	3.42	A5!_11	24	1200	-13.8987	409.5	12.3927	3.42
HR!_7	15.5	1080	-14.1007	366.9	15.1271	3.43	A5!_13	30	1200	-13.9614	408.8	12.1508	3.42
HR!_9	19.5	1184	-14.0638	403.9	15.065	3.42	A5!_15	36	1251	-14.2187	426.4	11.7287	3.42
HR!_11	23.5	1023	-14.1921	346.7	15.2266	3.44	A5!_17	42	1015	-14.3446	343.6	11.7094	3.45
HR!_13	27.5	1109	-14.2008	375.8	15.1922	3.44	A5!_19	48	1213	-14.3412	412.1	11.4111	3.43
HR!_15	32.0	1201	-14.2709	407.7	15.0621	3.44	A5!_21	56	1069	-14.4984	360.7	11.2588	3.46
HR!_17	38.0	1281	-14.3725	436.1	14.6821	3.43	A5!_23	64	1291	-14.5462	437.5	11.7776	3.44
HR!_19	44.0	1188	-14.7377	399.3	14.3936	3.47	A5!_25	72	1107	-14.5726	373.2	11.376	3.46
HR!_21	51.0	1248	-15.0127	423.2	13.5345	3.44	A5!_27	80	1071	-14.3404	360.2	12.7542	3.47
HR!_23	57.0	1030	-14.8751	346.2	13.4063	3.47	A5!_29	90	968.6	-14.3783	324.4	12.8702	3.48
HR!_25	63.0	924.3	-14.6535	309.2	13.3275	3.49	A5!_31	109	1089	-14.4304	364	12.3994	3.49
HR!_27	70.0	989.3	-14.6418	330.5	12.6608	3.49	Z3!_1	2	1.031	-14.34	0.351	15.6	3.43
HR!_29	77.5	974.2	-14.8923	324.9	12.8349	3.50	Z3!_2	4	1.169	-14.03	0.404	13.05	3.38
HR!_31	86.0	956.1	-14.9677	317.2	13.7351	3.52	Z3!_3	6	1.24	-14.05	0.429	13.21	3.37
HR!_33	96.5	1072	-14.8927	357.7	13.9646	3.50	Z3!_4	8	1.331	-13.95	0.461	14.01	3.37
B2!_1	2.5	1103	-14.2194	363.8	15.4347	3.54	Z3!_5	10	1.412	-13.67	0.49	14.5	3.36
B2!_3	6.5	1494	-13.9081	515	14.9019	3.38	Z3!_6	12	1.497	-13.52	0.52	15	3.36
B2!_5	10.5	1355	-13.8236	466.4	15.0595	3.39	Z3!_7	14	1.364	-13.56	0.467	15.27	3.41
B2!_7	14.5	1360	-13.7212	468.3	15.0097	3.39	Z3!_8	16	0.869	-13.7	0.292	15.52	3.47
B2!_9	19.0	1287	-13.7997	441.4	15.1901	3.40	Z3!_9	18	1.189	-13.64	0.407	15.45	3.41
B2!_11	24.0	1362	-14.0451	467.9	15.2141	3.40	Z3!_10	20	0.951	-13.68	0.323	15.61	3.43
B2!_13	29.5	1358	-14.2986	465.1	15.1282	3.41	Z3!_11	22	1.21	-13.72	0.415	15.64	3.40
B2!_15	34.5	1097	-14.8538	371.5	14.8998	3.45	Z3!_12	24	1.139	-13.74	0.39	15.68	3.41

B2!_17	40.0	1256	-15.2322	427	14.5845	3.43	Z3!_13	26	1.143	-13.8	0.392	15.62	3.40
B2!_19	46.0	1290	-15.0353	439	14.1839	3.43	Z3!_14	28	1.151	-13.76	0.392	15.72	3.43
B2!_21	52.5	1107	-15.0827	373.3	14.0919	3.46	Z3!_15	30	1.12	-13.85	0.384	15.68	3.40
B2!_23	60.5	1183	-15.5006	399.7	13.7012	3.45	Z3!_16	32	1.168	-13.85	0.402	15.57	3.39
B2!_25	68.5	1157	-15.6025	391.2	13.2471	3.45	Z3!_17	34	0.987	-13.93	0.337	15.66	3.42
B2!_27	77.0	1111	-14.9525	375.6	12.066	3.45	Z3!_18	36	0.759	-14.07	0.257	15.78	3.45
B2!_29	87.5	1101	-14.4693	370.6	13.8334	3.47	Z3!_19	38	0.919	-14.02	0.314	15.78	3.41
B2!_31	101.5	1238	-14.5311	417.3	14.5066	3.46	Z3!_20	41	1.275	-13.98	0.44	15.68	3.38
Q43!_1	3.0	638.6	-14.2231	204.6	15.4503	3.64	Z3!_21	44	1.218	-14.03	0.414	15.64	3.43
Q43!_3	8.0	1239	-13.1378	422.8	15.2492	3.42	Z3!_22	46.5	1.053	-14	0.357	15.7	3.44
Q43!_5	12.0	1075	-13.1457	366	15.2456	3.43	Z3!_23	49.5	1.339	-13.93	0.459	15.6	3.40
Q43!_7	16.0	1023	-13.2032	347.7	15.3568	3.43	Z3!_24	52.5	1.352	-14.09	0.463	15.22	3.41
Q43!_9	20.5	958.4	-13.3254	325.2	15.6994	3.44	Z3!_25	56	1.299	-14.11	0.444	15.3	3.41
Q43!_11	25.5	1183	-13.2768	404.5	15.7556	3.41	Z3!_26	59	1.086	-14.3	0.365	15.45	3.47
Q43!_13	31.5	1244	-13.239	426.2	15.8219	3.41	Z3!_27	62.5	1.293	-14.17	0.441	15.18	3.42
Q43!_15	37.5	1244	-13.2927	424.4	15.9605	3.42	Z3!_28	66	1.32	-14.2	0.449	15.12	3.43
Q43!_17	44.0	1037	-13.3593	351.1	15.6016	3.45	Z3!_29	69	0.998	-14.25	0.335	15.54	3.48
Q43!_19	51.0	1186	-13.3844	403	15.6072	3.43	Z3!_30	72.5	0.955	-14.22	0.323	15.73	3.45
Q43!_21	58.0	1115	-13.4329	378	15.7843	3.44	Z3!_31	76	1.023	-14.18	0.348	15.73	3.43
Q43!_23	66.0	1121	-13.6001	379.6	15.2347	3.45	Z3!_32	80.5	1.15	-14.28	0.392	15.71	3.42
Q43!_25	74.0	979.4	-13.5987	329.1	15.7941	3.47	Z3!_33	84.5	0.711	-14.5	0.234	13.51	3.54
Q43!_27	83.5	1009	-13.7176	338.6	15.5517	3.48	Z3!_34	89	1.082	-14.29	0.368	15.42	3.43
Q43!_29	94.5	1016	-13.9531	340.4	15.6488	3.48	Z3!_35	94	1.114	-14.22	0.379	15.63	3.43
Q43!_31	114.0	1418	-13.7677	479.8	15.5254	3.45	Z3!_36	100.5	1.156	-14.2	0.392	15.56	3.44
L7!_1	3.0	828.6	-14.8658	269.6	13.4578	3.59	Z3!_37	117.5	1.945	-14.16	0.673	15.46	3.37
L7!_3	7.0	1358	-14.9394	463	13.5315	3.42	L7!_17	41.5	1107	-14.9682	374.5	13.4185	3.45
L7!_5	11.0	1068	-15.0189	362	13.6036	3.44	L7!_19	48.5	1166	-14.685	393.8	12.2548	3.45
L7!_7	15.0	1172	-14.8894	397.5	13.5652	3.44	L7!_21	56.0	1154	-14.4298	389.8	12.4397	3.45
L7!_9	19.0	980.6	-14.9209	330.9	13.5816	3.46	L7!_23	64.5	1069	-14.4434	358.5	12.8562	3.48
L7!_11	23.0	995.3	-14.979	336.1	13.7077	3.45	L7!_25	74.0	1119	-14.5855	376	12.7546	3.47
L7!_13	29.0	959.6	-14.4832	323.1	13.044	3.46	L7!_27	85.5	1131	-14.6091	378.8	12.0762	3.48
L7!_15	35.0	1053	-15.255	355.8	13.8072	3.45	L7!_29	99.5	1231	-14.6355	412.4	12.4182	3.48

*X87_1	3.0	1270	-14.2979	431.2	13.2356	3.44	*X85_1	3.0	1270	-14.6047	423.9	11.605	3.50
*X87_3	7.0	1175	-14.2831	399.8	12.9138	3.43	*X85_3	7.0	1452	-14.3023	495.3	11.0867	3.42
*X87_5	11.5	1020	-14.0758	345.3	14.0163	3.45	*X85_5	11.0	1431	-14.2227	491.2	11.0422	3.40
*X87_7	16.5	966.3	-14.8503	327.1	14.244	3.45	*X85_7	15.0	1306	-14.2601	447.1	11.5687	3.41
*X87_9	21.5	1013	-14.4909	343.2	14.7764	3.44	*X85_9	19.0	1339	-14.2407	459.2	12.1781	3.40
*X87_11	27.5	991.4	-14.4587	334.8	14.7863	3.45	*X85_11	23.0	1387	-14.2866	476.2	13.1757	3.40
*X87_13	34.0	826.4	-14.9137	276.6	14.4186	3.49	*X85_13	28.5	1476	-14.4831	508.1	13.3019	3.39
*X87_15	41.5	793.7	-15.7969	264.9	14.1847	3.50	*X85_15	34.5	1689	-14.3172	584	13.4166	3.37
*X87_17	51.0	972.2	-15.6145	326.1	13.8165	3.48	*X85_17	40.5	1807	-14.1919	624.7	13.428	3.37
*X87_19	62.5	807.9	-15.1293	268.5	14.3839	3.51	*X85_19	47.0	1482	-14.125	506.7	13.2938	3.41
*X87_21	77.0	857.3	-14.581	281.7	14.3386	3.55	*X85_21	54.0	1690	-14.2963	581.6	13.6908	3.39
*X87_23	110.0	1492	-14.423	504.7	13.6026	3.45	*X85_23	61.0	1614	-14.6621	547.9	13.9765	3.44
*X47!_1	2.0	1227	-13.803	417	12.4385	3.43	*X85_25	68.5	1504	-14.401	511.5	13.3158	3.43
*X47!_3	6.0	1682	-13.4292	581	12.6683	3.38	*X85_27	77.5	1227	-14.5525	414.6	13.3875	3.45
*X47!_5	10.0	1572	-13.5219	542.9	12.6528	3.38	*X85_29	88.5	1745	-14.4291	594.3	13.2004	3.43
*X47!_7	14.0	1331	-13.574	457.3	12.8987	3.40	*X85_31	110.0	2674	-16.3853	960.9	11.9763	3.25
*X47!_9	19.0	1296	-13.6117	444	13.133	3.41	*1A_1	3.0	952.2	-14.2329	313.4	13.2809	3.54
*X47!_11	24.0	1448	-13.6884	497.2	13.1462	3.40	*1A_3	7.0	1411	-13.9773	481.1	12.7637	3.42
*X47!_13	30.0	1265	-13.6821	430.7	13.2542	3.43	*1A_5	11.0	1249	-13.6791	427.9	13.0215	3.41
*X47!_15	36.0	1286	-13.8565	437.9	12.8935	3.43	*1A_7	15.0	1187	-13.7589	403.7	12.9903	3.43
*X47!_17	42.0	1453	-13.7877	496.2	13.1376	3.42	*1A_9	19.0	1173	-13.6013	400.5	13.6992	3.42
*X47!_19	48.5	1517	-13.8817	518.7	13.0534	3.41	*1A_11	24.0	1082	-13.5956	368.3	13.9349	3.43
*X47!_21	55.5	1419	-14.0168	481.9	13.2829	3.44	*1A_13	29.0	975.5	-13.4775	329.3	14.195	3.46
*X47!_23	62.5	1416	-14.0217	480.6	13.3571	3.44	*1A_15	34.0	1152	-13.6116	391.2	14.1732	3.44
*X47!_25	70.0	1659	-14.022	565.3	13.1086	3.42	*1A_17	40.0	1527	-13.8199	523.6	13.5507	3.40
*7A_1	3.0	1409	-14.3071	469.6	13.1903	3.50	*1A_19	46.0	1296	-13.8229	441.6	13.7025	3.42
*7A_3	7.0	1517	-13.8697	511	13.6574	3.46	*1A_21	52.0	1529	-13.9563	524.5	13.7754	3.40
*7A_5	11.0	1252	-13.7096	426.7	13.6893	3.42	*1A_23	58.0	1308	-14.1802	443.2	13.2537	3.44
*7A_7	15.0	1221	-14.0031	416.3	13.8631	3.42	*1A_25	64.0	1413	-14.1692	477.5	13.8159	3.45
*7A_9	19.0	1225	-14.1942	418.2	14.0869	3.42	*1A_27	70.0	1197	-13.9312	404.4	14.5798	3.45
*7A_11	23.0	1176	-14.3001	400.3	14.5589	3.43	*1A_29	77.0	1148	-14.073	380.8	14.7279	3.52

*7A_13	28.0	1309	-14.4159	447	14.4202	3.42	*1A_31	84.0	1126	-14.0064	378.4	14.4658	3.47
*7A_15	33.0	1356	-14.5267	459.9	14.2899	3.44	*1A_33	92.0	1123	-14.1519	375.9	14.4277	3.49
*7A_17	38.5	1270	-14.4371	432.3	14.5794	3.43	*1A_35	100.5	1167	-14.4099	388	13.9429	3.51
*7A_19	44.5	1474	-14.4992	502.8	14.6537	3.42	*1A_37	117.5	1158	-14.2539	388.2	13.513	3.48
*7A_21	50.5	1450	-14.4478	493.3	14.7213	3.43	*TH_1	3	1226	-14.2618	408	13.5076	3.51
*7A_23	56.5	1226	-14.3911	414.2	14.7209	3.45	*TH_3	7	1946	-13.9697	676.1	13.2876	3.36
*7A_25	62.5	1178	-14.5	394.4	14.1821	3.48	*TH_5	11	1967	-13.821	684.3	13.4638	3.35
*7A_27	69.0	975	-14.4964	325	14.4411	3.50	*TH_7	13.5	1907	-13.7371	661.9	13.3028	3.36
*7A_29	76.0	1020	-14.4339	340.6	13.8784	3.49	*TH_9	19.5	1966	-13.9837	684.7	12.8637	3.35
*7A_31	83.0	885.7	-14.6234	292.3	15.1078	3.54	*TH_11	24	1310	-13.9643	447.8	12.8967	3.41
*Z8_1	3.0	1726	-15.4683	572.9	12.8443	3.51	*TH_13	30	1689	-14.024	582.4	12.9754	3.38
*Z8_3	7.0	1901	-14.6097	655.4	12.579	3.38	*TH_15	36	1669	-14.1402	574.7	12.5965	3.39
*Z8_5	11.0	1673	-14.4202	577.7	12.1278	3.38	*TH_17	42	1353	-14.0055	461.2	13.0259	3.42
*Z8_7	15.5	1705	-14.2146	589.4	12.5932	3.37	*TH_19	48.5	1708	-14.0941	587.6	13.7555	3.39
*Z8_9	20.5	1736	-14.1706	600.5	12.9244	3.37	*TH_21	55.5	1394	-13.9212	473.6	13.147	3.43
*Z8_11	26.0	1696	-14.1241	581.5	14.0986	3.40	*TH_23	63	1405	-13.9228	477.1	13.511	3.44
*Z8_13	32.0	1478	-14.0801	506.8	14.589	3.40	*TH_25	71.5	1095	-14.1435	367.6	13.9606	3.48
*Z8_15	38.0	1865	-13.9983	644.5	14.6064	3.38	*TH_27	83.5	1384	-14.0563	467.9	13.7278	3.45
*Z8_17	44.0	1920	-13.9325	662.6	14.6969	3.38	*TH_29	101.5	1516	-14.107	512.9	13.1096	3.45
*Z8_19	50.0	1547	-13.9609	529.2	15.1737	3.41	*Z7_1	2	1463	-13.6866	501.1	12.8423	3.41
*Z8_21	56.0	1640	-14.0627	561.3	15.2159	3.41	*Z7_3	6	1720	-13.7762	593.6	12.9988	3.38
*Z8_23	62.0	1396	-14.2232	474.6	15.193	3.43	*Z7_5	10	2006	-13.8903	699	12.3603	3.35
*Z8_25	68.0	1204	-14.1678	407.3	15.0178	3.45	*Z7_7	14	1707	-14.2893	590.6	12.9495	3.37
*Z8_27	74.0	1241	-14.3368	416.5	14.8237	3.48	*Z7_9	18	1577	-14.6129	543.6	13.5608	3.38
*Z8_29	81.0	1127	-14.4505	378.6	14.6793	3.47	*Z7_11	23	1868	-15.0399	645.8	12.8999	3.37
*Z8_31	101.0	2227	-14.3066	764.4	12.7004	3.40	*Z7_13	28	1706	-15.0005	587	13.5909	3.39
*X89_1	2.5	1404	-14.0883	473.6	13.5713	3.46	*Z7_15	34	1610	-15.16	550.9	13.4471	3.41
*X89_3	6.5	1725	-13.9996	595.1	13.2661	3.38	*Z7_17	40	1765	-15.2147	605.3	13.5751	3.40
*X89_5	10.5	1560	-13.831	536.9	13.1084	3.39	*Z7_19	46	1656	-14.667	566.1	15.2723	3.41
*X89_7	14.5	1295	-13.5318	442.9	14.7592	3.41	*Z7_21	52.5	1479	-14.6234	500.7	15.1803	3.45
*X89_9	18.5	1344	-13.5111	460	15.4321	3.41	*Z7_23	59.5	1393	-14.2721	471.5	15.6037	3.45
*X89_11	22.5	1218	-13.5782	414.9	15.5789	3.42	*Z7_25	66.5	1440	-14.1845	487	15.5561	3.45

*X89_13	26.5	1426	-13.6415	487.1	16.5245	3.42	*Z7_27	73.5	1223	-14.2979	410.8	15.1735	3.47
*X89_15	30.5	1350	-13.5491	460.5	16.198	3.42	*Z7_29	83	1203	-14.2983	403.2	14.5674	3.48
*X89_17	35.0	1401	-13.5218	477.4	16.1151	3.42	*Z7_31	96	1113	-14.2762	371.2	13.74	3.50
*X89_19	40.0	1502	-13.5515	514.1	16.194	3.41	*TL_1	2	1638	-14.6301	563.3	11.7075	3.39
*X89_21	45.0	1546	-13.5887	529.1	16.3876	3.41	*TL_3	6	1458	-14.5542	498.2	11.3328	3.41
*X89_23	50.0	1213	-13.608	410.9	16.527	3.44	*TL_5	10	1260	-14.5392	428.5	11.5028	3.43
*X89_25	55.0	1294	-13.6421	438.9	16.5258	3.44	*TL_7	14	1143	-14.5714	387.5	12.3068	3.44
*X89_27	60.0	1370	-13.6638	464.2	16.226	3.44	*TL_9	18.5	1192	-14.5411	404.7	12.3356	3.44
*X89_29	66.0	1136	-13.7835	381.5	16.5551	3.47	*TL_11	23.5	1254	-14.6764	425.8	13.8796	3.44
*X89_31	72.0	1344	-13.8657	454.2	16.2371	3.45	*TL_13	29	1228	-14.7573	415.3	15.0401	3.45
*A9_1	3.0	1346	-15.0007	445.2	11.5935	3.53	*TL_15	35	1302	-15.4053	441	14.6121	3.44
*A9_3	7.0	1192	-14.4347	404.5	11.903	3.44	*TL_17	41	1115	-14.95	375	14.768	3.47
*A9_5	11.0	1170	-14.457	398.1	10.808	3.43	*TL_19	48	1179	-15.0606	394.5	14.1783	3.49
*A9_7	17.0	1385	-14.0547	475.4	11.5856	3.40	*TL_21	56	1025	-15.0461	342.6	13.8866	3.49
*A9_9	23.0	1410	-14.1628	484.1	11.1072	3.40	*TL_23	64.5	1518	-14.6642	517.5	13.7933	3.42
*A9_11	29.5	1334	-14.1478	455.4	12.4304	3.42	*TL_25	76.5	1670	-14.1244	569.5	13.348	3.42
*A9_13	37.0	1627	-14.1547	558.6	13.322	3.40	*TL_27	101	1510	-14.2884	507.7	13.291	3.47
*A9_15	45.0	1567	-14.0293	536.3	13.9188	3.41	*TB_1	3	1414	-14.5501	468.4	13.3011	3.52
*A9_17	54.0	1228	-14.221	414.6	14.5294	3.46	*TB_3	7	1882	-14.2446	648.5	13.5294	3.39
*A9_19	65.5	1316	-14.0111	443	14.6893	3.47	*TB_5	11	1522	-14.1921	522.6	13.7295	3.40
*A9_21	90.0	1653	-14.4761	559.5	14.3336	3.45	*TB_7	15	1430	-14.0601	490.3	13.6716	3.40
*Z1_1	3.0	569	-14.5157	188.5	13.2181	3.52	*TB_9	20	1335	-14.0918	456.6	13.6674	3.41
*Z1_3	8.0	1366	-14.1205	465.8	12.1198	3.42	*TB_11	26	1443	-14.0597	494.6	13.8377	3.40
*Z1_5	13.0	1419	-14.0488	486.8	11.9111	3.40	*TB_13	32	1458	-15.5036	453.8	13.3944	3.75
*Z1_7	19.0	1252	-13.9508	424.6	14.3045	3.44	*TB_15	39	1174	-14.1528	398.5	13.6503	3.44
*Z1_9	25.5	1354	-14.0418	457.8	15.0918	3.45	*TB_17	46.5	1458	-14.2205	497.7	13.1324	3.42
*Z1_11	33.5	1146	-14.0149	387.9	15.3428	3.45	*TB_19	35	1215	-14.2707	411.4	13.2206	3.45
*Z1_13	42.0	1364	-14.0619	463.7	15.3533	3.43	*TB_21	64.5	1101	-14.3446	371.1	13.7358	3.46
*Z1_15	52.0	1315	-14.2764	443.2	15.2402	3.46	*TB_23	75.5	1313	-14.253	445.6	13.9296	3.44
*Z1_17	63.5	1167	-14.226	391.4	15.2723	3.48	*TB_25	90.5	1141	-14.5253	384.7	13.7704	3.46
*Z1_19	77.0	1248	-13.8757	419.8	14.9505	3.47	*TB_27	112.5	2022	-15.3877	691.8	14.1754	3.41

D_1	3	0.388	-16.27	0.129333	14.46	3.5	VT_1	3.5	0.38	-16.11	0.131553	14.07	3.37
D_3	7	0.446	-16.07	0.15259	14.35	3.41	VT_3	8.5	0.409	-16.65	0.139522	12.72	3.42
D_5	11	0.417	-16.18	0.141837	14.33	3.43	VT_5	14.5	0.434	-16.09	0.142629	13.25	3.55
D_7	15	0.412	-16.39	0.139729	14.15	3.44	VT_7	20.5	0.362	-15.69	0.117315	13.87	3.6
D_9	19	0.392	-16.37	0.13256	14.09	3.45	VT_9	27.5	0.369	-14.68	0.125145	15.07	3.44
D_11	23	0.4	-16.46	0.135659	14.54	3.44	VT_11	35.5	0.365	-14.91	0.12343	15.37	3.45
D_13	27.5	0.424	-16.41	0.143382	14.06	3.45	VT_13	45.5	0.355	-14.99	0.119013	15.35	3.48
D_15	32.5	0.45	-16.81	0.152616	13.86	3.44	VT_15	56.5	0.294	-14.18	0.098	16.97	3.5
D_17	38	0.504	-16.9	0.171429	13.61	3.43	VT_17	70.5	0.258	-14.84	0.084789	16.67	3.55
D_19	43	0.466	-17.12	0.158043	13.53	3.44	5H_1	2.5	0.393	-13.35	0.133285	16.28	3.44
D_21	48	0.426	-17.22	0.143642	13.48	3.46	5H_3	7.5	0.329	-13.4	0.111256	16.34	3.45
D_23	53	0.406	-17.28	0.136503	13.38	3.47	5H_5	13.5	0.373	-13.53	0.126502	16.19	3.44
D_25	58.5	0.456	-17.02	0.154203	13.6	3.45	5H_7	20	0.319	-13.71	0.107563	16.66	3.46
D_27	64.5	0.374	-16.54	0.125383	14	3.48	5H_9	27	0.328	-14.26	0.110279	16.49	3.47
D_29	71	0.428	-16.38	0.1439	14.03	3.47	5H_11	35	0.319	-14.55	0.107253	16.18	3.47
D_31	79.5	0.425	-16.49	0.142073	13.85	3.49	5H_13	43	0.296	-15.18	0.098949	15.57	3.49
D_33	88.5	0.439	-16.18	0.147598	14.82	3.47	5H_15	51.5	0.278	-15.66	0.092667	15.07	3.5
D_35	99	0.479	-16.09	0.161047	15.07	3.47	5H_17	62	0.251	-15.87	0.083667	15.32	3.5
D*_1	2.5	0.425	-16.33	0.142481	14.15	3.48	5H_19	83	0.299	-16.29	0.096898	15.05	3.6
D*_3	6.5	0.465	-15.82	0.157703	14.21	3.44	ZH*_1	2	0.287	-15.58	0.096773	16.3	3.46
D*_5	10.5	0.516	-15.79	0.17551	14.31	3.43	ZH*_3	7	0.352	-15.58	0.119728	16.55	3.43
D*_7	14.5	0.397	-16.24	0.134251	14.2	3.45	ZH*_5	12.5	0.4	-15.52	0.136852	16.61	3.41
D*_9	19	0.446	-16.23	0.152144	14.14	3.42	ZH*_7	18.5	0.381	-15.63	0.129592	16.44	3.43
D*_11	24	0.382	-16.28	0.129932	14.41	3.43	ZH*_9	24.5	0.387	-15.53	0.13125	16.64	3.44
D*_13	29.5	0.541	-16.46	0.186185	14.13	3.39	ZH*_11	30.5	0.33	-15.42	0.110951	16.51	3.47
D*_15	35.5	0.48	-16.49	0.163743	14.06	3.42	ZH*_13	38.5	0.398	-15.4	0.134589	16.38	3.45
D*_17	41.5	0.399	-16.39	0.135714	14.57	3.43	ZH*_15	47.5	0.453	-15.15	0.153634	16.27	3.44
D*_19	48	0.419	-16.86	0.142103	14.13	3.44	ZH*_17	58.5	0.397	-15.32	0.133863	16.14	3.46
D*_21	56	0.446	-16.9	0.15126	13.92	3.44	ZH*_19	70.5	0.324	-15.8	0.108309	15.82	3.49
D*_23	64	0.361	-16.96	0.120333	13.86	3.5	ZH*_21	92.5	0.569	-15.71	0.193537	15.26	3.43
D*_25	74	0.383	-17.27	0.126582	13.67	3.53	3B_1	2	0.251	-16.19	0.083428	13.66	3.51
D*_27	85	0.408	-17.51	0.135613	13.52	3.51	3B_3	7	0.277	-15.46	0.093401	15.38	3.46

D*_29	102.4	0.319	-17.46	0.104836	13.95	3.55	3B_5	12.5	0.379	-15.47	0.128912	15.17	3.43
X43_1	2	0.276	-15.02	0.092	15.13	3.5	3B_7	18.5	0.316	-15.59	0.105333	15.68	3.5
X43_3	6	0.316	-14.8	0.108113	15.52	3.41	3B_9	24.5	0.325	-15.42	0.109903	16.32	3.45
X43_5	11.5	0.339	-14.88	0.111408	15.67	3.55	3B_11	30.5	0.389	-15.75	0.131546	15.26	3.45
X43_7	17.5	0.356	-14.81	0.119007	15.69	3.49	3B_13	36.5	0.317	-15.53	0.10658	15.94	3.47
X43_9	24	0.375	-14.85	0.125718	15.68	3.48	3B_15	43.5	0.282	-15.35	0.093732	16.78	3.51
X43_11	32.5	0.429	-15.01	0.14341	15.79	3.49	3B_17	52	0.346	-15.4	0.115664	16.66	3.49
X43_13	42.5	0.369	-14.85	0.124783	16.03	3.45	3B_19	61.5	0.321	-15.51	0.106695	16.76	3.51
X43_15	54.5	0.35	-15.54	0.11406	15.52	3.58	3B_21	73	0.314	-15.46	0.104368	16.37	3.51
X43_17	75	0.543	-15.59	0.18204	15.08	3.48	3B_23	95	0.134	-15.9	0.042831	16.68	3.65
4H_1	3	0.201	-17.55	0.064423	13.44	3.64	C9_2	5	1.036	-16.2	0.349	13.85	3.46
4H_3	7	0.276	-17.28	0.090449	12.94	3.56	C9_4	9	1.426	-16.04	0.489	14.08	3.4
4H_5	12	0.316	-15.78	0.104143	13.66	3.54	C9_6	13	1.039	-15.93	0.353	14.43	3.44
4H_7	19	0.379	-15	0.128164	14.87	3.45	C9_8	17	1.049	-15.61	0.356	14.71	3.44
4H_9	27.5	0.327	-14.85	0.108689	15.91	3.51	C9_10	21	0.818	-15.37	0.275	15.31	3.47
4H_11	37	0.309	-15.9	0.099586	14.47	3.62	C9_12	25.5	1.164	-15.09	0.397	15.3	3.42
4H_13	51	0.273	-15.14	0.089972	15.64	3.54	C9_14	30.5	0.941	-15.18	0.32	14.91	3.42
DZ_1	2.5	0.224	-17.13	0.073203	13.46	3.57	C9_16	36.5	1.206	-15.18	0.412	14.78	3.41
DZ_3	7.5	0.388	-15.76	0.133925	13.65	3.38	C9_18	43.5	1.298	-15	0.443	15.43	3.42
DZ_5	13	0.398	-14.97	0.141998	14.35	3.27	C9_20	51	1.176	-15.54	0.385	15.42	3.56
DZ_7	19.5	0.358	-15.42	0.119675	14.93	3.49	C9_22	61	0.876	-15	0.293	15.96	3.49
DZ_9	28	0.497	-15.19	0.168556	15.39	3.44	C9_24	73	0.956	-15.18	0.319	15.8	3.49
DZ_11	40	0.551	-15.83	0.18579	14.79	3.46	C9*_1	2	0.351	-15.97	0.359	13.85	3.46
5B_1	3	0.232	-15.23	0.075185	14.61	3.6	C9*_3	6	0.375	-15.7	0.387	14.35	3.44
5B_3	8	0.241	-15.27	0.081973	14.28	3.43	C9*_5	10	0.348	-15.59	0.361	14.6	3.47
5B_5	15	0.293	-15.78	0.096291	14.51	3.55	C9*_7	14	0.277	-15.67	0.289	14.53	3.49
5B_7	23.5	0.309	-16.08	0.103592	13.53	3.48	C9*_9	19	0.389	-15.49	0.41	14.69	3.45
5B_9	32.5	0.252	-15.84	0.080769	14.49	3.64	C9*_11	24	0.423	-15.19	0.428	15.04	3.43
5B_11	44.5	0.277	-16.01	0.091809	14.87	3.52	C9*_13	30	0.452	-15.09	0.462	15.42	3.43
5B_13	69.5	0.178	-15.64	0.059846	15.46	3.47	C9*_15	36	0.466	-15.19	0.481	15.31	3.43
X44_1	2	0.335	-17.01	0.112958	12.84	3.46	C9*_17	43	0.417	-14.98	0.436	15.69	3.45
X44_3	6	0.335	-16.53	0.109477	13.33	3.57	C9*_19	51.5	0.425	-15.19	0.45	15.7	3.47

X44_5	10	0.28	-16.13	0.090741	13.62	3.6	C9*_21	62	0.341	-15.18	0.365	15.51	3.5
X44_7	15	0.304	-15.25	0.101624	14.96	3.49	C9*_23	78	0.244	-15.15	0.264	15.47	3.55
X44_9	20	0.278	-15.07	0.092403	15.77	3.51	1W_1	3.0	790.9	-15.6534	260.1	14.2037	3.55
x44_11	26	0.376	-14.56	0.126054	15.81	3.48	1W_3	7.0	1308	-14.799	447.7	13.9397	3.41
X44_13	32.5	0.354	-14.42	0.116011	16.09	3.56	1W_5	11.0	999.8	-13.6815	339.9	15.3386	3.43
X44_15	39.5	0.297	-14.87	0.094414	16.65	3.67	1W_7	16.0	1132	-13.5806	385.9	15.6837	3.42
X44_17	47	0.282	-14.78	0.090884	16.61	3.62	1W_9	22.0	1406	-13.4861	482	16.1277	3.40
X44_19	55	0.265	-14.65	0.084936	16.6	3.64	1W_11	30.5	1302	-13.4561	443.4	16.7145	3.43
X44_21	64	0.267	-14.92	0.085813	16.73	3.63	1W_13	40.5	1210	-13.6016	407.9	16.5967	3.46
X44_23	73.5	0.26	-14.96	0.084026	16.64	3.61	1W_15	54.0	1552	-13.5866	533.1	16.4112	3.40
X44_25	85	0.31	-15.06	0.101592	16.05	3.56	1W_16	72.5	1113	-13.6847	375.1	16.8384	3.46
D2_1	2.5	0.302	-17.21	0.102126	12.68	3.45	1W_17	96.5	641.5	-14.4809	211.8	16.8209	3.53
D2_3	9	0.385	-15.22	0.129817	15.3	3.46	H8_1	3.5	1128	-15.1655	382.8	15.8346	3.44
D2_5	16.5	0.406	-15.16	0.135721	15.38	3.49	H8_3	10.0	864.7	-15.5979	282.7	16.3614	3.57
D2_7	24.5	0.42	-15	0.14121	15.72	3.47	H8_5	18.5	869.6	-15.4382	291.3	15.6412	3.48
D2_9	33.5	0.383	-15.08	0.127303	15.44	3.51	H8_7	30.0	956.8	-15.9859	320.7	15.1575	3.48
D2_11	43.5	0.343	-15.43	0.114008	15.72	3.51	H8_9	43.5	1181	-15.8615	400	15.135	3.44
D2_13	55	0.333	-15.42	0.10732	15.84	3.62	H8_11	59.5	793.2	-16.2305	262.5	14.9115	3.53
D2_15	68	0.303	-15.33	0.098468	16.3	3.59	6C_1	3.5	0.221	-16.94	0.07202	14.62	3.58
							6C_3	10.5	0.373	-15.35	0.126871	14.63	3.43
							6C_5	18	0.374	-14.52	0.127583	15.79	3.42
							6C_7	21.0	1110	-15.7042	378.3	14.1999	3.42
							6C_9	30.0	1450	-15.8335	497.7	13.9535	3.40
D8!_1	3.0	1118	-15.5445	373.4	13.0709	3.49	2U!_1	3	1090	-15.9756	352.2	15.0262	3.61
D8!_3	7.0	1402	-15.9026	481	12.6483	3.40	2U!_3	7	1917	-15.6663	660.7	14.2977	3.39
D8!_5	11.0	1259	-15.8042	432.2	13.4045	3.40	2U!_5	11	1587	-14.6087	546.5	16.1311	3.39
D8!_7	15.0	1327	-15.5419	457.4	13.9839	3.38	2U!_7	15	1378	-14.5873	472.6	16.3492	3.40
D8!_9	21.0	1387	-15.5047	478.4	14.7253	3.38	2U!_9	20	1404	-14.8284	482.1	16.4042	3.40
D8!_11	27.0	1544	-15.6054	533.1	14.961	3.38	2U!_11	25.5	1179	-14.7292	402.1	16.3732	3.42
D8!_13	33.0	1707	-16.0559	589.4	14.6195	3.38	2U!_13	31.5	1326	-15.3182	453.2	15.6239	3.41
D8!_15	41.0	1572	-16.2824	540.3	14.5385	3.39	2U!_15	37.5	1576	-15.0129	542	16.1865	3.39

D8!_17	49.0	1761	-16.5959	606.1	14.3832	3.39	2U!_17	43.5	1385	-15.4755	473.7	15.8052	3.41
D8!_19	57.0	1590	-16.9072	544.3	13.9197	3.41	2U!_19	50.5	1523	-16.2698	522.5	14.6028	3.40
D8!_21	67.0	1800	-16.4803	616.9	14.5623	3.40	2U!_21	57.5	1235	-16.844	419.8	14.1617	3.43
D8!_23	80.0	1931	-16.4382	659.1	14.6635	3.42	2U!_23	65.5	1178	-17.03	399	14.0525	3.44
D8!_25	100.5	2504	-16.3449	862.3	14.8189	3.39	2U!_25	73.5	1121	-16.9034	378.5	14.3528	3.46
X6!_1	3.5	1424	-13.8894	481.5	15.1216	3.45	2U!_27	82.5	1150	-16.9328	388.5	14.0323	3.45
X6!_3	9.5	1773	-13.779	614.7	14.6334	3.37	2U!_29	92	1232	-17.1317	415	13.9555	3.46
X6!_5	15.5	1351	-13.3447	465.7	15.7692	3.38	2U!_31	105	1251	-17.1993	420.6	13.8894	3.47
X6!_7	21.5	1472	-13.3304	508.9	16.0571	3.37	XH!_1	3	1358	-15.6675	458.2	14.0404	3.46
X6!_9	27.5	1457	-13.3713	504.3	16.2611	3.37	XH!_3	7	1416	-15.7369	488	12.8892	3.39
X6!_11	34.5	1123	-13.4546	384.7	16.4611	3.41	XH!_5	11	1429	-16.0049	493.5	13.1499	3.38
X6!_13	42	1088	-13.4814	371.7	16.6457	3.41	XH!_7	15.5	1675	-15.7294	580.2	14.0989	3.37
X6!_15	50	1076	-13.6085	367.7	16.5481	3.41	XH!_9	19.5	1566	-14.9875	541.3	16.2633	3.38
X6!_17	59.5	913.8	-13.6811	309.2	16.4534	3.45	XH!_11	23.5	1575	-15.1501	544.5	16.3614	3.37
X6!_19	70	851.8	-14.0138	287	16.3832	3.46	XH!_13	28.5	1116	-14.8175	381.2	16.6107	3.42
X6!_21	83	1205	-14.0489	408.5	16.487	3.44	XH!_15	33.5	1015	-15.2107	345.3	16.453	3.43
1W!_1	3	1678	-14.7622	570.5	14.38	3.43	XH!_17	39.5	954.3	-15.1612	323.9	16.7098	3.44
1W!_3	7	1618	-15.3947	559.7	12.916	3.37	XH!_19	45.5	1249	-14.9929	427.3	16.9564	3.41
1W!_5	11	1275	-14.7105	437.6	13.8205	3.40	XH!_21	53.5	1498	-14.8458	515	17.0357	3.39
1W!_7	15.5	1647	-13.6605	570.8	15.4752	3.37	XH!_23	60.5	1222	-14.7465	415.9	16.8592	3.43
1W!_9	20.5	1407	-13.5027	484.3	15.7517	3.39	XH!_25	67.5	976.5	-15.0533	328.9	16.7595	3.46
1W!_11	26	1574	-13.4562	544.1	16.3975	3.37	XH!_27	75.5	1074	-15.4607	363.3	16.1198	3.45
1W!_13	32	1384	-13.5965	475.5	16.5295	3.40	XH!_29	84.5	949.4	-15.7248	318.7	15.7866	3.48
6L!_1	2	1131	-15.5991	380.1	13.9302	3.47	XH!_31	97	1064	-15.9301	357.6	15.4617	3.47
6L!_3	7	1583	-15.7737	549.2	13.3185	3.36	H3!_1	3	1075	-14.567	353.8	16.2984	3.54
6L!_5	11	1539	-15.9731	533.1	13.0848	3.37	H3!_3	7	1255	-13.8853	428.9	16.7843	3.41
6L!_7	15	1433	-16.0687	494.1	12.9198	3.38	H3!_5	11	1410	-13.9021	487.6	16.5999	3.37
6L!_9	19	1201	-15.5849	412	14.0924	3.40	H3!_7	14	1164	-14.3305	399.8	16.5371	3.40
6L!_11	23	1171	-15.5245	400.9	14.1237	3.41	H3!_9	18	1028	-15.6408	351.6	14.9488	3.41
6L!_13	27	1479	-15.7248	508.8	14.1337	3.39	H3!_11	23	1237	-15.4666	425.6	15.4948	3.39
6L!_15	32	1427	-15.84	489.7	14.1219	3.40	H3!_13	29	1229	-15.4501	422	15.9402	3.40
6L!_17	38	1233	-15.811	420.6	14.3227	3.42	H3!_15	35	1313	-15.5188	450.5	15.8828	3.40

6L!_19	44	1335	-15.6374	455	14.5627	3.42	H3!_17	42	1610	-16.1222	555.7	15.3832	3.38
6L!_21	50	1319	-16.0321	449.4	14.2871	3.42	H3!_19	49	1598	-16.3859	551.1	15.3083	3.38
6L!_23	58	1265	-16.1368	429	14.2863	3.44	H3!_21	56.5	1492	-16.3504	512.9	15.5534	3.39
6L!_25	66	1107	-15.9365	374.8	14.8517	3.45	H3!_23	64.5	1343	-15.9634	460.1	15.834	3.41
6L!_27	74	1139	-15.8665	384.6	14.5481	3.46	H3!_25	72.5	1184	-16.3896	401.3	15.2771	3.44
6L!_29	82	1055	-15.7742	353.8	14.6421	3.48	H3!_27	81.5	1022	-16.0944	345.1	15.3619	3.46
6L!_31	91	1070	-15.8926	359.4	14.9381	3.47	H3!_29	91.5	1214	-16.2123	409.3	15.3761	3.46
6L!_33	102	1228	-16.2681	412.4	15.2643	3.47	H3!_31	105	1102	-17.0285	370.9	13.896	3.47
6L!_35	117.5	1252	-16.4362	420.4	14.9631	3.47	H3!_33	125.5	1378	-17.0988	467.4	14.0822	3.44
4B!_1	3.5	1239	-13.7003	414.7	16.3809	3.49	3B!_1	3	798.6	-15.7146	262	14.5396	3.56
4B!_3	9.5	1305	-13.4307	446.2	16.5273	3.41	3B!_3	7	1321	-15.6873	453.1	13.3601	3.40
4B!_5	15.5	1157	-13.674	395.4	16.421	3.41	3B!_5	11	1350	-15.655	465	13.4468	3.39
4B!_7	21.5	1214	-14.5303	416.7	16.1064	3.40	3B!_7	15.5	1306	-15.7133	450.5	13.7106	3.38
4B!_9	27.5	1456	-14.9513	501.1	16.0414	3.39	3B!_9	20.5	1255	-16.0107	432	13.3346	3.39
4B!_11	33.5	1415	-14.7318	485.6	16.2907	3.40	3B!_11	25.5	1123	-15.4931	385.5	14.7169	3.40
4B!_13	40	1505	-14.4546	516.2	16.6065	3.40	3B!_13	31.5	1363	-15.4724	469.5	15.0236	3.39
4B!_15	47	1207	-14.8705	410	16.3832	3.43	3B!_15	37.5	1325	-15.2991	456.1	15.9019	3.39
4B!_17	54.5	1386	-15.191	472.9	16.2006	3.42	3B!_17	43.5	1274	-15.2409	436.6	16.0925	3.40
4B!_19	62.5	3.143	-43.6248	0.2662	-94.9645	13.77	3B!_19	49.5	1171	-15.1466	400.4	16.5878	3.41
4B!_21	70.5	1523	-15.1014	520.4	16.3774	3.41	3B!_21	55.5	1128	-15.2427	384.4	16.6207	3.42
4B!_23	78.5	1566	-15.4513	533.7	15.9473	3.42	3B!_23	622	1098	-15.3411	373.7	16.5196	3.43
4B!_25	88.5	1428	-15.7369	485.8	15.752	3.43	3B!_25	69.5	1114	-15.3759	378.2	16.4465	3.44
4B!_27	99.5	1450	-15.9774	493.8	15.5309	3.43	3B!_27	77.5	1010	-15.5748	341.5	15.7702	3.45
4B!_29	113	1292	-16.1799	437.6	15.2719	3.44	3B!_29	85.5	951.9	-15.5703	321	15.8511	3.46
4B!_31	131.5	1103	-16.8022	372.1	14.3861	3.46	3B!_31	94	1094	-15.3626	369.6	16.0153	3.45
D1!_1	3	1711	-15.1647	588.2	13.5755	3.39	3B!_33	105	1040	-15.3401	349.2	15.9065	3.47
D1!_3	7	1724	-14.9363	599.4	13.3581	3.36	3B!_35	119.5	1105	-15.874	370.6	15.6785	3.48
D1!_5	11	1581	-14.3636	548	14.748	3.37	H8!_1		916.4	-15.3508	295.3	13.9002	3.62
D1!_7	15	1658	-14.1261	575.9	15.6891	3.36	H8!_3		1450	-15.3035	495.3	13.7493	3.42
D1!_9	19	1442	-14.7337	498.1	14.903	3.38	H8!_5		1141	-14.888	385.6	15.1784	3.45
D1!_11	23	1267	-14.1912	435.2	15.7961	3.40	H8!_7		1368	-14.9845	468.2	15.289	3.41
D1!_13	27.5	1258	-14.0669	431.9	16.1072	3.40	H8!_9		1216	-14.9293	413.4	15.9983	3.43

D1!_15	82.5	1297	-14.0976	442.6	16.4446	3.42	H8!_11	1210	-15.1238	410.9	15.4428	3.44
D1!_17	38.5	1009	-14.4379	342.7	16.4948	3.43	H8!_13	1016	-15.0852	346.7	16.2219	3.42
D1!_19	44.5	996.4	-14.4718	337.3	16.5274	3.45	H8!_15	856.6	-15.2175	295.7	16.076	3.38
D1!_21	50.5	848.3	-14.1682	285.5	16.5709	3.47	H8!_17	791.8	-15.6519	269.5	15.721	3.43
D1!_23	57	1159	-14.2963	392.5	16.2357	3.45	H8!_19	647.4	-15.3815	220.1	15.9252	3.43
D1!_25	64.5	900.9	-15.4398	301.6	14.9495	3.48	H8!_21	521.5	-15.7588	177.3	15.4074	3.43
D1!_27	73.5	1018	-16.1379	342.3	14.5488	3.47	H8!_23	393.8	-16.2894	132	15.2551	3.48
D1!_29	87	1103	-15.8444	370.5	14.7393	3.47	H8!_25	424.3	-16.5569	142.6	15.0795	3.47
D1!_31	106	1587	-15.9726	536.5	14.6421	3.45	H8!_27	406.4	-16.715	137	14.0223	3.46
2W!_1	3	1311	-15.1586	440	15.8684	3.48	H8!_29	389.5	-16.6176	130.6	14.2384	3.48
2W!_3	7	1708	-15.3808	589.6	14.9479	3.38	H7!_1	438.7	-16.1442	143.6	13.4803	3.56
2W!_5	11	1399	-15.0605	481.5	15.062	3.39	H7!_3	479.1	-15.6372	163.1	13.812	3.43
2W!_7	15	1313	-15.322	450.7	15.407	3.40	H7!_5	406.6	-15.0019	138.6	15.5286	3.42
2W!_9	21	1369	-14.6995	471.5	16.3046	3.39	H7!_7	454.2	-14.9204	154.3	16.2141	3.43
2W!_11	27	1188	-14.7306	407.2	16.6945	3.40	H7!_9	499.9	-14.5896	170.8	16.6592	3.41
2W!_13	33	1217	-15.0475	416.2	16.522	3.41	H7!_11	432.6	-14.7571	146	16.3473	3.46
2W!_15	39	1440	-15.0209	496.9	16.884	3.38	H7!_13	439.1	-14.7025	148.6	16.524	3.45
2W!_17	45	1186	-14.9116	405.2	17.0834	3.41	H7!_15	489.4	-15.3744	166.2	16.114	3.44
2W!_19	51	1140	-15.0419	388.6	16.9059	3.42	H7!_17	425.3	-15.214	143.8	16.0831	3.45
2W!_21	57	1158	-15.0227	394.4	17.0561	3.43	H7!_19	462.2	-16.1143	153.6	15.5183	3.51
2W!_23	64	1211	-15.2966	411.8	16.6151	3.43	DZ!_1	428.2	-13.6996	141.7	15.9617	3.53
2W!_25	72	1167	-15.021	395.9	16.9558	3.44	DZ!_3	614	-13.4209	213.1	15.5164	3.36
2W!_27	80	1182	-15.1242	400.4	17.0489	3.44	DZ!_5	628	-14.2482	218.1	14.8113	3.36
2W!_29	89	1209	-15.2032	406.5	17.3343	3.47	DZ!_7	645.3	-15.1617	224.5	14.1151	3.35
2W!_31	101	1107	-14.9873	371.3	17.6134	3.48	DZ!_9	515.1	-15.0369	177.4	15.303	3.39
2W!_33	119	1192	-15.0943	399.9	17.9021	3.48	DZ!_11	525.2	-15.0303	180.1	15.8902	3.40
7J!_1	2.5	975.8	-16.3586	326.3	13.0535	3.49	DZ!_13	475.4	-15.425	161.4	15.4656	3.44
7J!_3	7.5	1501	-15.8614	517.6	14.5392	3.38	C9!_1	464.3	-15.9172	155.6	13.4179	3.48
7J!_5	12.5	1451	-16.307	499	12.8666	3.39	C9!_3	493.5	-15.7645	169.3	13.4444	3.40
7J!_7	17.5	1430	-15.7079	492.7	13.8901	3.39	C9!_5	508.2	-15.5318	174.9	13.9466	3.39
7J!_9	22.5	1289	-14.4808	442.3	16.4317	3.40	C9!_7	435	-14.8867	148.7	14.8819	3.41
7J!_11	28.5	1241	-14.746	425.4	15.8659	3.40	C9!_9	468.6	-15.0544	157	14.6533	3.48

7J!_13	34.5	1170	-14.8228	400.3	16.1298	3.41	C9!_11	450.7	-15.5911	154.4	14.2373	3.41
7J!_15	40.5	1083	-15.17	369.8	16.0327	3.42	C9!_13	519.9	-15.2477	178.8	14.8358	3.39
7J!_17	47.5	1225	-15.4451	419.3	15.8253	3.41	C9!_15	435.3	-15.2099	148.2	14.5923	3.43
7J!_19	54.5	1042	-16.6287	354.3	14.575	3.43	C9!_17	514.3	-15.1845	175.1	14.9373	3.43
7J!_21	62	1198	-16.7976	409	14.2225	3.42	6J!_1	296.9	-15.2289	97.91	13.6543	3.54
7J!_23	70.5	1226	-15.8323	418.2	15.5762	3.42	6J!_3	455.7	-15.0987	156.9	12.8696	3.39
7J!_25	80.5	1301	-16.5074	445	14.5867	3.41	6J!_5	405.9	-15.581	139.4	12.9631	3.40
7J!_27	93.5	1144	-16.7381	388	14.6523	3.44	6J!_7	430	-15.5727	147.7	13.6568	3.40
7J!_29	111.5	1492	-16.6025	509.5	14.7007	3.42	6J!_9	409	-15.4171	140.1	14.1842	3.41
F2!_1	3	723.1	-14.5582	236.1	14.3303	3.57	6J!_11	470.7	-15.3582	158.3	14.6941	3.47
F2!_3	9	1469	-14.1356	504.7	13.5523	3.40	6J!_13	469.5	-15.1247	159.9	15.2681	3.43
F2!_5	15	1112	-14.1777	381.3	13.3315	3.40	6J!_15	484.2	-15.4531	165.3	14.6759	3.42
F2!_7	21	1033	-14.1522	354	15.1116	3.40	6J!_17	484.9	-16.167	166.6	14.1831	3.40
F2!_9	27	873.1	-14.294	297	16.948	3.43	6J!_19	522.6	-15.649	179.6	14.7901	3.39
F2!_11	34.5	1050	-14.6237	358.7	17.1759	3.42	6J!_21	492.2	-15.5845	171.1	15.0074	3.36
F2!_13	44.5	1183	-14.8981	404.2	17.4188	3.41	6J!_23	518.7	-16.0233	178.7	15.114	3.39
F2!_15	54.5	1078	-14.1749	368	16.596	3.42	6J!_25	445	-16.2963	152.6	15.0585	3.40
F2!_17	66.5	952.7	-13.8573	322.6	16.382	3.45	6J!_27	444.7	-16.5089	148.8	15.0462	3.49
F2!_19	80.5	940.3	-14.1604	319.6	16.3434	3.43	5H!_1	426.1	-14.9696	143.7	15.37	3.46
F2!_21	101.5	1272	-14.4937	435.6	16.0557	3.41	5H!_3	736.4	-14.7171	261.2	14.7844	3.29
6C!_1	2	1595	-15.2992	553.7	13.2845	3.36	5H!_5	758.2	-14.7166	262.6	14.853	3.37
6C!_3	6	1622	-15.4047	563.1	13.4066	3.36	5H!_7	607	-14.6782	213.1	15.3116	3.32
6C!_5	10	1324	-15.45	455.7	13.2397	3.39	5H!_9	604.4	-13.7412	212.4	16.5197	3.32
6C!_7	14	1567	-15.519	543.2	13.2148	3.37	5H!_11	583.1	-13.4099	199.5	16.8097	3.41
6C!_9	18	1280	-15.5902	440.8	13.2423	3.39	5H!_13	630.2	-13.7265	218	16.9167	3.37
6C!_11	23	1365	-16.0148	470.8	13.2626	3.38	3H!_1	824.4	-14.1598	269.4	16.0432	3.57
6C!_13	33	1471	-16.1383	507.5	12.7835	3.38	3H!_3	1381	-14.563	472.8	14.9683	3.41
6C!_15	39	1415	-16.108	486.7	13.4034	3.39	3H!_5	1335	-14.5558	459	15.4118	3.39
6C!_17	45	1257	-15.9632	430.2	14.3732	3.41	3H!_7	1309	-14.958	449.5	15.9892	3.40
6C!_19	52	1125	-16.2726	383.1	13.6122	3.43	3H!_9	1135	-14.869	386.3	16.2158	3.43
6C!_21	59	1393	-16.1942	475.4	13.8358	3.42	3H!_11	1199	-14.874	407.5	16.3367	3.43
6C!_23	60	1348	-15.9229	460.5	14.3759	3.42	3H!_13	1241	-14.9348	419.6	16.2667	3.45

6C!_25	74	1198	-15.9398	405.7	14.7784	3.45	3H!_15	1102	-14.6697	371.1	16.6401	3.46	
6C!_27	83	1188	-16.2251	401	14.2061	3.46	3H!_17	1075	-15.3693	359.4	16.1037	3.49	
6C!_29	83	1523	-16.3708	519.9	13.9758	3.42	3H!_19	1148	-15.6079	385.7	15.7994	3.47	
6C!_31	94	1264	-16.6116	426.7	13.997	3.46	3H!_21	1197	-15.7213	402.2	16.1785	3.47	
6C!_33	109	1323	-16.8741	448.2	14.8719	3.44	3H!_23	1176	-15.9707	394.3	15.9119	3.48	
6C!_35	128.5	1440	-16.8854	487.4	14.8699	3.45	3H!_25	1273	-16.4895	426.5	15.4774	3.48	
M93_3	7.0	1.18	-14.97	0.394	14.29	3.49	M90_1	3.0	1.407	-14.94	0.476	16.3	3.45
M93_5	12.0	1.416	-14.07	0.485	13.81	3.41	M90_3	7.0	1.446	-13.71	0.486	14.67	3.47
M93_7	18.5	1.422	-14.43	0.489	13.76	3.39	M90_5	11.0	2.135	-13.96	0.744	13.26	3.35
M93_9	26.0	1.783	-14.21	0.619	13.76	3.36	M90_7	15.0	1.776	-14.36	0.614	13.61	3.38
M93_11	33.0	1.609	-14.35	0.553	13.63	3.39	M90_9	19.0	1.858	-14.39	0.643	13.34	3.37
M93_13	41.0	1.312	-14.26	0.446	13.66	3.43	M90_11	23.5	1.887	-14.68	0.651	13.61	3.38
M93_15	49.0	1.384	-14.34	0.47	13.16	3.43	M90_13	29.0	1.5	-15.26	0.511	13.07	3.42
M93_17	58.5	1.191	-14.42	0.401	13.66	3.46	M90_15	35.0	1.708	-15.2	0.586	13.49	3.4
M93_19	78.5	1.304	-14.7	0.439	13.49	3.46	M90_17	41.0	1.28	-14.68	0.433	15.62	3.45
M392_1	2.0	1.972	-15	0.676	12.99	3.4	M90_19	47.0	1.638	-14.59	0.56	16.13	3.41
M392_3	6.0	0.978	-14.69	0.318	14.9	3.59	M90_21	54.0	1.424	-15.02	0.483	16.37	3.44
M392_5	10.0	1.396	-14.03	0.478	13.64	3.41	M90_23	62.5	1.392	-14.76	0.472	16.74	3.44
M392_7	14.0	1.53	-13.94	0.526	13.34	3.4	M90_25	74.0	1.489	-14.95	0.505	16.46	3.44
M392_9	19.0	1.364	-13.8	0.467	13.46	3.4	M90_27	92.0	1.185	-14.84	0.398	16.43	3.47
M392_11	24.0	1.425	-13.84	0.489	13.73	3.4	M95_1	3.0	1.769	-14.56	0.604	16.19	3.42
M392_13	29.0	1.453	-13.88	0.499	13.59	3.4	M95_3	7.0	1.986	-14.05	0.686	13.57	3.38
M392_15	35.0	1.422	-13.95	0.487	13.64	3.4	M95_5	11.0	1.874	-14.05	0.651	12.79	3.36
M392_17	41.0	1.343	-14.1	0.458	13.81	3.42	M95_7	15.0	1.598	-14.21	0.549	14.28	3.4
M392_19	47.5	1.392	-14.25	0.475	13.59	3.42	M95_9	19.0	1.421	-14.36	0.484	14.39	3.42
M392_21	55.0	1.079	-14.4	0.362	13.89	3.48	M95_11	24.0	1.652	-14.43	0.566	14.54	3.4
M392_23	64.5	1.036	-14.3	0.346	13.44	3.5	M95_13	29.0	1.414	-14.69	0.48	15.17	3.44
M392_25	86.0	1.096	-14.31	0.365	14.82	3.51	M95_15	34.0	1.445	-14.92	0.491	15.57	3.43
M291*_1	2.0	2.4	-14.96	0.824	13.55	3.4	M95_17	39.0	1.32	-14.81	0.446	15.51	3.45
M291*_3	6.0	1.034	-14.49	0.345	17.16	3.5	M95_19	45.0	1.33	-15.03	0.448	15.13	3.46
M291*_5	10.0	1.416	-14.41	0.485	16.12	3.41	M95_21	51.0	1.242	-15.32	0.417	14.78	3.48

M291*_7	14.0	1.233	-14.57	0.42	15.98	3.42	M95_23	58.5	1.244	-15.43	0.418	14.44	3.47
M291*_9	18.0	1.181	-14.88	0.402	14.88	3.43	M291_1	2.5	1.059	-14.42	0.347	15.98	3.56
M291*_11	23.0	1.111	-14.05	0.376	15.74	3.45	M291_3	6.5	1.439	-13.82	0.492	15.23	3.41
M291*_13	28.0	1.035	-13.91	0.349	15.82	3.46	M291_5	10.5	1.187	-14.15	0.403	15.16	3.44
M291*_15	33.5	1.196	-13.68	0.405	15.92	3.44	M291_7	14.5	1.248	-14.43	0.425	15.5	3.43
M291*_17	39.5	1.216	-13.73	0.412	15.55	3.44	M291_9	19	1.236	-13.82	0.42	15.18	3.43
M291*_19	46.0	1.178	-13.85	0.399	15.86	3.44	M291_11	24.5	1.261	-13.86	0.429	14.62	3.43
M291*_21	53.0	1.28	-14.04	0.434	15.27	3.44	M291_13	30.5	1.224	-14.03	0.416	14.05	3.43
M291*_23	62.0	1	-14.43	0.336	15.79	3.47	M291_15	37.5	1.214	-14.21	0.412	13.84	3.44
M291*_25	72.0	1.23	-14.68	0.415	16.09	3.46	M291_17	45.5	1.137	-14.34	0.383	13.52	3.46
M291*_27	85.0	1.121	-14.21	0.376	15.26	3.48	M291_19	54	1.101	-14.36	0.369	13.88	3.48
M94_1	2.0	1.402	-13.98	0.472	14.87	3.46	M291_21	63.5	1.008	-14.27	0.335	15.09	3.51
M94_3	6.0	1.209	-15.69	0.404	14.06	3.49	M291_23	75.5	1.06	-14.52	0.351	15.23	3.52
M94_5	10.0	1.497	-15.35	0.511	14.74	3.42	M291_25	99	1.25	-14.55	0.416	16.37	3.5
M94_7	14.0	1.485	-15.71	0.509	14.26	3.4	M9_1	2	2.041	-14.1	0.713	12.68	3.34
M94_9	18.0	1.351	-15.29	0.462	14.49	3.41	M9_3	6	1.858	-14.18	0.646	13.14	3.36
M94_11	22.0	1.5	-14.55	0.514	14.96	3.4	M9_5	10	1.804	-14.45	0.624	13.99	3.37
M94_13	26.0	1.396	-14.52	0.477	14.66	3.41	M9_7	14	1.911	-14.51	0.662	14.2	3.37
M94_15	30.0	1.156	-14.69	0.393	14.21	3.44	M9_9	18	1.761	-14.8	0.605	14.89	3.4
M94_17	34.0	1.338	-14.38	0.457	14.53	3.41	M9_11	22	1.752	-14.9	0.602	15.36	3.4
M94_19	39.0	1.144	-14.47	0.387	14.48	3.45	M9_13	26.5	1.793	-14.82	0.616	15.07	3.4
M94_21	44.5	1.291	-14.42	0.441	14.13	3.42	M9_15	31.5	1.576	-15.14	0.536	14.85	3.43
M94_25	56.5	1.39	-14.33	0.476	13.59	3.41	M9_17	37	1.563	-15.35	0.531	14.61	3.44
M94_27	63.0	1.31	-14.45	0.447	13.93	3.42	M9_19	43	1.402	-15.42	0.474	14.43	3.45
M94_29	70.0	1.442	-14.86	0.494	13.98	3.41	M9_21	51	1.351	-15.34	0.454	14.72	3.47
M94_31	77.0	1.273	-14.86	0.433	14.45	3.43							
M94_33	84.5	1.305	-14.52	0.442	16.02	3.44							
M94_35	92.5	1.35	-15.2	0.45	15.86	3.5							
M94_37	102.0	1.33	-14.99	0.45	16.66	3.45							
M94_39	115.0	1.254	-14.89	0.422	16.24	3.46							
*6B_1	2.5	638.2	-14.6263	209.1	12.9438	3.56	*4H_1	3.0	1142	-14.3571	372.8	13.9803	3.57

*6B_3	6.5	1260	-14.3591	429.4	13.7644	3.42	*4H_3	9.0	1964	-13.745	674.4	13.7182	3.40
*6B_5	10.5	1246	-14.3909	426	13.3957	3.41	*4H_5	15.0	1746	-13.8749	603.7	13.2009	3.37
*6B_7	14.5	889.9	-14.8636	300.5	12.0631	3.45	*4H_7	21.0	1469	-14.1798	502.1	13.8179	3.41
*6B_9	18.5	952.8	-14.6722	322.6	12.8249	3.45	*4H_9	28.0	1394	-14.3146	475.5	13.8897	3.42
*6B_11	22.5	934.3	-14.5084	315.9	15.5052	3.45	*4H_11	35.0	1432	-14.268	490.2	14.3841	3.41
*6B_13	27.5	992.8	-14.6467	335.7	16.2386	3.45	*4H_13	43.0	1262	-14.3508	429	14.5641	3.43
*6B_15	32.5	1033	-14.8929	348.5	15.2663	3.46	*4H_15	51.0	1312	-14.4181	445.6	14.8253	3.44
*6B_17	38.0	1037	-15.0346	348.8	15.7452	3.47	*4H_17	59.0	1197	-14.5234	402.5	15.1722	3.47
*6B_19	44.0	1152	-15.1377	388.4	15.6262	3.46	*4H_19	67.5	1215	-14.6371	410.4	15.1127	3.45
*6B_21	50.5	1050	-14.8712	352.7	16.6029	3.47	*4H_21	77.5	1208	-14.4929	407.8	15.2768	3.46
*6B_23	58.0	1094	-15.1201	366.8	15.9148	3.48	*4H_23	91.0	2416	-14.4197	840	14.9248	3.36
*6B_25	67.5	1514	-14.7035	512.6	16.2589	3.45	*4H*_1	3.0	1307	-13.8509	443.9	13.9237	3.44
*6B_27	79.5	1126	-15.1344	374.8	16.2763	3.50	*4H*_3	8.0	1738	-13.7144	601.5	13.6586	3.37
*6B_29	104.5	1599	-14.2059	539.2	16.4302	3.46	*4H*_7	18.0	1426	-14.0072	487.1	13.2629	3.42
*6J_1	2.5	879.7	-14.3501	288	13.7997	3.56	*4H*_9	23.0	1518	-14.1944	521.1	13.6304	3.40
*6J_3	7.5	1194	-14.1068	404.2	13.3435	3.45	*4H*_11	29.0	1222	-14.1798	415.6	13.9806	3.43
*6J_5	12.5	1126	-14.0429	382.9	13.0595	3.43	*4H*_13	35.0	1233	-14.3146	417.2	14.4471	3.45
*6J_7	17.5	1011	-14.1004	342.1	13.4379	3.45	*4H*_15	41.5	1255	-14.4162	425	14.3638	3.45
*6J_9	23.0	1133	-14.325	384.2	13.3999	3.44	*4H*_17	48.5	1212	-14.3914	410	14.4989	3.45
*6J_11	29.0	1148	-14.6017	389.5	13.1928	3.44	*4H*_19	55.5	1123	-14.4792	377.5	15.0389	3.47
*6J_13	35.0	1103	-14.7926	372.5	13.2213	3.45	*4H*_21	64.0	1045	-14.5041	349.3	15.875	3.49
*6J_15	41.5	1126	-15.3206	378.5	13.2294	3.47	*4H*_23	73.5	1156	-14.7554	386.5	15.1568	3.49
*6J_17	48.5	1007	-15.5916	337.5	13.146	3.48	*4H*_25	98.5	960.2	-14.7743	318	15.263	3.52
*6J_19	55.5	1091	-15.1218	367.3	13.7985	3.47	*5B_1	2.5	970	-14.9482	319.4	14.5955	3.54
*6J_21	63.0	1004	-15.017	334.2	14.2088	3.50	*5B_3	6.5	1809	-14.3853	626.4	14.2677	3.37
*6J_23	71.0	1020	-14.2157	339.9	15.3426	3.50	*5B_5	10.5	1416	-14.6858	486.6	13.9131	3.39
*6J_25	80.0	940.6	-14.4618	308.1	15.5881	3.56	*5B_7	14.5	1370	-14.4588	468.5	14.4281	3.41
*6J_27	92.0	1054	-14.8109	350.4	14.9961	3.51	*5B_9	18.5	1330	-13.8764	454.8	15.3142	3.41
*6J_29	115.5	1446	-15.0421	484.8	14.1599	3.48	*5B_11	22.5	990.2	-13.7114	333.6	16.3924	3.46
*HT_1		1357	-14.3323	454.3	14.1413	3.48	*5B_13	27.0	1304	-13.368	446	16.7762	3.41
*HT_3		1303	-13.9487	445.4	14.9139	3.41	*5B_15	32.0	1170	-13.4677	397.3	16.8284	3.44
*HT_5		1224	-14.0191	417	14.8418	3.42	*5B_17	37.5	1181	-13.6101	399.6	16.7384	3.45

*4L_1	2.5	1008	-14.1165	332.3	16.8519	3.54	*5B_19	43.5	1397	-13.6183	475.6	16.5485	3.43
*4L_3	6.5	1109	-13.8026	362.5	16.6304	3.57	*5B_21	49.5	1259	-13.7324	425.5	16.6586	3.45
*4L_5	10.5	1161	-13.34	391.7	17.51	3.46	*5B_23	56.5	1234	-13.9816	413.9	16.6452	3.48
*4L_7	14.5	1149	-13.82	389.1	15.73	3.45	*5B_25	63.5	1202	-14.1739	404.7	16.443	3.47
*4L_9	18.5	922.9	-14.27	308.9	14.48	3.49	*5B_27	71.5	1159	-14.2522	390.6	16.3706	3.46
*4L_11	23.5	1183	-14.3	400.8	15.14	3.44	*5B_29	81.5	1431	-14.3086	484.4	16.3876	3.45
*4L_13	29.5	1090	-14.3	367.1	13.61	3.46	*5B_31	94.5	1651	-14.8218	564.4	15.3158	3.41
*4L_15	35.5	1111	-14.63	373.7	13.34	3.47	*5B_33	118.5	2680	-15.1963	950.7	14.0974	3.29
*4L_17	42.5	1102	-14.76	368.9	15.79	3.49	*6L_1	3.0	1371	-14.3652	470.7	13.756	3.40
*4L_19	50.5	1297	-14.28	437	16.87	3.46	*6L_3	7.0	1291	-14.3834	473.2	12.9082	3.18
*4L_21	58.5	1131	-14.58	378.7	16.75	3.48	*6L_5	11.0	1225	-14.6971	445.8	12.6486	3.21
*4L_23	68.5	1197	-14.86	402	15.84	3.47	*6L_7	16.5	1345	-14.9316	489.5	12.1659	3.21
*4L_25	79.5	1377	-14.93	463.5	16.25	3.47	*6L_9	22.5	1351	-15.2167	484.7	12.0079	3.25
*4L_27	96.0	1358	-14.93	454.5	16.75	3.49	*6L_11	30.0	1336	-15.9671	479.5	11.6929	3.25
*4L_29	134.0	1465	-15.06	488.8	16.45	3.50	*6L_13	37.0	1260	-16.303	434.1	12.3974	3.39
*ZH_1	3.0	1414	-14.5843	467.1	14.2313	3.53	*6L_15	44.5	1183	-16.8073	400.4	11.8114	3.45
*ZH_3	7.0	2259	-14.1536	786.2	13.2529	3.35	*6L_17	52.5	1236	-16.6451	410.1	12.3378	3.52
*ZH_5	11.0	1892	-14.0109	657.3	13.1602	3.36	*6L_19	61.5	1430	-16.2332	476.3	12.8529	3.50
*ZH_7	15.0	1728	-14.1357	597.7	13.1156	3.37	*6L_21	74.0	1317	-16.2855	438.3	13.3224	3.51
*ZH_9	19.0	1556	-14.1683	536.7	13.3835	3.38	*6L_23	107.0	2339	-15.9331	762.1	12.8399	3.58
*ZH_11	23.5	1450	-14.349	498.9	13.9528	3.39	*D2_1	2.5	1332	-15.8577	474.6	15.1534	3.27
*ZH_13	28.5	1731	-14.3309	598.3	15.6475	3.38	*D2_3	6.5	1438	-15.0583	519.9	15.5428	3.23
*ZH_15	33.5	1678	-14.1551	578.7	16.2274	3.38	*D2_5	10.5	1470	-14.8526	538	15.3836	3.19
*ZH_17	39.0	1314	-14.2259	448.4	16.0385	3.42	*D2_7	14.5	1174	-14.9208	411.8	15.0167	3.33
*ZH_19	44.0	1212	-14.2298	411.9	16.0989	3.43	*D2_9	18.5	965	-15.1126	340.5	15.0377	3.31
*ZH_21	49.5	1138	-14.7596	385.9	15.9234	3.44	*D2_11	22.5	878	-15.6511	302.6	14.3875	3.39
*ZH_23	56.5	1141	-15.3932	386.3	15.1359	3.45	*D2_13	26.5	956.9	-15.7036	337.4	14.5856	3.31
*ZH_25	64.0	1162	-15.3625	392.6	15.2228	3.45	*D2_15	31.5	959.9	-16.2474	337.4	14.1142	3.32
*ZH_27	73.0	1129	-14.9791	379.7	15.5122	3.47	*D2_17	37.5	1157	-16.5496	402.4	13.849	3.35
*ZH_29	88.5	1814	-14.5547	619.1	15.3817	3.42	*D2_19	43.5	1092	-16.6779	378.4	13.8565	3.37
*H7_1	3.0	1334	-14.5545	437.2	13.8401	3.56	*D2_21	50.5	1044	-16.4073	353.5	14.206	3.45
*H7_3	7.0	1510	-14.211	511.5	13.428	3.44	*D2_23	58.5	1092	-15.8934	374.1	14.6346	3.41

*H7_5	11.0	1381	-14.1464	469.2	13.7557	3.43	*D2_25	66.5	905.9	-15.5602	310.1	14.728	3.41
*H7_7	15.0	1293	-14.1936	437.7	13.4527	3.45	*D2_27	75.0	977.5	-16.1918	316.8	14.56	3.60
*H7_9	20.0	1224	-13.9483	414.4	15.4713	3.45	*D2_29	84.0	951.8	-16.1357	316.2	14.6467	3.51
*H7_11	25.5	1349	-13.8822	454.5	16.5614	3.46	*D2_31	94.0	1064	-16.1549	341.6	14.5521	3.63
*H7_13	31.5	1353	-13.937	457.2	16.687	3.45	*D2_33	105.5	1157	-16.0036	374.8	14.4485	3.60
*H7_15	37.5	1099	-14.0104	366.5	16.7108	3.50	*D2_35	119.5	1343	-15.6805	426.7	14.8501	3.67
*H7_17	43.5	1172	-14.0894	392.9	16.817	3.48	*6B_1	3.5	778.9	-16.2619	238.4	12.4196	3.81
*H7_19	49.5	992.2	-14.306	330	16.8894	3.51	*6B_3	9.5	1158	-15.6074	385.3	11.376	3.51
*H7_21	56.0	921.2	-14.3373	305	17.0459	3.52	*6B_5	12.5	939	-16.1077	307.1	11.6938	3.57
*H7_23	64.5	1001	-14.4269	332.9	16.9291	3.51	*6B_7	19.5	967.5	-16.1944	325.4	12.6417	3.47
*H7_25	76.5	888.1	-14.518	291.9	17.0261	3.55	*6B_9	27.5	1051	-15.9515	333.4	14.1071	3.68
*3H_1	2.5	1388	-13.8155	471.1	15.1496	3.44	*6B_11	36.5	1194	-15.8324	375.8	14.4771	3.71
*3H_3	6.5	1343	-13.6655	456.2	14.682	3.43	*6B_13	47.5	1341	-15.6974	433.3	14.584	3.61
*3H_5	10.5	1209	-13.8929	410.8	14.2522	3.43	*6B_15	59.5	1120	-15.9737	352.5	14.3314	3.71
*3H_7	14.5	1017	-14.0809	342.6	14.2407	3.46	*6B_17	72.0	958.6	-15.9934	301.8	14.1181	3.71
*3H_9	18.5	1159	-14.0902	395.1	14.3838	3.42	*6B_19	98.5	1368	-16.153	439.8	13.3237	3.63
*3H_11	22.5	1085	-13.9372	363.5	15.7248	3.48	*D8_1	3.0	1093	-15.1329	356	11.6521	3.58
*3H_13	26.5	1145	-14.2354	387.4	15.4044	3.45	*D8_3	7.0	972.5	-15.1673	331.6	11.4817	3.42
*3H_15	31.5	1192	-14.6437	402.6	14.9435	3.45	*D8_5	11.0	958.2	-15.5702	315.6	12.3785	3.54
*3H_17	36.5	1360	-14.1788	459.3	15.7127	3.45	*D8_7	16.5	1012	-15.9278	334.3	13.0878	3.53
*3H_19	41.5	992.2	-13.9426	331.2	17.2016	3.50	*D8_9	21.5	1125	-16.004	355.4	13.0911	3.69
*3H_21	47.5	1138	-13.7764	383	17.2896	3.47	*D8_11	27.0	1128	-16.2154	368.2	12.403	3.57
*3H_23	54.5	915.7	-13.9696	304	17.2741	3.51	*D8_13	34.0	1292	-16.2595	432.2	12.7821	3.49
*3H_25	62.0	891.9	-14.0672	296.8	16.9435	3.51	*D8_15	41.0	1189	-16.6085	393.4	12.5097	3.53
*3H_27	70.5	1179	-14.2124	393.4	16.5918	3.50	*D8_17	48.5	1006	-16.7513	326.2	12.743	3.60
*3H_29	79.5	1044	-14.344	349.1	16.6155	3.49	*D8_19	59.5	1087	-16.7576	350.9	12.6689	3.61
*3H_31	86.5	1128	-14.7039	373.8	16.5094	3.52	*D8_21	74.0	1040	-16.7449	328.9	12.8348	3.69
*3H_33	114.5	2300	-14.6422	785.3	15.4892	3.42	*5H_1	2.0	969.8	-15.0837	319.7	14.1999	3.54
*H8_1	3.0	1288	-14.6922	417.7	14.2172	3.60	*5H_3	6.0	1316	-14.9552	445.9	13.8928	3.44
*H8_3	7.0	1252	-14.2903	422.6	14.3025	3.46	*5H_5	10.0	1287	-15.0689	433.4	12.6113	3.46
*H8_5	11.0	1344	-14.5565	458.6	14.6409	3.42	*5H_7	14.0	1066	-15.144	359.1	11.8732	3.46
*H8_7	15.0	1155	-14.6342	390.4	15.809	3.45	*5H_9	18.0	1096	-15.1643	354.6	12.3771	3.61

*H8_9	21.0	1234	-14.7036	420.4	15.1868	3.42	*5H_11	22.5	1063	-15.3969	360.7	12.8906	3.44
*H8_11	27.0	1361	-14.5888	464.5	16.0135	3.42	*5H_13	27.5	846.1	-15.1347	269	14.4975	3.67
*H8_13	34.5	1464	-14.5501	501.8	16.0764	3.40	*5H_15	31.5	1005	-14.7813	317.7	15.1535	3.69
*H8_15	42.5	1416	-14.3699	484.9	16.5849	3.41	*5H_17	37.5	1091	-14.6385	358.1	15.4503	3.55
*H8_17	51.0	1258	-14.6157	428.4	16.0661	3.43	*5H_19	44.0	1222	-14.5221	384.8	15.5495	3.70
*H8_19	60.0	1193	-14.8829	404.6	16.2439	3.44	*5H_21	51.0	912.1	-14.6249	307.9	15.9343	3.46
*H8_21	69.5	1143	-14.7981	386.6	16.0772	3.45	*5H_23	58.0	1033	-14.6038	323.5	16.3694	3.73
*H8_23	80.0	1125	-15.3831	376.8	15.5587	3.48	*5H_25	65.5	901	-14.6821	285.9	16.353	3.68
*H8_25	92.5	1183	-15.2755	397	15.6715	3.48	*5H_27	75.0	1103	-14.8275	352	15.9831	3.66
*H8_27	115.0	2173	-15.1874	753.6	15.0726	3.36	*5H_29	89.5	1123	-14.8266	363.9	15.7971	3.60
*DZ_1	3.0	1114	-13.6726	367.2	15.3008	3.54	*SU_1	3	836.8	-14.816	272.3	13.9768	3.59
*DZ_3	8.5	1875	-13.3496	653.8	14.5309	3.35	*SU_3	7	1561	-14.1858	539.8	13.4481	3.37
*DZ_5	13.5	1441	-13.5714	487.6	14.6043	3.45	*SU_5	11	1482	-14.1252	512	13.3429	3.38
*DZ_7	19.0	1493	-14.2696	511.1	14.7719	3.41	*SU_7	15	1522	-14.1864	526.8	13.7929	3.37
*DZ_9	25.0	1399	-14.5024	478.9	14.9921	3.41	*SU_9	19	1283	-14.334	441.6	13.2907	3.39
*DZ_11	31.5	1502	-14.3696	512.1	15.2841	3.42	*SU_11	23	1349	-14.474	463.8	14.4432	3.39
*DZ_13	40.0	1447	-14.4275	492.7	15.7817	3.43	*SU_13	29	1329	-14.6426	456.6	14.9293	3.40
*DZ_15	62.0	1907	-13.7913	655.9	16.0741	3.39	*SU_15	35	1420	-14.9751	486.4	14.0886	3.41
*D1_1	3.0	1371	-14.3254	466.8	13.5407	3.43	*SU_17	41	1419	-15.1228	485.8	13.8371	3.41
*D1_3	8.0	1459	-14.1612	504.6	13.35	3.37	*SU_19	47.5	1461	-15.0322	498.9	14.1434	3.42
*D1_5	13.0	1327	-14.2576	457.6	13.1488	3.38	*SU_21	55	1362	-15.1726	463.2	13.7773	3.43
*D1_7	18.5	1447	-14.7572	500.9	13.9431	3.37	*SU_23	63	1270	-15.0553	430.6	14.0558	3.44
*D1_9	23.5	1142	-14.8198	390.3	14.1169	3.41	*SU_25	74	1352	-14.9637	457	14.4156	3.45
*D1_11	30.5	1256	-15.1417	427.4	14.3377	3.43	*SU_27	87	1011	-15.1177	339.2	14.453	3.48
*D1_13	41.5	1632	-14.3782	559.9	15.801	3.40	*SU_29	102	1963	-15.1825	670.7	14.3605	3.41
*D1_15	54.0	1250	-14.3984	423.7	16.0699	3.44	*1H_1	3	769.6	-16.1635	251.1	13.5172	3.58
*D1_17	69.0	1456	-14.4051	496.8	15.4581	3.42	*1H_3	9	1433	-15.6521	495.9	12.7758	3.37
							*1H_5	15	1587	-15.4598	553.6	13.134	3.34
							*1H_7	21	1400	-15.8581	485.8	12.8619	3.36
							*1H_9	27	1544	-14.6533	537.8	14.5101	3.35
							*1H_11	33	987.5	-14.9516	338.5	14.3779	3.40
							*1H_13	39.5	1026	-15.0067	350.9	14.7525	3.41

								*1H_15	46.5	1064	-15.1984	364	14.2579	3.41
								*1H_17	53.5	1110	-15.1781	378.7	14.6082	3.42
								*1H_19	61	1231	-15.3488	421.5	14.3581	3.41
								*1H_21	69	1190	-15.715	406.9	13.7125	3.41
								*1H_23	73	1036	-16.0158	350.4	13.5691	3.45
								*1H_25	77	1038	-16.0515	351.5	14.0608	3.45
								*1H_27	88	1105	-16.0441	373	14.3311	3.46
								*1H_29	102	1078	-15.9639	364.3	14.5848	3.45
G2_1	3.0	826.4	-15.6337	277.5	14.0398	3.47	G4_1	3.5	1063	-15.5533	355.9	14.5893	3.48	
G2_3	9.0	960.4	-15.9604	323.4	13.5242	3.46	G4_3	11	986.5	-15.8301	328.9	14.2711	3.50	
G2_5	15.5	1118	-16.0145	375.6	13.6262	3.47	G4_5	21.5	1169	-16.2692	391.2	13.3623	3.49	
G2_7	22.5	1149	-15.6597	387	13.533	3.46	G4_7	43.5	1227	-16.038	409.8	13.523	3.49	
G2_9	31.0	1305	-15.7336	441.6	13.7979	3.45	G6_1	4	1089	-15.013	370.3	14.0828	3.43	
G2_11	42.0	1177	-15.8036	394.3	13.7326	3.48	G6_3	12	1345	-15.0244	458.6	14.3182	3.42	
G2_13	59.0	1019	-15.6258	339.7	14.492	3.50	G6_5	23	1177	-15.0374	399.5	14.4291	3.44	
G3_1	3.0	1106	-15.1614	378.5	13.9883	3.41	G6_7	37	1276	-15.184	432.5	14.4462	3.44	
G3_3	9.0	1249	-15.6108	429	13.4748	3.40	G5_1	4	870.6	-15.4701	293.6	14.0384	3.46	
G3_5	15.0	1309	-15.5599	448.9	13.5544	3.40	G5_3	12	874.8	-15.6593	294.6	13.9234	3.46	
G3_7	21.0	1280	-15.6613	437.3	13.3727	3.41	G5_5	21	783.1	-16.1671	262.4	13.3269	3.48	
G3_9	28.0	1213	-15.6272	411.7	13.3558	3.44	G5_7	31	914.2	-16.2552	305.4	13.5474	3.49	
G3_11	36.0	1245	-15.7726	422	13.248	3.44	G5_9	44	916.8	-16.0365	308.1	13.4112	3.47	
G3_13	44.0	1041	-15.7392	351.4	13.44	3.46	G5_11	60	884.6	-16.0396	295	13.6779	3.50	
G3_15	53.0	979.8	-15.5054	329.7	14.3038	3.47	G1_5	3.0	852.5	-15.3445	285.5	14.0223	3.48	
G3_17	67.0	1137	-15.343	384.8	14.8372	3.45	G1_7	9.0	982.4	-15.7917	329.8	13.6052	3.48	
G3_19	82.0	1090	-15.3198	367.3	14.9584	3.46	G1_9	16.0	742	-16.27	246.4	13.0729	3.51	
*NRR*_1	4.0	1239	-14.0999	416.4	12.7761	3.47	A5a1	3.0	1342	-14.7709	442.8	11.7949	3.54	
*NRR*_3	11.0	1264	-13.8818	429.4	11.9038	3.43	A5a5	12.0	1495	-14.1336	515.3	11.5305	3.38	
*NRR*_5	19.5	1152	-13.6185	391.7	13.7607	3.43	A5a9	22.5	1604	-14.2865	553.3	11.6952	3.38	
*NRR*_7	31.5	1103	-14.0677	367.1	14.3913	3.51	A5a13	36.0	1631	-14.2984	561	11.9505	3.39	
*NRR*_9	55.5	1373	-14.2345	455.4	13.8267	3.52	A5a17	51.5	1182	-14.726	399.6	11.4462	3.45	

NRL\$_1	2.5	1126	-14.156	379.4	13.5503	3.46	A5a21	69.5	1166	-14.7121	393.4	12.0395	3.46
NRL\$_3	6.5	1501	-13.9383	513.2	11.9683	3.41	A5a25	86.5	970.8	-14.7064	323	12.18	3.51
NRL\$_5	10.5	1405	-13.8762	480.2	11.7053	3.41	A5a29	104.5	1336	-14.7365	448.8	11.9477	3.47
NRL\$_7	15.5	1247	-13.73	425.3	13.2932	3.42	A5b1	3.0	1183	-14.9847	388.8	11.3186	3.55
NRL\$_9	21.5	1042	-13.881	353.3	13.8066	3.44	A5b5	15.0	1339	-14.1727	460.7	11.4167	3.39
NRL\$_11	27.5	1028	-13.9032	346.9	14.3932	3.46	A5b9	29.0	1235	-14.2202	420.1	11.3508	3.43
NRL\$_13	35.5	940.1	-14.0202	316.4	14.5093	3.47	A5b13	45.0	1162	-14.3673	393.2	11.6961	3.45
NRL\$_15	44.0	987.5	-14.0542	330.6	14.5034	3.48	A5c5	3.0	1387	-14.9616	462.2	11.4362	3.50
NRL\$_17	53.5	922.2	-14.2638	308	13.9967	3.49	A5c9	11.0	1413	-14.1977	487.4	11.3292	3.38
NRL\$_19	67.5	973.6	-14.1464	326.3	13.8414	3.48	A5c13	21.0	1336	-14.2621	458.8	11.4304	3.40
*NRR\$_1	2.5	976.2	-14.2062	328.8	13.7197	3.46	A5c17	31.5	1185	-14.3702	402.9	11.5399	3.43
*NRR\$_3	6.5	1407	-13.946	481.2	12.6862	3.41	A5c21	43.5	859.2	-14.4545	286.2	12.3784	3.50
*NRR\$_5	10.5	1283	-13.9598	438.2	12.0583	3.42	A5c25	57.5	1035	-14.6312	346.2	11.8027	3.49
*NRR\$_7	15.5	1207	-13.9876	410.9	11.8476	3.43	A5c29	85.5	952.9	-14.6527	317.2	12.0067	3.50
*NRR\$_9	21.0	1245	-13.9848	423.9	12.8294	3.43	A5d1	3.5	901.6	-14.9325	299.9	11.3027	3.51
*NRR\$_11	27.0	1452	-13.6787	495.1	13.6944	3.42	A5d5	16.0	1335	-14.2164	459.9	11.6107	3.39
*NRR\$_13	30.0	1227	-13.9364	416	13.9187	3.44	A5d9	33.0	1276	-14.4394	434.6	11.7615	3.43
*NRR\$_15	37.0	1278	-13.9265	433.2	14.3611	3.44	A5e1	3.0	1029	-14.8022	342.8	11.4956	3.50
*NRR\$_17	45.5	1362	-13.83	462.1	14.1276	3.44	A5e5	17.0	1498	-14.123	516.7	11.3854	3.38
*NRR\$_19	55.0	1280	-13.9618	432.6	14.198	3.45	A5e9	37.0	1204	-14.3401	408.6	11.9157	3.44
*NRR\$_21	66.5	1364	-14.1245	461.2	13.6357	3.45	A5f1	3.0	958.1	-14.5203	319.5	11.5764	3.50
NRL_1	3.0	1419	-13.9822	484	13.0485	3.42	A5f5	18.0	1234	-14.2908	423.3	11.6688	3.40
NRL_3	7.0	1250	-13.8932	427.4	12.3367	3.41	A5f9	45.5	1090	-14.6554	368.9	12.1183	3.45
NRL_5	11.0	1202	-13.8985	410.9	11.754	3.41	Ba_1	3	1122	-14.4188	376.6	12.5468	3.48
NRL_7	15.5	1272	-13.7416	432	12.9743	3.44	Ba_3	9	1498	-14.0467	517	14.9604	3.38
NRL_9	21.0	1253	-13.7653	423	13.9852	3.46	Ba_5	15	1361	-14.0448	469.3	17.2916	3.38
NRL_11	27.5	1242	-13.8552	418.9	14.4006	3.46	Ba_7	21	1578	-14.0178	547.9	17.6602	3.36
NRL_13	35.0	1076	-14.0044	361.1	14.6776	3.48	Ba_9	27	1343	-14.3534	462.2	16.6667	3.39
NRL_15	45.5	1297	-13.9972	435.9	14.5219	3.47	Ba_11	33	1289	-14.3115	443.8	15.3928	3.39
NRL_17	59.5	1012	-14.4865	337.7	14.2361	3.50	Ba_13	39	1286	-14.2534	441.5	15.5397	3.40
NRL*_1	3.0	1562	-14.0476	530.2	13.2763	3.44	Ba_15	47	1121	-14.6492	383.1	15.8731	3.41
NRL*_3	7.0	1411	-14.032	479.3	12.4872	3.43	Ba_17	56	1153	-14.722	391.8	16.5484	3.43

NRL*_5	11.0	1370	-13.9886	466.9	11.8093	3.42	Ba_19	66	1056	-14.7362	355.1	16.3621	3.47
NRL*_7	16.0	1318	-13.9773	449	12.4938	3.42	Ba_21	79	1166	-14.5698	393.7	14.5229	3.46
NRL*_9	21.0	1226	-13.8835	416.1	14.1055	3.44	Db1	3	1052	-14.98	349.6	13.0162	3.51
NRL*_11	27.0	1291	-13.9351	437.9	13.8648	3.44	Db5	9	1628	-14.8682	562.7	12.0243	3.38
NRL*_13	33.0	1207	-13.9538	406	14.5682	3.47	Db9	16	1400	-14.7022	481.1	11.7359	3.39
NRL*_15	40.0	1138	-14.1018	380.6	14.5648	3.49	Db13	26	1388	-14.5469	474.9	11.9062	3.41
NRL*_17	48.0	1112	-14.1201	372.1	14.5882	3.49	Db17	37	1572	-14.45	538.3	12.164	3.41
NRL*_19	59.0	1104	-14.3975	368.6	13.9881	3.49	Db21	49	1400	-14.5513	474.2	11.949	3.44
NRL*_21	77.0	1970	-13.9561	666.2	13.177	3.45	Dc1	4	940.3	-14.9649	314.3	12.3939	3.49
NRR_1	3.0	1626	-14.1421	553.2	12.6912	3.43	Dc5	13	1144	-14.5427	390.2	12.8255	3.42
NRR_3	9.0	1625	-14.0028	556.3	11.6205	3.41	Dc9	22	1281	-14.7239	437.6	11.9696	3.42
NRR_5	15.0	1556	-13.8624	533.4	12.0912	3.40	Dc13	34	1228	-14.7965	417.5	11.9295	3.43
NRR_7	21.0	1432	-13.7503	487.2	13.6272	3.43	Dc17	75	1171	-14.83	394.2	12.0004	3.47
NRR_9	27.0	1346	-13.8825	455.6	13.9844	3.45	Dd1	3	831.5	-14.7658	278.5	12.4533	3.48
NRR_11	34.0	1398	-13.8	3252	14.2	0.50	Dd5	12	1073	-14.5559	365.5	12.8149	3.42
NRR_13	42.0	1247	-14.2906	418.7	14.4312	3.47	Dd9	23	1147	-14.9378	391.6	11.8896	3.42
NRR_15	55.0	2385	-13.9537	810.4	13.2526	3.43	Dd13	36	1185	-14.8786	401	11.8573	3.45
Bb1	2.0	649	-14.366	210.2	16.5829	3.60	Dd17	57	1112	-14.8729	373	12.0035	3.48
Bb5	11.0	1248	-14.2067	422.7	16.0821	3.44	De1	4	944.3	-14.8859	313.9	12.6635	3.51
Bb9	24.0	1091	-14.4116	370.8	15.8033	3.43	De5	17	917.9	-14.7608	312.4	12.0076	3.43
Bb13	39.0	1116	-14.4135	377.5	15.5226	3.45	Df1	3	1254	-14.6389	421.3	12.3747	3.47
Bb17	54.0	1215	-14.7114	410	11.4099	3.46	Df5	15	1309	-14.59	447.3	11.8751	3.41
Bc1	3.0	978.4	-14.3351	325	12.8774	3.51	Df9	28	1394	-14.6244	477.1	11.7053	3.41
Bc5	11.0	1336	-13.913	457.3	16.7472	3.41	Df13	48.5	1132	-14.4831	381.2	12.0476	3.46
Bc9	23.5	1429	-13.9806	490.7	17.4779	3.40	Dg1	3	969.7	-14.6918	323.2	12.4722	3.50
Bc13	37.5	1045	-14.1445	353.7	15.8269	3.45	Dg5	11	1259	-14.7962	430.2	11.6951	3.41
Bc17	54.5	1201	-14.795	403.4	16.6472	3.47	Dg9	21	1133	-14.7291	386.8	11.6576	3.42
Bd1	3.0	1187	-14.2825	400.3	12.7242	3.46	Dg13	32	1307	-14.4929	447.1	11.846	3.41
Bd5	15.0	1427	-13.8184	493.6	17.7393	3.37	Dg17	45	1198	-14.4972	406.6	12.163	3.44
Bd9	34.0	965.3	-14.2768	325.8	15.2656	3.46	Dg21	63.5	1109	-14.6646	373.5	12.1575	3.46
Be1	3.0	1106	-14.27	368	13.7524	3.51	Dh1	2.5	966.2	-15.0299	322.8	12.1557	3.49
Be5	15.0	1381	-13.9582	473	17.7627	3.41	Dh5	6.5	1637	-14.4324	566	11.7619	3.37

Be9	27.0	1237	-14.3284	418.3	15.4542	3.45	Dh9	10.5	1690	-14.2849	584.3	12.0889	3.37
Be13	42.0	1634	-14.6426	561	16.3909	3.40	Dh13	20	1463	-14.4493	501.7	11.8927	3.40
Be17	59.0	1061	-14.4274	357	13.6445	3.47	Dh17	30.5	1373	-14.5523	467.1	11.7441	3.43
Bf1	3.0	1198	-14.3144	402	12.7798	3.48	Dh21	42.5	1528	-14.5872	521.3	11.8426	3.42
Bf5	15.0	1634	-13.9866	565.3	16.6944	3.37	Dh25	56.5	1512	-14.7666	513.1	11.4413	3.44
Bf9	24.0	1602	-13.9815	553.2	17.542	3.38	Da_1	2	1218	-14.7577	409.3	12.8638	3.47
Bf13	44.0	1362	-14.1359	465.9	15.8547	3.41	Da_3	6	1786	-14.5793	616.2	12.2982	3.38
Bf17	63.5	1161	-14.7479	392.1	16.6712	3.45	Da_5	10	1572	-14.845	539.7	11.8618	3.40
Bf21	105.5	2365	-14.5705	816.3	13.0925	3.38	Da_7	14	1405	-14.7795	482.5	11.93	3.40
							Da_9	20	1565	-14.707	540.3	11.8789	3.38
							Da_11	26	1718	-14.5795	593.1	12.0121	3.38
							Da_13	32	1609	-14.4952	552.6	12.0477	3.40
							Da_15	38	1364	-14.3509	465.1	12.4086	3.42
							Da_17	45	1337	-14.5775	452.6	12.1902	3.45
							Da_19	53	1559	-14.5646	532.6	12.0453	3.42
							Da_21	62	1525	-14.6236	518.8	12.1482	3.43
							Da_23	73	1367	-14.7943	460.1	12.0713	3.47
							Da_25	86	1454	-14.7731	489.8	11.9955	3.46

Appendix 2: Southern Elephant Seal Data

Appendix 2

Sample	Length	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C/N ratio	Sample	Length	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C/N ratio
m17_1	2	1446	-17.2066	490.7	12.328	3.44	M16\$ _2	4.5	0.789	-17.43	0.266	10.63	3.46
m17_2	4	1384	-17.2635	468.3	12.3454	3.45	M16\$ _4	9.5	0.942	-17.4	0.319	10.48	3.45
m17_3	6	1109	-17.2927	373.1	12.3487	3.47	M16\$ _6	15.5	0.875	-17.23	0.294	10.39	3.47
m17_4	8	1218	-17.2618	411.7	12.2477	3.45	M16\$ _8	22	1.028	-16.76	0.347	10.72	3.45
m17_5	10.5	1384	-17.1473	470.4	12.0147	3.43	M16\$ _10	31	1.206	-16.22	0.408	11.76	3.45
m17_6	12.5	1504	-17.1971	513	12.0833	3.42	M16\$ _12	41.5	0.959	-16.77	0.321	12.99	3.49
m17_7	14.5	1221	-17.0885	412.4	11.8129	3.45	FO_2	4	1.268	-16.3	0.432	10.79	3.43
m17_8	16.5	1001	-17.0793	336	11.9535	3.48	FO_4	8	1.091	-16.28	0.37	10.91	3.44
m17_9	18.5	1006	-17.0475	337.9	11.913	3.47	FO_6	12	1.066	-16.03	0.36	11.52	3.45
m17_10	21	1179	-17.0136	397.9	11.7892	3.46	FO_8	16	1.318	-15.81	0.448	12.89	3.43
m17_11	23.5	1184	-16.9808	400.1	11.6736	3.45	FO_10	21	1.276	-15.69	0.432	13.74	3.45
m17_12	25.5	964.4	-16.978	324	11.6967	3.47	FO_12	25	1.148	-15.99	0.389	12.09	3.44
m17_13	28	1167	-16.9216	395.2	11.5648	3.45	FO_14	29.5	1.293	-16.14	0.441	11.11	3.42
m17_14	30.5	1143	-16.8578	384.3	11.4436	3.47	FO_16	35	1.21	-16.34	0.409	10.55	3.45
m17_15	33.5	1572	-16.7704	532.4	11.5347	3.44	FO_18	42	1.292	-16.44	0.438	10.58	3.44
m17_16	36.5	1725	-16.8715	583.8	11.6356	3.45	FO_20	49	1.152	-16.49	0.389	10.88	3.45
m17_17	39.5	1941	-17.0931	653.7	11.2087	3.46	FO_22	56.5	1.038	-16.6	0.345	11.24	3.51
m17_18	43	2370	-17.1896	798.2	10.9741	3.46	FO_24	64.5	1.035	-16.34	0.347	11.92	3.48
m17_19	46.5	2291	-17.2062	768.7	11.0509	3.48	FO_26	75.5	0.975	-16.54	0.326	12.74	3.49
m17_20	51.5	3922	-17.155	1330	11.0455	3.44	FO_28	91	0.955	-16.12	0.318	15.15	3.5
m17_21	56	4074	-17.0884	1381	11.4771	3.44	SX_2	8	1.207	-15.63	0.407	12.52	3.46
m17_22	62	2670	-16.9764	897.5	11.7765	3.47	SX_4	14.5	1.409	-15.8	0.478	11.99	3.44
m17_23	68.5	1714	-16.9871	571.6	11.9711	3.50	SX_6	20.5	1.398	-15.62	0.475	12.33	3.44
m17_24	76.5	1378	-17.139	458.2	11.5392	3.51	SX_8	26.5	0.983	-15.55	0.328	12.69	3.49
m17_25	94	430.2	-17.3891	136.5	12.2555	3.68	SX_10	33.5	1.037	-15.49	0.346	13.09	3.49
S*_1	2	962.7	-16.7942	323.2	10.2104	3.48	SX_12	40.5	0.88	-15.52	0.292	13.23	3.52
S*_2	4.5	1118	-16.8834	374.3	10.2695	3.48	SX_14	48	0.809	-15.64	0.268	13.33	3.53
S*_3	7.5	1133	-16.7662	381.1	10.4704	3.47	SX_16	59	0.698	-15.83	0.228	13.19	3.56

S*_4	10.5	1175	-16.6391	396.3	10.4722	3.46	SX_18	75	1.08	-16.08	0.361	12.56	3.49
S*_5	14	971.3	-16.5788	326.1	10.4862	3.47	Q*_4	6.5	1.145	-16.96	0.387	10.8	3.45
S*_6	17.5	1107	-16.4708	372.8	10.4337	3.46	Q*_6	10.5	1.437	-16.78	0.491	10.77	3.42
S*_7	21	888.1	-16.4105	297.3	10.2468	3.49	Q*_8	14.5	1.278	-16.75	0.435	10.88	3.43
S*_8	25.5	1233	-16.3581	416.9	10.4381	3.45	Q*_10	18.5	1.127	-16.87	0.383	10.63	3.44
S*_9	30	975.3	-16.3709	326.4	11.8873	3.49	Q*_12	22.5	1.345	-16.81	0.458	10.7	3.43
S*_10	35	1012	-16.5128	340	12.5567	3.47	Q*_14	26.5	1.174	-16.62	0.398	11.08	3.45
S*_11	41	976	-16.6829	327.1	12.5584	3.48	Q*_16	30.5	1.103	-16.59	0.373	11.16	3.45
S*_12	49	1032	-16.6783	348.7	12.4189	3.45	Q*_18	34.5	1.128	-16.69	0.382	10.77	3.45
S*_13	69	1501	-16.9635	501	11.7056	3.50	Q*_20	39.5	1.208	-16.72	0.41	10.74	3.44
S_1	2	1540	-16.5145	532.8	10.6032	3.37	Q*_22	44.5	1.14	-16.67	0.386	11.05	3.44
S_2	4	1899	-16.4993	662.7	10.3903	3.34	Q*_24	50.5	1.027	-16.64	0.346	11.25	3.46
S_3	6	1542	-16.5165	534.3	10.2227	3.37	Q*_26	57	1.07	-16.58	0.36	11.15	3.46
S_4	8	1210	-16.5761	415.5	10.1314	3.40	Q*_28	64.5	1.158	-16.56	0.39	11.11	3.46
S_5	10	1420	-16.5354	489.8	10.1319	3.38	Q*_30	73.5	1.084	-16.52	0.363	10.79	3.48
S_6	12	1261	-16.5629	433.6	10.0723	3.39	Q*_32	85	1.278	-16.53	0.43	10.62	3.46
S_7	14	1180	-16.4769	404.4	10.3268	3.40	Q*_34	102	1.032	-17.08	0.344	12.8	3.49
S_8	16	1.33	-16.32	0.456	10.23	3.4	N\$_2	4	1.411	-18.93	0.475	9.25	3.47
S_9	18	1.189	-16.44	0.407	10.18	3.41	N\$_4	8	1.335	-18.77	0.448	9.33	3.48
S_10	20	1.521	-16.53	0.524	10.08	3.39	N\$_6	12	1.231	-18.55	0.413	9.25	3.48
S_11	22	1.309	-16.71	0.448	10	3.41	N\$_8	16	1.124	-18.46	0.377	9.24	3.48
S_12	24	1.129	-16.84	0.385	9.99	3.42	N\$_10	20	1.153	-18.36	0.388	9.06	3.47
S_13	26	1.362	-16.85	0.467	9.9	3.4	N\$_12	24	1.132	-18.2	0.38	8.91	3.48
S_14	28.5	1.13	-16.93	0.385	10.01	3.42	N\$_14	28.5	0.895	-18.35	0.301	8.93	3.47
S_15	31	1.005	-16.96	0.342	9.99	3.43	N\$_16	33.5	1.089	-18.23	0.369	9.24	3.45
S_16	33	1.072	-17.04	0.362	10.19	3.45	N\$_18	39.5	1.194	-18.17	0.406	9.54	3.43
S_17	36	1.431	-16.88	0.49	10	3.41	N\$_20	47.5	1.33	-18.25	0.45	9.8	3.45
S_18	39	1.092	-16.69	0.371	10.26	3.44	N\$_22	55.5	1.128	-17.32	0.381	10.8	3.46
S_19	42.5	1.207	-16.53	0.411	10.36	3.43	N\$_24	64.5	1.272	-16.49	0.429	11.83	3.46
S_20	46.5	1.324	-16.44	0.453	10.38	3.41	N\$_26	76.5	1.289	-16.88	0.435	12.57	3.46
S_21	51	1.262	-16.42	0.431	10.47	3.42	N\$_28	91.5	1.521	-16.92	0.519	12.42	3.42
S_22	56	1.303	-16.36	0.439	11.8	3.46	FI*_2	3	0.872	-17.03	0.292	11.63	3.48

S_23	61	1.161	-16.38	0.39	12.33	3.47	FI*_4	7	1.01	-17.45	0.341	10.95	3.46
S_24	67	1.227	-16.37	0.414	12.35	3.46	FI*_6	11	1.18	-17.5	0.401	10.36	3.43
S_25	74	1.068	-16.37	0.36	12.18	3.46	FI*_8	16	1.227	-17.24	0.417	10.37	3.43
S_26	80	1.171	-16.24	0.396	11.98	3.45	FI*_10	21	1.137	-17.11	0.383	10.65	3.46
S_27	91	0.856	-16.41	0.285	11.91	3.51	FI*_12	27	1.455	-16.68	0.494	10.59	3.43
S_28	108	0.75	-16.57	0.248	11.76	3.52	FI*_14	33	1.131	-16.49	0.38	11	3.47
m17*_1	2.5	1.866	-16.38	0.644	11.09	3.38	FI*_16	39	0.974	-16.46	0.328	11.15	3.47
m17*_2	4.5	1.405	-16.45	0.479	11.17	3.42	FI*_18	46	0.905	-16.68	0.303	11.18	3.48
m17*_3	6.5	1.295	-16.56	0.44	11.13	3.44	FI*_20	54	1.058	-16.87	0.356	10.81	3.46
m17*_4	8.5	1.209	-16.7	0.41	11.01	3.44	FI*_22	63	1.243	-17.08	0.416	11.3	3.49
m17*_5	10.5	1.229	-16.82	0.417	10.92	3.44	FI*_24	75	1.095	-17.46	0.368	12.28	3.48
m17*_6	13	1.378	-16.92	0.47	10.65	3.42	V_2	3.5	1.172	-16.5	0.398	10.94	3.44
m17*_7	15.5	1.287	-16.96	0.44	10.52	3.42	V_4	7.5	1.269	-16.49	0.432	10.8	3.43
m17*_8	18	1.186	-17.01	0.404	10.49	3.43	V_6	11.5	1.215	-16.36	0.414	11	3.42
m17*_9	21	1.124	-17.01	0.383	10.38	3.43	V_8	15.5	0.96	-16.42	0.323	11.28	3.47
m17*_10	24.5	1.131	-17	0.384	10.56	3.43	V_10	19.5	0.989	-16.72	0.333	11.07	3.46
m17*_11	29	1.485	-16.89	0.505	10.71	3.43	V_12	24.5	1.002	-17.34	0.339	10.59	3.45
m17*_12	35.5	1.298	-16.77	0.44	11.89	3.44	V_14	30.5	1.315	-17.64	0.45	10.2	3.41
m17*_13	39	1.205	-17.09	0.405	12.37	3.47	V_16	36.5	1.32	-17.29	0.453	10.47	3.4
m17*_14	44	0.753	-17.32	0.249	12.53	3.53	V_18	44	1.63	-16.88	0.561	10.62	3.39
m17*_15	51	1.057	-17.31	0.35	12.31	3.52	V_20	53	1.52	-16.49	0.522	11.63	3.4
m17*_16	60	0.763	-17.38	0.249	12.15	3.57	V_22	64	1.366	-16.41	0.465	13.41	3.43
F\$_1	3	1.538	-19.05	0.471	14	3.81	V_24	77.5	0.989	-16.41	0.334	13.16	3.46
F\$_2	5	1.718	-18.7	0.558	12.73	3.59	SX*_2	4.5	1.327	-16.49	0.448	11.55	3.45
F\$_3	8	2.266	-18.25	0.774	11.78	3.41	SX*_4	8.5	1.275	-16.55	0.431	11.39	3.45
F\$_4	11	1.553	-17.49	0.525	11.67	3.45	SX*_6	12.5	1.04	-16.72	0.348	11.38	3.48
F\$_5	13.5	1.296	-17.54	0.435	11.69	3.48	SX*_8	16	1.098	-16.6	0.369	11.21	3.47
F\$_6	15.5	1.795	-17.47	0.621	11.31	3.37	SX*_10	20	1.273	-16.44	0.43	11.2	3.46
F\$_7	17.5	1.472	-17.4	0.502	11.32	3.42	SX*_12	24	1.234	-16.28	0.415	11.28	3.47
f\$_8	19.5	1.52	-17.44	0.522	11.14	3.4	SX*_14	28	1.352	-16.08	0.456	11.28	3.46
f\$_9	21.5	1.785	-17.37	0.618	11.06	3.37	SX*_16	33	1.242	-16.01	0.418	11.68	3.47
f\$_10	23.5	1.322	-17.5	0.45	11.09	3.43	SX*_18	38	1.245	-15.98	0.419	11.62	3.47

f\$ _11	25.5	1.458	-17.39	0.499	10.87	3.41	SX*_20	44	1.282	-16.07	0.431	11.53	3.47
f\$ _12	27.5	1.168	-17.57	0.393	10.88	3.47	SX*_22	51	1.511	-16.1	0.511	11.29	3.45
f\$ _13	30	1.375	-17.45	0.471	10.75	3.4	SX*_24	59.5	1.428	-16.19	0.482	11.12	3.46
f\$ _14	32.5	1.587	-17.35	0.546	10.36	3.39	SX*_26	70	1.384	-16.21	0.464	11.56	3.48
f\$ _15	35	1.502	-17.3	0.515	10.16	3.4	SX*_28	84	1.299	-16	0.435	13.28	3.48
F\$ _16	38	1.794	-17.1	0.615	10.21	3.4	SX*_30	114	1.422	-15.96	0.477	13.38	3.48
F\$ _17	40.5	1.558	-17.06	0.527	10.35	3.45	OI_2	4	1.263	-17.73	0.431	9.37	3.42
F\$ _18	43	1.549	-16.8	0.524	10.61	3.45	OI_4	8	1.147	-17.61	0.388	9.35	3.45
F\$ _19	45.5	1.256	-16.66	0.423	10.77	3.47	OI_6	12	1.191	-17.68	0.402	9.42	3.46
F\$ _20	48	1.337	-16.52	0.456	10.82	3.42	OI_8	16	1.055	-17.41	0.356	9.81	3.46
F\$ _21	51.5	1.652	-16.37	0.567	10.66	3.4	OI_10	20.5	1.2	-17.14	0.408	9.89	3.43
F\$ _22	54	1.071	-16.41	0.361	10.68	3.46	OI_12	25.5	1.24	-16.94	0.422	10.01	3.43
F\$ _23	56.5	1.232	-16.38	0.42	10.6	3.42	OI_14	30.5	1.001	-16.97	0.336	10.34	3.47
F\$ _24	59	1.223	-16.38	0.418	10.58	3.42	OI_16	36.5	0.932	-16.82	0.311	10.52	3.49
F\$ _25	61.5	1.402	-16.28	0.483	10.6	3.39	OI_18	42.5	1.019	-16.61	0.342	10.73	3.48
F\$ _26	64.5	1.186	-16.31	0.404	10.79	3.42	OI_20	49.5	0.958	-16.46	0.32	10.97	3.49
F\$ _27	68	1.227	-16.17	0.418	11.02	3.42	OI_22	57.5	0.921	-16.18	0.308	11.34	3.48
F\$ _28	71.5	0.934	-16.27	0.315	11.04	3.46	OI_24	66.5	0.971	-16.41	0.323	11.12	3.51
F\$ _30	80	1.101	-16.32	0.372	10.59	3.45	AdP_1	2.5	1.297	-15.87	0.441	11.85	3.43
F\$ _31	84.5	1.033	-16.49	0.346	10.62	3.48	AdP_3	7.5	1.302	-15.84	0.445	11.97	3.41
F\$ _32	90	1.272	-16.51	0.434	11.08	3.42	AdP_5	12.5	1.081	-15.9	0.365	11.91	3.46
F\$ _33	95	1.226	-16.89	0.413	12.93	3.46	AdP_7	18	0.997	-16.03	0.335	11.85	3.48
F*_1	2	1.063	-19.2	0.327	13.82	3.8	AdP_9	24	1.266	-16.05	0.43	11.62	3.43
F*_2	4	1.204	-18.74	0.381	12.34	3.69	AdP_11	30.5	1.09	-16.4	0.368	11.29	3.46
F*_3	6	1.441	-17.85	0.475	11.92	3.54	AdP_13	38	1.147	-16.51	0.385	11.31	3.48
F*_4	9	2.479	-17.52	0.85	11.16	3.4	AdP_15	46	0.726	-16.55	0.236	12.62	3.58
F*_5	12	2.049	-17.47	0.697	11.03	3.43	AdP_17	58.5	1.067	-16.58	0.355	13.05	3.51
F*_6	14.5	1.942	-17.43	0.666	11.19	3.4	AdP_19	87	0.934	-16.56	0.305	12.46	3.57
F*_7	16.5	1.296	-17.51	0.436	11.27	3.47	AdF_1	2	1.349	-19.06	0.413	12.42	3.81
F*_8	18.5	1.578	-17.4	0.541	11.03	3.4	AdF_3	6	1.557	-18.19	0.514	11.27	3.53
F*_9	20.5	1.274	-17.48	0.431	11.03	3.45	AdF_5	10	1.708	-17.37	0.589	10.73	3.39
F*_10	22.5	1.441	-17.39	0.49	10.69	3.43	AdF_7	14	1.781	-17.38	0.616	10.75	3.38

F*_11	25	1.6	-17.31	0.548	10.45	3.41	AdF_9	18	1.661	-17.67	0.572	10.68	3.39
F*_12	27.5	1.227	-17.31	0.414	10.48	3.46	AdF_11	22	1.402	-17.65	0.479	10.46	3.41
F*_13	29.5	1.253	-17.27	0.425	10.47	3.44	AdF_13	26	1.419	-17.92	0.485	10.57	3.41
F*_14	31.5	1.163	-17.18	0.392	10.56	3.46	AdF_15	30	1.336	-18.07	0.456	10.39	3.42
F*_15	33.5	1.161	-16.83	0.393	10.78	3.45	AdF_17	34	1.613	-17.98	0.556	10.19	3.39
F*_16	36	1.348	-16.67	0.46	10.73	3.42	AdF_19	38	1.283	-17.69	0.436	10.17	3.43
F*_17	39	1.439	-16.38	0.491	10.63	3.42	AdF_21	42.5	1.208	-17.29	0.409	10.47	3.44
F*_18	42.5	1.202	-16.39	0.407	10.73	3.44	AdF_23	47.5	1.268	-16.83	0.43	10.52	3.44
F*_19	46	1.296	-16.31	0.444	10.71	3.41	AdF_25	53	1.305	-16.69	0.444	10.79	3.43
F*_20	50	1.574	-16.21	0.545	10.57	3.37	AdF_27	59.5	1.461	-16.56	0.501	10.8	3.4
F*_21	54.5	1.306	-16.25	0.447	10.77	3.41	AdF_29	66.5	1.106	-16.49	0.373	10.95	3.46
F*_22	59.5	1.446	-16.1	0.497	10.93	3.4	AdF_31	74	1.119	-16.82	0.375	11.32	3.48
F*_23	64.5	1.217	-16.16	0.414	11	3.43	AdF_33	84.5	1.095	-17.61	0.367	12.24	3.48
F*_24	69.5	1.156	-16.23	0.392	10.89	3.44	AdF_35	98	0.966	-17.89	0.32	12.12	3.52
F*_25	74.5	1.085	-16.33	0.369	10.65	3.43	AdF_37	127	0.858	-17.52	0.277	11.63	3.61
F*_26	80	1.076	-16.48	0.367	10.79	3.42	AdT*_1	2	1.07	-16.96	0.361	10.85	3.46
F*_27	86	0.955	-16.67	0.322	11.92	3.46	AdT*_3	6	1.166	-16.85	0.395	10.97	3.44
F*_28	93	0.965	-16.96	0.324	12.96	3.48	AdT*_5	10.5	1.261	-16.8	0.429	11.05	3.43
F*_29	105	1.179	-17.05	0.396	13.05	3.47	AdT*_7	16	1.167	-16.82	0.395	10.98	3.45
T_1	2.5	2.589	-17.64	0.925	9.5	3.27	AdT*_9	23	1.469	-16.69	0.505	11.09	3.4
T_2	4.5	2.307	-17.65	0.802	9.47	3.36	AdT*_11	31	1.304	-16.53	0.443	12.59	3.43
T_3	7	2.379	-17.48	0.829	9.87	3.35	AdT*_13	40.5	1.29	-17.02	0.436	13.02	3.45
T_4	9	2.13	-17.28	0.739	10.33	3.36	AdT*_15	51	1.131	-17.17	0.381	12.92	3.46
T_5	11	1.828	-17.15	0.628	10.64	3.4	AdT*_17	62.5	0.782	-17.22	0.262	12.68	3.49
T_6	13	1.747	-17.12	0.599	10.57	3.41	AdT*_19	76.5	0.609	-17.24	0.201	12	3.54
T_7	15	1.451	-17.15	0.49	10.57	3.45	AdL_1	2.5	1.693	-16.52	0.587	11.34	3.37
T_8	17	1.322	-17.12	0.447	10.58	3.45	AdL_3	7.5	1.605	-16.46	0.554	11.47	3.38
T_9	19	1.574	-16.99	0.536	10.4	3.43	AdL_5	13	1.749	-16.4	0.608	11.54	3.36
T_10	21	1.507	-16.91	0.517	10.36	3.4	AdL_7	19	1.739	-16.45	0.603	11.45	3.36
T_11	23	1.458	-16.89	0.5	10.46	3.4	AdL_9	25.5	1.643	-16.66	0.568	11.39	3.38
T_12	27	1.12	-16.98	0.381	10.59	3.43	AdL_11	33.5	1.562	-16.46	0.537	11.28	3.39
T_13	29	1.348	-16.97	0.464	10.6	3.39	AdL_13	41.5	1.471	-16.11	0.505	11.28	3.4

T_14	31	1.08	-17.22	0.367	10.61	3.43	AdL_15	51	1.368	-16.21	0.468	11.59	3.41
T_15	33	1.239	-17.21	0.425	10.54	3.4	AdL_17	63	1.061	-16.38	0.357	13.39	3.47
T_17	35	1.023	-17.2	0.344	10.6	3.47	AdL_19	77	0.983	-16.46	0.328	13.05	3.49
T_18	37	0.86	-17.34	0.291	10.6	3.44	Ad2*_1	2.5	0.835	-16.41	0.278	11.29	3.51
T_19	39.5	0.941	-17.4	0.321	10.63	3.42	Ad2*_3	8.5	0.98	-16.4	0.328	11.5	3.49
T_20	42	1.019	-17.42	0.348	10.65	3.41	Ad2*_5	16	0.938	-16.55	0.311	13.05	3.52
T_21	45	0.962	-17.26	0.326	10.56	3.44	Ad2*_7	22.5	0.928	-16.75	0.308	13.13	3.52
T_22	48.5	1.123	-16.97	0.383	10.62	3.42	Ad2*_9	37	0.599	-16.83	0.195	13.8	3.58
T_23	52.5	1.105	-16.77	0.376	11.03	3.43	AdT_1	2	1.387	-17.67	0.476	10.38	3.4
T_24	57	0.909	-16.59	0.307	12.28	3.45	AdT_3	6	1.258	-17.25	0.428	10.26	3.43
T_25	61.5	0.845	-16.61	0.28	12.86	3.52	AdT_5	9	1.036	-16.72	0.35	11.24	3.46
T_26	66.5	0.819	-16.67	0.273	13.12	3.5	AdT_7	15	1.276	-16.69	0.436	10.99	3.41
T_27	72	0.752	-16.86	0.25	12.9	3.51	AdT_9	20.5	1.352	-16.66	0.462	11.2	3.42
T_28	79.5	0.707	-16.82	0.235	12.69	3.5	AdT_11	26.5	1.101	-16.77	0.373	10.97	3.44
T_29	95	0.698	-17.87	0.214	11.76	3.8	AdT_13	32.5	1.108	-16.76	0.375	11.07	3.45
T*_1	2.5	2.348	-17.45	0.838	9.95	3.27	AdT_15	38.5	0.958	-16.55	0.322	12.48	3.48
T*_2	4.5	1.464	-17.62	0.503	9.97	3.4	AdT_17	46	1.194	-16.99	0.405	12.96	3.44
T*_3	6.5	1.496	-17.68	0.51	9.8	3.42	AdT_19	55	0.945	-17.32	0.316	12.96	3.49
T*_4	9	2.235	-17.6	0.786	9.5	3.32	AdT_21	66.5	1.014	-17.26	0.342	12.6	3.46
T*_5	11	1.488	-17.66	0.509	9.64	3.41	AdT_23	81.5	0.865	-17.15	0.29	12.24	3.48
T*_6	13	1.296	-17.61	0.442	9.91	3.42	AdM_1	2.5	1.281	-18.27	0.437	9.48	3.42
T*_7	15	1.317	-17.5	0.452	10.27	3.4	AdM_3	7.5	1.242	-18.02	0.424	9.54	3.42
T*_8	17	1.799	-17.23	0.629	10.42	3.33	AdM_5	12.5	1.191	-17.97	0.405	9.66	3.43
T*_9	19.5	1.712	-17.07	0.595	10.58	3.36	AdM_7	18.5	1.325	-17.78	0.452	9.76	3.42
T*_10	21.5	1.162	-17.18	0.395	10.57	3.43	AdM_9	25.5	1.189	-17.6	0.404	10.13	3.44
T*_11	24	1.549	-17.07	0.538	10.44	3.36	AdM_11	32.5	1.026	-17.47	0.345	10.55	3.47
T*_12	26.5	1.883	-16.99	0.659	10.33	3.33	AdM_13	40.5	1.113	-17.26	0.375	10.72	3.46
T*_13	29.5	1.738	-16.94	0.603	10.31	3.36	AdM_15	50	1.166	-17.22	0.392	10.81	3.47
T*_14	32	1.331	-16.97	0.455	10.41	3.42	AdM_17	61	1.05	-16.93	0.349	10.86	3.51
T*_15	34.5	1.242	-16.93	0.425	10.42	3.41	AdM_19	73	1.113	-16.77	0.368	12.72	3.53
T*_16	37	1.335	-16.92	0.46	10.48	3.39	Ad2_1	3	1.131	-16.33	0.381	11.33	3.46
T*_17	40	1.463	-16.94	0.504	10.47	3.39	Ad2_3	9	1.199	-16.31	0.406	11.26	3.45

T*_18	43	1.153	-17.12	0.393	10.57	3.42	Ad2_5	15.5	1.131	-16.39	0.382	11.14	3.45
T*_19	46	1.338	-17.17	0.461	10.43	3.39	Ad2_7	22.5	1.15	-16.34	0.389	11.16	3.45
T*_20	49	1.306	-17.18	0.448	10.56	3.4	Ad2_9	31	1.2	-16.37	0.4	12.51	3.5
T*_21	52	1.045	-17.21	0.355	10.65	3.44	Ad2_11	42	1.055	-16.76	0.348	13.2	3.54
T*_22	55.5	1.113	-17.28	0.38	10.57	3.42	Ad2_13	61	0.944	-16.69	0.308	12.65	3.58
T*_23	58.5	0.912	-17.55	0.307	10.69	3.46	AdM*_1	3	1.683	-18.03	0.579	8.94	3.39
T*_24	62	1.21	-17.26	0.415	10.53	3.4	AdM*_3	8	1.366	-17.83	0.467	9.16	3.41
T*-25	65.5	0.944	-17.1	0.318	10.52	3.46	AdM*_5	13	1.251	-17.78	0.426	9.46	3.43
T*-26	69.5	1.267	-16.81	0.434	10.73	3.4	AdM*_7	18	1.283	-17.71	0.437	9.6	3.42
T*-27	74.5	1.246	-16.53	0.425	11.78	3.42	AdM*_9	23	1.127	-17.55	0.382	10.08	3.45
T*-28	79.5	0.98	-16.63	0.33	12.64	3.47	AdM*_11	29	1.104	-17.45	0.372	10.41	3.46
T*-29	84.5	0.984	-16.68	0.331	12.86	3.47	AdM*_13	35.5	0.942	-17.27	0.316	10.84	3.48
T*-30	89.5	0.835	-16.8	0.279	12.84	3.5	AdM*_15	43	1.069	-17.17	0.359	10.87	3.48
T*-31	96.5	0.972	-16.76	0.328	12.55	3.46	AdM*_17	52	0.836	-17.14	0.276	10.93	3.53
T*-32	105.5	1.132	-16.58	0.384	11.63	3.44	AdM*_19	66	1.137	-16.81	0.38	11.22	3.5
T*_33	117.5	0.684	-16.69	0.224	11.84	3.56	AdP*_1	2.5	1.146	-15.86	0.388	11.94	3.45
F-1	2.5	1.233	-18.16	0.366	13.35	3.93	AdP*_3	7.5	1.179	-15.82	0.401	11.79	3.43
F-2	5	1.572	-18.4	0.502	12.63	3.65	AdP*_5	12.5	1.102	-15.87	0.374	11.81	3.43
F-3	7.5	2.067	-18.03	0.703	11.78	3.43	AdP*_7	18	1.14	-15.82	0.388	11.74	3.43
F-4	9.5	1.33	-18.02	0.444	11.64	3.5	AdP*_9	24	1.031	-15.93	0.349	11.61	3.45
F-5	11.5	1.379	-18.09	0.463	11.51	3.47	AdP*_11	30	1.02	-15.94	0.344	11.41	3.46
F-6	13.5	1.436	-17.94	0.485	11.37	3.46	AdP*_13	37	0.951	-16.35	0.319	11.28	3.48
F_7	15.5	1.651	-17.5	0.561	11.35	3.43	AdP*_15	44	0.866	-16.54	0.289	11.4	3.5
F_8	17.5	1.416	-17.28	0.479	11.38	3.45	AdP*_17	54	0.892	-16.53	0.293	13.17	3.55
F_9	19.5	1.504	-17.27	0.512	11.37	3.42	AdP*_19	69	0.881	-16.58	0.291	13.14	3.53
F_10	21.5	1.349	-17.37	0.458	11.42	3.44	Adf\$_1	3	1.139	-18.67	0.348	12.16	3.82
F_11	23.5	1.313	-17.5	0.444	11.43	3.45	Adf\$_3	7	1.252	-18.27	0.415	10.85	3.52
F_12	25.5	1.457	-17.35	0.497	11.45	3.42	Adf\$_5	11	1.482	-17.87	0.504	9.96	3.43
F_13	27.5	1.245	-17.21	0.421	11.41	3.45	Adf\$_7	15	1.268	-17.86	0.43	10.14	3.44
F_14	29.5	1.126	-17.15	0.381	11.28	3.45	Adf\$_9	20	1.412	-17.9	0.481	9.68	3.43
F_15	31.5	1.33	-17.07	0.456	11.12	3.4	Adf\$_11	25.5	1.413	-17.3	0.482	9.78	3.42
F_16	34	1.347	-16.99	0.462	10.9	3.4	Adf\$_13	31.5	1.306	-16.8	0.443	10.26	3.44

F_17	36.5	1.429	-16.84	0.492	10.87	3.39	Adf\$ _15	39	1.327	-16.52	0.451	10.31	3.44
F_18	39.5	1.413	-16.53	0.485	10.94	3.4	Adf\$ _17	48	1.27	-16.51	0.431	10.57	3.44
F_19	42	1.325	-16.4	0.452	11.08	3.42	Adf\$ _19	59	1.32	-17.34	0.446	11.88	3.45
F_20	45	1.437	-16.16	0.494	11.14	3.4	Adf\$ _21	73.5	1.134	-17.71	0.379	11.98	3.49
F_21	48.5	1.352	-16.06	0.461	11.19	3.42	Adf\$ _23	101.5	0.56	-17.56	0.179	12.05	3.65
F_22	52	1.27	-16.05	0.432	11.3	3.43	AdP\$ _1	3	0.694	-16.11	0.23	12.09	3.52
F_23	56	1.372	-16.05	0.469	11.27	3.41	AdP\$ _3	9	1.391	-15.89	0.476	11.39	3.41
F_24	60	1.417	-16.02	0.485	11.11	3.41	AdP\$ _5	15	1.33	-15.83	0.453	11.14	3.43
F_25	64	1.16	-16.06	0.392	11.14	3.45	AdP\$ _7	22	1.246	-16.05	0.422	11.15	3.44
F_26	68	1.16	-16.03	0.393	11.2	3.44	AdP\$ _9	29	1.171	-16.33	0.395	11.11	3.46
F_27	70	1.065	-16.11	0.361	11.28	3.44	AdP\$ _11	36.5	1.248	-16.3	0.421	11.4	3.45
F_28	74.5	1.288	-16.08	0.442	11.5	3.4	AdP\$ _13	44.5	0.936	-16.38	0.311	13.13	3.51
F_29	79.5	1.223	-16.25	0.412	11.62	3.46	AdP\$ _15	54	0.94	-16.42	0.312	13.21	3.51
F_30	85.5	1.104	-16.62	0.369	12.88	3.49	AdP\$ _17	67	0.988	-16.35	0.328	12.7	3.52
F_31	91.5	0.949	-16.79	0.314	12.79	3.53	AdP\$ _19	94.5	1.19	-16.34	0.391	12.24	3.55
F_32	101	1.137	-16.51	0.384	12.49	3.45	Adf* _1	2.5	1.114	-18.58	0.338	12.33	3.84
F_33	117	1.054	-16.54	0.349	12.02	3.53	Adf* _3	6.5	1.377	-18.54	0.461	10.35	3.48
N_1	2	1.381	-17.96	0.469	10.79	3.44	Adf* _5	11	1.309	-18.37	0.446	9.43	3.42
N_3	6	1.19	-17.97	0.401	11.56	3.47	Adf* _7	16	1.364	-18.38	0.465	9.91	3.43
N_5	10.5	1.328	-17.54	0.448	11.87	3.46	Adf* _9	21	1.296	-18.41	0.441	10.37	3.43
N_7	15	1.552	-17.16	0.529	12.1	3.42	Adf* _11	26.5	1.26	-18.08	0.427	10.15	3.45
N_9	19	1.226	-17.01	0.413	10.43	3.46	Adf* _13	32.5	1.357	-17.69	0.461	9.94	3.43
N_11	24.5	1.363	-16.95	0.462	10.56	3.44	Adf* _15	39	1.232	-17.82	0.417	9.92	3.45
N_13	29.5	1.235	-16.77	0.416	10.69	3.46	Adf* _17	47	1.274	-17.32	0.433	10.46	3.44
N_15	35	1.311	-16.6	0.443	10.8	3.45	Adf* _19	58	1.293	-16.32	0.436	11.37	3.46
N_17	40	1.038	-16.47	0.348	11.33	3.48	Adf* _21	74	0.909	-16.54	0.302	11.52	3.51
N_19	46	1.01	-16.46	0.339	11.3	3.48	FI_2	4	1.113	-16.78	0.376	10.89	3.46
N_21	52	1.043	-16.71	0.347	11.32	3.5	FI_4	8	1.259	-16.99	0.427	11.14	3.44
N_23	59.5	1.13	-16.62	0.38	10.85	3.47	FI_6	6	1.12	-16.95	0.378	11.68	3.46
N_25	67	1.038	-16.68	0.348	11.09	3.48	FI_8	12	1.197	-16.82	0.403	11.78	3.46
N_27	77	1.038	-16.89	0.346	12.46	3.5	FI_10	16	1.163	-17.21	0.394	11.31	3.45
N_29	90.5	0.932	-17	0.311	12.4	3.49	FI_12	20	1.042	-17.43	0.352	10.76	3.46

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N_31	115	0.819	-16.91	0.271	11.86	3.53	FI_14	24	1.195	-17.46	0.407	10.25	3.43
N*_1	2	1.188	-18.18	0.401	9.78	3.46	FI_16	28	1.208	-16.98	0.411	10.78	3.43
N*_3	6	1.091	-17.97	0.368	10.11	3.45	FI_18	32.5	1.139	-16.92	0.385	10.8	3.45
N*_5	10	1.197	-17.47	0.407	10.19	3.43	FI_20	37.5	1.417	-16.51	0.485	10.68	3.41
N*_7	14	1.179	-17.24	0.397	10.35	3.46	FI_22	43	1.214	-16.28	0.412	11.09	3.44
N*_9	18	1.154	-17.04	0.389	10.42	3.46	FI_24	49	1.23	-16.36	0.418	11.09	3.44
N*_11	22	1.014	-17	0.342	10.77	3.46	FI_26	55.5	1.095	-16.56	0.369	11.23	3.46
N*_13	26.5	1.243	-16.73	0.421	10.67	3.45	FI_28	63	1.346	-16.81	0.456	10.64	3.45
N*_15		1.344	-16.46	0.456	10.88	3.44	FI_30	72.5	1.264	-17.31	0.426	12.22	3.46
N*_17		1.103	-16.34	0.372	11.33	3.45	FI_32	82	0.871	-17.5	0.29	12.37	3.5
N*_19		1.081	-16.48	0.364	11.34	3.46	Q_2	4	1.079	-16.44	0.366	11.82	3.44
N*_21		1.142	-16.7	0.384	11.14	3.47	Q_4	8	1.216	-16.36	0.416	11.58	3.41
M16£_2	5	1.081	-17.37	0.366	10.64	3.44	Q_6	12	1.05	-16.19	0.357	11.35	3.43
M16£_4	10	0.926	-17.13	0.314	10.43	3.44	Q_8	16	1.003	-16.05	0.34	11.1	3.44
M16£_6	15	0.831	-17.24	0.276	10.68	3.51	Q_10	23	0.952	-16.05	0.322	11.32	3.45
M16£_8	22.5	0.81	-16.53	0.272	11.24	3.47	Q_14	30.5	0.899	-16.33	0.304	11.15	3.45
M16£_10	32.5	1.103	-16.22	0.373	12.32	3.45	Q_16	36.5	0.978	-16.46	0.331	11.05	3.44
M16£_12	39	0.752	-16.79	0.251	13.14	3.5	Q_18	44	1.007	-16.79	0.34	11.15	3.46
							Q_20	53	0.95	-16.93	0.318	11.04	3.49
							Q_22	64	0.989	-16.77	0.332	11.78	3.48
							Q_24	78	0.744	-17.19	0.246	12.81	3.53
SA\$_1	2	0.982	-14.24	0.327	17.09	3.51	SA34b_1	2	1.114	-15.26	0.376	14.12	3.45
SA\$_2	4.5	0.551	-14.68	0.179	17.4	3.6	SA34b_3	6	1.327	-15.09	0.455	13.56	3.41
SA\$_3	7	1.132	-14.33	0.385	17.15	3.43	SA34b_5	10	1.371	-15.08	0.466	13.31	3.43
SA\$_4	9.5	1.142	-14.35	0.388	17.12	3.43	SA34b_7	14	1.151	-15.02	0.397	13.68	3.39
SA\$_5	12.5	1.37	-14.34	0.467	16.98	3.42	SA34b_9	18.5	1.772	-15.18	0.609	12.55	3.39
SA\$_6	16	1.558	-14.28	0.535	16.83	3.4	SA34b_11	23.5	1.66	-15.3	0.572	12.19	3.39
SA\$_7	19	1.313	-14.35	0.448	16.81	3.42	SA34b_13	28.5	1.236	-15.5	0.422	12.68	3.42
SA\$_8	21	1.26	-14.49	0.427	16.41	3.44	SA34b_15	33.5	1.47	-15.37	0.503	12.83	3.41
SA\$_9	24	1.248	-14.46	0.425	16.08	3.43	SA34b_17	38.5	1.35	-15.26	0.461	13.21	3.42
SA\$_10	27	1.084	-14.45	0.368	15.72	3.43	SA34b_19	44	1.763	-15.05	0.609	13.21	3.38

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SA\$_11	29.5	0.875	-14.52	0.296	15.65	3.45	SA34b_21	50	1.561	-14.56	0.536	14.36	3.4
SA\$_12	32	0.933	-14.48	0.316	15.56	3.45	SA34b_23	56	1.189	-14.45	0.413	15.06	3.36
SA\$_13	35	0.941	-14.56	0.319	15.38	3.44	SA34b_25	62	1.326	-14.45	0.453	15.07	3.42
SA\$_14	38	0.947	-14.52	0.321	15.33	3.44	SA34b_27	68.5	1.081	-14.47	0.365	15.44	3.46
SA\$_15	41	0.884	-14.6	0.296	15	3.49	SA34b_29	75.5	0.966	-14.44	0.325	15.82	3.47
SA\$_16	44.5	1.05	-14.62	0.356	14.76	3.44	SA34b_31	83	1.159	-13.87	0.395	15.85	3.42
SA\$_17	49	1.393	-14.56	0.478	14.68	3.4	SA34b_33	92	1.318	-13.88	0.444	15.61	3.47
SA\$_18	53.5	1.055	-14.64	0.356	15.04	3.46	SA34b_35	105	0.992	-14.59	0.332	15.58	3.49
SA\$_19	58.5	1.036	-14.65	0.347	15.47	3.48	SA34b_37	134	0.941	-15.61	0.31	14.76	3.54
SA\$_20	63.5	1.211	-14.31	0.415	16.98	3.4	SAY*_1	2	1.16	-15.82	0.39	12.78	3.47
SA\$_21	69.5	1.159	-14.41	0.395	17.35	3.42	SAY*_3	6	1.345	-15.92	0.455	12.94	3.45
SA\$_22	76	0.865	-14.62	0.29	17.54	3.48	SAY*_5	10	1.114	-15.98	0.374	12.85	3.47
SA\$_23	87.5	1.091	-14.52	0.372	17.29	3.42	SAY*_7	14	1.169	-16.05	0.394	12.71	3.46
SA\$_24	106	1.052	-14.79	0.354	16.3	3.47	SAY*_9	18	1.115	-16.14	0.372	12.54	3.49
SA*_1	2	1.495	-14.12	0.516	16.13	3.38	SAY*_11	22.5	1.375	-16.09	0.467	12.6	3.43
SA*_2	4	1.785	-13.95	0.619	15.86	3.36	SAY*_13	25.5	1.478	-16.12	0.502	12.37	3.43
SA*_3	6	1.381	-13.89	0.471	15.94	3.42	SAY*_15	31.5	1.414	-16.06	0.479	12.7	3.44
SA*_4	8	1.345	-13.76	0.459	15.93	3.42	SAY*_17	38	1.411	-16.17	0.475	14.2	3.47
SA*_5	10	1.183	-13.77	0.403	15.98	3.42	SAY*_19	45	1.3	-16.4	0.433	14.27	3.5
SA*_6	12	1.077	-13.82	0.364	15.9	3.45	SAY*_21	53	1.132	-16.33	0.381	14.27	3.47
SA*_7	14	1.277	-13.84	0.434	15.78	3.43	SAY*_23	62.5	1.325	-16.42	0.443	14.06	3.49
SA*_8	16	1.387	-13.77	0.475	15.76	3.4	SAY*_25	74.5	1.156	-16.24	0.386	13.66	3.49
SA*_9	18	1.507	-13.73	0.519	15.7	3.39	SA4A*_1	2	1.463	-20.69	0.501	13.02	3.4
SA*_10	20	1.249	-13.81	0.426	15.76	3.42	SA4A*_3	6	1.385	-20.7	0.473	13.13	3.42
SA*_11	22	1.403	-13.78	0.481	15.72	3.4	SA4A*_5	10	1.391	-20.73	0.476	13.13	3.41
SA*_12	24	1.394	-13.74	0.478	15.83	3.4	SA4A*_7	14	1.218	-20.79	0.413	13.26	3.44
SA*_13	26	1.102	-13.77	0.375	16.01	3.43	SA4A*_9	18	1.262	-20.93	0.429	13.16	3.43
SA*_14	28	1.052	-13.88	0.349	16.1	3.51	SA4A*_11	22.5	1.368	-21.33	0.467	12.42	3.42
SA*_15	30	1.001	-13.92	0.336	16.19	3.48	SA4A*_13	27.5	1.334	-21.27	0.454	12.78	3.43
SA*_16	32	1.036	-13.95	0.349	16.27	3.46	SA4A*_15	32.5	1.108	-21.13	0.373	12.8	3.46
SA*_17	34	1.097	-13.93	0.371	16.2	3.45	SA4A*_17	38.5	1.147	-21.29	0.387	13.21	3.46
SA*_18	36.5	1.15	-14.1	0.389	16.4	3.45	SA4A*_19	44.5	1.073	-21.49	0.36	13.75	3.48

SA*_19	39	1.068	-14.01	0.36	16.26	3.46	SA4A*_21	52	1.008	-21.65	0.337	13.67	3.49
SA*_20	41.5	1.073	-14.32	0.362	16.4	3.46	SA4A*_23	61	0.91	-21.63	0.303	13.44	3.5
SA*_21	44	1.125	-14.42	0.375	16.4	3.5	SA4A*_25	82	0.955	-21.56	0.317	12.93	3.52
SA*_22	46.5	1.012	-14.4	0.34	16.83	3.47	OSA4_1	2	1.162	-15.49	0.392	13.85	3.46
SA*_23	49.5	1.037	-14.34	0.352	17.1	3.44	OSA4_3	6	1.222	-15.27	0.413	13.82	3.45
SA*_24	52.5	1.031	-14.48	0.35	17.21	3.43	OSA4_5	10	1.193	-15.35	0.403	13.81	3.45
SA*_25	55.5	0.974	-14.5	0.329	17.33	3.45	OSA4_7	14	1.15	-15.56	0.384	13.85	3.49
SA*_26	59	1.037	-14.51	0.351	17.27	3.45	OSA4_9	18	1.067	-15.5	0.358	13.79	3.48
SA*_27	64	1.3	-14.42	0.444	17.1	3.41	OSA4_11	22.5	1.234	-15.56	0.417	13.72	3.45
SA*_28	69.5	1.171	-14.44	0.393	17	3.48	OSA4_13	27.5	1.402	-15.68	0.471	13.65	3.47
SA*_29	74.5	0.868	-14.58	0.29	17.06	3.49	OSA4_15	33	1.411	-15.45	0.48	13.79	3.43
SA*_30	80	0.867	-14.56	0.293	17.14	3.46	OSA4_17	39	1.56	-15.43	0.527	13.86	3.45
SA*_31	87.5	1.011	-14.82	0.34	17	3.47	OSA4_19	45	1.47	-15.29	0.499	13.86	3.44
SA*_32	110.5	0.975	-14.7	0.299	15.98	3.81	OSA4_21	53	1.344	-15.12	0.447	15.2	3.51
SA_1	2	1.556	-13.85	0.537	15.96	3.38	OSA4_23	62.5	1.232	-15.2	0.411	16.09	3.5
SA_2	4	1.373	-13.85	0.469	15.88	3.42	OSA4_25	76.5	1.237	-15.32	0.413	15.61	3.5
SA_3	6	1.244	-13.97	0.422	15.98	3.44	SA4T_1	2.5	1.339	-15.21	0.451	13.66	3.47
SA_4	8	1.529	-13.94	0.515	15.79	3.46	SA4T_3	7.5	1.254	-15.13	0.421	13.77	3.48
SA_5	10	1.368	-13.96	0.461	15.88	3.46	SA4T_5	12.5	1.319	-15.1	0.443	13.66	3.47
SA_6	12	1.255	-13.94	0.424	15.9	3.45	SA4T_7	17.5	1.138	-15.18	0.38	14.06	3.49
SA_7	14	1.222	-13.96	0.412	16	3.46	SA4T_9	22.5	1.112	-15.24	0.371	14.99	3.49
SA_8	16	1.199	-13.92	0.407	15.93	3.44	SA4T_11	28.5	1.143	-15.38	0.382	15.48	3.49
SA_9	18	1.08	-13.95	0.366	15.89	3.45	SA4T_13	34.5	1.119	-15.36	0.374	15.43	3.49
SA_10	20	1.189	-13.91	0.405	15.95	3.43	SA4T_15	41	1.262	-15.26	0.425	15.35	3.46
SA_11	22	1.136	-13.92	0.387	15.91	3.43	SA4T_17	49	1.226	-15.1	0.411	15.05	3.48
SA_12	24	1.013	-13.91	0.341	15.98	3.47	SA4T_19	57.5	1.23	-14.97	0.411	14.74	3.49
SA_13	26	1.095	-13.95	0.374	15.85	3.41	SA4T_21	68	0.968	-15.05	0.32	14.77	3.53
SA_14	28	1.14	-13.93	0.39	15.82	3.41	SA4T_23	81	1.137	-15.15	0.377	14.83	3.52
SA_15	30	1.02	-14	0.347	15.91	3.43	SA4T_25	104	1.073	-15.71	0.354	14.33	3.54
SA_16	32.5	1.195	-13.97	0.409	15.89	3.41	SA4A_1	2	1.259	-20.97	0.429	13.36	3.43
SA_17	35	1.102	-14.01	0.375	15.95	3.43	SA4A_3	6	1.242	-20.87	0.422	13.27	3.43
SA_18	37.5	1.147	-13.97	0.392	16	3.42	SA4A_5	10	1.146	-20.88	0.387	13.05	3.45

SA_19	40.5	1.426	-13.95	0.492	15.91	3.38	SA4A_7	14	1.273	-20.7	0.433	13.18	3.43
SA_20	43.5	1.277	-13.86	0.432	15.88	3.45	SA4A_9	19	1.319	-20.81	0.448	13.29	3.43
SA_21	46.5	1.154	-13.93	0.391	15.93	3.44	SA4A_11	24	1.265	-20.82	0.428	13.39	3.44
SA_22	49.5	1.187	-13.93	0.404	15.96	3.43	SA4A_13	29.5	1.138	-21	0.385	13.2	3.45
SA_23	52.5	1.083	-13.97	0.368	16.04	3.43	SA4A_15	35.5	1.094	-21.44	0.37	12.18	3.45
SA_24	55.5	1.169	-14.03	0.396	15.96	3.44	SA4A_17	42	1.206	-21.36	0.409	12.76	3.44
SA_25	58.5	1.079	-14	0.365	16.04	3.45	SA4A_19	49	1.073	-21.25	0.361	12.96	3.46
SA_26	61.5	1.035	-14.09	0.35	16.23	3.45	SA4A_21	57.5	0.973	-21.43	0.324	13.63	3.5
SA_27	65	1.294	-14.05	0.439	16.08	3.44	SA4A_23	67	0.951	-21.68	0.315	13.76	3.52
SA_28	69	1.139	-14.29	0.384	16.28	3.46	SA4A_25	79.5	0.867	-21.78	0.286	13.63	3.53
SA_29	73	1.075	-14.17	0.365	16.82	3.44	SA4A_27	106.5	0.836	-21.69	0.273	13.09	3.57
SA_30	78	1.184	-14.23	0.403	17.18	3.43	SA2*_1	2	0.801	-14.81	0.246	20.61	3.8
SA_31	83	1.141	-14.44	0.384	17.06	3.46	SA2*_3	6	0.797	-14.36	0.255	19.59	3.65
SA_32	88	0.831	-14.43	0.279	17.28	3.48	SA2*_5	10	0.975	-13.95	0.322	19	3.53
SA_33	94	0.836	-14.43	0.282	17.05	3.46	SA2*_7	15	1.13	-13.31	0.378	18.94	3.49
SA_34	100	0.7	-14.37	0.233	16.83	3.5	SA2*_9	20	1.068	-13.2	0.36	18.79	3.46
SA_35	118	0.793	-14.41	0.266	16.66	3.49	SA2*_11	26	1.191	-13.49	0.405	18.47	3.44
MS3_1	2	0.865	-17.42	0.288	13.24	3.51	SA2*_13	34	1.253	-13.54	0.427	18.16	3.42
MS3_3	6.5	0.965	-17.28	0.321	13.38	3.5	SA2*_15	42.5	1.066	-13.57	0.36	18.06	3.46
MS3_5	11.5	0.994	-17.05	0.33	13.45	3.51	SA2*_17	51.5	0.887	-13.4	0.297	18.62	3.49
MS3_7	18	1.186	-16.93	0.392	13.62	3.53	SA2*_19	64.5	0.942	-13.76	0.313	17.77	3.51
MS3_9	26	1.195	-17.16	0.399	13.28	3.49	SA2*_21	80	1.611	-13.26	0.548	20.41	3.43
MS3_11	34.5	0.895	-17.26	0.299	13.97	3.49	SA2_1	3.5	1.573	-14.23	0.492	20.06	3.73
MS3_13	45	0.688	-17.46	0.23	14.59	3.5	SA2_3	7.5	1.094	-13.69	0.358	18.99	3.56
SA34a_1	2	1.262	-14.36	0.429	16.08	3.43	SA2_5	11.5	1.208	-13.55	0.407	18.79	3.46
SA34a_3	6	1.519	-14.27	0.521	15.98	3.4	SA2_7	15.5	1.071	-13.49	0.36	19.98	3.47
SA34a_5	10		-14.44		15.8	3.42	SA2_9	19.5	1.025	-13.44	0.345	20.09	3.47
SA34a_7	14	1.434	-14.41	0.491	15.47	3.4	SA2_11	23.5	1.023	-13.33	0.342	19.64	3.49
SA34a_9	18	1.257	-14.49	0.428	15.58	3.42	SA2_13	27.5	1.172	-13.31	0.395	19.2	3.46
SA34a_11	22	1.452	-14.41	0.498	15.25	3.4	SA2_15	32	1.296	-13.37	0.442	18.48	3.42
SA34a_13	26	1.437	-14.35	0.492	15.23	3.41	SA2_17	38	1.389	-13.09	0.475	18.26	3.41
SA34a_15	30	1.449	-14.29	0.498	15.36	3.4	SA2_19	43	1.116	-12.91	0.378	18.33	3.45

SA34a_17	34	1.247	-14.35	0.426	15.35	3.41	SA2_21	50	1.196	-12.92	0.406	18.31	3.44
SA34a_19	38	1.205	-14.19	0.411	15.58	3.42	SA2_23	58	1.064	-13	0.359	18.41	3.45
SA34a_21	42	1.359	-13.88	0.466	15.59	3.4	SA2_25	68.5	1.07	-13.07	0.358	19.51	3.48
SA34a_23	46	1.343	-14.04	0.46	15.35	3.41	SA2_27	81.5	1.026	-13.36	0.341	20.93	3.51
SA34a_25	51	1.529	-13.86	0.526	15.66	3.39	SA2_29	104.5	0.951	-13.5	0.316	20.79	3.51
SA34a_27	56	1.192	-14.31	0.405	15.45	3.43	SA23_1	3.5	1.166	-14.25	0.358	20	3.8
SA34a_29	61	1.213	-14.52	0.412	15.37	3.43	SA23_3	9.5	1.238	-13.65	0.412	19	3.51
SA34a_31	66	1.217	-14.55	0.415	15.4	3.42	SA23_5	17	1.238	-13.46	0.418	18.84	3.46
SA34a_33	72	1.236	-15.07	0.42	15.14	3.43	SA23_7	25	1.032	-13.08	0.347	18.81	3.47
SA34a_35	80	1.363	-15.27	0.466	14.51	3.41	SA23_9	35.5	0.98	-13.56	0.327	18.44	3.49
SA34a_37	89	1.381	-15.17	0.472	13.96	3.41	SA23_11	47.5	0.971	-13.59	0.323	19.85	3.51
SA34a_39	99	1.114	-15.17	0.376	13.62	3.45	SA23_13	61.5	0.888	-13.79	0.293	20.22	3.53
SA34a_41	111	1.212	-15.06	0.41	13.38	3.45	SA23_15	80	0.527	-13.77	0.171	19.31	3.6
SA34a_43	138.5	1.744	-15.64	0.589	12.24	3.46	SA34b*_1	2	1.274	-15.37	0.434	14.22	3.42
SA4*_1	2	1.64	-12.57	0.567	18.12	3.37	SA34b*_3	6	1.324	-15.18	0.453	13.86	3.41
SA4*_3	6	1.675	-12.74	0.58	17.75	3.37	SA34b*_5	10	1.251	-15.14	0.426	13.8	3.42
SA4*_5	10	1.617	-12.66	0.559	18.05	3.37	SA34b*_7	14	1.262	-15.16	0.429	13.71	3.43
SA4*_7	14	1.41	-12.68	0.484	18.08	3.4	SA34b*_9	18	1.481	-15.43	0.507	12.9	3.41
SA4*_9	18	1.438	-12.58	0.495	18.35	3.39	SA34b*_11	22.5	1.57	-15.46	0.54	13.18	3.39
SA4*_11	22	1.43	-12.43	0.492	18.34	3.39	SA34b*_13	27.5	1.579	-15.3	0.543	13.71	3.39
SA4*_13	26	1.525	-12.25	0.526	18.58	3.38	SA34b*_15	32.5	1.34	-15.24	0.456	13.95	3.43
SA4*_15	28.5	1.487	-12.25	0.511	18.79	3.39	SA34b*_17	38	1.365	-14.97	0.464	14.43	3.43
SA4*_17	33.5	1.432	-12.32	0.49	18.85	3.41	SA34b*_19	44	1.324	-14.57	0.45	15.08	3.44
SA4*_19	38.5	1.29	-12.34	0.44	18.93	3.42	SA34b*_21	50	1.233	-14.38	0.417	15.42	3.45
SA4*_21	43.5	1.333	-12.34	0.454	18.84	3.43	SA34b*_23	57	1.266	-14.48	0.428	15.51	3.45
SA4*_23	49	1.296	-12.71	0.439	18.11	3.45	SA34b*_25	64	1.144	-14.5	0.385	15.65	3.47
SA4*_25	55	1.167	-12.97	0.395	17.83	3.45	SA34b*_27	71.5	1.093	-14.46	0.366	16.07	3.48
SA4*_27	61.5	1.077	-13.2	0.364	17.64	3.45	SA34b*_29	80	1.174	-13.9	0.394	16.21	3.48
SA4*_29	68.5	1.142	-13.07	0.387	18.5	3.44	SA34b*_31	89.5	0.991	-14.01	0.33	16.08	3.5
SA4*_31	76.5	1.196	-13.07	0.404	19.4	3.45	SA34b*_33	101.5	1.017	-14.45	0.337	15.75	3.52
SA4*_33	86	1.312	-13.13	0.444	19.41	3.45	SA34b*_35	132	1.254	-15.41	0.415	15.07	3.52
SA4*_35	98.5	1.191	-13	0.403	19.3	3.45	SA2\$_1	2	1.253	-14.2	0.386	20.49	3.79

SA4*_37	122.5	1.248	-13	0.418	19.17	3.48	SA2\$_3	6	1.344	-13.33	0.448	19.37	3.5
SA4_1	2	1.356	-12.82	0.464	17.87	3.41	SA2\$_5	10	1.153	-13.39	0.386	18.99	3.49
SA4_3	6	1.251	-12.8	0.425	18.08	3.43	SA2\$_7	14	1.239	-13.26	0.416	18.91	3.47
SA4_5	10	1.16	-12.83	0.394	18.16	3.43	SA2\$_9	18	1.239	-13.39	0.415	19.01	3.48
SA4_7	14	1.305	-12.57	0.446	18.25	3.41	SA2\$_11	22	1.178	-13.52	0.395	18.88	3.48
SA4_9	18	1.312	-12.42	0.448	18.58	3.42	SA2\$_13	26	1.407	-13.43	0.473	19.63	3.47
SA4_11	22	0.961	-12.44	0.324	19.04	3.46	SA2\$_15	30	1.252	-13.34	0.42	20.45	3.48
SA4_13	26	0.928	-12.57	0.312	19.21	3.46	SA2\$_17	35	1.502	-13.27	0.512	20.93	3.42
SA4_15	30.5	1.323	-12.35	0.452	18.72	3.42	SA2\$_19	40	1.39	-13.17	0.473	20.88	3.43
SA4_17	35.5	1.306	-12.38	0.444	18.85	3.43	SA2\$_21	45.5	1.3	-13.1	0.44	20.45	3.45
SA4_19	40.5	1.166	-12.52	0.392	18.92	3.47	SA2\$_23	51.5	1.263	-12.99	0.426	20.52	3.45
SA4_21	46	1.154	-12.72	0.39	18.27	3.45	SA2\$_25	58	1.322	-13.19	0.438	19.92	3.52
SA4_23	52	1.205	-13.11	0.408	18.1	3.45	SA2\$_27	66	1.357	-13.08	0.45	18.92	3.52
SA4_25	58.5	1.216	-13.3	0.411	17.68	3.45	SA2\$_29	75.5	1.313	-13.01	0.442	18.9	3.47
SA4_27	65.5	1.124	-13.1	0.381	18.66	3.44	SA2\$_31	87.5	1.35	-13.06	0.446	18.61	3.53
SA4_29	73	1.308	-13.04	0.442	19.28	3.45	SA23*_1	3	1.329	-14.7	0.406	20	3.82
SA4_31	83	1.195	-13.11	0.405	19.64	3.44	SA23*_3	9	1.666	-13.64	0.565	20.08	3.44
SA4_33	93	1.091	-13.06	0.368	19.48	3.46	SA23*_5	15.5	1.667	-13.39	0.57	18.99	3.41
SA4_35	104.5	0.934	-13.14	0.312	19.46	3.49	SA23*_7	22.5	1.482	-13.15	0.502	18.23	3.45
SA4_37	119.5	0.795	-13.26	0.262	19.37	3.54	SA23*_9	30.5	1.379	-13	0.468	18.11	3.44
SA34a*_1	2	1.728	-14.44	0.596	16.01	3.38	SA23*_11	39.5	0.956	-13.24	0.316	18.54	3.53
SA34a*_3	6	1.629	-14.51	0.561	16.02	3.39	SA23*_13	51	0.791	-13.64	0.256	20.76	3.6
SA34a*_5	10	1.651	-14.43	0.569	15.74	3.39	SA23*_15	82	1.533	-13.44	0.511	20.85	3.5
SA34a*_7	14	1.893	-14.22	0.657	15.55	3.36	SA3*_1	2	1.02	-20.57	0.344	12.31	3.46
SA34a*_9	18	1.53	-14.29	0.524	15.86	3.41	SA3*_3	6	0.911	-20.78	0.304	11.9	3.49
SA34a*_11	22	1.596	-14.37	0.549	15.41	3.39	SA3*_5	10	0.862	-20.23	0.286	11.43	3.51
SA34a*_13	26	1.601	-14.37	0.55	15.25	3.39	SA3*_7	15	1.085	-19.66	0.363	11.49	3.49
SA34a*_15	30	1.417	-14.52	0.483	15.3	3.42	SA3*_9	20	1.023	-18.75	0.342	12.09	3.49
SA34a*_17	34	1.606	-14.37	0.551	15.16	3.4	SA3*_11	27	1.08	-17.76	0.362	13.28	3.48
SA34a*_19	38	1.301	-14.32	0.443	15.35	3.42	SA3*_13	35.5	0.909	-18.35	0.301	14.4	3.52
SA34a*_21	42	1.397	-14.29	0.478	15.42	3.41	SA3*_15	46	0.787	-18.6	0.259	14.19	3.55
SA34a*_23	46.5	1.36	-14.32	0.464	15.31	3.42	SA3*_17	77.5	1.179	-18.44	0.39	13.63	3.52

SA34a*_25	51.5	1.376	-14.1	0.47	15.45	3.41	SA3_1	2	1.238	-19.74	0.377	14.66	3.83
SA34a*_27	56.5	1.335	-13.81	0.456	15.73	3.42	SA3_3	6	1.393	-19.97	0.442	13.71	3.68
SA34a*_29	61.5	1.204	-14.06	0.408	15.57	3.44	SA3_5	10	1.59	-20.15	0.525	12.25	3.53
SA34a*_31	67.5	1.182	-13.92	0.401	15.81	3.44	SA3_7	14	1.58	-21.07	0.532	11.02	3.46
SA34a*_33	74	1.239	-14.49	0.417	15.48	3.47	SA3_9	18	1.752	-21.37	0.598	10.66	3.42
SA34a*_35	81	1.266	-14.55	0.43	15.23	3.43	SA3_11	22	1.591	-21.62	0.541	10.58	3.43
SA34a*_37	89	1.088	-14.75	0.368	15.39	3.45	SA3_13	26	1.493	-21.65	0.507	10.55	3.43
SA34a*_39	97.5	0.993	-15.32	0.335	15	3.46	SA3_15	30	1.77	-21.53	0.606	10.63	3.41
SA34a*_41	107	0.971	-15.59	0.322	14.58	3.51	SA3_17	34	1.254	-21.37	0.421	11.59	3.48
SA34a*_43	118.5	0.936	-15.55	0.311	14.12	3.51	SA3_19	38	1.384	-21.15	0.467	11.91	3.46
SA34a*_45	133.5	0.676	-15.56	0.219	13.61	3.6	SA3_21	42	1.452	-20.99	0.49	12.22	3.45
SAY_1	2	1.111	-16.2	0.372	12.38	3.48	SA3_23	46	1.202	-20.93	0.403	12.55	3.48
SAY_3	6	1.311	-16.03	0.445	12.28	3.43	SA3_25	50	1.311	-20.84	0.441	12.63	3.47
SAY_5	10	1.384	-15.92	0.472	12.27	3.42	SA3_27	55	1.468	-20.76	0.498	12.49	3.44
SAY_7	14	1.242	-15.96	0.42	12.49	3.45	SA3_29	60	1.565	-20.78	0.532	12.24	3.43
SAY_9	18	1.227	-15.98	0.416	12.45	3.44	SA3_31	65	1.409	-20.93	0.474	12.15	3.47
SAY_11	22.5	1.274	-16.01	0.433	12.53	3.43	SA3_33	71	1.443	-20.99	0.489	11.69	3.45
SAY_13	27.5	1.574	-16.1	0.531	12.22	3.46	SA3_35	77	1.33	-21.13	0.451	11.23	3.44
SAY_15	33	1.476	-16.06	0.506	12.52	3.4	SA3_37	84	1.39	-20.32	0.471	10.58	3.45
SAY_17	39	1.248	-16.11	0.421	13	3.46	SA3_39	91.5	1.315	-19.27	0.442	11.2	3.47
SAY_19	45.5	1.391	-16.15	0.472	12.97	3.44	SA3_41	99.5	1.242	-17.8	0.416	12.7	3.49
SAY_21	52.5	1.19	-16.27	0.398	13.19	3.49	SA3_43	109.5	1.042	-18.7	0.347	13.75	3.51
SAY_23	60	1.115	-16.3	0.374	13.25	3.48	SA3_45	135.5	0.816	-19.31	0.263	13.39	3.62
SAY_25	68	0.948	-16.55	0.312	13.48	3.54	SA3\$_1	2	1.24	-20.84	0.42	12.62	3.44
SAY_27	77.5	1.015	-16.12	0.338	13.33	3.51	SA3\$_3	6	1.317	-20.8	0.445	12.67	3.45
SAY_29	92	1.088	-16.08	0.365	14.38	3.48	SA3\$_5	10	1.206	-20.75	0.407	12.56	3.45
							SA3\$_7	14	1.313	-20.82	0.445	12.39	3.45
							SA3\$_9	18.5	1.302	-20.87	0.442	12.17	3.44
							SA3\$_11	23.5	1.331	-20.98	0.452	11.77	3.44
							SA3\$_13	29	1.424	-21.14	0.484	11.25	3.43
							SA3\$_15	35	1.278	-20.59	0.432	10.74	3.45
							SA3\$_17	41	1.46	-19.6	0.496	10.86	3.43

SA3\$_19	48	1.269	-18.3	0.428	12.05	3.46
SA3\$_21	56.5	1.17	-17.9	0.393	13.16	3.47

Appendix 3: South American Sea lion Data

Appendix 3

Sample	Length	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C/N ratio	Sample	Length	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C/N ratio
OF*_1	3	1.116	-13.16	0.373	20.69	3.49	OA_1	2	1132.00	-12.42	395.20	20.45	3.34
OF*_3	8	1.215	-12.61	0.419	20.78	3.38	OA_3	6	1203.00	-12.41	421.90	20.78	3.33
OF*_5	13	1.173	-12.6	0.407	20.44	3.36	OA_5	10	1427.00	-12.72	503.80	20.86	3.30
OF*_7	19	1.355	-12.34	0.474	20.27	3.33	OA_7	14	1245.00	-12.99	435.00	19.78	3.34
OF*_9	25	1.229	-12.48	0.428	20.1	3.35	OA_9	19	1327.00	-12.62	465.90	20.07	3.32
OF*_11	31	1.105	-12.5	0.383	20.11	3.36	OA_11	24	1431.00	-12.47	503.50	20.28	3.32
OF*_13	38.5	1.118	-12.53	0.388	20.1	3.36	OA_13	29	1348.00	-12.53	473.10	20.07	3.32
OF*_15	47.5	1.276	-12.77	0.443	19.5	3.36	OA_15	34	1292.00	-12.47	453.20	20.18	3.33
OF*_17	58.5	1.163	-12.74	0.402	19.65	3.37	OA_17	39	1183.00	-12.76	414.50	20.25	3.33
OF*_19	71.5	1	-13.11	0.345	19.8	3.38	OA_19	45	1227.00	-12.98	428.70	20.06	3.34
OF*_21	86.5	1.052	-13.46	0.363	19.11	3.38	OA_21	51	1230.00	-12.91	429.70	21.01	3.34
OF*_23	132.5	1.47	-13.03	0.515	22.29	3.33	OA_23	58	1320.00	-13.23	461.40	19.90	3.34
OF_1	3	0.503	-13.75	0.162	21.18	3.62	OA_25	65	1031.00	-12.59	358.50	20.43	3.36
OF_3	8	1.302	-12.89	0.45	20.68	3.37	OA_27	73	1172.00	-12.35	408.10	20.47	3.35
OF_5	13	1.238	-12.8	0.43	20.47	3.36	OA_29	81	992.60	-12.47	345.30	20.35	3.35
OF_7	18	1.237	-12.63	0.43	20.43	3.35	OA_31	89	976.90	-12.77	339.50	20.22	3.36
OF_9	23	1.191	-12.6	0.413	20.28	3.36	OA_33	99	1135.00	-12.93	394.50	21.23	3.36
OF_11	28	1.214	-12.66	0.421	20.04	3.37	OA_35	109	1045.00	-13.16	362.40	19.93	3.36
OF_13	34	1.245	-12.64	0.432	20	3.36	OA_37	119.5	910.30	-12.72	314.10	20.15	3.38
OF_15	40.5	1.164	-12.62	0.403	20.17	3.37	OA_39	131	1091.00	-12.92	379.40	19.56	3.35
OF_17	49.5	1.244	-12.91	0.431	19.44	3.37	OA_41	143	986.60	-12.76	339.70	20.97	3.39
OF_19	60.5	1.162	-12.82	0.402	19.84	3.37	OA_43	158	1038.00	-12.78	359.00	20.33	3.37
OF_21	73.5	1.097	-13.35	0.378	19.57	3.38	OA_45	177	1076.00	-12.49	372.10	20.16	3.37
OF_23	93.5	0.75	-13.78	0.254	19.29	3.44	OA_47	207	1065.00	-12.84	367.70	20.08	3.38
OF\$_1	3	0.658	-13.54	0.216	21.04	3.56	OB_1	3	1110.00	-12.98	375.80	21.89	3.45
OF\$_3	8	1.19	-12.91	0.411	20.74	3.38	OB_3	7	1123.00	-12.56	391.90	21.11	3.34
OF\$_5	13	1.282	-12.74	0.448	20.45	3.34	OB_5	11	1093.00	-12.65	382.10	20.75	3.34
OF\$_7	18.5	1.356	-12.64	0.474	20.1	3.34	OB_7	15	1214.00	-12.85	425.10	20.34	3.33

South American Sea Lion Data

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OF\$_9	24.5	1.362	-12.51	0.478	20.17	3.33	OB_9	19	1244.00	-12.77	435.40	20.38	3.33
OF\$_11	30.5	1.41	-12.55	0.496	19.89	3.32	OB_11	23	1287.00	-12.46	450.70	20.73	3.33
OF\$_13	36.5	1.365	-12.72	0.478	19.83	3.33	OB_13	27	1137.00	-12.34	397.90	20.48	3.33
OF\$_15	42.5	1.173	-12.76	0.408	20.01	3.35	OB_15	32	1403.00	-12.42	492.60	20.18	3.32
OF\$_17	50.5	1.425	-12.77	0.501	19.83	3.32	OB_17	38	1410.00	-12.33	495.10	20.30	3.32
OF\$_19	58.5	1.319	-12.81	0.462	19.72	3.33	OB_19	44	1206.00	-12.40	421.30	20.31	3.34
OF\$_21	67.5	1.392	-13.19	0.489	18.9	3.32	OB_21	50	1280.00	-12.34	447.40	20.41	3.34
OF\$_23	78.5	1.524	-12.8	0.538	19.49	3.3	OB_23	56	1244.00	-12.34	434.70	20.49	3.34
OF\$_27	103.5	1.241	-13.67	0.428	19.01	3.38	OB_25	62	1699.00	-11.81	602.00	21.70	3.29
OF\$_29	133.5	1.927	-13.3	0.686	20.24	3.28	OB_29	78	1659.00	-11.84	581.40	21.39	3.33
Oca_1	3	594.90	-13.70	188.90	21.27	3.67	OFa_1	3	665.50	-13.17	225.10	20.89	3.45
Oca_3	9	1010.00	-12.77	347.00	21.24	3.40	OFa_3	9	1144.00	-12.71	398.30	20.61	3.35
Oca_5	15	855.30	-12.75	294.60	20.53	3.39	OFa_5	15	1068.00	-12.58	371.60	20.28	3.35
Oca_7	22	937.40	-12.46	326.70	20.58	3.35	OFa_7	21	1089.00	-12.46	380.10	20.43	3.34
Oca_11	43	912.10	-12.86	314.00	20.09	3.39	OFa_9	27	1037.00	-12.46	361.50	20.23	3.35
Oca_13	75	843.20	-12.97	286.80	19.79	3.43	OFa_11	33	1006.00	-12.86	345.40	19.97	3.40
							OFa_13	41	1125.00	-12.64	392.60	20.04	3.34
							OFa_15	49	977.40	-12.53	340.20	20.13	3.35
							OFa_17	59	1087.00	-12.72	379.70	19.65	3.34
							OFa_19	73	1393.00	-12.57	488.40	19.86	3.33
							OFa_21	92	1444.00	-13.25	505.40	19.36	3.33
							OFa_23	118	1234.00	-13.41	428.00	20.17	3.36

Appendix 4: Northern Hemisphere Fish Data

Appendix 4

Species	Sample	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C:N ratio	Species	sample	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C:N ratio
haddock	1ec	1040	-16.1969	324.1	12.6601	3.74	hake	4ca	2251	-16.1923	684.8	13.2105	3.83
haddock	1bc	1058	-16.848	329.4	12.7501	3.75	hake	4aa	1282	-16.2833	398	13.4032	3.76
haddock	1ea	1130	-16.2072	353.6	12.5239	3.73	hake	4ba	1833	-15.8965	558.5	13.5052	3.83
haddock	1ca	1648	-15.3391	499.3	14.9264	3.85	hake	4da	1476	-16.1032	451.9	13.2207	3.81
haddock	1da	1274	-15.5616	397.5	13.8189	3.74	hake	4bc	2085	-15.7846	632.2	13.6288	3.85
haddock	1aa	1254	-15.8039	395.8	14.4529	3.70	hake	4cc	1817	-16.1663	561.2	13.2105	3.78
haddock	1ba	1688	-16.5686	525.5	12.7937	3.75	hake	4ac	2077	-16.2858	633.3	13.4487	3.83
haddock	1cc	1363	-15.338	421	14.5701	3.78	hake	4dc	2374	-16.1106	718.1	12.8807	3.86
haddock	1dc	1406	-15.589	432.4	13.9717	3.79	sprat	5bc	2474	-19.0629	487	10.9962	5.93
haddock	1ac	1171	-16.002	360.4	14.588	3.79	sprat	5cc	1132	-16.0312	347.1	13.586	3.80
Monk	2ca	1254	-16.078	393.8	13.8656	3.72	sprat	5dc	1528	-19.5788	450	10.3518	3.96
Monk	2ea	1810	-16.1806	567.4	13.7831	3.72	sprat	5aa	2018	-18.2636	597.3	10.8781	3.94
Monk	2aa	1277	-17.2031	401.5	12.8364	3.71	sprat	5da	1287	-19.7994	379.3	10.546	3.96
Monk	2ba	1170	-16.6973	360.7	13.5859	3.78	sprat	5ba	1380	-20.0602	493.5	10.9327	3.26
Monk	2da	1322	-16.6058	405.8	13.3803	3.80	sprat	5ca	1260	-17.1121	370.5	13.3933	3.97
Monk	2bc	969.6	-16.6563	298.8	13.8287	3.79	sprat	5ac	1120	-17.5273	349	11.0937	3.74
Monk	2dc	1457	-16.4257	446.7	13.1997	3.81	witch	6bma	1775	-15.476	541.2	12.3377	3.83
Monk	2ac	1898	-17.1957	576.9	12.7794	3.84	witch	6ca	2189	-14.5765	665.1	12.2499	3.84
Monk	2cc	1646	-16.1273	503.7	13.788	3.81	witch	6da	1376	-15.803	428.4	12.2392	3.75
Monk	2ec	1775	-16.5209	536.5	13.9792	3.86	witch	6aa	2016	-15.5922	595.6	12.0834	3.95
Monk	2fa	1751	-16.4774	528.4	14.3489	3.87	witch	6bma	1647	-15.2623	507	12.3425	3.79
Monk	2fb	1307	-16.2056	404.6	14.2889	3.77	witch	6dc	1805	-15.6835	552.9	12.296	3.81
Monk	2fc	1391	-16.6113	422.8	14.3265	3.84	cod	7da	2028	-15.9421	620.6	13.3627	3.81
Monk	2fa	1661	-16.1569	504.6	13.876	3.84	cod	7ca	1210	-15.7167	370.5	13.8672	3.81
Monk	2fb	1007	-16.1333	312	13.9892	3.77	cod	7ba	1256	-15.9883	393.6	13.9727	3.72
Monk	2fc	1497	-16.3209	459.7	13.3267	3.80	cod	7aa	1587	-15.4393	492.6	13.6025	3.76
whiting	3ac	1610	-15.9246	505.4	14.1242	3.72	cod	7ea	1767	-15.18	544.1	13.8218	3.79
whiting	3aa	1762	-16.0883	553.3	14.1919	3.72	cod	7fa	1239	-15.0495	386.3	13.5098	3.74
whiting	3fa	1462	-16.4411	442.6	13.8797	3.85	cod	7dc	1766	-15.9048	541.3	13.6154	3.81

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whiting	3ca	1990	-16.1571	616.3	13.8331	3.77	cod	7cc	1589	-15.0799	500.6	13.8056	3.70
whiting	3ba	1645	-16.5073	510.6	13.8703	3.76	cod	7bc	1200	-15.9349	378.2	13.8421	3.70
whiting	3ea	1764	-15.7776	538.3	14.603	3.82	cod	7ac	1746	-15.4676	535.3	13.4503	3.81
whiting	3da	1366	-16.2111	412.3	14.1244	3.87	cod	7ec	1511	-15.3233	469.3	13.8934	3.76
whiting	3fc	1405	-16.092	432.2	13.3622	3.79	cod	7fc	1676	-14.9728	516.1	13.6327	3.79
whiting	3cc	1897	-16.0462	583.1	13.8637	3.80							
whiting	3bc	1266	-16.3621	396.4	13.9331	3.73							
whiting	3ec	1227	-15.9264	372.8	14.4839	3.84							
whiting	3dc	1153	-16.115	354.8	13.9032	3.79							
cod	1ma	1.334	-16.06	0.427	17.14	3.65	haddock	5mc*	0.879	-15.96	0.285	13.13	3.61
cod	1mb	1.451	-16.05	0.462	17.15	3.66	haddock	6ma	1.473	-17.28	0.429	14.44	4
cod	1mc	1.558	-16.21	0.494	17.21	3.68	haddock	6mc	2.092	-17.27	0.616	13.14	3.96
cod	1mba	1.01	-16.36	0.309	17.37	3.81	haddock	6ma*	1.448	-16.68	0.462	14.8	3.65
cod	1mbb	1.172	-16.37	0.36	17.26	3.79	haddock	6mb*	1.787	-16.61	0.576	14.69	3.62
cod	1mbc	1.065	-16.56	0.318	17.35	3.9	haddock	6mc*	1.46	-16.58	0.467	14.71	3.65
cod	1mb*	1.63	-16.19	0.517	17.28	3.68	pollock	7ma	0.778	-17.33	0.265	9.84	3.42
cod	1ma*	1.202	-16.32	0.377	17.59	3.72	pollock	7mb	1.411	-17.1	0.507	9.19	3.25
cod	1mc*	1.67	-15.98	0.538	17.33	3.62	pollock	7mc	1.208	-17.13	0.427	9.36	3.3
cod	1mba*	1.572	-15.57	0.512	17.22	3.58	pollock	7ma*	1.131	-19.5	0.375	7.2	3.51
cod	1mbb*	1.534	-16.07	0.491	17.46	3.65	pollock	7mb*	1.6	-18.79	0.579	6.61	3.23
cod	1mbc*	1.634	-15.84	0.526	17.18	3.63	pollock	7mc*	1.072	-19.78	0.337	7.12	3.71
mackerel	2ma	1.513	-18.11	0.459	15.02	3.84	herring	8ma	1.687	-19.66	0.494	9.44	3.98
mackerel	2mb	1.388	-18.19	0.425	14.16	3.81	herring	8mb	1.673	-20.05	0.492	10.08	3.97
mackerel	2mc	1.436	-18.15	0.431	15.06	3.89	herring	8mc	1.704	-18.7	0.499	9.05	3.98
mackerel	2ma*	2.031	-17.77	0.665	14.34	3.56	herring	8ma*	1.705	-18.36	0.499	10.34	3.99
mackerel	2mb*	1.83	-18.13	0.591	13.46	3.61	herring	8mb*	1.868	-17.94	0.575	10.01	3.79
mackerel	2mc*	1.812	-18.16	0.586	13.46	3.61	herring	8mc*	1.29	-18.57	0.379	10.47	3.97
mackerel	3ma	1.542	-18.04	0.476	13.86	3.78	witch	11ma	1.28	-17.31	0.378	12.89	3.95
mackerel	3mb	1.432	-18.04	0.441	14.06	3.79	witch	11mb	1.591	-17.2	0.474	12.54	3.92
mackerel	3mc	1.619	-18.31	0.481	14.62	3.92	witch	11mc	1.979	-17.3	0.579	12.59	3.99
mackerel	3ma*	1.704	-17.51	0.559	14.14	3.56	witch	11ma*	2.007	-15.8	0.635	13.26	3.69
mackerel	3mb*	1.631	-17.53	0.534	14.18	3.57	witch	11mb*	1.64	-15.95	0.519	13.39	3.69

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mackerel	3mc*	1.06	-17.28	0.349	13.93	3.55	witch	11mc*	1.626	-15.85	0.515	13.52	3.68
plaice	4ma*	1.599	-16.61	0.512	13.17	3.64	haddock	12ma	1.245	-17.92	0.368	13.52	3.97
plaice	4mb*	1.484	-16.62	0.474	13.01	3.66	haddock	12mb	1.882	-18.43	0.481	14.07	3.95
plaice	4mc*	1.731	-16.62	0.555	12.72	3.64	haddock	12mc	1.33	-17.79	0.391	13.8	3.97
plaice	4ma	1.352	-17.47	0.399	11.58	3.95	haddock	12ma*	1.608	-16.9	0.525	14.66	3.57
plaice	4mb	1.783	-17.62	0.517	11.31	3.99	haddock	12mb*	1.213	-16.96	0.39	14.84	3.63
plaice	4mc	1.482	-17.46	0.442	11.36	3.91	haddock	12mc*	1.668	-16.86	0.549	14.36	3.54
haddock	5ma	1.568	-17.27	0.466	13.3	3.92	herring	14ma	1.241	-17.32	0.417	8.09	3.47
haddock	5mb	1.717	-17.35	0.512	12.84	3.91	herring	14mb	1.669	-17.91	0.54	7.79	3.6
haddock	5mc	2.09	-17.04	0.648	12.6	3.76	herring	14mc	1.378	-17.66	0.454	8.07	3.54
haddock	5ma*	1.157	-16.62	0.363	13.95	3.72	herring	14ma*	1.237	-18.41	0.375	10.18	3.85
haddock	5mb*	1.263	-16.52	0.402	13.95	3.67	herring	14mb*	1.818	-18.22	0.566	9.78	3.75
							herring	14mc*	1.864	-18.33	0.576	9.74	3.77

Appendix 5: Southern Hemisphere Fish Data

Appendix 5

Sample	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C:N ratio	Sample	Mass C	$\delta^{13}\text{C}$	Mass N	$\delta^{15}\text{N}$	C:N ratio
10a1	1.383	-17.37	0.419	15.39	3.85	34b1	1.268	0.472	-15.22	14.75	3.13
10a2	1.414	-16.97	0.429	16.25	3.85	34b2	1.293	0.498	-14.81	14.74	3.03
10c1	2.552	-17.3	0.767	17.13	3.88	34c1	2.073	0.735	-15.91	16.76	3.29
10c2	1.715	-17.46	0.516	16.99	3.88	34c2	2.304	0.8	-15.71	16.83	3.36
12b1	2.706	-19.67	0.544	17.35	5.81	34d1	2.27	0.871	-15.32	15.31	3.04
12b2	1.829	-19.99	0.358	17.47	5.96	34d2	1.779	0.686	-15.28	15.14	3.02
12d2	1.741	-20.41	0.268	17.22	7.59	34e_1	1.001	0.357	-15.81	15.45	3.27
12d1	3.315	-20.12	0.551	17.17	7.02	34e_2	1.169	0.455	-15.85	15.49	3
12g1	1.58	-21.91	0.17	17.37	0.83	35c1	2.428	0.654	-18.67	11.55	4.33
12g2	3.175	-21.3	0.375	17.17	9.88	35c2	1.864	0.519	-18.74	11.56	4.19
13b1	1.127	-15.81	0.453	16.4	2.9	35k1	2.54	0.722	-18.4	12.57	4.1
13b2	1.274	-15.86	0.439	16.48	3.39	35k2	1.25	0.345	-18.55	11.93	4.23
16a1	1.408	-16.32	0.48	15.98	3.42	37b1	2.57	0.753	-18.45	13.01	3.98
16a2	1.474	-16.43	0.494	15.95	3.48	37b2	2.217	0.651	-18.33	13.34	3.97
16b1	1.337	-16.37	0.452	16	3.45	40b1	1.511	0.42	-17.01	14.46	4.2
16b2	1.112	-16.31	0.374	16.22	3.47	40b2	1.265	0.354	-17.01	14.42	4.16
16d1	2.229	-16.98	0.77	15.74	3.38	40c1	1.004	0.228	-18.49	14.02	5.14
16d2	0.927	-16.98	0.317	15.47	3.42	40c2	1.112	0.284	-17.88	14.2	4.57
17a1	0.997	-17.2	0.35	13.07	3.32	40e_1	2.061	0.572	-17.64	14.24	4.21
17a2	0.94	-17.04	0.338	13.1	3.24	40e_2	1.776	0.373	-18.88	14.32	5.55
17b1	2.757	-16.55	0.863	32.85	3.73	40h1	1.204	0.33	-17.2	15.72	4.25
17b2	1.029	-17.27	0.364	13.27	3.3	40h2	2.254	0.63	-16.94	15.52	4.18
20a2	1.221	-15.84	0.447	16.59	3.19	40i1	1.137	0.244	-19.22	13.63	5.44
20a1	1.3	-15.46	0.497	16.46	3.05	40i2	2.078	0.336	-19.52	15.34	7.23
21a1	1.273	-15.72	0.464	15.21	3.2	40k2	1.376	0.314	-18.57	13.82	5.11
21a2	1.128	-15.65	0.437	15.3	3.01	40k1	1.328	0.31	-18.5	13.6	5
21b1	1.351	-15.87	0.512	15.08	3.08	40n1	2.54	0.558	-17.6	13.87	5.31

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21b2	1.517	-15.83	0.564	15.38	3.14	40n2	1.321	0.334	-16.49	13.57	4.62
21d1	1.949	-15.91	0.671	15.6	3.39	41c1	1.344	0.438	-16.16	16.52	3.58
21d2	1.897	-15.85	0.665	15.54	3.33	41c2	1.573	0.455	-16.72	16.71	4.04
22b1	2.129	-18.83	0.439	16.55	5.66	41d2	2.154	0.657	-16.29	16.54	3.82
22b2	0.989	-19.14	0.212	16.37	5.45	41e_1	2.04	0.622	-16.15	16.71	3.83
23a1	2.64	-19.73	0.297	14.59	3.36	41e_2	1.128	0.344	-16.69	16.27	3.83
23a2	3.039	-18.88	0.462	14.41	7.68	42a1	2.352	0.729	-17.57	12.69	3.76
23c1	1.044	-18	0.314	14.08	3.88	42a2	1.042	0.327	-18.01	12.61	3.72
23c1	2.08	-20.86	0.311	15.44	7.8	45_1	2.223	0.699	-16.1	18.05	3.71
23c2	1.151	-17.75	0.352	14.04	3.81	45_2	2.026	0.62	-16.3	17.81	3.81
23c2	1.714	-21.26	0.241	15.22	8.3	46_1	2.281	0.706	-17.4	14.79	3.77
23e_1	2.694	-19.76	0.334	14.37	9.42	46_2	2.419	0.738	-17.37	14.87	3.82
23e_2	2.196	-18.99	0.336	14.5	7.63	49a1	2.6	0.775	-16.18	16.09	3.91
24b1	1.826	-17.37	0.558	13.67	3.82	49a2	1.113	0.336	-16.68	16.64	3.87
24b2	1.678	-17.56	0.521	12.65	3.76	50b1	2.371	0.683	-17.79	13.33	4.05
25b1	2.598	-18.11	0.791	13.41	3.83	50b2	2.233	0.645	-17.71	13.43	4.04
25b2	2.308	-18.04	0.695	13.6	3.87	51a1	1.979	0.59	-19.87	12.52	3.92
26a2	1.148	-18.37	0.35	14.9	3.82	51a2	1.248	0.375	-19.95	12.75	3.88
26a1	1.375	-18.27	0.407	15.11	3.94	51b1	1.782	0.543	-16.73	12.1	3.83
26c1	2.094	-17.39	0.622	15.13	3.93	51b2	2.187	0.675	-16.25	12.71	3.78
26c2	2.782	-17.8	0.722	15.98	4.5	54a1	1.338	0.23	-19.83	17.04	6.78
28c1	1.07	-17.18	0.352	14.16	3.55	54a2	1.137	0.244	-18.79	16.09	5.43
28c2	1.34	-17.15	0.437	14.09	3.57	m8b1	1.388	0.351	-18.43	16.04	4.61
29a1	2.173	-17.4	0.644	14.5	3.93	m8b2	1.736	0.312	-19.96	14.77	6.5
29a2	1.578	-18.07	0.436	14.19	4.22	m8c1	1.767	0.521	-16.8	17.44	3.95
30a2	2.299	-16.04	0.702	17.89	3.82	m8c2	1.761	0.518	-16.65	17.59	3.97
32a1	0.979	-15.41	0.406	17.04	2.82	m8d1	3.434	0.689	-19.07	16.1	5.81
32d1	1.683	-18.86	0.41	13.73	4.79	m8d2	1.724	0.456	-17.56	17.51	4.41
32d2	2.594	-18.6	0.63	13.76	4.8	m8e_1	1.333	0.253	-20.43	16.15	6.16
32f1	2.307	-18.13	0.574	16.95	4.69	m8e_2	1.357	0.263	-20.27	16.41	6.02
32f2	1.712	-17.86	0.44	16.87	4.54	m4b1	1.456	0.289	-19.35	13.82	5.88
32g1	1.023	-17.28	0.307	17.15	3.89	m4b2	1.452	0.444	-16.9	14.12	3.81

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32g2	1.117	-18.06	0.29	17.04	4.5	m4e_1	1.327	0.37	-17.74	13.09	4.18
32h1	1.321	-17.45	0.386	15.12	3.99	m4e_2	1.131	0.342	-17.56	12.62	3.86
32h2	2.964	-18.14	0.724	14.93	4.78	m5c1	1.524	0.466	-18.17	12.89	3.82
33a1	2.186	-16.86	0.647	16.61	3.94	m5c2	1.495	0.468	-18.28	12.31	3.72
33a2	1.229	-17.19	0.366	16.78	3.92	m2a1	1.558	0.477	-16.84	15.32	3.81
33b1	2.157	-19.59	0.516	11.8	4.88	m2a2	1.894	0.582	-16.97	15.01	3.8
33b2	2.857	-19.05	0.722	12.09	4.62	m2c1	1.445	0.431	-17.57	15.82	3.91
33c1	1.103	-18.15	0.384	12.27	3.35	m2c2	1.372	0.392	-17.86	16.48	4.09
33c2	1.693	-18.67	0.566	12.2	3.49	m6b1	1.518	0.347	-19.14	16.14	5.1
						m6b2	1.507	0.313	-19.79	16.39	5.63
						m6c1	2.172	0.635	-17.94	16.07	3.99
						m6c1	1.688	0.486	-17.87	16.34	4.05
						m6c2	1.783	0.506	-18.2	16.14	4.11
						m6c2	2.593	0.752	-17.51	16.38	4.02
merlvza f1	2262	15.2362	582.5	-17.0496	4.5304721	salmon f4	3119	18.4265	811.2	-15.9239	4.4857413
merlvza f1	1981	15.3609	514.3	-16.9977	4.4938104	squida f5	2846	15.4133	916.2	-14.7134	3.6240268
merlvza f1	1723	15.4218	447.6	-16.9953	4.490989	squida f5	2193	15.6618	731.2	-14.7481	3.4990427
abaderio f2	1748	15.2201	488.5	-16.7917	4.1746844	squida f5	1321	15.6582	458.3	-14.5909	3.36279
abaderio f2	2306	14.6783	620.1	-17.0925	4.3385475	squida f5	2796	16.3475	904	-14.7258	3.6084071
abaderio f2	2060	15.1523	548.8	-16.9595	4.3792517	sqidb f6	2684	17.6813	792.1	-15.8645	3.9532046
abaderio f2	1855	15.0239	511.1	-16.8992	4.2343312	sqidb f6	2251	17.515	669	-15.8163	3.9255107
tuna f3	1014	15.4332	274.6	-17.0867	4.3080845	sqidb f6	3799	27.9866	1078	-15.7722	4.1114719
tuna f3	2467	15.165	638.8	-16.9432	4.5055834	sqidb f6	3333	17.3755	963.7	-15.9836	4.0349694
tuna f3	2775	14.466	690.4	-17.1499	4.6893105	sqiuidc f7	3168	14.0478	903.5	-17.5869	4.0907582
tuna f3	1016	15.1707	268	-17.317	4.4228856	sqiuidc f7	3520	14.2376	1004	-17.4428	4.0903054
salmon f4	1887	18.7624	569.6	-14.8937	3.864993	sqiuidc f7	1072	14.7309	324.7	-17.6474	3.8517606
salmon	1559	18.4477	473.5	-15.1016	3.8412531	sqiuidc f7	2340	14.6409	689	-17.5048	3.9622642

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