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Sex Differences in the Foraging Ecology of a Size-dimorphic Marine Carnivore

By

Charlotte Anne (Carrie) Beck

Submitted in partial fulfillment of the requirements for the degree
of Doctor of Philosophy in Biology

at

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Signature of Author

For Nana - who always encouraged my
interest in nature and shared my
fascination and love of Sable Island

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ABSTRACT

Sex differences in foraging ecology have been noted in a variety of taxa and are most commonly attributed to sexual size dimorphism, inter-specific competition, and the differing reproductive roles of males and females during the breeding season. More recently, sex differences in foraging behaviour have been linked to the differing trade-off solutions of the sexes that allow an individual's reproductive success to be maximized. Among marine carnivores, such as pinnipeds, sex differences in foraging ecology have been difficult to study due to the wide-ranging, at-sea nature of foraging outside of the breeding season and the fact that feeding often occurs at depth where direct observation is rarely possible. I examined sex differences in the foraging ecology of adult grey seals, *Halichoerus grypus*, in the Northwest Atlantic, over the 8-month period prior to breeding using of time-depth data-loggers and satellite telemetry to measure temporal and spatial scales of foraging, hydrogen isotope dilution methods to examine longitudinal changes in body composition and energy gain, and quantitative fatty acid signature analysis to estimate diet composition. The influence of seasonal changes in body composition and hence buoyancy on diving behaviour was also examined.

Grey seals are size dimorphic, with males being 1.5 times larger than females; thus, sex-differences in foraging were expected given the higher absolute energy requirement of males. However, the sex-specific seasonal pattern of diving behaviour, found at multiple temporal scales (i.e., individual dives, bouts of diving and trips) indicated that females had a higher level of dive effort than males in the periods directly following the spring moult and in the 3-months directly prior to breeding. This suggests that males and females make different decisions about the allocation of time to foraging and other activities (e.g. resting at the surface) with females spending more time foraging than males. Sex differences in the seasonal pattern of energy storage mirrored these patterns in diving behavior with females accumulating stored body energy earlier in the pre-breeding foraging period than males. These results suggest that sex differences in the seasonal pattern of foraging likely reflect sex-specific decisions for dealing with the costs and benefits of storing energy for reproduction during the foraging period. During the mid-late 1990s, the diet of both males and females was dominated by capelin during the 3-months prior to breeding. However, diet composition differed significantly between sexes with females consuming a higher proportion of sandlance and a lower proportion of skates and squid relative to males. Among individuals foraging on the eastern Scotian Shelf, males had a more diverse but lower energy-density diet than did females. In combination with differences in diving behaviour, these differences in diet suggest that males are less selective than females and including more prey species of lower energy density in their diet to increase overall intake and meet the energy demands imposed by larger body size. Thus, both sexual size dimorphism and the sex differences in the costs and benefits of energy storage for reproduction appear to influence the foraging ecology of this species.

ABBREVIATIONS

ABT:	Accumulated bottom time/day
AIC:	Akaike's information criterion
ANOVA:	Analysis of variance
BC:	Bout cluster
CPM:	Counts per minute
DA:	Dive analysis
DFA:	Discriminant Function Analysis
DSL:	Dorsal standard length
EB:	End of breeding
EM:	End of moult
ESS:	Eastern Scotian Shelf
FAME:	Fatty acid methyl ester
FAS:	Fatty acid signature
GLTDR:	Geolocation time-depth recorder
HTO:	tritiated water
IM:	intramuscularly
LME:	Linear mixed effects model
MANOVA:	Multivariate analysis of variance
MF:	Mid-foraging
MUFA:	Monounsaturated fatty acid
NAFO:	Northwest Atlantic Fisheries Organization
PB:	Pre-breeding
PM:	Post-moult
PUFA:	Polyunsaturated fatty acid
QFASA:	Quantitative fatty acid signature analysis
SB:	Start of breeding
SM:	Start of moult
TBE:	Total body energy
TBF:	Total body fat
TBP:	Total body protein
TBW:	Total body water
TDR:	Time-depth recorder
SLTDR:	Satellite-linked time-depth recorder
WSS:	Western Scotian Shelf

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There's always time to take the train... - WDB

No matter what happens...you can ALWAYS cut it in half! - SJI

Chapter 1. Sex differences in foraging behaviour: The influence of size dimorphism, competition and reproduction

Introduction

Foraging is the process whereby food energy is acquired; allocation of this energy to growth, reproduction and survival is determined by the life history of the individual. Life history patterns – the way in which organisms allocate resources to maximize fitness – vary greatly among species. For example, some species begin reproduction early in life and, as a consequence, have shorter life spans whereas other species delay reproduction in favor of increased size at first reproduction resulting in bigger or more offspring (Stearns 1992). In the past several decades, there has been increasing interest in the evolution and variation of life history patterns utilized by organisms (e.g., Stearns 1992; Roff 1992). An important component in understanding life history evolution is understanding the factors which affect an individual's ability to acquire nutrients (Clutton-Brock *et al.*, 1982; Sculley & Boggs, 1996). A variety of factors (e.g., inter-annual changes in prey distribution, condition or state of the individual) can influence foraging success and these must be addressed when examining how energy is acquired and subsequently allocated to growth and reproduction.

Much has been written about the foraging behaviour of animals from both a theoretical and empirical perspective. The development of "foraging theory" dominated much of the early work (e.g., MacArthur & Pianka 1966; Emlen 1966; Schoener 1969; Schoener 1971; Hughes 1980; Stephens & Krebs, 1986). Models were developed on the assumption that an individual's foraging behavior maximizes its net rate of energy intake (Schoener 1971). Many of these earlier studies were deterministic and failed to consider the stochastic environment in which organisms live. Critics of the original foraging models pointed out that foraging is not independent of other vital activities (e.g., predator avoidance, provisioning of young, mate acquisition) and it is therefore unreasonable to assume that foraging alone would be maximized (Pierce & Ollason 1987). From a life history perspective, foraging behaviour should maximize fitness, subject to trade-offs between foraging and other vital activities. Some models of foraging behaviour attempt to reflect this by including the influence of such extrinsic factors as prey distribution (in time and space), prey quality, risk of predation, central place foraging and environmental stochasticity (e.g., temperature, weather; Stephens & Charnov 1982; Oaten 1977; Orians & Pearson 1979). Intrinsic factors, such as sex, may also play a role in determining what is optimal foraging behaviour given the differing energetic requirements of males and females (Trivers 1972).

Sex-differences in foraging behaviour are evident in a variety of taxa (e.g., mammals - Clutton-Brock *et al.* 1983, birds - Ligon 1968, reptiles - Parmelee & Guyer 1995, and invertebrates - Jormalainen *et al.* 2001). Given that selection operates on individuals, understanding how each sex responds to selection in order to maximize fitness is fundamental to our understanding of the evolution of life histories. In fact recent studies have linked sex differences in foraging behaviour to sex-specific fitness maximizing strategies (Clutton-Brock & Parker 1992; Merilaita & Jormalainen 2000; Jormalainen *et al.* 2001), that is, the differing trade-off solutions of the sexes that allow an individual's reproductive success to be maximized. However, most often the evolution of sex differences in foraging behaviour has been attributed to sexual dimorphism, intra-specific competition, and the differing reproductive roles of males and females during the breeding season. It is doubtful that these factors are mutually exclusive, but rather work together to bring about differences in the way males and females acquire energy and nutrients. In this chapter, I present a review of how these factors can foster sex-differences in foraging behaviour and provide a brief description of the natural history of the species used in my research.

Sexual size-dimorphism and foraging behaviour

Sexual size dimorphism is relatively common in the animal kingdom with male-based size dimorphism being most common in birds and mammals (see Fairbairn 1997). The evolution of sexual size dimorphism is most often attributed to sexual selection (Darwin 1871; Selander 1972; Clutton-Brock *et al.* 1982; Fairbairn 1997). Briefly, any genetic trait, which confers an advantage in reproductive success over other individuals of the same sex, will be under sexual selection. When resources (e.g., food, space), used by females, are distributed such that female distribution is clustered, the opportunity for male defense arises (Emlen & Oring 1977). The ability of individual males to defend and monopolize females leads to variation in the reproductive success of males. In cases where size confers an advantage over other males, increased body size in males will be selected.

Sexual size dimorphism is likely a significant factor in producing divergent foraging tactics between males and females. Intuitively, the larger sex will have higher energetic requirements. Resting metabolism increases with body mass, thus larger individuals require more total energy per unit time relative to smaller individuals (Klieber 1961). To attain and maintain their larger size, the larger sex would require a higher energy intake and thus might be expected to modify their foraging behaviour relative to that of the smaller sex. This may result in the larger sex consuming greater quantities of the same prey, consuming different prey types (potentially higher energy prey), or foraging more efficiently.

Dimorphic body size also imparts differential physiological and anatomical mechanisms which may affect foraging ability and hence behaviour (Drunzinsky 1993; LeBoeuf *et al.* 1993). One example of this is the allometric relationship between gut size and body mass (Demment 1982; Gross *et al.* 1995). A larger individual has a larger gut capacity than a smaller individual and is theoretically able to extract more nutrients per unit intake. This gives larger individuals the ability to digest food more efficiently than smaller individuals and may be particularly important for herbivores where digestion of plant material increases with retention time. Bite size should also increase with body size assuming bite size is isometrically related to the size of the buccal apparatus. However, chewing frequency is allometrically related to body size in mammals (Druzinsky 1993) such that individuals with shorter jaws (i.e., smaller animals) can masticate food at a faster rate than individuals with larger jaws. As a result of these allometric relationships, sex-differences in foraging behaviour would be expected in size dimorphic species. Members of the larger sex should be able to efficiently utilize lower quality food sources, take larger bites and consume greater quantities of food to satisfy the energy requirements. Individuals of the smaller sex would be expected to ingest higher quality food and have a higher chew frequency.

The foraging behaviour of several ungulate species has been investigated in relation to size dimorphism and these predictions (Clutton-Brock *et al.* 1983; Ginnett &

Demment 1997; Perez-Barberia & Gordon 1999). Clutton-Brock *et al.* (1983) examined the feeding behaviour of male and female red deer (*Cervus elaphus*) on the island of Rum in Scotland. As these authors pointed out, it is difficult to directly compare the nutritional requirements of males and females because costs associated with reproduction differ not only in magnitude but also in timing. Nevertheless, stags in general should have the larger energy requirements due to their substantially larger size. Results of the study showed that stags had a smaller home range and tended to use habitats inferior to those used by hinds. Additionally, males spent more of their daily activity budget grazing than did females. These findings suggest that males were less selective in their choice of diet in order to increase overall intake, while females roamed over a larger area in search of higher quality food. However, a more recent and comprehensive study of the red deer population on the Isle of Rum has indicated that this may not always be the case (Conradt *et al.* 2001) and that further studies of other red deer populations are necessary.

Sex differences in foraging behaviour due to body size and physiological mechanisms can also be expected in air-breathing, aquatic carnivores. Marine mammals and sea birds are constrained in the time available for foraging beneath the surface by their oxygen storage capacity. Oxygen storage is a direct function of body size – larger individuals have a larger lung capacity, a larger muscle (myoglobin) mass and blood pool in which to store oxygen and have a slower mass-specific metabolic rate (i.e., slower utilization of oxygen stores; Castellini & Kooyman 1989; Scheer 1997). In a review of diving capacity among air-breathing vertebrates, Scheer (1997) found that 71% of the variation in dive duration could be explained by body mass, with larger species staying beneath the surface for longer periods of time. As a consequence of larger oxygen storage capacity, larger individuals can also dive to greater depths, presuming that dive depth is not limited by habitat. In species that exhibit extreme size dimorphism, males and females would have different oxygen storage capacities and hence divergent foraging ability.

The logistic difficulties associated with examining the foraging behaviour of aquatically feeding species are such that both males and females have been studied in only a few species outside of the breeding season. LeBoeuf *et al.* (1993, 2000) examined the foraging and diving behaviour of male and female northern elephant seals, *Mirounga augustrioustris*. In this species, males can be between 1.5 and 10 times larger than females. Thus, males have energetic requirements and oxygen storage capacities that far exceed that of females. Not unexpectedly, diving behaviour of males and females differs significantly. Based on dive depth and location, males appear to forage on benthic prey located at the continental margin. Females, on the other hand, concentrate foraging effort off the continental shelf. The strong diurnal pattern of dive depth shown by females suggests that individuals pursue vertically migrating pelagic prey species. LeBoeuf *et al.* (1993) speculate that males are foraging more efficiently by pursuing benthic prey which, relative to pelagic prey, tend to be larger and have a higher energy density. In this way, males forage so as to increase energy intake relative to females. Surprisingly, mean dive duration did not differ significantly between the sexes. However, the maximum dive duration recorded for males was 35 minutes longer than that for females, indicating that the potential for longer dives in males may sometimes be realized. Castellini & Kooyman (1989) point out that the physiological capabilities of an individual will only affect its behaviour when physiological limitations are reached. Hence, similar dive durations for male and female elephant seal may simply indicate that males are not normally limited by oxygen capacity, but return to the surface for some other reason. This suggests that oxygen balance may be another factor in the optimization of fitness.

Sexual size dimorphism and the scaling relationships of body size to other anatomical structures appear to play a large role in the sex-specific divergent foraging tactics of many mammalian species. Evidence of this can also be found among avian foragers. In many bird species, beak size is proportional to body size such that size dimorphism results in the larger sex having a larger beak. Beak size in turn affects the type and size of food an individual can ingest (Downhower 1976) resulting in males and females having different diet compositions.

While this section has focused on sexual dimorphism in body size, sexual dimorphism of feeding structures also effects the foraging ability of males and females, which could result in different foraging tactics. The now extinct woodpecker species Huia, *Neomorpha acutirostris,* of New Zealand, provided an excellent example of this phenomenon. Males and females of this species did not differ significantly in body size, however beak structure was dramatically different between sexes. Males used their short, broad, and relatively straight beak to bore into rotting wood to find grubs and insects. In contrast females, which had longer, slender, curved beaks probed existing crevices in the wood to obtain prey (Selander 1966; Morse 1968). This anatomical difference allowed for different foraging techniques, with each sex using the technique most efficient to their capabilities. Sexual dimorphism in beak structure of the purple-throated carib hummingbird, *Eulampis jugularis*, has also been linked to the divergent foraging behaviours of males and females (Temeles *et al.* 2000).

Intra-specific competition and social structure

Competition between male and female con-specifics for resources has often been invoked as an explanation for divergent foraging behaviour observed within species (Schoener 1969; Hughes 1980; Clarke *et al.* 1998). An investigation of inter-sexual niche partitioning by the Downy woodpecker (*Dendrocopos pubescens*), a monomorphic species, revealed significant differences in foraging behaviour outside the breeding season. Sexes differed not only in pattern of foraging activity but also in foraging technique and diet composition. By using different foraging techniques, males and females can utilize different food sources and thus competition for resources is reduced (Williams 1980). To further support for this hypothesis, Williams (1980) indicated that when inter-specific competition increased, the extent of niche overlap between male and female Downy woodpeckers became even more reduced as each sex specialized on the prey type they could most efficiently obtain.

Sex-specific foraging techniques and the associated reduction in inter-sexual competition may also arise as a result of a species social structure. Ligon (1968) found that in certain species of woodpeckers, males are dominant over females. As a result, males are able to monopolize the most productive foraging areas, forcing females to find alternative, and likely less productive areas. Ligon (1968) speculated that natural selection would favor females that can most efficiently utilize these inferior areas by the development of new foraging techniques, thus resulting in sex-specific foraging behaviours. Social structure and competition may account for divergent foraging strategies in the Nuttall woodpecker (*Picoides nuttallii*; Jenkins 1979). In this species, repeated competition for resources is hypothesized to weaken the pair bond between males and females, possibly to the extent of clutch failure. By partitioning the area in which they forage, males and females are less likely to create friction through competition and hence have a stronger, more efficient pair bond (Kilham 1965; Ligon 1968; Jenkins 1979).

Segregation of the sexes, for example in matrilineal societies, may also result in males and females foraging in different locations and on different prey. Sexual size dimorphism is a likely contributor to the evolution of social segregation of males and females. In several size dimorphic mammalian species where males are larger than females, females and juveniles stay together while sub-adult and adult males form bachelor groups or forage independently. When foraging in a group, competition between members may reduce energetic intake, although there are also many benefits related to group foraging. However, as juvenile males grow they require greater food intake to support their increasing body mass and as a result leave the group to forage independently. Alternatively, young males may leave their natal group and join other males to travel to more profitable foraging areas where competition between group members does not significantly limit energy intake. Empirical evidence of this can be found in the terrestrial white-nosed coati, (*Nasua narica*; Gompper 1996). In this species females are approximately 25% smaller than males and foraging success of solitary adult males is higher than that of adult females and juveniles foraging together. This advantage for males appears to be the result of decreased competition for food. As juvenile males become larger and require higher energy intake, they begin to spend more time foraging than the other members of the group by staying slightly longer at foraging sites, often having to "catch-up" to the group later. Eventually males leave the maternal group and begin foraging alone in order to attain enough resources. Group living among females appears to be a trade-off between foraging success and predator defense. In aggressive encounters, small groups of females could not defend themselves at a foraging site against larger solitary males or predators whereas larger female groups were able to defend the area (Gompper 1996).

Sex-specific reproductive roles and foraging behaviour

While rearing offspring, males and females take on parental duties to increase the probability of offspring survival. Several studies have suggested that the divergent foraging behaviour of males and females during the breeding period is a consequence of these reproductive or parental roles (Williamson 1971; Petit *et al.* 1990). For example, in Prothonotary warblers (*Protonotaria citrea*), males and females partition their foraging range vertically with males maintaining territorial vigilance and feeding in the higher branches while females feed closer to the ground and nest (Petit *et al.* 1990). Morse (1968) and Williamson (1971) reported similar results and conclusions regarding the divergent foraging strategies of the sexes in four species of spruce-wood warblers and the Red-eyed Vireo, *Vireo olivaceus*, respectively. Williamson (1971) further supported his conclusions by noting that such sex-differences are not observed during the non-breeding period.

The role of each sex during the parental care period and its influence on sex-differences in foraging behaviour may also be indirect, via an affect on sexual size dimorphism. Jonsson & Alerstam (1990) investigated the relationship between the division of parental care and sexual size dimorphism in 57 species of shorebirds. They found a clear relationship between the degree of sexual dimorphism and the relative level of parental care provided by each sex. They concluded that, assuming both pair members have similar rates of energy intake (regardless of size), smaller body size would be selected for in the sex that provides the higher level of parental care. Body size and maintenance energetic costs are directly related, such that a smaller parent would be able to provide a greater portion of their acquired energy to their offspring.

Fitness maximizing strategies

The potential reproductive rates of males and females often differ as a result of the unequal energetic expense of gamete production in males and females and in some cases the degree of parental care provided by either sex (Trivers 1972). In general, male fitness is most closely associated with the number of mating opportunities obtained whereas a female's fitness is more closely associated with her energetic ability to successfully rear offspring (Trivers 1972). As a result, fitness-maximizing strategies of males and females typically differ (Clutton-Brock & Parker 1992; Jormalainen *et* al. 2001) and may be expected to influence the foraging behaviour of males and females. In a series of studies on the isopod *Idotea baltica*, Jormalainen & colleges (Merlilaita & Jormalainen 1997, 2000; Jormalainen *et al.* 2001) showed that the foraging behaviour and microhabitat choice of male and female isopods differed due to differing solutions to the trade-off between foraging and predator avoidance. In males, reproductive success depends on size with larger males having higher fitness. As a result, high food intake for growth is critical to reproductive success and males take greater predation risks by foraging on high quality, apical parts of *Fucus vesiculosus* where they are exposed to visually searching fish predators. In female *I. baltica*, reproductive success depends mainly on survival from the time of breeding to the release of juveniles. In this species incubation of offspring by the female is a relatively long period during which anti-predator behaviour is more important than high food intake (Tuomi *et al.* 1988). As a result, females feed on the lower quality basal parts of *F. vesiculosus*, which provide more cover and less exposure to visually searching predators. Thus, males and females have differing fitness maximizing strategies with sex-specific solutions when balancing the need to acquire food energy and the need to avoid predation, resulting in sex differences in their feeding ecology.

Difference in fitness maximizing strategies may also be responsible for sex differences in foraging behaviour among some mammalian species. Among many ungulate species, sexual segregation outside the rut has often been explained by the "reproductive-strategy" hypothesis (Main & Coblentz 1990). In these species, male reproductive success is influenced by their competitive capabilities which in turn are influenced by the individuals ability to maximize rates of growth and increase body mass. As a result males exploit areas where food is abundant. In contrast, female reproductive success is dependent on the survival of offspring, such that females occupy areas that reduce the risk of predation to the neonate, even when this results in lower quality or quantity of food intake (Main *et al.* 1996; Perez-Barberia & Gordon 1999).

Conclusion

Sex differences in foraging ecology can be expected when energy or resource requirements differ between males and females. Whether these differing requirements are a result of dimorphic body size or a function of the reproductive ecology of a species will determine the extent and timing of divergent foraging tactics. Differential foraging ability as a result of size dimorphism can also result in differing behaviour, however other factors such as prey distribution or habitat features may limit the effect of differential foraging ability. Habitat or resource partitioning by sex, either as a result of intra-specific competition, social structure or fitness maximizing strategies also leads to differences in foraging ecology between sexes. Size dimorphism is linked to many aspects of a species' ecology, but appears to be a prominent driving force in the evolution of sex-specific foraging strategies. However, reproductive strategies and the associated energetic costs also play a significant role. In this thesis, I examined sex differences in the foraging ecology of grey seals, *Halichoerus grypus*, a size dimorphic marine carnivore in which males and females are expected to differ both in the timing and magnitude of energetic costs associated with reproduction.

The grey seal is a relatively large phocid species found on both sides of the North Atlantic Ocean. Adult male and female grey seals in the Northwest Atlantic population reach lengths of up to 2.65 m and 2.20 m, respectively. Although, both sexes go through dramatic seasonal changes in body mass and composition as a result of alternating periods of foraging and fasting, adult males are approximately 1.5 times heavier than adult females throughout the annual cycle (Mohn & Bowen 1996, Chapter 2 & 4). As in all pinnipeds, foraging at sea is temporally and spatially interrupted by the need to return to terrestrial breeding and moulting grounds. In the Northwest Atlantic population, parturition and mating occur from late December through early February with the largest breeding colony being located on Sable Island, Nova Scotia. Females give birth to a single offspring and wean their pup after a 16-day lactation period during which females fast (Iverson *et al.* 1993). During the late stages of lactation females enter estrous and are mated by one or more males (Boness & James 1979; Ambs *et al.* 1999). Grey seals have a polygynous mating system with males competing for access to groups of females (Boness & James 1979; Godsell 1991).

Following the breeding season, grey seals return to the sea to forage for approximately 4 months. During this period little is known about the duration of foraging trips or the amount of time spent on land. In May and June, both sexes moult. This is a period of reduced food intake over approximately 4-5 wk during which considerable time is spent on land. Grey seals have an annual moult, completely shedding and re-growing their pelage. After moulting, adults return to sea to forage, however again, little is known about the foraging behaviour of grey seals during this 7-month period leading up to the breeding season.

To date, knowledge of the diets of grey seals has been based on analysis of otoliths and other hard parts recovered from grey seal stomachs (e.g., Bowen *et al.* 1993) and faecal samples (e.g., Bowen & Harrison 1994; Mohn & Bowen 1996; Hammond *et al.* 1994a & b). Unfortunately these methods of diet analysis are subject to unavoidable biases (see Jobling 1987, Harvey 1989 and Prime & Hammond, 1990). For example, seals tend to digest their meals relatively quickly (Harvey 1989), such that fecal samples collected at haul-out sites represent only the last meal of an individual and likely reflects foraging near the haul-out site only. Thus, these samples may not be representative of the overall offshore diet that these animals rely on during most of the year. Despite these biases, stomach content and fecal analysis have provided useful information about the diet of grey seals (e.g., Bowen *et al.* 1993). A study based on faecal samples collected on Sable Island indicated that sandlance, *Ammodytes dubius*, dominated the diet of grey seals, accounting for over 80% of the diet by weight (Bowen & Harrison 1994). Atlantic cod, *Gadus morhia*, capelin, *Mallotus villosus*, redfish, *Sebates* spp., squid, *Illex illecebrocus*, and a variety of flatfish (flounders & American plaice, *Hippoglossoides platessoides*) were also found to be important prey items (Bowen & Harrison 1994; Mohn & Bowen 1996).

The population of grey seals in the Northwest Atlantic has increased rapidly over the last several decades and is suspected of playing a large role in the predation on and mortality of commercially important fish populations. The collapse of many commercial fish stocks in the North Atlantic since the late 1980's has raised questions about changes in the marine food-webs, with particular attention to predator-prey relationships. Mohn & Bowen (1996) indicate that the rapidly growing population of grey seals on the Scotian Shelf may represent an important source of predation on Atlantic cod populations. A better understanding of grey seal foraging ecology in the Northwest Atlantic is required for a more accurate accounting of seal predation on fish populations in this area.

In this thesis I examined several aspects of the foraging ecology of adult male and female grey seals. Sex differences in the foraging behaviour of this species were expected both because males are considerably larger than females and because each sex should differ in its fitness maximizing strategy. In Chapters 2 and 3, I examine diving behaviour at the level of individual dives and at the larger temporal scales of dive bouts and foraging trips, respectively. In Chapter 4, I examine the effects of large seasonal changes in body composition and hence buoyancy on diving behavior. Chapter 5 looks at the energetic consequences of diving behaviour in terms of the seasonal changes in energy storage and expenditure of males and females. In the final chapter, I examine differences in the diet composition of male and female grey seals using quantitative fatty acid signature analysis (Iverson *et al*, in prep) and investigate how diet characteristics are linked to measures of dive effort, foraging location and mass gain.

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Chapter 2. Sex differences in the diving behaviour of a size dimorphic capital breeder: the grey seal

Introduction

Survival, growth and reproductive success are ultimately linked to an individual's ability to acquire food energy. Foraging behaviour should therefore maximize an individual's fitness, subject to trade-offs between foraging and other activities such as predator avoidance and mate acquisition. Extrinsic factors, such as the spatial and temporal distribution of prey, prey quality, risk of predation, and environmental stochasticity influence the strategy used to obtain food (e.g. Stephens & Charnov 1982; Oaten 1977; Orians & Pearson 1979). However, intrinsic factors, such as sex, can also influence the foraging behaviour of an individual (e.g., Jenkins 1979; Clutton-Brock *et al.* 1982; LeBoeuf *et al.* 1993; Ginnett & Demment 1997).

Intra-specific differences in the foraging behaviour of males and females have been found in a variety of taxa (e.g., Williams 1980; Clutton-Brock *et al.* 1982; Petit *et al.* 1990; LeBoeuf *et al.* 2000). Among the explanations for these differences, the three most prominent hypotheses to account for the occurrence of sex differences in foraging behaviour are sexual size dimorphism, reduced inter-sexual competition for food, and the differential roles of each sex during reproduction and parental care.

Sexual size dimorphism is relatively common with male-based size dimorphism being more prevalent in birds and mammals (Fairbarin 1997). As absolute metabolic requirements increase with body mass, larger individuals require more energy per unit time than smaller ones (Klieber 1961). Therefore, to attain and maintain their larger size, the larger sex will require a higher energy intake and thus may forage differently than the smaller sex. As an example, studies on the foraging behaviour of several size dimorphic ungulate species (e.g., red deer (*Cervus slsphas)* - Clutton-Brock *et al.* 1982; giraffes (*Giraffa camelopardalis)* - Ginnett & Demment 1997) suggest that the larger males are less selective in their choice of diet in order to increase overall intake, while females roam over a larger area in search of higher quality food.

Competition for resources between male and female con-specifics also may account for differences in foraging behaviour (Schoener 1969; Hughes 1980; Clarke *et al.* 1998). In the Downy woodpecker (*Dendrocopos pubescens*), a monomorphic species, sexes differed not only in their pattern of foraging activity, but in foraging technique and diet composition, thereby reducing competition for food resources (Williams 1980). During periods of increased inter-specific competition, the niche overlap between male and female Downy woodpeckers was further reduced as each sex specialized on the prey type they could most efficiently obtain, providing further support for this hypothesis (Williams 1980).

Sex-differences in foraging behaviour have also been attributed to the different parental duties of males and females (Morse 1968; Williamson 1971; Petit *et al.* 1990). For example, in Prothonotary warblers (*Protonotaria citrea*), Petit *et al.* (1990) found that during the pre-nesting period males and females partition their foraging range vertically, with males foraging higher than females. During this period females are building nests and, as a result, are often searching for materials near to the ground. Since energy acquisition is also necessary at this time, females forage at lower levels. Males, on the other hand, maintain territorial vigilance from higher more conspicuous branches and thus, forage at a higher level.

Males and females may forage differently as the result of differences in the sex-specific energetic costs of reproduction (Clutton-Brock *et al.* 1983; Parmelee & Guyer 1995; Ginnett & Demment 1997, Petit *et al.* 1990). These costs may differ not only in origin, but also in magnitude. In mammals the immediate energetic expenditure to females for gestation and lactation often outweigh the immediate expenditure of males in acquiring mates and defending resources (Gittleman & Thompson 1988; Wilkinson & Barclay 1997; Perrigo 1990). The fitness consequences associated with not acquiring sufficient resources to support these expenditures may also differ, such that the costs and benefits of storing energy for reproduction differs between males and females. For example, in polygynous mammalian species where females are capital breeders (i.e. relying only on stored body energy for reproduction), females that fail to store sufficient energy prior to the breeding season may unsuccessfully wean the current offspring, or wean an offspring that has a low probability of subsequent survival (e.g., Hall et al. 2001). In species where males compete for mates, returning to the breeding season in poor condition may result in a reduction of mating opportunities but such males may still obtain some matings by using alternate mating tactics (e.g., sneak matings) and thus the loss of fitness may be less dramatic than in females.

Sex differences in foraging behaviour among birds have been studied mainly during the breeding season (but see Williams 1980 and Morrison & With 1987). Among mammals, sex differences in the foraging behaviour of ungulates have been studied throughout the year (eg. Main *et al.* 1996; Ruckstuhl 1998; Barboza & Bowyer 2000) and have been interpreted in relation to size dimorphism and reproduction. Little is known about the sex differences in foraging behaviour of carnivorous marine mammals.

Although there is a considerable understanding of the allocation of time between foraging and reproduction during the breeding season in female pinnipeds (eg., Gobel *et al.* 1991; Bowen *et al.* 1999a; Arnould & Hindell 2001), few studies (and these deal with only one species, LeBoeuf *et al.* 1993, 2000) have examined the foraging behaviour of both males and females with sufficient sample size to examine sex differences prior to the breeding season (e.g., Folkow & Blix 1999).

Grey seals are a polygynous, size dimorphic species in the Family Phocidae, with males and females in the Northwest Atlantic population reaching lengths of up to 2.65 m and 2.20 m, respectively (McLaren 1993). Grey seals alternate periods of terrestrial fasting during moulting and breeding periods with foraging at sea. As a result of this life history strategy, individuals go through dramatic seasonal changes in body mass and composition, however adults males are approximately 1.5 times heavier than adult females throughout the year (Table 2.1).

Female grey seals use stored body energy accumulated over the previous 7-month period to support the high energetic cost of lactation and their own metabolic expenditures during the breeding season. Females with low body mass (and hence energy stores) at parturition tend to wean smaller pups or wean their pups pre-maturely (Iverson *et al.* 1993; Mellish *et al.* 1999; Pomeroy *et al.* 1999) increasing the probability of juvenile mortality (Coulson 1960; Coulson & Hickling 1964; Hall *et al.* 2001). Male grey seals use a variety of mating strategies ranging from tenure of several weeks on land to roving, in which males alternate short foraging trips to sea with attempts at mate acquisition on land (Boness & James 1979; Amos *et al.* 1993; Twiss *et al.* 1994; Lidgard *et al.* 2001). Despite these trips to sea, foraging by males is greatly reduced during the breeding period and individuals rely on energy stores accumulated during the foraging period to extend the period of time they can remain ashore competing for and acquiring mates. While the quantity of stored energy is important for this purpose, Godsell (1991) and Lidgard *et al.* (2001) found that for male grey seals on Sable Island, the correlation between body mass at the start of the breeding season and mating success is weak. Hence, reproductive success of males should be less dependent on the amount of stored body energy at the beginning of the breeding season than is the reproductive success of females.

The benefits associated with storing energy for reproduction are reasonably well understood (Chapin *et al.* 1990; Jonsson 1997). However there may be fitness costs associated with storing energy for long periods of time (Witter & Cuthill 1993; Gosler *et al.* 1995; Bonnet *et al.* 1998; Gentle & Gosler 2001). Such costs could include an increased risk of predation or increased cost of transport during diving. For example, studies on the effect of buoyancy on air-breathing aquatic foragers (Webb *et al.* 1998; Chapter 4) indicate that, at the level of individual dives, descent rate decreases as animals fatten. As a result, it takes animals longer to reach depth and they spend longer periods of time underwater (Chapter 4).

In this study, I investigated sex differences in the diving behaviour of adult grey seals, *Halichoerus grypus*, a species in which size dimorphism and a capital breeding strategy are expected to influence foraging behaviour prior to breeding. I hypothesized that both sexual size dimorphism and sex differences in the relative costs and benefits associated with acquiring energy for reproduction would be reflected in diving behaviour prior to reproduction. As the larger sex, males were expected to show higher levels of diving effort than females, assuming that diving is closely linked to foraging during this period. I also predicted that males and females would differ in their seasonal patterns of diving behaviour. Male and female grey seals are in the poorest condition following the spring moult (Chapter 5). Evidence from a variety of mammalian species indicate that females in poor condition are less likely to be pregnant or carry the pregnancy to term (Boyd 1984; Albon *et al.* 1986; Stewart *et al.* 1989; Cameron *et al.* 1993; Lunn & Boyd 1993; White *et al.* 1997; Pitcher *et al.* 1998). Therefore, female grey seals need to recover body condition quickly to support early pregnancy and to begin storing the body energy required to support the high energetic cost of lactation. On the other hand, I expected males to recover body condition more gradually, increasing energy storage only as the breeding season approaches. This is because the accumulation of body energy should be mediated by fitness costs associated with supporting increased body mass for long periods of time (Jonsson 1997). Although females will also have to deal with such costs, they may do so differently because the predicted reproductive benefit from early storage of body energy is higher for females than for males.

Methods

The study was carried out between May 1992 and January 2000 on Sable Island (43°55'N, 60°00'W), a crescent-shaped, partially vegetated sandbar approximately 300 km south-east of Halifax, Nova Scotia, Canada. Sable Island is the largest haul-out and breeding location for grey seals in the Northwest Atlantic population. Animals congregate in large numbers on the island in May and June to moult, in late December and January to rear offspring and mate, and in smaller numbers throughout the year between foraging trips.

Grey seals, of known age (8 - 27 yr.), were captured on-shore following the spring moult (May and June) or in the fall (late September and early October) using hand-held nets (Bowen *et al.* 1992). Seals were weighed to the nearest 0.5-kg on Salter spring balances suspended from an aluminum tripod and anesthetized using Telazol (equal parts of tiletamine and zolazepam) with males and females receiving an average dose of 0.45 mg kg^{-1} body mass and 0.90 mg kg^{-1} body mass, respectively (Bowen *et al.* 1999b). Beginning in 1995, dorsal standard length (DSL; McLaren 1993) was measured on all animals while anesthetized.

To study diving behaviour, time-depth recorders (TDRs) were secured to netting and then the netting was attached to the pelage of the anesthetized animals using a 5-min marine epoxy. TDRs were positioned between the shoulders along the dorsal midline of the individual. These instruments weighed between 65 and 300 g (< 0.3 % of animal's initial body mass) depending on the model used. In January, when animals returned to Sable Island for the breeding season, instrumented animals were recaptured to remove the data-loggers and then released. Beginning in January 1998, instrumented animals were also weighed at recapture.

Instrument Sampling

Various models of TDRs (Mk3e, Mk5, Mk 6 and Mk7 -Wildlife Computers, Richmond, Washington) were used to collect information on diving behaviour. TDRs recorded depth every 20 seconds and a wet/dry sensor was used to determine when the animal was hauled out on land. Most instruments were duty-cycled to prolong the memory and battery life over the deployment period. Depending on the duty cycle, between 33% and 100% of diving behaviour was sampled over the length of deployment (3 to 8 mon.).

Dive Analysis

Upon recovery, TDR data were processed using software supplied by the manufacturer (Wildlife Computers, Richmond, Washington). Initially, data were examined graphically (Strip Chart) to provide a visual representation of the diving pattern of each individual (Fig. 2.1). Zero-offset correction software was used to account for shifts in the calibration of the pressure transducer of the instrument over the data collection period. Dive analysis software was then used to analyze the corrected records and provide numerical descriptions of each dive (see Boness *et al.* 1994 for details).

Transducer drift introduces noise in depth measurements that cannot be completely removed by the zero-offset correction. Therefore, I excluded dives less than 5 m in depth from the analysis. Dives of longer than 30 minutes were also excluded from analysis as visual inspection of these long dives showed that they generally represented situations where two dives were not properly separated by the zero-offset correction software. These erroneous dive durations accounted for < 0.05% of the total number of dives sampled.

To examine the effects of age on diving behaviour, animals were assigned to one of three age classes (young: < 17 y, middle: 17 - 22 y, and old: > 22 y). Age classes

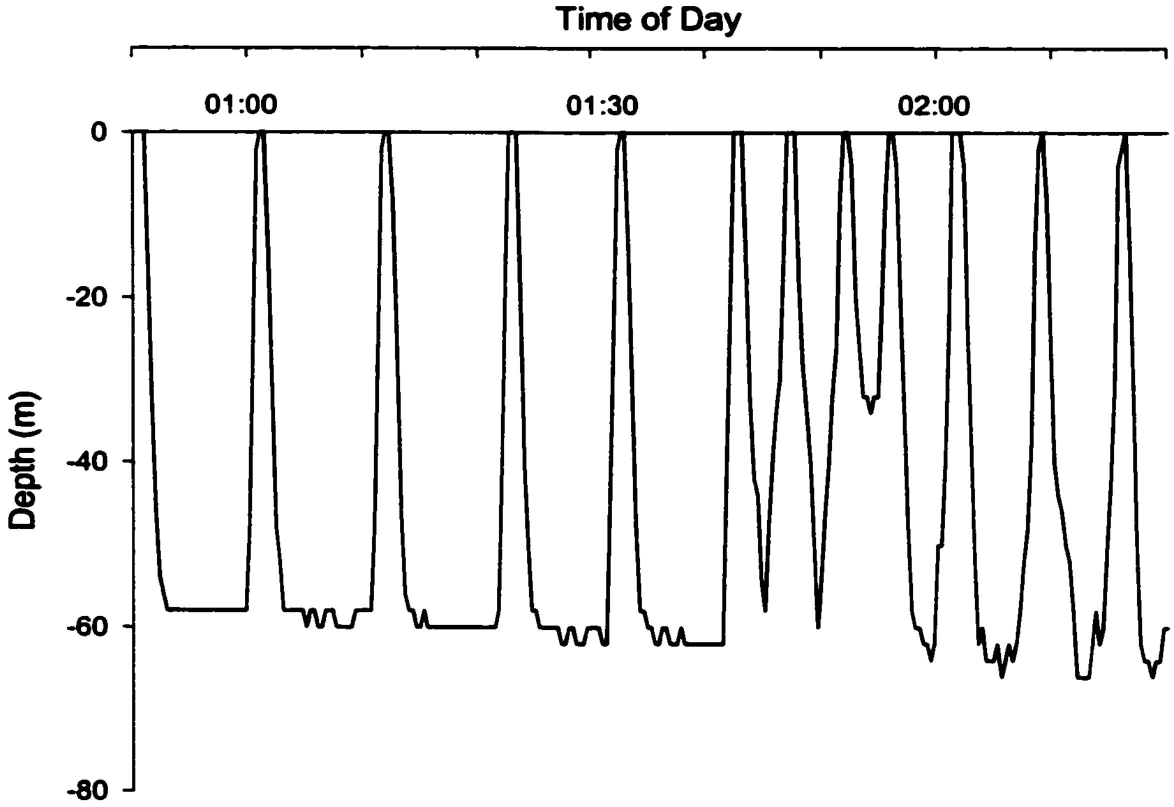


Figure 2.1. An illustration of individual grey seal dives over a period of 90 min.

represent the 33rd and 66th percentiles of age for all study animals. Similarly, seals were classified as one of three length classes (small: < 183.5 cm, medium: 183.5 - 208 cm, and large: > 208 cm) based on the 33rd and 66th percentile values of DSL to examine the effect of overall body size on diving behaviour.

Individual dive characteristics

Prior to analysis, dive variables were checked for normality and transformed if necessary. To examine seasonal changes in diving behaviour, data were averaged by month for each individual. Only individuals with dive data in > 3 months were used in the seasonal analysis. May was excluded from all seasonal analysis due to the small number of males sampled. Linear mixed-effects models (LME; S-Plus 4.5) were used to examine the effect of month, sex, and age on the individual dive characteristics of adult grey seals. This method uses maximum-likelihood parameter estimation. Given the nature of the data, I assumed an auto-regressive (i.e., AR1) variance-covariance matrix for the within-subject error terms. All possible models with two-way interactions were examined and all models were compared to the mean model: $y = \mu + \varepsilon$. Variables included in each model were entered simultaneously. To select the best predictive model, the five models with the lowest Akaike's information criterion (AIC) were compared using a log-likelihood ratio test. I used this approach, rather than relying only on the lowest AIC, due to the non-orthogonal nature of my data (i.e., not all animals were measured in each month). The explained variance was calculated using Cox & Snell's (1989, pp. 208-209) generalized coefficient of determination (R^2) modified to incorporate the effective degrees of freedom (Wade Blanchard, pers. comm.). Other statistical analyses were performed using SPSS 10.0.

Diurnal pattern of depth and duration distribution

To determine if male and female grey seals dived differently throughout the day, I compared the distribution of dive depth and duration during periods of light and darkness and during eight 3-h periods. The duration of light and darkness was determined daily based on the times of sunrise and sunset at Sable Island. Repeated-measures ANOVAs were used to examine whether the distribution of dive depth and duration differed between sex by light level. For this analysis dive depth was binned at 30-m intervals and dive duration by 2-min intervals. LME analysis (see above) was conducted on mean dive depth, mean duration and dive activity (% dives) to examine the effect of month, time period, sex and age-class on the diurnal distribution of these dive variables.

Dive Shape Classification

The shape of individual dives can be represented in 2-dimemsions as a function of time and depth. Different shapes are thought to represent different behaviours (Bengtson & Stewart 1992; Asaga *et al.* 1994; Crocker *et al.* 1994; Slip *et al.* 1994; Wilson *et al.* 1996; Martin *et al.* 1998; Lesage *et al.* 1999; Hochscheid *et al.* 1999). Dive shapes were classified using a combination of manual identification and discriminant function analysis (DFA) as described by Scheer & Testa (1996). Briefly, a random subset of 2000 dive profiles stratified by sex were individually inspected and classified as one of five shapes – square, wiggle, V, left-skewed square and right-skewed square. Discriminant functions were derived from this subset using the following dive variables: depth, duration, bottom time, bottom time/depth, rate of descent, rate of ascent and skew (ascent/descent). The presence or absence of wiggles (vertical movement at depth) was also used to classify individual dives. DFA correctly classified 96.1 % of the dives in the subset with a cross-validation error rate of 4.0%. The discriminant functions resulting from this analysis were used to classify the larger data set. Repeated measures MANOVA was used to examine the effect of month, year, sex and age on the distribution of dive shapes by individuals. Given our sampling rate of 20 seconds, dives of less than 1 minute were V-shape by definition. To avoid introducing a bias, all dives less than 1 minute were excluded from this analysis.

Dive Effort

Dive effort, measured as accumulated bottom time/day (ABT), was calculated from individual dive records as follows:

$$\mathrm{ABT} = \left[\left(\sum_{d=1}^{k} \mathrm{BT}\right)/60\right]/\mathrm{N} \qquad \text{Equation 1}$$

where BT is bottom time for individual dives (min), d and k are dive number and the number of dives recorded for each individual, respectively, and N is the number of days sampled. Thompson et al. (1991) indicated that adult grey seals spent approximately 60% of individual dives at or near the seabed feeding on demersal and benthic fish. Assuming that most foraging takes place during the "bottom time" of individual dives this was deemed the measure of dive effort most likely representative of foraging effort. LME models (as described above) were used to examine the influence of month, sex, and age-class on accumulated bottom time/day.

Results

As expected, adult male grey seals were significantly heavier and longer than adult females throughout the year (Fig. 2.2, Table 2.1). Rate of mass gain differed significantly between males and females with males having higher gain/day than females. Rate of gain by females did not differ between the two deployment periods (i.e. June-January vs. October-January, $t_{24} = 0.604$, $p = 0.559$). However, males had significantly higher rates of mass gain during the October-January period ($t_{26} = -3.346$, $p = 0.008$) compared to the June-January deployment period (Table 2.1). DSL ranged from 2.0 to 2.4 m in males and from 1.5 to 2.0 m in females. The mean age of study animals did not differ between sexes and all animals were sexually mature (Table 2.1).

Between spring 1992 and fall 1999, instruments were deployed on 140 adult grey seals (66 males, 74 females). Of these animals 111 (79.2%) returned to Sable Island the following January, however detailed dive data were obtained from only 95 individuals (46 males, 49 females) due to instrument loss or failure. On average, 10238 ± 768.5 dives were recorded from males and 9774 ± 622.9 dives from females, with a median sampling period of 189 and 142 days for males and females, respectively. There was no significant difference in the number of dives sampled in males and females ($t_{93} = 0.471$, $p = 0.639$).

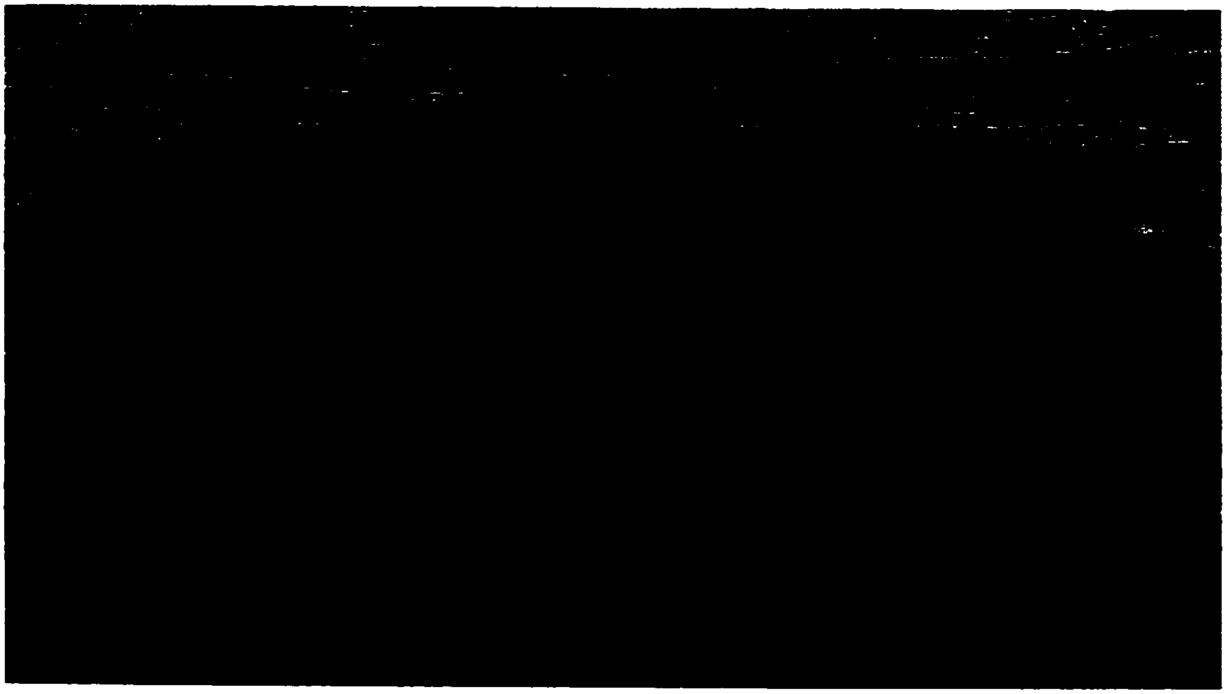


Figure 2.2: Male and female grey seal, *Halichoerus grypus*, on Sable Island, NS, Canada, illustrating the 1.5-fold greater body size of males than females in this population. Photo courtesy of W.D. Bowen.

Table 2.1. Age, body length and rate of mass gain in adult grey seals.

	Males				Females				t-test
	n	Mean	SE	CV	n	Mean	SE	CV	p-value
Age (years)	46	19	0.7	0.236	49	17	0.9	0.341	0.166
Length (m)	38	2.12	0.02	0.044	38	1.78	0.01	0.048	<0.001
Mass (kg)									
June	24	200.8	7.0	0.17	37	141.0	3.2	0.14	<0.001
October	14	227.4	6.6	0.11	16	167.0	5.0	0.12	<0.001
January	28	303.7	6.9	0.12	26	208.1	4.6	0.11	<0.001
Mass Gain (kg/d)									
June-January	19	0.47	0.03	0.25	16	0.34	0.03	0.34	0.002
October-January	9	0.76	0.08	0.33	10	0.39	0.08	0.61	0.005

Characteristics of individual dives

Overall, mean dive variables of males and females differed significantly (MANOVA: $F_{6,54} = 7.32$, $p < 0.001$, $n = 95$) with females diving longer and spending longer at the bottom of dives (Table 2.2) but diving shallower than males. Diving variables did not differ by age-class or year (MANOVA: age class: $F_{12,110} = 1.36$, $p = 0.197$; year: $F_{42,354} = 1.18$, $p = 0.219$) nor were there any significant interaction terms. Once the effect of sex had been removed, length-class had no significant effect on dive variables. Given that sex accounted for the variability seen between length-classes, length-class became a redundant factor and was removed from further analysis.

The maximum dive depths recorded for a male and female grey seal were 412 m and 354 m, respectively. Mean maximum dive depths differed by more than 30 m between males and females. However, this difference was not statistically significant ($t_{93} = 1.90$, $p = 0.061$, $n = 95$; Table 2.2.). Mean maximum dive duration and maximum bottom time also did not differ significantly between males and females (Table 2.2).

Seasonal changes were evident in three of the six dive variables: duration, bottom time, and rate of descent. For all three of these dive variables, the sex and age of individuals influenced the observed seasonal pattern of behaviour. The best predictive models for duration ($R^2 = 0.184$) and bottom time ($R^2 = 0.255$) included a quadratic month term, sex and age-class. There was also a significant interaction between the quadratic month effect and sex for dive duration (Table 2.3). In both males and females, dive duration (Fig. 2.3a) and bottom time (Fig. 2.3b) steadily increased from June through September and then decreased from October through January. From June through September, males and females did not differ significantly in their dive durations

Table 2.2. Dive characteristics of adult grey seals.

	Males, n = 46			Females, n = 49			t-test
Dive Variables	Mean	SE	CV	Mean	SE	CV	p-values
Depth (m)	57	1.7	0.201	49	2.1	0.299	0.009
Duration (min)	4.9	0.09	0.129	5.5	0.15	0.188	0.002
Bottom Time (min)	2.7	0.08	0.196	3.4	0.12	0.246	< 0.001
Surface time (min)	2.2	0.12	0.367	2.4	0.17	0.505	0.350
Descent rate (m/s)	1.0	0.03	0.232	1.0	0.04	0.313	0.242
Ascent rate (m/s)	-0.8	0.03	-0.218	-0.9	0.05	-0.413	0.265
Max Depth (m)	252	12.9	0.349	219	11.6	0.370	0.061
Max Duration (min)	20.3	1.05	0.352	22.0	0.75	0.240	0.179
Max Bottom Time (min)	16.2	0.94	0.395	17.8	0.74	0.290	0.175

Table 2.3. Results of Linear Mixed Effects Analysis on individual dive variables.

Dive Variable (n)	Source	Coefficient	SE	z	p	df	Pseudo R^2
Depth (87)	Constant	63.54	4.73	13.446	<0.001		
	Sex	- 8.25	2.95	-2.792	0.003	85	0.023
Duration (87)	Constant	-1.70	1.26	-1.349	0.089		
	Month	1.71	0.23	7.374	<0.001	409	
	Month^2	-0.09	0.01	-7.247	<0.001	409	
	Sex	-0.27	0.46	-0.625	0.268	85	
	Ageclass	-0.74	0.36	-2.079	0.019	84	
	Month^2 x Sex	0.40	0.21	1.862	0.031	71	0.184
Bottom time (87)	Constant	-4.20	0.92	-4.563	<0.001		
	Month	1.52	0.20	7.777	<0.001	409	
	Month^2	-0.08	0.01	-7.676	<0.001	409	
	Sex	0.63	0.14	4.519	<0.001	85	
	Ageclass	-0.23	0.08	-2.806	0.003	84	0.255
Surface interval (87)	Constant	0.74	0.06	12.063	<0.001		

Table 2.3. continued

Dive Variable (n)	Source	Coefficient	SE	z	p	df	Pseudo R^2
Descent rate (85*)	Constant	1.59	0.17	9.300	<0.001		
	Month	-0.05	0.02	-2.997	0.001	397	
	Sex	-0.27	0.11	-2.597	0.005	83	
	Ageclass	-0.04	0.02	-2.022	0.022	82	
	Month x Sex	0.02	0.01	1.918	0.028	389	0.087
Ascent rate (83*)	Constant	-0.78	0.02	-50.46	<0.001		

* outliers removed prior to analysis

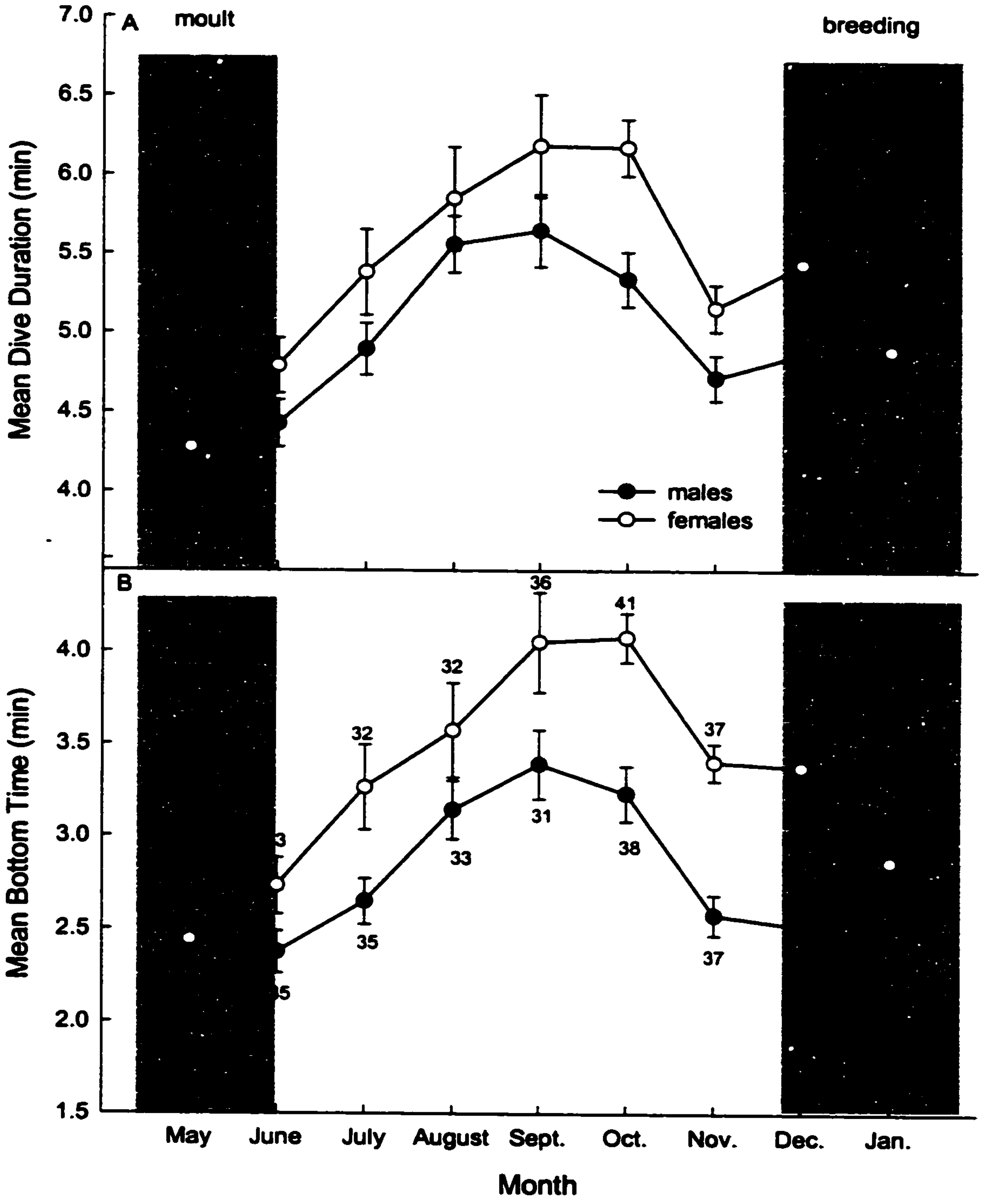


Figure 2.3: Seasonal changes in (A) duration (min) and (B) bottom time (min) of dives by male and female grey seals. Values are means ± 1 SE. Numbers above or below each mean represent sample size (i.e., number of individuals) in each month and are the same for both panels. May was not included in statistical analyses since only one male was sampled.

or in the amount of time spent at the bottom of the dive. However, from October through December females spent significantly more time at the bottom of dives than males. Young seals had longer dives (5.5 min vs. 5.2 min) and spent more time at the bottom of dives (3.5 min vs. 3.0 min) than the two older age-classes throughout the foraging period ($P< 0.02$, Table 2.3).

Seasonal changes also were observed in the rate at which individuals descended to depth. However, the best model explained only 8.7% of the variability in descent rate (Table 2.3). Overall descent rate decreased from a peak of 0.98 ± 0.04 m/s in July to 0.66 ± 0.05 m/s in January. However, this seasonal pattern was generated by changes in male behaviour alone. From June to September males had faster rates of descent than females, but from October to January descent rates were similar for both sexes as indicated by the significant month/sex interaction term (Table 2.3). Age class also had a significant effect on descent rate with older animals descending to depth more slowly (0.88 m/s) than middle and young age-classes (1.01 m/s).

Rate of ascent and time spent at the surface between dives did not differ by season, sex or age class. Of the factors investigated, only sex explained a significant, although small ($R^2 = 0.023$), fraction of the variability in dive depth.

Diurnal patterns of dive depth and duration

Diurnal patterns of diving differed between males and females and by month. Males distributed their dive activity evenly throughout the day (Fig. 2.4). In contrast,

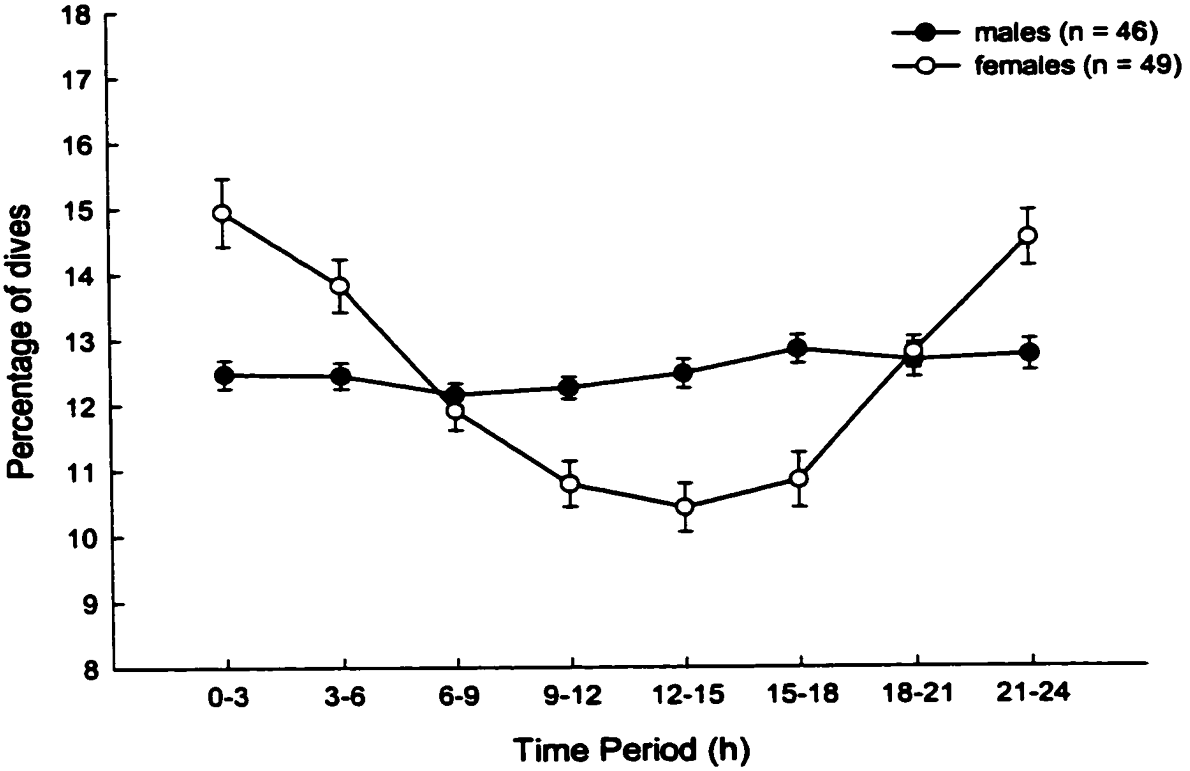


Figure 2.4. Diurnal pattern of dive activity by male and female grey seals. Values are means ± 1 SE of the percentage of total dives that occurred during each time period.

females showed increased dive activity between 1800 h and 600 h local time, with a corresponding decrease in activity during mid-day. This pattern of dive activity was relatively consistent during the 7-month foraging period. However, there were slight changes in the magnitude of the sex differences by month. The best predictive model of the diurnal pattern of diving activity (number of dives) included month, sex, and quadratic time-period factors as well as month x time-period and month x sex interactions (Table 2.4).

Overall, 95.9 ± 0.60 % of dives by adult grey seals were less than 120 m. However, the distribution of dive depths differed between periods of light and darkness (Repeated measures: $F_{7,87} = 16.566$, $p < 0.001$). At night, 73.9 % of dives were < 60 m, whereas only 59.4% of daytime dives were < 60 m. This difference was generated by the behaviour of females alone. During the day females dived significantly more often to depths between 90 and 150 m, whereas at night dives were concentrated in shallower depths. The depth distribution of male dives was similar during light and dark periods.

Mean dive depth varied with time of day and sex. The best model included a quadratic time-period term, sex and an interaction term (Table 2.4). Season was not a significant factor. Male grey seals dived deeper than females during the night and early morning periods. However, depth was similar between males and females from mid-day to evening periods. Both sexes showed the deepest diving during the mid-day period.

Dive duration by individuals was similarly skewed with 90.8 ± 0.79% of dives being less than 8 min. As with depth, the distribution of dive duration differed between light and dark periods and between sexes (Repeat Measures: $F_{7,87} = 3.409$, $p = 0.003$).

Table 2.4. Results of Linear Mixed-Effects Analysis on Diurnal Patterns of Dive Variables.

Diurnal Patterns (n)	Source	Coefficient	SE	z	p	df	Pseudo R^2
Dive activity (87)	Constant	14.249	0.819	17.394	<0.001		
	Month	0.300	0.078	3.845	0.001	3815	
	Sex	1.162	0.532	2.128	0.017	85	
	Time Period	-2.393	0.202	-11.845	<0.001	3814	
	Time Period^2	0.312	0.030	10.432	<0.001	3814	
	Month x Period^2	-0.118	0.056	- 2.110	0.017	3766	
	Month x Sex	-0.005	0.002	- 2.576	0.005	3808	0.054
Dive Depth (87)	Constant	6.206	0.124	50.145	<0.001		
	Sex	-0.359	0.109	- 3.301	<0.001	85	
	Time Period	0.526	0.036	14.561	<0.001	3814	
	Time Period^2	-0.059	0.004	-15.031	<0.001	3814	
	Sex x Period^2	0.002	0.001	2.562	0.005	3806	0.268

Table 2.4 continured

Diurnal Patterns (n)	Source	Coefficient	SE	z	p	df	Pseudo R^2
Dive Duration (87)	Constant	0.538	0.190	2.835	0.002		
	Month	0.373	0.041	9.121	<0.001	3815	
	Month^2	-0.020	0.002	-9.159	<0.001	3815	
	Sex	0.051	0.021	2.390	0.008	85	
	Time Period	0.044	0.009	5.088	<0.001	3814	
	Time Period^2	-0.004	0.001	-3.968	<0.001	3814	
	Month x Period^2	-0.00001	5×10^{-6}	-2.127	0.015	3766	
	Sex x Period^2	0.0003	2×10^{-4}	2.031	0.021	3806	0.105

Female behaviour generated most of the difference between light and dark periods with dives being of shorter duration at night (71.1% < 6 min) and longer during the daytime (63.8% < 6 min). The distribution of dive duration of males was similar throughout the day.

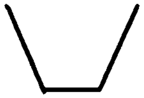
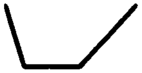
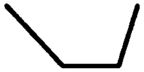
The diurnal pattern in dive duration was best described by a model that included sex and quadratic month and time-period effects. However, there were significant month x time-period and sex x time-period interactions. Females dived longer than males during the day, but had similar dive durations at night. The magnitude of these sex differences in diurnal patterns of dive duration varied by month, being most evident in September and November and less prominent in the early summer.

Dive Shape

One of five shapes was assigned to the 923,477 dives from 95 individuals (Table 2.5). Square dives were the most common, relatively deep and of medium duration (Table 2.5). Right-skewed square dives were the second most common shape. These dives were also deep and of medium duration, however right-skewed dives had faster rates of descent than of ascent (Table 2.5). Left-skewed dives were shallow, of medium duration, and had slower rates of descent than of ascent. V-shaped dives were also shallow and of short duration, with no significant amount of time spent at depth. Finally, wiggle dives tended to be deep and long relative to other dive types and were characterized by vertical movement at depth.

The distribution of dive shapes was significantly different between males and females (Repeated measures MANOVA: $F_{3,92} = 6.566$, $p < 0.001$, $n = 95$).

Table 2.5. Characteristics of shapes assigned to dives by 95 grey seals.

Dive Shape	Profile	% of dives	Depth (m)	Duration (min)	Bottom Time (min)	Descent Rate (m/s)	Ascent Rate (m/s)	Skew Ratio Ascent/Descent
Square		68.2 ± 1.70	62 ± 3.5	5.5 ± 0.86	3.3 ± 0.07	1.0 ± 0.03	0.9 ± 0.04	0.96 ± 0.132
Right Skewed Square		14.2 ± 1.08	53 ± 3.9	5.4 ± 0.12	3.0 ± 0.09	1.5 ± 0.05	0.6 ± 0.02	0.41 ± 0.004
Left Skewed Square		7.0 ± 0.59	32 ± 1.7	5.2 ± 0.07	3.0 ± 0.06	0.4 ± 0.05	1.2 ± 0.12	3.65 ± .117
V-shape		5.7 ± 0.70	26 ± 1.1	3.3 ± 0.13	0.1 ± 0.03	0.5 ± 005	0.7 ± 0.11	3.19 ± 0.467
Wiggle		5.0 ± 0.70	57 ± 1.6	6.8 ± 0.23	4.4 ± 0.20	1.0 ± 0.04	0.9 ± 0.08	1.43 ± 0.108

Females had a significantly higher proportion of left-skewed dives than males (t_{94} = -3.426, p = 0.001), whereas males had a significantly higher proportion of right-skewed square dives (t_{94} = 2.441, p = 0.016). The proportion of square, wiggle and v-shape dives did not differ between males and females (t_{94} = -0.610, -0980, and 1.895, p = 0.543, 0.329 and 0.061, respectively). Dive shape distribution also did not differ between age classes ($F_{6,178}$ = 1.402, p = 0.209, n = 95) or by year ($F_{12,213}$ = 1.516, p = 0.120).

Dive shapes used by grey seals changed seasonally in a non-linear pattern ($F_{18,30}$ = 7.274, p < 0.001, n = 49; Fig. 2.5). There was a significant decrease in the proportion of square dives from June to August and then a significant increase from October through December followed by a significant decrease in January. The proportion of V-shaped dives increased 1.8 % in December compared to the previous month and was compensated for by a decrease in the proportion of square dives. January was not included in the above repeated measures analysis due to reduced sample size (n = 30). However, there was a sharp increase in the proportion of v-shape (6.0 ± 0.58% to 16.3 ± 3.75%) and left skewed (6.1 ± 0.64% to 12.1 ± 2.29%) dives from December to January with a corresponding decrease in square dives (74.3 ± 1.59% to 57.9 ± 4.71%; Fig. 2.5).

The seasonal change in dive shape distribution did not differ among age classes ($F_{36,60}$ = 1.299, p = 0.182, n = 49). There was also no statistically significant difference between males and females ($F_{18,30}$ = 1.581, p = 0.130, n = 49) in the pattern of seasonal change from June to December. I re-examined sex as a factor using a larger sample where months were grouped into two periods (June - September, n = 61 and October-December, n = 71). Using this larger sample, dive shape distribution did not differ during the June- September period ($F_{9,51}$ = 1.706, p = 0.112, n = 61), but males used

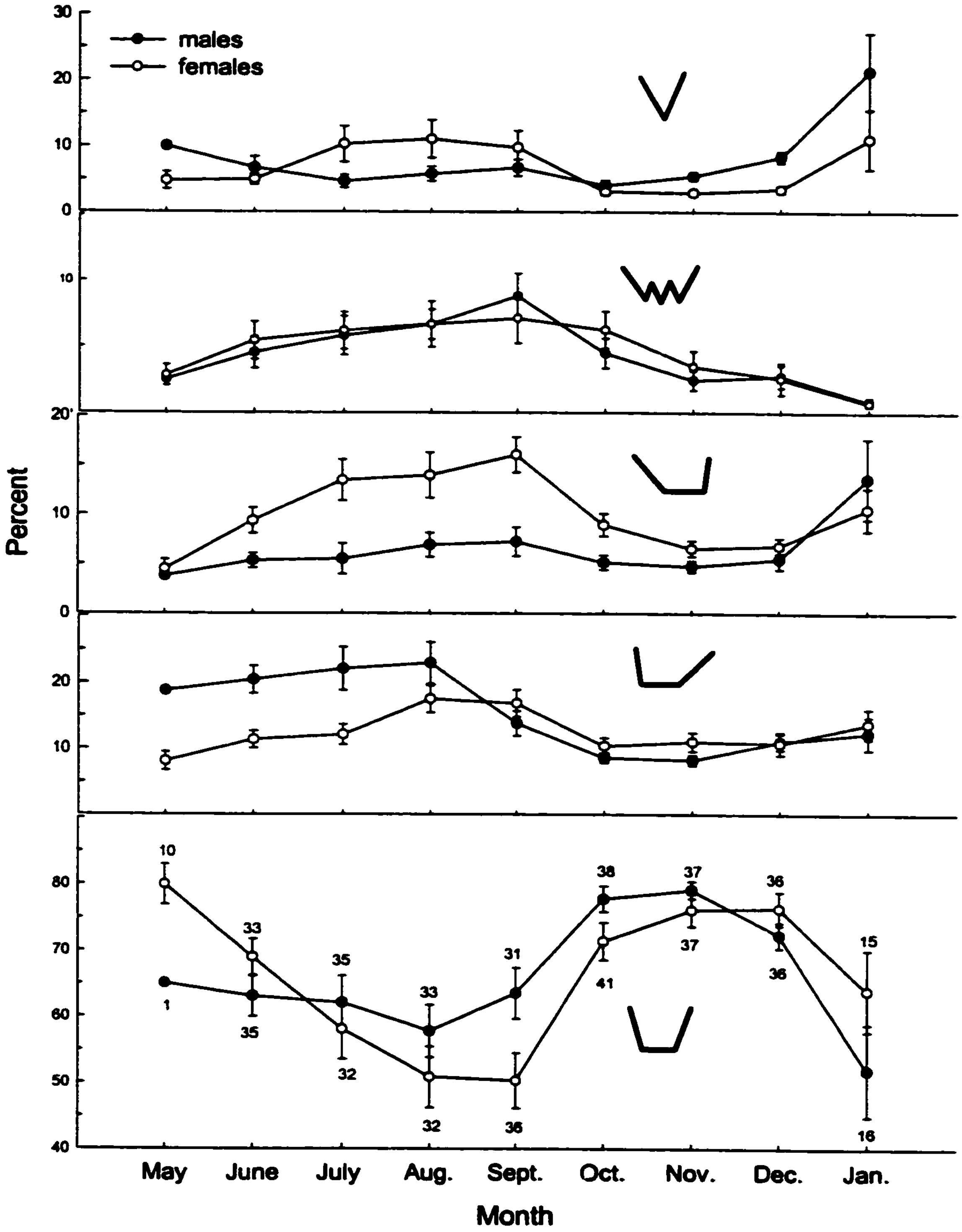


Figure 2.5. Seasonal changes in the percentage of dive shapes used by male and female grey seals. Shape profiles are indicated in each panel. Values are means ± 1 SE. Numbers above or below each mean in the bottom panel indicate the number of animals sampled in each month and are the same for all panels. May was not included in statistical analyses since only one male was sampled.

a greater proportion of V-shape dives and a reduced proportion of square dives during the October to December period ($F_{6,64} = 4.848$, $p < 0.001$, $n = 71$). Among females, there was a decrease in wiggle dives and a corresponding increase in square dives during this latter period.

Dive Effort

Dive effort differed significantly between males and females. Overall, females spent 7.69 h/day at depth compared to the 6.47 h/day spent at depth by males ($t_{93} = -3.421$, $p = 0.001$). Accumulated bottom time/day also differed by month and there was a significant month x sex interaction (Fig 2.6, Table 2.6). The best model for accumulated bottom time ($R^2 = 0.517$; Fig. 2.6) included a cubic month term, sex and a month-sex interaction. Age-class had no effect on seasonal patterns of dive effort.

Discussion

My findings demonstrate sex differences in diving behaviour of adult grey seals. These differences occurred at the level of individual dives (e.g., duration, shape), diurnal patterns and dive effort. The most prominent feature of these differences was the sex-specific seasonal pattern in diving behaviour, suggesting that males and females have different long-term foraging strategies. I interpret these sex differences in the seasonal pattern of diving as evidence that males and females make different foraging decisions as a result of sex-specific costs and benefits associated with storing energy for reproduction.

Given that adult grey seal males are about 1.5 times heavier than adult females throughout the year and that males likely require 1.3 times more energy than females

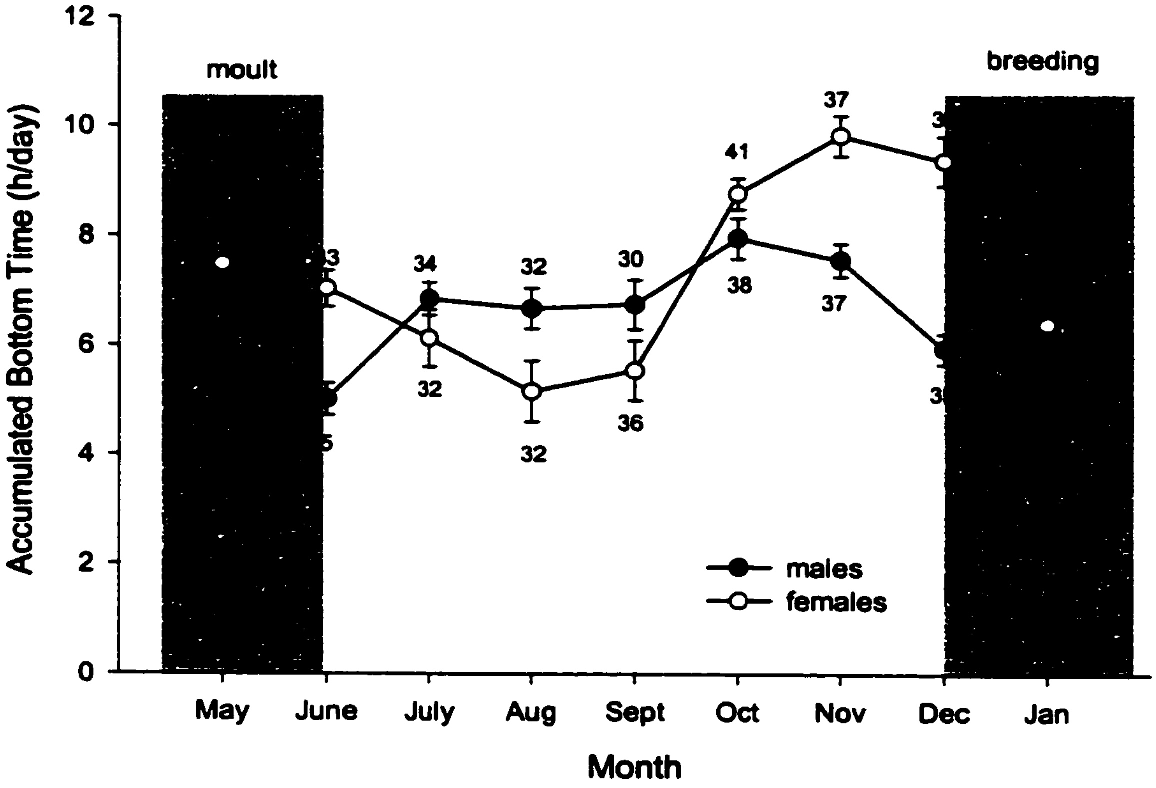


Figure 2.6. Seasonal changes in accumulated bottom time (h/day). Values are means ± 1 SE. Numbers above or below each mean indicate the number of individuals sampled in each month. May was not included in statistical analyses since only one male was sampled.

Table 2.6. Results of Linear Mixed Effects Analysis on Dive Effort

Dive Effort	Source	Coefficient	SE	z-score	p-value	df	Pseudo R^2
Accumulated Bottom Time (h/day)	Constant	35.38	5.829	6.069	<0.001		
N=87	Month	-10.53	1.996	-5.274	<0.001	409	
	Month^2	1.23	0.221	5.592	<0.001	409	
	Month^3	- 0.05	0.007	-5.845	<0.001	409	
	Sex	0.06	0.294	0.208	0.417	85	
	Month^3 x Sex	0.0005	0.0001	4.307	<0.001	401	0.517

(Mohn & Bowen 1996), sex differences in the diving behaviour of adult grey seals were expected. However, the direction of the observed differences was contrary to that predicted based on size dimorphism, with males showing less overall dive effort, having shorter dives and spending less time at depth than females. Two possible explanations for this inconsistency are that males are more efficient predators (i.e., higher energy intake/unit time) than females or are less selective when searching for prey. As mass-specific energy requirements decrease with body mass while gut capacity scales isometrically, larger males should have the ability to digest lower quality foods than females, thus being less selective foragers (Mysterud 2000). As a result, in size dimorphic herbivore species, males are more efficient, spending less time foraging than females despite their larger size and absolute energy requirement (e.g., Ginnett & Demment 1997; Ruckstuhl 1998; Pérez-Barberia & Gordon 1999). These scaling relationships imply that grey seal males should have a higher ratio of gut capacity to metabolic requirement than females and as such could be more efficient than females. Females, with a lower gut capacity/metabolic requirement ratio may be more selective and search for higher quality prey types, thus having longer dives and spending more time at the bottom of dives. Males may also be more efficient if their larger size allows them to more easily capture and handle larger prey than females.

Sexual size dimorphism in grey seals does not explain the sex-specific seasonal patterns of diving behaviour seen in this study. Satellite telemetry data from adult males and females in this population indicate that there is a broad overlap in their foraging areas (unpublished data, D.A. Austin, W.D. Bowen, C.A. Beck & J.I. McMillan). Thus, males and females should be affected by the same seasonal changes in environmental conditions and prey availability. Rather I suggest that seasonal differences in the diving behaviour of males and females can be better explained by the sex differences in the ratio between the costs of transporting stored body energy and the benefit of having stored that energy for reproduction. This argument is similar to the "reproductive-strategy hypothesis" used to explain the ecological segregation of male and females in size dimorphic ungulate species (Main et al. 1996; Mysterud 2000).

Female grey seals have a lower cost/benefit ratio for stored body energy than do males because the reproductive benefit of having sufficient stores at parturition is greater than the reproductive benefit to a male's mating success and likely has greater consequences for a female's fitness. Coulson (1960) and Hall *et al.* (2001) showed that undersized grey seal pups have lower survival probability than average or above average sized pups at weaning. Female size and milk energy output are the best predictor of weaning mass in grey seals (Iverson *et al.* 1993; Mellish *et al.* 1999), emphasizing the importance of maternal energy storage to offspring survival and female fitness. In contrast, mating success in male grey seals is likely to be more flexible with respect to body energy reserves and as a result is more variable (Anderson & Fedak 1987; Godsell 1991; Lidgard *et al.* 2001). Age, body mass, operational sex ratio and length of stay within a breeding colony all influence the reproductive success of grey seal males (Boness & James 1979; Godsell 1991; Twiss *et al.* 1994; Lidgard *et al.* 2001). In addition, a recent study has shown that some males take short foraging trips during the breeding season presumably to supplement energy stores (Lidgard *et al.* 2001). Therefore, female reproductive success is much more dependent on energy stores available at the start of the breeding season than is male mating success.

Immediately following the spring moult females exhibited high levels of dive effort in which approximately 80% of all dives were square shaped (Fig 2.5 & 2.6). Maternal condition has an important influence on early fetal development in grey seals, with females in poorer condition implanting later than females in better condition (Boyd 1984). Thus, females need to recover body condition quickly to ensure maintenance of pregnancy. Given that this early recovery of body condition is not required in males, it is not surprising that females out-dived males in the first two months following the moult (Fig. 2.6). Support for this hypothesis comes from seasonal changes in sternal blubber thickness from this population, which shows that blubber thickness in females increases at a faster rate than in males following the moult (Brian Beck, pers. comm.).

During the late summer and early fall female grey seals reduced their dive effort and the proportion of square shaped dives. This reduction may indicate that females are simply maintaining body condition during this period. Given that there are likely costs associated with the accumulation and maintenance of stored body energy over long periods of time (J nsson 1997), females may not benefit from further accumulation of energy stores during this period. These costs could include increased metabolic costs associated with maintaining and transporting additional body mass (Jonsson 1997) including an increased cost of transport during the descent phase of dives due to increases in buoyancy (Webb *et al.* 1998; Chapter 4). Increased dive effort in the months immediately prior to parturition would suggest that the benefit of additional accumulation of body energy over the period just prior to parturition outweigh those costs.

The seasonal pattern of diving behaviour and effort observed among male grey seals was less dynamic than that observed among females. This was also reflected in a more constant use of square shaped dives throughout the spring and summer relative to females. Following the moult, male dive effort increased gradually, reaching a peak in late fall and declining just prior to the breeding season. Rate of mass gain was significantly lower in males measured over the June - January period (0.47 ± 0.03 kg/d) compared to males sampled over the second half of the foraging period (October - January; 0.76 ± 0.08 kg/d). This suggests that in males, the majority of stored body energy for reproduction is accumulated during the last 3 months of the foraging period. Given the less certain reproductive pay-off in males associated with energy stores (see above), the costs associated with storage and transportation of extra body mass throughout the entire 7-month foraging period may outweigh the benefit of early accumulation of stored energy to fitness. Although males did exhibit a decline in dive effort just prior to the breeding season, this may reflect increased travel as males return to the breeding colony. An increase in the proportion of V-shape dives used by males during December and January support this hypothesis (Fig. 2.5). V-shaped dives are generally thought to represent travel in other diving species although direct evidence is still needed to confirm this (Fedak & Thompson 1993; Asaga *et al.* 1994; Slip *et al.* 1994; Martin *et al.* 1998; LeBoeuf *et al.* 2000).

Males and females also differed in their diurnal patterns of diving (Fig 2.4). However in this respect, season accounted for little of the observed differences between males and females. These diurnal patterns were reflected in the dive activity, distribution of dive depths and durations. Without additional information it is difficult to interpret these differences. However, they could indicate that males and females were feeding on different prey types or using different tactics on similar prey. Diurnal patterns of dive depth have been observed in another phocid species, the northern elephant seal, *Mirounga augustrioustris*. In this species, it is thought that males forage on demersal prey whereas females forage on vertically migrating pelagic prey (LeBeouf *et al.* 2000).

Sex differences in the foraging behaviour of birds and mammals have also been explained by the need to reduce intra-specific competition. Males and females may forage in different locations (Schoener 1969; Clarke *et al.* 1998), on different prey (Hughes 1980; Williams 1980) or at different times within the same habitat. However, as stated above, male and female grey seals do not appear to forage in different locations. The estimated diet of grey seals from this population is based on fecal collections (Bowen & Harrison 1994) from individuals of unknown sex. Nevertheless, Bowen & Harrison (1994) showed that a single species, northern sandlance (*Ammodytes dubius*), comprised between 50 and 85% of the diet by weight depending on the time of year. Given the dominance of a single prey, it seems unlikely that males and females have significantly different diets, but this remains a possibility that should be examined more closely. For example, sex differences in the diurnal patterns of diving (Fig. 2.4) suggest that females may be consuming a higher proportion of vertically migrating prey than males. Although I think it unlikely that males and females show seasonal differences in foraging behaviour to reduce intra-specific competition, I cannot exclude this hypothesis.

The only other pinniped species for which sex differences in diving behaviour has been studied with significant sample size outside of the breeding season are northern and southern elephant seals, *Mirounga leonina* (LeBeouf *et al.* 1993, 2000; Slip *et al.* 1994). Both species exhibit extreme sexual size dimorphism with males being 1.5 to 10 times larger than females (LeBoeuf *et al.* 1993). As in our study, female southern elephant seals had longer dive durations compared to males following the moulting period (Slip *et al.* 1994). Among northern elephant seals, males and females have similar dive durations and spent a similar amount of time submerged per day despite the larger body size and energy requirements of males (LeBoeuf *et al.* 1993). In the less dimorphic harbour seal, *Phoca vitulina*, males have longer dives than females during the breeding season (Coltman *et al.* 1997; Bowen *et al.* 1999a), however female diving may be constrained by the diving ability of her pup during this period.

An unexpected finding in my study was the effect of age on diving behaviour, given that all seals studied were adults ranging in age from 8 to 27 years. Younger adults (mainly 8-14 years old) had longer dives and spent more time at depth than older animals (> 17 years). However, there were no differences between the two older age classes. As these young adults are still growing (McLaren 1993), this difference in behaviour may reflect the need for greater energy intake to account for metabolic rate and growth. It is also possible that foraging ability continues to develop over many years. Comparable data from other marine mammal species are rare. In northern elephant seals, age had no influence on dive depth or duration in animals over the age of 2 years (LeBoeuf 1994). In ringed seals, *Phoca hispida*, age had no influence on diving behaviour, but only 10 adults were studied (Kelly & Wartzok 1996).

Size dimorphism may account for some of the differences observed in the diving behaviour of males and females (e.g., dive depth and duration). However, I suggest that seasonal differences in diving behaviour result from sex differences in the costs and benefits associated with long-term energy storage for reproduction. The pattern of diving behaviour used by females appears more risk-averse with high levels of diving and presumably foraging effort occurring earlier than in males. This risk-aversion is likely due to the higher importance of stored body energy for reproduction (McNamara *et al.* 1991). In contrast, males appear to have adopted a less risk-averse pattern due to lower reproductive cost. Additionally, males appear to be more efficient in terms of energy intake/time and therefore may be less sensitive to environmental variation than are females. One test of this hypothesis would be to study the diving behaviour of juvenile grey seals. Given that juveniles are not storing energy for reproduction I would not expect a sex-season interaction in diving behaviour or effort. It will also be important to compare the diets of males and females to further test alternative explanations for sex differences in diving behaviour.

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Chapter 3: Sex differences in diving behaviour at multiple temporal scales in a marine predator: the grey seal

Introduction

Foraging decisions of individuals are influenced, and in some cases constrained, by a variety of factors including prey patchiness and abundance, current physical state, risk of predation, and reproductive status (e.g., provisioning offspring). As a result, predators may make foraging decisions at varying spatial and temporal scales to maximize energy intake and ultimately fitness (Clutton-Brock *et al.* 1982; Allan & Hoekstra 1992). Although our general understanding of the foraging behaviour of aquatic predators has increased, our understanding of the scales of foraging remains limited (Boyd 1996). Recent studies show that temporal variation in foraging behaviour can be used to gain insight into both the temporal and spatial scales of foraging (Boyd 1996; Mangel & Adler 1994).

Air-breathing aquatic predators (marine mammals, seabirds and reptiles) are a particularly interesting group in which to examine temporal scales of foraging. In addition to having to deal with prey that are patchily distributed and temporally variable, scales of foraging may be further constrained by oxygen stores during diving (Kramer 1988). Thus, these predators must make foraging decisions at several temporal scales. At the smallest scale (an individual dive), animals make decisions about how long and deep to dive, how fast to swim, and about how much time to spend at depth and at the surface between dives. These decisions may be influenced by the predator's aerobic dive limit (Kramer 1988; Houston & Carbone 1992; Castellini & Kooyman 1989), foraging tactics (i.e., ambush vs. search & pursue predator; Hughes 1980), sex (Chapter 2) and by the anti-predator behaviour of prey (e.g., benthic vs. pelagic; Feldkamp *et al.* 1989). At a larger temporal scale, pinnipeds and seabirds make foraging trips (defined as the period between going from land to sea and returning to land). Decisions about the duration and timing of foraging trips depend on the predator's physical state, energetic requirements, the distance to a food source, and the abundance and patchiness of prey (Gentry & Kooyman 1986; Boyd *et al.* 1994; Merrick & Loughlin 1997; Thompson *et al.* 1998; Hull *et al.* 1997; Kirkwood & Robertson 1997). Trip duration during the breeding season should also reflect constraints such as the need to provision offspring at a central place and the fasting ability of offspring (Gentry & Kooyman 1986; Hull *et al.* 1997; Weimerskirch & Lys 2000).

Within foraging trips, several pinniped and seabird species cluster individual dives into bouts of activity (e.g., Boyd *et al.* 1994; Boness *et al.* 1994; Watanuki *et al.* 1996; Mori 1997). In otariid pinnipeds and seabirds, it is reasonably assumed that dive bouts represent periods of foraging and that the duration of a bout, as well as other characteristics, reflects the quality and size of a prey patch (Feldkamp *et al.* 1989; Boyd 1996). This is because otariids are known to travel at the surface between bouts of diving and seabirds fly between foraging locations. Boyd (1996) found that in Antarctic fur seals, *Arctocephalus gazella*, surface intervals between bouts could be used to distinguish two scales of spatial distribution in prey. Short intervals between bouts were suggested to reflect the fine scale distribution of krill, *Euphausia superba*, within a prey patch, whereas longer inter-bout surface intervals are consistent with the predator travelling between prey patches (Boyd 1996). Although it is clear that many phocid pinniped species also organize their diving behaviour into bouts (Boness *et al.* 1994; Nordoy *et al.*

1995; Kelly & Wartzok 1996; Bengtson & Stewart 1992), telemetry data have shown that phocid seals do not travel at the surface to any significant degree. Therefore, unlike otariids and seabirds, bouts of diving in phocids are used both to forage and travel (Thompson *et al.* 1991; Asaga *et al.* 1994; Schreer & Testa 1996). As a result, it may be more difficult to identify spatial scales of foraging from the temporal pattern of diving behaviour in these species. Nevertheless, the temporal pattern and characteristics of bouts should still provide insight into how males and females forage, as much of diving behaviour is necessarily associated with this activity.

Studies examining the organization of diving behaviour at the level of bouts within foraging trips have generally been limited to foraging during the breeding season. In the case of pinnipeds, such studies have focused on female otariids that alternate regular foraging trips to sea with periods on land to suckle their offspring (Gentry & Kooyman 1986; Boyd & Croxall 1992, Boyd *et al.* 1994, Boyd 1996; McCafferty *et al.* 1998; but see Boness *et al.* 1994). Among seabirds, bout characteristics of both males and females have been examined during the period in which parents are provisioning offspring (Williams *et al.* 1992; Watanuki *et al.* 1993; Watanuki *et al.* 1996; Mori 1997; Jodice & Collopy 1999). However, the foraging behaviour of adults may differ when not provisioning or otherwise caring for offspring and therefore studies during the non-breeding season are needed to fully understand differences in foraging strategies.

In this study, I examined how male and female grey seals, *Halichoerus grypus* (Family Phocidae), organize bouts of diving behaviour during the 7-month, pre-breeding foraging period when adults are not constrained to a central place. The grey seal is a polygynous, size-dimorphic species, with adult males being approximately 1.5 times heavier than adult females in the Northwest Atlantic population (Mohn & Bowen 1996). Males and females differ in their seasonal pattern of diving behaviour when measured at the level of individual dives (Chapter 2). However, these differences could not be explained by the difference in the body size of males and females, but rather appeared to reflect sex-specific differences in the costs and benefits of storing body energy for reproduction. By examining diving behaviour at the larger temporal scales of bouts and foraging trips, I hoped to gain further insight into the sex differences in grey seal diving behaviour and the causes underlying these differences. Inter-annual variation in bout characteristics of lactating Antarctic fur seals has been linked to changes in the availability and distribution of prey species (Boyd 1996). Therefore, I also investigated how the bout characteristics of grey seals responded to environmental variability over the 7 years of the study.

Methods

The study was carried out between May 1993 and January 2000 on Sable Island (43°55'N, 60°00'W), a partially vegetated sandbar approximately 300 km southeast of Halifax, Nova Scotia, Canada. This site is the largest haul-out location for grey seals in the Northwest Atlantic population. Animals congregate in large numbers on the island in May and June to moult, in late December and January to rear offspring and mate, and in smaller numbers throughout the year between foraging trips.

Known-age, adult grey seals (8 to 27 yr) were captured on-shore following the spring moult (May and June) or in the fall (late September and early October) using hand-held nets (Bowen *et al.* 1992). Seals were weighed to the nearest 0.5 kg on Salter spring balances suspended from an aluminum tripod. Males and females were anesthetized with an intramuscular injection of Telazol (equal parts of tiletamine and zolazepam) at an average dose of 0.45 mg kg^{-1} body mass and 0.90 mg kg^{-1} body mass, respectively (Bowen, Beck & Iverson 1999) to allow the fastening of data loggers to the animals and to take body measurements. Roughly equal numbers of males and females were instrumented in each year (Table 3.1).

To study diving behaviour, we used time-depth recorders (TDRs) manufactured by Wildlife Computers (Redmond, Washington; models: Mk3e, Mk5, Mk6 and Mk7). TDRs were secured to netting, which was then attached to the pelage just posterior to the shoulders along the midline using a 5-min marine epoxy. Instruments weighed between 65 - 300 g (< 0.3 % of initial body mass) depending on the model used. TDRs were programmed to sample depth every 20-sec and a wet/dry sensor indicated when the animal was hauled out on land. Most instruments were duty-cycled to prolong the period of data collection. Given the duty cycle schedules used, between 33% and 100% of diving behaviour was sampled over the 3- to 8-mon period. In January, when animals returned to Sable Island for the breeding season, instruments were recovered and the seals released.

Dive Analysis

Upon recovery, TDR data were processed using software supplied by the manufacturer (Wildlife Computers, Redmond, Washington). Zero-offset correction software was used to correct for shifts in the calibration of the pressure transducer of the

Table 3.1: Number of adult grey seals by year that were instrumented, returned to Sable Island and had useable data for seasonal and inter-annual analysis.

Year	# of animals instrumented		# of animals returning		# of animals used in seasonal analysis		# of animals in inter-annual analysis	
	Males	Females	Males	Females	Males	Females	Males	Females
1993	4	6	4	5	4	5	3	3
1994	5	6	3	3	2	3	2*	1*
1995	7	12	6	11	6	8	5	6
1996	18	17	16	12	7	7	5	5
1997	13	12	12	8	3	5	3	5
1998	9	8	7	7	5	4	5	4
1999	8	9	8	7	4	6	3	4
Total	64	70	56	43	31	38	26	28

*not included in analysis of inter-annual variation instrument over the period of data collection. Dive analysis software was then used to calculate a number of variables describing individual dives (see Boness *et al.* 1994 for details).

Transducer drift and sea surface conditions introduce noise in depth measurements that cannot be completely removed by the zero-offset correction program. Therefore, I excluded dives < 5 m in depth from the analysis. Dives of longer than 30 min were also excluded from analysis as visual inspection of these long dives indicated that they generally represented two dives that were not properly separated by the zero-offset correction software. These erroneous "dives" accounted for < 0.05% of the total number of dives sampled.

Dive Bouts

To determine the extent to which grey seals organize their diving in bouts, I only analyzed data from animals with TDRs that were duty cycled on for ≥ 2 consecutive days. Bouts were defined using a modification of an iterative statistical method presented in Boyd *et al.* (1994). A bout started when three or more dives occurred within 35 min. This 35-minute start window allowed for three dive cycles to be completed based on the mean dive duration and surface interval between dives for this species (Chapter 2). Once a bout had begun, subsequent dives were added to the bout if the next surface interval was not significantly greater than the mean of the previous surface intervals within the bout (t-test, $p > 0.05$) or was < three 20-sec sampling units. This last criterion reflected the imprecision of estimating when the animal had surfaced, given the accuracy of the depth transducer. If the subsequent surface interval did not meet these criteria, the bout was ended. Bouts that were truncated by the TDR's duty cycle were omitted from the analysis.

Diagnostic statistics were used to determine the accuracy of the bout identification method (Boyd *et al.* 1994). I examined the distribution of significant p-values that resulted in bout termination. This analysis indicated that 92.8% of bouts ended with p-values < 0.01 and 83.5% of bouts ended with p-values < 0.001, suggesting that surface intervals ending a bout represented genuine changes in behaviour and were not the result of random variation in surface intervals. Bouts were also examined to determine if there was a systematic increase in surface interval as the bout progressed, resulting in over-estimation of bout length. Linear regressions of surface interval against dive number for each bout showed that 77.8% of bouts had no systematic variation in surface interval within bout. In 15.3 % of bouts, surface intervals between dives decreased as the bout progressed whereas in only 6.9% did surface intervals between dives increase. Thus, in general, there was no systematic trend in the length of surface intervals between dives within bouts, and in cases where a significant trend was present, surface intervals generally decreased as the bout progressed.

Each dive within a bout can be characterized by depth, duration, and percentage of time spent at the bottom of the dive. In addition to these characteristics, the time/depth profile or "shape" of each dive over 1-minute in duration was determined. This was done using supervised discriminate function analysis (DFA; Schreer & Testa 1996) as is described in Chapter 2, resulting in the identification of five dive shapes. I used only two of these shapes (i.e., square and V-shaped dives) to investigate possible bout functions as these two shapes accounted for over 70% of all dives (Chapter 2) and have been associated with different behaviours in other phocid species (e.g., LeBoeuf *et al.* 2000).

To examine how bout characteristics differed by sex, month and year, I used MANOVA and linear-mixed effect models (LME; S-Plus 4.5). LME analysis uses maximum-likelihood parameter estimation to determine the significance of factors included in the model. Given the nature of the data, I assumed an auto-regressive (i.e., AR1) variance-covariance matrix for the within-subject error terms. All possible models with two-way interactions were examined and all models were compared to the mean model: $y = \mu + \varepsilon$. Variables included in each model were entered simultaneously. To select the best predictive model, the five models with the lowest Akaike's information criterion (AIC) were compared using a log-likelihood ratio test. I used this approach, rather than relying only on the lowest AIC, due to the non-orthogonal nature of our data (i.e., not all animals were measured in each month). The explained variance was calculated using Cox & Snell's (1989, pp. 208-209) generalized coefficient of determination (R^2) modified to incorporate the effective degrees of freedom (Wade Blanchard, pers. comm.). Only individuals with dive data in > 3 months were included in the seasonal analysis. May was excluded from all statistical analyses because only one male was sampled during this month. However, I have included May data for females in the figures because they provide additional insight into female tactics. Age had little influence on the diving behaviour of males and females at the level of individual dives (Chapter 2). Therefore, I did not include age in the present analysis to limit the number of LME models to be examined. The males and females used in this study did not overlap in length measurements such that when sex was included in the model, body size did not account for significant variation in diving behaviour. To examine inter-annual variability in bout characteristics only animals with data from June through December were used in the MANOVA.

The percentage of square and v-shaped dives within a bout were arcsin transformed and other bout variables were transformed as necessary prior to analysis to meet the assumptions of parametric analyses. In cases where a variable was transformed using natural logarithms, the mean and variability about the mean are reported as the re-transformed mean (i.e., geometric mean of raw data) with 95% confidence limits. In all other cases the mean and standard error are given.

Classification of Dive bout types

The analysis of different types of bouts may provide further insight about how predators organize their behaviour. Bout types were determined using cluster analysis (based on Euclidean distances) following Boyd *et al.* (1994). This method uses both the characteristics of individual dives within a bout (dive duration, surface interval, and depth) and characteristics of the bout itself (number of dives, bout duration, percentage of the bout duration spent at depth, and the percentage of square and V-shape dives/bout). A general problem with cluster analysis is determining how many clusters are appropriate. To determine the optimal number of clusters representing different types of dive bouts, the mean r^2 value for cluster analyses with 1-10, 15 and 20 clusters (weighted for the variance of the original variables) was plotted against the number of clusters (Fig. 3.1). The point where the tangent from the origin to the resulting curve met was defined

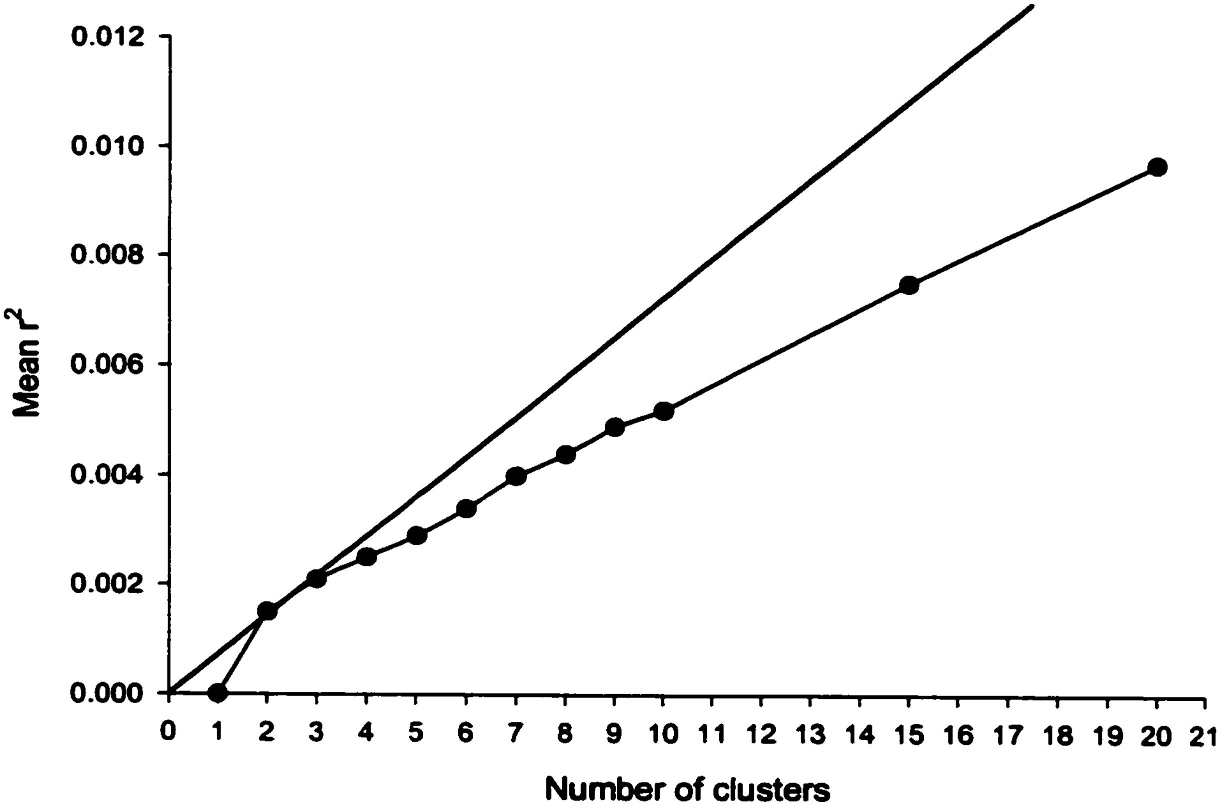

Figure 3.1: The variation between cluster groupings explained by the clusters of bout types (Mean r^2) vs. the number of clusters used. Where the tangent from the origin meets the curve defines the optimum number of clusters (Boyd *et al.*, 1994).

as the optimum number of clusters (Boyd *et al.*, 1994). Using this method, two or three bout types seemed optimal. I chose to use three bout types in this analysis to provide finer resolution of the temporal variation in diving behaviour. I then used DFA to determine the accuracy of bout classifications. DFA indicated that 97.8 % of dive bouts were classified correctly with a cross-validation error rate of 2.2%. Repeated-measures MANOVAs were used to examine the effect of sex, month, and year on the use of different bout types.

Bout Clusters

I then asked if grey seals organized their diving bouts at larger temporal scales into bout clusters (BCs) as suggested by the pattern seen in Fig. 3.2. Bout clusters were identified using a modification of the bout algorithm such that a BC started when the cumulative surface-interval time between three bouts was < 44 minutes in duration (e.g., Fig. 3.2). This cumulative surface interval threshold was based on the distribution of post-bout surface intervals, which indicated that 80% of all bout intervals lasted < 22 min. Hence, a bout cluster began when the cumulative surface time between 3 bouts was < 44 min. Once started, subsequent bouts were added if the next surface-interval was not significantly different than the mean of the previous intervals in the BC (t-tests, $p > 0.05$). BCs truncated by the duty-cycle of the TDR were omitted from the analysis. The influences of sex, month and year on the characteristics of bout clusters were examined using repeated-measures MANOVA and LME models as above.

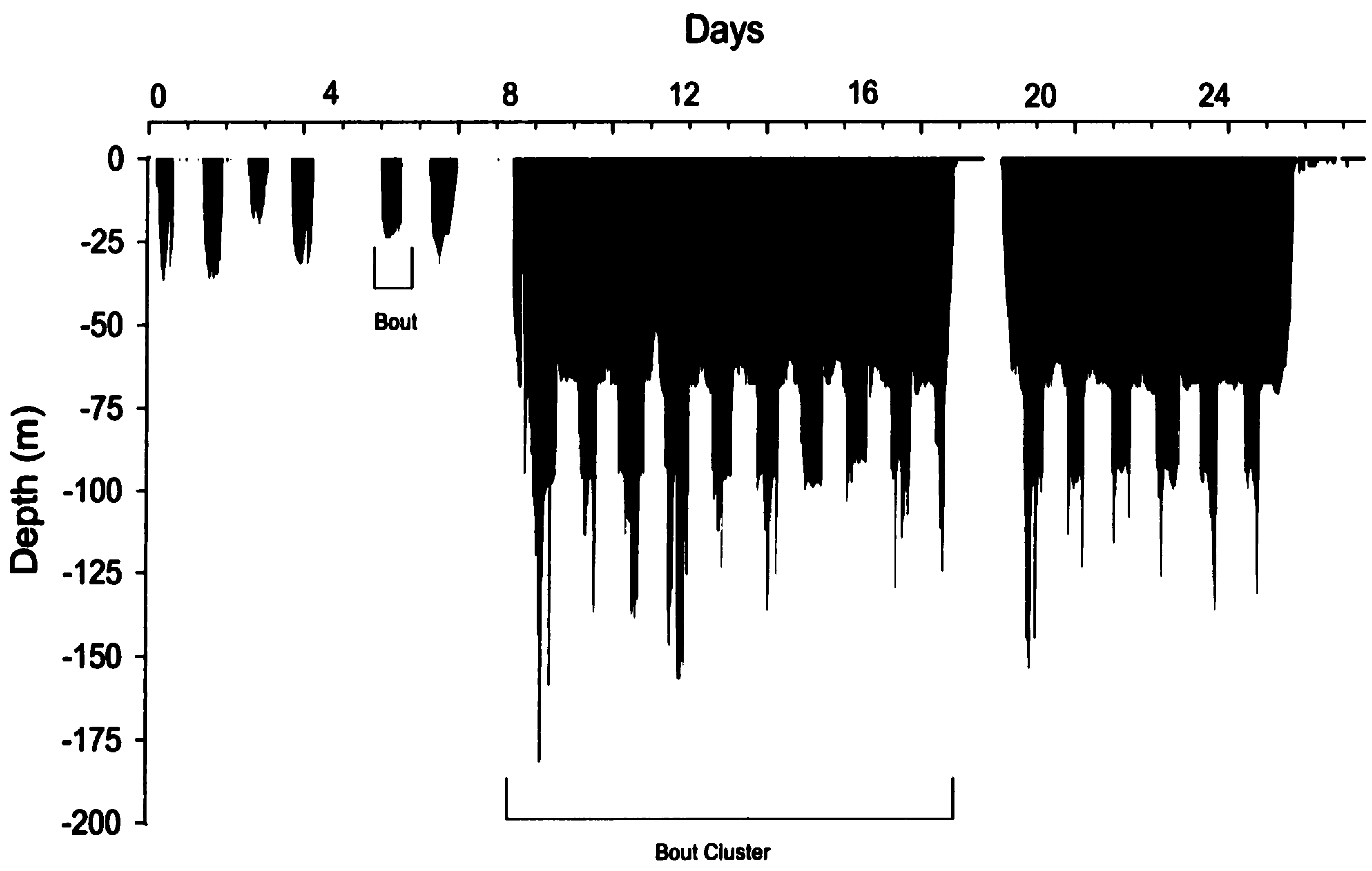

Figure 3.2: Illustration of an individual grey seal dive record measured over a period of 27 days. See methods for definitions of bouts and bout clusters.

Foraging trips

I examined sex differences in trip characteristics using 16 seals (n = 7 males and 9 females) that were equipped with non-duty cycled TDRs. For these animals, the duration of foraging trips was estimated as follows: a trip started when a period of haulout (i.e., extended dry time) was followed by five or more dives and ended when > 20 min of accumulated dry time was recorded between successive dives. Too few individuals were studied to examine month and year effects.

Inter-annual variability in small pelagic prey

To examine the influence of inter-annual variation in prey abundance on the diving effort of grey seals, I constructed an annual abundance index of small pelagic fishes (capelin - *Mallotus villosus*, Northern sandlance - *Ammodytes dubius*, herring - *Clupea harengus*, and mackerel - *Scomber scombrus*) known to be important prey for adult grey seals (Bowen *et al.* 1993; Bowen & Harrison 1994). For this index of abundance, I summed the mean number of fish/30-min tow of each species from stratified-random, groundfish surveys conducted on the Scotian Shelf (NAFO sub-areas 4VWX) each July. Satellite telemetry studies show that the eastern Scotian Shelf is the main foraging area for grey seals from Sable Island (Austin, Bowen, McMillan & Beck, unpublished data). The eastern Scotian shelf was surveyed in the last two weeks of the month-long July survey, therefore, I examined the correlation between the prey index and the mean dive effort (hrs spent in bouts/d) of males and females in July and August of each year.

Results

Data Logger Recovery

Between May 1993 and January 2000, 134 animals (64 males, 70 females) were captured and outfitted with TDRs (Table 3.1). Overall 73.9% (56 males, 43 females) of these animals returned to Sable Island the following January, however due to instrument loss, failure or short duty cycling schedules (e.g., 1 day on, 1 day off), only 69 animals could be included in the seasonal analysis (31 males, 38 females). Of these only 54 animals (26 males, 28 females) had complete dive data from June through December such that they could be used to examine inter-annual differences (Table 3.1). Only 3 (2 males & 1 female) of these 54 individuals were from 1994, thus, 1994 was excluded from analysis of inter-annual variation.

Bout Characteristics

A total of 27,548 bouts was identified from the dive records of 69 grey seals. Of these bouts, 7.1% were truncated by duty cycling and omitted from statistical analyses. Omitted bouts were equally distributed between males and females. Overall, 99.4 ± 0.07% of dives by individuals were contained within dive bouts.

The mean duration of the 25,590 bouts analyzed was 1.40 h (95% CL: 1.38 and 1.42 h) with a mean of 14.6 ± 1.02 dives/bout. On average the post-bout surface interval was 6.37 min (95% CL: 6.28 and 6.45 min) in duration. Bout characteristics of males and females differed significantly (MANOVA: $F_{6,34} = 7.950$, $p < 0.001$, $n = 51$). Bouts by males were significantly deeper (57 ± 2.3 m vs. 44 ± 3.1 m) than bouts by females. Females had significantly longer bouts than males (1.85 h (95%CI: 1.55, 2.20h) vs. 1.37

h (95%CI: 1.24, 1.51 h) and spent a significantly higher percentage of the bout at depth (45.7 ± 1.32 % vs. 38.4 ± 1.36%). There was a significant year effect on bout characteristics (year: MANOVA: $F_{30, 190} = 1.631$, $p = 0.043$) with the percentage of square dives/bout being higher in 1995 and 1996 compared to other years of the study (Fig. 3.3). There was no significant sex by year interaction (MANOVA: $F_{30, 190} = 0.959$, $p = 0.532$).

All but one of the bout characteristics had a significant month effect (Table 3.2; Figs. 3.4 and 3.5). The exception was the percentage of V-shaped dives/bout, which was best described by the mean model. The best predictive models for bout duration ($R^2 = 0.104$) and percentage of bout spent at depth ($R^2 = 0.138$) included a cubic (quadratic) month term, sex, and a month by sex interaction (Table 3.2, Fig.3. 4).

Mean bout depth and the percentage of square dives within a bout were best described by models which included a cubic month term, year and sex ($R^2 = .101$ and 0.243, respectively). There was also a significant month by sex interaction term in the model describing percentage of square dives within bouts (Table 3.2, Fig. 3.5). Although the mean depth of bouts by males was significantly deeper than that of females, both sexes followed the same seasonal pattern. Bout depth decreased from June to September (males: 54 ± 2.9 m to 49 ± 3.56; females: 45 ± 3.5 m to 29 ± 3.2 m) before increasing from September to December (peak: males = 63 ± 4.15; females = 51 ± 4.1 m). Bout depth then decreased in January to a mean of 36 m for both sexes. Average bout depth also exhibited annual variation, being shallower in the last three years of the study for both males and females.

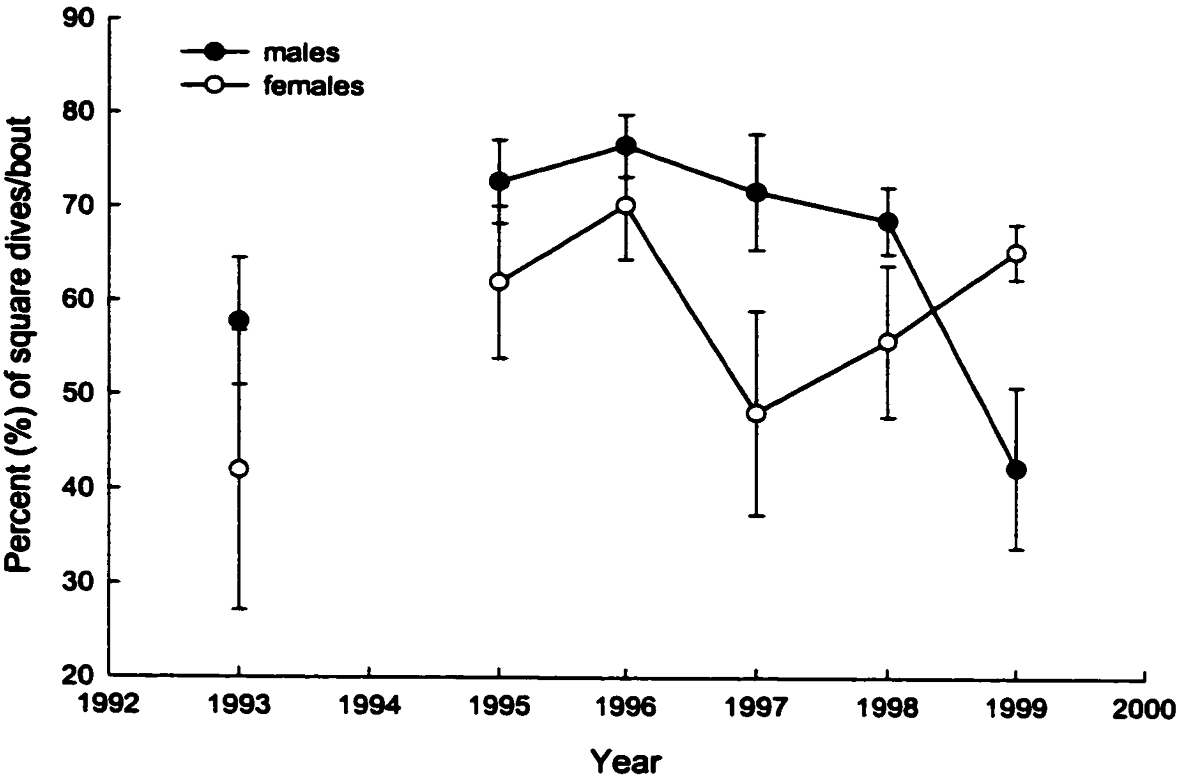

Figure 3.3: Inter-annual variation in the percentage of square dives per bout for males and females. Since diving behavior differed across months, only animals from which data was available from June to December were used in this analysis. Values are means ± 1 SE. Sample size is as shown in Table 3.1.

Table 3.2: Linear mixed effects models of individual bout characteristics.

Bout Variable ($n = 69$)	Source	Coefficient	SE	z-score	p-value	df	Pseudo R^2
Bout Duration	Constant	-2.989	2.552	-1.17	0.121		0.104
(ln transformed)	Month	1.011	0.869	1.16	0.123	357	
	Month^2	-0.082	0.096	-0.85	0.198	357	
	Month^3	0.001	0.003	0.39	0.348	357	
	Sex	-0.074	0.145	-0.51	0.305	67	
	Month^2 x Sex	0.0003	0.0001	3.01	0.001	349	
% Bout at depth	Constant	-3703	1552.0	-2.39	0.008		0.138
(arcsine transformed)	Month	4.484	1.454	3.08	0.001	357	
	Month^2	0.270	0.295	0.91	0.181	357	
	Year	76.023	32.396	2.35	0.009	62	
	Year^2	-0.388	0.169	-2.29	0.011	62	
	Sex	0.074	1.067	0.070	0.472	67	
	Month^2 x Year^2	0.00006	0.00003	-1.88	0.030	309	
	Month^2 x Sex	0.18	0.009	1.86	0.031	349	
Mean Bout Depth	Constant	457.454	114.161	4.01	< 0.001		0.101
	Month	-92.851	27.435	-3.38	< 0.001	357	
	Month^2	10.498	3.020	3.48	< 0.001	357	
	Month^3	-0.078	0.108	-3.52	< 0.001	358	
	Year	-1.569	0.827	-1.90	0.029	62	

Table 3.2 continued

	Sex	-5.615	1.521	-3.70	< 0.001	67	
% Square dives/bout	Constant	-9007.8	2480.2	-3.63	<0.001		0.243
(arcsine transformed)	Month	-118.338	16.200	-7.31	<0.001	357	
	Month^2	13.006	1.784	7.30	<0.001	357	
	Month^3	- 0.456	0.064	-7.19	<0.001	357	
	Year	195.344	51.704	3.78	< 0.001	62	
	Year^2	-1.015	0.269	-3.77	< 0.001	62	
	Sex	- 3.815	1.401	-2.72	0.003	67	
	Month^3 x Sex	0.002	0.001	1.86	0.032	349	
% "V" dives/bout	Constant	1.825	0.133	13.72	< 0.001		
(ln transformed)							
Post-bout surface interval	Constant	102.396	98.183	1.04	0.149		0.050
(ln transformed)	Month	1.608	0.804	2.00	0.023	357	
	Month^2	- 0.175	-0.088	-1.98	0.024	357	
	Month^3	0.006	0.003	2.06	0.020	357	
	Year	-2.246	2.047	-1.10	0.156	62	
	Year^2	0.012	0.011	1.12	0.131	62	
	Sex	0.246	0.116	2.15	0.016	67	
	Month^3 x Sex	- 0.0001	0.00009	-1.77	0.038	349	

Seasonal analysis did not include animals sampled in May, as only one male was sampled.

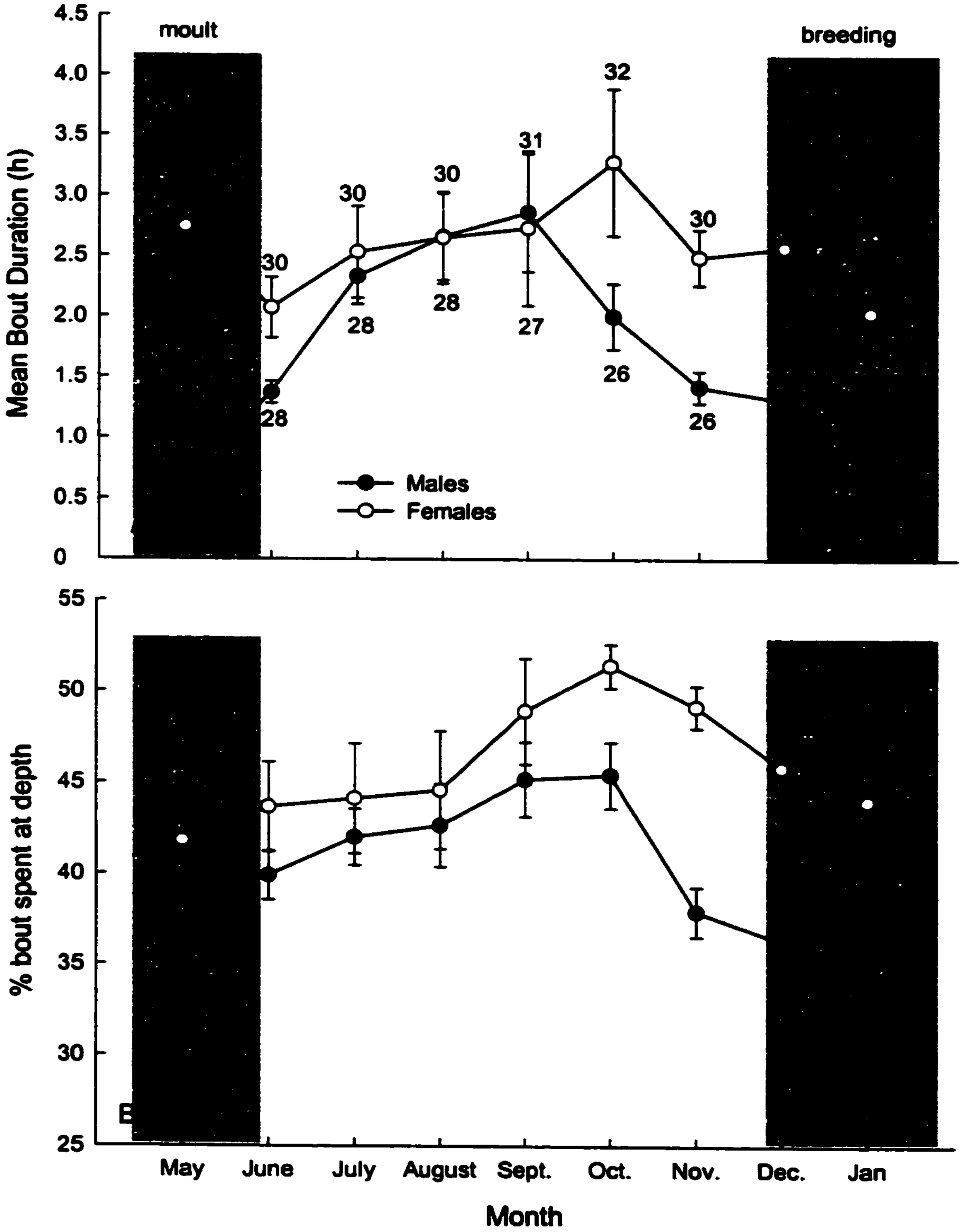

Figure 3.4: Seasonal changes in (A) bout duration (h) and (B) percent bout spent at depth (%) by male and female grey seals. Values are means ± 1 SE. Numbers above or below each mean represent sample size (i.e., number of individuals) in each month and are the same for both panels. May was not included in statistical analyses since only one male was sampled.

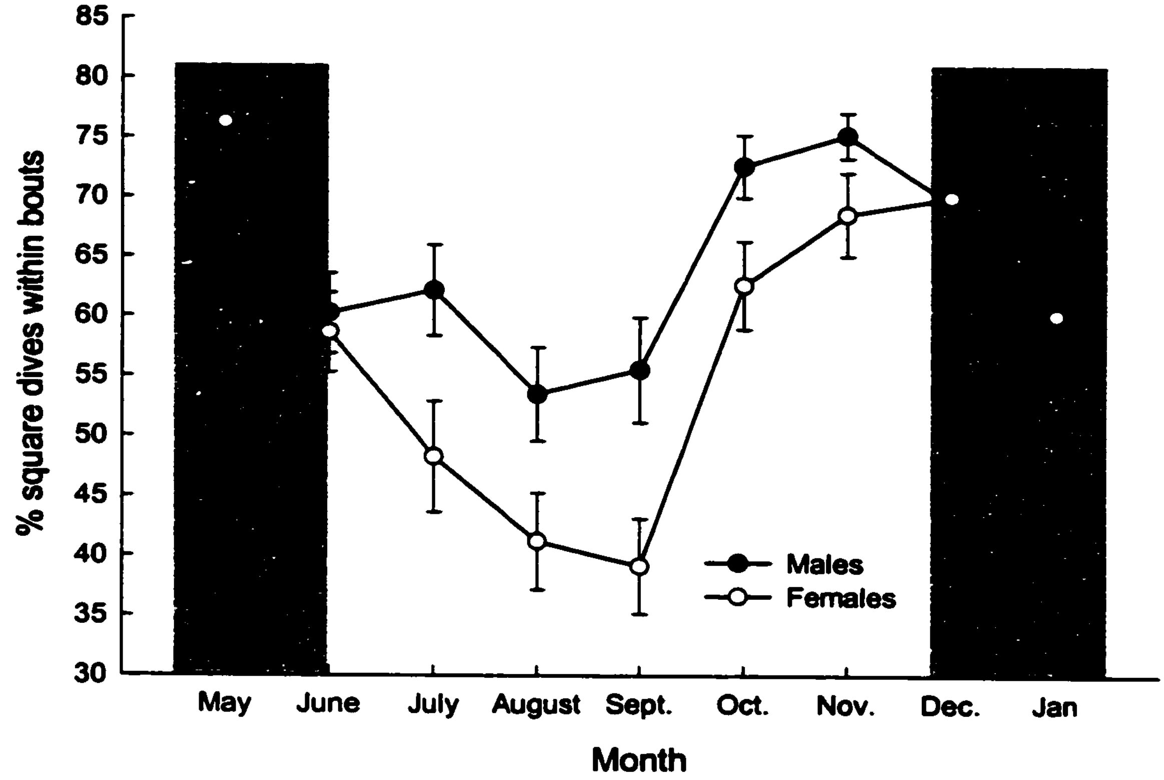

Figure 3.5: Seasonal changes in the percentage of square dives within a dive bout for male and female grey seals. Values are means ± 1 SE. Sample size is as shown in Figure 3.4. May was not included in statistical analyses since only one male was sampled.

Post-bout surface interval was best described by a model that included a cubic month term, a quadratic year term, sex, and a month by sex interaction term. However, this model explained only 5% of the variation found in post-bout surface interval (Table 3.2). For both sexes, mean post-bout surface interval increased from June through September and then declined through the fall and winter. The magnitude of increase in the duration of post-bout surface intervals was greater for females than for males during the summer months resulting in the significant month by sex interaction term. Mean post-bout surface intervals were significantly higher in 1997 (8.5 ± 0.91 min) and 1998 (11.8 ± 2.02 min) compared to other years (6.8 ± 0.29 min).

Bout types

Three types of bouts were identified using cluster analysis (Fig. 3.2, Table 3.3). Type-1 bouts accounted for 19.4% of all bouts. These bouts were relatively shallow, of short duration, with approximately 8 dives/bout and followed by a relatively long surface interval. Type-1 bouts had relatively more V-shaped dives/bout than the other two bout types, accounting for the relatively low percentage of time spent at depth (Table 3.3). Type-2 bouts accounted for 29.4% of all bouts. These bouts were intermediate in depth, longer in duration and had double the number of dives compared with Type-1 bouts (Table 3.3). Time spent at depth within bouts accounted for almost half of bout duration, reflecting the higher percentage of square-shape dives and the lower percentage of V-shape dives compared to Type-1 bouts (Table 3.3). Type-3 bouts, accounting for 51.2% of all diving bouts, were deeper than the other two bout types and were comprised of about 90% square dives (Table 3.3). Type-3 bouts were of similar duration as Type-2

Table 3.3. Characteristics of three different bout types identified from 69 grey seal dive records. Values are means ± 1 SE or with (95% confidence intervals).

	Type 1	Type 2	Type 3
Bout duration (h)	0.59 (0.57, 0.61)	1.59 (1.55, 1.63)	1.82 (1.78, 1.85)
Dives/ bout	8 ± 1.0	16 ± 1.0	18 ± 1.0
Mean bout depth (m)	27 ± 0.4	44 ± 0.3	63 ±0.3
% bout spent at depth	22.9 ± 0.26	44.9 ± 0.19	45.1 ± 0.11
% square dives	9.1 ± 0.20	49.8 ± 0.20	89.0 ± 0.10
% V dives	39.4 ± 0.50	9.7 ± 0.10	2.2 ± 0.04
Post-bout surface interval (min)	9.7 (9.39, 10.08)	6.3 (6.08, 6.42)	5.6 (5.47, 5.66)
Mean dive duration (min)	3.5 ± 0.03	5.1 ± 0.02	5.1 ± 0.01
Mean surface interval between dives (min)	2.2 ± 0.03	1.3 ± 0.01	1.4 ± 0.01

Bout types determined using cluster analysis (see Methods, Fig. 3.1).

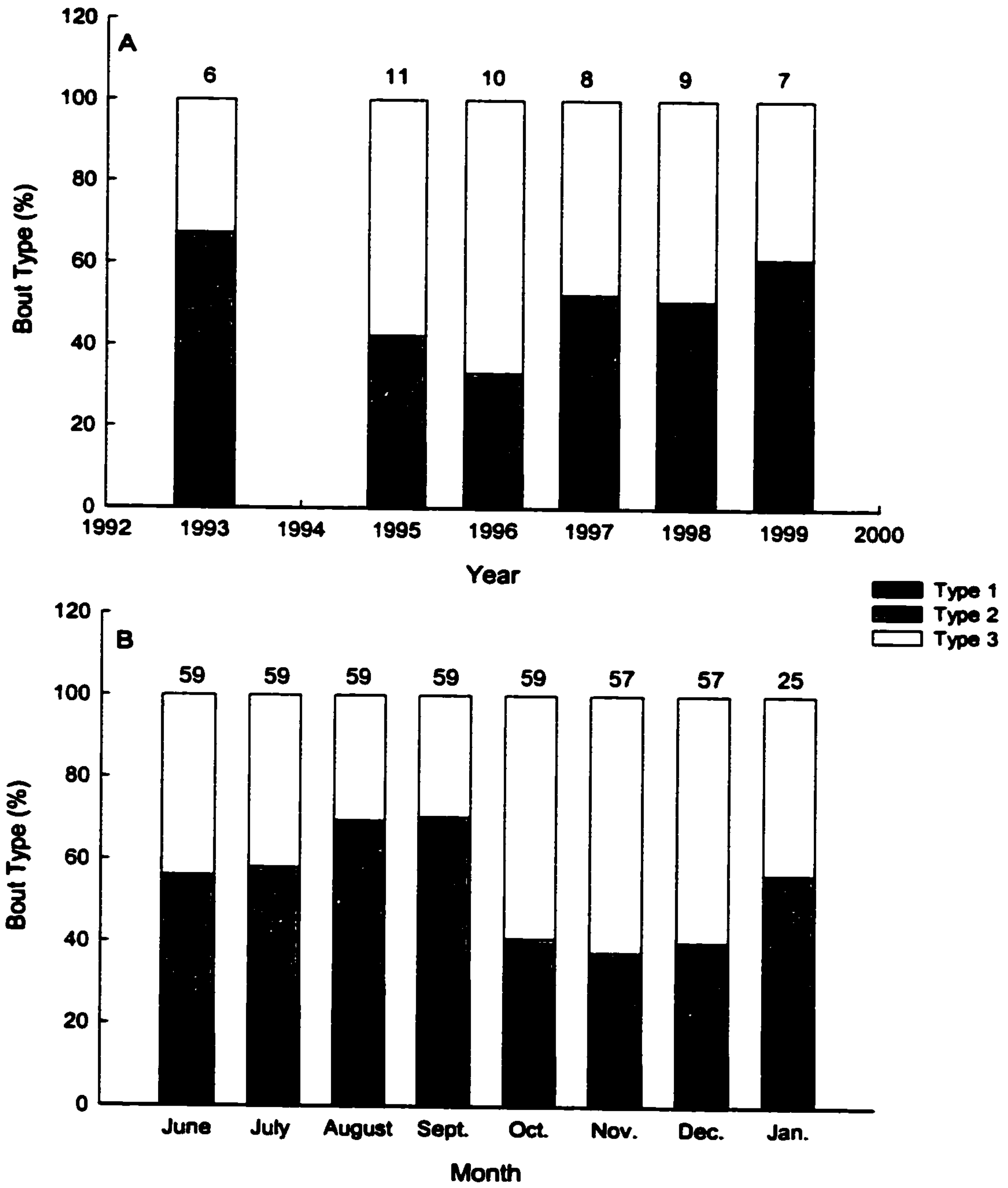

Figure 3.6: Inter-annual (A) and seasonal (B) variation in the distribution of bout type use. Numbers above each bar represents sample size. Given that there were no significant differences between males and females in the inter-annual and seasonal distribution of bout types used data was averaged across all animals by year and month.

bouts, but were followed by shorter inter-bout intervals.

The percentage of each bout type did not differ between male and female grey seals (Repeat measures MANOVA: $F_{1,39} = 1.744$, $p = 0.194$), but showed significant inter-annual variation ($F_{5,39} = 2.858$, $p = 0.027$, Fig 3.6a). The percentage of type-2 bouts increased significantly in the last two years of the study while type-3 bouts declined during this same period. The use of type-1 bouts varied throughout the 7-year study period, being particularly high in 1993 (32.6%). The use of different bout types also changed seasonally (Repeat Measures: $F_{6,28} = 7.048$, $p < 0.001$; Fig 3.6b) with type-3 bouts increasing significantly during the fall relative to the summer months. This seasonal change was consistent through all 7 years of the study ($F_{6,28} = 1.247$, $p = 0.313$).

The temporal sequence of bout types may contain information on how seals organized their diving/foraging behaviour. To investigate this, I conducted a non-parametric Runs test on the sequence of bout types used by each individual. For 61 of the 69 grey seals (88.4%), the pattern of bout type use was significantly non-random (p-value < 0.05). To determine the pattern of bout type use and the factors that influenced the temporal organization of bout types, transition probabilities were calculated (the proportion of time each bout type was followed by each of the three bout types) for each individual. Overall, bouts were most often followed by bouts of the same type (Table 3.4) suggesting that animals often perform a series of one bout type before changing their behaviour. While the most common transition was from a type-3 bout to another type-3 bout, there was significant inter-annual variation in transition matrices and this inter-annual variation differed between males and females (Repeat Measures MANOVA: Transition x Year X Sex: $F_{10.5,81.7} = 2.144$, $p = 0.028$, Fig. 3.7). Male grey seals showed

Table 3.4: Transition probabilities for 69 grey seals over the entire pre-breeding foraging period and by season.

Current / Next	Type 1	Type 2	Type 3
	June - January		
Type 1	0.12 ± 0.021	0.06 ± 0.005	0.03 ± 0.002
Type 2	0.06 ± 0.005	0.15 ± 0.014	0.10 ± 0.005
Type3	0.03 ± 0.002	0.10 ± 0.005	0.37 ± 0.028
	Season 1 (June - September)		
Type 1	0.17 ± 0.028	0.08 ± 0.006	0.03 ± 0.003
Type 2	0.08 ± 0.006	0.21 ± 0.020	0.09 ± 0.005
Type 3	0.03 ± 0.003	0.09 ± 0.005	0.27 ± 0.03
	Season 2 (October - January)		
Type 1	0.05 ± 0.011	0.05 ± 0.007	0.03 ± 0.003
Type 2	0.05 ± 0.006	0.13 ± 0.017	10.3 ± 0.50
Type 3	0.03 ± 0.003	0.10 ± 0.005	0.48 ± 0.030

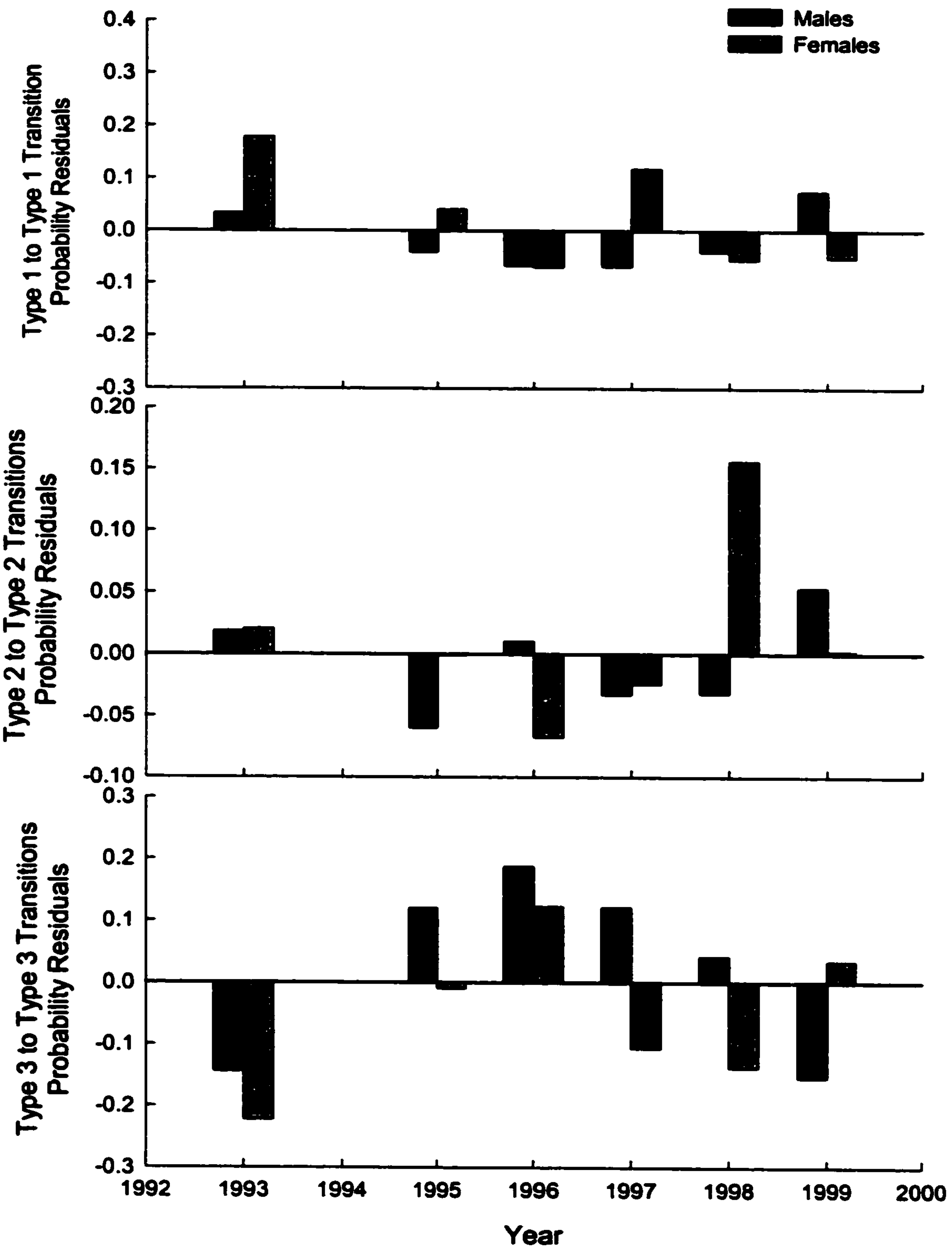

Figure 3.7: Inter-annual variation in bout type transition probabilities for male and female grey seals. Values are residuals from the overall mean for the three most common transition types. Sample size is shown in Table 3.1.

less inter-annual variability than females. In all years the most common transition performed by males was from a type-3 bout to another type-3 bout. This transition type dominated male behaviour (i.e. represented > 45% of all transitions) from 1995 to 1998 with lower values (24.5% and 23.5%) in 1993 and 1999, respectively. The transition frequencies of bout types by females were more variable. In 1993 and 1997 the most common transition was from a type-1 to a type-1 bout while in 1995, 1996 and 1999 type-3 to a type-3 transitions were dominant. In 1998, type-2 to type-2 transitions were the most frequent, representing over 30% of transitions by females.

It was not possible to examine the monthly variation in transition probabilities, as there were many empty transition cells. To examine larger temporal-scale changes in the pattern of bout type use, transition matrices were re-calculated for the period from June through September (season 1) and for October through December (season 2; Table 3.4). Repeat Measures MANOVA indicated seasonal effects ($F_{3.2, 210} = 6.371$, $p < 0.001$) with fewer transitions involving type-1 bouts in season 2. During season 2, 81.7% of all transitions involved type-2 and 3 bouts (Table 3.4).

Dive Effort

I used hours spent in bouts/day as an index of effort for each individual. Effort was calculated for all bout types combined and type-3 bouts separately because the characteristics of type-3 bouts suggested that they were most likely to represent foraging behaviour. While total effort did not show any significant year or sex effects (ANOVA: year - $F_{5,39} = 1.932$, $p = 0.111$; sex - $F_{1,39} = 1.721$, $p = 0.197$), when measured using only type-3 bouts, dive effort varied annually (ANOVA: $F_{5,39} = 3.097$, $p = 0.019$). Type-3 effort was low in 1993 but peaked in 1995 and 1996 before declining during the last 3 years of the study. Type-3 effort did not differ by sex (ANOVA: $F_{1,39} = 0.452$, $p = 0.505$) nor was there a sex by year interaction (ANOVA: sex by year - $F_{5,39} = 2.104$, $p = 0.085$).

There was significant monthly variation in both measures of dive effort. However, only the results for total effort are reported here as the results were similar in both cases. The best LME model explained 21.8% of the monthly variation in dive effort and included significant month (cubic), year, sex, month by sex and year by sex interaction terms (Table 3.5). Female effort was relatively high immediately following the spring moulting period (May-June), but showed a marked decrease from June to September before increasing again through the fall and then declining in January (Fig. 3.8). In contrast, male effort increased more variably from June through November before decreasing abruptly in December and January.

Bout Clusters

In total, 4280 bout clusters (BC) were identified. However, 21.6% of BC were truncated by the duty cycling such that only 3357 were used in the analysis. Omitted BCs were evenly distributed between males and females. The degree to which bouts clustered varied by individual (range: 30.6 to 96.7% of bouts by individual seals were included in BCs; CV = 0.21) and between males and females (Table 3.6). Bouts not included in bout clusters had an average duration of 1.56 h (95% CL: 1.50 h and 1.63 h) contained 16 ± 1.0 dives and had longer than average post-bout surface intervals (23.6 min vs. 6.4 min, $p < 0.001$) than those that were included.

Table 3.5: Linear mixed effects model of total dive effort

Effort Measure (n = 69)	Source	Coefficient	SE	z-score	p-value	df	Pseudo R^2
Hrs in bouts/day	Constant	496.710	0.0824	0.602	0.274		0.218
	Month	- 47.612	6.8931	-6.907	<0.001	357	
	Month^2	5.259	0.7579	6.939	<0.001	357	
	Month^3	- 0.186	0.0270	-6.880	<0.001	357	
	Year	- 6.478	0.1720	-0.377	0.352	62	
	Year^2	0.030	0.0896	0.332	0.378	62	
	Sex	14.306	8.122	1.761	0.039	67	
	Month^3 x Sex	0.001	0.0004	3.305	<0.001	349	
	Year^2 x Sex	- 0.002	0.0009	-1.932	0.027	55	

Seasonal analysis did not include animals sampled in May, as one male was sampled.

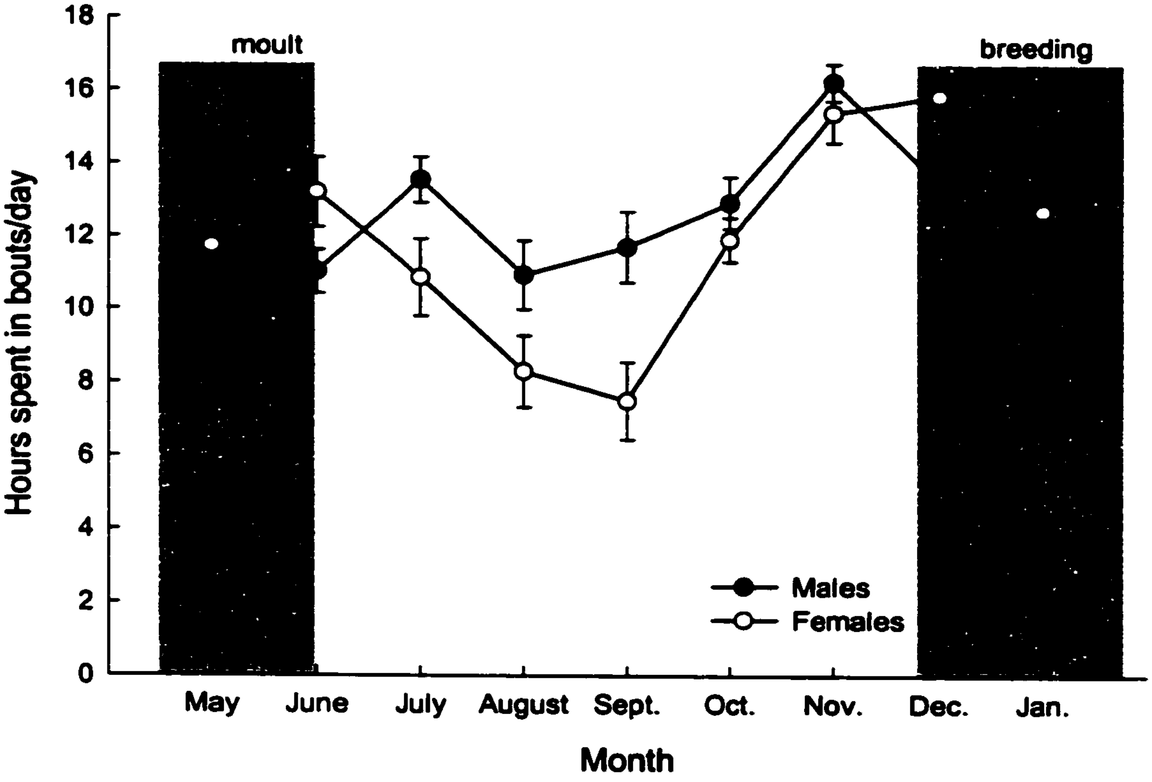

Figure 3.8: Seasonal changes in dive effort (h/day spent in bouts) of male and female grey seals. Values are means ± 1 SE. Sample size is as shown in Figure 3.4. May was not included in statistical analyses since only one male was sampled.

Table 3.6: Characteristics of bout clusters by male and female grey seals. Values are means ± 1 SE or means (95% confidence intervals).

	Males, n=31	Females, n=38	t, p
% of bouts included in BC	83.2 ± 1.61%	69.9 ± 2.91%	3.761, < 0.001
BC duration (h)	9.8 (8.4, 11.06)	11.2 (9.6, 13.2)	-1.310, 0.195
Post-BC surface interval (min)	17.9 (15.7, 20.4)	19.4 (16.7, 22.7)	-0.765, 0.447
# bouts/BC	5.1 ± 0.10	4.67 ± 0.13	2.797, 0.007

BCs averaged 10.56 h (95% CL: 9.51 h and 11.73 h) in duration, were comprised of 4.9 ± 0.09 bouts and were followed by a mean surface interval of 18.7 min (95% CL: 16.9 min and 20.8 min). Bout cluster characteristics did not differ significantly between males and females (MANOVA: $F_{2,38} = 2.989$, $p = 0.062$) however, females tended to having longer bout clusters (11.0 h (95%CI: 9.4, 12.9 h) vs. 9.1 h (95% CI: 8.3, 10.1)) than males. There was no significant inter-annual variation in bout cluster characteristics (MANOVA: $F_{10,78} = 0.748$, $p = 0.820$) and no year by sex interaction (MANOVA: $F_{10,78} = 0.469$, $p = 0.905$).

Both BC duration and post-BC surface interval exhibited significant monthly variation (Table 3.7). The best model for BC duration contained a significant month by sex interaction, with both sexes having BCs of relatively similar lengths from June through September, after which male BCs become significantly shorter while female BCs become longer until January (Fig. 3.9). However the best LME model for this characteristic explained only a small percentage of the variation ($R^2 = 0.073$). The best LME model for post-BC surface interval explained only 11.3% of the variation. This model included month, year and sex terms. Surface intervals following bout clusters decreased through the summer and fall but increased in January.

Foraging trips

In total, 147 trips were recorded from the 7 males and 9 females whose TDRs were not duty cycled, with an average of 9.2 ± 1.03 trips per seal. Trips ranged between 1 h and 78.3 d with a mean duration of 8.3 ± 1.25 d. Haulout periods following foraging trips ranged from 3.6 to 37.5 h with a mean of 16.2 ± 2.09 h. Although male and female

Table 3.7: Linear mixed effects model of bout cluster duration and post-bout cluster surface interval.

BC characteristic (n = 66)	Source	Coefficient	SE	z-score	p-value	df	Pseudo R^2
BC duration	Constant	2.737	2.411	1.14	0.079		0.073
	Month	-0.237	0.825	-0.29	0.386	296	
	$Month^2$	0.044	0.091	0.49	0.312	296	
	$Month^3$	-0.002	0.003	-0.70	0.242	296	
	Sex	-0.098	0.069	-1.42	0.078	64	
	$Month^3$ x Sex	0.0001	0.00005	3.10	0.001	288	
Post-BC surface interval	Constant	134.23	211.75	0.634	0.264		0.113
	Month	5.36	1.965	2.730	0.003	280	
	$Month^2$	-0.57	0.217	-2.606	0.005	280	
	$Month^3$	-0.019	0.008	2.426	0.008	280	
	Year	-3.154	4.415	-0.714	0.239	59	
	$Year^2$	0.017	0.230	0.734	0.233	59	
	Sex	0.301	0.081	3.714	0.0001	64	

Seasonal analysis did not include animals sampled in May, as only one male was sampled.

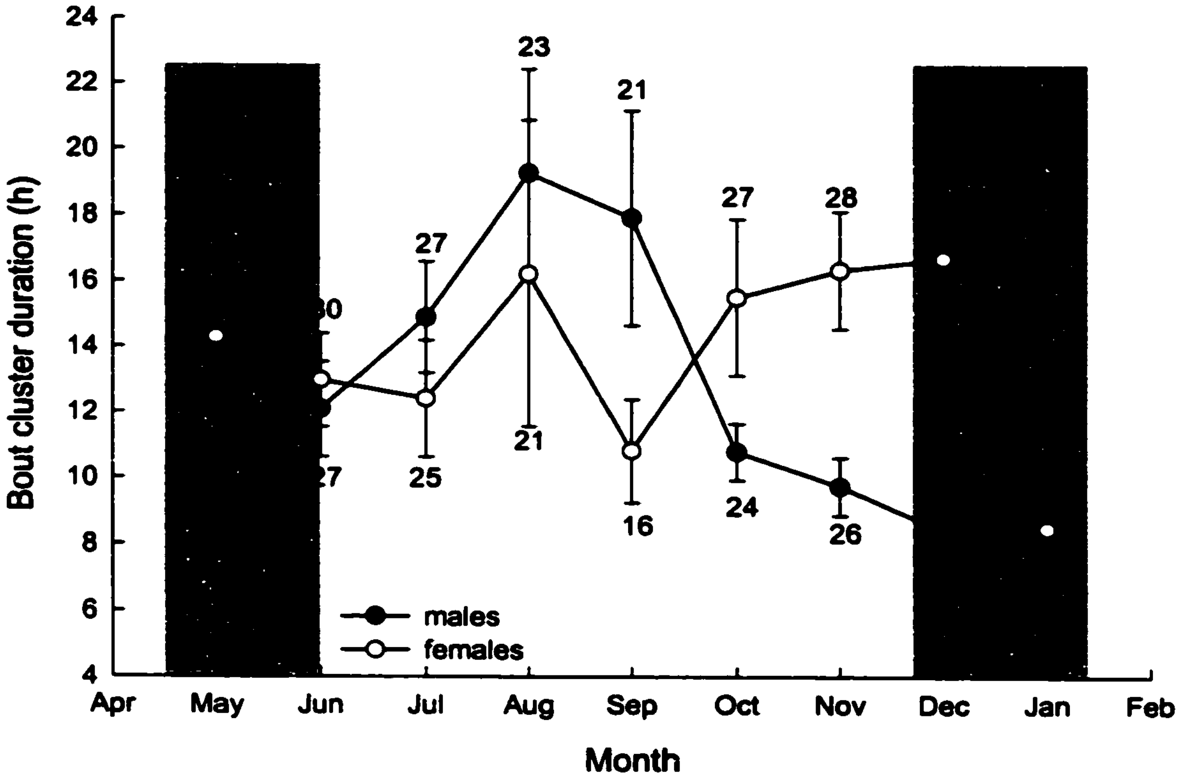

Figure 3.9: Seasonal changes in bout cluster duration (h) by male and female grey seals. Values are means ± 1 SE. Numbers above or below each mean represent sample size (i.e., number of individuals) in each month. May was not included in statistical analyses.

trip durations did not differ ($t_{14} = 0.123$, $p = 0.904$), males had significantly longer post-trip haulout periods than females (20.8 ± 2.98 h vs. 12.5 ± 2.38 h, $t_{14} = 2.194$, $p = 0.046$). The percentage of time spent diving while on foraging trips also differed, with females (58.7 ± 3.56%) spending significantly more time diving than males (36.8 ± 5.91%; $t_{14} = -3.328$, $p = 0.005$).

Dive effort and inter-annual variability in prey

The estimated overall abundance of small pelagic prey on the Scotian Shelf increased over the 7-year study period and particularly on the eastern part of the Shelf, from 1997 to 1999 (Fig. 3.10). There was a significant negative correlation between the index of prey abundance and estimated dive effort in males ($r = -0.856$, $p = 0.014$), but not in females ($r = -0.531$, $p = 0.220$), suggesting that in years of lower prey abundance, male grey seals spent more time foraging, although the case for females is less clear (Fig. 3.10).

Discussion

The temporal clustering of diving behaviour into bouts is a common feature of air-breathing marine predators (e.g., Goebel *et al.* 1991; Ralls *et al.* 1995; Jodice & Collopy 1999; Watanuki *et al.* 1999). Among pinnipeds, the temporal characteristics of diving behaviour of Antarctic fur seals has been particularly well studied, but only in lactating females (Boyd & Croxall 1992; Boyd *et al.* 1994; Boyd 1996; McCafferty *et al.* 1998). To my knowledge, only elephant seals have been studied with sufficient sample size to make reasonable inferences about the foraging ecology of both sexes (Slip *et al.*

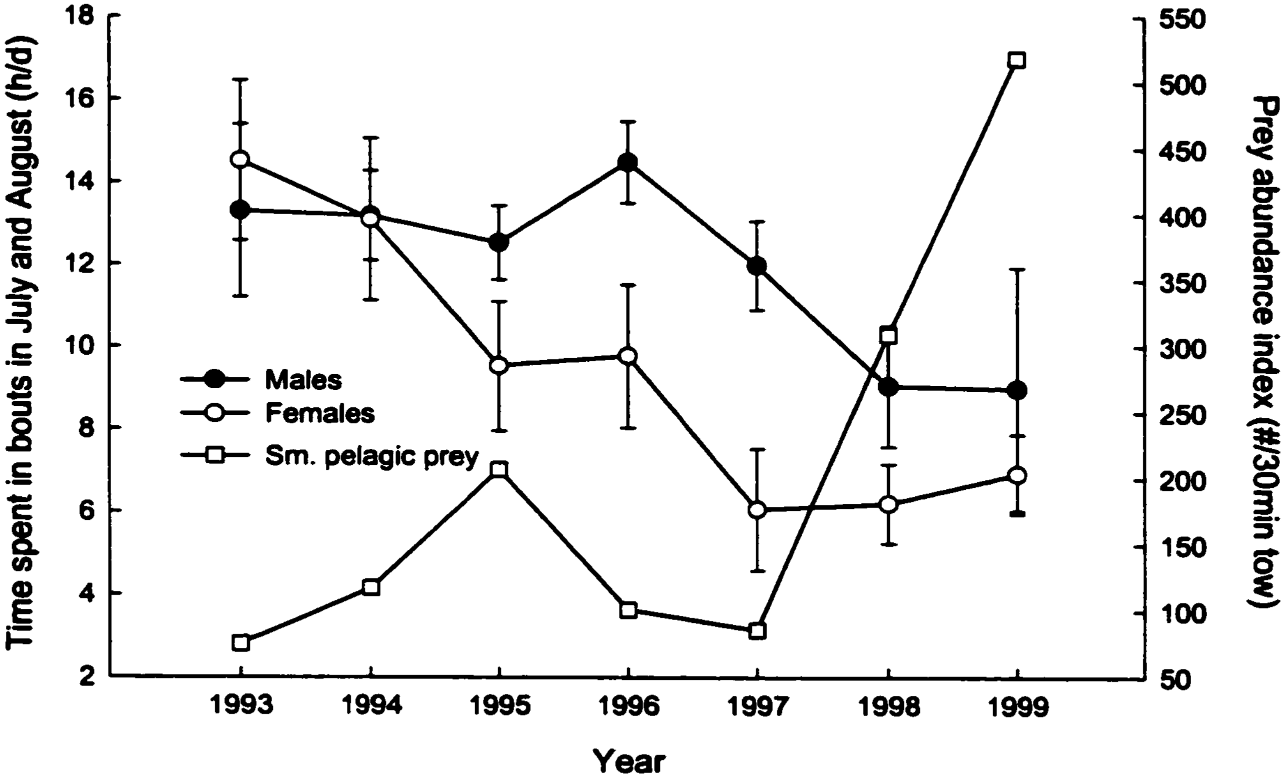

Figure 3.10: Inter-annual variation in July abundance index of small pelagic prey on the Eastern Scotian Shelf and the dive effort (h/day in bouts) of males and females during July and August.

1993; LeBoeuf *et al.* 2000). However, unlike grey seals, elephant seals are highly migratory and foraging is organized into two major trips each year during which diving is virtually continuous (LeBoeuf *et al.* 1988, 1989, 1993, & 2000).

The results of this study show that adult male and female grey seals make different decisions about the allocation of time to diving compared to other behaviours (e.g., resting at the surface, hauled out on land). These sex differences in diving behaviour are evident at multiple temporal scales: individual dives (minutes; Chapter 2), bouts (1-2 h) and trips (days) and in the way bouts are organized seasonally and inter-annually.

Function of Bout types

Grey seals organize their diving behaviour into temporal clusters, with few dives (< 1%) performed outside of bouts. I identified three types of diving bouts differing primarily in duration, depth, the percentage of square-shaped dives/bout and the percentage of bout spent at depth. In the same way that some authors have used the shape of individual dives to infer behaviour (Crocker *et al.* 1994, Asaga *et al.* 1994; Kirkwood & Robertson 1997; Lesage *et al.* 1999), it is tempting to conclude that different bout types represent different behaviours. This has been suggested for another apex marine predator, the Antarctic fur seal. In this species four bout types were identified, each thought to represent a different aspect or type of foraging (Boyd *et al.* 1994). The association of bout type with foraging seems reasonable in this species, as fur seals are known to travel at the surface both to foraging areas and among prey patches. However, grey seals, northern elephant seals (*Mirounga angustirostris*) and harbour seals (*Phoca* *vitulina*) apparently do not travel at the surface (Thompson *et al.* 1991; LeBoeuf *et al.* 2000, Bowen *et al.* submitted), such that diving measurements have necessarily included both foraging and travel to and among prey patches. Therefore the functional interpretation of different bout types is more complex in phocids. For instance, a study of male harbour seals fitted with the Crittercam video system indicated that dives with significant bottom time (e.g., square-shaped dives) can represent a variety of behaviours, including foraging, travelling, and courtship (Bowen *et al* submitted). Nevertheless, evidence indicates that grey seals and harbour seals usually forage at or near the seabed (Bowen *et al.* submitted; Thompson *et al.* 1991). Thus, although interpretations of diving are not as clear-cut in phocids, it seems reasonable to suggest that most foraging in grey seals is associated with type-2 and particularly type-3 bouts (see Table 3.3) because a large fraction of the bout is spent at depth. Seasonal changes in the percentage of bout type used are also consistent with this interpretation, as higher percentages of type-3 bouts in October, November and December (Fig 3.6b) are associated with periods of higher mass gain and energy storage in males (Chapter 2).

Sex differences in the temporal organization of diving

It is interesting that males and females exhibited sex-specific differences in the temporal organization of diving at multiple temporal scales. At the level of individual dives, grey seals have sex-specific seasonal patterns of diving behaviour that could not be accounted for by the sexual size dimorphism of this species (Chapter 2). Rather, these differing seasonal patterns appear to reflect differences in the magnitude and timing of the reproductive costs of males and females (Clutton-Brock *et al.* 1983; Gittleman &

Thompson 1988; Wilkinson & Barclay 1997; Perrigo 1990). I suggested that the reproductive requirements of each sex result in different behavioural responses to the costs (Jonsson 1997) and benefits (Pomeroy *et al.* 1999; Hall, McConnell & Barker 2001; Godsell 1991; Lidgard *et al.* 2001) of long-term energy storage for reproduction. Due to the higher relative importance of stored body energy to female reproductive success, females appear to be more risk-averse by showing high levels of diving (and presumably foraging) effort early in the pre-breeding foraging period (Chapter 2; McNamara *et al.* 1991). In contrast male grey seals seem less risk averse, increasing dive effort gradually and gaining mass at a higher rate during the last few months prior to breeding (Chapter 2).

The results of this study showed that sex differences and sex specific seasonal patterns of diving behaviour are also evident at longer temporal scales. At the longest scale, although male and female grey seals had similar foraging trip durations, males spent almost twice as long hauled-out on land between trips and spent less time diving while on a foraging trip compared to females. This suggests that females are either less efficient predators (i.e., lower energy intake/time) or are more selective than males when searching for food. Evidence of this type of sex difference is found among size dimorphic ungulate species. Differences in the digestive efficiency, due to size dimorphism (Mysterud 2000), results in males (the larger sex) spending less time foraging than females, presumably because males can consume and digest abundant, lower quality foods while females are more selective and spend more time searching for higher quality forage (Ginnett & Demment 1997; Ruckstuhl 1998; Pérez-Barberia & Gordon 1999; Barboza & Bowyer 2000, but see Conradt *et al.* 2001). Given the size dimorphism seen in adult grey seals and the scaling relationships between body size, mass-specific metabolic rate and gut capacity (Klieber 1961; Mysterud 2000), similar, although less pronounced, effects may be expected in this carnivore species (Stirling & Derocher 1990).

Within foraging trips, grey seals organize their diving behaviour into bouts and bout clusters (Fig. 3.2). At both scales, there was a significant sex by month interaction. However, this interaction explained relatively little of the observed variability in bout cluster characteristics compared to bouts. Patterns of bout characteristics were sex-specific, similar to those seen at the level of individual dives (Chapter 2). Females had longer bouts and exhibited a higher level of effort immediately following the moult and again in the 3 months prior to the breeding season (Figs. 3.4 & 3.8) than during the summer months. In contrast, bout duration among males increased gradually through the summer and early fall and then decreased as the breeding season approached. In addition to shorter bouts, males also spent a smaller portion of bouts at depth (Fig. 3.4b). However, dive effort by males was not significantly different than females during the months immediately prior to breeding (Fig. 3.8). This indicates that while both sexes forage intensely during the last few months prior to breeding, they do so differently with males performing a larger number of short bouts whereas females perform a smaller number of longer bouts. Since grey seals dive both to forage within a patch and to travel among prey patches, longer bouts could be associated with greater distances traveled among patches or more time spent within a patch. Thus, the observed differences may reflect sex differences in both the spatial scale and efficiency of foraging. To test this hypothesis will require data on the spatial patterns of foraging, the temporal distribution of foraging success (Wilson *et al.* 1995; Weimerskirch, Wilson & Lys 1997; Bost *et al.* 1997) and the diet composition of males and females.

In addition to seasonal variability, bout characteristics, percentage of bout type used and dive effort varied inter-annually (Figs. 3.3, 3.6a, 3.10). During the period of this study, inter-annual variability and longer-term trends in both ocean bottom temperatures and prey abundance were documented on the Scotian Shelf (Zwanenburg *et al.* 2002). In general, the eastern Scotian Shelf was characterized by colder than average bottom temperatures and greatly reduced populations of the larger gadoid fishes. It is thought that both colder temperatures and reduced fish predation resulted in an increased abundance of small pelagic fishes, such as sandlance and capelin. Although I used a limited set of data to correlate grey seal diving with prey variability, the negative correlation between the index of small pelagic prey abundance and summer dive effort suggests that when such prey were more abundant, males satisfied their energy requirements in significantly fewer hours of diving. The non-significant, negative correlation between female dive effort and the index of prey abundance may be the result of the seasonal pattern of foraging in females. Across all years, July and August represent a period when females began to reduce both the total hours spent in bouts per day (Fig. 3.8) and the percent of square dives in bouts (Fig. 3.5), suggesting that this is a time of year when females are foraging less in general. As a result one might not expect to have a pronounced correlation between dive effort and prey abundance during these months. In contrast, July and August generally appear to be a time of higher dive effort in males (Figs. 3.8) and as a result may be more influenced by prey abundance as measured during the July fisheries survey. Given that only 7 years are available for this analysis, the lack of a significant correlation between female dive effort and the abundance of small pelagic prey may also be the result of low statistical power.

Sex-specific inter-annual variability in the pattern of bout type use (Fig. 3.7) suggests that males and females may respond differently to inter-annual environmental variability. Although the pattern of bout type varied among males, the type-3 to type-3 transition was dominant in all years of the study, whereas female transition probabilities were more variable. The interpretation of these transition probability residuals (Fig. 3.7) is hampered by the inability to assign a specific function to the different bout types. However, the strong sex by year interaction suggests that the temporal sequence of bout type contains information about the way in which males and females organize their behaviour in time and space, in response to changes in their physical environment and their strategy of storing energy for reproduction.

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Chapter 4. Seasonal Changes in Buoyancy and Diving Behaviour of Adult Grey Seals

Introduction

Two vertical forces affect objects that are immersed in fluid: the force of gravity and the buoyant force. The force of gravity is directed downward and has a magnitude determined by the mass of the object. The buoyant force is directed upward and is equal to the weight of the fluid displaced by the object (Cromer 1977). When the gravitational force is greater than the buoyant force the object is negatively buoyant and will sink. Conversely, when the buoyant force is greater than the gravitational force the object is positively buoyant and will float upward. Aquatic organisms must deal with these forces in the course of their daily activities. Individuals that are negatively or positively buoyant must expend energy to maintain their place in the water column or move in the direction opposite to the total force acting upon them. Organisms that are neutrally buoyant must exert effort to move vertically within the water column, regardless of direction.

In pinnipeds (true seals, fur seals, sea lions and walruses), as in other marine mammals, buoyancy is determined by the ratio of adipose to lean body tissue and the mass of the individual. Adipose tissue is positively buoyant while lean tissue is negatively buoyant; hence an animal with a high ratio of adipose to lean tissue is more buoyant than an animal of similar mass but with a lower ratio. Mass affects buoyancy since the force of gravity is related to the mass of an object. Thus, a large animal, with the same ratio of adipose to lean tissue as a small animal, would be less buoyant (e.g. Webb *et al.* 1998, Table 1). In phocids (true seals), terrestrial reproduction and moulting result in periods of fasting on land alternating with periods of foraging at sea. This pattern results in dramatic seasonal changes in body mass and composition (Sergeant 1976; Ryg *et al.* 1990; Lager *et al.* 1994; Chabot *et al.* 1996; Worthy *et al.* 1992; Costa *et al.* 1986). For example, following the moulting period, female grey seals (*Halichoerus grypus*) have a mean body mass of 126.2 kg and a fat concentration of 13.2%. In contrast, females average 210.2 kg, with fat accounting for 32.8% of body mass at the start of the breeding season 7 months later (Chapter 5). These large seasonal changes in body mass and composition will affect the buoyancy of individuals.

In many aquatic species, physiological mechanisms or anatomical structures have evolved which allow individuals to regulate buoyancy (e.g. the swim-bladders of fish, increased lung volume in sea otters, the ability of deep sea shrimp to replace heavy ions in their tissues with lighter ions). In general, phocids cannot adjust body mass or composition over the short-term to regulate buoyancy, thus Webb *et al.* (1998) argue that phocids may modify their diving behaviour in response to changes in buoyancy.

Webb *et al.* (1998) experimentally examined the effect of buoyancy on the diving behaviour of 13 juvenile northern elephant seals, *Mirounga angustirostris*. They found that descent rate differed significantly between buoyancy groups, with less buoyant animals having a faster rate of descent than more buoyant animals. Surprisingly, ascent rate of individual seals did not vary with buoyancy in the elephant seal study. Webb *et al.* (1998) concluded that the effect of buoyancy on ascent rate would be minimal relative to the lift generated by active swimming of individuals towards the surface. Webb *et al.* (1998) also concluded that differences in descent rate between buoyancy groups, and the strong correlation between descent rate and buoyancy among animals, confirmed the influence of buoyancy on diving behaviour. While this relationship appears fairly strong, the adjusted buoyancy of animals in the Webb *et al.* (1998) study ranged from +1.07 to -65.05 Newtons (N) or 43.7% to 24.2% adipose tissue, respectively. With the exception of newly weaned pups and some tentative evidence regarding pregnant elephant seals (Crocker *et al.* 1997), phocid seals do not obtain a body composition which would result in positive buoyancy (e.g., grey seals – this study, *Phoca vitulina*, - Bowen *et al.* 1992, *Phoca hispida* – Ryg *et al.* 1990, elephant seals – Williams 1995, Worthy *et al.* 1992). Thus by including individuals that had been manipulated to be positively buoyant, Webb *et al.* (1998) may have extended the relationship between descent rate and buoyancy over a range of buoyancy that is not entirely representative of that found in nature.

In the present study, I tested the hypotheses of Webb *et al.* (1998) that phocids modify their diving behaviour in response to seasonal changes in buoyancy. Specifically, I address the hypothesis that less buoyant individuals descend more rapidly than more buoyant individuals but have similar rates of ascent. To test this hypothesis, I measured longitudinal changes in buoyancy and diving behaviour of free-ranging adult grey seals during two periods that represent the maximum contrast in buoyancy of this species.

The grey seal is a relatively large phocid species found on both sides of the North Atlantic Ocean. Sable Island, Nova Scotia in the northwest Atlantic supports the largest breeding colony of grey seals in the world. Grey seals in this population congregate on Sable Island in May and June to moult and again in late December and January for the breeding period. As indicated above, adult grey seals are particularly lean (and consequently least buoyant) following the terrestrial moulting period in May. During the 7-month period following the moult, grey seals equipped with time-depth data loggers spend much of their time at-sea diving and presumably foraging (Chapters 2 & 3). Animals return to the island in late December and January for the breeding season having increased their body mass and adipose tissue mass by approximately 45% and 68%, respectively (Chapter 5). Thus, adult grey seals are most buoyant at the start of the breeding season.

Methods

Body composition and buoyancy measures

This study was conducted between May 1997 and January 1999 on Sable Island, a 45-km long, crescent-shaped, vegetated sandbar, located 300-km southeast of Halifax, Nova Scotia, Canada (43°90' N, 60°00' W). Fourteen adult grey seals (6 males and 8 females) were captured using hand-held nets (see Bowen *et al.* 1992) shortly following the spring moulting period in May 1997 or 1998 and again in January of the following year when these individuals returned to Sable Island at the beginning of the breeding season.

Body composition of each seal was measured using tritium (HTO) dilution at initial capture and again when recaptured in January. Individuals were weighed to the nearest 0.5 kg using Salter spring balances and then administered a precisely weighed dose of HTO ($0.5 \text{ mCi} * \text{mL}^{-1}$; at $0.02 \text{ g} * \text{kg}^{-1}$ body mass). HTO was injected intramuscularly (IM) and the needle and syringe were rinsed with unlabeled water (also injected) to insure complete delivery of the weighed isotope. A blood sample was taken from the extradural vein at 90 min post-administration and again 15-20 min later to confirm that isotope equilibration had occurred. Previous studies on grey seals have shown that HTO injected IM equilibrates with body water in $\leq$ 90 min and that 15-20 minute intervals are sufficient to detect any continued changes (Mellish 1999; Appendix 5.1).

Blood samples were collected into Vacutainers without additives and later centrifuged for 20-30 min. Serum aliquots (5 mL) were stored frozen (-20°C) in cryovials until analysis. Total water was recovered from each sample by distilling 50 µl aliquots of serum directly into pre-weighed scintillation vials, using the evaporated-freeze-capture method described by Ortiz *et al.* (1978). The vials were then re-weighed to obtain the mass of distillate to the nearest 0.1-mg and 10-mL of Scintiverse II was added to each vial. Each sample was counted for 5 min in a Beckman scintillation counter. Samples were analyzed in triplicate and the average specific activity was expressed as count per minute per gram distillate ($\text{CPM} * \text{g}^{-1}$). In cases where the triplicate samples had a coefficient of variation greater than 2%, the two closest samples were used. The specific activity of the injectant was determined at the same time as that of the serum samples.

HTO dilution space (D_{HTO}) was calculated using published equations (Bowen *et al.* 1999) and total body water (TBW) was estimated from a regression of isotope dilution space on TBW (Bowen & Iverson 1998). Percentage of total body fat was then calculated using the equation:

$$\%\text{TBF} = 105.1 - 1.47(\%\text{TBW})$$

developed for grey seals by Reilly and Fedak (1990).

In January, females were not recaptured until 1-3 days postpartum to allow mothers time to bond with newborns. As mean female mass loss during the first 5 days of lactation is 4.3 kg/day with fat comprising 58% of loss (Mellish *et al.* 1999), these rates of mass and fat loss were used to correct female body mass and percent fat to initial postpartum levels. Pup birth mass (5% of which is fat; Iverson *et al.* 1993; Mellish *et al.* 1999) was added to female mass to estimate body composition during late-term pregnancy. Mass lost in the placenta and amniotic fluid was not considered in this back-calculation of female mass and composition due to lack of data. Male grey seals were usually captured within 2 days of appearing on the breeding grounds, as indicated by the dry time (i.e., time on land) recorded by their time-depth recorders. During the breeding season male grey seals on Sable Island lose mass at an approximate rate of 2.5 kg/day with fat comprising 62% of mass loss (Godsell, 1991; Lidgard, Boness, & Bowen, unpublished; Coltman *et al.* 1998). These rates of loss and my best estimate of when the male returned to the island (first sighting of the male on the island or from diving data) were used to correct body mass and composition of males to pre-breeding conditions.

Adipose mass was calculated assuming that fat accounts for 76.9% and 92.3% of adipose tissue following the moulting period and at the beginning of the breeding season, respectively. In the absence of data on grey seals, these estimates of the lipid content in adipose tissue were based on the equation developed by Bowen *et al.* (1992) for female harbour seals (*Phoca vitulina*) during lactation. We used this equation to determine the lipid content of adipose tissue for an animal in a high-fat condition (i.e. at the start of lactation/pre-breeding season) and in a relatively low-fat condition (i.e. post-moulting season/at the end of lactation).

Buoyancy was calculated for each animal at initial post-moult (PM) capture and again at pre-breeding (PB) recapture using the equation from Webb *et al.* (1998):

$$B_T = (0.8871 * \text{adipose tissue (kg)}) + (-0.6689 * \text{lean body mass (kg)})$$

where B_T is total buoyancy in Newtons (N), 0.8871 is the mass-specific buoyancy of adipose tissue (N/kg) and –0.6689 is the mass-specific buoyancy of lean tissue (N/kg). Mass-specific buoyancy coefficients from Webb *et al.* (1998) were determined by calculating the buoyancy of 1 kg of tissue based on published estimates of tissue density (Webb, pers. comm.; Webb *et al.* 1998; Worthy *et al.* 1992; Nordoy & Blix, 1985).

Diving behaviour

At the initial PM capture, animals were anesthetized using Telazol (equal parts of tiletamine and zolazepam) immediately after the first equilibration blood sample was taken. Males and females were given an average dose of 0.45 and 0.85 mg/kg body mass, respectively (Bowen *et al.* 1999). Once immobilized, time-depth recorders (TDRs) or satellite-linked, time-depth recorders (SLTDRs) were glued to the pelage of the animal using 5-minute epoxy. TDRs, weighing 65 - 300 g or < 0.3 % of initial body mass, were placed on the lower back of the animals. SLTDRs, weighing approximately 600g or < 0.6% of initial body mass, were placed on the seals' head. TDRs and SLTDRs were programmed to record depth every 20 seconds. Because the memory capacity of instruments differed, instruments were duty-cycled (25% - 60% of days sampled) such that data were collected every few days over the entire 7-month deployment period.

In January, at the PB recapture, instruments were removed and TDR dive data were processed using software from Wildlife Computers (Woodinville, WA, USA). Zero-Offset Correction software was used to correct for shifts in the calibration of the instruments' pressure transducer over the data collection period. Data files could only be corrected for transducer drift in blocks of dives. Therefore, only dives > 4 m were analyzed, as instrument noise causes drift that is slightly greater than the depth resolution of the instrument (2m). Dive Analysis software (DA) was used to analyze the corrected dive records and to provide estimates of the individual dive variables: depth, duration, bottom time, surface interval between dives, descent rate and ascent rate. Dives during the first two weeks after PM deployment were selected to represent diving behaviour when animals were thin and consequently least buoyant. Dives during the two weeks prior to haul-out on Sable Island in January (PB) were considered to represent diving behaviour when animals were the fattest and most buoyant.

Statistical Analysis

Statistical analyses were performed using SPSS 8.0. Standard error (SE) is given as a measure of variability about the mean. Dive variables were examined for normality and transformed where necessary. Depth was strongly correlated with rates of descent and ascent (Spearman's rho = 0.553 and –0.555; p =0.002 and 0.002 respectively). Thus, repeated-measures ANOVAs with depth as a covariate was used to examine differences in rates of travel between the PM and PB period. Paired t-test analysis was used to compare all other dive variables between PM and PB periods.

The shape of individual dives can be represented in 2-dimemsions as a function of time and depth. Dive shapes were classified using discriminate function analysis (DFA) as described in Scheer & Testa (1995). Briefly, a subset of 2000 dives was visually inspected with individual dives being classified as one of five shapes – square, wiggle, V, left-skewed square and right-skewed square. Discriminate functions were derived from this subset such that DFA correctly classified 96.2 % of the dives. The resulting discriminate functions were used to classify the remaining dives. A repeated-measures, 2-way ANOVA was used to determine whether dive shape frequency differed between the PM and PB period.

Results

Buoyancy

Mean body mass of the recently moulted grey seals was 155.2 kg, with adipose tissue accounting for about 14% of body mass (Table 4.1). At the beginning of the breeding season, mean body mass of the same individuals had increased to 249.1 kg (i.e., by 60.5 %), with adipose tissue more than doubling to 34% of body mass. At both times, animals were negatively buoyant (Table 4.1). however, buoyancy was 47.9 ± 5.51% greater at the beginning of the breeding season than in recently moulted seals (Paired t-test: $p < 0.001$, n=14).

Diving Behaviour

A total of 13,307 dives was sampled in the two weeks following the moult. During this PM period, the number of dives per seal ranged between 318 and 1631, representing 3 to 9 days of sampling. In the two weeks prior to the breeding season on Sable Island, 10,118 dives were recorded from these same individuals. The number of dives per seal ranged between 213 and 1059, representing 4 to 6 days of data during the PB period.

Table 4.1. Body composition and buoyancy of individuals during post-moult (PM) and pre-breeding (PB) periods.

Seal	Sex	Mass (kg) PM	Mass (kg) PB	Fat (kg) PM	Fat (kg) PB	% adipose tissue PM	% adipose tissue PB	Buoyancy (N) PM	Buoyancy (N) PB
B541	F	150.0	287.5	18.5	99.6	16.0	37.5	-63.0	-24.4
E358	F	127.0	220.5	14.6	64.3	15.0	31.6	-55.4	-39.0
E463	F	126.5	195.0	19.2	63.2	19.8	35.1	-45.7	-23.9
M538	M	195.0	288.0	23.4	95.6	15.6	36.0	-83.1	-31.5
1C1	F	131.0	266.2	14.3	86.6	14.2	35.2	-58.7	-32.1
M523	M	155.0	227.0	6.2	67.7	5.2	32.3	-91.1	-37.7
M190	M	192.0	301.0	21.3	83.7	14.4	30.1	-85.3	-60.2
K448	F	116.0	148.0	12.5	47.5	14.0	34.8	-52.2	-18.9
8C9	F	111.0	222.7	10.1	76.9	11.8	37.4	-53.8	-19.3
K171	F	117.5	210.1	24.7	65.6	27.3	33.8	-28.7	-29.9
M18	M	170.0	269.0	26.2	93.3	20.0	37.6	-60.7	-22.6
F757	F	138.0	230.7	17.0	66.0	16.0	31.0	-58.0	-43.1
S-4272	M	201.5	305.0	7.3	92.1	4.7	32.7	-120.1	-48.7
S-4274	M	242.0	316.0	14.5	97.3	7.8	33.4	-132.5	-47.3
Mean		155.2	249.1	16.4	78.5	14.4	34.2	-70.6	-34.2
SE		10.55	13.05	1.66	4.34	1.60	0.66	7.69	3.31

Table 4.2. Summary diving statistics for study animals during post-moult (PM) and pre-breeding (PB) periods.

		# Dives		Mean Depth (m)		Mean Duration (min)		Mean Bottom Time (min)		Mean Surface Interval (min)		Mean Descent Rate (m/s)		Mean Ascent Rate (m/s)	
Seal	Sex	PM	PB	PM	PB	PM	PB	PM	PB	PM	PB	PM	PB	PM	PB
B541	F	601	712	39.6	49.3	3.9	6.2	2.4	3.7	5.1	1.8	1.0	0.7	0.9	0.6
E358	F	1324	812	48.7	41.3	6.0	5.6	3.5	3.7	2.6	1.2	0.7	0.9	0.6	0.8
E463	F	1155	911	27.4	10.9	4.1	4.6	1.9	3.0	1.8	1.8	0.4	0.3	0.4	0.3
M538	M	597	609	80.1	85.6	4.5	6.0	2.4	2.7	1.7	4.3	1.5	0.9	1.1	0.7
1C1	F	1631	796	55.0	68.9	3.9	5.2	1.8	2.4	1.2	2.4	0.9	0.9	0.8	0.8
M523	M	987	276	45.3	46.2	4.1	6.0	2.4	3.6	1.2	2.9	1.1	0.8	0.9	0.7
M190	M	1178	988	34.9	53.8	3.2	4.6	1.8	1.8	1.4	1.2	1.0	0.6	0.8	0.5
K448	F	743	859	38.0	51.2	3.7	6.8	2.2	4.2	2.6	1.0	1.0	0.9	0.8	0.7
8C9	F	1182	1059	59.2	66.7	3.6	4.2	1.9	1.9	2.2	1.5	1.2	0.9	1.2	0.9
K171	F	903	966	33.8	34.6	4.1	4.9	3.0	2.9	2.0	1.2	1.1	0.6	1.1	0.6
M18	M	1074	811	26.6	56.1	3.6	6.0	2.4	3.5	0.9	3.0	0.9	0.9	0.8	0.7
F757	F	836	725	76.8	75.3	5.8	7.0	3.4	4.4	3.5	1.7	1.2	1.0	1.1	0.9
S-4272	M	778	381	45.9	12.8	5.1	4.0	2.7	2.2	2.5	8.1	0.8	0.3	0.5	0.3
S-4274	M	318	213	58.4	55.4	5.6	5.9	2.9	3.1	10.8	5.0	0.9	0.7	0.5	0.5
Overall:															
Mean		950.5	722.7	47.8	50.6	4.4	5.5	2.5	3.1	2.8	2.7	1.0	0.7	0.8	0.6
SE		90.84	70.59	4.44	5.68	0.24	0.25	0.15	0.22	0.68	0.53	0.07	0.06	0.06	0.05
P-value[1]				0.520		0.003		0.008		0.850		[2]		[2]	

[1] Paired-sample t-test; [2] see Table 3

There were no significant differences in mean dive depth (Paired t-test: $p = 0.520$, $n = 14$) or surface time between dives (Paired t-test: $p = 0.850$, $n = 14$) between the two periods (Table 4.2). Mean dive duration and mean bottom time were significantly longer during the PB period compared to the PM period (Paired t-test: $p = 0.003$ and $p = 0.008$, $n = 14$, respectively; Table 4.2). Rates of descent and ascent increased with dive depth (Fig. 4.1) and were significantly faster (Table 4.3) during the PM period, when animals were less buoyant, than during the PB period, when they were more buoyant.

I also examined the effect of changes in buoyancy on diving behaviour by calculating the difference between descent and ascent rate for each dive. The mean difference between descent and ascent rate was significantly correlated with buoyancy within the PM period ($r = -0.829$, $p < 0.001$) but not during the PB period ($r = -0.055$, $p = 0.853$). In almost all cases, descent rate was faster than ascent rate (Fig. 4.2) and as individual animals became more buoyant (from PM to PB) the magnitude of the difference between the two rates decreased (Paired t-test: $p = 0.010$, $n = 14$).

Changes in buoyancy might also be reflected by the frequency distribution of dive shapes used by grey seals during the PM and PB periods. However, the distribution of dive shapes did not differ between the two periods (Fig. 4.3). A repeat-measures, 2-way ANOVA also showed no significant interaction between dive shape and condition of the individual ($F = 2.13$, $df = 4,65$, $p = 0.087$). Square-shaped dives were by far the most frequently used, accounting for over 70% of dives during both periods. Right-skewed square dives were the second most common shape, representing 12.1 and 13.9 % of dives during the low and high buoyancy periods, respectively. None of the remaining dive shapes accounted for more than 6.6% of dives used during either period.

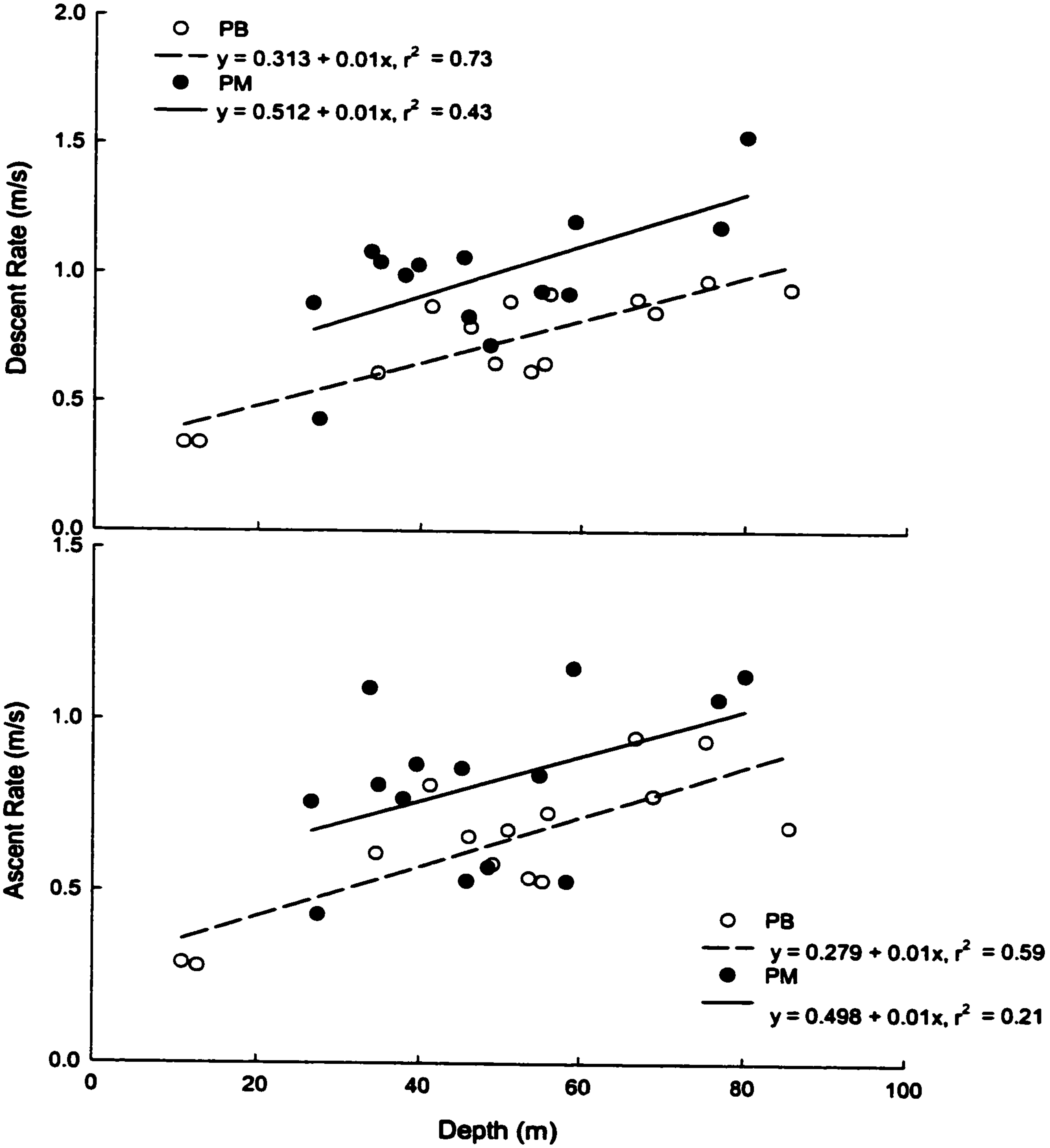

Figure 4.1: Relationships between mean depth and a) mean descent rate and b) mean ascent rate during the PM and PB periods for 14 adult grey seals. See Table 4.3 for statistical results.

Table 4.3. Results of repeated measures ANOVA comparing PM and PB grey seals with depth as covariate.

		Descent Rate, n = 14			Ascent Rate, n = 14		
		Parameters	t	p	Parameters	t	p
Condition (PB) on depth							
	constant	0.5071	4.058	0.002	0.4508	2.748	0.017
	slope	0.0103	6.030	< 0.001	0.0084	3.749	0.003
Within subject difference (PM vs. PB)							
	constant	0.1809	4.370	< 0.001	0.1186	3.197	0.008
	slope	0.003	0.658	0.523	-0.0001	-0.018	0.986

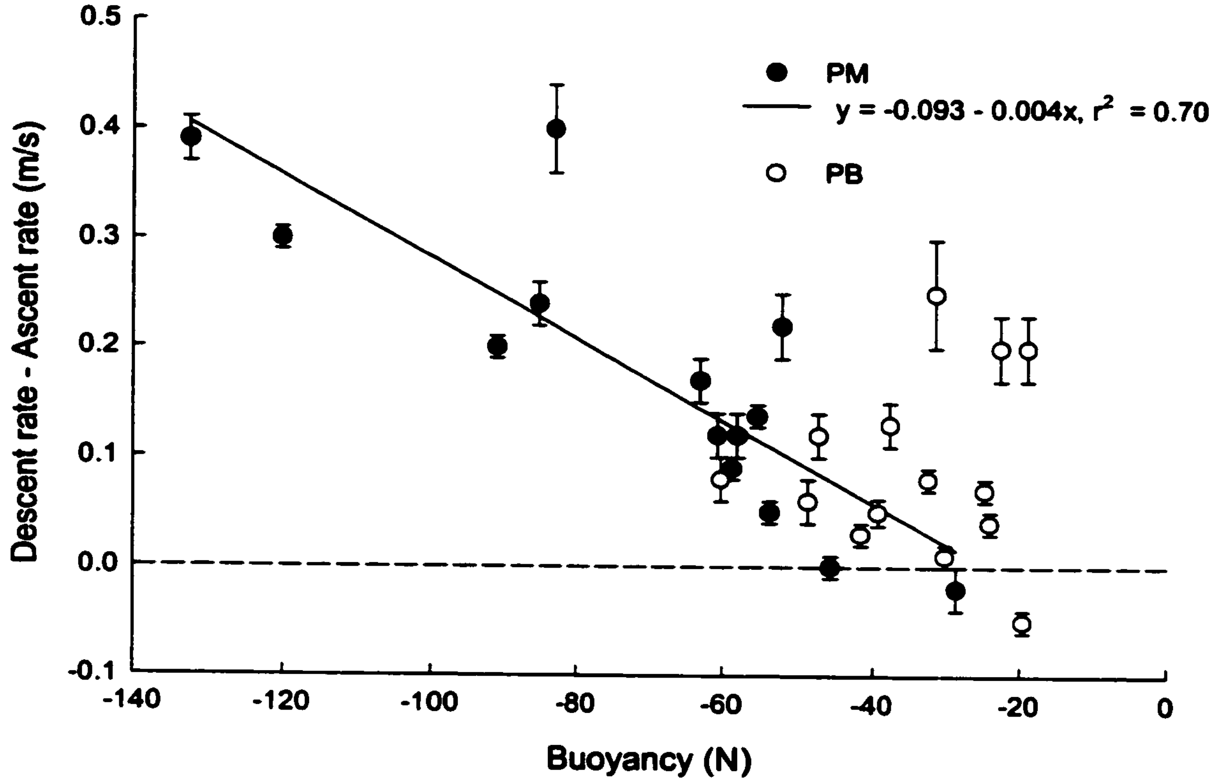

Figure 4.2: Relationship between buoyancy and the difference between descent and ascent rate of individual dives for 14 adult grey seals during both the PM and PB period. Error bars are one SE. r and p values refer to Pearson's correlation statistics

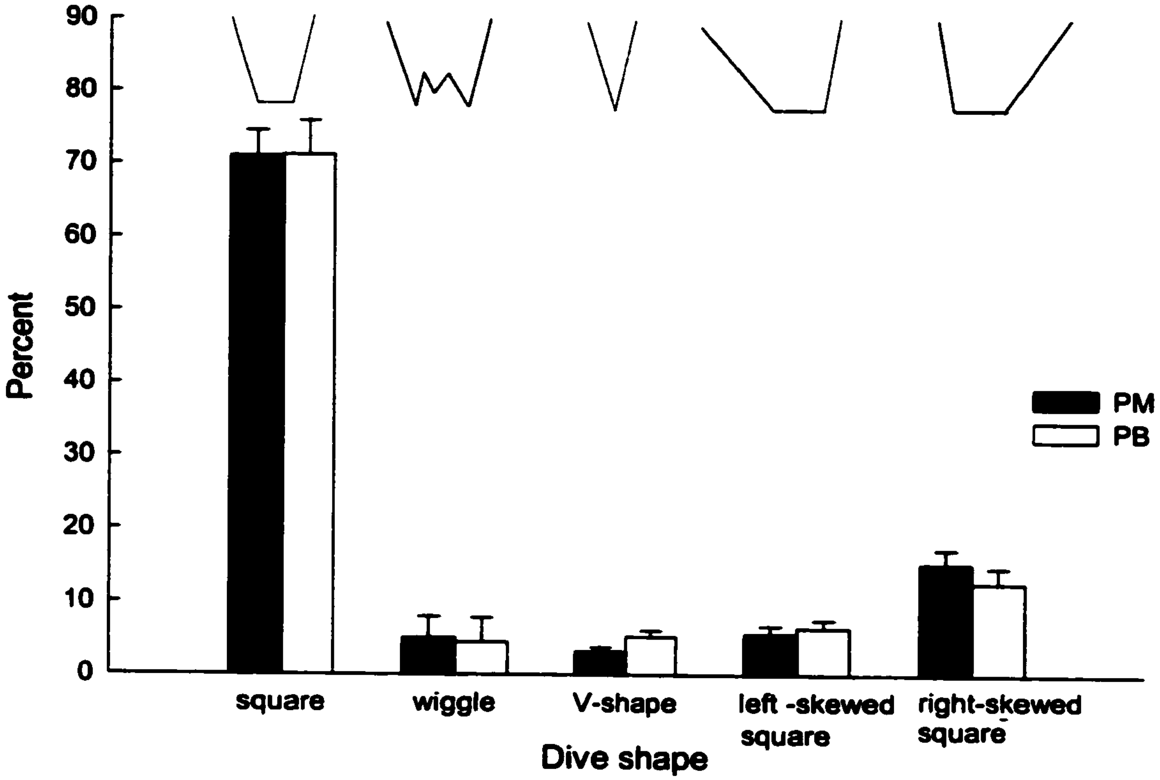

Figure 4.3: Dive shape distribution of 14 adult grey seals during both the PM and PB periods.

Discussion

Buoyancy estimation

My calculations of buoyancy are affected by two potential sources of error. The equation developed by Webb *et al.* (1998) for determining buoyancy uses mass-specific values of buoyancy for adipose and lean tissue and requires accurate measurements of the masses of both tissues. Thus, the first source of error involves the estimation of the masses of these tissues. In estimating body composition from total body water, lipid mass, not adipose tissue mass, is estimated. Adipose tissue mass must subsequently be calculated from fat mass based on the percent lipid in adipose tissue. While adipose tissue is composed primarily of lipid, water and protein are also significant components. It is reasonably well established that when animals fatten, fat cells (adipocytes) fill with lipid. Conversely, when animals lose fat, adipocytes empty resulting in a lower lipid and greater water and protein content of adipose tissue (Emery 1969). This change in adipose tissue composition will have substantial effects on the estimation of adipose tissue mass from lipid mass and hence on the calculation of buoyancy. Data on the lipid content of adipose tissue in grey seals is not available during the PM or PB periods. However, Bowen *et al.* (1992) found that the adipose tissue of fattened female harbour seals at parturition contained 92.3% fat, 2.2% protein and 5.5% water. In contrast, 20 days later, after substantial mass and fat loss during lactation, adipose tissue contained 76.9% fat, 5.9% protein and 17.2% water. Individual grey seals at the end of the moulting period and harbour seal females near the end of lactation appear similarly depleted, thus, lipid content of adipose tissue at these times is likely similar. Body fat content is similar in both species at the start of the breeding season (Bowen *et al.* 1992; Chapter 5). Hence, these values for the proximate composition of harbour seal blubber should provide reasonable estimates of grey seal adipose tissue and thus buoyancy during the PM and PB periods. The assumption of a constant value of lipid content in adipose tissue would clearly lead to erroneous estimates of buoyancy, particularly in studies examining temporal changes in buoyancy.

The second source of error involves the relationship between mass-specific buoyancy and tissue density (Webb *et al.* 1998; Webb pers. comm.). Given the expected large seasonal changes in the lipid content (see above), the density of adipose tissue will not be a constant. As individuals become depleted in fat, adipose tissue should become denser as the relative lipid content decreases and protein content increases. This being the case, the density and hence mass-specific buoyancy of adipose tissue would differ between the PM and PB periods. However, seasonal changes in the density of adipose tissue are not available for grey seals or other phocid species. By assuming a constant mass-specific buoyancy of adipose tissue, I have likely underestimated the seasonal change in buoyancy of individuals.

Buoyancy and drag effects on diving

Adult phocid seals undergo dramatic seasonal changes in body composition and body mass. These changes in turn affect the force of buoyancy acting on individuals. Despite these dramatic seasonal changes, I found that adult grey seals were always negatively buoyant. However, the magnitude of this downward force decreased significantly as individuals increased their lipid stores for reproduction. Changes in buoyancy should be most evident in the rates of ascent and descent. Consistent with this expectation, grey seals descended at a significantly faster rate when less buoyant (PM), suggesting that individuals were aided by negative buoyancy during descent. This finding confirms the results of Webb *et al.* (1998) that descent rate in elephant seal is affected by changes in buoyancy. Given the relationship between descent rate and buoyancy, I expected grey seals to ascend faster during the PB period (i.e., relatively more buoyant) than during the PM period. Although fatter individuals would not be aided by lift from buoyancy (i.e. they are not positively buoyant), they would have less downward force to work against while actively swimming to the surface. Webb *et al.* (1998) found no difference in the ascent rate of elephant seals relative to changes in buoyancy. In contrast, less buoyant grey seals ascended faster than more buoyant seals (Table 4.2) contradicting the predicted effect of buoyancy. These results indicate that grey seals travel to and from the surface faster when they are thin and consequently less buoyant.

Mobile aquatic organisms are also affected by drag. The force of drag impedes movement through a fluid and is a function of velocity, fluid density, cross-sectional area and hydrodynamic shape (i.e., coefficient of drag). In the present study, drag would be greater on an animal during the PB period compared to the PM period, given the increase in cross-sectional area associated with fattening (assuming the same travel speed). To decrease drag, grey seals could travel more slowly during the PB period. This is consistent with the observed slower rates of travel when animals were more buoyant. To compare the relative magnitude of drag and buoyancy during vertical travel, I calculated drag (D) for PM and PB individuals based on girth measurements for grey seals in eastern Canada (M. Hammill, unpublished data). Drag was calculated using the equation:

$$D = 0.5\rho a U^2 C_d$$

where ρ is the density of seawater (1024 kg/m^3), a is the frontal area of the seal calculated from girth measurements (thin: girth = 1.12 m, $a = 0.10$ m^2; fat: girth = 1.84 m, $a = 0.27$ m^2), U is the swim velocity, and C_d is the drag coefficient (0.09 - Williams & Kooyman 1985; Webb *et al.* 1998). The calculated drag for a thin and fat grey seal traveling at an average swim speed of 0.9 m/s is 3.73 N and 10.08 N, respectively. While the force of drag is almost three times larger for a fat seal, the magnitude of drag is small relative to the buoyant force affecting the animals in their respective conditions (Table 4.1). Hence, buoyancy increases by a larger magnitude than drag as the animal fattens. As a result, the effect of drag cannot explain the association of increased buoyancy and decreased rate of ascent.

Descent rate was almost always faster than ascent rate for individual dives (Table 4.2). When considering the combined role of buoyancy and drag on rate of vertical movement this result seems logical (Webb *et al.* 1998). During descent, the force of buoyancy and drag work in opposite directions. However, since the negative buoyancy exceeds the magnitude of drag, the animal is aided in descent by a downward force. On ascent, individuals are faced with the cumulative force of negative buoyancy and drag and as a result will have to work harder to ascend (Webb *et al.*, 1998). Thus, regardless of buoyancy, descent is energetically less costly than ascent, resulting in faster rates of descent. As an animal fattens and becomes less negatively buoyant the differential cost of descent and ascent lessens (Fig. 4.2) providing evidence for the effect of buoyancy.

Webb *et al.* (1998) suggested that animals with greater fat stores might have to exert greater effort to maintain a position at the bottom while feeding benthically due to lift from buoyancy. If this were the case, given finite oxygen capacity, more buoyant animals would be expected to have dives of shorter duration and spend less time at the bottom during the PB period. In this study, grey seals had significantly longer dive durations and bottom-times when they were most buoyant, contradicting Webb *et al.*'s (1998) prediction. However, grey seals in this study were always negatively buoyant and as a result they would not have to expend energy to maintain position on the bottom for benthic feeding. Given that dive depth did not differ with respect to changes in buoyancy, the increased dive duration may be the result of slower rates of descent and ascent in more buoyant individuals. However, this does not explain why time spent at the bottom of dives should increase with buoyancy. Alternatively, increased dive duration and bottom time might be associated with increased foraging effort just prior to the breeding season. Seasonal changes in dive effort and presumably foraging occur in both male and female grey seals equipped with TDRs (Chapter 2 & 3), and show that both sexes increase dive effort as the breeding season approaches.

The interpretation of longitudinal measurements of diving behaviour in free-ranging grey seals is potentially confounded by several factors. In addition to the changes in body mass and buoyancy, differences in foraging location and diet may also have affected the characteristics of diving. For example, as discussed above, the observed differences in dive duration and bottom time between the PM and PB period may be the result of increased foraging effort. However, these confounding factors are unlikely to be the cause of the observed differences in vertical rates of travel for several reasons. First, grey seals exhibited a similar distribution of dive shapes (Fig. 4.3) and mean dive depth (Table 4.2) between the two periods, suggesting that individuals were foraging in similar habitats and using similar foraging tactics. Second, animal-borne video data shows that rates of vertical travel during diving did not differ significantly among prey types in adult harbour seals (Tully 1999, Bowen *et al.* submitted). Nevertheless, including these potentially confounding factors in future analyses would provide a stronger test of the influence of buoyancy on diving behaviour.

This study confirms the hypothesis of Webb *et al.* (1998) and demonstrates that seasonal changes in buoyancy in individual adult grey seals affect rates of descent during diving. Seasonal differences in descent rate are convincingly associated with changes in buoyancy. However, seasonal changes in ascent rates require another explanation. Seasonal changes in the cost of transport with changes in body mass may better explain the observed seasonal changes in ascent rate. To test this hypothesis, it will be necessary to measure the cost of transport during ascent in thin (less buoyant) and fat (more buoyant) individuals.

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Chapter 5. Sex differences in seasonal energy storage and utilization in a size dimorphic phocid seal

Introduction

Recent interest in state-dependent life histories has focused on the importance of the physical state of an animal to its reproductive decisions and fitness (McNamara & Houston 1996; Pitcher *et al.* 1998; Boyd 2000; Glazier 2000). Body mass and energy content are important components of an individual's state and are expected to vary throughout an individual's lifetime. For instance, many northern and temperate herbivores go through seasonal changes in body mass, composition and energy content that coincide with the seasonal changes in food availability (Mautz 1978; Adamczewski *et al.* 1987; Worden & Pekins 1995; Chan-McLeod *et al.* 1999). However, seasonal changes in mass and body condition are also often linked to reproduction (e.g., Kenagy *et al.*1989; Ryg *et al.* 1990; Virgl & Messier 1992; White *et al.* 1997). Reproduction represents a period of increased energy demand, associated with rearing offspring, mate acquisition, and resource defense. These reproductive costs can alter the magnitude and timing of seasonal fluctuations in body mass brought about by changes in food availability (Mitchell *et al.* 1976; Leader-Williams & Ricketts 1981; Hewison *et al.* 1996). More directly, reproductive behaviour may severely limit foraging (e.g., phocid and male otariid seals, baleen whales, Holarctic bears, and male ungulates) such that individuals must use previously stored body energy to meet maintenance metabolic requirements and the additional costs of reproduction. Females which rely solely on previously stored energy during offspring rearing are referred to as "capital breeders" (Jonsson 1997) and are subject to especially pronounced seasonal patterns of energy accumulation and depletion. Reliance on stored energy to support reproductive costs also applies to the males of some species.

In mammals, the magnitude of reproductive costs differs between males and females (Gittleman & Thompson 1988; Perrigo 1990; Munks & Green 1995; Wilkinson & Barclay 1997) with the energetic costs to females (gestation and lactation) being considerably higher than the energetic costs to males (mate acquisition and resource defense). The timing and duration of reproductive costs also differ between the sexes. In most mammalian species males do not contribute to parental care, such that male reproductive costs are generally limited to the breeding period. In contrast, females incur energetic costs from the early stages of gestation until the offspring is weaned. The fitness consequences of not obtaining sufficient energy to meet these energetic costs can also differ between males and females. A male's fitness is most closely associated with the number of mating opportunities whereas a female's fitness is more closely associated with her energetic ability to successfully wean offspring (Trivers 1972). As a result, fitness-maximizing strategies of males and females typically differ (Clutton-Brock & Parker 1992; Jormalainen *et* al. 2001) and may be expected to influence the foraging behaviour and pattern of energy storage by males and females.

Despite the number of studies that have examined sex differences in seasonal changes of body energy, these have included only a few carnivore species (Buskirk & Harlow 1989; Prestrud & Nilssen 1992; Poulle *et al.* 1995). Unlike northern and temperate herbivores that experience dramatic seasonal reductions in food quality and quantity, most carnivores ought to be less affected by seasonal variability in prey characteristics. As a result, in non-growing individuals, seasonal fluctuations in energy stores are more likely to result solely from the allocation of energy to reproduction. In capital breeding species, depletion of body energy stores can be extreme. For example, in polar bears (*Ursus maritimus*), females lose approximately 44% of their stored body energy during the denning period (calculated from Atkinson & Ramsay 1995). Thus, capital breeding carnivores provide a good opportunity to examine how patterns of energy storage differ between males and females as a result of differing reproductive costs.

I examined the seasonal pattern of energy storage and allocation by male and female grey seals, *Halichoerus grypus*. The grey seal is a polygynous, size-dimorphic species (Family Phocidae), with adult males being approximately 1.5 times heavier than adult females in the Northwest Atlantic population (Mohn & Bowen 1996). Female grey seals are capital breeders, relying solely on stored body energy accumulated prior to parturition to support the high energetic costs of lactation and their own metabolic expenditures during the breeding season. Females with low body mass (and hence low energy stores) at parturition tend to wean smaller pups or wean their pups pre-maturely (Iverson *et al.* 1993; Mellish *et al.* 1999; Pomeroy *et al.* 1999), thus increasing the probability of juvenile mortality (Coulson 1960; Coulson & Hickling 1964; Hall *et al.* 2001). Female grey seals enter estrous and are mated during the late stages of lactation, however implantation does not occur for 3 - 4 months. Male grey seals use a variety of mating tactics during the breeding season. These range from tenure of several weeks on land to roving, in which males alternate short foraging trips to sea with attempts at mate acquisition on land (Boness & James 1979; Amos *et al.* 1993; Twiss *et al.* 1994; Lidgard *et al.* 2001). Despite these trips to sea, foraging by males is greatly reduced during the breeding period and individuals rely on previously accumulated energy stores to extend the period of time they can remain ashore competing for and acquiring mates. While the quantity of stored energy is important for this purpose, Godsell (1991) and Lidgard *et al.* (2001) found that the correlation between body mass and male mating success is weak. Hence, reproductive success of males should be less dependent on the amount of stored body energy at the beginning of the breeding season than is the reproductive success of females. Although all individuals begin foraging immediately after the breeding season, 4-5 months later they are subject to another period of fasting while they moult on land.

As a result of these alternate periods of terrestrial fasting and foraging at sea, grey seals go through dramatic seasonal changes in body mass and composition. Both sexes deplete body energy stores during periods of terrestrial fasting, however, I predicted sex differences in the seasonal pattern of energy accumulation due to sex-specific reproductive costs (magnitude and timing) and differential fitness consequences associated with having insufficient stored body energy to meet reproductive needs. Female mammals in poor condition are less likely to become pregnant or carry the pregnancy to term (Mitchell *et al.* 1976; Thomas 1982; Boyd 1984; Albon *et al.* 1986; White *et al.* 1997; Pitcher *et al.* 1998). Thus, I expected female grey seals to recover body condition quickly following the breeding and moulting periods to support both pregnancy and the future energetic costs of lactation. While males should also recover body condition after these extended periods of fasting, I expected the accumulation of energy stores for reproduction to occur more gradually as there is no immediate reproductive requirement and lower risk associated with reduced body condition.

Finally, while the benefits of stored body energy are well understood (Chapin *et al.* 1990; Jonsson 1997), there are also potential costs associated with the storage of body energy (Witter & Cuthill 1993; Gosler *et al.* 1995; Jonsson 1997; Bonnet *et al.* 1998; Gentle & Gosler 2001). In phocids, such costs could include an increased risk of predation, decreased mobility on land, and increased cost of transport during diving (Webb *et al.* 1998; Chapter 4). The way in which male and female grey seals deal with the costs associated with energy storage is likely to differ since the relative reproductive benefit from early storage of body energy is predicted to be higher for females. Thus, I predicted that the seasonal pattern of energy storage and allocation would differ between male and female grey seals as a result of sex differences in the benefits of storing energy for reproduction and the costs of storing that energy over long periods of time.

Methods

The study was carried out between January 1997 and May 2000 on Sable Island (43°55'N, 60°00'W), a crescent-shaped, partially vegetated sandbar approximately 300 km south-east of Halifax, Nova Scotia, Canada. Sable Island is the largest haul-out location for grey seals in the Northwest Atlantic population. Animals congregate in large numbers on the island in May and June to moult, in late December and January to rear offspring and mate, and in smaller numbers throughout the year between foraging trips.

Adult grey seals were captured on-shore using hand-held nets (see Bowen *et al.* 1992) five times throughout their annual cycle (Fig. 5.1): Start of the moult (May), End of the moult (June), Mid-foraging period (early October), Start of breeding (late December/early January) and End of breeding (February). In addition, a subset of

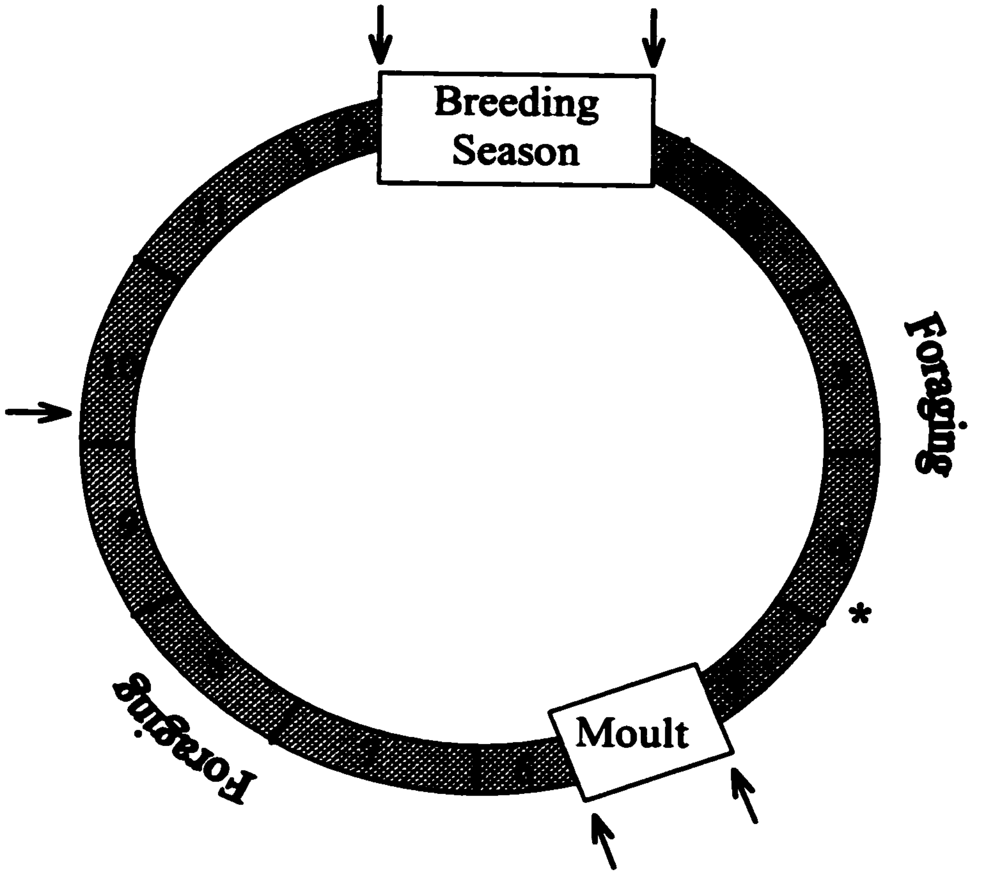

Figure 5.1: Annual cycle of terrestrial fasting and at-sea foraging for grey seals in the Northwest Atlantic. Numbers indicate month of the year. Periods of terrestrial fasting and their associated activities are shown in boxes, arrows depict times of sampling and the star denotes time of implantation in females.

animals sampled in June or October were re-captured the following January and February to measure longitudinal changes in body mass and composition.

Individuals were weighed to the nearest 0.5 kg using Salter spring balances and then administered a known quantity of tritiated water (HTO; 0.5 mCi * mL^{-1}; at 0.02 g * kg^{-1} body mass). HTO was injected intramuscularly (IM) and the needle and syringe were rinsed with unlabeled water (also injected) to insure complete delivery of the weighed isotope. A blood sample was taken from the extradural vein at 90 min post-administration and again 15-20 min later to confirm that isotope equilibration had occurred. Previous studies on grey seals have shown that HTO injected IM equilibrates with body water in $\leq$ 90 min and that 15-20 minute intervals are sufficient to detect any continued changes (Mellish 1999; Appendix 5.1).

Blood samples were collected into Vacutainers without additives and later centrifuged for 20-30 min. Serum aliquots (5 mL) were stored frozen (-20°C) in cryovials until analysis. Water was recovered from each sample by distilling 50 µl aliquots of serum directly into pre-weighed scintillation vials, using the evaporated-freeze-capture method described by Ortiz *et al.* (1978). The vials were then re-weighed to obtain the mass of distillate to the nearest 0.1-mg and 10-mL of Scintiverse II was added to each vial. Each sample was counted for 5 min in a Beckman scintillation counter. Samples were distilled and analyzed in triplicate and the average specific activity was expressed as count per minute per gram distillate (CPM * g^{-1}). In cases where the triplicate samples had a coefficient of variation greater than 2%, the two closest samples were used. The specific activity of the injectant was determined at the same time as that of the serum samples.

HTO dilution space was calculated according to Bowen *et al.* (1999) and total body water (TBW) was estimated from a regression of isotope dilution space on TBW (Bowen & Iverson 1998). Total body fat (TBF), protein (TBP) and energy (TBE) were calculated from the following equations developed for grey seals by Reilly & Fedak (1990):

$$\%TBF = 105.1 - 1.47(\%TBW)$$

$$\%TBP = 0.42(\%TBW) - 4.75$$

$$TBE\ (MJ) = 40.8(\text{Body Mass}) - 48.5(TBW) - 0.4.$$

In January, females were not recaptured until 1-3 days postpartum to allow mothers time to bond with their pups. For females sampled at the beginning and end of the breeding season, I corrected mass and composition to parturition levels using each individual's rates of mass and composition loss, which is usually linear (Mellish *et al.* 1999). Where mass and composition was not obtained at the end of breeding, I used the average rate of mass and fat loss in female grey seals (Mellish *et al.* 1999 and this study) to predict parturition mass and composition. Male grey seals were captured within 2 days of appearing on the breeding grounds based on daily surveys of the island. During the breeding season, male grey seals on Sable Island lose mass at an approximate rate of 2.5 kg/day with fat comprising 62% of mass loss (Godsell, 1991; Lidgard, Boness, and Bowen, unpublished). These rates of loss were used to correct body mass and composition of males to arrival conditions. As with females, when males were sampled at both the beginning and end of the breeding season, I used each individual's rate of mass and composition loss to correct mass and composition. During the moult in May, individuals were considered to be at the start of the moult if 95% or more (visual estimate) of the previous year's pelage was still present. Individuals were considered to be at the end of moult only when they were fully moulted.

Statistical analyses were done with SPSS 10.1. Standard error (SE) is given as a measure of variability about the mean. Total body energy was significantly correlated with body mass (Pearson's correlation = 0.900, $p < 0.001$). As a result, analysis of variance with body mass as a covariate was used to examine sex-differences in the seasonal pattern of TBE. Homogeneity of regression slopes between groups was tested prior to conducting the covariance analysis. This method was considered the most appropriate way of correcting for the effects of body mass given that the two variables are not isometrically related (Raubenheimer & Simpson 1992; Raubenheimer 1995). To maintain statistical independence, in cases where a seal was sampled more than once, a single randomly selected observation was used. Longitudinal analyses were used to examine the rate and composition of mass change by individuals during the annual cycle.

Results

Cross-sectional data

Body mass and composition was measured in 135 adult grey seals (67 males and 68 females). With the exception of the start of breeding sampling period, equal numbers of males and females were studied in each period (Table 5.1). It was not possible to sample at all time periods in every year of the study due to logistic constraints. However, start

Table 5.1: Seasonal mass and body composition of male and female grey seals (n = 135). Mean ± SE (CV)

		Sampling Period[1]				
	Sex	EB	SM	EM	MF	SB
Body Mass (kg)	M	241 ± 10.5 (0.14)	240 ± 6.4 (0.10)	199 ± 9.7 (0.19)	239 ± 11.9 (0.17)	291 ± 7.7 (0.10)
	F	144 ± 4.7 (0.11)	160 ± 4.6 (0.11)	133 ± 5.9 (0.17)	153 ± 4.0 (0.09)	207 ± 8.5 (0.16)
% Water	M	57.1 ± 1.03 (0.06)	58.8 ± 0.69 (0.05)	63.7 ± 0.97 (0.06)	56.2 ± 1.15 (0.07)	52.9 ± 1.01 (0.07)
	F	59.5 ± 1.54 (0.9)	55.9 ± 0.72 (0.05)	60.9 ± 1.01 (0.06)	56.9 ± 0.99 (0.06)	49.4 ± 0.85 (0.07)
% Protein	M	19.2 ± 0.42 (0.07)	19.9 ± 0.29 (0.06)	22.0 ± 0.40 (0.07)	18.8 ± 0.49 (0.09)	17.4 ± 0.42 (0.09)
	F	20.2 ± 0.65 (0.11)	18.7 ± 0.30 (0.06)	20.8 ± 0.43 (0.08)	19.2 ± 0.42 (0.08)	16.0 ± 0.36 (0.09)
% Fat	M	21.2 ± 1.51 (0.24)	18.7 ± 1.00 (0.21)	11.5 ± 1.41 (0.47)	22.5 ± 1.68 (1.68)	27.5 ± 1.51 (0.20)
	F	17.7 ± 2.26 (0.42)	23.0 ± 1.07 (0.18)	15.6 ± 1.49 (0.37)	21.4 ± 1.45 (0.23)	32.5 ± 1.25 (0.15)
Total Body Energy (MJ)	M	3180 ± 223.8 (0.23)	2956 ± 125.7 (0.16)	2014 ± 196.3 (0.38)	3292 ± 272.7 (0.29)	4460 ± 246.9 (0.23)
	F	1729 ± 134.5 (0.26)	2205 ± 110.6 (0.19)	1534 ± 142.9 (0.36)	2030 ± 110.9 (0.19)	3504 ± 187.0 (0.21)
N	M	11	15	15	12	14
	F	11	15	15	12	15

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[1] Sampling periods are as follows: EB = End of breeding, SM = start of moult, EM = end of moutl, MF = Mid-foraging, and SB = start of breeding.

and end of breeding samples were collected for both sexes in 1998, 1999 and 2000. Animals were sampled at the start of the moult in May of 1999 and 2000, the end of the moult in June of 1997, 1998 and 1999, and mid-foraging samples were collected in October of 1997 and 1999. Given the relatively small sample size when stratified by period and year, I did not investigate inter-annual changes in body composition. However, equal numbers of males and females were sampled in each year/season group.

Average body mass ranged from 199 to 291 kg in males and from 133 to 207 kg in females (Fig. 5.2, Table 5.1). Both sexes were lightest following the spring moult and heaviest at the beginning of the breeding season 7 months later. However, males and females showed significantly different seasonal patterns of energy storage and depletion (ANCOVA with body mass as a covariate: $F_{4, 124} = 2.479$, $p = 0.047$; Fig. 5.3) with females having a higher energy density throughout the year. By the beginning of the spring moult, females had increased their TBE by 27.5% relative to their end of breeding condition whereas males had lost a further 7.1% of TBE (Table 5.1). Both sexes lost mass and body energy during the spring moult, but females remained in better condition than males (Fig. 5.3). However this difference was only significant at the beginning and end of the moulting period. By the middle of the subsequent foraging period, males and females were in relatively similar body condition with 22.5 and 21.4 % fat, respectively (Fig. 5.4). From the end of the moult to the beginning of the breeding season both males and females more than doubled their body energy stores (Table 5.1). However, males gained more TBE between the end of moulting and mid-foraging season, whereas females gained more TBE during the three months prior to parturition (Fig. 5.3). Both

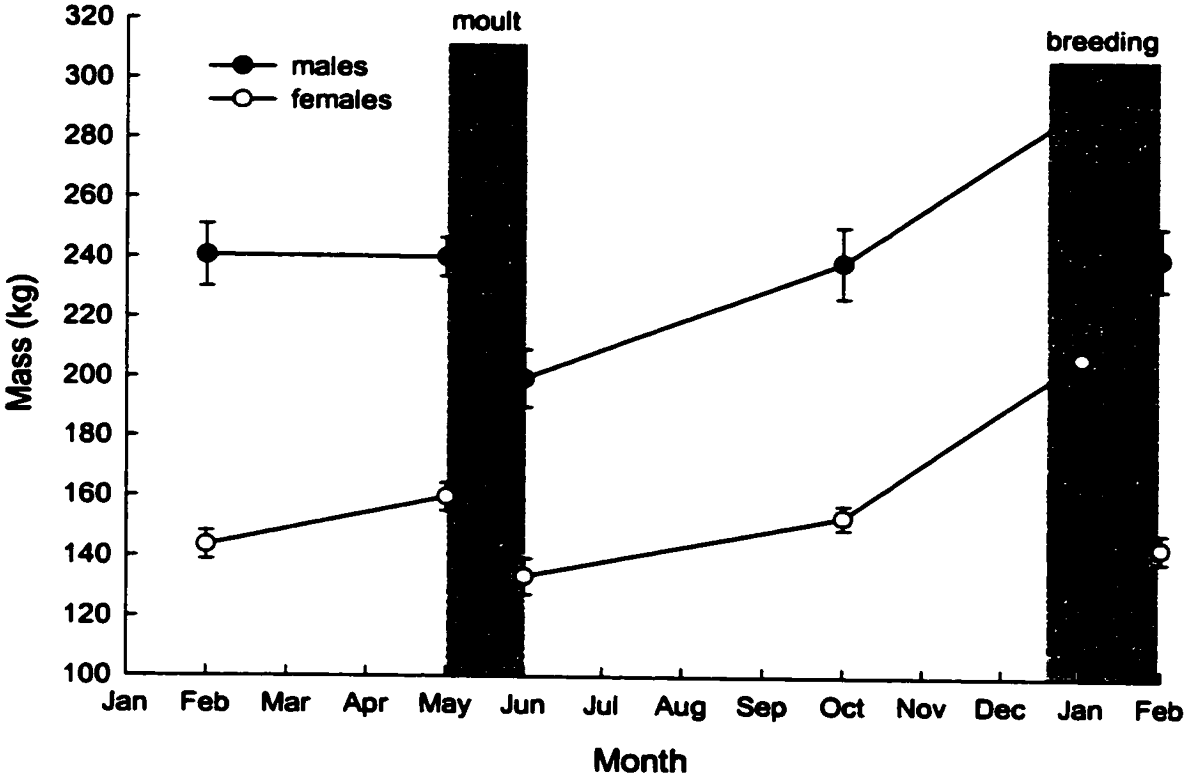

Figure 5.2: Seasonal changes in body mass in male and female grey seals (mean ± SE). Sample sizes are as indicated in Table 5.1.

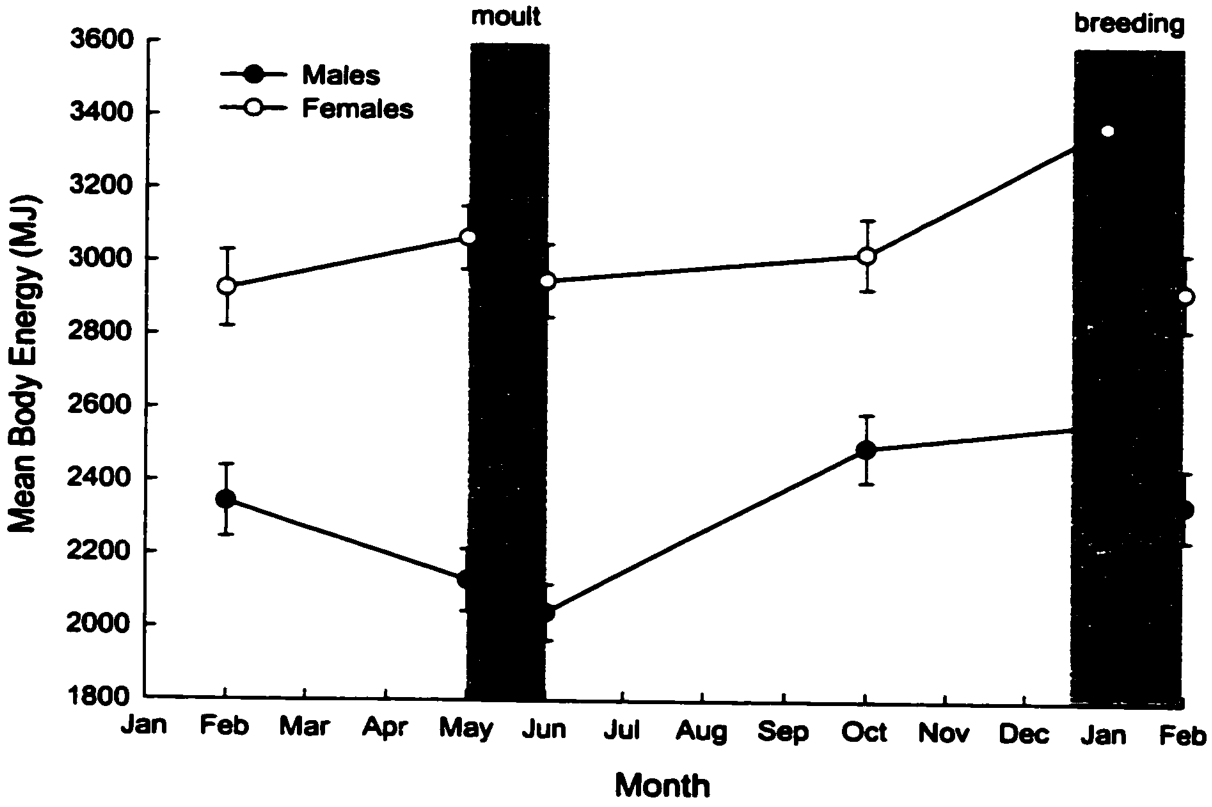

Figure 5.3: Seasonal changes in total body energy. Values are means from an ANCOVA with body mass as the covariate ± 1 SE. Sample sizes are indicated in Table 5.1.

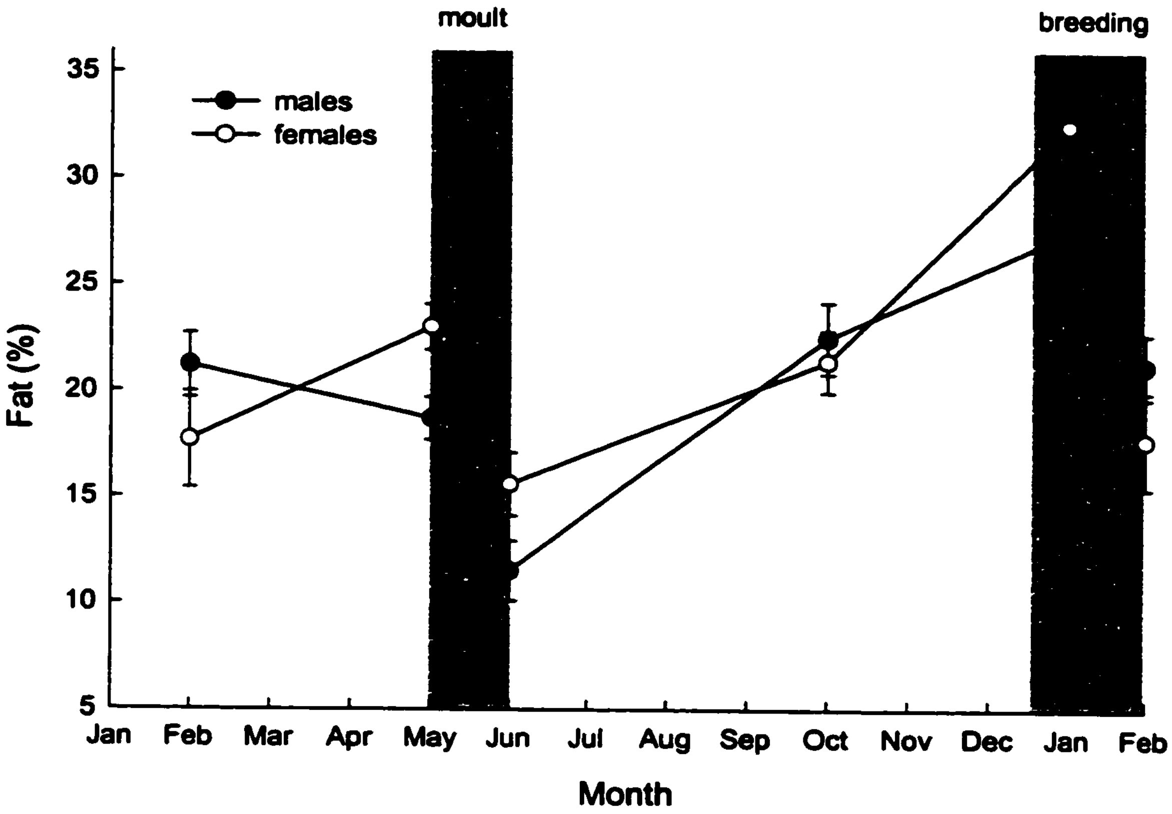

Figure 5.4: Seasonal changes in percent body fat in male and female grey seals (mean ± SE). Sample sizes are as indicated in Table 5.1.

sexes lost mass during the breeding period, however females lost significantly more energy than males during this period.

Within the annual cycle, both the mass and energy gained during foraging roughly balanced that which was spent during periods of terrestrial fasting and reproduction. However this balance occurred differently for males and females. Males accumulated energy only during the pre-breeding foraging period and continuously lost body energy from the start of the breeding season through the end of the moult, some 5 months later. In contrast, females accumulated body energy during both the pre-moult and pre-breeding foraging periods and expended this energy during the moult and breeding seasons, respectively.

Longitudinal data

Longitudinal data were obtained from 73 individuals (35 males and 38 females). Nineteen males and 15 females sampled after the moult were resampled at the beginning of the breeding season, 16 of which were sampled again at the end of the breeding season. Eighteen of the animals sampled in October (mid-foraging period) were also resampled at the beginning of the next breeding season, with 7 being sampled again at the end of that breeding season. A further 7 males and 14 females were sampled at the beginning and end of the breeding season to examine the composition of mass loss during this period.

To look at the temporal pattern of energy gain I compared the rate of mass gain in the last 3-months of the pre-breeding foraging period to that over the entire 7-month period. Females gained mass at a relatively constant ($t_{22} = -0.712$, $p = 0.484$), but

Table 5.2. Rate of mass and energy change in adult grey seals studied longitudinally. Mean ± SE (CV).

		Period of Mass/Energy Change[1]		
	Sex	EM - SB	MF - SB	SB-EB
Mass change (kg)	M	97 ± 5.3 (0.24)	65 ± 7.0 (0.33)	-52 ± 2.9 (0.24)
	F	75 ± 6.7 (0.35)	34 ± 7.0 (0.62)	-65 ± 1.5 (0.12)
Rate of Mass Change (kg/d)	M	0.47 ± 0.03 (0.25)	0.76 ± 0.08 (0.33)	-2.45 ± 0.09
	F	0.34 ± 0.03 (0.34)	0.39 ± 0.08 (0.62)	-4.22 ± 0.10
Total Body Energy Change (MJ)	M	2727 ± 172.9 (0.28)	1512 ± 212.9 (0.42)	-1285 ± 161.8 (0.55)
	F	2002 ± 191.2 (0.37)	1081 ± 181.7 (0.50)	-1724 ± 60.3 (0.18)
Rate of Energy Change (MJ/d)	M	13.1 ± 0.83 (0.27)	17.7 ± 2.50 (0.43)	-59.0 ± 6.54 (0.48)
	F	9.0 ± 0.82 (0.36)	12.5 ± 2.12 (0.51)	-114.9 ± 4.02 (0.17)
N	M	19	9	19
	F	15	9	25

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[1] Sampling period abbreviations as in Table 5.1.

significantly lower rate than males throughout the pre-breeding foraging period ($F_{1,48}$ = 26.598, $p < 0.001$; Table 5.2). Between post-moult and pre-breeding, males gained mass at a rate of 0.47 kg/d, however rate of mass gain in the 3 months prior to breeding (0.76 kg/d) was significantly higher than the 7-month average ($F_{1,48}$ = 12.058, $p = 0.001$, Table 5.2). Mean energy gain during the 7-month foraging period was 2727 MJ for males and 2002 MJ for females. Females had a significantly lower rate of energy gain (9.0 MJ/d) than males (13.1 MJ/d) during this period ($F_{1,48}$ = 10.521, $p = 0.002$), however, in both sexes, rate of energy gain during the three months prior to breeding was significantly higher than the 7-month average ($F_{1,48}$ = 8.048, $p = 0.007$; Table 4.2).

During the breeding season both absolute mass and energy loss were significantly higher in females than in males (t_{42} = 3.790, $p = 0.001$ and t_{42} = 2.800, $p = 0.008$, respectively, Table 5.2). Daily rate of mass loss was also significantly higher in females than in males (t_{42} = 13.461, $p < 0.001$) as was rate of energy expenditure (t_{42} = 7.630, $p < 0.001$).

Composition of mass gained over the entire 7-month foraging period did not differ significantly by sex ($F_{1,32}$ = 0.287, $p = 0.596$; Fig. 5.5 & Table 5.3). However, the composition of mass gained during the last 3-months prior to the breeding season did ($F_{1,16}$ = 9.942, $p = 0.006$; Fig. 5.5). During this period, fat accounted for most of the mass gain by females, whereas lean body mass accounted for more of the mass gained by males (Table 5.3). During the breeding season, fat accounted for 62% of mass loss in females compared to 54% in males. However this difference was not significant ($F_{1,42}$ = 1.898, $p = 0.176$).

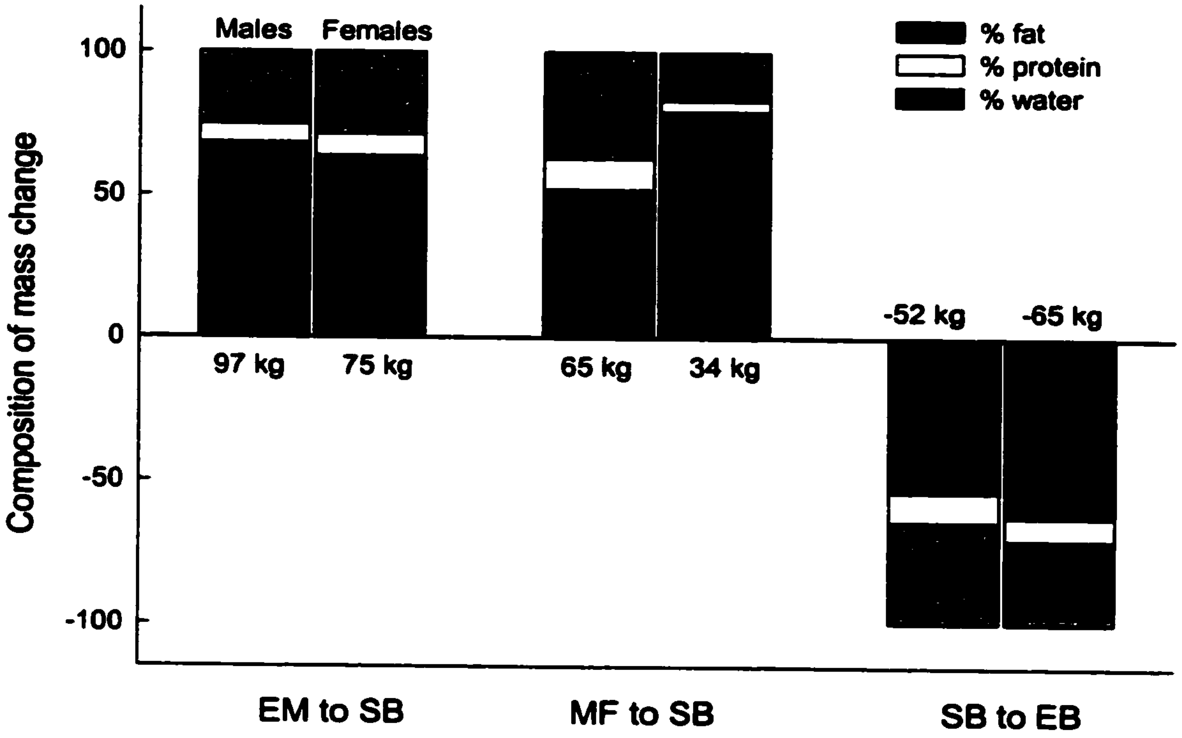

Figure 5.5 Composition of mass change in male and female grey seals between key points in the annual cycle. Numbers represent the average absolute change in mass. Bars on the left and right represent male and female mass change respectively. Sampling period abbreviations as in Table 5.1.

Table 5.3: Longitudinal estimates of the composition of seasonal mass change in male and female grey seals. Sample size represents the number of animals sampled at the beginning and end of each period. Total mass change for each period is shown in Table 5.2.

Composition of Mass Change	Gain between the EM and SB (7-months)		Gain between MF and the SB (3-months)		Loss between SB and EB (1 month)	
Sex	M	F	M	F	M	F
% TBW	25.5 ± 3.79	28.4 ± 2.93	37.1 ± 3.60	16.6 ± 4.67	35.4 ± 4.63	29.2 ± 1.64
% Protein	6.3 ± 1.42	7.5 ± 1.05	10.7 ± 1.52	3.9 ± 1.34	10.4 ± 1.72	8.1 ± 0.79
% Fat	68.3 ± 5.17	63.0 ± 4.08	52.2 ± 5.51	79.0 ± 6.11	53.5 ± 6.77	62.1 ± 2.38
N	19	15	9	9	19	25

I was also interested in the timing and composition of energy gain for reproduction within sex (Fig. 5.5, Table 5.3). Because only a few animals were sampled in all periods, I was unable to analyze these data statistically. Nevertheless, the composition and magnitude of male mass loss during the breeding season (e.g., 52 kg, 54% fat) was more similar to that gained during the 3-months prior to breeding (65 kg, 52% fat) than to that gained over the entire 7-month foraging period. In contrast, female mass loss during the breeding season (65 kg) was approximately double that gained in the 3 months prior to breeding (34 kg). Mass gained by females over the entire 7-month foraging period was more similar to that expended during the breeding season both in magnitude (75 kg) and composition (63% and 62% fat, respectively, Table 5.3, Fig. 5.5).

Discussion

The manner in which an individual allocates energy between survival and reproduction depends on the animal's current condition, the energetic demand of reproduction and the time until reproduction (McNamara *et al.* 1991). Individuals are expected to employ the strategy that maximizes their lifetime reproductive success and hence fitness. In this paper, I demonstrate that males and females in a capital-breeding carnivore differ in their pattern of seasonal energy storage and expenditure for both reproduction and moult. Females store body energy after both periods of terrestrial fasting whereas males only accumulate body energy during the pre-breeding foraging period. I propose that this difference reflects both the earlier reproductive costs in females as well as sex differences in the benefit of stored body energy for reproduction and the cost of storing that energy over long-periods. While females should reduce uncertainty in future reproductive success by accumulating body energy as soon as possible, if males can afford the risk of waiting longer, and avoid the costs of carrying excess body mass and energy, they should do so.

Between the breeding season and the beginning of the moult, females increased their total body energy by 27.5%. Maternal condition has an important influence on early fetal development in grey seals, with females in poorer condition implanting later than females in better condition (Boyd 1984). Thus, females should recover body condition quickly following the breeding season to ensure successful implantation and to fuel the early stages of pregnancy. In contrast, males maintained their body mass during the post-breeding to pre-moulting foraging period, but continued to lose body energy (Figs 5.2 & 5.3). Thus, the percentage of total body fat in males decreases during this period while lean body mass increases (Fig. 5.4). This pattern may reflect the need to replace protein lost during the breeding season and the fact that males do not have early reproductive costs that require an increase in body energy stores. This also implies that subsequent reproductive success in males is relatively insensitive to body condition during the pre-moult foraging period. Thus, as predicted, males appear to make quite different decisions than females about when and how fast to recover body condition from the last breeding event.

The observation that the amount of energy stored during the pre-breeding foraging period appears to balance that which is spent during reproduction further indicates that there must be both costs and benefits to storing body energy (Jonsson 1997; Witter & Cuthill 1993; Bonnet *et al.* 1998). Yet the fact that males and females store energy for reproduction over different lengths of time implies that they have different solutions to balancing these costs and benefits, suggesting sex-specific fitness-maximizing strategies (Trivers 1972; Clutton-Brock & Parker 1992; Jormalainen *et al.* 2001). On average the quantity and composition of mass spent by females during lactation was equal to that gained over the entire 7-month, pre-breeding foraging period. In contrast, male energy expenditure during the breeding season was similar to that gained in only the last 3-months of this foraging period (Fig. 5.5). Although males gained mass during the first four months of this period (Fig. 5.2), this gain appears to simply replace mass lost during the previous breeding and moulting periods, with energy storage for reproduction not commencing until the 3 months prior to breeding. Females appear willing to pay increased costs of long-term storage of body energy because the risks of storing insufficient energy is more critical to successful weaning of offspring. The higher energy density in females throughout the year (Fig. 5.3) may be another reflection of this. Male reproductive success is not so tightly linked to stored body energy (Anderson & Fedak 1987; Godsell 1991; Lidgard *et al.* 2001). Various studies on male reproductive strategies have indicated that age, body mass, length of stay within a breeding colony and the operational sex ratio in the colony all influence the reproductive success of grey seal males (Boness & James 1979; Godsell 1991; Twiss *et al.* 1994; Lidgard *et al.* 2001). In addition, recent studies have shown that some males take short foraging trips during the breeding season, presumably to supplement energy stores (Lidgard *et al.* 2001). Thus, males may not benefit from early storage of body energy to the same degree as females, such that the costs associated with long-term storage are not worth supporting until the 3 months prior to breeding.

Asynchronous patterns of change in body mass or fat content between the sexes have been found in two herbivore species. Hewison *et al.* (1996) found that female roe deer, *Capreolus capreolus*, recovered from the energetically expensive reproductive period earlier than males. Early recovery of body condition in females has been shown to increase the probability of subsequent pregnancy in several ungulate species (White *et al.* 1997; Thomas 1982; Chan-McLeod *et al.* 1999; Mitchell *et al.* 1976). In contrast, male roe deer continue to lose body condition for several months after the rutting period. As in my study, this suggests that subsequent reproductive success in males is less dependent on body condition during this early period and therefore males can delay increasing body mass in order to forgo costs of carrying and maintaining extra body mass. Muskrats, *Ondatra zibethicus*, also show asynchronous patterns of seasonal changes in fat mass with females increasing fat mass earlier following the breeding season than males (Virgl & Messier 1992).

I would expect to find similar sex-specific patterns of energy storage and expenditure in other pinniped species, particularly among other capital breeders. Although body mass and condition have been examined in several other phocid species (e.g., Pitcher 1986; Deutsch *et al.* 1990; Ryg *et al.* 1991; Worthy *et al.* 1992; Boyd *et al.* 1993), I was unable to find comparable annual data to those presented here. In the present study, males and females were sampled explicitly in conjunction with the beginning and end points of key events in the annual cycle (breeding and moulting) and mid-way through the pre-breeding foraging period. In other studies, samples were taken on a monthly basis without specific reference to moult or lactation stage (Chabot *et al.* 1996), did not sample all key times throughout the annual cycle (e.g., Ryg *et al.* 1990, Worthy *et al.* 1992), or investigated only one sex (Carlini *et al.* 1999). Nevertheless, like grey seals, female elephant seals (*Mirounga angustirostris, M. leonina*) appear to gain mass after both periods of terrestrial fasting (LeBeouf *et al.* 2000; Boyd *et al.* 1993, Carlini *et al.* 1999). Male northern elephant seals also appeared to gain mass after both periods of terrestrial fasting. However only two males were studied over the post-moult period (LeBoeuf *et al.* 2000). Ryg *et al.* (1990) and Chabot *et al.* (1996) examined changes in body mass in various age-sex groups in ringed seals, *Phoca hispida*, and harp seals, *Phoca groenlandica*, respectively. While not directly comparable to the present study, both studies found sex-specific seasonal changes in carcass mass among adults, but not in immature animals. Juveniles do not have reproductive costs and so would not be expected to show sex-specific seasonal patterns. This supports the hypothesis that seasonal patterns of energy storage and expenditure by males and females likely reflect differences in the costs and benefits of energy storage for reproduction.

Previous studies on terrestrial carnivores have shown synchronous seasonal patterns of body condition by males and females (*Canis latrans* - Poulle *et al.* 1995; *Aloplex lagopus* - Prestrud & Nilssen 1992; *Martes americana* - Buskirk & Harlow 1989). However, these terrestrial carnivore species are income breeders, acquiring the energy necessary for reproduction at the time it is required (Jonsson 1997). As individuals are not relying on stored body energy for reproduction, I would not expect to see marked sex-specific seasonal patterns in energy storage.

Finally, while the benefits of energy storage for reproduction are reasonably well understood, the costs are not. Understanding the costs associated with obtaining energy and its long-term storage and maintenance of body mass for reproduction would improve our understanding of the different seasonal patterns of fat and protein storage in pinnipeds and other mammals and how each sex has balanced the costs and benefits of storing energy for reproduction.

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Appendix 5.1: Equilibration of tritiated water (HTO) injected intra-muscularly in adult grey seals.

Hydrogen-isotope dilution methods are frequently used to determine body composition of pinnipeds and other mammals. These methods rely on the assumption that the hydrogen isotope (deuterium oxide, D_2O, or tritiated water, HTO) mixes completely with body fluids of the animal (Nagy and Costa 1980). If the isotope is not allowed to equilibrate completely with body water, dilution space of the isotope is underestimated leading to inaccurate estimates of body composition. In order to determine the time required for complete equilibration of HTO in adult grey seals, I sampled 6 adult male in June 1997 and an additional 6 adults (3 females and 3 males) in October 1997.

Animals were captured on Sable Island as described earlier. Immediately after capture, seals were weighed to the nearest 0.5 kg and a known quantity of HTO was administered intramuscularly (0.5 mCi $*$ mL^{-1}; approximately 0.02 mL $*$ kg^{-1} body mass). In June 1997, blood samples (10 mL) were taken from the extradural vein every 30-min post HTO administration for 3 h. In October, blood samples were taken prior to HTO administration and every 15-min for the first 60 min followed by bleeds at 90 and 120 min. Blood samples were processed and analyzed for HTO concentration in triplicate as described in the results section of Chapter 5. Equilibration was considered to have occurred when CPM/g distillate was within analytical precision (2%) of the CPM/g distillate at the last bleed. Results are expressed as mean and the standard error of the mean (SE).

HTO equilibrated with body water in all males studied in June 1997 within 90 min of intramuscluar administration (Figure 5.6a). Four individuals (M656, E84, M18,

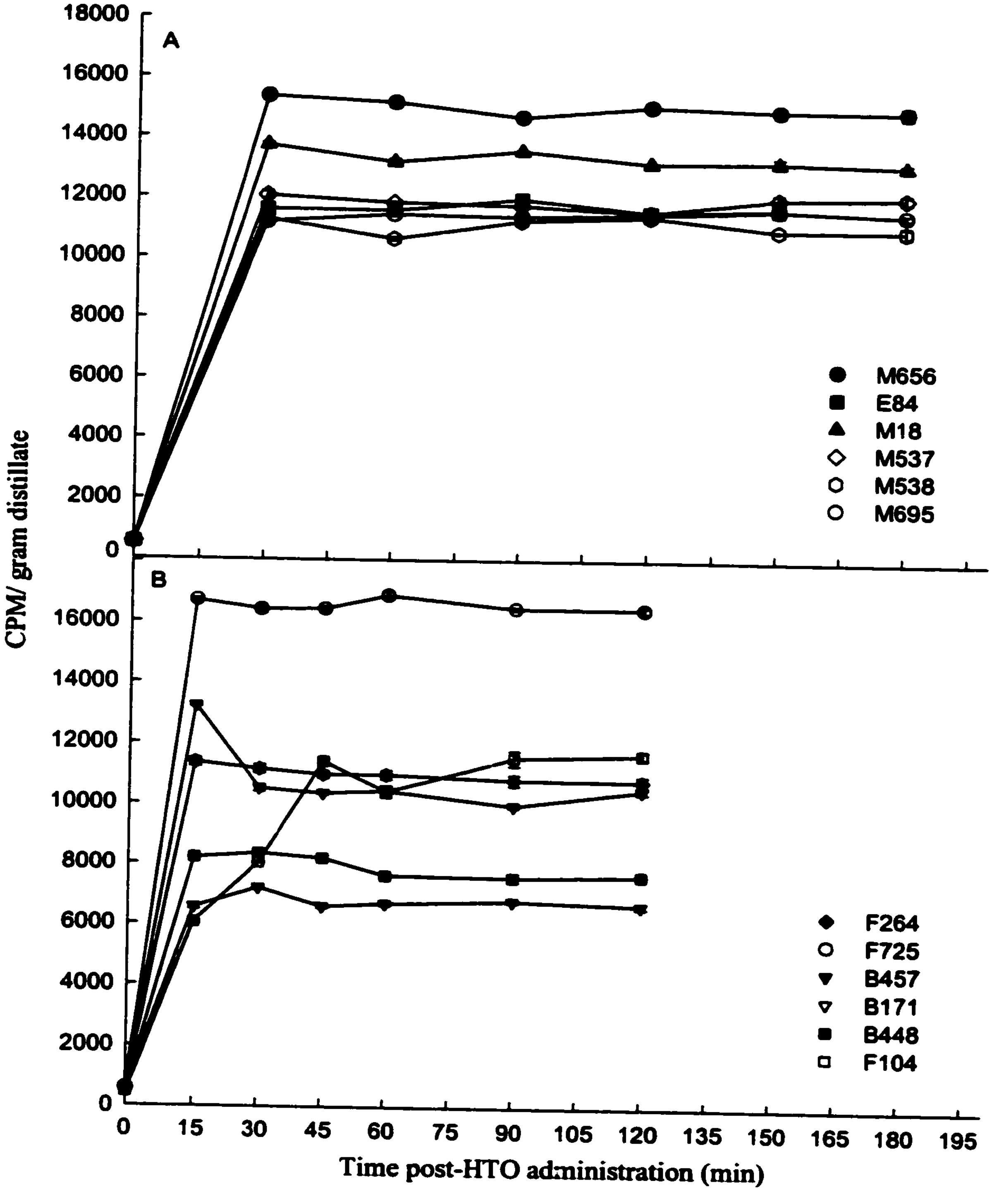

Figure 5.6: Equilibration Curves for a) 6 adult males in June 1997 and b) 3 males and 3 females in October 1997 given HTO through intermuscular injection.

and M537) were equilibrated within 30min. M695 and M538 were equilibrated by 60 and 90-min post-isotope administration, respectively. All six adults (3 females and 3 males) studied in October 1997 were equilibrated within 60 min (Figure 5.6b). Two females (F264 and F725) equilibrated within 15 min whereas, the third female took 45 min to reach equilibration. Male B457 equilibrated by 30 min whereas, B171 and B448 equilibrated by 45 and 60 min, respectively. Equilibration time was not related to body mass ($F = 1.591$, $p = 0.236$, $n = 12$; body mass range: 144.0 to 294.0 kg) or sex (Kruskal-Wallis: $p = 0.178$, $n = 6$) of the individual.

Chapter 6: Linking fatty acid estimates of diet composition to dive effort and location in a size dimorphic marine carnivore

Introduction

Inter-specific differences in foraging behaviour and diet composition of males and females have been examined for a variety of taxa (e.g., mammals - Clutton-Brock *et al.* 1983, birds - Ligon 1968, reptiles - Parmelee & Guyer 1995, and invertebrates - Jormalainen *et al.* 2001). Sexual size dimorphism has often been cited as the driving force of sex differences in foraging ecology. As absolute metabolic requirements increase with body mass, larger individuals require more energy per unit time than smaller ones (Klieber 1961). Therefore, to maintain their larger size, the larger sex will require a higher energy intake and thus may forage differently, perhaps by consuming different prey items, than the smaller sex. This has been shown among size dimorphic ungulate species (e.g., red deer *(Cervus slsphas)* - Clutton-Brock *et al.* 1982*a*; giraffes *(Giraffa camelopardalis)* - Ginnett & Demment 1997). In these herbivores, males (the larger sex) appear to be less selective than females in their food choice in order to increase overall intake and meet the higher energy requirements imposed by their larger body size. Additionally, the allometric relationships between body size and gut capacity results in males having longer retention time of plant material in their digestive tract such that males extract nutrients more efficiently from high-fiber (lower-quality) food (Ginnett & Demment 1997). In contrast, females roam over a larger area in search of higher quality food, which can be more easily digested (Main *et al.* 1996; Ruckstuhl 1998; Pérez-Barberia & Gordon 1999; Barboza & Bowyer 2000, but see Conradt *et al.* 2001).

Other factors thought to contribute to the evolution of sex differences in foraging ecology include the sex-specific roles of males and females during the breeding season (Williamson 1971; Petit *et al.* 1990), intra-specific competition (Schoener 1969; Hughes 1980; Clarke *et al.* 1998) and sex-specific fitness-maximizing strategies (Clutton-Brock & Parker 1992; Jormalainen *et al.* 2001). As stated in Chapter 1, it is unlikely that these factors are mutually exclusive, as more than one may be relevant to the way males and females differ in acquiring energy.

Among air-breathing marine carnivores, sex differences in foraging ecology have been difficult to study due to the wide-ranging, at-sea nature of foraging outside of the breeding season and the fact that feeding often occurs at depth where direct observation is rarely possible (Bowen *et al.* submitted). Despite this, the development of time data-loggers and telemetry techniques has vastly increased our knowledge of how and where individuals of several pinniped species forage (e.g., northern elephant seals, *Mirounga angustirostris,*- LeBoeuf *et al.* 2000; crabeater seals, *Lobodon carcinophagus* - Nordoy *et al.* 1995; Subantarctic fur seals, *Arctocephalus tropicalis* - Georges *et al.* 2000; Australian fur seals, *Arctocephalus pusillus doriferus* - Arnould & Hindell 2001). Information pertaining to diet composition and dominant prey species has been limited to indirect measures that rely on the recovery of prey structures from feces and stomach content samples (e.g., Murie & Lavigne 1992; Bowen *et al.* 1993;Thompson *et al.* 1996; Brown & Pierce 1997). These methods, while providing information about prey species, are known to be biased (Jobling & Breiby 1986; Jobling 1987; Harvey 1989; Bowen 2000). For example, prey species that do not contain hard parts are difficult to identify due to rapid digestion and are often under-represented or omitted in diet estimates.

Diagnostic hard parts of prey species, such as sagittal otoliths from fish species and the beaks of cephalopods, may be eroded during digestion such that identification of the prey species is not always possible. Additionally, as a result of rapid digestion rates, hard parts recovered from either fecal samples or stomach contents likely represent only the last meal consumed. In the case of fecal samples collected at haulout sites, prey identified may only represent near-shore feeding and not accurately characterize the overall at-sea diet. Furthermore, it is usually not possible to determine the age and sex of individuals that contributed samples, thus differences in diet among demographic groups can not be investigated.

These biases have lead to the development of alternative methods of diet composition analysis, which do not rely on the recovery of prey hard parts and for which demographic comparisons are possible. Stable isotopes ratios of nitrogen and carbon in various animal tissues have been used to examine tropic levels of predators and geographic areas of foraging, respectively (Wada *et al.* 1987; Fry 1988; Schell *et al.* 1989; Rau *et al.* 1992). However, stable isotopes do not provide determination of specific prey species (Bowen & Siniff 1999).

Another recent technique developed to examine the diet of marine predators and clarify the structure of marine food webs is fatty acid signature analysis (Iverson 1988; 1993; Iverson *et al.* 1997*a,b*; Graeve *et al.* 1997; Raclot *et al.* 1998). This method allows diet to be inferred from the quantitative comparison of the fatty acid signature (FAS; the suite of fatty acids present in adipose tissue) of the predator and those of potential prey. Fatty acids are the primary components of lipids, commonly consisting of a carbon chain 14 to 22 atoms in length with varying degrees of unsaturation. Due to biochemical limitations and the nature of fatty acid deposition in monogastric carnivores (such as pinnipeds), many dietary polyunsaturated fatty acids (PUFA) are ingested and deposited directly into the adipose tissue of marine mammals with little or no modification, such that the FAS of the predator reflects the fatty acid composition of ingested prey. Within the marine ecosystem, fatty acids are diverse, containing many unique long-chain monounsaturated fatty acids (MUFA) and PUFA originating from unicellular phytoplankton (Ackman 1980). As a result of the conservation of these marine fatty acids through the food chain and the complex array of fatty acids in marine ecosystems, both qualitative (Hooper *et al.* 1973, Iverson *et al.* 1997*a*; Graeve *et al.* 1997; Kirsch *et al.* 2000) and quantitative (Iverson *et al.* in prep) FAS analyses are possible, allowing for prey items to be identified and quantified in diets of individuals.

In this chapter I use qualitative and quantitative FAS analysis to examine differences in the diet composition of male and female grey seals foraging in the Northwest Atlantic during the three months prior to breeding. The grey seal is a size-dimorphic, capital breeding, marine carnivore with males being approximately 1.5 times as large as females. Previous studies (Chapter 2, 3 and 5) have shown that male and female grey seals differ significantly in their foraging ecology and have sex-specific seasonal patterns of both diving behaviour and energy accumulation. These sex-specific seasonal patterns suggest that males and females have different fitness-maximizing strategies, such that females accumulate energy for reproduction earlier during the pre-breeding foraging period than males. However, size dimorphism should also contribute to the divergent foraging strategies in this species. Male grey seals spent less time diving while on foraging trips than females (Chapter 3) and exhibited lower levels of dive effort when measured at the scales of individual dives and dive bouts (Chapter 2 & 3). Given the larger size of males, and thus their higher energy requirements, this result was somewhat unexpected. However, this result may be explained if, like terrestrial ungulates, females are more selective and spend more time at depth searching for high quality prey while males simply increase overall intake by consuming a wider variety of, perhaps lower-quality, prey species. Alternatively or perhaps in addition, male grey seals may be more efficient foragers (i.e., higher energy intake/time) if their larger size allows them to more easily capture and handle different, larger prey items relative to females (Druzinsky 1993; LeBoeuf *et al.* 1993).

The link between diet and diving behaviour may be further influenced by foraging location since diet composition and diving behaviour may be constrained by the spatial distribution of prey and foraging habitat (e.g., bathymetry), respectively (Hughes 1980; Belovsky *et al.* 1989; Slip *et al.* 1994; LeBeouf *et al.* 2000). Satellite telemetry data (unpublished data, D.A. Austin, W.D. Bowen, J.I. McMillan, and C.A. Beck) for male and female grey seals in this population indicate that there is a broad overlap in their foraging areas throughout their Atlantic Canadian distribution. To examine the influence of foraging location on the diet composition I use geolocation techniques (Hill 1994; see methods) and satellite telemetry (see methods) to determine the broad-scale foraging location of individual grey seals for which diet estimation and dive effort data were also available.

Throughout this thesis, differences in the foraging ecology of male and female grey seals during the pre-breeding foraging period have been linked to the differential requirements of individuals to accumulate stored body energy for reproduction. Here I examine how diet characteristics, diving effort and foraging location influenced mass gain which is used here as an index of foraging success.

Thus, the main objectives of this chapter were to test hypotheses relating size dimorphism to sex differences in the diet composition of males and females and to examine the influence of foraging location and dive effort on diet. Following from the example of size dimorphic ungulates, I predicted that male grey seals would be less selective than females. As a result, the diet of males may be more diverse and have a lower energy density relative to females, due to the larger suite of prey types consumed. Finally, the role of diet, dive effort and location on foraging success were examined to see how energy accumulation was influenced by these factors.

Methods

Field Sampling

The study was carried out between May 1993 and January 2000 on Sable Island (43°55'N, 60°00'W), a partially vegetated sandbar approximately 300 km southeast of Halifax, Nova Scotia, Canada. This site is the largest haul-out location for grey seals in the Northwest Atlantic population. Animals congregate in large numbers on the island in May and June to moult, in late December and January to rear offspring and mate, and in smaller numbers throughout the year between foraging trips.

Adult grey seals were captured on-shore following the spring moult (May and June) or in the fall (late September and early October) using hand-held nets (Bowen *et al.* 1992). Seals were weighed to the nearest 0.5-kg on Salter spring balances suspended from an aluminum tripod and anesthetized with an intramuscular injection of Telazol (equal parts of tiletamine and zolazepam). Males and females were given an average dose of 0.45 mg kg^{-1} body mass and 0.90 mg kg^{-1} body mass, respectively (Bowen *et al.* 1999).

To study diving behaviour, I used geolocation time-depth recorders (GLTDRs - models Mk3e, Mk5, Mk6 and Mk7) and satellite-linked time-depth recorders (SLTDR - models SDR-T6 and SDR-T10) manufactured by Wildlife Computers (Redmond, Washington). GLTDRs were secured to netting, which was then attached to the dorsal pelage of the animal between the shoulders using a 5-min marine epoxy. Satellite transmitters were similarly secured to netting and attached to the pelage on the head of the anesthetized individual just behind the ears. Instruments weighed 65 - 600 g (< 0.6 % of initial body mass) depending on the type and model used. Both GLTDRs and SLTDRs were programmed to sample depth every 20-sec and a wet/dry sensor indicated when the animal was hauled out on land. Most instruments were duty-cycled to prolong the period of data collection. Given the duty cycle schedules used, between 33% and 100% of diving behaviour was sampled over a 3- to 8-mon period.

Instrumented animals were recaptured in January when they returned to Sable Island for the breeding season. Instruments were removed by trimming the surrounding pelage and a sample of blubber was taken by biopsy. To do so, a small area was shaved and cleaned on the posterior flank of the animals and a 1-cm incision was made in the skin with a scalpel. A sterile 6-mm biopsy punch was then inserted through the incision and a core was taken through the full depth of the blubber layer. The incision was then cleaned, sutured and sprayed with an antibacterial antiseptic. Biopsies were wrapped in tinfoil and kept chilled for several hours until they were weighed, placed in a solution of

2:1 Chloroform/Methanol containing 0.005% 2,6-di-*tert*-butly-4-methyl-phenol (BHT) and stored frozen until analysis. Beginning in January 1997 study animals were also weighed upon returning to the colony in order to assess foraging success.

Laboratory Procedures

Lipid was extracted from each blubber core in chloroform using a modified Folch method (Folch *et al.* 1957; Iverson *et al.* 2001). Fatty acid methyl esters (FAME) were prepared from ≥100 mg of the pure lipid (filtered and dried over anhydrous sodium sulfate) by transesterification using 1.5 ml 8% boron trifluroide in methanol (v/v) and 1.5 ml of hexane, capped under nitrogen and heated for 1 h at 100°C. FAME were then extracted into hexane, concentrated and brought up to volume (50 mg ml^{-1}) with high purity hexane.

FAME were analyzed in duplicate using temperature-programmed gas liquid chromatography according to Iverson *et al.* (1992; 1997*a*). This analysis was carried out on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30 m by 0.25 mm i.d. column coated with 50% cyanopropyl poly-siloxane (0.25 μm film thinckness; J&W DB-23; Folsom, CA, USA) and linked to a computerized integration system (Turbochrom 4 software, PE Nelson). Identification of fatty acids and isomers were determined using known standard mixtures (Nu Check Prep., Elysian, MN), silver nitrate (argentation) chromatography and GC-mass spectrometry (Iverson *et al.* 1997). All chromatograms were individually checked to ensure correct fatty acid identification, with correction and reintegration where necessary. Fatty acids are expressed as mass percent of the total fatty acids identified and are designated by shorthand nomenclature of carbon chain length:number of double bonds and location (n-x) of the double bond nearest the terminal methyl group.

Fatty acid signature (FAS) analysis and diet composition

Initially, FASs were examined using multivariate analysis of variance (MANOVA) to determine whether FASs differed with the sex of the animal and year in which it was sampled. For these analyses, the number of samples must exceed the number of variables in order to meet certain statistical assumptions and provide reasonable assurance that covariance matrices are homogeneous (Stevens 1986). As a result only 11 fatty acids were used given that 12 animals were included in each sex/year group (see below). The 11 fatty acids chosen (Table 6.1) were those that were most variable and/or represented the most abundant dietary fatty acids (i.e., those that are most indicative of dietary intake) when averaged across all samples. These 11 fatty acids accounted for 69.4 ± 0.11% of total fatty acids identified. Prior to these analyses, fatty acid data were normalized according to Budge *et al* (in press).

Quantitative fatty acid signature analysis (QFASA; Iverson *et al.* in prep) was then used to estimate the diet composition of individual animals. This method provides an estimate of the observed predator FAS given a mixture of FASs of potential prey species. In this analysis, the entire suite of fatty acids identified and quantified in predator and prey was used, omitting only fatty acids that originate solely from biosynthesis in the predator and/or those trace-level fatty acids that may be problematic in detection. Briefly, given the mean FASs of all potential prey species, a computer

Table 6.1. Fatty acids used in multivariate analysis of variance. Values are the mean ± 1 SD of total % fatty acid by weight for the 164 animals from which blubber samples were taken.

Fatty Acid	Males (n = 82)	Females (n = 82)	Total (n =164)
14:0	4.56 ± 0.53	4.85 ± 0.62	4.71 ± 0.597
16:1n-7	13.39 ± 1.37	13.26 ± 1.76	13.32 ± 1.574
18:1n-9	12.07 ± 2.42	11.82 ± 2.26	11.94 ± 2.338
18:1n-7	4.65 ±0.82	4.09 ± 0.78	4.38 ± 0.854
18:2n-6	1.13 ± 0.17	1.23 ± 0.22	1.18 ± 0.204
18:4n-3	1.07 ± 0.21	1.22 ± 0.31	1.14 ± 0.271
20:1n-11	1.81 ± 0.42	1.99 ±0.49	1.90 ± 0.464
20:1n-9	7.63 ± 1.75	8.10 ± 1.91	7.87 ± 1.842
20:5n-3	6.21 ± 0.80	6.89 ± 0.99	6.55 ± 0.960
22:1n-11	3.81 ± 1.65	3.68 ± 1.50	3.75 ± 1.573
22:6n-3	12.41 ± 2.29	11.89 ± 1.85	12.15 ± 2.089
Total	69.82 ± 1.05	70.07 ± 1.25	69.94 ± 1.159

simulation calculates the relative mixture of prey FASs that is closest to the FAS of the predator. Closeness is determined by minimizing the Kulback-Liebler distance, which measures the relative similarity of the distribution of fatty acids in the signatures of the predator and simulated prey mixture. Once the closest estimate of the prey mixture is obtained, diet composition can be calculated using a weighting according to the relative fat content (i.e., total fatty acid contribution) of the different prey types. For example, if two prey species are consumed in equal proportions of the diet, but one is of higher fat content, this species will contribute relatively more to the actual FAS of the predator.

To employ this method of diet estimation, it is essential to have as complete a database of potential prey FASs as possible. Prey species not included in the prey database will not be present in the estimation of diet composition. An additional concern is the variability of FASs within prey type. Fatty acid signatures within prey species can differ significantly between broad geographical areas, size classes and age groups (Iverson *et al.* 1997*a*; Budge *et al.* in press). As a result, it is important to have an adequate number of samples from each potential prey species to evaluate variability and to ensure that the average FAS for each prey type is representative of the species. For the present analysis, I used a prey library that consisted of 32 species (n = 1475) collected over the entire study area (Gulf of St. Lawrence, Scotian Shelf and Georges Bank) between 1993 and 2000 (Table 6.2; Budge *et al.* in press). For each prey species a minimum of 10 individuals was represented in the database.

Variability within prey FASs is expected to produce variation in the estimate of diet composition (Iverson *et al.* in prep). To measure this variability, a bootstrapping procedure was followed whereby new mean prey FASs were created by sampling with replacement from the prey library (within species). These bootstrapped mean prey FASs were then used estimate diet composition as described above. This bootstrapping procedure was performed 100 times for each individual and then used to calculate the standard error of the diet estimation for each prey type within seal (see Iverson *et al.* in prep). The average within seal standard error for each prey type was calculated as:

$$\text{Average within seal SE} = \sqrt{\left(\sum \text{SE} * \text{SE}\right)/n},$$

where SE is the standard error for each individual seal using the bootstrapping procedure and n is the number of seals. To calculate the total SE for each prey type (see Table 6.4) the within SE and among SE (SE of mean diet estimate) were squared, summed and then the square root taken.

Another consideration when using QFASA is the degree to which the specific fatty acids are directly deposited in the predator's adipose tissue in relation to their abundance in the prey. Due to metabolic processes in the predator, the fatty acid signature of the prey will never be exactly reflected in the predator's adipose tissue. For instance while some fatty acids can arise only from the dietary intake (e.g., fatty acids with n-3, n-6 and n-11 double bonds), others can also be biosynthesized from components such as amino acids consumed in excess of metabolic needs (e.g., 18:1n-9 and 16:1n-7) (Cook 1991). Alternatively, some dietary fatty acids show reduced (but still proportional) deposition relative to their intake (e.g., 22:1n-11 and 20:5n-3), such that the amount of the specific fatty acid found in the adipose tissue is consistently lower than that found in the prey (Lin & Connor 1990; Jandacek *et al.* 1991). As a result, it is important to account for the relative deposition of each fatty acid consumed (i.e., from prey) into the predator's adipose tissue prior to generating a diet estimate. To date,

Table 6.2. Potential prey species used to estimate diet composition of adult grey seals in the Northwest Atlantic Ocean.

Common name	Scientific name	N
Butterfish	*Peprilus triacanthus*	10
Capelin	*Mallotus villosus*	56
Gaspereau	*Alosa pseudoharengus*	61
Herring	*Clupea harengus*	146
Mackerel	*Scomber scombrus*	60
Northern Sandlance	*Ammodytes dubius*	71
Snake Blennie	*Lumpenus lumpretaeformis*	11
Cod	*Gadus morhua*	109
Haddock	*Melanogrammus aeglefinus*	131
Longhorn Sculpin	*Myoxocephalus octocdecmspinosus*	20
Lumpfish	*Cyclopterus lumpus*	10
Monkfish	*Lophius americanus*	10
Ocean Pout	*Macrozoarces americanus*	18
Pollock	*Pollachius virens*	32
Redfish	*Sebastes sp.*	72
Sea Raven	*Hermitropteris americanus*	25
Red Hake	*Urophycis chuss*	25
Silver Hake	*Merluccius bilinearus*	38
White Hake	*Urophycis tenuis*	69
American Plaice	*Hippoglossides platessoid*	99
Halibut	*Hippoglossus hippoglossus*	10
Windowpane Flounder	*Scophthalum aquosus*	10
Winter Flounder	*Pseudopleuronectes americanus*	25
Yellowtail Flounder	*Limanda furruginea*	117
Thorny Skate	*Raja radiata*	36
Winter Skate	*Raja ocellata*	14
Lobster	*Homarus americanus*	10
Rock Crab	*Caner irroratus*	37
Snow Crab	*Chionoecetes opilio*	46
Toad Crab	*Hyas sp.*	12
Shrimp	*Pandalus borealis*	96
Squid	*Illex illecebrosus*	18
Total		1475

several captive studies on grey seals have been conducted to examine this issue (Iverson *et al.* in prep; Cooper *et al.* 1999). In these studies, seals were fed diets with known fatty acid composition for extended periods of time, allowing for the relative deposition of each fatty acid ("calibration coefficient") to be measured. For the present study I used the average calibration coefficients from a captive study of 8 adult grey seals fed a moderate fat diet of herring (Iverson *et al.* in prep) and 17 grey seal pups fed the high fat diet of their mother's milk (Iverson *et al.* in prep). These average coefficient values performed better in predicting the diet of other seals on controlled diets than either set of coefficients alone (Iverson *et al.*, in prep).

Once the diet composition of each study animal was estimated from the blubber FAS, I calculated the energy density (kJ/g) and diet diversity of individuals' diets. To calculate energy density, I used proximate composition data of prey species included in the Scotian Shelf prey database where the prey samples were know to be collected in the fall or winter (Budge *et al.* in press; S.J. Iverson & W.D. Bowen unpublished data). These calculations were performed using the values of 39.3 kJ/g and 23.6 kJ/g for fat and protein, respectively (Blaxter 1989). For species in which fall proximate composition data were not available in the database, I used proximate composition data from the literature (Appendix 6.1). Diet diversity was calculated using Levins' diet breadth (Krebs 1989, p. 372):

$$B = 1/\Sigma\, p_j^2$$

where B is the measure of diversity and p_j is the proportion of prey species j in the diet. This index of diet diversity is minimized for specialists and maximized for generalists.

To compare the overall diet composition between males and females, a randomization test was conducted. The mean diet composition for each sex was first calculated and the distance between these two distributions measured using the Kulback-Liebler distance measure. The diet estimates of individuals were then randomly assigned to males or females with the mean diet composition for each sex and the distance between the new means computed again. This randomization was done 10,000 times to give a distribution Kulback-Liebler distances against which to test the actual distance between the diets of males and females. Similar randomization analyses were conducted to examine sex within year differences in the diet composition of adult grey seals. A Bonferroni correction was applied to the resulting p-values to account for multiple comparisons.

Dive data

Upon recovery of GLTDRs and SLTDRs, detailed dive data were downloaded and processed using software supplied by the manufacturer (Wildlife Computers, Redmond, Washington). Zero-offset correction software was used to correct for shifts in the calibration of the pressure transducer of the instrument over the period of data collection. Dive analysis software was then used to calculate a number of variables describing individual dives (see Boness *et al.* 1994 for details).

Transducer drift and sea surface conditions introduce noise in depth measurements that cannot be completely removed by the zero-offset correction. Therefore, I excluded dives < 5 m in depth from the analysis. Dives of longer than 30 minutes were also excluded from analysis as visual inspection of these long dives showed that they generally represented situations where two dives were not properly separated by the zero-offset correction software. These erroneous "dives" accounted for < 0.05% of the total number of dives sampled.

From the remaining data I calculated dive effort and the mean depth of dives performed from the beginning of October until the animal returned to the breeding colony in January. I used this subset of data instead of the entire dive record (in some cases dive records extended from May to the breeding season) in order to examine the diving behaviour most likely associated with the period of pre-breeding fattening, and thereby diet, reflected in the blubber (Iverson *et al* 1997*a*). Thompson et al. (1991) indicated that adult grey seals spent approximately 60% of individual dives at or near the seabed feeding on demersal and benthic fish. Assuming that most foraging takes place during the "bottom time" of individual dives, accumulated time spent at depth was deemed the measure of dive effort most likely to represent foraging. Dive effort was therefore calculated as:

$$\mathrm{ABT} = \left[\left(\sum_{d=1}^{k} \mathrm{BT}\right)/60\right]/\mathrm{N}$$

where ABT is accumulated bottom time (h/d), BT is the time spent at depth (min) for individual dives, d and k are dive number and the number of dives recorded for each individual, respectively, and N is the number of days sampled.

Location data

Foraging locations of individual animals were determined using one of two methods depending on the type of instrument deployed on the individual. For animals with GLTDRs, daily locations were first estimated using software provided by the manufacturer (Wildlife Computers, Redmond). This software calculates geographical position by means of solar navigational equations, given estimates of day length and local noon (Hill 1994). These estimates of day length are derived from light-levels recorded every 10 min throughout the day by the instrument. However, estimates of day length are subject to errors caused by weather (i.e., cloud cover) and by the diving behaviour of the individual (Hill 1994; Welch & Eveson 1999; Beck *et al.* in review). These errors degrade the accuracy of location such that it is important to validate the positions derived using other methods (e.g., DeLong *et al.* 1992; LeBoeuf *et al.* 2000). For this study, I used the algorithm developed by Beck *et al.* (in review) to improve the accuracy of location estimates derived from the manufacturer's software. This algorithm matches sea surface temperature data and dive depth recorded by the GLTDR with existing sea surface temperature and bathymetry databases for the study area and has been shown to significantly improve the accuracy and precision of geolocation estimates (Beck *et al.* in review).

For animals deployed with SLTDRs, whenever the Service ARGOS satellite system received 2 or more consecutive transmissions from theSLTDR, the surface position of the animal could be calculated based on Doppler shift in the frequency of signals (Priede & Swift 1992). SLTDRs transmitted to Service ARGOS approximately ever 45 sec when the animal was at the surface. An increase in the number of consecutive transmissions received by the satellite improves the accuracy (i.e., quality) of the ARGOS location estimate, such that when 4 or more messages are received the estimated position is said to be accurate to within 1 km (Harris *et al.* 1990). Given the variability in the accuracy of ARGOS location estimates, I identified acceptable ARGOS locations using a three-stage location filter (Austin *et al.* submitted). Briefly, in stage 1, four rates of travel were calculated for each location (regardless of location quality) – the rate to each of the two previous locations and the two subsequent locations. If all four rates exceeded 2 m sec^{-1}, the location was removed. At the second stage, the surviving data were filtered using the McConnell *et al.* (1992) forward-backward averaging filter. Finally, the remaining locations were evaluated against a distance threshold, defined as the 99th percentile of the cumulative straight-line distance traveled over a period of 7 d. Locations exceeding this threshold were rejected as being highly unlikely. The daily mean of the acceptable satellite locations was determined to be the geographical position of the individual for that day, making this location data comparable to the daily position estimates derived for individuals with GLTDRs.

Once position estimates were obtained, study animals were classified visually based on their locations from October to January using Arcview GIS software. As with the diving data, this subset of locations was selected because they were most likely associated with the period of fattening and diet reflected in the blubber sample. Individuals were classified as using the Eastern Scotian Shelf (ESS), Western Scotian Shelf (WSS), George's Bank, Gulf of St. Lawrence or St. Pierre Bank (Fig. 6.1). In cases where individuals used two areas they were classified as using both areas. Chi-square analysis was used to test for differences in the distribution of animals among these broad

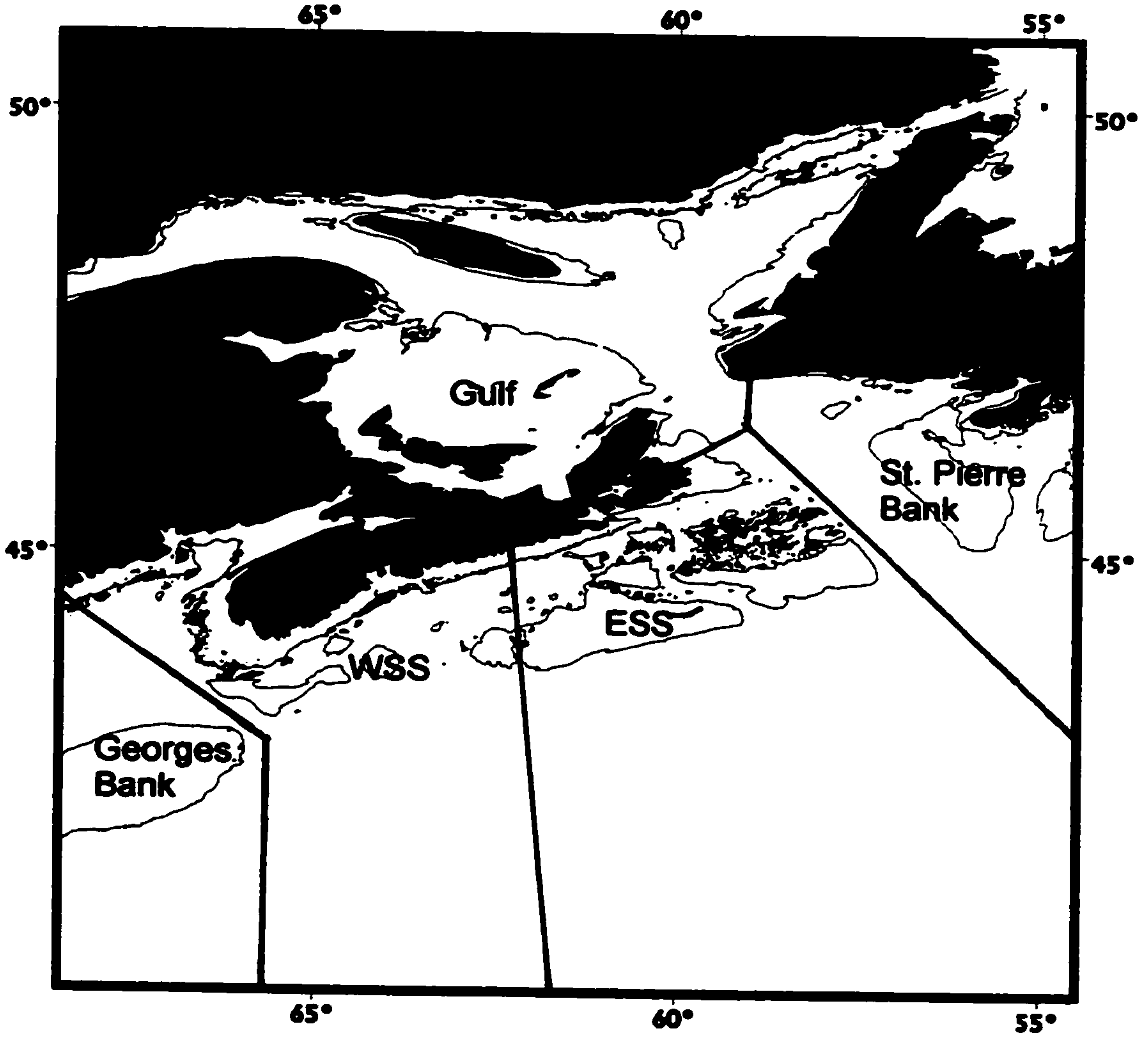

Figure 6.1: Foraging Areas of adult grey seals in the Northwest Atlantic

scale areas based on the method of location estimate and by sex. Sample size by year limited inter-annual comparison of foraging location.

Results

Data recovery

Between May 1993 and January 2000 a total of 134 animals (64 males, 70 females) were captured and outfitted with GLTDRs (43 males, 49 females) or SLTDRs (21 males, 21 females). Overall 73.9% (56 males, 43 females) of these animals returned to Sable Island the following January. However, due to instrument loss or failure, dive effort and mean dive depth could be calculated for only 80 (41males, 39 females) adult grey seals between October and January. In 1994, only 3 individuals (2 males, 1 female) had useable dive data, and as a result these 3 animals were excluded from analysis until the influence of year had been determined. In cases where it was determined that year had no influence on variability these three animals were included in subsequent analysis.

Broad scale foraging areas were identified for 68 of the animals. The foraging location of 37 animals was determined using geolocation with the remaining 31 animals being classified based on filtered ARGOS satellite position estimates. Foraging location could not be identified for 12 animals due to large errors (or failure) in the light-levels and surface temperatures recorded by individual GLTDR units which could not be sufficiently corrected using the algorithm developed by Beck *et al.* (in review).

Blubber samples were taken from most of the returning animals (n = 104). Blubber samples were taken from additional adult grey seals known to have recently arrived on the breeding colony such that there was a minimum of 12 blubber samples from each sex in most years of the study (Table 6.3). Diet estimates were computed for a total of 164 animals, 70 of which had corresponding dive effort data (Table 6.3).

Fatty acid signature (FAS) analysis

Based on the 11 fatty acids indicated in Table 6.1, male and female grey seals differed significantly in their FASs (MANOVA: $F_{11,140} = 17.293$, $p < 0.001$, $n = 164$). Females exhibited significantly higher levels of 18:2n-6, 18:4n-3 and 20:5n-3 but lower levels of 18:1n-7 compared to males. FASs of adult grey seals also differed by year (MANOVA: $F_{66,870} = 4.614$, $p < 0.001$) and had significant sex by year interactions (MANOVA: $F_{66,870} = 1.426$, $p = 0.017$). Seven fatty acids (18:1n-9, 18:1n-7, 18:2n-6, 18:4n-3, 20:1n-11, 20:1n-9, 22:6n-3) exhibited significant annual changes in abundance. In general, FASs did not differ between animals foraging in the fall of 1993 and 1994. However, after 1994 there was a gradual increase in the levels of 18:1n-7 and 22:5n-3 while 20:1n-11 and 20:1n-9 showed a decreasing trend. Additionally, animals foraging in the fall of 1995 had particularly high levels of 18:2n-6 and 18:4n-3 compared to other years. Female grey seals also had relatively higher levels of these two fatty acids in 1997. However males did not, resulting in a significant sex by year interaction in overall FASs.

Diet composition

QFASA indicated that 15 of the 32 potential prey species contributed to the diets of the 164 adult grey seals sampled (Table 6.4). Error associated with diet composition estimates due to the variability of FAS within prey species (see above; Iverson *et al.*, in

Table 6.3: Number of male and female grey seals by year of study included in various statistical analyses.

Year	Diet Composition		Diet and Dive Data		Diet, Dive and Location Data		Diet, Dive, Location and Mass Gain Data	
	Male	Female	Male	Female	Male	Female	Male	Female
1993	12	12	3	3	2	2	0	0
1994	12	12	1	1	1	1	0	0
1995	5	12	5	7	4	7	0	2
1996	17	14	8	9	7	9	0	0
1997	12	8	5	7	5	6	5	7
1998	12	12	5	4	5	2	4	3
1999	12	12	6	6	3	4	6	6
Total	82	82	33	37	27	31	15	18

Table 6.4: Average diet composition of adult grey seals estimated using QFASA.

Prey	# (%) seals consuming	% diet				
		Range	Mean	Total SE	Within seal SE	Among seal SE
Capelin	164 (100.0)	2.5 - 78.5	39.2	4.33	4.17	1.21
Herring	16 (9.8)	0 - 37.3	1.2	1.69	1.64	0.41
Mackerel	1 (0.6)	0 - 0.8	0.0	0.38	0.38	
Sandlance	105 (64.0)	0 - 70.0	11.3	3.89	3.72	1.16
Snake Blennie	136 (82.9)	0 - 65.0	19.2	3.97	3.79	1.18
Cod	8 (4.9)	0 - 22.7	0.4	2.01	2.00	0.18
Lumpfish	16 (9.8)	0 - 43.4	1.7	2.40	2.34	0.05
Redfish	92 (56.1)	0 - 51.7	9.4	3.78	3.65	1.01
Halibut	4 (2.4)	0 - 8.1	0.1	0.80	0.80	0.06
Windowpane Flounder	35 (21.3)	0 - 38.3	3.6	3.99	3.94	0.63
Thorny Skate	24 (14.6)	0-39.0	2.1	5.11	5.08	0.53
Winter Skate	38 (23.2)	0 - 61.2	3.5	7.88	7.85	0.66
Lobster	1 (0.6)	0 - 0.8	0.0	0.21	0.21	
Shrimp	1 (0.6)	0 - 14.9	0.1	1.60	1.60	
Squid	102 (62.2)	0 - 34.1	8.3	3.80	3.72	0.74

prep) was highest for Winter Skate, *Raja ocellata*, which had an average within-seal SE of 7.85%. This was followed by Thorny Skate, *Raja radiata*, and Capelin, *Mallotus villosus* (Table 6.3). With the exception of these three species, the average within-seal SE error associated with predicted prey species was less than 4%.

On average 3.8 ± 0.08 (range: 2 - 7) prey species were consumed by individual seals in more than trace amounts (defined as > 5% of the diet, Krebs 1989). Capelin, was the most common prey type, being present in the diet of all study animals (Table 6.4), and represented on average 39.2 ± 4.33% of the diet. Snake blennie, *Lumpenus lumpretaeformis*, was the second most common prey item, being found in the diet of 136 individuals and accounting for 19.2 ± 1.18% of diets. Northern sandlance, *Ammodytes dubius*, squid, *Illex illecebrosus*, and redfish, *Sebastes sp.*, were also common prey items and accounted for 11.3%, 8.3%, and 9.4% of the diet of adult grey seals, respectively. Other prey species were found in ≤ 24% of individuals sampled and accounted for between 0.1 and 3.6 % of the average diet (Table 6.4).

Although capelin dominated the diet of both sexes (Fig. 6.2) the overall diet composition of male and female grey seals differed significantly ($p<0.001$). Diets of females contained a significantly higher proportion of sandlance (17.3 ± 1.91% vs. 5.2 ± 0.93%, $p <0.001$) and lumpfish, *Cyclopterus lumpus*, (2.8 ± 0.95% vs. 0.5 ± 0.29%, $p = 0.016$) compared to males. Relative to females, males consumed a higher proportion of skates (Thorny skate: 3.9 ± 1.02% vs. 0.3 ± 0.17%, $p <0.001$; Winter Skate: 6.4 ± 1.22% vs.0.6 ± 0.17%, $p<0.001$) and squid (10.5 ± 1.14% vs. 6.1 ± 0.89%, $p = 0.003$). These differences in the overall diet composition of male and female grey seals were not consistent across all years of the study (Table 6.5). The diets of males and females did

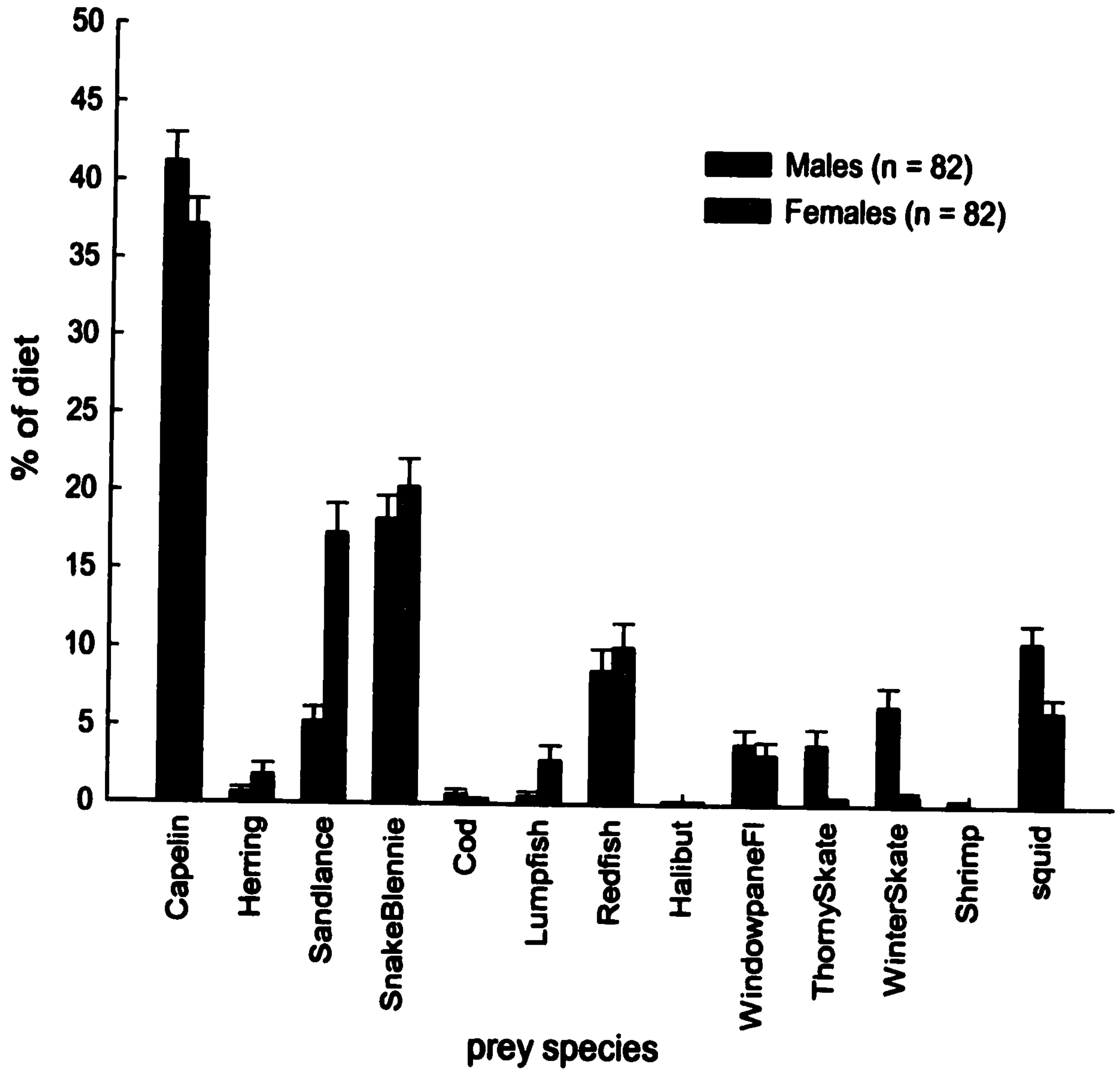

Figure 6.2: Diet composition of male and female grey seals. Mean +/- 1 SE

not differ significantly in 1993,1994, 1995, 1997 or 1999 when a Bonferroni correction for multiple tests was applied to the significance values. In 1996 and 1998, the diets of male and females differed significantly (p-values = 0.003 and < 0.001) with females consuming a significantly higher proportion of sandlance (p-values: <0.001 and 0.004) and lower proportion of winter skate (p-values: 0.003 and 0.005) relative to males in all three years. In 1996, females also consumed a lower proportion of squid relative to males (p = 0.024).

Despite these differences in species composition of diets, energy density and diet diversity of individual seals did not differ by sex or year. Average diet diversity, measured as Levin's diet breadth, was 3.2 ± 0.08, with a 30% coefficient of variation. This variation was not attributable to sex (2-way ANOVA: $F_{1, 150} = 1.513$, p= 0.221) or year of study ($F_{6, 150} = 1.997$, p = 0.070) and there was no significant sex by year interaction effect ($F_{6, 150} = 1.583$, p = 0.156). The energy density of individual diets exhibited less variation (CV = 11%) than diet diversity. The average energy density of grey seal diets was 6.2 ± 0.05 kJ/g and did not differ between males and females ($F_{1, 150}$ = 1.520, p = 0.219). However, energy density did exhibit significant annual variation ($F_{6,150}$ = 3.136, p = 0.006) with the diet of animals in the fall of 1998 having a slightly but significantly lower energy density (5.8 ± 0.09 kJ/g) than in other years. In 1998, the average diet included less redfish and sandlance which are relatively high energy density prey, and more flatfish and squid, which have a lower energy density (Table 6.5;Appendix 6.1). There was no significant year by sex interaction effect ($F_{6, 150} = 1.017$, p = 0.415) on the energy density of grey seal diets.

Table 6.5: Diet composition of male and female grey seals by year of study. Values are mean percent ± 1 SE (among).

Year	Sex	Capelin	Herring	Sandlance	Snake Blennie	Cod	Lumpfish	Redfish	Squid	Flatfish[1]	Skates[2]	Other[3]
1993	M	39.7 ± 2.74	1.4 ± 1.39	9.8 ± 3.46	13.2 ± 2.83	1.9 ± 1.89	1.5 ± 1.49	16.9 ± 3.34	9.2 ± 2.59	0.7 ± 0.73	4.5 ± 3.21	1.2 ± 1.24
	F	30.2 ± 3.00	1.2 ± 1.18	22.4 ± 5.33	13.8 ± 4.20	0.0 ± 0.0	6.2 ± 4.21	21.3 ± 5.10	4.0 ± 1.38	0.8 ± 0.84	0.0 ± 0.0	0.1 ± 0.06
1994	M	39.5 ± 4.61	0.0 ± 0.0	0.1 ± 0.04	26.1 ± 4.85	0.6 ± 0.39	1.6 ± 1.29	7.8 ± 4.28	7.1 ± 3.00	5.8 ± 2.38	11.6 ± 3.98	0.0 ± 0.0
	F	39.1 ± 3.93	0.0 ± 0.0	2.4 ± 1.36	27.1 ± 4.79	0.1 ± 0.11	2.5 ± 2.43	12.7 ± 4.99	8.4 ± 2.81	3.8 ± 2.26	3.8 ± 1.78	0.1 ± 0.07
1995	M	38.7 ± 5.13	0.0 ± 0.0	9.5 ± 5.01	15.1 ± 6.42	0.0 ± 0.0	0.0 ± 0.0	5.5 ± 4.74	11.3 ± 2.98	1.9 ± 1.63	18.0 ± 10.50	0.0 ± 0.0
	F	47.3 ± 4.69	0.8 ± 0.83	24.3 ± 4.41	11.2 ± 4.58	0.0 ± 0.0	1.4 ± 1.38	10.8 ± 4.05	2.2 ± 1.99	1.9 ± 1.31	0.0 ± 0.0	0.0 ± 0.0
1996	M	37.5 ± 3.98	0.0 ± 0.0	5.0 ± 1.33	21.3 ± 3.11	0.8 ± 0.82	0.2 ± 0.17	2.7 ± 1.49	14.6 ± 2.82	6.0 ± 2.41	11.8 ± 2.78	0.0 ± 0.0
	F	36.8 ± 5.10	2.8 ± 2.66	20.8 ± 5.11	20.0 ± 4.78	0.0 ± 0.0	0.0 ± 0.0	7.7 ± 2.63	6.0 ± 1.91	4.8 ± 2.79	1.0 ± 0.73	0.0 ± 0.0
1997	M	44.7 ± 3.74	1.2 ± 0.91	6.3 ± 3.15	18.7 ± 4.63	0.5 ± 0.48	0.0 ± 0.0	10.7 ± 4.73	12.0 ± 3.72	0.8 ± 0.53	5.0 ± 4.12	0.0 ± 0.0
	F	33.8 ± 6.57	0.0 ± 0.0	23.0 ± 8.62	23.6 ± 6.33	0.0 ± 0.0	4.1 ± 4.10	9.0 ± 4.78	0.7 ± 0.65	4.8 ± 4.79	1.0 ± 0.95	0.0 ± 0.0
1998	M	33.9 ± 3.92	1.9 ± 1.33	1.1 ± 0.68	20.5 ± 3.97	0.0 ± 0.0	0.0 ± 0.0	7.6 ± 3.71	12.8 ± 2.74	6.1 ± 3.30	16.2 ± 5.32	0.0 ± 0.0
	F	34.2 ± 2.91	0.0 ± 0.0	10.0 ± 2.87	28.4 ± 3.15	1.3 ± 0.90	3.2 ± 2.25	2.8 ± 1.29	14.8 ± 2.44	5.2 ± 2.24	0.0 ± 0.0	0.0 ± 0.0
1999	M	54.5 ± 6.14	0.0 ± 0.0	7.5 ± 2.53	9.3 ± 1.88	0.0 ± 0.0	0.0 ± 0.0	9.6 ± 3.05	5.5 ± 2.06	4.8 ± 3.29	8.7 ± 4.53	0.0 ± 0.0
	F	37.4 ± 2.97	7.0 ± 3.59	19.3 ± 4.84	19.0 ± 4.94	0.0 ± 0.0	3.4 ± 2.32	6.3 ± 2.10	4.5 ± 1.89	2.1 ± 1.50	0.9 ± 0.64	0.0 ± 0.0

[1] Flatfish includes Halibut and Windowpane flounder, [2] Skates includes Thorny and Winter Skate, [3] Other includes Mackerel, Lobster and Shrimp.

Foraging Location

Over 70% of study animals were located exclusively on the ESS between October and January (Fig 6.1; Table 6.6). Another 11.7% of individuals were located in this area but also used either the southern Gulf of St. Lawrence or St. Pierre Bank off southern Newfoundland. Six and two animals, respectively, were located exclusively in the Gulf of St. Lawrence and St. Pierre Bank. Several animals used areas on the WSS and Georges Bank. To examine the effect of method (i.e., geolocation vs. satellite data) on location estimate, I performed a chi-square analysis. However, due to the low number of animals in most categories several assumptions were violated. To accommodate this, I further classified animals in to three groups: i) those using the ESS exclusively, ii) those using areas west of the ESS (Georges and WSS) and iii) those using areas east of the EES (Gulf of St. Lawrence and St. Pierre Bank). This analysis showed that the method used to determine foraging location had no significant effect on the distribution estimate of animals between these three groups ($\chi^2 = 2.826$, df = 3, p = 0.243). There was also no significant difference in the distribution estimate of male and female grey seals between these groups ($\chi^2 = 0.4028$, df = 2, p = 0.133). However, only males used areas west of the ESS.

Diving effort

Diving effort differed significantly between males and females ($F_{1,58} = 42.151$, $p < 0.001$) with females spending significantly more time at depth/day than males (9.1 ± 0.30 h/d vs. 6.7 ± 0.25 h/d). However, mean dive depth ($F_{1,65} = 3.073$, p= 0.084) did not differ significantly between sexes (males: 54.3 ± 2.12 m, females: 49.4 ± 2.30 m) from

Table 6.6: Foraging location of male and female grey seals between October and January in the Northwest Atlantic.

Geographical Location	# males	# females	% Total
Eastern Scotian Shelf	23	25	70.6
Gulf of St. Lawrence	2	4	8.8
Eastern Scotian Shelf/Gulf of St. Lawrence	4	2	8.8
Western Scotian Shelf	2	0	2.9
Georges Bank	2	0	2.9
St. Pierre Bank	0	2	2.9
Eastern Scotian Shelf/St. Pierre Bank	2	0	2.9

October and January. There was no significant year or sex by year interaction effect on either of these measures of dive effort.

The effect of foraging location and dive effort on diet characteristics

The small number of animals foraging outside of the ESS area limited statistical comparison of the diet composition of individuals foraging in different locations. However, at a qualitative level, there were some differences in diet composition associated with foraging location (Table 6.7). For instance, only individuals feeding on St. Pierre Bank consumed lumpfish. Animals feeding on Georges Bank and the WSS did not consume redfish, but had higher levels of flatfish and skates compared to individuals foraging in other areas. Sandlance was eaten by individuals in all foraging locations but accounted for a higher proportion of diet among animals foraging on the ESS and on St. Pierre Bank.

Among animals foraging on the ESS, diet composition differed between males and females (Table 6.7). As in the larger sample, capelin dominated the diet. However, females consumed more sandlance and less squid and skate than did males. Within the ESS, energy density of the diet was significantly higher for females (Table 6.7). A limited number of individuals foraging within other areas limited statistical, comparisons, however the energy density of females foraging in the Gulf of St. Lawrence was higher than that of males.

Among the 70 individuals (33 males and 37 females) for which diet and diving effort were obtained, the energy density and diversity of individual diets differed significantly between males and females (energy density: $t_{68} = 2.888$, $p = 0.006$;

Table 6.7: Diet composition of adult grey seals foraging in different areas. Values are mean percent ± 1 SE.

Foraging Area	Sex (N)	Capelin	Herring	Sandlance	Snake Blennie	Cod	Lumpfish	Redfish	Squid	Flatfish[2]	Skates[3]	Other[4]	Energy[5] Density (kJ/g)
Eastern SS	M (23)	39.2±3.14	0.6 ±0.49	6.9±1.96	16.0±1.76	1.1±1.03	0.0±0.0	6.5±2.28	10.7±2.10	3.1±1.57	15.0±1.57	0.0±0.0	6.1±0.13
	F (25)	38.6±3.58	3.0±1.58	25.6±3.43	11.1±2.52	0.0±0.0	0.0±0.0	13.6±5.62	5.6±1.82	2.2±1.44	0.2±1.44	0.04±0.03	6.6±0.12
Western SS	M (2)	38.3±1.65	0.0±0.0	5.9±5.85	28.0±3.17	0.0±0.0	0.0±0.0	0.0±0.0	13.5±13.45	0.0±0.0	14.5±14.47	0.0±0.0	5.9±0.04
George's Bank	M (2)	20.4±0.12	0.0±0.0	4.0±4.01	14.2±3.26	0.0±0.0	0.0±0.0	0.0±0.0	9.3±6.98	26.4±6.16	25.7±7.95	0.0±0.0	5.3±0.03
Gulf of St. Lawrence	M (2)	31.2±13.03	0.0±0.0	0.0±0.0	32.9±3.07	0.0±0.0	0.0±0.0	1.6±1.64	14.9±1.44	10.6±10.61	8.7±10.61	0.0±0.0	5.5±0.41
	F (4)	42.5±2.79	0.0±0.0	10.1±4.51	36.2±7.60	2.1±2.05	0.0±0.0	3.0±2.37	6.0±3.35	0.0±0.0	0.0±0.0	0.0±0.0	6.1±0.18
St. Pierre Bank	F (2)	36.1±10.7	0.0±0.0	12.9±12.06	24.8±11.23	0.0±0.0	16.4±16.41	9.8±4.87	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	6.1±0.70

[1] Individuals that foraged in more than one area between October and January were not included in this table.

[2] Flatfish includes Halibut and Windowpane flounder. [3] Skates includes Thorny and Winter Skate. [4] Other includes Mackerel, Lobster and Shrimp.

[5] The energy density of diets (kJ/g) was significantly higher for females relative to males foraging on the eastern Scotian Shelf ($t_{42} = -3.141$, $p = 0.003$)

diversity: $t_{68} = -3.403$, $p = 0.001$) with female diets being of lower diversity (2.99 ± 0.12 vs. 3.66 ± 0.19) but higher energy density (6.4 ± 0.11 kJ/g vs. 5.9 ± 0.10 kJ/g) than the diets of males.

Diet diversity was not significantly influenced by dive effort, mean dive depth or foraging location in males or females (GLM: all p-values > 0.05). However, 35.9% of the variation in the energy density in female diets was explained by a GLM that included these variables. In this model, dive effort, measured as accumulated bottom time/d was a significant factor ($F_{1,25} = 4.582$, $p = 0.042$), with the energy density of diets increasing with increasing effort. Foraging location and mean dive depth were not significant factors ($F_{3,25} = 1.689$, $p = 0.195$ and $F_{1,25} = 1.763$, $p = 0.196$, respectively). For males, dive effort, foraging location and mean dive depth had no significant influence on the energy density of diets (GLM: all p-values > 0.05). Given the dominance of capelin as a prey species for adult grey seals, I also constructed a GLM to determine whether the variation among individuals in the proportion of capelin (arcsine transformed) in the diet could be attributed to foraging location, dive effort or mean dive depth. This analysis showed that dive effort was a significant factor in predicting the proportion of capelin in the diet ($F_{1,49} = 11.474$, $p = 0.001$), such that as dive effort increased so did the percentage of capelin in the diet.

Year was not included as a factor in these models given the reduced number of animals in each year (particularly 1994) for which I had diet estimates in combination with diving and foraging location data (Table 6.3).

Foraging Success

Measures of mass gain during the pre-breeding foraging period were obtained for 33 (15 males, 18 females) of the individuals with diving data and diet estimates, in order to serve as a proxy of foraging success. Foraging location was found to have no influence on the amount of mass gained during the foraging period (ANOVA: $F_{4,22} = 1.174$, $p = 0.349$) likely due to the fact that most animals were in the same broad scale foraging area. To examine if other aspects of an individual's foraging ecology could predict mass gain, and hence foraging success, dive effort, mean dive depth, diet energy density, and the proportion of capelin in the diet were included in a stepwise regression. Sex, initial mass and the number of days over which mass gain was measured for each individual were also included in this analysis to determine their influence on mass gain. Only sex and the length of time over which mass gain was measured were included as significant predicting factors but accounted for 50% of the variation in mass gain.

Discussion

This study demonstrates that sex differences in the diving behaviour of adult grey seals are reflected in diet composition and are likely associated with the sexual size dimorphism in this species. Male and female grey seals exhibit differences in diving behaviour at the level of individual dives and bouts of dives, in the diurnal pattern of dive activity and in dive effort (Chapter 2 & 3). The contribution of sexual size dimorphism to the evolution of these differences has been unclear in previous chapters with the larger sex spending less time diving, and thus foraging, despite their higher energy requirements. In the present study, sex differences in the diet composition and diet characteristics of animals known to be feeding in the same area (Table 6.7), demonstrate that male grey seals actually have a more diverse but lower energy density diet than females. This finding supports the hypothesis that with their increased body size, males may be able to more efficiently process larger quantities of lower-quality prey. This may be due to a proportionally larger gut capacity (see Chapter 2 & 3; Ginnett & Demment 1997) and/or indicate that males are simply less selective in order to increase overall intake. In addition, the larger size of males may allow them to more readily consume larger species (e.g., Schoener 1971) compared to the prey more commonly consumed by females (i.e., sandlance). In contrast, females appear to be more selective and spend more time searching for higher quality prey, resulting in the longer dives and higher levels of dive effort.

Diet Composition of adult grey seals

Capelin was the dominant prey consumed by both male and female grey seals (Fig 6.2), being present in the diet of all animals sampled and accounting for almost 40% of the diet (Table 6.4). Four species (snake blennie, northern sandlance, redfish and squid) made up another 48.2% of the diet. Previous studies of grey seal diets based on prey hard parts recovered from fecal or stomach samples have similarly indicated that while a variety of prey species appear to contribute to diet, a large portion of the diet is accounted for by relatively few species (Prime & Hammond 1990; Murie & Lavigne 1992; Bowen *et al.* 1993; Bowen & Harrison 1994; Thompson *et al.* 1996).

On the Scotian Shelf, studies based on fecal and stomach content data (Bowen & Harrison 1994; Bowen *et al.* 1993) have indicated that sandlance is the dominant prey species of grey seals in this area. Atlantic cod, squid, and flatfish were also identified as being important prey during the fall and winter months. In the Gulf of St. Lawrence, Murie & Lavigne (1992) found that cod (36%), herring (26%) and capelin (10%) were the dominant prey types by mass, based on the stomach contents of 41 individuals.

While sandlance was identified as a common prey item in the present study, the proportion of diet represented by this species was significantly lower (11.3 ± 3.89%) than previously reported on the Scotian shelf. Capelin and redfish were also identified in previous studies of grey seal diet but were not found to account for a major portion of the diet (1.3 and 0.4% by weight, respectively) and occurred in only 3.8 and 2% of the samples, respectively (Bowen & Harrison 1994). The differences between the diet composition of grey seals reported here and in previous studies are not completely unexpected. As discussed earlier, diet composition based on fecal samples will be biased towards prey species available near the haul-out location and are likely not representative of the overall diet. In contrast, diet composition estimated from the FAS of blubber represents diet over a longer period of time during which individuals are storing body energy for reproduction. Thus, diets estimated in this study represent prey consumed over a longer temporal and broader spatial scale, and equally identify prey regardless of the presence of hard parts. Additionally, prey assemblages are not static, but show temporal and spatial variability (e.g., Garrison 2000). Since the early 1990's there has been a progressive increase in the abundance of capelin on the Scotian Shelf (Department of Fisheries and Oceans 1997) associated with an influx of colder water from the Labrador Current (Department of Fisheries and Oceans 2000). The previous studies on grey seal diet composition on the Scotian Shelf were conducted in the late 1980s and early 1990s, prior to this increase and the present study. Thus, differences in the distribution of prey species over time may also contribute to the differences in diet composition reported.

Snake blennie was an important prey species for both male and female grey seals (Fig. 6.2) using QFASA. This species had not previously been identified as a prey item for grey seals although its distribution and habitat (Scott & Scott 1988) overlap with the known distribution and dive depths of grey seals (Chapter 2; this study). The absence of this species from previous diet estimates may be related to the relatively small size of the species and the correspondingly small otoliths, which may be more easily digested than the otoliths of other prey species (Bowen 2000). Additionally, the distribution and abundance of snake blennie (Marine Fish Division Virtual Data Center, Bedford Institute of Oceanography) is such that individuals foraging within a day's travel to Sable Island, where the fecal samples were collected (Bowen & Harrison 1994), were likely not feeding on this species. Furthermore, according to groundfish surveys conducted by the Department of Fisheries and Oceans, little snake blennie was found on the ESS prior to 1993. Since then, the abundance of this species has increased, being particularly high in 1995.

Given that snake blennie was identified as a major prey item using a new method of diet estimation and that the mean snake blennie FAS was based on only 11 samples (Table 6.2), this raises the concern that snake blennie might be incorrectly identified as a prey item (i.e., a false positive). To examine the effect of removing snake blennie on conclusions regarding sex differences in diet, QFASA was again performed to estimate diets, excluding snake blennie as a potential prey species. The average remodeled diet was similar to the original diet estimation with capelin, sandlance, redfish and squid identified as the major prey species (Fig. 6.3). In addition, yellowtail flounder, *Limanda furruginea*, which was not previously identified as a prey item using this method, became an important component of the diet, representing on average 7.4 ± 1.00% of the diet and present in the diet of 56 (34.1%) individuals. Two other flatfish species (American Plaice, *Hippoglossus platessoid*, and Winter Flounder, *Pseudopleuronectes americanus*) also appeared in the remodeled diets with males consuming significantly more of these prey types than females. With the removal of snake blennie, crustacean species also increased (lobster and shrimp) or appeared (i.e., snow crab, *Chionoecetes opilio*) in the diet (Fig. 6.3). All analyses reported above were repeated using these new diet estimates. The removal of snake blennie from the diet had no effect on the conclusions or statistical findings regarding sex differences in diet composition and diet characteristics.

Sex differences in the diet

The diet of male and female grey seals differed significantly (Fig. 6.2), with females consuming a higher proportion of sandlance and lower proportion of skates and/or squid, depending on the year of study, compared to males. These differences were observed in the quantitative estimates of diet but were also suggested by differences in the FAS of males and females. Females had relatively higher levels of 18:2n-6, 18:4n-3, and 20:5n-3 in their blubber tissue compared to males. These three fatty acids are relatively higher in sandlance compared to the skates and squid consumed in higher abundance by males. Conversely 18:1n-7, which was observed to contribute more to

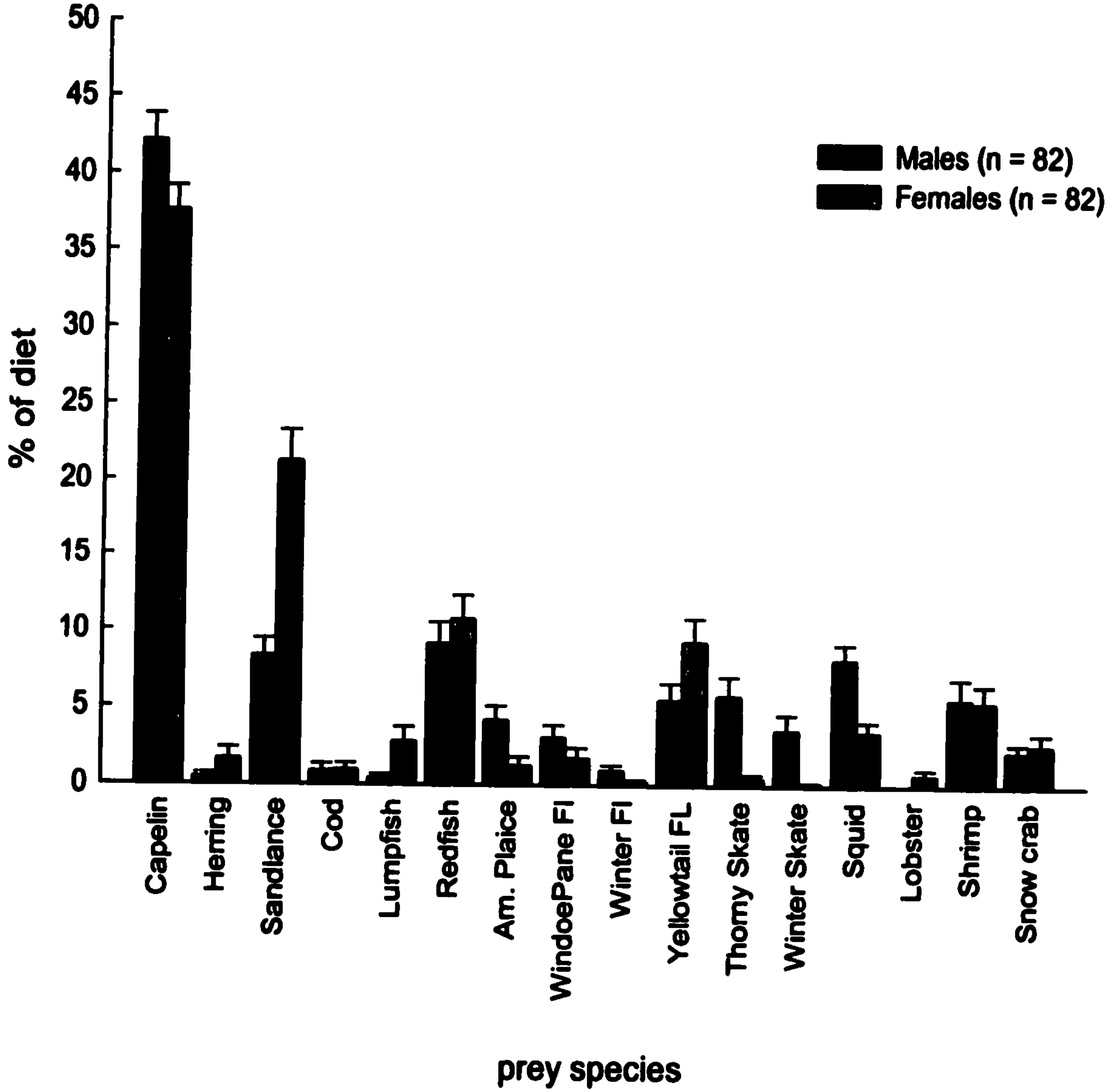

Figure 6.3: Diet composition estimate of male and female grey seals when snake blennie is removed as a potential prey species. Mean +/- 1 SE.

male FAS than females, is higher in skates compared to sandlance (Budge *et al.* in press; Kirsch *et al.* 1998).

Females consumed a diet that included a larger proportion of relatively higher energy density prey (Appendix 6.1) relative to males. Despite this, energy density and diet diversity did not differ significantly by sex for the 164 animals sampled. However, among the 70 individuals for which dive effort data was also obtained (Table 6.3), most of which (n = 58) foraged on the ESS, female grey seal diets were significantly less diverse (i.e., more specialized) and of greater energy density compared to the diets of males. The reason for this discrepancy is not clear but may be due to the potentially confounding influence of diet variation between foraging locations.

Sex differences in the diets of grey seals foraging on the ESS and the influence of dive effort on the energy density of the diet, suggest that females spend more time at depth searching for higher quality prey. Indeed, three of the four prey species that account for 84% of the average female diet (capelin, redfish and sandlance) are the prey ranked first, third and fourth in terms of energy density (Appendix 6.1). Males, in contrast, appear less selective and have a more diverse diet, which includes prey of lower energy density (e.g., skates, Appendix 6.1) than in female diets. Diurnal patterns of dive activity are consistent with sex differences in diet composition and characteristics (Fig. 2.4). Female grey seals exhibited higher levels of dive activity and dived to shallower depths at night compared to during the day. Such patterns are consistent with the pursuit of vertically migrating, pelagic prey (Croxall *et al.* 1985; LeBoeuf *et al.* 1993; 2000). In contrast, male grey seals do not exhibit the diurnal pattern in diving behaviour (Fig. 2.4) but rather dive to similar depth with similar frequency through out the day (Chapter 2).

This type of diurnal dive activity pattern is consistent with foraging on benthic prey species, such as skates and flatfish (LeBoeuf *et al.* 2000).

These sex-specific foraging tactics are likely influenced by the sexual size dimorphism of the species. As a result of their larger size, male grey seals need to acquire more absolute energy than females and may be capable of digesting lower-quality food items than females (Chapter 2 & 3). Thus, to increase absolute intake males should consume a larger number of prey items. By consuming a more diverse suite of prey, males may be able to satisfy their daily energy requirements more efficiently than females. In addition, the larger body size of male grey seals may allow them to consume larger prey that are less profitable to the smaller-bodied females due to the greater handling costs associated with these prey (Schoener 1971; Vaudry *et al.* 1990).

Among the extremely size dimorphic northern elephant seals, *Mirounga angustirostris*, sex differences in diving behaviour and foraging location are consistent with similar (although presently unconfirmed) sex differences in diet composition. In this species, males and females have distinct foraging locations with males foraging on the continental shelf margin and females ranging widely over deeper water off the continental shelf (LeBoeuf *et al.* 2000). Sex differences in the diurnal pattern of diving behaviour of this species strongly suggest that females are foraging on vertically migrating pelagic prey whereas males feed predominantly on benthic species found on the shelf (LeBoeuf *et al.* 1993; 2000). LeBoeuf *et al.* (1993; 2000) suggest that males are foraging more efficiently by pursuing benthic prey which, relative to pelagic prey, tend to be larger and thus are of higher energy value compared to smaller, pelagic prey items. In this way, it appears that males are foraging so as to increase energy intake relative to females. Hindell *et al.* (1991) made similar inferences about the diet composition of male and female southern elephant seals, *Mirounga leonina*, based on the dive depths and the diurnal pattern of dive behaviour of each sex.

In terrestrial size dimorphic species, female ungulates forage longer than males and are more selective in their choice of food (Owen-Smith 1988; Ginnet & Demment 1997; Ruckstuhl 1998). Sexual dimorphism in body size, and the scaling relationships between energy requirements, digestive efficiency and body mass, is one of the leading hypothesis explaining sex differences in these herbivores. Among terrestrial carnivores, Raymond *et al.* (1990) showed that male ermines, *Mustela erminea*, were generalist feeders while the smaller-bodied females appeared to specialize on meadow voles, *Microtus pennsylvanicus*. This difference was linked to prey profitability and the high costs to females of capturing more aggressive prey items such as the short-tailed shrew, *Blarina brevicauda*. Another study on ermines showed similar results and also suggested that the mean handling time for females was significantly higher than for males when foraging on shrews due to the smaller body size of females and its influence on foraging ability (Vaudry *et al.* 1990).

It is also possible that the differing reproductive costs of males and females contribute to differences in diet composition observed. During the months prior to reproduction both males and females exhibit high levels of dive effort and rates of energy gain. However, energy accumulation prior to the terrestrial breeding season is expected to be more critical to the reproductive success of females (Chapter 2, 3, 5). Thus the higher energy density of diets consumed by females relative to males foraging in the same area during the 3-months prior to reproduction may be a reflection of higher reproductive costs in females and the relative importance of stored body energy to each sex. Among several dolphin species (Bottlenose, *Tursiops truncatus*, spotted, *Stenella attenuata* and common dolphin, *Delphinus delphis*) differences in diet composition have been correlated with differing reproductive status (and thus costs) both within and between sexes (Cockcroft & Ross 1990; Bernard & Hohn 1989; Young & Cockcroft 1994). Similarly, the differences in foraging behaviour and diet composition between lactation and non-lactating female red deer, *Cervus elaphus*, have been attributed to the differing reproductive costs of these individuals (Clutton-Brock *et al.* 1982*b*). In order to clarify the contribution of differing reproductive costs to differences in diet composition between male and female grey seals it will be important to examine diet composition throughout the annual cycle. However, it seems unlikely that the influences of reproductive costs and of sexual size dimorphism are mutually exclusive in fostering the sex differences observed in this study.

Foraging success

Diving effort, foraging location and characteristics of the diet did not significantly influence mass gain in adult grey seals. The lack of explanatory power of dive effort and energy density on mass gain is perhaps not surprising for several reasons. First, it is the total quantity of food energy consumed above maintenance requirements that determines mass gain. Hence actual energy consumption may not be correlated with either energy density of the diet (i.e., as above) or with diving effort (i.e., our measure of foraging effort). Furthermore, the long time periods over which mass gain was measured may obscure relationships occurring over shorter time scales, particularly given the seasonal pattern of mass gain evident in this species (Chapter 5).

Conclusion

Adult grey seals exhibit sex differences in several aspects of their foraging ecology including diet composition. The pattern of these sex-differences in diving behaviour (Chapter 2 & 3), energy accumulation (Chapter 5) and diet (this study) indicate that both sexual size dimorphism and different fitness-maximizing strategies of males and females likely contributed to the evolution of these differences. Further investigation into the foraging ecology of juvenile grey seals will help to clarify the relative role body size and reproductive considerations play in fostering these sex differences, given that energy storage for reproduction would not be expected to influence the diving behaviour of immature animals.

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Appendix 6.1: Proximate composition and energy density of prey species found in the diet of adult grey seals.

Prey Species	% Lipid	% Protein	Energy Density (kJ/g)[a]
Capelin	9.70[1]	16.13[1]	7.62
Herring	7.16[1]	18.00[3]	7.06
Mackerel	3.37[1]	18.60[3]	5.71
Sandlance	7.54[1]	15.34[1]	6.58
Snake Blennie	2.21[1]	15.00[1]	4.41
Cod	2.00[1]	15.35[1]	4.41
Lumpfish	2.52[1]	15.00[3]	4.53
Ocean Pout	2.73[1]	15.00[1]	4.61
Redfish	6.92[1]	16.45[1]	6.60
American Plaice	2.62[1]	15.95[1]	4.79
Halibut	1.87[1]	20.80[3]	5.49
Windowpane Flounder	1.91[1]	16.30[3]	4.60
Winter Flounder	2.03[1]	16.30[3]	4.64
Yellowtail Flounder	2.34[1]	17.10[3]	4.96
Thorny Skate	2.50[1]	17.00[4]	4.99
Winter Skate	1.43[1]	17.00[4]	4.57
Lobster	1.52[1]	18.80[3]	5.03
Rock Crab	0.82[1]	18.50[3]	4.69
Snow Crab	2.37[1]	18.50[3]	5.30
Shrimp	1.87[1]	17.20[2]	4.79
Squid	2.00[1]	17.00[2]	4.80

Proximate Composition data on prey species from [1] Scotain Shelf prey base, [2]Lawson *et al.* 1998, [3]Government of Newfoundland Fisheries and Aquaculture website: www.gov.nf.ca/fishaq/species, [4] Scotain Shelf prey base value for Smooth Skate. [a] energy density = ((%lipid/100) x 39.3 kJ/g) +((% protein/100) x 23.6 kJ/g)