Movement, diving and foraging success in a large, sexually dimorphic

marine predator: Insights from telemetry

By

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*For my parents,
who always encouraged
me to pursue
education to its
fullest.*

*And for Strahan,
for helping me to
believe I could.*

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ABSTRACT

Establishing where and when predators forage is essential to understanding trophic interactions. Recently, the abundance of grey seals (*Halichoerus grypus*) in the Northwest Atlantic has raised concerns about the impact of predation on commercial fish species. However, current predation models are limited by assumptions that predation is constant in time and space. Therefore, the goal of my research was to examine the spatial and temporal scales of foraging in grey seals. Advances in telemetry make it possible to study diving, movement and distribution of feeding at sea. Given evidence of sex-specific differences in diving and energy storage in this body-size dimorphic species, I predicted that sex would be important in structuring foraging behaviour.

I examined the use of space by grey seals by quantifying movement patterns using locations from satellite telemetry. Using correlated random walk (CRW) and Lévy Flight models, I found that individuals used three types of movement: those which followed a CRW, those which were over-predicted by the model and used Sable Island year-round (residents), and those which were under-predicted by the model and used larger-scale directed travel. Movement type was related to sex, with males more likely to exhibit directed travel. The failure of most to fit a Lévy Flight suggested that prey were not randomly distributed. The temporal pattern of feeding success using stomach temperature telemetry revealed considerable individual variation, some of which was related to sex. The number of feeding events and average time associated with feeding was greater in males. By linking distribution and feeding success with dive data from time-depth-recorders, I investigated how feeding was related to both movement and diving behaviour. Foraging trip length, accumulated bottom time and angular variance were all predictors of successful feeding. Diving characteristics differed by movement type, independent of sex, such that residents had longer bouts and dove to shallower depths. My research demonstrated that although grey seals exhibited marked individual variation in movement, diving and feeding patterns, males and females differed both in the characteristics of feeding and the way they used space. These findings have implications for the way we model predation in marine ecosystems.

ABBREVIATIONS

AIC:	Akaike's information criterion
ANOVA:	Analysis of Variance
CRW:	Correlated Random Walk
DFA:	Discriminant Function Analysis
DM:	Directed Mover
GLM:	Generalized Linear Model
GLMM:	Generalized Linear Mixed Model
HR:	Home Range
KEI:	Keating's Error Index
LI:	Linearity Index
MANOVA:	Multivariate Analysis of Variance
MCP:	Minimum Convex Polygon
MVT:	Marginal Value Theorem
OFT:	Optimal Foraging Theory
QFASA:	Quantitative Fatty Acid Signature Analysis
SMM:	State Space Model
SLTDR:	Satellite-Linked Time Depth Recorder
SRDL:	Satellite Relay Data Logger
STT:	Stomach Temperature Transmitter
TDR:	Time Depth Recorder
ZOC:	Zero Offset Correction

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Chapter I: General Introduction

The spatial and temporal organization of animal behaviour fundamentally affects the nature and dynamics of ecological interactions. Nowhere is this more evident than in the case of top predators. Establishing where and when predators forage is primary to understanding ecosystem functioning (Everson 1984, Trathan *et al.* 1998). Top predators tend to integrate variability in the productivity of the ecosystem across large spatial and temporal scales (Boyd *et al.* 2002). The distribution of predation introduces heterogeneity in prey mortality, which can have significant effects on prey and community dynamics (Boyd 1996). Therefore, temporal variation in predator behaviour is likely to provide insight into the spatial distribution of dynamic prey that may otherwise be difficult to track (Mangel and Adler 1994). Consequently, in marine ecosystems, top vertebrate predators have been cited as potential indicators of change, due to their position at the top of marine food chains (Montevecchi 1993, Boyd *et al.* 2002).

To survive, a predator must continuously track changing prey patterns and respond to heterogeneity at different spatial and temporal scales (Benoit-Bird and Au 2003). Therefore, the spatial and temporal distribution of prey has a strong effect on the energetic costs of foraging, foraging success and overall predator survival (Boyd 1996). The extent at which apex predators respond to prey variability will be an indication of the scales at which they can detect change. The relative mobility, home range and size of an organism may affect the resolution at which an animal recognizes environmental heterogeneity (Kotliar and Wiens 1990, Rose and Leggett 1990, Russell *et al.* 1992). Consequently, the concept of scale is one that is largely species-specific, but can vary between individuals, between sexes, (Sjöberg and Ball 2000, Ball *et al.* 2001, Stirrat

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2004), or seasonally (Boyd *et al.* 2002). To understand the relationship of an organism to its environment, one must understand the interactions between the intrinsic scales of heterogeneity within the environment and the scales at which the organism can respond to this heterogeneity.

Recent declines of upper-trophic level predators in ecosystems worldwide have raised awareness of potential human impacts on non-target species (Agardy 2000, Lotze 2004, Baum *et al.* 2003). In particular, we have seen the decline of many top marine predators, including sharks (Baum and Myers 2004), large piscivorous fish (Pauly *et al.* 1998, Jackson *et al.* 2001) and marine mammals (Trites *et al.* 1999, Brownell *et al.* 2001, Donahue *et al.* 2001, Doroff *et al.* 2003). Proposed reasons for these declines are varied, but in many cases causes are inferred such as the removal of predators from the community as a result of bycatch from commercial fishing (Morizur *et al.* 1999, Baum *et al.* 2003), commercial whaling (Springer *et al.* 2003) or ecosystem regime shifts mediated either by natural processes or large-scale commercial fisheries (Benson and Trites 2002). The decrease of marine mammal populations are of particular concern given their low population growth rates and life history characteristics: they reach sexual maturity late in life, produce single offspring, and have long inter-birth intervals. Consequently populations can be slow to respond even once ecological conditions have turned favourable (Taylor 2002). In order to resolve these issues of decline and to fully appreciate the consequences of anthropogenic threats, we must first identify the range of spatial and temporal scales at which top predators operate, and understand the mechanisms of their survival, including their behaviour, distribution and habitat.

Conversely, the end of centuries of exploitation has led to the recovery of other marine mammal populations to historic levels (Bowen *et al.* 2003, Olesiuk 2003). This has led to perceived conflict with commercial fisheries, based on the belief that marine mammal predation may result in significant removal of prey populations that are of commercial interest to humans (Bowen 1997, Trites *et al.* 1997). In recent years, a number of predator-prey models have been developed to quantify the relative importance of marine mammal predation on fish stocks (Overholtz *et al.* 1991, Bax 1992, Punt and Butterworth 1995, Mohn and Bowen 1996, Stenson *et al.* 1997). However, current models are limited by our understanding of how predators use time and space. The resolution of these two broad issues, marine mammal conservation and their conflict with fisheries, as diametrically opposed as they may seem, is together limited by our current inability to predict the spatial and temporal scales over which these animals make their living. Only once we have a basic understanding of the foraging behaviour of marine mammals can we begin to develop appropriate conservation and management plans.

Until recently, the ability to study marine mammals as top predators has been limited given that they spend as much as 90% of their time submerged (Read 2002) and are often extremely wide ranging, sometimes occupying very remote locations (Bowen 1997). These difficulties have resulted in a general lack of knowledge of foraging behaviour in marine mammals, particularly in comparison to terrestrial animals. Telemetry, the process of obtaining data remotely by transmitting information or storing information for later retrieval (Read 2002), has enabled ecologists to bridge the frontier of behavioural ecology; essentially liberating them from the logistical difficulties of making physical observations or the tedium of constant tracking. In the case of the

marine mammal, information about diving behaviour, spatial distribution and feeding success can all be collected and/or transmitted by free-ranging individuals using telemetry. Obviously, the potential afforded by such developments has marked a significant turning point for ecologists attempting to understand the role of marine mammals in marine ecosystems.

Yet, it is not only community or ecosystem wide studies that can benefit from the use of data collected via telemetry. Perhaps even more momentous has been the shift to an individual-based ecology resulting from the ability to collect large amounts of information pertaining to a single organism. The very means by which telemetry data is collected necessitates that we consider the effect of individual variation on the overall outcome; in statistical terms, the "subject effects". This represents a philosophical change in the focus of ecological studies, from that of creating population or species specific generalizations, to the study of individuals. For example, Optimal Foraging Theory (OFT) has traditionally been used to predict general decision rules in foraging behaviour, as a population-level phenomenon (Charnov 1976, Stephens and Krebs 1986). However, recent studies have indicated that individuals within a single population often exhibit marked individual variation, or specialization, in foraging behaviour (Bolnick *et al.* 2003). For example, Goebel *et al.* (1991) suggested that female northern fur seals (*Callorhinus ursinus*) demonstrated two distinct diving patterns, each characterized by either deep or shallow diving and each associated with different feeding behaviours. In a more extreme example, Estes *et al.* (2003) established that adult female sea otters (*Enhydra lutris*) from the same region studied over seven years demonstrated extreme inter-individual variation in diet. Further, they suggested that given the specialist nature

of their prey selection, individual otters probably require radically different sensory skills. Given that natural selection operates at the level of the individual, ecological concepts that paint all individuals with the same sweeping brush effectively disregard this sort of variation (Judson 1994).

Intraspecific variation in foraging behaviour may also reflect sex-specific differences. Evidence for sex-specific foraging behaviour is widespread across various taxa, including mammals, birds and invertebrates, (e.g. Clutton-Brock *et al.* 1983, Parmelee and Guyer 1995, Stokke 1999, Jormalainen *et al.* 2001). Sex-specific differences have been attributed to a number of factors, including sexual dimorphism, intra-specific competition, and differing reproductive roles of males and females. Sexual size dimorphism results in unequal energetic requirements between males and females. Obviously, the larger sex will require a greater absolute energy intake in order to attain and maintain their larger size (Klieber 1961) and thus might be expected to modify their foraging behaviour relative to that of the smaller sex.

Sex differences in foraging behaviour have been shown in a number of marine mammal species. Sperm whales (*Macrocephalus physeter*) show the greatest size dimorphism of any cetacean, and studies indicate that adult males have dissimilar distribution patterns and use different habitats than female sperm whales. Males appear to spend the majority of time feeding at high latitudes, while female sperm whales tend to remain in the warmer, equatorial areas of the ocean, and it is thought that warmer waters provide better thermoregulatory conditions in which females can successfully rear young. In this example, the divergent foraging strategies demonstrated by males and female

sperm whales may be related to differing reproductive roles of the sexes (Best 1979, Whitehead *et al.* 1991, Weilgart *et al.* 1996).

Pinnipeds show the greatest range in sexual size dimorphism of any vertebrate group (Ralls and Mesnick 2002), and therefore one might expect profoundly divergent requirements between the sexes which may be manifested in foraging behaviour (e.g., Le Boeuf *et al.* 2000). Indeed, sex-specific differences in both foraging areas and diurnal patterns of dive depth have been observed in Northern elephant seals (*Mirounga angustirostris*; DeLong and Stewart 1991, Le Boeuf *et al.* 2000), a highly size-dimorphic species. These differences are assumed to reflect dietary seclection between the sexes. Males are thought to feed on demersal prey while females feed on vertically migrating pelagic prey, although direct evidence of diet is still lacking (Le Boeuf *et al.* 2000). Subsequently, it has been suggested that this variation in both location and diving behaviour are consistent with a hypothesis of intra-specific competition between male and female northern elephant seals (Le Boeuf *et al.* 2000).

Sex-specific differences in the foraging behaviour of grey seals (*Halichoerus grypus*) have been well documented (Beck *et al.* 2003a,b,c). Grey seals are a size-dimorphic pinniped, with adult males approximately 1.5 times larger than females. They are a relatively large phocid species; adult males and females in the Northwest Atlantic population reach lengths of up to 2.65 m and 2.20 m, respectively. Based on diving behaviour obtained from time-depth-recorders (TDRs), males and females exhibit markedly different seasonal patterns in dive characteristics and overall dive effort. For example, female grey seals had higher levels of dive effort immediately following molting, and in the three months prior to the breeding season (Beck *et al.* 2003a).

Females also had longer dives than males, and spent more time at depth, although males dove to deeper depths (Beck *et al.* 2003a). These seasonal differences in diving were also observed at the temporal scale of bouts. Dive bouts of female grey seals were of longer duration and with greater time spent at depth (Beck *et al.* 2003b). Further, patterns of energy accumulation and storage throughout the year reflected these patterns of diving effort (Beck *et al.* 2003c).

Size dimorphism may account for some of the differences observed in diving, for example, the ability for males to dive deeper and longer than females. However, the seasonal differences in diving patterns cannot be as easily explained. Beck *et al.* (2003b) suggest that seasonal differences in diving behaviour result from sex differences in the costs and benefits associated with long-term energy storage for reproduction. Females must amass sufficient reserves early on in the year post-moult in order to ensure a viable pregnancy, and again just prior to the breeding season in order to sustain lactation. Males are not faced with the dire consequences of failing to procure sufficient energy reserves until closer to the breeding season, and hence they can adopt a more consistent strategy of feeding (Beck *et al.* 2003b).

These findings of sex differences are critical for modeling predator-prey relationships; the downfall of many current models (e.g., Punt and Butterworth 1995, Mohn and Bowen 1996, Stenson *et al.* 1997) being the assumption that predation (prey selection and consumption rates) is distributed equally across individuals. By recognizing inherent variability of feeding within a population through studies of this nature, existing models can be fine-tuned to account for the differing roles of predators within a population. The development of predator-prey models that that are more

representative of grey seal foraging in time and space is of timely importance. In particular, the collapse of commercial fisheries in the last decade has renewed concerns over the role of pinniped predation in the Northwest Atlantic marine food webs (Harris 1990, Fu *et al.* 2001). Recent studies indicate that the grey seal population in the Northwest Atlantic is increasing at an exponential rate of 12.8% with an estimated population of 300 000 animals in 2003 (Bowen *et al.* 2003). As a consequence, Mohn and Bowen (1996) predicted that grey seals might represent an important source of predation on Atlantic cod (*Gadus morhua*) populations. Other studies (Mansfield and Beck 1977, Murie and Lavigne 1992, Bowen *et al.* 1993, Bowen and Harrision 1994) have shown that other commercial fish species are also eaten by grey seals.

A key limitation of the predation model proposed by Mohn and Bowen (1996) is the assumption that predation by grey seals is distributed uniformly within season over a range of prey species. However, the studies by Beck *et al.* (2003a,b,c) demonstrate that grey seal foraging effort varies significantly within season and between the sexes. Similarly, very recent work on grey seal diet suggests that the suite of prey species consumed also varies extensively between seasons and individuals (Beck *et al.* in review). These findings will aid in the development of future models, but there are still a number of major gaps in our understanding of grey seal foraging (Mohn and Bowen 1996), including the spatial extent of foraging distribution and the temporal distribution of foraging success. If models are to be truly representative, they must sufficiently address the spatial and temporal scales at which foraging takes place.

Therefore, the overall goal of my research was to examine the spatial and temporal scales of foraging grey seals. The purpose of which was to further our

understanding of the role of top predators in marine ecosystems, and contribute to the conceptual development of further models to predict the effects of grey seal predation in the Northwest Atlantic. This objective had three constituent parts. Firstly, I examined the use of space by foraging grey seals by quantifying movement and distribution patterns based on satellite telemetry. Secondly, I studied the temporal pattern of feeding success using stomach temperature telemetry. Thirdly, I used records of diving obtained from TDRs to test hypotheses about how dive effort changes with feeding success, and used satellite locations to describe the spatial distribution of feeding. In addition, with each objective I tested for the presence of individual variation, and in particular, sex-specific differences in foraging behaviour. Given the existence of sex-specific diving behaviour and energy storage in grey seals (Beck *et al.* 2003a,b,c), I predicted that sex differences in may be an important factor in structuring patterns of movement, distribution and feeding success.

In Chapter II, I begin with a review of animal movement theory, and follow by considering various components of movement within the context of OFT, the purpose being to stress the importance of a unified theory of animal foraging behaviour and life history. Chapter III describes an improved filtering algorithm to remove erroneous satellite locations from an individual's track. Using filtered satellite locations, I then analyze the movement patterns of grey seals using quantitative movement models and home ranges in Chapter IV. In Chapter V, I present the first quantitative analysis of the temporal pattern and frequency of feeding in free-ranging pinnipeds. Finally, in Chapter VI, I examine the relationships between feeding and the temporal pattern of diving, foraging location and movement patterns.

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Chapter II: Linking Optimal Foraging Theory to Animal Movement

Introduction

Animals must eat to survive. This premise forms one of the most basic concepts in biology, and yet, behavioural ecologists are still attempting to understand how animals organize their feeding behaviour. Optimal foraging theory was developed over thirty-five years ago, with seminal papers from MacArthur and Pianka (1966) and Emlen (1966). The logic they developed is that of classic optimization theory- that complex behaviours are to be interpreted in terms of the contribution they make to Darwinian fitness (Maynard-Smith 1978). An immediate reward, or "currency" is to be maximized at the cost of conflicting behaviours, and is directly related to the amount of food obtained, and hence the net energy received (Schoener 1971, Pyke *et al.* 1977, McNamara and Houston 1986). In turn, it was assumed that maximizing this rate was equivalent to maximizing fitness (Schoener 1971, Houston *et al.* 1988). Given that for every individual, there is a range of potential foraging behaviours (Pyke *et al.*1977), optimal foraging theory (OFT) attempts to predict which is the most profitable, in terms of the least number of tradeoffs for maximum benefit to reproductive success (Perry and Pianka 1997).

Despite the initial excitement that OFT afforded behavioural ecologists, it was followed by a backlash from those who did not concur with the basic tenet of optimization theory. Many argued that optimization was inherently untestable in living organisms, and hence there was no absolute way to reject optimality (Heinrich 1983, Pierce and Ollason 1987). Regardless of the intense scrutiny, it appears that OFT remains

a useful concept in behavioural ecology (Perry and Pianka 1997). Imperative to our understanding is that there is not one single model of OFT, nor is there a single model which is globally applicable to all organisms. Instead, theories of optimal foraging are considered to be a suite of models, for which optimization is the shared approach to their construction (Stearns and Schmid-Hempel 1987, Nonacs 1993). According to Perry and Pianka (1997), OFT should offer essential theory to ecologists through its ability to predict the optimum performance of organisms by comparing predictions to empirical behaviour, and to guide future research.

OFT models developed in seminal papers (e.g. MacArthur and Pianka 1966, Emlen 1966) were moderately successful in predicting short-term behaviours (Stephens and Krebs 1986, Houston *et al.* 1988). However, they suffered from critical limitations because they were entirely deterministic, and hence did not consider the stochasticity of the natural world (Stephens and Charnov 1982, Oaten 1977). Generally, deterministic models assume that the forager is omniscient of the resource conditions; e.g., they know the prey-encounter rate or time to renewal and that the currency being maximized is static (Stephens and Charnov 1982). Constraints on maximizing the net rate of energy intake, such as starvation or predation risks, were not considered, nor did models account for the energetic state of the organism (Houston *et al.* 1988) and hence they fell short in their predictive ability.

In response, ecologists formulated models that were both dynamic and state-dependent (Mangel and Clark 1986, Houston *et al.* 1988). These developments included: extensive models of optimal patch use (e.g., Charnov 1976, Stephens and Charnov 1982), central place foraging theory (e.g., Orians and Pearson 1979, Schoener 1979), risk

sensitive foraging theory, a collection of models which considered variance about the food reward, (e.g., Caraco 1980, 1981, 1983) and models of optimum movement or search paths (Norberg 1977, Pyke 1977, 1978a,b, 1981).

Of the above OFT models, the latter category has received the least attention (Pyke 1983, 1984). This is surprising given that most animals must undertake some form of movement in order to amass sufficient food reserves; hence, animals must also move to survive. As previously mentioned, the decision-making process for free-ranging animals faced with stochasticity in food resources and in their environment is not as simple as optimal foraging hypotheses would suggest (McFarland 1977, Schluter 1981, Mangel and Clark 1986). Many other factors, movement being one of them, must be included to achieve a realistic sense of the rules governing foraging decisions. The need to quantify animals' search paths became evident in many of the initial studies of OFT (e.g. Pyke *et al.* 1977, Krebs 1978, Krebs *et al.* 1983, Pyke 1983, 1984).

According to Johnson et al. (2001), foraging behaviour is simply a series of consecutive decisions, such as: What to eat? When to eat? Where to eat? And how to get there? (Johnson *et al.* 2001). Consequently, therein lies the potential to model the way in which an animal should navigate or approach a specific food resource in an optimal manner. For the most part, only models that predict "why" and "when" an animal should move in relation to a food resource have been developed (Pyke 1983, Swingland and Greenwood 1983); largely owing to the establishment of the Marginal Value Theorem (MVT) by Charnov (1976). Charnov (1976) predicted that an animal will forage optimally if it remains in each patch until its net rate of energy gain in that patch has decreased to the overall background rate in the habitat, at which point it should leave.

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Cowie (1977) provides the best empirical demonstration of the MVT. Using great tits (*Parus major*), he was able to show that the observed times spent in a patch agreed closely with the optimal times predicted by the MVT.

Still, even with Charnov's theorem and the establishment of patch departure rules by the early 1980's, the development of theory to outline efficient search strategies, to answer the question of *how* animals should move when traveling between patches, (Swingland and Greenwood 1983) had received little attention in the literature (Pyke 1983). Given that the mode of movement may influence the type and amount of prey consumed (Huey and Pianka 1981), it begs to be a fundamental element in models of optimal foraging (Schoener 1971). Therefore, in order to fully understand the physiological, ecological and evolutionary complexity of foraging decisions, we should consider both the "how" and the "why"; the former question considers the mechanisms, while the latter concerns evolutionary significance (Heinrich 1983).

Mode of movement can be varied by altering certain characteristics, including: directionality (turning angles), speed, and distance traveled. In turn, these aspects are influenced by the type of resources or patches present within the environment (Russell *et al.* 2003), the type of landscape surrounding a patch (Pither and Taylor 1998, Jonsen *et al.* 2001), perceived risks of travel (Bhattacharya *et al.* 2003) and the state of the animal (e.g., degree of satiation; Kareiva and Odell 1987, Wallin 1991). In more recent years, movement has garnered attention from ecologists and mathematicians; yet, these studies have generally remained distinct from advances in OFT. However, I argue that movement should be fitted within an OFT framework (Bovet and Benhamou 1988), thus providing a means of predicting optimal movement patterns.

The main objective of the following synthesis is to emphasize that current foraging theory needs to be coupled with the rules that predict how animals move. The focus of the paper is not to model the two concepts together, but instead to stress the importance of a unified theory of energy acquisition, which would include both foraging and movement. I begin with a brief synopsis of animal movement theory, and follow by considering various movement characteristics and how these have or have not been considered within the context of OFT. In turn, the mechanisms that may be responsible for observed movement patterns, namely search strategies and energetic state, will be considered for their contribution to OFT. Finally, I will give a critical overview of the applicability of OFT to empirical data, and finish with a look to the future of OFT in the field of ecology.

A Brief History of Animal Movement Theory

Prior to 1950, the requirement of feeding was not even considered as a possible incentive for movement. Animal movement in the form of dispersal was ascribed to a "steady leakage of individuals out of an area, a forced exodus due to overcrowding and accidental transport," (Wellington 1979). Further, the risks of movement were emphasized more often than the benefits, and population ecology usually ignored dispersal altogether since it was difficult to observe and explain quantitatively (Turchin 1998, Byers 2001). However, with increasing knowledge of population dynamics over the following decades, it became clear that animal movement was a missing link in understanding the interplay between population distribution and environmental heterogeneity (Turchin 1998). More and more, ecologists recognized that movement

could alter populations by subtracting or adding individuals, imparting genetic variability, changing resource distribution and influencing organism interactions.

A general definition of movement is given by Turchin (1998) as, "The process by which individual organisms are displaced in space over time". Hence, movement has a spatial and temporal component, and is a process that implicates individuals, though for many species group dispersal (e.g., with a herd) may be a critical feature. Consequently then, movement can be considered at a number of relevant spatial and temporal scales. At the longest time scale and over large spatial scales, can occur sporadic or rare metapopulation movements, such as immigration and emigration. Migration, also on a large spatial scale, but occurring consistently in time, is another form of movement as suggested by Baker (1978). At conflicting scales, are those small scale movements associated with foraging. Migratory movement generally implies a substantial distance component, but foraging movement can refer to a distance as short as that undertaken by a bee flying between two inflorescences (Greenwood and Swingland 1983). Throughout this review, I will be referring to the latter category of movement, those movements associated directly with acquisition of resources.

Though the assumption that the distribution of animals in space is linked to the distribution of food supplies has existed for centuries (Greenwood and Swingland 1983), the study of movement did not progress beyond this until much more recently. As previously mentioned, movement behaviour received increased attention with the onset of OFT in the 1970's, however, most studies focused on the outcome of different movement patterns, without describing the movement itself (Kareiva 1982). For example, Charnov's (1976) MVT describes the way in which an animal should appropriate its time

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between patches- hence, when an animal should leave a patch in search for another. His model does little to describe the way in which an animal should move from patch to patch and still optimize net energy received, i.e. in terms of speed, angular variation or type of movement. Thus, Charnov's theory, although an important advancement, is limited in its deterministic view and its lack of application to overall animal behaviour.

Shortly thereafter, Pyke (1978a) made one of the first attempts to create a model that maximizes rate of energy gain as a function of movement rules. He suggested simple rules for an animal moving on a grid of uniformly distributed "patches" or grid points, where each move length is constant, the animal obtains no food by re-visiting grid points, and the animal can turn right, left, forward or backwards, the probability of which is obtained by discrete approximation to a normal distribution. While a useful contribution in providing one of the first attempts to predict direction of travel, it was rather limited in that it did not consider that the animal might have some memory of previously visited "patches". In addition, since it offered only four directions and was applicable to uniformly distributed food resources, it suffered from being overly simplistic.

Subsequently, Pyke (1978c) offered a second model, to describe a bumblebee moving between inflorescences. The corresponding "rules of movement" depended upon on an animal's assumed memory level, and hence was innately stochastic. The model assumed that each bee had a theoretical "scanning sector", within which it chose the closest resource point. The aim of the model was to determine the optimal relationship between the arrival and aimed departure directions and the optimal width of the scanning sector. Many useful predictions were provided, some of which were validated empirically. The model still suffered from a number of limitations. Namely, it resulted in

qualitative, not quantitative predictions, and the model assumed that the animal chose the closest resource point within a scanning sector, however, this would result in an animal simply moving back and forth between the same two points (Pyke 1983). As a result of these difficulties, Pyke (1978c) concluded that the best way to avoid these difficulties and provide the most realistic model of movement would be to use computer simulation.

Following these two pivotal modeling efforts, a large number of empirical studies were conducted to test the predictions of both the Charnov (Zach and Falls 1976, Cook and Hubbard, 1977, Cowie 1977, Waage 1979, Bond 1980, Stanton 1982) and Pyke (Heinrich 1979, Zimmerman 1979, 1982) models. Hereafter, we see a distinct divergence of OFT theory from movement studies. Theoretical contributions were largely focused upon the latest development in OFT, that being stochastic dynamic programming and theories of risk-sensitivity. Meanwhile, understanding and modeling animal movement became the undertaking of insect ecologists, presumably due to the relative ease with which insects could be observed in the field. Departing from the original algorithmic rule models of Pyke, these researchers approached the theory of animal movement from two different directions.

At this point in time in the mid 1970's, computer simulations had just commenced to play a role in movement analysis (e.g. Siniff and Jessen 1969, Kaiser 1976, Jones 1977). Jones (1977) provided one of the first such simulations to generate extended movement sequences to predict how cabbage butterflies, *Pieris rapae*, should distribute their eggs to maximize reproductive success. Computer simulations based on field observations of individual behaviour are tightly linked to empirical data (e.g., Cain 1985, Turchin 1987), but may suffer by being very species-specific, and thus make

contributions to general theory difficult (Turchin 1991). Nevertheless, they still play a large role in movement analysis today, and are used by many ecologists to answer questions of a species-specific nature.

In addition, we see the development of another theoretical approach to explaining movement using diffusion based models; the majority of which took their roots from the formative diffusion models of Skellam (1951), and later modified by Kareiva and Shigesada (1983). These are based on the null hypothesis that movement patterns can be represented by random movement (also known as a random walk), and that departures from a random pattern indicate a propensity to move according to alternate rules (e.g., tracking patch distribution). The random walk hypothesis was later modified by introducing a correlated element to the random walk, which reflects the cephalo-caudal polarization and the bilateral symmetry observed in most animals, giving them an inherent tendency to go forward (Bovet and Benhamou 1988). Kareiva and Shigesada (1983) developed an equation which used move lengths, turning angles and total number of moves to calculate an expected net squared displacement of a correlated random walk (CRW). This results in a quantitative representation of observed animal movement, which can be compared to simulated random paths that predict expected movement. The CRW approach has been used with relative success in many studies of insect movement (Kareiva and Shigesada 1983, Turchin 1991, Crist *et al.* 1992, Byers 1999, 2000, 2001), and even vertebrates (Bergman *et al.* 2000, Austin *et al.* 2004).

Despite the amount of attention that movement modeling has had over the last twenty years, it still lags behind that of other ecological processes (Marsh and Jones 1988), particularly in the case of larger vertebrates (Bergman *et al.* 2000). Further, many

published studies have a focus on methodology alone, and as a result many researchers have neglected their raison d'être, or the greater context in which their studies should be considered. Namely, in the case of foraging animals, the theoretical background represented by OFT.

Components of Movement

I. Optimal Directionality

Historically, turning angles in animal search paths have received a great deal of attention by behaviourists (Levin *et al.* 1971, Smith 1974a, b, Kareiva and Shigseda 1983). Directionality refers to the sequence of turning angles used by an animal whilst moving. If the direction of one movement at t_1 is independent of the previous movement at t_1-1, then the distribution of turning angles that describe a path should be uniformly distributed around a circle. The more negatively serially correlated the angles are, as typically occurs when turning angles are grouped around ±180°, the more sinuous, or tortuous is the path. However, if successive turning angles are positively correlated to one another, then one can infer that the animal is demonstrating directionality, also known as directional persistence or directional bias (Turchin 1998). In such an instance, often the turning angles are clustered around 0° and display alternation in sequential turn directions, resulting in a nearly straight path. Pyke's (1978c) model described above predicted that both the mean turning angle should approximate 0°, and that animals should alternate right and left turns to remain in a near straight line.

Optimal directionality in an animal's path should lead to a decrease in the number of patches revisited and increase the possibility of encountering new patches (Wolf and

Hainsworth 1990). The "lost opportunity principle" coined by Stephens and Krebs (1986) refers to the re-visitation of already exploited patches; by doing so, an animal loses the opportunity to seek out other patches where resource availability is higher. Bovet and Benhamou (1991) developed a model to predict the optimal sinuosity of a search path of a central place forager. They proposed that to bring a search path within the constraints of optimal foraging theory, it should constitute a compromise between an overly straight path, which would result in a lengthy return trip to the central place, and an over-sinuous path which results in too much patch re-visitation. The model depends in part upon the energetic demands of the trip back to the central place, i.e. the amount of food the animal must carry. For example, to account for heavier loads on the trip back to the central place, the model would result in a higher optimal sinuosity. As the survey area increased, they found that optimal sinuosity decreased.

Although Bovet and Benhamou (1991) did not provide an explanation for this phenomenon, Zollner and Lima (1999) proposed that the closer the path approaches to being straight (without actually being perfectly straight), the greater the area that can potentially be searched. Using computer simulated models, they found that the best search paths were nearly straight, i.e. with a relatively high amount of correlation between successive steps. Intuitively, completely straight paths resulted in an animal leaving the landscape and hence, missing available patches, but nearly straight search paths were effective across a range of circumstances, including conditions of increased mortality risk, fluctuating reserve levels and differing patch densities.

A considerable number of empirical studies have suggested that foragers will maximize net energy intake, by traveling in a straightened path (Cody 1971, Levin *et al.*

1971, Pyke 1978a,c, Zimmerman 1979, 1982, Root and Kareiva 1984, Bascompte and

Vila 1997, Zollner and Lima 1999). Pyke (1978c) predicted that bumblebees, (*Bombus*

flavifrons) foraging optimally amongst inflorescences would maintain a constant

direction in order to avoid revisiting flowers, and he supported this data empirically.

Soon afterwards, Zimmerman (1979) proposed an alternative hypothesis which predicted

that in a system where the probability of revisiting a specific flower was small, such as in

an area of high flower density, the bees would not maintain a constant direction, and

hence would have a random distribution of turning angles. Thus, in a case where resource

density is high, directionality may not be the optimal strategy. Alternatively, if the

forager is non-destructive in its feeding, revisiting patches would not be as grave a

problem, and hence randomness in directionality might be favoured. Experimental results

using the same species of bumblebees supported this hypothesis, and Zimmerman (1979)

concluded that as a result, the probability of flower revisitation in high density areas was

low. Interestingly, this species of bumblebee is able to maximize its energy intake by

altering its behaviour to best fit the distribution of resources encountered; therefore

emphasizing that models of OFT should include consideration of resource distribution

(Zimmerman 1979).

Therefore, we see that animals may change their directionality, and hence their

mode of movement, depending upon the distribution of patches and the density of

resources within, and dependent upon whether they are searching for food, or feeding.

For longer travel, such as that between patches, observations suggest that straight line

movements are most common for a number of species including moose (*Alces alces*,

Pastor *et al.* 1997), narwhals (Laidre *et al.* 2004), red foxes (*Vulpes vulpes,* Phillips *et al.*

2004) and salamanders (*Ambystoma maculatum*, Madison 1997). Root and Kareiva (1984) found that ovipositing female cabbage butterflies (*P. rapae*) travel differently than females foraging for nectar. Ovipositing females tended to follow linear routes of flight and demonstrated strong directionality, while nectar foraging females readily abandoned linear flight paths by engaging in tight turning behaviour in clumps of flowers. This suggests that different modes of movement may be appropriate for different foraging-related activities.

However, individuals within a species may also demonstrate different degrees of directionality while foraging. For example, in a comparison of the movement patterns of migratory versus resident caribou (*Rangifer tarandus*), Bergman *et al.* (2000) demonstrated that over the course of a year, migratory animals tended to move in straight paths over long distances, with the majority of turning angles concentrated around a mean of 4.0°. However, during important feeding periods the variance of turning angles increased to result in a wider distribution of move angles. On the other hand, paths of resident caribou were much more tortuous throughout the entire year because they did not leave the immediate area, and hence resulted in successive turns which tended to reverse the direction of movement.

Although Bergman *et al.* (2000) did not discuss their findings in light of OFT, they provide an important contribution towards our understanding of intra-specific differences in movement behaviour (Swingland 1983). Within a single species, we have two very distinct foraging modes- resident, or area restricted search, and migratory, or area extended search. The reasons for the occurrence of more than one strategy in a single species and not known, but may include different energetic requirements, other

phenotypic traits or genotypes. For example, similar results were reported for the giant tortoise, *Geochelone gigantea* (Swingland *et al.* 1989), and these were in part related to morphometry (migrating tortoises were longer and narrower than sedentary tortoises). Nor can one purport that one group is more "successful" than another according to OFT. Yet, it demonstrates that for whatever reason, these individuals are able to survive by optimizing two different strategies, and potentially two different currencies as well. While the occurrence of behavioural polymorphisms is not a new discovery, few studies have attempted to provide such quantitative mechanistic explanations beyond an observation of behavioural difference. Thus, movement models can provide measurable parameters which enable behavioural ecologists to distinguish between two opposing behaviours.

II. Optimal Distance Traveled

Another manner in which animals are able to change how they move is by altering the distance traveled between successive turning angles, or simply, the distance at which animals choose to travel in a straight line before stopping. Zimmerman (1979, 1982) showed that even when bees were moving randomly with regard to direction, they were minimizing flight distances by moving to neighbouring flowers. The resulting distribution of distances traveled was strongly leptokurtic. He suggested that by minimizing time and energy spent in transit, bees were able to maximize net energy gained. Similar distributions of distance traveled have been described for bees in other studies (i.e. Levin and Kerster 1969, Smith 1974a, Pyke 1978c).

In the model of Pyke (1978c) described above, it was demonstrated that when nectar resources are patchily distributed, the rate of net energy intake is maximized when

foragers utilize area-restricted searching behaviour. He proposed that as food resources increase, the average distance moved to the next resource point should decrease. Similarly, Stanton (1982) was able to show that female butterflies (*Colias philodice eriphyle*) make shorter flights when preferred plants are locally abundant. This strategy is considered to be optimal because when a high quality resource is encountered, the patchy nature of the environment suggests that nearby flowers will also be of high quality. Thus, by using information gained at the last patch visited, and adjusting travel distances in response, animals can increase their chances of encountering more high quality patches.

Focardi *et al.* (1996) studying fallow deer (*Dama dama*) looked at the cross-correlation coefficients of turning angles with their subsequent displacements and found that long displacements are correlated with large turns (i.e. around 180°). In this manner, an individual tends to retrace its path if in some previous step its movement was characterized by a long displacement. This mechanism also reduces the probability of leaving the habitat.

More recently, ecologists have "borrowed" concepts from the physical sciences in order to determine optimal search strategies for randomly located objects. In the past, path lengths of a randomly foraging animal were considered to have a characteristic distribution, e.g. gaussian or Rayleigh. However, Viswanathan *et al.* (1999) suggest that an inverse square power-law distribution of path lengths, a Lévy Distribution, is a more optimal strategy. Lévy distributions or Lévy flights have been found to characterize physical phenomena, such as fluid dynamics. It is characterized by a number of short moves, followed by a large displacement. Viswanathan *et al.* (1999) propose that a Lévy

distribution is advantageous when patches are randomly distributed because the probability of returning to a previously visited site is smaller than for a normal distribution. Similarly, but for different reasons, Klafter *et al.* (1996) proposes that a Lévy distribution is preferable because the number of new sites visited is greater than for simple random walkers under typical Brownian motion. Lévy flights have been demonstrated in nature in a few cases including foraging ants (Shlesinger 1986), *Drosophila* (Cole 1995), wandering albatross, *Diomedea exulans* (Viswanathan *et al.* 1996) and minke whales, *Balaenopta acutorostrata* (Stern and Hoelzel, unpublished data).

III. Optimal Speed

Although there has been a great deal of physiological study of maximum travel speeds in many animals, less is known about optimal travel speeds in animals in the context of optimal foraging (Ware 1975, Pyke 1981,1984). For example, Weihs (1977) demonstrated theoretically that fish will maximize the distance traveled for a given amount of energy if they swim at approximately 1 fish length per second, which is well within the range of aerobic metabolism. He also predicted optimum cruising speeds for fish, based on physiological and mechanical concepts. However, because foraging animals must perceive resources and decide which ones to consume, the dynamics of travel while foraging may differ from that of maximum travel velocity or critical speed (Speakman and Bryant 1993). As foraging animals travel faster, rates of energy expenditure should increase, followed by a corresponding increase in the rate of potential patches encountered (Pyke 1984).

Obviously, optimal speed is a trade-off between energetic costs of travel and encountering as many foraging opportunities as is needed. In a notable effort, Ware (1975) attempted to bring similar concepts into the realm of ecology by calculating the relationship between swimming speed and rate of food gain in a planktivorous fish. Using existing physiological relationships developed by Ivlev (1960), combining swimming speeds and rate of energy expenditure, he was able to determine the swimming speed that maximizes the net rate of energy gain. This he compared to the observed swimming speed, and found a close match. He then concluded that we can use empirically determined factors to assess optimality criteria. Although, it is not discussed in light of OFT, it was an important advance in looking at the ecological consequences of physiological mechanisms and abilities.

Pyke (1981) provided a model to predict optimal speeds for a theoretical animal while foraging which resulted in two broad predictions: (1) If fitness increases with net daily energy gain and decreases with time spent foraging, then the animal should employ a foraging speed that results in the maximum net rate of energy gained during foraging; (2) If fitness depends on the amount of time spent in a particular activity which involves travel, but does not depend on distance traveled, then the animal should employ the travel speed that results in the lowest rate of energy expenditure. He also indicated that in instances where predation risk is significant, and the energetic cost of travel is slight, the animal should travel at the maximum critical speed, i.e. the greatest speed that the animal can sustain over the distance. However, in more realistic terms, the optimal travel speed will depend on the trade-off between decreased predation risk, increased distance covered, and increased energetic costs, all of which arise from increased travel speed.

Norberg (1977) provided a model for optimal flight speeds of birds provisioning their young. Because the energetic costs of flight do not increase with speed, as in the case of running or swimming, he found that regardless of the distances flown, birds should increase their speed as long as the concomitant increase in travel costs can be more than compensated by foraging in the travel time saved. Gendron and Staddon (1983) developed a model incorporating all of the consequences of increasing speed, and using computer simulations demonstrated that the optimal foraging speed should always be lower than the rate that maximizes the gross rate of energy gain. They also determined that optimal foraging speed depends on the density and crypticity of each food type. The difficulty with both of these models is that they do not consider speeds between patches as being different to the speed once an animal encounters a patch. One would expect that as food density increases, assuming some degree of handling time, travel should be decreased in most species, e.g., herbivores (Shipley *et al.* 1996) and filter feeders (Sims 2000), but might be increased in others, e.g., predators, such as seals (Bowen *et al.* 2002) or fish (Weihs and Webb 1983). Additionally, before either model can be applied, there is a great deal of information that must be gathered about the animal before optimality criteria can be applied. Thus, it is difficult to apply these models to genuine situations.

For herbivores feeding on stationary food items, encounter rate is a function of the spatial distribution of foods, an ability to perceive that distribution, and the rate of travel among perceived items (Shipley *et al.* 1996). Although it was originally thought that the foraging rate of herbivores was constant because of a simple, linear function of plant density, further studies suggest that foraging velocity varies as a function of the distance

between plants (Spalinger *et al.* 1988, Speakman and Bryant 1993, Shipley *et al.* 1996). It has also been suggested that observed foraging speed is below attainable critical speeds because of the failure for previous models to include acceleration and deceleration upon departure and arrival at plants (Shipley *et al.* 1996). Thus, a model that describes an animal's acceleration when leaving a plant to an asymptotic velocity, as that proposed by Shipley *et al* (1996), resulted in good model fit to empirical data. Their model predicts that foraging velocity of mammalian herbivores increases asymptotically as the distance between plants increases.

Surprisingly, Shipley *et al.* (1996) also found similar foraging velocities amongst nine different species of mammalian herbivores. As size of the animals increased, so did acceleration time, such that smaller animals were able to reach maximum foraging velocity more quickly than larger animals and hence have better success foraging where plants were more closely situated. However, they did not find the inverse- maximum foraging velocity did not vary with body size. They attribute this, at least in part to the fact that large and small animals may require approximately the same foraging velocities to provide the best chance of detecting food items of a size scaled to their own size, while still maintaining a high encounter rate. Or, conceivably, smaller herbivores may move faster while foraging to optimize food intake relative to metabolic cost. Shipley *et al.* (1996) link their findings nicely with OFT. They conclude that the dynamics of foraging velocity may influence the way patches are exploited, particularly in herbivores. The example given is that if an animal must slow down to stop to take a bite, and in doing so increase overall foraging time and expend energy to overcome inertia when it leaves the plant, the animal may choose to exploit many bites in one area before moving on,

therefore in fact defining a herbivore "patch" in an otherwise uniform resource distribution.

To create OFT models that are truly stochastic, one needs to consider other factors that may be of importance in structuring foraging behaviour. Evidence exists that suggests animals may make changes in movement speed in response to perceived risks of predation, variation in food quality, quantity and spatial distribution (Stephens and Krebs 1986, Werner and Anholt 1993). Werner and Anholt (1993) propose a family of stochastic models that consider how movement speed would change under predation risk and changing resource conditions. Given the assumption that predation risk increases with increased speed due to increased detectability, they predict that under predation risk, optimal speed will decrease. They take it one step further to suggest that in instances when both rate of resource acquisition and mortality risk increase linearly with speed, foragers should switch from the sit-and-wait tactic to active search when resources increase. This is due to increased growth incurred from accrual of additional food under high resource density.

The first few models presented in this section (i.e., Ware 1975, Norberg 1977, Pyke 1981, Shipley *et al.* 1996) are relatively simple and attempt to identify an optimum foraging speed in order to maximize resource acquisition, considered tantamount to energy intake. Though parsimonious in their design, these models are embodiments of simple optimal foraging theories. One difficulty with these models is that they tend to be taxonomically specific, and it presents a challenge for ecologists to generate all encompassing rules of optimal speed beyond what was established in simple terms by Pyke (1981). However, the latter model (Werner and Anholt 1993) is more universal in

its application and uses stochastic dynamic programming to create a model that is far more complex because it considers additional parameters which may be key contributors to varying movement rates. Although the consideration of predation rates and varying resource distribution projects the model into a more realistic framework, the authors do not refer to seminal theories of OFT. This is unfortunate as their model is a significant example of the type of models which need to become the next generation of foraging theory.

Mechanisms of Movement

Although we have looked at the components of movement which can be altered by a foraging organism, we have not considered the forces which may be driving individual movement behaviour, i.e. potential reasons why an animal would change from directed to tortuous movement. One such mechanism, which has already received a fair amount of attention above, is resource distribution. Obviously, animals must move to find resources, and will alter movement patterns to reach these resources. This is an example of an extrinsic force, but there are a number of intrinsic factors that may mediate movement patterns. Individuals may use various mechanisms to find and procure food resources. The search strategies used by an animal may be determined by learned behaviour, heritability or cognitive abilities, and may be species specific, or may demonstrate intra-specific variation. Energetic state, affected by changing energetic requirements fuelled by growth, travel costs, level of satiation or proximity to the reproductive season is another key mechanism which will ultimately influence

movement. In the following section, I will examine these two factors, which I consider to be critical in determining optimal movement patterns of individuals.

I. Search Strategies

Predictions of OFT models depend directly upon the assumed search strategy (Focardi *et al.* 1996). Search strategies may take a number of approaches, including systematic search, random search or resource oriented strategies. In essence, an animal moving in a systematic manner will not correspond to predictions from an OFT model for randomly distributed resources. Types of non-systematic search have already been considered in light of OFT in previous sections of this paper. Correlated random walks, Lévy flights and the benefits of near-straight line search have been discussed. However, we have not discussed systematic searching, which relies on the animal moving according to a specific rule.

Evidence of systematic search rules in empirical studies has been few and far between, and comparisons of effectiveness versus random or resource-oriented search mechanisms are nonexistent (Zollner and Lima 1999). Systematic search methods have been described for bumblebees by a handful of researchers. Heinrich (1983) observed that bumblebees always move up inflorescences and suggested that systematic searching may be advantageous for two reasons. First, by moving up the inflorescence the bees circumvent the problem of revisiting patches because they automatically restrict themselves to those flowers that they have not already visited. Second, systematic foraging behaviour could also increase efficiency of flower handling by consistently approaching hanging flowers from underneath. This is the simplest example of a systematic rule because the bumblebee consistently moves in the same direction. More

complicated rules, such as Archimedean spirals, have also been described for foraging animals (Dusenberry 1992). For example, Mexican bean beetle (*Epilachna varivestis*) movement patterns have a significant spiralling component to them. The beetles tend to make several turns in a row in the same direction, thereby creating a positive autocorrelation in the direction of their turns (Turchin 1998). Typically the distance between the concentric circles created by an Archimedean spiral is twice the searcher's perceptual range. According to Bell (1991), a spiralling pattern of movement is a very efficient mode of searching, because it allows the animal to spread out in a concentric fashion, thereby exhaustively searching the area without overlapping on previously visited terrain.

Another type of systematic search strategy is the average distance rule (Zollner and Lima 1999). Although similar to the Archimedean spiral, it differs in that the distance between circular loops is equal to the average inter-patch distance in the landscape. This rule does not lead to exhaustive searching of the landscape, but is effective because it is determined in part by landscape configuration. Zollner and Lima (1999) tested the efficiency of Archimedean spirals, average distance rules, and correlated random walks using computer simulations. They found that the average-distance rule had the highest probability of successful dispersal, particularly in a uniform landscape, where this rule quickly moves the searcher to the vicinity of neighbouring patches. In contrast, Archimedean spirals were ineffective given that simulated animals spent too much time searching empty space near their starting patches. A correlated random walk provided results intermediate to the two forms of systematic search.

Trapline foraging is a specific type of systematic search that refers to repeated sequential visits to a series of fixed resource points or "stations" (Thomson et al. 1997). The analogy refers to a trapper checking traps on a regular basis and has been observed by many researchers working on bees (Heinrich 1979, Anderson 1983, Thomson et al. 1996, 1997), hummingbirds (Gill 1988) and even ungulates (Garber 1988). Though a documented phenomenon, no one has proposed a succinct method of validation by statistical testing (Thomson et al. 1997). Typically it is restricted to a small, local foraging area, and the animals are presumed to remember the location of the resource points, presumably having chosen resource points that were consistently profitable. "Flower constancy" is a similar strategy which describes how bees systematically return to certain flowers regularly (Goulson 2000). This may be an alternate form of an OFT model which maximizes net energy intake and minimizes reward variability by having a reliable source of consistently profitable rewards.

Spatial structure of the landscape may influence search strategies (Crist et al. 1992, Ferguson et al. 1998, Edwards et al. 2001, Vesa and Hanski 2003), as long as there is a perceived difference in quality of varying landscape types. According to OFT, the greater the rate of return of resources within a habitat type, the more time an animal will spend foraging in that habitat. The greater the distance between patches, the more energy an animal must invest in traveling between patches, and therefore, the more time an animal will spend in a patch (Phillips et al. 2004). For example, red fox movements (*V. vulpes*) were straighter across landscapes with a low grassland composition, indicating directed movement, but red fox trajectories tended to be more tortuous in landscapes with

a high grassland composition (Phillips *et al.* 2004). This indicates that overall search strategies will vary according to the spatial structure and scale of the landscape.

Search strategies may vary intra-specifically, as previously demonstrated by foraging caribou in Bergman *et al.* (2000). Sperm whales (*Macrocephalus physeter*) in the South Pacific have also been shown to use differing search strategies dependent upon their habitat, and their social clan (Whitehead and Rendell 2004). Members of one clan typically moved in relatively straight lines while other clan groups had more convoluted tracks and a more inshore distribution, patterns which were consistent across years. Further, clans appeared to have differential foraging success, which may be dependent on their inherent search strategy. Whitehead and Rendell (2004) suggested that the mechanism for the transmission of search strategies within members of the clan may result from cultural inheritance.

II. Energetic State

The awareness that metabolic factors resulting from body size and diet may affect home range size, and hence dispersal, is one that is well appreciated (McNab 1963, Turner *et al.* 1969, Milton and May 1976, Clutton-brock and Harvey 1977, Harestad and Bunnell 1979, Mace and Harvey 1983, Swihart *et al.* 1988, Kelt and Van Vuren 1999, 2001). As body mass increases, so does the absolute requirement for food, and as a result, larger animals may have to travel further to attain sufficient resources. Although a reasonable hypothesis when proposed by McNab (1963) over 40 years ago, it is still one which requires considerable empirical and theoretical testing (Reiss 1988). Recent studies have demonstrated that the relationship between home range size and body mass is non-linear, and hence, the allometric scaling relationship between the two factors has

been especially hard to explain (Kelt and Van Vuren 2001). Numerous hypotheses have been invoked to attempt to explain this discrepancy. Harestad and Bunnell (1979) postulated that large mammals experience a greater proportion of energetically useless space within their home range, and hence productivity of the environment might scale negatively with size; such that larger species require larger feeding areas relative to their metabolic requirements. In contrast, Kelt and Van Vuren (2001) suggested that the relationship between home range size and body mass may be better described by a constraint space that sets an energetically based limit to how small a home range can be for a species of a given mass.

In comparison, far fewer are studies that demonstrate how energetic status or degree of satiation may influence actual movement, speed or directionality. It has been suggested that decreases in speed may come about from constraints due to digestive time or feeding motivation, which would limit the energy available for movement (Werner and Anholt 1993). A number of studies have indicated that level of hunger may influence the motivation to forage (Bell 1991, Wallin 1991, Zhang and Sanderson 1993). Ernsting and Van der Werf (1988) argue that hungry predatory beetles are more willing to take a risk than satiated ones, and this may affect prey selection.

Perhaps one of the best studies demonstrating the way in which satiation affects how animals move is by Wallin (1991). He demonstrated that the movements of the caterpillar hunter beetle, *Calosoma affine*, varied significantly when an animal was satiated, compared to hungry individuals. Hungry beetles displayed directed movements in areas of low prey density (short grass), until they reached areas of high prey density (long grass). At this point, they adopted a correlated random walk strategy, presumably to

search for prey items, and to extend patch residence time. As a result, velocity decreased considerably, while sinuosity increased. Conversely, satiated beetles displayed random movement in both high density and low density habitats. Satiated beetles were also observed climbing the plant canopy, an activity that is energetically expensive, indicating that satiated beetles are more willing to spend spare energy on energetically expensive behaviour. Similar findings were reported by Kareiva and Odell (1987) who showed that turning frequency of a predator increases with satiation, leading to area-restricted search. Thus, Wallin (1991) concluded that his study emphasized the importance of incorporating energy measurements into foraging models in order to obtain a more comprehensive picture of the cost of foraging, and the decision making due to intrinsic mechanisms. Similarly, Zhang and Sanderson (1993) determined that as hunger increases in predatory mites, individuals were more likely to display an increase in turning frequency, thereby causing them to remain within a patch longer and attack more prey.

In addition to energy requirements, nutrient limitations and the need to regulate nutrient intake are key factors which may affect the foraging strategies of organisms, particularly insect herbivores. These animals can attempt to regulate protein and carbohydrate intake by feeding on different plants or plant parts (Chambers *et al.* 1996). However, as the distance between nutritionally complementary food resources increases, the demands on the regulatory systems as well as associated costs with travel also increase. Behmer *et al.* (2003) demonstrated that locusts, *Locusta migratoria*, adjusted their foraging strategies such that their protein-carbohydrate ratio did not change even with increasing distance between food sources. They did this by increasing fidelity to

rare foods, decreasing energy budgets and increasing foraging efficiency by taking more directed feeding excursions.

Air-breathing animals who dive for food resources are subject to a number of energetic constraints not experienced in non-diving species. They are theoretically limited in their ability to search for food by their oxygen capacity (Kramer1988), which is in turn affected by the energetic demands of feeding activity (Acevedo-Gutiérrez *et al.* 2002). Thus, a diving animal has an additional cost of foraging- it must travel to the surface to breathe, and consequently, these animals must optimize movement patterns not only in 2 dimensions, but in 3 dimensions as well. To bring this into the context of OFT, if net energy gain increases with time spent at depth, optimal diving behaviour should favour animals that maximize the proportion of their total time budget spent in the site of resource gain. Kramer (1988) predicted that as depth of feeding sites increases, so should the bout lengths of surface time and dive time. One of the ways in which diving animals can balance the additional energetic costs of diving longer is by adjusting swim speeds. For example, Boyd *et al.* (1995) demonstrated that Antarctic fur seals (*Arctocephalus gazella*) swam within a narrow range of their potential speeds while diving, and predicted that this was likely due to a minimum cost of transport at lower speeds. Hence, by choosing lower speeds, they are able to increase the net energy gained by keeping oxygen requirements lower. Conversely, when moving between patches by swimming at or near the surface, fur seals exhibited a wider range of swim speeds, likely because they are not limited by their access to oxygen. Therefore, diving animals can adjust their movement patterns on one of two dimensions: surface travel, and diving to depth.

Criticisms of OFT Theory Applied to Movement Behaviour

As mentioned at the outset, OFT has received a fair amount of criticism over the years, and hence we should consider the potential pitfalls of coupling OFT to movement behaviour. Pyke (1978b) hypothesized that bumblebees are optimal in their movement patterns as they forage in groups of inflorescences. Since it is well documented that on most vertical inflorescences the flowers having the greatest amount of nectar are at the bottom, and that nectar concentrations decrease with increased flower height (Pyke 1978b, Waddington 1979), his model predicted that bees should start at the bottom flowers because they have the highest rewards, and then move upwards. Pyke (1978b) tested the model in the field and found that the bees did indeed move as predicted; in this sense, they were foraging optimally.

However, Waddington and Heinrich (1979) performed the same experiment using artificial vertical inflorescences, and observed that bumblebees almost always move upwards, regardless of whether the rewards were distributed in the bottommost or the topmost flowers. Similarly, Corbet *et al.* (1981) observed that bumblebees foraging on *Linaria vulgaris*, also showed movement up the flower, even though the nectar concentrations of this flower increase with height. Therefore, we see that Pyke's (1978b) model only demonstrated what he expected, but it did not answer the question of why the bees moved as they did (Heinrich 1979, 1983). Without more stringent testing it is impossible to determine whether the bees are moving according to nectar concentrations (and thus "optimally"), or whether the animals are using some other proximal mechanism. For example, perhaps bees move in an upwards manner because it allows them to perform more systematic foraging, or may be due to handling efficiency or vision

(Heinrich 1983). This emphasizes the importance of considering optimality to be one of a number of working hypotheses (Ward 1993), and not the only foreseeable outcome, inherently limiting the testability of OFT.

Of course, simply because models of OFT are disproved in empirical testing, it does not imply that the animals are suboptimal, simply that we do not know the currency the animals are attempting to maximize, or alternatively, the specification of the model is wrong. For example, perhaps it is more optimal for an animal to travel at night due to lower air temperatures, which subsequently results in fewer energetic costs, but not because the number of prey items are greater. Often net energy intake depends not only on food levels, but also on habitat conditions, such as the thermal environment- the consequence of this being that net energy gain can still be maximized by selecting patches that are "suboptimal" with respect to food density (Huey 1991). Nevertheless, using an optimality approach allows us to consider all the possible cues to which an animal may be responding.

Conclusions and Future Directions

In its original form, OFT was intended to develop a more mechanistic way of thinking about community dynamics by linking evolutionary biology with behaviour and population and community ecology (Belovsky 1997, Schmitz 1997). By including movement as a meaningful parameter in OFT models, we are in fact facilitating this union, as movement is in part responsible for the dynamic nature of population ecology, given that movement is a process by which demographic rates are realized. According to Jones (1977), one cannot hope to understand the population dynamics of a species

without knowing its movement patterns; one cannot be completely understood without the other. Hence, it is imperative that we combine the two fields of research to create a more absolute understanding of population ecology.

Optimal foraging theory should also be considered a tool used to derive predictions of how an animal should organize its foraging behaviour to in order to optimize net energy intake. As demonstrated herein, movement is a fundamental component of foraging. It is the manifestation of foraging behaviour driven by the requirement to acquire energy. Therefore, movement by definition should be an intrinsic part of OFT. Incorporating movement within OFT allows us to use an overall theoretical framework to derive predictions of how foraging animals should move, such as: how an animal should move between patches, or how an animal should move once in a patch.

The recent development of state-space models (SSMs) for use in animal movement behaviour (Sibert and Fournier 2001, Jonsen *et al.* 2003) may provide the analytical means for incorporating measures of animal energetic or physiological state and corresponding OFT predictions into movement models. SSMs are models which describe the evolution of two time series running in parallel, one as the state or unobserved process and the other as the observation process, which is in fact a function of the state process (Buckland *et al.* 2004). There are two main benefits to using SSMs. Firstly, they are able to account for measurement error and process noise in locations, a key issue with movement data, particularly when collected remotely via telemetry (Jonsen *et al.* 2003). Secondly, stochasticity can be accounted for by modeling animal behaviour as a dynamic variable that changes as a function of an animal's energetic state (e.g., satiation), or environment (Jonsen *et al.* 2003). Models which allow for the

dynamic state of the individual to be included can be used for determining optimal behaviours in an OFT context, and for testing predictions empirically. SSMs may pave the way for future studies capable of linking movement parameters to theoretical models of OFT.

Given that parameters of movement can be measured and quantified, the key advantage to integrating OFT and movement is that it allows one to gain insight into the behaviour of animals for which we cannot possibly measure all parameters. For example, consider the case of a large marine predator for whom food resources cannot be quantified. Using satellite telemetry, one can measure movement characteristics (e.g., turning angle or distances) and based on what we know from the integration of movement to OFT, make inferences about food availability, patch distribution and patch size (e.g., short distances and a non-normal distribution of turning angles could indicate the presence of a patch). Clearly, without being able to quantify food resources, it becomes very difficult to test OFT models, however, by coupling theory to simple measures of movement, we can begin to interpret the way in which an animal perceives its environment.

Understanding movement behaviour is a huge gap in our knowledge of the ecology of most animals. To date, most of our insight of movement patterns is based on studies of insects and small mammals. Only with the advent of new technologies, such as satellite telemetry, have we begun to understand the movement patterns of large and widely-dispersing species. As a result we are only beginning to analyze movement patterns of these animals in a qualitative manner. Consequently, there is a distinct paucity of analyses which endeavor to quantitatively describe movement across all species.

Other components of foraging behaviour, such as diet, ingestion rates, handling time and cognition remain gaps in our knowledge as well. However, new technologies and tracer techniques are generating quantitative estimates of these elements (e.g. animal-borne imaging systems, Marshall 1998; fatty acids, Iverson 1993, contaminant-consumption rate models; Rowan and Rasmussen 1996). Therefore, as methods of examining these aspects of foraging continue to improve, we can hope to increase our understanding of foraging behaviour, and further enhance the integration of movement patterns and OFT.

In an even larger context, understanding the magnitude and importance of cross-habitat fluxes of matter, energy and information are necessary to form a unified understanding of the spatial and temporal framework of ecological interactions and should be an important future direction in ecology. In order to do so, we must characterize patterns of movement across space and through time, and break them down into their constituent rules (Thompson *et al.* 2001). Herein lies the importance of a unified theory of optimal foraging and movement- both the consumption and transfer of energy can be considered in a single predictive framework.

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Chapter III. A three-stage algorithm for filtering erroneous Argos satellite locations

Introduction

Satellite telemetry has increased our knowledge of the spatial distribution and movements of wide-ranging vertebrates. This is particularly true in the case of marine mammals and birds, where the large spatial scale of movements usually precludes direct observation. However, the requirement for initial processing of satellite locations to remove potentially erroneous positions has often limited researchers in their ability to carry out subsequent analyses.

Argos is a satellite-based location and data collection system (Service Argos, Toulouse, France and Landover, Maryland, USA). Argos transmitters, attached to study animals, send signals to Argos receivers carried on board National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites. Animal locations from Argos are calculated by measuring the Doppler effect on the transmitted frequency provided that two or more signals are received during a single pass of the satellite (Harris *et al.* 1990a, Priede and French 1991). Standard locations are calculated on reception of four or more signals and vary according to the estimated accuracy of the location. Auxiliary locations are estimated when <4 signals have been received from the transmitter.

Primarily, the number of signals (uplinks) received by a satellite during each orbit determines the accuracy of locations. The number of uplinks received is in turn affected by latitude, animal behaviour, transmission rate, number of receiving satellites, and transmitter power (Harris *et al.* 1990a). Each location is assigned a location class (LC) as

predicted by the Argos system. The best location classes are those that have received a minimum of 4 uplinks from the transmitter, and which meet other standards of transmission set by service Argos. These standard locations include LC3, for which locations are predicted to be ≤ 150 m from the animal's actual position; LC2, for which locations are predicted to be ≤ 350 m; and LC1, for which locations are predicted to be $\leq$ 1km. The stated precision is the standard deviation of the distribution of locations, such that 68% of a series of locations would be expected to fall within the given distance (Harris *et al.* 1990a). Service Argos offers no predictions for LC = 0, as these are locations which have failed certain class checks. Auxiliary locations, LCA, LCB, or LCZ have no associated accuracy as they are estimated with only 3, 2 or 1 uplink, respectively.

Field studies comparing known locations to standard Argos positions indicate that Argos estimates of accuracy underestimate the true error. For example, Le Boeuf *et al.* (2000) found that while the animals were on the rookery, the mean error for northern elephant seal (*Mirounga angustirostris*) locations for LC = 3, 2, 1 and 0 was 0.8 ± 0.1km, 1.4 ± 0.6 km, 2.7 ± 2.1 km, and 9.3 ± 15.5 km, respectively. Mean error of LC = A and B locations was 28.3 ± 50.7 km and 48.4 ± 70.4 km, respectively (Le Boeuf *et al.* 2000). Hull *et al.* (1997) calculated mean errors associated with latitudinal and longitudinal errors and suggested that mean errors for individual positions of LC = A may vary from 9.0 km of latitude to 14.9 km of longitude, and that mean errors for individual positions of LC = B may vary from 4.0 km of latitude to 4.6 km of longitude. However, given that the nature of transmission reception is likely to be more stochastic for diving animals, it is perhaps unrealistic to compare accuracies based on terrestrial vs. at-sea transmissions. Vincent *et al.* (2002) used captive, but diving, juvenile grey seals (*Halichoerus grypus*) to

assess the degree of error associated with Argos locations. They determined that error is generally greater in longitude than in latitude, resulting in an elliptical distribution of locations with the major axis aligned along east-west, thereby in fact widening the satellite track.

Few standard locations (LC ≥ 1) are obtained in most animal-tracking studies (e.g., Stewart *et al.* 1989, Harris *et al.* 1990a, Keating 1994, Burns and Castellini 1998, Goulet and Hammill 1999, Vincent *et al.* 2002). Therefore, using only standard locations would result in the elimination of a high proportion of most data sets. Even the best quality standard locations may have a considerable amount of associated error, in fact White and Sjöberg (2002) found that the smallest location error is not always associated with the best LC. Similarly, Vincent *et al.* (2002) reported that errors associated with LC0 were actually greater than those associated with auxiliary location LCA.

To deal with these problems, a number of methods have been suggested to eliminate inaccurate locations. McConnell *et al.* (1992) suggested an iterative forward/backward-averaging filter to remove locations with large error, using rate of travel as the determining factor. For each location, the previous two rates of travel and the subsequent two rates of travel were used to compute a geometric mean rate of travel. If this rate of travel was greater than the maximum feasible rate of travel (based on knowledge of the distribution of measured speeds), then the location was rejected, and the next location considered. This resulted in the rejection of approximately 40% of standard locations in McConnell *et al.* (1992). This method has been used with varying rejection rates (14% to 78% of locations rejected) for a number of satellite-based telemetry studies of marine animals (Hindell *et al.* 1999, Hull *et al.* 1997, McConnell and

Fedak 1996, McConnell *et al.* 1999, Le Boeuf *et al.* 2000, Sjöberg and Ball 2000,

Vincent *et al.* 2002).

Although this method represents an important advance in the processing of satellite-derived locations, this filtering algorithm has two limitations. First, auxiliary locations that pass the filter may eliminate some standard locations. For example, this can occur when the distance from a 'B' class auxiliary location to a standard location does not meet the speed filter criteria. This results in the elimination of the standard location, even if the error is associated with the auxiliary location. Second, if the elapsed time between two consecutive locations is sufficiently large, it may result in the use of locations that are not feasible. For instance, if the time between two consecutive locations L_1 and L_2, is 7 d, and one estimates that the animal can travel no more than 120 km/d, then the animal could have traveled up to 840 km from L_1 and thus any location < 840 km away would pass the filter.

I developed a three-stage filter that builds on the algorithm introduced by McConnell *et al.* (1992). I tested this approach on data from satellite-linked transmitters fitted to free-ranging grey seals (*Haliochoerus grypus*). The objective was to reduce the number of erroneous satellite locations used in the analysis of animal movement while at the same time using both standard and auxiliary locations, thereby including as many locations as possible while improving confidence in resulting interpretations of dispersion and movements. The first stage involves the removal of locations that are highly inaccurate, which might otherwise cause the elimination of subsequent accurate locations. The second stage filters the remaining locations using the algorithm developed by McConnell *et al.* (1992), and the final stage removes locations for which the distance

traveled is unreasonable based on the observed distribution of linear distances traveled over time.

Methods

Thirty-seven adult grey seals were captured on Sable Island between October 1995 to January 2000. Sable Island (43°55'N, 60°00'W) is a partially vegetated sandbar approximately 300 km southeast of Halifax, Nova Scotia, Canada. Seals were captured on-shore using handheld nets (see Bowen *et al.* 1992) following the spring moult (June) or in the fall (late September and early October). I used half-watt satellite-linked platform terminal transmitters (PTTs) from Wildlife Computers (Redmond, Washington). Of the 18 PTTs deployed, 17 were version ST-6 and 1 PTT was version ST-10. Each PTT weighed $\leq$ 650g (<0.6% of body mass). Instruments were secured to netting and then the netting was attached to the pelage of the head or neck of the anaesthetized animals using 5-min epoxy. Seals were anaesthetized using Telazol (equal parts of tiletamine and zolazepam). Males and females received 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 extend battery life and to reduce processing fees, some transmitters were programmed to transmit 8 h day^{-1}, and depending on the duty cycle, between 25% and 100% of days were sampled over a 3- to 8-month period. A salinity sensor on the instrument detected whether the animal was wet or dry, and suppressed transmissions when the instrument was wet. The instruments were removed in January when animals returned to Sable Island to give birth or mate.

<u>Programming the filtering algorithm</u>

For each animal, the first location was Sable Island, on the date the seal was fitted with the Argos satellite transmitter. A filtering algorithm was developed with the programming language 'ObjectPAL' a component of the relational database Paradox 8. Locations were extracted from Service Argos data using the SatPak program version 3.04 from Wildlife Computers, and processed using the location filter described below. The location filter proceeds in three stages described as follows:

Stage 1: Reject locations that fail all four travel rate tests.

Using a dataset that was sorted in ascending order by position and time within each animal, and beginning from the deployment date, a subset of the first five positions was retrieved. If rate ($i,i+2$) > 2 m/s and rate ($i+1,i+2$) > 2 m/s and rate ($i+2,i+3$) > 2 m/s and rate ($i+2,i+4$) > 2 m/s then reject position $i+2$; where, for example, rate ($i,i+2$) is the rate to move from position (i) to position ($i+2$) where i = 1...n positions. The rate of 2 m/s was chosen as the maximum travel speed of grey seals in this study, based on the 99th percentile of travel speeds between standard class locations. This speed appeared to be a reasonable compromise between the slower speeds used during foraging, and the faster speeds associated with long distance travel.

If the current position was accepted then the next subset of 5 positions was retrieved, beginning with the position previously accepted to the currently accepted position, and processed. If the location was rejected then a new subset of 5 positions was retrieved beginning with the same position and skipping all the rejected positions. The entire dataset was processed in this manner, and each position was either accepted or rejected.

Stage 2: Reject locations that fail the McConnell *et al.* (1992) filter.

Beginning with the resulting sorted dataset, the iterative forward/backward

averaging filter described by McConnell *et al.* (1992) was applied to all locations

accepted in Stage 1. A velocity V_i was associated for each location i, where $v_{i,j}$ is

the velocity between successive locations i and j:

$$V_i = \sqrt{\frac{1}{4} \sum_{j=-2, j \neq 0}^{j=2} (v_{i,j+i})^2}$$

Locations with V_i greater than the predicted mean velocity of grey seals (2 m/s)

were rejected.

Stage 3: Reject locations that fail the realized distance test.

During processing of stage 2, the mean distance that separated each location from

each of the 4 neighbouring locations (2 previous and 2 subsequent locations) was

calculated and stored. If (distance ($i,i+2$) + distance ($i+1,i+2$) + distance

($i+2,i+3$) + distance ($i+2,i+4$)) /4 > 160 km, regardless of time, then reject

position ($i+2$). This threshold was the 99th percentile of distances moved as a

function of time using locations of class ≥ 1. Stage 3 was developed to remove

locations that survived the previous stages simply because enough time had lapsed

between observations to generate a rate of travel that was ≤ 2 m/s.

Statistical Analyses

All statistical analyses were conducted using SPSS version 10.0. Means are given

with standard errors. Transmitter power may affect the number and quality of Argos

locations (Harris *et al.* 1990a). Further, some studies have suggested that the number of

Argos locations may be affected by sex of the instrumented animals (Le Boeuf *et al.*

2000). A GLM, two-way ANOVA was used on arcsine-square root transformed data to

determine if PTT type and sex had an effect on the proportion of accepted locations. All

locations were mapped using Arcview 3.2 (Environmental Systems Research Institute,

Inc.).

Results

The duration of data collection for the 37 instrumented seals ranged from 76 to 301

d. Of the 15,987 locations obtained, 34% were standard locations and 66% were

auxiliary locations (Table 3.1). The mean number of locations per day was 5.7 ± 0.28 (*n*

= 37 seals). Overall, the filter eliminated 30.7%, or 4,905 satellite locations and reduced

the mean number of locations per day to 4.1 ± 0.20. The majority of locations failed the

filter at the second stage, followed by the 1st and the 3rd stages. Most standard locations

were retained and 85.7%, 76.6%, and 41.9% of location class 0, A, and B, respectively,

were also retained as good positions (Table 3.1). For LCB locations, the greatest number

were rejected in stages one (69%) and three (76%) compared to stage 2 (53%). The

performance of each stage of the filter is illustrated in Figure 3.1 and 3.2 for two adults

with quite different patterns of movement. The four circled-locations in Figure 3.1a

illustrate the rejection of highly erroneous locations in stage 1 of the filter. Figure 3.2

illustrates the spatial distribution of the locations rejected at each stage of the filter. As

expected, rejected locations are more tightly clustered at successive stages of the filter.

Table 3.1. Percentage of 15,987 locations rejected by Location Class (LC) and the percentage rejected within LC, given in brackets, at each stage of the filter

LC	Pre-filtered locations (%)	Rejected by filter (%)			
		Stage 1	Stage 2	Stage 3	Total
3	1.8	0 (0)	0.11	0.006	0.11
			(0.5)	(0.9)	(0.4)
2	4.2	0 (0)	0.23	0.012	0.24
			(1.0)	(1.8)	(0.8)
1	9.5	0.001	0.93	0.006	0.94
		(0.2)	(4.1)	(0.9)	(3.1)
0	18.6	0.57	3.75	0.05	4.37
		(7.9)	(16.5)	(7.3)	(14.3)
A	24.6	1.63	5.47	0.087	7.18
		(22.4)	(24.0)	(12.8)	(23.4)
B	41.3	5.04	12.27	0.52	17.83
		(69.5)	(53.9)	(76.1)	(58.1)
Total	100	7.25	22.75	0.70	30.70
		(100)	(100)	(100)	(100.1)

Figure 3.1. a. Unfiltered satellite locations, **b.** locations retained after stage 1, **c.** locations retained after stages 1 and 2, and **d.** final locations following the application of all three stages of the filter of an adult female grey seal (2986). Dashed line is the 200 m isobath; circled locations indicate highly erroneous positions.
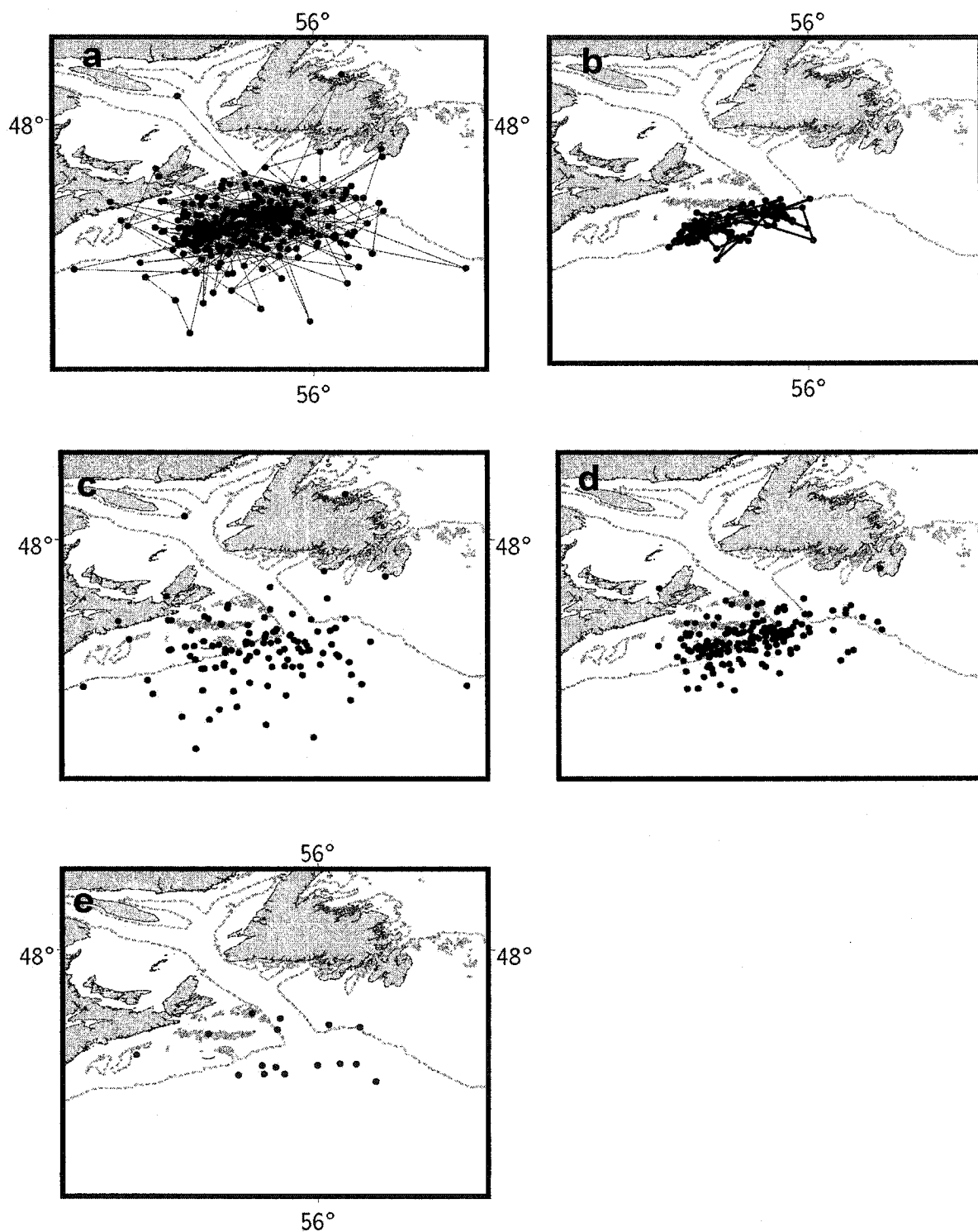
Figure 3.2. Satellite locations of an adult male (617) prior to and following each stage of filtering: **a.** unfiltered locations, **b.** final locations following filtering, **c.** locations rejected following stage 1 of the filter, **d.** locations rejected following stage 2 of the filter, **e.** locations rejected following stage 3 of the filter. Dashed line is the 200 m isobath.

The mean rejection rate for all seals was $30.7 \pm 1.62\%$ of all locations, though the percentage of rejected locations varied among seals from 8.6% to 50%. To investigate the source of variability in rejection rate, a two-way ANOVA was performed using the GLM with sex as a fixed effect and PTT as a random effect. Only the seven PTTs that were deployed more than twice on both males and females were used in the analysis. A repeated measures design was not used because each PTT was refurbished with new batteries and a new antenna between deployments and thus essentially each PTT represented a new tag on each subsequent deployment. There was no effect of individual PTT on the percentage of locations accepted by the filter ($F_{6,6} = 0.50$, $P = 0.79$). However, there was a significant effect of sex on the number of locations accepted by the filter ($F_{1,6.3} = 13.3$, $P = 0.010$), with 11 females having a significantly greater number of accepted locations (73.0%) than 11 males (60.5%) . There was no significant interaction between sex and PTT ($P = 0.06$).

Discussion

The use of any filter will result in a reduction in the number of locations available for analysis. Auxiliary locations are often not used in studies on marine mammals due to their lack of accuracy (e.g., Boyd *et al.* 1998, McConnell *et al.* 1999, Le Boeuf *et al.* 2000, Bonadonna *et al.* 2000). As most locations calculated for marine mammals at sea are based on auxiliary processing, objective criteria are needed to use these locations with confidence. This 3-stage algorithm was designed to meet this objective. The algorithm efficiently identified erroneous locations and retained a large fraction of auxiliary locations, thus increasing the overall sample size while augmenting the confidence in

standard locations. As auxiliary processing by Service Argos incurs an additional cost, the use of auxiliary locations improves the cost efficiency of using Argos telemetry data. These results also demonstrate that the nature of the filter used can affect analyses of the way animals use space.

A number of filtering methods have been suggested to deal with inaccuracies in Argos satellite locations. Choosing the appropriate algorithm is often a trade-off between accuracy and sample size; the most conservative filtering approach often results in the lowest number of locations being preserved. The simplest method available is to edit each location for reasonableness, evaluating whether it is possible for the animal to be in the observed position based on what is known of the bounds to the animals range (e.g., cetaceans must be in the ocean). Although simple, this approach is too subjective to have much confidence in the results. A quantitative extension of this approach is to evaluate the distances between successive locations for feasibility given the elapsed time between the fixes and the animal's maximum speed (Merrick and Loughlin 1997).

Another relatively simple method, recommended by Harris *et al.* (1990a), is to specify a time window during which only one location is to be selected. An algorithm identifies the cluster of locations falling within the specified window and chooses the best location offered based on LC - it then finds the next cluster of locations, beginning with the first observation not in the previous cluster. Alternatively, one could also specify other criteria in choosing the best location, such as optimum satellite overpass elevation. Mean error in location is smallest when satellite orbits have maximum elevations between 40° and 50° (Harris *et al.* 1990a). Hence, mean error could be reduced by restricting locations to those resulting from the best overpasses, but only with

considerable loss of data, making it rather costly (Keating 1994). Clark (1989) proposed using the standard deviation around locations to eliminate incorrect locations. However, this is limited by the unrealistic assumption that the distribution of locations is circular bivariate normal (Keating 1994).

Keating (1994) suggested an alternative index of location error that uses distances and relative directions between consecutive satellite locations. This is based on the reasoning that locations are more likely to be incorrect when the data indicate a single, relatively large movement, followed by an immediate return to a point near the original location. The resulting Keating's Error Index (KEI) integrates effects of all determinants of error and is a ratio-scaled continuous index (as opposed to the LC ordinal index) which offers great control over the trade off between sample size and accuracy, and consequently cost effectiveness

In a study on harbour seal (*Phoca vitulina*) movements, Lowry *et al.* (2001) suggested using a three-step process, which expands upon the KEI. Firstly, all satellite locations that were calculated by Argos using fewer than two signals (i.e., LC = Z) were discarded. Secondly, the KEI was calculated for each record, and all records with a KEI > 20 and a LC <1 were omitted. These records were screened between sequential positions and any improbable locations given the time, distance and the maximum velocity of the seals were removed, based on what was known of maximum sustainable swim speed. Finally, following the removal of these records, the KEI was recalculated, and all records with a KEI > 20 were omitted. Although it has been used in a number of studies (e.g., Burns *et al.* 1999, Lowry *et al.* 2001), this filtering approach may reject a

large number of locations. For example, Lowry *et al.* (2001) used only standard locations and 36% of those locations were removed using the above filtering criteria.

Although the KEI has been used with success in studies of terrestrial animals (e.g., Bergman *et al.* 2000), it is problematic when applied to studies of diving animals where there are fewer uplinks and thus fewer locations. As a result, it is possible for a diving animal to "disappear" from satellite contact for an extended period of time, and traverse a considerable distance prior to the next successful satellite transmission. Given enough time, large movements are theoretically possible for marine animals and to remove those locations may incorrectly represent an animal's movements.

The McConnell *et al.* (1992) filter attempts to deal with this problem by averaging several speeds. However, adding a 1st and 3rd step in the filtering process effectively improves on the existing McConnell algorithm. When only the McConnell *et al.* (1992) filter was used on this data, 32.3% of locations were rejected, compared to 30.7% when all three stages were applied. More importantly, the 3-stage filter rejected more of the auxiliary locations than the McConnell filter alone, but fewer standard locations (18.6% vs. 21.8%) than the McConnell filter.

Still, the percentage of locations rejected does not tell the whole story. The use of even a few erroneous locations may affect interpretations of habitat use. To illustrate this, I compared the track of several seals filtered using only stage 2 (the McConnell *et al.* 1992 filter) and the three-stage filter (Figure 3.3). In each case, there are fewer unusual movements when using the three-stage filter than when using only the McConnell filter.
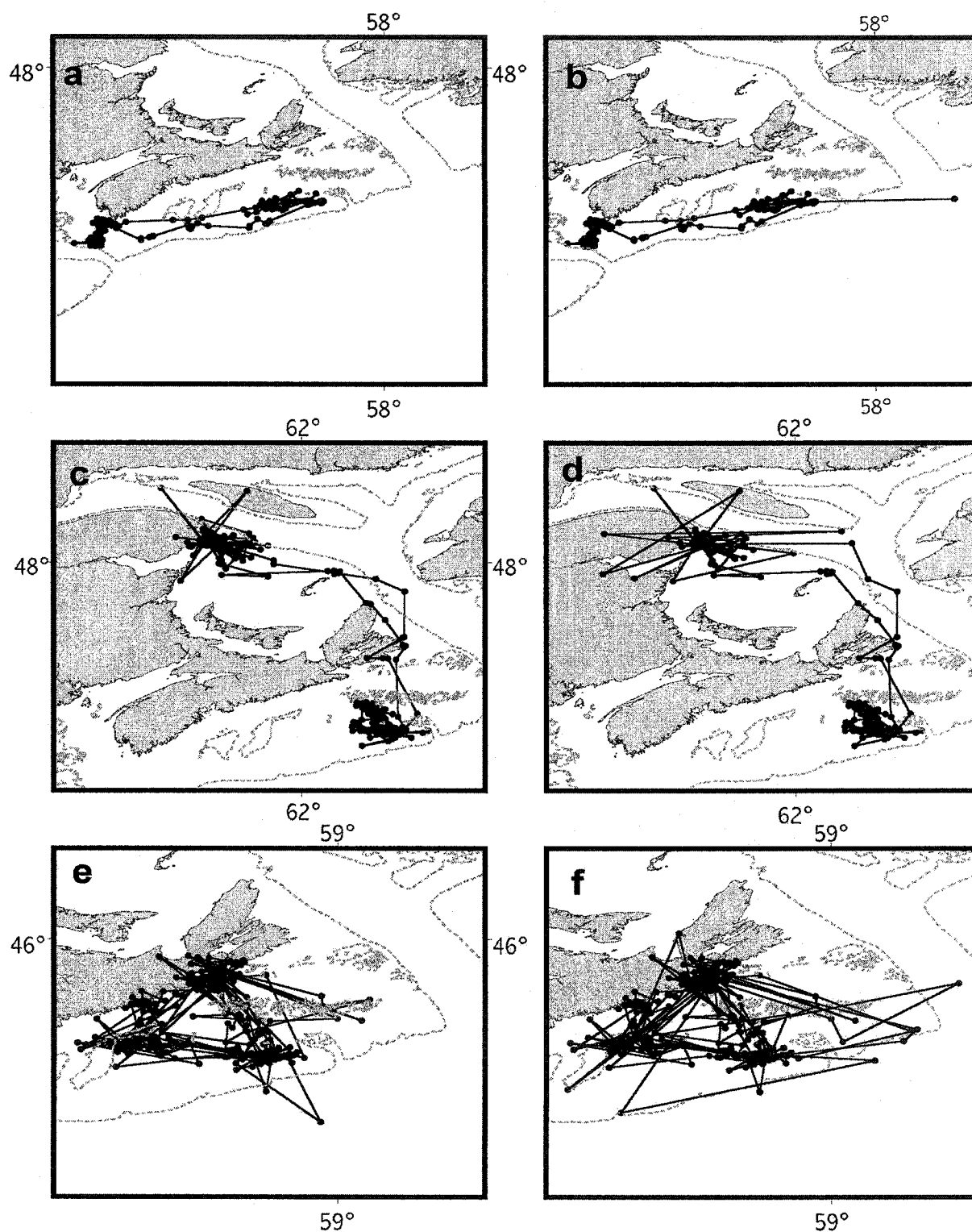
Figure 3.3. Satellite tracks of 3 adult grey seals, comparing the proposed filtering algorithm and the McConnell *et al.* (1992) filter: **a.** seal 3662, our filter, **b.** seal 3662, McConnell filter; **c.** seal 2667, our filter, **d.** seal 2667 McConnell filter; **e.** seal 3617, our filter, **f.** seal 3617, McConnell filter. Dashed line is the 200 m isobath.

Such unusual movements can have significant effects on estimates of home range size and our understanding of search tactics used by marine mammals. I calculated home range estimates for 10 grey seals using kernel and minimum convex polygon methods and both the 3-stage filter and the McConnell *et al.* (1992) filter (Table 3.2). Both the 95% kernel and MCP home range estimates differed significantly and although there was no significant difference between the 50% kernel home range estimates based on the 3-stage filtering criteria and the stage two-only filtered data, the mean estimates differed by almost a factor of two (Table 3.2). However, the direction of difference was not consistent between the two estimation methods. The mean MCP area calculated from the 3-stage filter was significantly smaller than the McConnell filter. This is to be expected to a certain degree simply because the MCP method for estimating home rage area is calculated by connecting the outermost points of an animal's track, and thus is extremely sensitive to peripheral locations. Any single erroneous location, which represents a large displacement from the core area of activity, may greatly increase MCP area (Harris *et al.* 1990b). Thus, highly erroneous locations, if not filtered out, may result in overestimates of the true area used.

Conversely, the mean 95% and 50% kernel home range areas were greater for the 3-stage filtered data. Kernel analysis is a probabilistic method that provides a utilization distribution, and as a result denotes core areas of particularly high home range usage (Worton 1989). Because of the nature of the kernel distribution, as locations are more clustered, the utilization distribution area increases as a result of increased density (Seaman *et al.* 1999). Thus, with elimination of dispersed erroneous points, there is an increase in kernel home range size. Further, Seaman *et al.* (1999) stress the importance

Table 3.2. Comparison of kernel and 100% minimum convex polygon (MCP) home range size estimates (mean ± SE) of 10 grey seals based on the 3-stage filter and the McConnell *et al.* (1992) filter

Method	Filter type		Wilcoxon Z	P
	3-stage (km^2)	McConnell filter (km^2)		
95% kernel	318,952	204,203	-2.599	0.009
	± 80,015	± 53,960		
50% kernel	57,553	31,730	-1.580	0.114
	± 22,694	± 13,024		
MCP	126,817	206,717	-2.803	0.005
	± 33,513	± 39,256		

of sufficient sample size to ensure the correct application of the smoothing factor in kernel estimations. Consequently, maintaining the highest number of Argos locations is a distinct advantage for home range estimation. Therefore, these results suggest that comparisons of home range size among studies may only be meaningful if the same filtering algorithm has been used.

The number of locations rejected varied considerably among grey seals. This variation may arise both from differences in hardware (the transmitter and the satellite) and the behaviour, particularly diving behaviour, of the animal. Internal hardware inconsistencies, subtle differences in attachment of the instrument to the animal, and length of deployment have all been shown to affect transmitter performance (Harris *et al.* 1990a). I found no significant effect of PTT type on the percentage of accepted locations, suggesting that behaviour may be a more significant source for the observed variability than hardware. This is consistent with the finding of a significant effect of sex on the percentage of accepted locations, with females having a greater number than males. Although one might assume that this results from a greater amount of time spent at the surface by females, data from time-depth recorders shows that females do not spend significantly more time at the surface than males (Beck 2002). Instead, it is likely that this difference is relatively subtle, but results in consistent differences in behaviours between the sexes. For example, female grey seals are more buoyant that male grey seals (Beck *et al.* 2000), and thus more of their head may be exposed when at the surface resulting in a more consistent presentation of the PTT during satellite overpasses. Sex accounted for about 68% of the observed variability among grey seals. Similarly, Le

Boeuf *et al.* (2000) found that the mean number of locations per day was higher in female northern elephant seals than in males. Other sources of variability among individuals may include differences in time spent at the surface seasonally (Nordøy *et al.* 1995, Stewart and Delong 1995, Goulet *et al.* 1999), by time of day (Le Boeuf *et al.* 1988), and individual behaviour (McConnell *et al.* 1999).

This three-stage filtering algorithm should be applicable to other species, including terrestrial vertebrates. Although the logic should apply broadly, the filter will produce the best results if certain parameters are based on species-specific behaviour. Both the maximum travel rate and the straight-line, distance-traveled threshold will need to be derived for each species. Even within species, there may be differences in travel rate or maximum distance traveled per day based on sex, age or habitat characteristics. Such differences could be used to fine-tune algorithm parameters and therefore improve the quality of the resulting data.

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Chapter IV. Intraspecific Variation in Movement Patterns: Modeling Individual Behaviour in a Large Marine Predator

Introduction

Most animals must move to locate and capture food. Thus, patterns of movement are considered a key factor in the survival of most organisms (Turchin 1998, Bergman *et al.* 2000). In any given environment, there is a range of behaviours (i.e., phenotypes) that can be considered successful. These can be learned behaviours, or alternatively, the products of longer-term selection for specific traits (Komers 1997). Intraspecific variation in movement behaviour reflects the different tactics used by individuals or sexes within a species or population to meet the demands of survival. We expect natural selection to favour those strategies that maximize fitness or some proxy of fitness, such as the rate of resource acquisition, or production of offspring. Given that natural selection operates at the level of the individual, ecological models that lump all individuals into the same behavioural category effectively disregard this variation (Judson 1994, Zollner and Lima 1999). Consequently, examining average responses across populations obscures variability in behavioural ecology. Animal movement often becomes most intriguing by examining how individuals fail to fit model predictions (Bergman *et al.* 2000).

One difficulty in studying movement patterns within a population lies in distinguishing one pattern from another. Ecologists interested in movement patterns have used mathematical models to bring studies of movement out of the purely descriptive realm (Kareiva and Shigesada 1983, Root and Kareiva 1984, Viswanathan *et al.* 1996, Barrett and Lowen 1998). Perhaps the simplest means of quantitative description is that of home range (Burt 1943). Kernel methods of estimating home range produce a density

estimate that can be interpreted as a utilization distribution (Worton 1989) and are useful because they provide an interpretation of the key areas used by an individual (Worton 1995). Home range analysis has a long history in terrestrial wildlife ecology (e.g., Damuth 1981, Bowen 1982, Anderson and Rongstad 1989). However, the difficulty with home range indices is that they provide a single picture of the area occupied by an animal's trajectory, without lending any understanding to the decision rules which led the animal to move across the landscape in such a manner.

In contrast, a Lagrangian approach to modeling focuses on aspects of the moving individual; for example, velocity or direction can be used to derive information about an animal's trajectory and delineate the search strategies employed (Turchin 1998). Instead of a single picture, individual modeling projects movement patterns along a continuum, such that decisions over time and their influence on the resulting distribution can be described in terms of the behavioural mechanisms involved (Zollner and Lima 1999).

The simplest stochastic model is that of Brownian motion; this is the basis of the classical "random walk". However, this model does not consider the cephalo-caudal polarization which gives the tendency for an animal to go forward, and thus does not give an accurate representation of most animal movement (Bovet and Benhamou 1988). Alternatively, a correlated random walk (CRW) assumes independent distributions of move lengths and turning angles that describe an animal's movement trajectory. Although each step length or turning angle is randomly chosen, a probability distribution can be derived which allows the formulation of equations that predict the probability of future behaviour (Shlesinger 2001). By examining departures from a random walk, we

may gain insight into the foraging behaviour of individuals and the variability in search tactics used while foraging.

More recently, ecologists have borrowed concepts from the physical sciences to determine optimal search strategies for randomly located objects (Viswanathan *et al.* 1996, 1999, Atkinson *et al.* 2002, Mårell *et al.* 2002). Rather than considering a normal Gaussian or Rayleigh distribution of trajectory lengths of a randomly foraging animal, Viswanathan *et al.* (1999) suggest that an inverse square power-law distribution of move lengths, a Lévy distribution, is a more optimal strategy because it results in a greater number of patches being visited, with fewer repeat visits. Such distributions are characterized by many short moves and few large displacements. Evidence of Lévy Flights have been found in foraging ants (Shlesinger 1986), *Drosophila* (Cole 1995), wandering albatross, *Diomedea exulans* (Viswanathan *et al.* 1996), reindeer, *Rangifer tarandus tarandus* (Mårell *et al.* 2002), and jackals, *Canis adustus* (Atkinson *et al.* 2002).

To date, our knowledge of the movement patterns of large predators have been limited by the sheer spatial scale of their ranges. Consequently, the rules that influence movement patterns and distributions of larger animals in relation to food resources remain poorly understood. In contrast, the movement of insects and smaller animals has received more attention, resulting in the modeling of individual movements, population distribution and scale- specific resource use (Kareiva and Shigesada 1983, Cain 1985, Bovet and Benhamou 1988, Turchin 1991, Gustafson and Gardner 1996).

Understanding the foraging behaviour of marine predators has presented an even greater challenge, given that nearly all foraging takes place beneath the surface of the water. With recent advances in satellite telemetry, we have begun to produce qualitative

descriptions of the movement of large marine predators, including pinnipeds, (Stewart and DeLong 1995, Folkow *et al.* 1996, McConnell and Fedak 1996), cetaceans (Read and Westgate 1997, Mate *et al.* 1998, 2000), seabirds (Davis *et al.* 1996, Hull *et al.* 1997), polar bears (Ferguson *et al.* 1997), and turtles (Polovina *et al.* 2000). Nevertheless, few studies have modeled the movement patterns used by large predators in a quantitative manner. Given that individual movement behaviour drives population spatial structure and resource use (Turchin 1998), this is a substantial gap in our understanding of these animals (Bergman *et al.* 2000).

In this paper I apply quantitative models of movement to satellite derived trajectories of a large marine predator, the grey seal, *Halichoerus grypus*. Grey seals are abundant apex predators inhabiting both sides of the North Atlantic and there is increasing evidence that marine mammals can have significant top-down effects on ecosystem functioning (Estes 1996, Bowen 1997). In recent years, there have been several attempts to model the impact of pinniped predation on commercially important fish stocks (e.g., Overholtz *et al.* 1991, Punt and Butterworth 1995, Mohn and Bowen 1996). A significant limitation of these models is our lack of understanding of how foraging is distributed in time and space.

I had two main objectives in this study. Firstly, I tested the applicability of CRW and Lévy Flight models to predict the trajectories of individual grey seals at two temporal scales of movement. I tested the null hypothesis that all grey seals moved in the same random fashion. Secondly, I examined sex, age, season, and body mass as predictor variables of the type of movement exhibited by grey seals, and considered the individual variability in movement patterns with movement type. Since sex effects have been found

in grey seal diving behaviour (Beck *et al.* 2003 a,b), I predicted that sex might also be an important factor in structuring movement patterns in grey seals. Given the variability in prey characteristics in marine ecosystems, I expected that foraging experience and seasonal changes in prey availability might affect search tactics thus giving rise to age and season effects. I regard these analyses as the first steps toward a better understanding of the spatial distribution of foraging in marine apex predators.

Methods

Study Area

The study was conducted on Sable Island (44°53'N, 60°00'W), a vegetated sand bar approximately 300 km from Halifax, Nova Scotia, Canada from June 1995 to January 2002 (Figure 4.1). Sable Island is the largest breeding site for grey seals worldwide. The number of pups born on Sable Island has been increasing exponentially for four decades and in 1997 more than 25,000 pups were born (Bowen *et al.* in press).

Known-aged, adult grey seals were captured using hand-held nets (Bowen *et al.* 1992) and weighed to the nearest 0.5 kg prior to being anaesthetized with Telazol (equal parts of Tiletamine and Zolazepam). Males and females received an average dose of 0.45 mg kg^{-1} body mass and 0.90 mg kg^{-1} body mass, respectively (Bowen *et al.* 1999). Once the animals had been anaesthetized, dorsal standard length (McLaren 1993) was measured.

To study the pattern of movement, animals were instrumented with satellite-relay data loggers (SRDL - Wildlife Computers, Redmond WA or ST-18 - Telonics, Mesa AZ). Instruments were secured to netting and then the netting was attached to the pelage
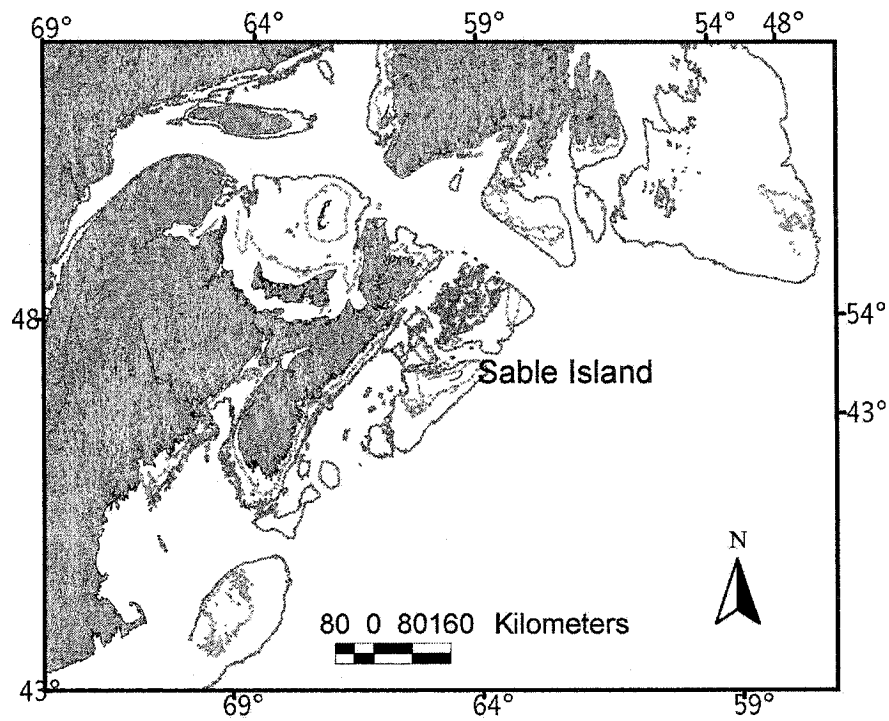
Figure 4.1. Map of study area showing Sable Island. Dark grey lines represent the 100 m isobath, and light grey lines represent the 50 m isobath.

on top of the head or neck of the anaesthetized animals using 5-min epoxy. A salinity sensor on the instrument detected whether the animal was wet or dry, and suppressed transmissions when the instrument was wet. Most instrumented seals returned to Sable Island during the breeding season in December/January, at which point they were re-weighed and the satellite tag was removed.

Instrumented females were not recaptured until several days postpartum to permit females to form a strong bond with their pup. The rate of mass lost by females during the first 5 d of lactation is linear at 4.3 kg/d (Mellish *et al.* 1999). Thus, I corrected the mass at recapture to initial postpartum mass to estimate the total mass gained during foraging. Similarly, male grey seals were usually captured within several days of appearing on the island in December/January. I used the average daily mass lost during the breeding season (2.5 kg/d, Godsell 1991), to back-calculate male body mass on arrival.

Data Processing

Satellite transmitters were duty cycled to transmit for 8 h every day or every 2nd day to conserve battery power and reduce satellite fees. Locations of grey seals were determined from data collected by polar orbiting satellites operated by Service Argos. Service Argos provides a location quality index (LQ) for each estimated location. Standard locations (LQ = 3,2,1 or 0) have known theoretical precision, but auxiliary locations (LQ = A or B) do not (Priede and French 1991). Calibration studies have shown that considerable location errors can occur for all location qualities (Le Boeuf *et al.* 2000, Hull *et al.* 1997). Therefore, all locations for each seal (including auxiliary locations) were filtered using a three-stage algorithm (Austin *et al.* 2003) to remove erroneous data. I used these filtered data in subsequent analyses.

To estimate the overall area used by individuals, kernel home ranges (Worton 1989) were calculated using the Animal Movement Extension (Hooge and Eichenlaub 1999; available on http://www.absc.usgs.gov/glba/gistools.htm) in Arcview 3.1 (Environmental Systems Research Institute, Inc. 1996). Fixed-kernel home ranges at the 50% and 95% utilization distributions were calculated based on mean daily locations, and mean bi-daily locations using least squares cross-validation (LSCV) to select the smoothing factor. Seaman and Powell (1996) demonstrated that the fixed-kernel estimator using LSCV provided the least biased and most accurate measure of home range size, particularly on data that is multi-modal and non-normal.

I used the Kareiva and Shigseda (1983) modification of the CRW model of Skellam (1973) to calculate the net squared displacement (R_n^2) of individuals. This model measures the rate of change in area over time by incorporating move lengths (the measured distance from one location to the next) and turning angles (the change in angle from one location to the next) into a quantitative description of an animal's trajectory (Turchin 1998). I calculated the net squared displacement R_n^2 for each seal at successive moves, assuming that there is no predisposition to turn in a preferential direction (Turchin 1998):

$$R_n^2 = nl^2 + 2l^2 \frac{c}{1-c} \left(n - \frac{1-c^n}{1-c} \right)$$

where R_n^2 (km) is the displacement from the first location, n is the number of moves from the first location, l is mean move length (km) and c is the mean of the cosines of the turning angles.

Using the empirical distribution of move lengths and turning angles from all grey seals, an expected R_n^2 was generated using a bootstrapped simulation of 10 000 iterations, with 95% confidence intervals determined by the percentile method (Turchin 1998). The observed (O) and expected R_n^2 (E) were plotted over time to visualize how each seal fit the correlated random walk model - the null hypothesis. In most cases it was clear if the seal fit the model or not, but in some cases the track crossed the 95% confidence interval for some portion of the track. To determine if seals fit the model, I developed a statistic (I_p) which provided an index of the proportion of the track that was outside of the confidence limits:

$$I_p = \sum_{i=1}^{n} \left[\frac{(E_{ui} - O_i) * j}{E_{ui} - E_{mi}} + \frac{(E_{li} - O_i) * k}{E_{li} - E_{mi}} \right]$$

where $i = 1 \ldots n$ locations, $j = 1$ if $O > E_u$ and $j = 0$ if $O < E_u$, $k = 1$ if $O > E_l$ and $k = 0$ if $O < E_l$, and u and l are the upper and lower 95% confidence limits.

The 95th percentile of the expected values was used as the critical value and compared to the observed trajectories. All seals with an observed I_p greater than the critical value were considered to significantly differ from the CRW model. Those animals that fit the model were termed Correlated Random Walkers (CRWs). An individual's trajectory was overpredicted by the model if the observed track lay below the expected R_n^2; hereafter, these individuals are termed Residents because they had a lower displacement than predicted by the model. If the observed trajectory was above the expected R_n^2, these individuals had a greater displacement than predicted by the model and were termed Directed Movers.

Due to the nature of seal diving behaviour and satellite coverage, there are occasional days in which no locations were available for some animals. To determine if missing days in the satellite record would affect the fit to the CRW model, I randomly removed from 1 to 12 consecutive daily locations from the 30 seals with complete records and generated 1000 simulated tracks of each individual and level of deletion. At each level of deletion, the animals were classified as fitting the CRW model or not, and these results were compared with the original data.

Simulations used in this study showed that data quality could affect the overall results of CRW fit. As expected, increasing the size of the missing data gap, increased the overall distance traveled per move length- thus, animals appeared to have greater overall move lengths. Prior to deleting daily locations from those seals, 25 animals fit the CRW model, 15 animals were overpredicted by the model, and 12 animals were underpredicted. Of the observed animals having missing data, the mean duration of the gap was 4.2 ± 0.72 days. Using simulations with 4 missing locations, 31 animals fit the CRW model, 10 animals were overpredicted by the model, and 11 animals were underpredicted. Thus, when data was missing, I was more likely to overestimate the number of animals that fit the CRW. Nevertheless, the objective of this paper was not to examine the proportion of movement types, but instead to examine inherent variability in movement types, which seems not to have been affected by a modest amount of missing data.

To assess whether significant directionality occurred in the distribution of turning angles between successive moves, mean turning angles were calculated for each individual seal (ranging from $-180°$ to $180°$), and across each movement type using

circular statistics (Batschelet 1981). Rayleigh's test statistic was used to test the null

hypothesis that the distribution of turning angles was random, (Batschelet 1981). Angular

concentration, whether the angles were uniformly distributed around a 360° circle, was

measured by calculating a mean vector (r) for each animal (Batschelet 1981).

To test for the presence of autocorrelation between successive turn angles, I used

a non-parametric approach to estimate the autocorrelation function (ACF). I estimated

the mean autocorrelation coefficient between pairs of turn directions at lags up to six

moves (Turchin 1998). An ACF was considered significant if greater than 2 standard

errors from zero. Autocorrelations between successive move lengths were tested using

Pearson's correlation coefficient (Nolet and Mooij 2002). Other location statistics such

as mean distance traveled, total distance traveled, and overall linearity of trajectories

were measured using the Animal Movement extension in Arcview. An index of linearity

(LI) of each trajectory was calculated as the distance between the first and last point

divided by the total distance traveled.

The distribution of move lengths was also examined to see if it fit a Lévy

distribution: $P(l) \sim l^{-\mu}$, where l is move length and μ is a fitted parameter taking on

values of $1 \leq \mu \leq 3$ under a Lévy Flight (see Viswanathan *et al.* 1999, Mårell *et al.* 2002).

For each seal, move lengths between successive locations were divided into fifteen equal

bins, and the frequency of move lengths in each bin calculated. I estimated the Lévy

parameter μ from a regression of log frequency on log move length, and then examined

trends in residuals that would indicate lack of fit.

To investigate how each seal moved relative to the common initial location,

distance from Sable Island was calculated at successive satellite locations. Trip duration

was calculated as the period from the time a seal left a "box" extending 20 km in all directions from the island until the seal once again entered this box. I adopted this approach because location errors associated with Argos data meant that locations within this box could not be reliably determined as being on or off the island. Given that most grey seal locations were of LQ = 0 and LQ = A, I chose the distance of 20 km because it is roughly the midpoint of the mean error of these Argos satellite location classes (9.3 km and 28.3 km, respectively, Le Boeuf *et al.* 2000).

To compare movement characteristics of those seals that fit the CRW model and those that did not fit the model, I used a single factor MANOVA on six movement variables (kernel home range size at the 95% utilization distribution, mean move length, total distance traveled, index of linearity, mean vector, mean speed and mean net squared displacement). Although it is possible that oceanographic influences might affect movement patterns of marine organisms on an inter-annual basis (e.g., Boyd *et al.* 1994, Thompson *et al.* 1996), for the purpose of this study, year of deployment was treated as random variation. Sample size was not large enough to look at season and year simultaneously. Where multiple testing was done, *P*-values were Bonferroni corrected. Statistical analyses were conducted using SPSS version 10.0. Means are given with standard errors.

Results

Sixty-four animals were instrumented during the 7 years of study. Of these, six instruments did not transmit and another six could not be used for this study due to the nature of their duty cycle program. Seven animals had valid satellite records but did not

return to Sable Island in January and therefore could not be weighed a second time to estimate mass gain. Therefore, I obtained satellite records from 52 seals (26 males and 26 females) that ranged in duration from 3 to 10 months; 12 records beginning in May/June, and 40 in September/October. The satellite tags on 27 seals were not duty cycled, permitting estimates of daily locations to be used for analysis of movement. The satellite tags on the other 35 seals were 50% duty cycled (one day on, one day off). Thus, I calculated mean location every 2 days for the entire set of 52 satellite records.

I received 21,747 locations from these 52 seals, for an average of 5.4 ± 0.16 locations per day. Filtering the data eliminated 6,414 locations (29.5 %) leaving 15,333 useable locations (daily mean = 3.9 ± 0.13) for this analysis (Table 4.1). Males had a significantly greater number of mean locations per day than females (5.8 ± 0.23 locations/d, 5.0 ± 0.20 locations/d, respectively; $t = 2.60$, $df = 52$, $P = 0.012$).

Bi-daily movements

Of the 52 seals for which locations were calculated every second day, the trajectories of 25 animals (48.1 %) fit the CRW model (Figure 4.2a,b). The tracks of another 15 animals (28.8%) were overpredicted by the CRW model, and thus were classified as Residents. These seals had low net squared displacement (R_n^2), and typically made short foraging trips from Sable Island (Figure 4.2c,d). The remaining 12 animals (23.1 %) were underpredicted by the CRW model and exhibited greater directionality of movement and longer move lengths than expected (Directed Movers, Figure 4.2e, f).

Table 4.1. Percentage of locations (n) by Argos location quality index (LQ), prior to filtering and post-filtering using the algorithm in Austin *et al.* (2003).

Argos LQ	Unfiltered (%)	Filtered (%)
3	3.2	4.3
2	6.2	8.1
1	11.1	14.0
0	17.5	18.6
A	23.8	23.9
B	38.2	31.1
N	21,747	15,333
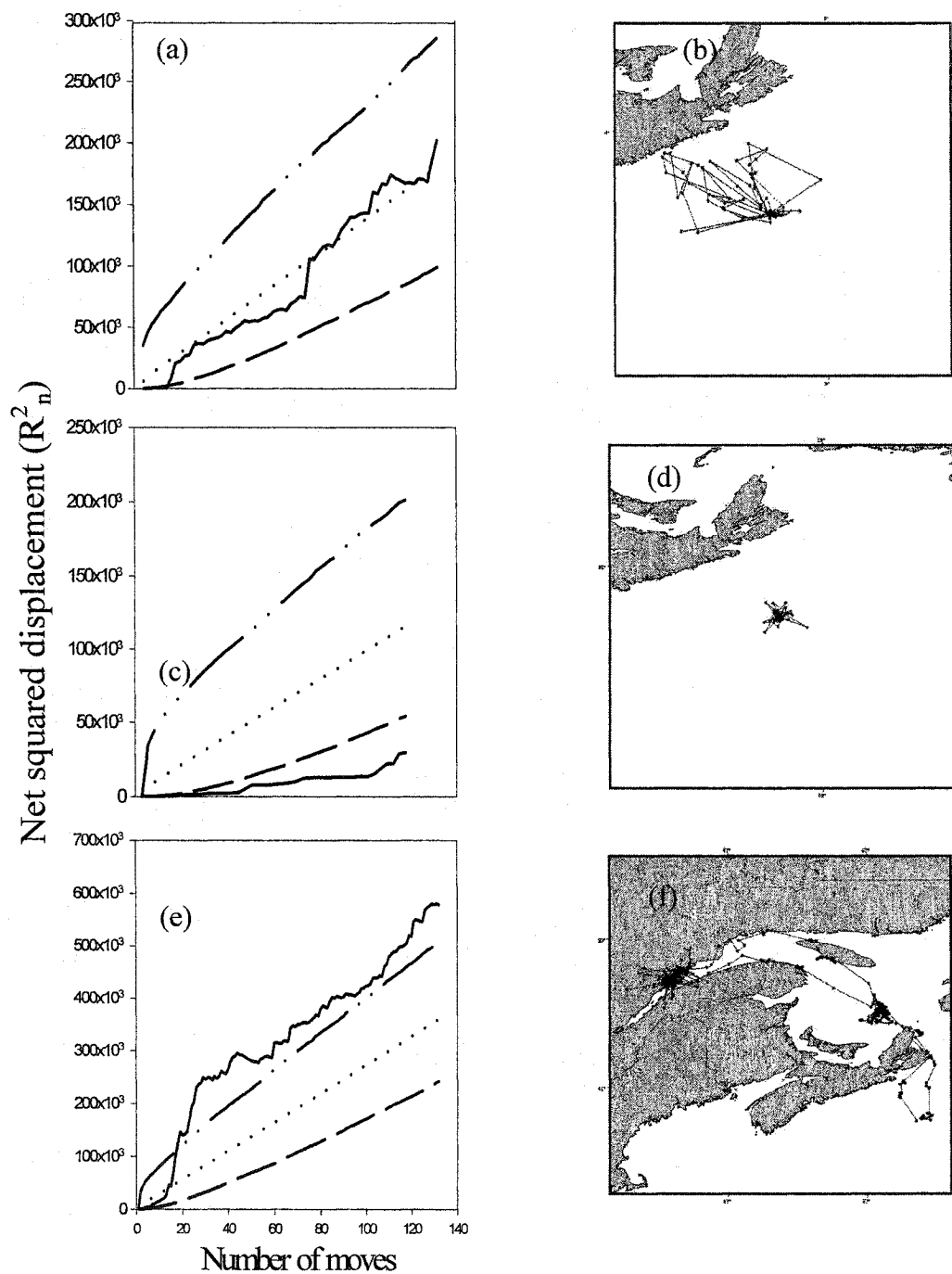
Figure 4.2. Three examples of observed vs predicted R and the corresponding trajectories a) R_n^2 of Seal 23, a correlated random walker, b) Satellite trajectory of Seal 23, c) R_n^2 of Seal 146, a Resident, d) Satellite trajectory of Seal 146, (e) R_n^2 of Seal 2986, a Directed Mover. (f) Satellite trajectory of Seal 2986. Dotted line (..........) indicates expected R_n^2, solid line (_____) indicates observed R_n^2, dashed line (------) indicates lower 95% confidence interval, and dot-dash line (__..__..) indicates upper 95% confidence interval.

Movement characteristics differed significantly among movement types

(MANOVA Pillai's Trace, $F_{14, 88} = 6.47$, $P < 0.001$). Based on Tukey's *post hoc* tests,

significant differences in kernel 95% home range, mean R_n^2, sum of distances traveled,

mean distance traveled, and mean speed were found among all three movement types

(Table 4.2). Mean vector also differed significantly between CRWs and Residents, and

between Directed Movers and Residents. The index of linearity differed between the

Residents and Directed Movers (Table 4.2). With the exception of mean move length and

mean speed, the coefficients of variation (CV) for measured characteristics were high,

indicating considerable individual variability within each movement type.

Mean turning angle approached 180° in Residents, suggesting a propensity to

make successive turns which reversed the direction of movement (Table 4.2). In addition,

only in Residents did successive angles show a significant directional bias (Rayleigh's z

$= 2.95$, $P < 0.05$). Across all animals, a significant positive ACF was found at Lag $= 1$,

but all other lags were non-significant (Table 4.3). When each movement type was

considered separately, a significant positive ACF was found at Lag $= 1$ only in CRWs

and Residents, whereas a significant negative ACF was found at a Lag $= 2$ in Directed

Movers (Table 4.3). Sequential move lengths were not autocorrelated across all animals

(Pearson's $r = 0.03$, $P = 0.09$), however, when Pearson's correlation coefficients were

calculated for each movement category, there was a strong autocorrelation in the move

lengths of the Directed Movers (Pearson's $r = -0.13$, $P < 0.001$).

I next examined if sex of the animal affected movement behaviour. Males were

more likely to be Directed Movers than females, whereas females were more likely to be

Table 4.2. Mean movement characteristics ± SE and coefficient of variation (CV, in parentheses) by movement type for bi-daily locations. Significant differences based on Tukey's post hoc tests.

Movement Characteristic	CRW	Resident	Directed Mover
Mean Move Length (km)	$35.40 \pm 1.33^{a*,b*}$ (18.8)	$19.61 \pm 0.96^{b*,c*}$ (18.9)	$46.08 \pm 2.09^{a*,c*}$ (15.8)
Total Distance Traveled (km)	$1785.9 \pm 235.7^{a*,b*}$ (66.0)	$849.8 \pm 96.1^{b*,c*}$ (43.8)	$3452.3 \pm 510.5^{a*,c*}$ (51.2)
Index of Linearity	0.059 ± 0.008 (69.6)	0.088 ± 0.019^{b} (82.1)	0.038 ± 0.009^{a} (85.0)
Mean R_n^2 (km^2/t)	$87,796 \pm 16,103^{a*,b*}$ (56.8)	$56,511 \pm 21,757^{b*,c*}$ (61.3)	$93,438 \pm 23,256^{a*,c*}$ (46.0)
Mean Vector (r)	0.167 ± 0.017^{a} (64.7)	0.211 ± 0.033^{c} (43.0)	0.181 ± 0.037^{a} (56.7)
Mean Travel Rate (km/h)	$0.762 \pm 0.029^{a*,b*}$ (18.71)	$0.423 \pm 0.021^{b*,c*}$ (18.91)	$1.00 \pm 0.046^{a*,c*}$ (15.93)
Mean Turning Angle	$61.09°$	$-176.33°$	$158.02°$
Kernel HR 95% (km^2)	$25,879 \pm 5,068^{a*,b}$ (97.9)	$3,965 \pm 436^{b*,c*}$ (42.6)	$70,680 \pm 21,210^{a*,c}$ (104.0)
Kernel HR 50% (km^2)	$3,710 \pm 832$ (112.2)	543 ± 92 (65.8)	$12,564 \pm 3,602$ (99.3)

[a] significantly different from Residents at $P \leq 0.05$

[b] significantly different from Directed Movers at $P \leq 0.05$

[c] significantly different from CRWs at $P \leq 0.05$

[*] indicates significance at $P < 0.001$

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Table 4.3. Autocorrelation Function (ACF) of turning angles for each movement type for up to 6 successive lags for bi-daily locations (n=52), with ± standard errors. Significant ACFs are indicated with an *.

Lag	CRW	Resident	Directed Mover	All Seals
1	0.17 ± 0.032*	0.101 ± 0.039*	0.020 ± 0.035	0.11 ± 0.022*
2	-0.047 ± 0.038	-0.024 ± 0.049	-0.071 ± 0.031*	-0.035 ± 0.026
3	-0.064 ± 0.036	-0.051 ± 0.027	0.043 ± 0.026	-0.040 ± 0.021
4	0.0064 ± 0.037	0.0024 ± 0.058	0.011 ± 0.045	0.0020 ± 0.026
5	-0.015 ± 0.032	0.047 ± 0.046	0.020 ± 0.060	0.010 ± 0.022
6	-0.034 ± 0.038	0.066 ± 0.054	0.010 ± 0.037	0.014 ± 0.027

Residents (Likelihood Ratio = 7.43, df = 2, P = 0.024, Table 4.4). A consequence of this

difference was that the 95% kernel home range size of males was significantly larger than

females ($F_{1,50}$ = 17.44, P < 0.001, Table 4.4). Similarly, mean distance traveled between

locations was significantly greater in males than in females ($F_{1,50}$ = 12.21, P < 0.001),

as was mean speed ($F_{1,50}$ = 12.01, P < 0.001).

The probability of exhibiting a particular movement pattern also differed by the

season of instrument deployment. Animals instrumented in spring were more likely to be

Directed Movers, whereas animals instrumented in autumn were more likely to be

Residents or CRWs (Likelihood Ratio = 11.64, df = 2, P = 0.003) independent of sex.

The mean 95% kernel home range size of seals whose record began in spring (41,029 ±

12,413 km^2) was greater than those instrumented in the fall (26,909 ± 7266 km^2),

although this difference was not significant. Mean move length was significantly greater

in seals instrumented in spring (42.5 ± 3.4 km) than in fall (30.8 ± 1.6 km; $F_{1,50}$ = 8.17, P

= 0.006), as was linearity index (spring: 0.046 ± 0.013, fall: 0.067 ± 0.008); $F_{1,50}$ = 3.87,

P = 0.05) and mean R_n^2 (spring: 197,166 ± 29,593, fall: 48 737 ± 5582; $F_{1,50}$ = 24.59, P

< 0.001).

Although all the seals in this study were adults (mean = 18.2 ± 0.9 yr), ages

ranged from 8 to 28 yr. Males in the study were significantly older than females (20.8 ±

1.2 yr, 16.4 ± 1.2 yr, respectively; t_{50} = 2.85, P = 0.006). As foraging and thus movement

behaviour might be affected by experience, I divided my sample into two groups based

on the median age of 18. I found that older seals were more likely to be CRWs, whereas

younger seals were more likely to be Residents. Both older and younger seals

Table 4.4. Number of male and female grey seals by movement type and mean movement characteristics ± SE based on bi-daily locations. Significance as determined from a one-way GLM at $P \leq 0.05$ denoted with an *.

Movement Type	Males (n = 25)	Females (n = 27)
CRW	14	11
Resident*	3	12
Directed Mover*	8	4
95% Kernel Home Range (km^2)*	45,814 ± 11,249	15,157 ± 4,944
50% Kernel Home Range (km^2)	7,725 ± 1,933	2,169 ± 854
Mean distance traveled (km)*	38.39 ± 1.93	28.61 ± 2.14
Total Distance Traveled (km)	2,171.0 ± 292.1	1,650.0 ± 294.1
Mean R_n^2 (km^2/t)	94,783 ± 14,235	66,573 ± 17,155
Mean Speed (km/h)*	0.83 ± 0.042	0.62 ± 0.47

were equally likely to be Directed Movers (Likelihood Ratio = 10.72, $df = 2$, $P = 0.005$).

Using a univariate GLM with age class as a factor, 95% kernel home range size was significantly greater in older ($40,859 \pm 10,488$ km^2) vs. younger animals ($18,056 \pm 5,959$ km^2; $F_{1,50} = 4.12$, $P = 0.05$, R$^2 = 0.076$). The low R^2 value indicates that only a small amount of the variation can be accounted for by age, and thus may not be a biologically significant factor.

Neither body mass at deployment nor rate of mass gain from deployment to recapture differed among movement types ($F_{2,49} = 1.95$, $P = 0.15$; $F_{2,28} = 1.98$, $P = 0.16$, respectively, Table 4.5).

<u>Daily movements</u>

Of the 27 seals located daily, 17 were CRWs (63.0%), 7 were Residents (25.9%) and 3 were Directed Movers (18.5%). At this scale there were proportionately more CRWs and fewer Directed Movers and Residents. The movement type of 6 out of 27 animals (22.2%) changed when they were modeled at daily rather than bi-daily temporal scale, suggesting that movement type may be scale dependent. Five animals that had been classified as Residents using bi-daily data were classified as CRWs using daily locations, whereas one CRW was reclassified as a Directed Mover.

Kernel home range sizes estimated using mean daily locations did not differ significantly from those estimated using bi-daily locations (paired t-test, $t_{26} = -2.09$, $P > 0.05$, Bonferroni corrected), nor did mean vector (paired t-test, $t_{26} = 0.15$, $P > 0.05$, Table 4.6). However, linearity (paired t-test, $t_{26} = -4.51$, $P < 0.001$) was significantly greater for the bi-daily data. This was presumably because more of the tortuosity in the

Table 4.5. Mean body mass at deployment and rate of mass change by day for each movement type.

Movement Type	Mass at deployment (kg)	Rate of mass change per day (kg/d)
CRW	201.24 ± 8.14	0.56 ± 0.06
Resident	176.83 ± 7.58	0.53 ± 0.13
Directed Mover	182.70 ± 12.09	0.57 ± 0.09

Table 4.6. Mean movement characteristics ± SE of 27 seals sampled bi-daily and daily. Significant differences based on paired t-tests at $P \leq 0.05$ (Bonferroni corrected) are denoted with an *.

Movement Characteristic	Bi-daily Locations	Daily Locations
Mean Move Length (km)*	29.1 ± 2.2	24.7 ± 1.9
Total Distance Traveled (km)*	1,163.4 ± 143.6	1,755.0 ± 174.3
Index of Linearity*	0.082 ± 2.21	0.027 ± 0.01
Mean R_n^2 (km²/t)*	39,050 ± 8,130	55,229 ± 9,522
Mean Vector (r)	0.20 ± 0.02	0.21 ± 0.02
Kernel HR 95% (km²)	25,987 ± 10,223	23,976 ± 9,133
Kernel HR 50% (km²)	3,753 ± 1,458	3,395 ± 1,347

trajectory was captured at shorter time scales. Both cumulative distance traveled (paired t-test, $t_{26} = 10.89$, $P < 0.001$) and mean R_n^2 (paired t-test, $t_{26} = 5.07$, $P < 0.001$) were significantly greater at the shorter time scale (Table 4.6).

The mean turning angle was $32.0°$ for CRWs, $167.3°$ for Residents and $114.0°$ for Directed Movers. Both the Residents and Directed Movers showed a propensity for turning in a particular direction (Residents: Rayleigh's $z = 6.31$, $P < 0.05$; Directed Movers: Rayleigh's $z = 0.71$, $P < 0.05$). Examining the ACF for the mean daily locations across all non-duty cycled animals indicated a significant positive correlation at a Lag = 1 (Table 4.7), and a significant negative correlation at a Lags = 3 and 4. Across all three movement types, there was a significant positive ACF at a Lag = 1. However, there was a significant negative ACF for the Residents at a Lags = 3 and 6. Directed Movers had a significant negative ACF at a Lag = 5 and a significant positive ACF at a Lag = 6 (Table 4.7).

Using the daily locations, again males had larger kernel 95% home ranges than females (males: $39,781 \pm 16,726$ km^2, females: 6956 ± 1552 km^2; $F_{1,25} = 9.75$, $P = 0.004$, $R^2 = 0.28$). Similarly, a one-way GLM with age class as a factor and 95% kernel home range as a dependent factor showed that kernel home range was significantly greater in older animals ($40,917 \pm 16,590$ km^2) than in younger animals ($5,731 \pm 887$ km^2; $F_{1,25} = 7.18$, $P = 0.013$, $R^2 = 0.22$).

Lévy Flight

The CRW model fit the observed trajectories of approximately half of all seals studied. An examination of the distribution of move lengths suggested that a Lévy Flight

Table 4.7. Autocorrelation Function (ACF) of turning angles for each movement type for up to 6 successive lags for mean daily locations (n=27), with ± standard errors. Significant ACFs are indicated with an *.

Lag	CRW	Resident	Directed Mover	All Seals
1	0.099 ± 0.029*	0.142 ± 0.037*	0.105 ± 0.016*	0.12 ± 0.013*
2	-0.0042 ± 0.034	-0.0035 ± 0.034	-0.026 ± 0.092	-0.011 ± 0.007
3	-0.010 ± 0.044	-0.075 ± 0.024*	-0.071 ± 0.054	-0.052 ± 0.021*
4	-0.070 ± 0.036	-0.075 ± 0.040	-0.051 ± 0.053	-0.065 ± 0.007*
5	0.0094 ± 0.032	-0.029 ± 0.035	-0.077 ± 0.034*	-0.032 ± 0.025
6	-0.0081 ± 0.038	-0.056 ± 0.025*	0.068 ± 0.029*	0.0020 ± 0.036

might also be an appropriate model. However, only 8 of the 52 seals (15.3%), had

frequency distributions of movement lengths that fit the negative power law distribution

of a Lévy Flight indicating that long movements occurred more often than expected if the

distribution of movement lengths was normal (Mårell *et al.* 2002). Five of the animals

that fit the Lévy distribution also fit the CRW model, whereas the other three animals

were Residents.

To investigate if the temporal scale of sampling affected the number of seal

trajectories fit by the Lévy model, I repeated the analysis using the daily sampled seals.

In this sample, 9 of the 27 animals, or 33.0 % of trajectories fit a Lévy Flight (Figure

4.3). Of these, 4 were males and 5 were females. However, among the 27 seals, there was

no evidence that one sex is more likely to fit a Lévy Flight than another (Log-likelihood

ratio = 0.30, *df* = 1, *P* = 0.59). Of the animals that fit the Lévy Flight distribution, 5 were

CRWs and 4 were Residents, but no one movement type was more likely to fit the Lévy

Flight (Log-likelihood Ratio = 4.21, *df* = 2, *P* = 0.122). None of the seals classified as

Directed Movers fit the Lévy Flight distribution. Directed Movers had a frequency

distribution characterized by more long move lengths than short ones, resulting in a

distribution with no descending right tail.

Distance from Sable Island

Although the analysis of the movement trajectories using quantitative models

provided considerable insight into how animals use space, it did not capture all aspects of

movement. Since all seals began their trajectory at the same location, the mean distance

from Sable Island provided another way to quantify movement behaviour over the course
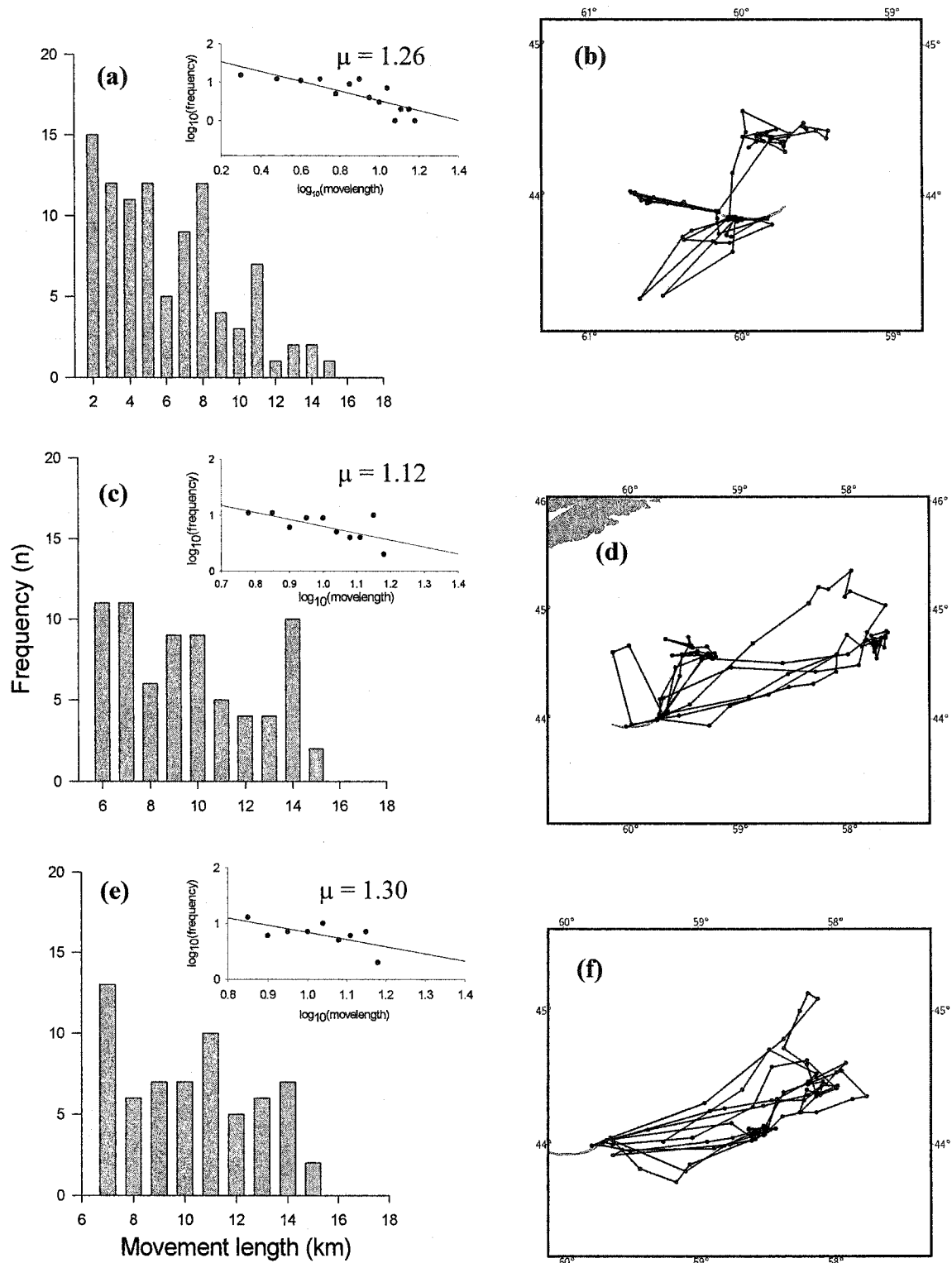
Figure 4.3. Average frequency distributions of movement lengths for each three seals which fit the Lévy distribution. (a) Seal 6118, a Resident, (b) Seal 6124, a CRW and (c) Seal 6125, a CRW. Inserted is a double-log plot of the same data fitted with a regression line, where μ is the power-law exponent of the frequency distribution. Lévy Flights follow a distribution of $1 < \mu \leq 3$.

of the trajectory. Distance from Sable Island over time varied significantly among

movement types, with the average distance being greatest in Directed Movers (258.8 ±

59.6 km), least in Residents (38.8 ± 39.7 km) and intermediate in CRWs (90.7 ± 7.3 km,

Kruskal-Wallis Chi-Square = 31.34, df = 2, P < 0.001).

The way in which distance from Sable changed over the course of the trajectory

provided insight into the structure of foraging trips (Figure 4.4a. to f.). Directed Movers

made one long trip from Sable Island, whereas Residents undertook many short trips.

Directed Movers may have used other haul-out areas other than Sable Island and hence I

did not calculate trip statistics for this group of animals. Mean trip duration from Sable

Island in Residents (6.8 ± 0.78 d; CV = 103.2) was significantly less than that of CRWs

(10.6 ± 0.77 d, CV = 91; t_{225} = 4.04, P < 0.001). Residents also spent a lower percentage

of time spent away from Sable (i.e., outside the 20 km box) than CRWs (33.4 ± 3.6 % d

and 53.9 ± 3.9 % d, respectively; t_{38} = 3.5, P = 0.001). Plots of travel speed over time

demonstrated that high speeds were typically associated with rapidly changing distance

from Sable (Figure 4.4).

Discussion

The correlated random walk model, based on mean population distribution of

turning angles and move lengths, did not describe the movement behaviour of over half

the grey seals in this study. However, this does not mean that correlated random walks

could not be fit to these individuals using parameters other than the population means as

indicated by Levy Flight analysis. Nevertheless, testing the trajectories of individual seals

against predictions of the CRW model provided a useful way to differentiate among types
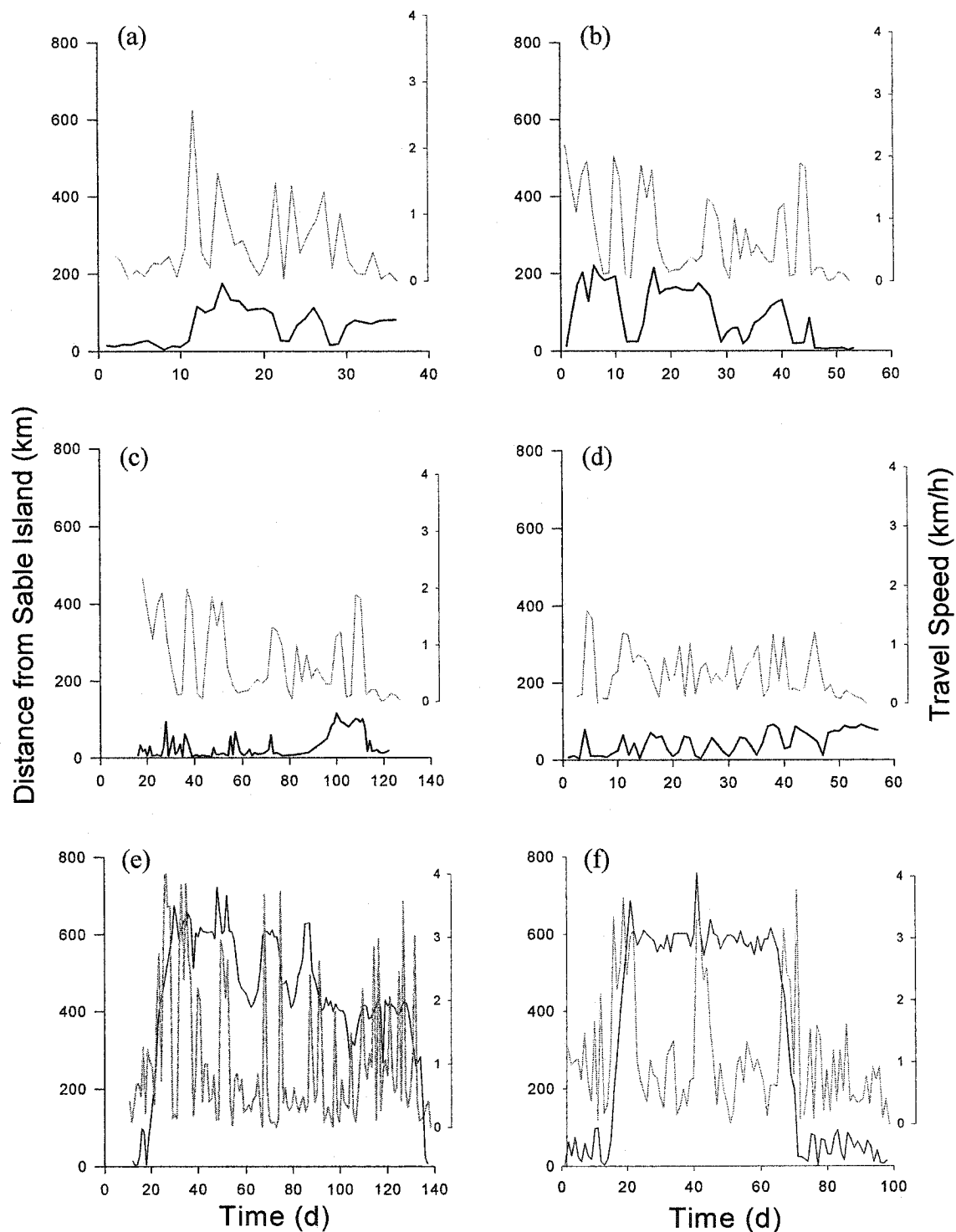
Figure 4.4. Distance (in km) from Sable Island over time (solid black line) and travel speed over time (solid grey line) for 6 seals. (a) Female 24, a CRW. (b) Male 3099, a CRW. (c) Female 2999, a Resident. (d) Male 6115, a Resident. (e) Female 3616, a Directed Mover. (f) Male 3662, Directed Mover.

of movement: (1) those which moved in a random fashion, the CRWs, (2) those whose movement patterns were characterized by short return trips from a single place, the Residents, and (3) those seals which undertook long distance, directed movements away from the island, only returning to the island just prior to the breeding season, the Directed Movers. Most animals did not fit the Lévy Flight, which indicates that other search tactics are involved, and that prey items consumed by grey seals are not randomly distributed. These results also show that there is considerable individual variability within each of the three movement types (i.e., high CVs), with movement tactics seemingly varying along a continuum from short, localized trips to distant, extended trips.

My primary goal here was not to estimate the proportion of each movement type within the population. Nevertheless, I identified several factors that will affect such estimation. Directed Movers were more likely among seals tagged after the spring molt, whereas Residents were more common among seals tagged in the fall, suggesting that there may be seasonal changes in the proportion of movement types used by grey seals. Or, alternatively, Directed Movers may simply spend less time on Sable Island in the fall and thus are less available to capture than seals exhibiting other movement types. Sex of the animal also affected the proportion of movement types. Male and female grey seals exhibit different seasonal patterns of body mass and energy storage (Beck *et al.* 2003c) and diving behaviour (Beck *et al.* 2003 a, b) and as a result may use different search tactics. Finally, the frequency of sampling location affected the perception of the proportion of seals exhibiting different movement tactics (e.g., the proportion fitting a Lévy Flight).

An examination of the assumptions of the CRW model may indicate why some animals failed to meet the predictions of the model. The two key assumptions of a CRW are that move lengths and turning angles are not serially autocorrelated. Such autocorrelation in move lengths is the primary reason for rejection of CRW models (Turchin 1998). Move lengths were strongly autocorrelated in Directed Movers indicating that the distance traveled at t_1 is a function of the distance traveled at $t_1 - 1$, indicating that distance traveled between successive satellite locations was relatively constant. As a result, the majority of move lengths in the Directed Movers were of similar size. Furthermore, the distribution of move lengths in the Directed Movers tended to be strongly biased towards longer move lengths, with the mean distance traveled considerably greater than that seen in the CRWs and Residents. Long move lengths are generally associated with traveling, whereas shorter move lengths are characteristic of foraging behaviour (Pyke 1978, Stanton 1982). Therefore, by using many long, similarly sized move lengths, Directed Movers reduce travel time to distant feeding areas. Mean travel speed of Directed Movers (see Figure 4.4) was also higher than that of Residents and CRWs. A number of studies suggest that foraging speed varies as a function of the distance between patches (Spalinger *et al.* 1988, Speakman and Bryant 1993, Shipley *et al.* 1996), such that as distance increases so should optimal speed. According to optimal foraging theory (OFT), animals should attempt to minimize time spent between patches in favour of time spent within patches (Pyke 1978). Long-distance travel should only be taken if there is a high probability of reward from the distant patch. In all cases, the destination of the Directed Movers in this sample was a known offshore or coastal area of high prey abundance. For example, seal 2986 (Figure 4.2c) moved quickly to an area of

the St. Lawrence Estuary known to contain a productive upwelling, used by other marine mammals (Simard and Lavoie 1999). Although I could not determine the quality of prey patches directly, I can assume that these were areas of high quality given that these animals returned to the Sable Island having gained sufficient reserves to withstand prolonged fasting period associated with the breeding season.

The second reason for failing to fit a CRW is the autocorrelation of turning angles. Turning angles were significantly positively correlated at a time Lag = 1 across all animals, and for Residents, CRWs, and Directed Movers (daily locations only), indicating the propensity to make sequential turns in the same direction from one move to the next, also known as directional persistence or directional bias. While perfectly correlated angles result in a straight trajectory, in general, positive autocorrelation of turning angles will result in a more tortuous trajectory (Zollner and Lima 1999), thereby lowering the overall net squared displacement. This is generally characteristic in areas where animals may be foraging (Bovet and Benhamou 1991).

In addition to testing first order autocorrelations at a Lag = 1, I also examined higher-order autocorrelations up to Lag = 6 (Turchin 1998). Most Lags > 1 had autocorrelations that were negative in all three movement types, indicating the tendency to turn in opposite directions, particularly observed in the Residents. As expected, Residents chose turning angles which approach 180° at both the bi-daily and daily temporal scales. In this manner, an individual tends to reverse its direction ensuring that it remains within the vicinity of Sable Island, thereby reducing the probability of leaving the habitat.

There may be several reasons for Residents to forage near Sable Island. First, proximity to a haul-out site has a suite of potential advantages. Hauling out on land may be necessary for rest, to engage in social interaction and to reduce risk of predation from killer whales (*Orcinus orca*) and white sharks (*Carcharodon carcharias*). McConnell *et al.* (1999) found that, in the North Sea, most foraging by grey seals apparently occurred in close proximity to haul-out sites. Second, Sable Island Bank is a relatively shallow (50-100 m), sandy region, which is habitat for a number of important grey seal prey, such as sandlance (*Ammodytes dubius*) and capelin (*Mallotus villosus*) (Beck 2002). Thus, by remaining near Sable Island, travel costs to prey patches are minimized.

In contrast, mean turning angle of the CRWs is closer to 0°, and distribution of turning angles is not significantly clustered around any given direction. Generally, a normal distribution of turning angles suggests that an animal's movement pattern is random (Levin *et al.* 1971). In the seals for which there were daily movements, I found a significant negative autocorrelation for the Residents at a Lag = 3 and a Lag = 6. This indicates some long-term memory in movement behaviour, although this effect is not as strongly correlated as at a Lag = 1 and consequently has less influence (Turchin 1998). The longest-term autocorrelations are seen in the Directed Movers (daily trajectories, Lag = 5 and Lag = 6) as would be expected of animals exhibiting long distance, directed travel, indicating memory in the direction of movement.

Within the context of OFT, optimal directionality in an animal's trajectory should lead to a decrease in the number of patches revisited and increase the possibility of encountering new patches (Wolf and Hainsworth 1990). The "lost opportunity principle" refers to the revisitation of already exploited patches; by doing so, an animal loses the

opportunity to seek out other patches where resource availability is higher (Stephens and Krebs 1986). Zollner and Lima (1999) found through simulation that the best search tactic to avoid "lost opportunities" is to use non-systematic search trajectories that are nearly straight, with optimal angular concentration being > 0.9. Nevertheless, I found a relatively low angular concentration (mean vector) of my animals of 0.19 ± 0.02, also reported in foraging swans (*Cygnus columbianus bewickii*, Nolet and Mooij 2002) and caribou (*Rangifer tarandus*, Bergman *et al.* 2000). Zollner and Lima (1999) concluded that when food patches are clumped, the optimal angular concentration does not matter, provided the trajectory is neither perfectly straight nor random. I know from studies of the diving patterns of grey seals that the preferred foraging depth is 50-100 m (Beck *et al.* 2003 a). In the Northwest Atlantic, distribution of shallow offshore banks in the 50-100 m depth range is not uniform, rather they tend to be clumped across the Scotian Shelf, particularly in the area surrounding Sable Island (Figure 4.1). This may account for the low angular concentration observed in grey seals.

According to existing theory, the probability of successful dispersal across a habitat is increased by employing a strongly correlated random walk (Zollner and Lima 1999). Nonetheless, my results show that only about half of the adult grey seals studied fit the CRW model. Another type of random walk, the Lévy Flight, also predicted the movement of about a third of grey seals whose location was sampled daily. A Lévy Flight search tactic is advantageous when resources are randomly distributed because the probability of returning to a previously visited site is smaller than for a normal distribution (Viswanathan *et al.* 1999). In addition, a Lévy distribution is preferable because the number of new sites visited is greater than for simple random walkers under

typical Brownian motion (Klafter *et al.* 1996). Thus, my results suggest that some grey

seals do not use random search tactics to locate prey patches. I suggest that both the

clumped distribution of foraging habitats and many years of foraging experience in these

adult grey seals may account for these results.

Age was a significant predictor of movement type and home range size (this

study), as well as aspects of diving behaviour (Beck *et al.* 2003a). Swingland *et al.*

(1989) found that the proportion of migratory and sedentary tortoises (*Geochelone*

gigantea) varies with age, with young, immature animals appearing inconsistent in their

movement patterns, and older animals being more likely to migrate. Grey seals are long

lived, and adults certainly will have had many years for foraging experience to learn the

location of profitable prey patches. This could explain the rapid direct movements of

Directed Movers to distant areas followed by a subsequent change in search behaviour

(Figure 4.4). The younger animals in this study were more likely to exhibit movements

characteristic of Residents, whereas older animals were more likely to display a random

search or directed travel pattern. Nevertheless, age explained relatively little of the

variation in movement type and so the biological significance of this difference remains

unclear.

Differences in diet preferences or dietary requirements among individuals might

also affect movement patterns to the extent that prey distributions differ in time and

space. For example, the distribution of some important grey seal prey, such as capelin

and sand lance, are highly clumped in time and space over shallow and sandy habitats

(Scott and Scott 1988). However, other important prey items such as flounders and other

flatfish (Beck 2002) tend to have a more uniform distribution at the scale of the offshore

banks shown in Figure 4.1 (Groundfish Survey Database, Department of Fisheries and Oceans, Canada). It is likely that the costs and gross amounts of food consumed in order to reach similar levels of energy storage vary between individuals, and this difference will be reflected in prey selection. Indeed, by examining diet at an individual level using techniques such as Fatty Acid Signature Analysis (Iverson *et al*. 1997), in future I will be able to link seal movement and prey distribution in these animals.

Variation in movement tactics within a population have been observed in other taxa. For example in the cane toads, *Bufo martinus*, some individuals are nomadic, while others remain in a single small area for most of their existence (Schwarzkopf and Alford 2002). Among birds, many species show distinct migratory and sedentary behavioural morphs, known as partial migration. For example, in goshawks (*Accipiter gentiles*) and the chaffinch (*Fringilla coelebs*), the proportion of migrants in the population fluctuates, likely as a result of changing food conditions, and is related to the sex or age of the individual (Newton 1979). Variation in movement behaviour has also been observed in ungulate populations. For example, within the same habitat in Northern Sweden, half of a population of moose (*Alces alces*) migrated while the other half remained sedentary (Ball *et al*. 2001), similar to the behavioural variation exhibited by the seals in this study.

Swingland and Lessells (1979) suggest that migrant and non-migrant individuals will persist in a population if they receive approximately equal pay-offs. I found no difference in amount of mass gained by grey seals among the three movement types, indicating that each of these are successful search tactics. Furthermore, 20 of the 27 study females (74%) returned to Sable Island, gave birth, and nursed healthy pups. Among these 27 females reproductive success was independent of movement type (Log-

likelihood ratio = 1.27, $P = 0.53$). I could not conduct a similar analysis in males because I do not have a reasonable measure of the reproductive success of the study seals.

Sex-specific foraging behaviour has been found in several taxa (Pérez-Barbería and Gordon 1999, Le Boeuf *et al.* 2000, Jormalainen *et al.* 2001, Ishikawa and Watanuki 2002), including grey seals (Beck *et al.* 2003 a,b). Male and female grey seals exhibited different seasonal patterns of diving at several temporal scales, with males generally diving deeper, but with less overall dive effort (shorter dives with less time at depth). There is also evidence that males consume a lower energy density diet than females (Beck 2002). Therefore it is not entirely surprising that males and females also differ in the way in which they search for food. Females show a greater tendency to remain in the vicinity of Sable Island as Residents, and use a smaller home range size, while males exhibit more long distance travel, and as a result have significantly greater home range sizes. By using a larger foraging range, males presumably encounter a greater diversity of prey species. This coupled with their larger body size (males are 1.5 times heavier than females) may enable males to process larger quantities of lower quality prey (Beck 2002). Consequently, males may be more efficient predators than females, spending less time foraging despite their larger size and absolute energy requirement, a dichotomy also observed in ungulates (e.g., Ginnett and Demment 1997, Ruckstuhl 1998, Pérez-Barbería and Gordon 1999).

Although there is evidence of sex-differences in the proportions of movement types exhibited by grey seals, nevertheless, both sexes used all three search tactics. Thus, there remains a great deal of individual variability in the movement patterns in this population of grey seals (this study), as well as in the North Sea (McConnell *et al.* 1992)

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and in the Baltic Sea populations (Sjöberg and Ball 2000). In addition there is a considerable amount of variation in movement patterns between populations. Some of this variation is captured in estimates of kernel home ranges. For example, the mean 95% kernel home range of Baltic seals (2,658 ± 508 km^2) is significantly less than that in this study (23,976 ± 9133 km^2, $t = -4.17$, $df = 36$, $P < 0.001$; Sjöberg and Ball 2000). This difference seems to reflect the greater complexity of the continental shelf habitat used by grey seals in the Northwest Atlantic compared to the relatively uniform and shallow Baltic Sea. Ungulates also show differences in home range size between populations (Lesage et $al.$ 2000), seemingly as a result of density-dependent competition (Nelson and Mech 1984) and habitat differences (Lincoln 1992).

Understanding movement, and hence increasing our knowledge of the foraging behaviour of grey seals has many implications. I have used new technology to shed light on previously unknown movement patterns of an apex predator. Moreover, I have increased our comprehension by using quantitative methods of modeling which allow us to predict the decision rules used by a large marine predator, and interpret them in the context of optimal foraging theory and intraspecific variation. The ability to predict the population distribution and spread through the environment has important consequences for modeling resource and habitat use (Bergman et $al.$ 2000). Understanding individual variability in movement patterns of grey seals will improve existing models of predation (e.g., Mohn and Bowen 1996) by permitting more spatially explicit estimates of predation mortality on prey populations.

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Chapter V. Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal

Introduction

Establishing when predators forage is fundamental to understanding ecosystem function (Everson 1984, Trathan *et al.* 1998). Although patch structure is expressed in both time and space; temporal variation often constitutes a major source of spatial patchiness (Wiens 1976). Thus, temporal variation in predator behaviour may provide insight into the spatial distribution of a highly dynamic prey that can be difficult to track in other ways (Mangel and Adler 1994). In addition, the spatial and temporal distribution of predation introduces heterogeneity in prey mortality, which can have significant effects on prey and community dynamics (Boyd 1996). The way that predators perceive the patchiness of prey can have considerable implications for understanding the temporal distribution of feeding; hence, this is a major gap in our capacity to model predator-prey relationships (e.g., Abrams 1991, Mohn and Bowen 1996).

Our inability to determine the frequency and temporal pattern of feeding also limits our understanding of foraging behaviour (Wilson *et al.* 2002a). For instance, such information is essential in predicting the timing of feeding according to optimal foraging theory (Krebs 1978). Observation of feeding is difficult because many species feed in dense cover, feed at night or forage over large and remote areas. In particular, the temporal distribution of successful foraging is largely unknown in marine mammals and seabirds, as direct observation is precluded because feeding generally occurs during diving. Consequently, the timing of feeding has been merely inferred from the shapes of

dives (i.e., their 2-dimensional time-depth profile; Schreer and Testa 1996, Le Boeuf *et al.* 2000), the temporal structure of bouts of diving (Boyd 1996, Beck *et al.* 2003a), and for some species (e.g., Murie and Lavigne 1986), the state of digestion of stomach contents. Marine mammals are upper trophic-level predators in the marine ecosystem (Estes 1996, Bowen 1997), yet we know little about the frequency and timing of successful feeding in these animals.

Sex-specific foraging behaviour has been found in several taxa (Pérez-Barbería and Gordon 1999, Le Boeuf *et al.* 2000, Jormalainen *et al.* 2001, Ishikawa and Watanuki 2002) and may affect the temporal distribution of feeding. In grey seals (*Halichoerus grypus*), males and females exhibit different seasonal patterns of diving at several temporal scales (Beck *et al.* 2003a,b). Additionally, males and females tend to differ in the way in which they search for food, with females using a smaller foraging range than males (Austin *et al.* 2004). This coupled with size dimorphism (males are 1.5 times heavier than females), differences in diet (Beck *et al.* in review) and seasonal differences in energy storage (Beck *et al.* 2003) might suggest the presence of sex specific differences in the temporal record of foraging grey seals.

Moreover, individual variation independent of sex may also affect foraging behaviour. Movement patterns of grey seals show a great deal of deviation between individuals (Austin *et al.* 2004), and there is evidence of individual variation in their diet as well as between the sexes (Beck *et al.* submitted). Dietary preferences or dietary requirements among individuals might also affect the temporal record of foraging given that prey distributions differ in both time and space. For example, the distribution of some important grey seal prey, such as capelin and sand lance, are highly clustered in

time and tend to be found in large schools (Scott and Scott 1988). However, other important prey items such as flounders and other flatfish (Beck 2002) tend to have a more uniform distribution (Groundfish Survey Database, Department of Fisheries and Oceans, Canada). Thus, prey behaviour may determine whether individual grey seals may have single prey ingestions or a multiple ingestion event. Therefore, it is likely that the distribution of feeding in time may reflect differences in prey selection.

Despite the application of new methods that have resulted in a better understanding of the diets of marine animals, such as quantitative fatty acid signature analysis (Iverson *et al.* 2004) and stable isotopes (Schell *et al.* 1989, Ramsay and Hobson 1991); we still have little indication of when food ingestion occurs, or how animals might structure their food intake over time. Thus, rapid growth in our knowledge of marine mammal and seabird diving behaviour and diet, and by inference, their foraging behaviour (Grémillet *et al.* 1999, Lesage *et al.* 1999, Le Boeuf *et al.* 2000, Wilson *et al.* 2002), has not been mirrored by an increase in our understanding of the timing or frequency of feeding success.

The development of stomach temperature telemetry (Wilson *et al.* 1992) has enabled feeding frequency to be studied in free-ranging marine animals. This method is based on the principle that the body temperature of prey in the marine environment is colder than that of the core body temperature of its endothermic predators resulting in a predictable drop in stomach temperature following prey ingestion. The magnitude of the temperature drop and the amount of time the temperature takes to recover to pre-ingestion levels has also been used to derive estimates of meal size (Wilson *et al.* 1992, Gales and Renouf 1993, Pütz and Bost 1994, Hedd, Gales and Renouf 1996). Stomach

temperature telemetry has been used with considerable success on free-ranging seabirds, e.g., albatross, (*Diomedea exulans*; Wilson *et al.* 1992), King penguins, (*Aptenodytes patagonicus*; Pütz and Bost 1994) and northern gannets, (*Sula bassana*; Garthe *et al.* 1999). However, the use of stomach temperature telemetry in marine mammals has been limited by the difficulty of keeping the stomach temperature transmitter in the stomach (Bjørge *et al.* 1995, Lesage *et al.* 1999; Wilson *et al.* 1995, Wilson *et al.* 1998). Although there has been some success in captive pinnipeds, e.g., harbour seals (*Phoca vitulina*, Bekkby and Bjørge 1995; Hedd *et al.* 1995), and harp seals (*Phoca groenlandica*, Gales and Renouf 1993) stomach temperature telemetry has had limited success in free-ranging pinnipeds (Bjørge *et al.* 1995, Lesage *et al.* 1999).

I studied the temporal distribution of feeding events in free-ranging grey seals using stomach temperature telemetry. Recently, the collapse and failure to recover of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic has focused attention on grey seals as predators (Mohn and Bowen 1996; Fu *et al.* 2001). Delineating the frequency of feeding will provide increased information on the temporal scales of foraging success in these animals. I had two objectives in this study. The first was to measure the frequency of foraging success in a marine predator to reveal how success is distributed over time. Secondly, I tested whether sex, time of day and time since the last feeding event significantly affected the temporal pattern of feeding. Given the documented variation in diving, movement and seasonal energy storage between the sexes, I predicted that the temporal pattern of feeding should differ between males and females.

Methods

Field Site

Seals were captured on Sable Island (44°53'N, 60°00'W), a vegetated sand bar in the Northwest Atlantic, approximately 300 km from Halifax, Nova Scotia, Canada in September/October from 1999 to 2001. Known-aged, adult grey seals were caught using hand-held nets (Bowen *et al.* 1992) and weighed to the nearest 0.5 kg prior to being anaesthetized with Telazol (equal parts of Tiletamine and Zolazepam). Males and females received an average dose of 0.45 mg kg^{-1} body mass and 0.90 mg kg^{-1} body mass, respectively (Bowen *et al.* 1999).

Data Sampling

The stomach temperature telemetry system consisted of two separate instruments: a stomach temperature radio transmitter (STT; 56 x 20 mm, 32 g) placed in the stomach of the seal and a radio receiver with an integrated microprocessor data logger (10 x 50 x 70 mm, 60 g) attached to the seal's pelage along the dorsal midline over the stomach using 5-min epoxy (both from Wildlife Computers, Redmond WA, USA). The receiver was programmed to record stomach temperature every 3 seconds in 1999 and 2000 and every 10 seconds in 2001. To ensure that the STT remained in the stomach of the animal for an extended sampling period, I devised an assembly that increased the size of the device without endangering the health of the animal. To minimize the potential for rejection of the device, the STT was glued into the center of an oval shaped piece (20 x 15 x 2 cm) of biodegradable ethafoam with 10-min epoxy. The sides of the STT remained exposed to gastric fluids and ingested prey in the stomach, the exposed surface area being only slightly reduced by the ethafoam. Hence, I assume that the estimated response time of the STT to changes in temperature of 6 s (Lesage 1999) was not significantly delayed.

As soon as the animal was anaesthetized such that the jaw musculature of the animal was relaxed, the STT was delivered to the stomach by fastening the assembly to the end of an equine intubation tube. Prior to intubation the STT assembly was compressed with biodegradable paper tape to reduce its cross-sectional area and lubricated. Once in the stomach, the STT assembly was dislodged using a rod inserted through the equine tube. The assembly expanded back to its full size as the paper tape was broken down by stomach acids and peristalsis. Through consultation with veterinarians, the assembly was made large enough to delay passage, but small enough so that as the foam broke down in the stomach over time, it would eventually be passed.

Seals returned to Sable Island during the breeding season in December/January at which point they were re-weighed and the stomach temperature data logger removed.

Data Analysis

Stomach temperature data were downloaded using software provided by the manufacturer. The resulting data file was then run through a custom software program (Visual Basic within the Microsoft Access) designed to identify individual feeding events. Before analysis, electronically generated noise (occasional erroneous transmissions yielding temperatures that were not biologically possible), was eliminated from the record by discarding all readings greater than 105% or less than 90% of the running mean temperature calculated over a 1 min window. The onset of a feeding event was defined as a temperature reading that was greater than two standard deviations from the calculated running mean. If the difference was greater than two standard deviations for ≥ 2 minutes- a feeding event was considered to have started. The end of a feeding event was defined by calculating the mean temperature for each 1-minute period and

subtracting this amount from the calculated mean prior to the onset of the feeding event. When this difference was less than 2 % then the feeding event was considered finished. A random sample of putative feeding events was then manually scored to ensure that identified feeding events showed the characteristic precipitous drop followed by slow asymptotic rise (e.g., see Figure 5.1a). For each feeding event, I measured: pre-feeding (body) temperature (A, Figure 5.1a), minimum temperature during an event (B, Figure 5.1a), time to reach the minimum temperature, time to return to body temperature post-feeding, rate of temperature decrease (amplitude of temperature drop/time to minimum temperature), post-feeding temperature (C, Figure 5.1a) and time between the end of a feeding event to the onset of the next. Grey seals feed on non-schooling demersal fish and schooling pelagic fish, hence feeding events might be characterized by single prey consumption or multiple prey consumption. Therefore, I categorized each feeding event as either "single", corresponding to a single drop in temperature (Figure 5.1a) or "multiple", as corresponding to a large drop followed by many smaller drops in temperature(Figure 5.1b).

Experimental studies in seabirds have shown that there is a linear relationship between the integral under the asymptote and the energy supplied to warm the ingested food (Wilson *et al.* 1992) and this may be used to estimate ingested prey mass. However, Hedd *et al.* (1996) suggested that this relationship was not robust enough to allow quantitative estimation of consumption rates in pinnipeds due to a number of factors that may confound quantification, including animal activity, heat transfer, fullness of the
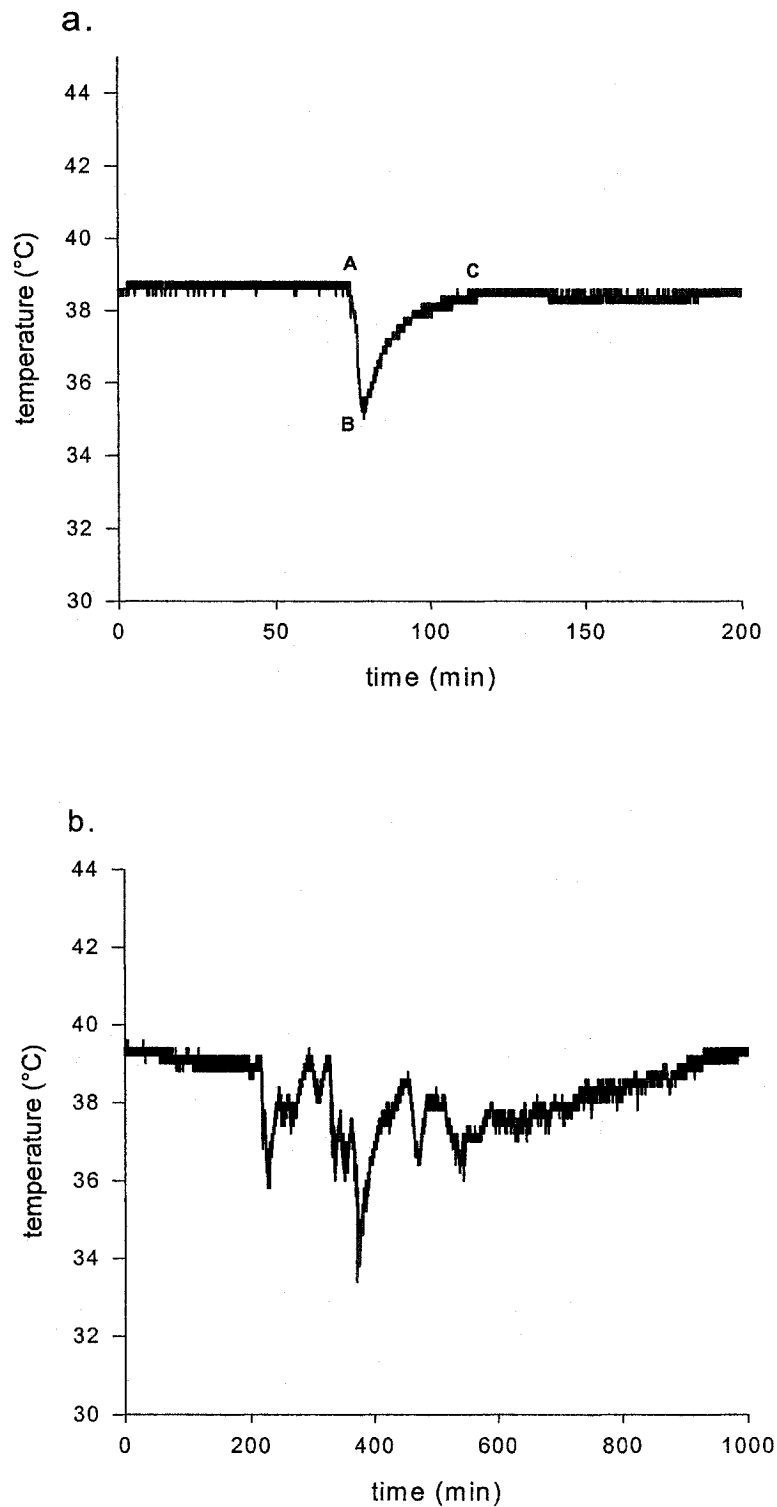
Figure 5.1. Example of a stomach temperature profile over time, demonstrating **a.** a typical single feeding event (where A = pre-feeding stomach temperature, B = minimum temperature attained during feeding and C = post-feeding recovery temperature), and **b.** a typical multiple feeding event.

stomach and degree of stomach churning (Grémillet and Plos 1994, Wilson *et al.* 1995, Hedd *et al.* 1996). While I use this relationship to estimate ingested prey mass in this study, I offer the caveat that feeding event size as presented should be considered a relative estimate of the quantity of ingested prey (Wilson *et al.* 1995).

The integral area enclosed by the temperature curve and bounded by points A to C (Figure 1a) was calculated using a geographic information system (GIS). By designating the temperature field as latitude and the time field as longitude, I imported the file into Arcview 3.1 (Environmental Systems Research Institute, Inc. 1996), and determined the spatial area bounded by the curve in km^2 using the extension Xtools (Mike Delaune 1999; http://www.odf.state.or.us.sfgis) point to polygon function in an unprojected planar view. Although these are not the appropriate units (i.e., km^2 instead of °C/sec), this method nevertheless permitted calculation and comparison of feeding event size within and among individuals.

To examine the pattern of feeding events over time, I examined the non-feeding interval, i.e., the time between feeding events. The satiety concept (LeMagnen 1985, Tolkamp *et al.* 1998, Tolkamp and Kyriazakis 1999) predicts a low probability that animals will initiate a feeding event shortly after terminating one, but as the duration of non-feeding increases, hunger or motivation will increase; thereby increasing the probability of feeding. Under this model, feeding will not be randomly distributed in time and the distribution of intervals between feeding will correspond to physiological state. I used bout analysis, as outlined in Tolkamp *et al.* (1998), to estimate the distribution and duration of feeding events (Sibly, Nott and Fletcher 1990) of six grey

seals having the longest stomach temperature records. To do this, I estimated a critical time interval for each seal that determined whether successive events were part of the same meal, or a part of an altogether different meal. I binned non-feeding intervals into equal time bins and used a maximum likelihood to fit log-transformed intervals (Tolkamp *et al.* 1998). Using the model parameters, I estimated the percentage of intervals that occur within or between meals, and estimated the mean inter-meal interval for each seal.

To test for the effects of sex and time of day on meal size and meal frequency, I used Generalized Linear Mixed Models (GLMM) with Penalized Quasi-Likelihood (PQL) estimation in S Plus version 6.2 (Copyright 1988, 2003 Insightful Corp.). In order to test how the percentage of simple vs complex meals varied between the sexes, I used a Generalized Linear Model (GLM). All possible models with two-way interactions were examined, and residuals were verified to ensure there was no obvious lack of fit or alternative pattern present. To select the best predictive model, I compared the models with the lowest Akaike's information criteria (AIC). All other statistical analyses (runs tests, t-tests) were conducted using SPSS version 11.5. Means are reported with ± standard errors.

Results

Stomach Temperature Records

A total of 32 (16 males and 16 females) grey seals were equipped with STTs: 8 in 1999, and 12 each in 2000 and 2001. Four of those animals did not return to the breeding colony the January following deployment, although one detached data logger was recovered on Sable Island during the breeding period. Of the 29 recovered recorders, 8

recorders collected no data, leaving 21 with stomach temperature data. The mean body mass was significantly greater in males than in females at the time of deployment ($t = 4.28$, $p < 0.001$, n = 21) and at time of recapture ($t = 5.57$, $p < 0.001$, n = 21; Table 5.1). In addition, the rate of mass gain per day of deployment was also significantly greater in males than in females ($t = 3.51$, $p = 0.003$; Table 5.1).

The number of days sampled was highly variable among seals (Table 5.2). Twelve stomach temperature loggers sampled ≥ 14 days, to a maximum of 40 days. A single logger sampled 8 days and the remaining 8 instruments recorded for < 1 week. Two of these recorders recorded no feeding events, though it appears that the instrument was retained in the stomach of these animals for almost a week. A total of 343 days of stomach temperature data was collected from the 21 seals, for an average of 16.33 ± 2.67 d/seal, median = 14.0. Mean deployment length did not vary between males (15.92 ± 3.46 d) and females (16.11 ± 3.95 d; $t = 0.106$, $P = 0.92$). Average body temperature calculated from the mean body temperature of each seal prior to each feeding event was $38.1°C \pm 0.13$ °C.

I recorded a total of 555 feeding events in the 21 seals with an average of 26.4 ± 5.56 events per seal (median = 22 events). Mean feeding event duration was 56.9 ± 6.88 min (time from temperature drop A to temperature recovery C, Figure 5.1). There was considerable individual variation in the frequency of feeding events (Figure 5.2), and feeding events did not occur every day in most seals. For example, seal 6122 went 13 days without feeding, while seal 5112 fed on each of 13 consecutive days of its 14-day record (Figure 5.2). Seal 5114 appeared to alternate between 3 or 4 days of feeding and several days of not feeding (Figure 5.2).

Table 5.1. Differences in mean age, body length and the rate of mass gain ± SE in males and females.

	Males	Females
Age (years)	22.42 ± 1.21	20.11 ± 2.46
Length (cm)	218.08 ± 2.42	183.00 ± 2.82
Mass at deployment (kg)	223.50 ± 8.50	173.78 ± 2.82
Mass gain (kg/d)	0.79 ± 0.097	0.32 ± 0.075

Table 5.2. Number of days in which stomach temperature was sampled in 21 male and female grey seals and number and proportion of days with feeding.

Seal id	Sex	Year	Record length (d)	Days with feeding (d)
6122	Female	2001	32.0	10 (31.3%)
24	Female	2000	28.0	17 (60.7%)
5683	Female	2000	28.0	12 (42.3%)
5108	Female	1999	24.0	16 (66.7%)
5110	Female	1999	14.0	9 (64.3%)
6116	Female	2001	6.0	4 (66.7%)
6120	Female	2001	5.0	0 (0.0%)
3271	Female	2000	4.0	2 (50.0%)
2690	Female	2001	3.0	1 (33.3%)
6117	Male	2001	40.0	13 (32.5%)
5114	Male	1999	36.0	24 (66.7%)
6124	Male	2001	32.0	19 (59.4%)
5111	Male	1999	17.0	7 (41.2%)
5684	Male	2000	17.0	7 (41.2%)
5687	Male	2000	17.0	14 (82.3%)
5112	Male	1999	14.0	13 (92.9%)
6125	Male	2001	8.5	7 (82.4%)
6126	Male	2001	6.0	6 (100.0%)
3661	Male	2000	5.0	5 (100%)
5116	Male	1999	4.5	0 (0.0%)
5685	Male	2000	2.0	2 (100.0%)

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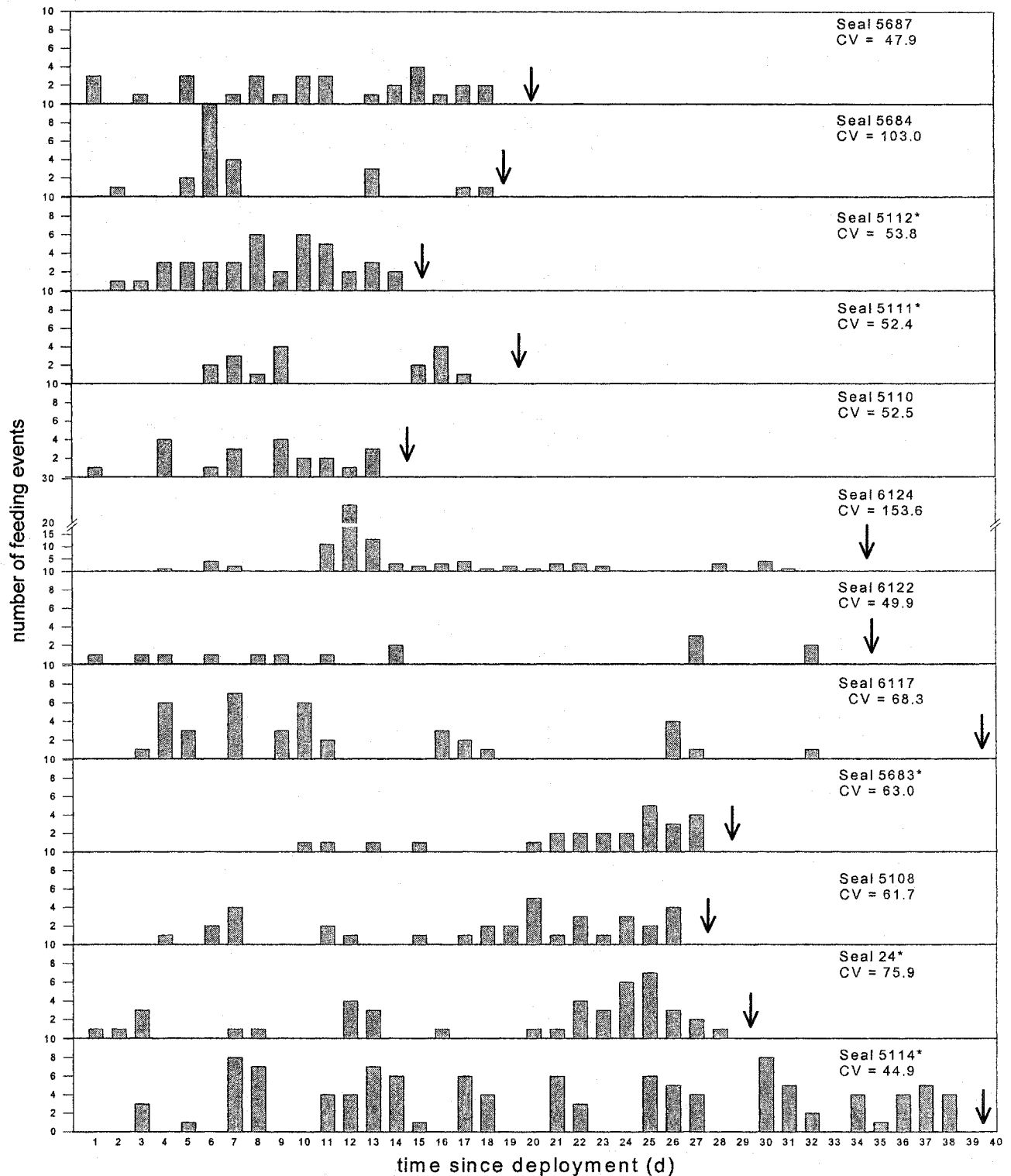
Figure 5.2. Frequency of feeding events by day in individual seals having stomach temperature records ≥ 2 weeks (n = 12). Time is measured as days since deployment. Arrows indicate the end of the stomach temperature record. Seals marked with an asterisk are those with a significant runs test. Coefficients of variation (CV) are given for each seal.

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On average, seals fed on 57.8 ± 6.46 % of days and had a mean number of 1.7 ±

0.26 meals per day (including non-feeding days), but the number of meals per day was

highly variable among seals, (mean coefficient of variation [CV] = 69.0%; Figure 5.2).

To investigate the temporal pattern of feeding in those seals having records ≥ 14 days (n

= 12), I did runs tests at three temporal scales (1 d, 12 h, and 6 h). At the scale of 1 d, the

temporal distribution of feeding was significantly different from random in only 5 of the

12 seals (Figure 5.2). However, as I increased the temporal scale to 12 h, the number of

seals showing a significant pattern of feeding increased to 7 out of 12, and this remained

the same at the 6h scale. Seals with a temporal patterning of feeding events were those

having the longest records, (i.e., greater than 2 weeks), suggesting that the probability of

detecting temporal patterns of feeding is higher in longer records.

For the six seals having the longest records, bout analysis suggested that each

animal had a different distribution of non-feeding intervals, and the best fit to the data

varied from a log-normal to a double log-normal model (Table 5.3, Figure 5.3). Four of

the animals fit a log-normal distribution, indicating that there was no evidence for

discontinuity in the length of time between-feeding intervals. When transformed back

from the log scale, the geometric mean non-feeding interval for these animals ranged

from 0.82 to 346.7 min (the geometric mean is closer to the median value of the inter-

feeding event time across all seals= 145.2 min). Intervals from two seals did fit to a

double log- normal model (Table 5.3). This resulted in two populations of intervals: short

intervals within meals and longer intervals effectively separating individual meals (>75%

of all intervals). For these two animals, I calculated the mean non-feeding interval of the

first and second populations of intervals. Using model parameters, I calculated a meal

Table 5.3. Results of maximum likelihood fitting of log normal distributions to the non-feeding intervals of six seals. Given P values are based on the goodness of fit, p values < 0.05 indicate significantly poor model fit. Asterisks indicate which distribution better fits the data. Mean non-feeding interval is transformed back from the log value and is given in minutes with upper and lower confidence intervals in brackets. The T_c describes the point in time where the two log normal distributions intersect and therefore all between-feeding intervals < T_c occurred within a meal, and all between-feeding intervals > T_c represent separate meals.

seal id	single log normal P value	double log normal P value	mean non-feeding interval length (min)	T_c (min)
24	0.400*	0.997	253.5 (140.6, 457.1)	
5108	0.381*	0.896	346.7 (192.3, 625.2)	
5112	0.157*	0.992	190.5 (118.6, 306.2)	
5114	0.058	0.180*	0.82 (0.66, 1.0)/ 108.7 (76.8, 153.8)	1.6
6117	0.506*	0.705	154.9 (82.4, 291.1)	
6124	0.005	0.746*	1.6 (1.4, 1.9)/ 189.2 (117.8, 304.1)	20.0
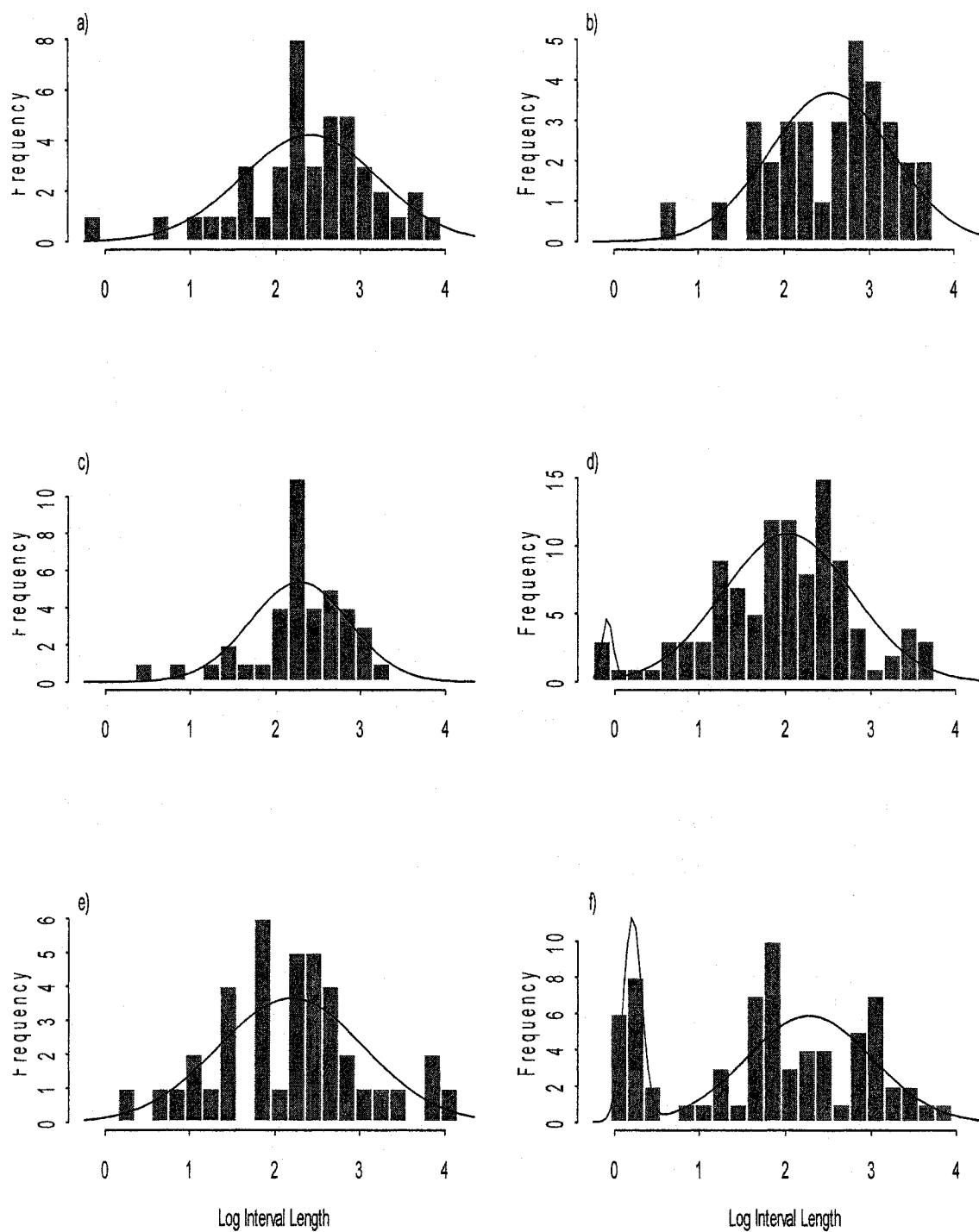
Figure 5.3. Frequency distribution of log-transformed intervals between feeding events. Solid line demonstrates fit to a single or double log-normal distribution. a) Seal 24, b) Seal 5108, c) Seal 5112, d) Seal 5114, e) Seal 6117 and f) Seal 6124.

criterion (T_c) where the two log-normal distributions intersect (Table 5.3). Thus, all between-feeding intervals < T_c occurred within a meal, and all between-feeding intervals > T_c represented separate meals.

There was no significant difference in mean body temperature between males (38.2 ± 0.15°C) and females (37.9 ± 0.21°C; $t = 1.16$, $P = 0.268$). Similarly, there was no significant difference between the sexes in the temperature drop from pre-feeding (A, Figure 5.1) to the minimum temperature attained during a feeding event (males = 4.3 ± 0.21°C; females = 4.1 ± 0.32 °C; $t = 0.52$, $P = 0.60$). However, there were significant sex differences in the temporal distribution of feeding events. The mean number of feeding events per day was significantly greater in males (2.2 ± 0.38) than in females (1.0 ± 0.20; $t_{19} = 2.45$, $P = 0.024$). Similarly, the average time spent feeding per day was greater for males (56.6 ± 5.84 min) than females (43.8 ± 9.42 min; $t_{17} = 1.70$, $P = 0.05$). Consequently, the time elapsed between feeding events in males (541.42 ± 63.54 min, median = 111.20 min) was significantly less than in females (1092.63 ± 169.94 min, median 384.50; median test, 26.56, $P < 0.001$). Males had a greater percentage of days with feeding (66.54 ± 9.32 %) than females (46.2 ± 7.38 %), but this difference was not significant ($t_{19} = 1.71$, $p = 0.10$). Meal size was greater in males (58,667 ± 14,743 units) than in females (53,338 ± 27,619 units), although this difference was not significant (Mixed-effects GLM, $F_{(1, 17.13)} = 0.20$, $P = 0.66$).

Grey seals exhibit diurnal variation in diving behaviour (Beck *et al.* 2003c). To examine if feeding incidence is related to time of day, I binned time of day into 6 h blocks corresponding to light levels throughout a 24 h period (dusk, night, dawn and day)

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and calculated the number of feeding events per bin. Using a GLMM with a poisson distribution, the number of feeding events varied with time of day (b = 0.22, P = 0.0075, DF = 47, observations = 67, groups = 19) with the least number of feeding events occurring during dawn hours. Sex was not a significant factor in the number of feeding events by time of day (b = -0.53, P = 0.10, DF = 17, observations = 67, groups = 19). Similarly, the mean feeding event size between time bins differed significantly (GLMM,b = 0.074, P = 0.02, DF = 535, observations = 555, groups = 19), with mean meal size greater during the dawn and least throughout the night (Figure 5.4). Although males appear to have larger meals during dusk, night and dawn, and females appear to have larger meals during the day (Figure 5.4), there was no sex effect ($F_{1,14}$ = 0.58, P = 0.81) or sex-time bin interaction ($F_{7,84}$ = 2.01, P = 0.05).

In order to determine if time between feeding events affected feeding event size, I used another GLMM with feeding event size as the response variable, and the inter-event time as predictor variable. Feeding event size was significantly predicted by the length of time between feeding events (b = 0.14, P < 0.0001, DF = 519, observations = 538, groups =18), but sex was not a significant predictor variable (b = 20,244.5, P < 0.42, DF = 519, observations = 538, groups =18).

The overall percent of simple feeding events (those characterized by a single temperature drop) by seal was 45%, compared to 55% of complex feeding events (those characterized by multiple temperature drops). The ratio of simple to complex feeding events did not vary significantly by sex (GLM; b = 0.17, P = 0.73, DF = 17), although females tended to have a higher percentage of complex meals (63%) than males (51%).
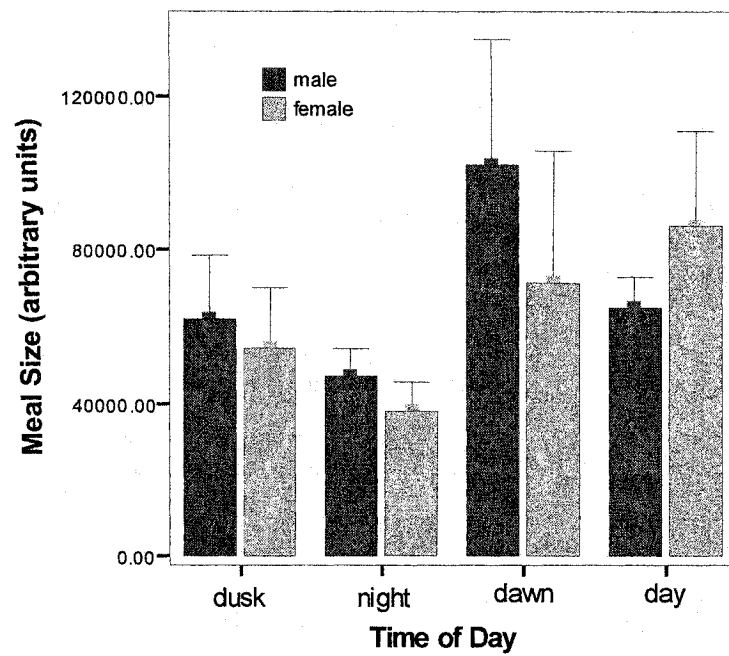
Figure 5.4. Mean feeding event size by time of day and sex. Standard error bars given.

Discussion

This study is the first quantitative analysis of feeding in a free-ranging marine mammal based on data collected by stomach temperature telemetry. I succeeded in keeping the STTs in the stomach long enough to obtain records of greater than 2 weeks in a number of animals; providing insight into individual variability in the temporal distribution of feeding behaviour of large marine predators. I found significant differences in the number of feeding events and the time spent feeding between males and females. Feeding distribution appears to vary by time of day and the time between meals is a predictor of meal size. These results provide new insight into the basis of sex differences in diving and diet in this size-dimorphic species.

Individual variability in feeding frequency was one of the most salient features of my findings, as evidenced by high CVs and significant subject effects. This underscores the importance of examining individual variability; otherwise we risk obscuring interesting patterns in pursuit of simplification and generality (Judson 1994). For instance, a comparable degree of individual variability was found in a recent study of movement and distribution of grey seals (Austin *et al.* 2004). Individual variability in feeding frequency has also been found in other species such as wandering albatross, *Diomedea exulans* (Weimerskirch *et al.* 1997) and King Penguins, *Aptenodytes patagonicus* (Pütz and Bost 1994). Likewise, in foraging hamadryas baboons (*Papio hamadryas*), there was considerable within and between individual variation in time spent feeding and ingestion rate, with a CV of 68% (Zinner 1999). In this study it was not possible to determine whether observed variability resulted from variation in individual foraging behaviour (mediated by diving differences or diet) or a consequence of the

patchiness of prey. However, a departure from a random sequence (based on runs test results) was found in four of the seven animals with records longer than a month, suggesting that those 4 seals may be exploiting prey that are predictable in time, or simply organizing their foraging behaviour in a predictable manner over time.

One of the most interesting findings of this study was that grey seals do not feed every day, and it was not uncommon for many days to separate feeding events. This is undoubtedly related to the large body size and the ability of marine mammals to store energy reserves as a thick blubber layer which gives them a degree of insurance against periods of non-feeding (Iverson 2002). For example, during the breeding period, adult grey seals fast for 3 to 4 weeks; hence we know that they can withstand extended periods of fasting. In wolves (*Canis lupus*), time between predation events on ungulates can vary from 3 – 19 days (Hayes *et al.* 2000). Carey *et al.* (1982) suggest that a 4.6 m white shark could survive 1.5 months between successive meals of 30 kg of whale blubber, which may in part be driven by their poikilothermy. However, as the time between feeding events increased, the subsequent meal size also appeared to increase in grey seals (this study), suggesting that they are compensating for the lack of feeding with a larger meal. The duration of between-feeding intervals is directly correlated to fullness of the stomach in shrews (*Sorex* sp., Saarikko and Hanski 1990).

The temporal organization of feeding events in grey seals differed between individuals. Bout analysis revealed that four of the six grey seals having the longest records had between-feeding intervals that fit a log-normal distribution. However, two of the six grey seals organized their feeding intervals into two categories: those that were short (i.e., breaks within a meal) and those that were longer (i.e., separating meals). The

majority of intervals in both seals were composed of the latter, and given that the other four seals did not demonstrate a distinct population of these very short intervals, this may indicate that grey seals tend to have many single feeding events, with a relatively longer time period separating each event.

The mean between feeding interval in grey seals as determined using bout analysis was approximately 150 min. Thus individual feeding events were separated by relatively long periods of time, particularly in comparison to other species such as free-ranging horses (Mayes and Duncan 1986) or starlings (Langton et al. 1995) where mean inter-feeding interval is typically only 50 minutes. Grey seals probably need to feed more frequently than would other predators that gorge on large prey items (e.g., coyote, Canis latrans, feeding on ungulates), given that they tend to feed on small prey items (0.01–3.0 kg) relative to their body size (150–350 kg).

Nevertheless, these results differ considerably from the distribution of feeding in herbivores or domestic animals, where the typical structure involves many short within-meal intervals, and fewer long inter-meal intervals, with a clear distinction between the two populations of intervals (Simpson and Ludlow 1986, Tolkamp et al. 1998). Herbivores often have a continuous supply of food and hence feed to satiation with occasional brief interruptions in feeding for predator vigilance, social interactions or searching for a new food patch. In contrast, grey seals are upper trophic-level predators, which actively search for individual prey or aggregations of individual prey. Therefore, feeding is more likely to be limited by opportunity rather than stomach fullness.

As well, physiological studies show that most predators employ a "batch-reactor" type of digestion, which involves the consumption of discreet meals (Penry and Jumars

1987). The ideal batch reactor operates intermittently, and remains idle between additions of food, as opposed to herbivores, which digest via a "continuous-flow-reactor" system, characterized by a continuous flow of material (Penry and Jumars 1987). Evidence from studies of digestion in captive southern elephant seals (*Mirounga leonina*) indicates a capacity for rapid transit of digesta, suggesting that they can consume frequent, relatively large meals such as they would encounter in prey patches (Krockenberger and Bryden 1994).

Sex differences were observed in the distribution of feeding events in grey seals. There are several reasons why one might expect males to spend more time feeding and have longer (and potentially larger) feeding events than females. Since absolute metabolic requirements increase with body size, larger individuals require more energy per unit time than smaller ones (Klieber 1961). Thus, a larger animal requires greater energy intake, and may forage differently as a result (Clutton-Brock *et al.* 1982). For example, male hamadryas baboons fed more often and had larger feeding events, accounted for by the presence of sexual dimorphism, and associated increased energetic demands (Zinner 1999). Male grey seals require 1.3 times the energy intake of females (Mohn and Bowen 1996); hence one might expect that they will organize their foraging accordingly. Evidence from yearly seasonal patterns of energy storage indicates that males only begin to accumulate energy stores during the pre-breeding foraging period following a 6 month period of body energy loss (Beck *et al.* 2003b). Energy gain increases in September, corresponding to this study period. Male have greater energy requirements and gain a greater amount of body mass at a faster rate during the fall. Thus it is not surprising that I found that males spend more time feeding.In contrast, females

have a more consistent strategy of energy accumulation throughout the year, and do not demonstrate as marked an increase in the fall months (Beck *et al.* 2003b). Additional support from studies of grey seal diving behaviour indicate that in early fall, time spent in foraging bouts is greater in males than in females (Beck *et al.* 2003c). All of these factors provide additional rationale beyond simply that of greater energetic requirement, as to why one might expect males to spend more time feeding during the present study period.

Feeding event size tended to be greater in males, though not significantly so. In theory, the observed difference in feeding event size should be substantially larger when one considers the principles of thermodynamics as related to body size. Females, having a smaller body size, would have a greater mass-specific heat production than males by about 10% (Cossins and Bowler 1987), which might suggest that females would warm ingested prey faster than males. Nevertheless, males are roughly 50% heavier than females, and hence would warm the ingested prey faster than females because heat storage capacity is proportional to body mass (Cossins and Bowler 1987, Berteaux 2000). Therefore, if males are warming ingested prey faster, then one would expect feeding event size in males to appear smaller than in females. Yet, we see the opposite phenomena, with females having smaller feeding events than males, which suggests that the observed difference in feeding event size is even greater than it appears through this analysis.

In addition to feeding more frequently, males may also feed on different prey than females. Recent dietary analysis of grey seals using fatty acid signatures and stable isotopes suggests that grey seals may also exhibit a sexual dichotomy in diet selection. Male grey seals appear to feed heavily on benthic prey that is low in energy density,

while females prefer pelagic prey items, which tend to be higher in energy density (Beck *et al.* submitted).

I have demonstrated that the distribution of foraging success is highly variable among individuals and between the sexes, providing new insight into the basis of sex differences in foraging behaviour and diet in this size dimorphic species. This is critical information for understanding predator-prey relationships in upper trophic-level predators.

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Chapter VI: Linking successful foraging with movement and diving behaviour in grey seals

Introduction

Predator behaviour can be used to make inferences about prey distribution and prey patch quality, over both spatial and temporal scales (e.g., Boyd 1996, Hooker and Baird 2001). Ideally, one should attempt to study predator behaviour relative to prey abundance and distribution (e.g., Baumgardner *et al.* 2003, Benoit-Bird *et al.* 2003). However, this is not a simple task in air-breathing aquatic predators. Often it is impossible to concurrently observe both predator and prey. Consequently, information on prey is collected at scales of time or space that are logistically convenient for the researcher, but may not be entirely relevant to the predator. Therefore, in general, information about how large marine predators alter their behaviour in response to their prey is poorly understood.

Marine mammals are long-lived, k-selected individuals, and therefore must have evolved the ability to adapt to different scales of environmental variation within their lifetime (Whitehead 1996). Thus, individuals may be expected to modify their behaviour in response to changes in prey abundance and distribution (e.g., McCafferty *et al.* 1998, Boyd 1999, Bradshaw *et al.* 2000, Georges *et al.* 2000, Jaquet and Gendron 2002, Harcourt *et al.* 2002). Variation in food availability occurs at multiple temporal and spatial scales, resulting in changes in the diet, from fine-scale daily changes in prey behaviour (Bowen *et al.* 2002) to seasonal/geographic (Perez and Bigg 1986, Iverson *et al.* 1997) and longer-term variation (Bailey and Ainley 1982, Thompson *et al.* 1996). Given that most marine mammals must dive to forage, diving effort can serve as a

reasonable proxy for foraging effort in relation to changes in prey availability, as evidenced by studies on pinnipeds (Boyd *et al.* 1994, Thompson *et al.* 1996).

However, given the difficulty of directly observing foraging in a diving animal, we have little way of knowing how diving effort is related to foraging success. Presumably, animals which spend more time diving should encounter more prey and have greater feeding success. Still, studies have shown that there can be substantial variation in diving behaviour among individuals within the same species (Le Boeuf *et al.* 2001, Beachler *et al.* 2002, Beck *et al.* 2003a,b). Presumably, individuals respond differently to changes in prey distribution and these changes are discernable to some extent in their diving behaviour. Still, we have no way of knowing how the distribution of foraging success in time may affect the temporal structure of diving, or alternatively, how characteristics of diving may influence the probability of successful foraging.

A number of approaches have been used to extract additional information on foraging behaviour from diving. Dive shape classification has been used to infer different behaviours from the shape of individual dives as a function of time and depth (Le Boeuf *et al.* 1988, Bengston and Stewart 1992, Martin *et al.* 1998, Lesage *et al.* 1999, Hochscheid *et al.* 1999, Beachler *et al.* 2002, Beck *et al.* 2003a). Another approach has been to examine the temporal pattern of diving. Pinnipeds often dive episodically such that dives may be clustered in time into bouts of diving, which may also differ in predictable ways. Boyd *et al.* (1994) suggested that the analysis of different types of bouts may provide insight about how predators organize their behaviour over a longer temporal scale. This type of analysis has been useful in understanding the diving behaviour of adult pinnipeds (Beck *et al.* 2003b).

If diving behaviour reflects variation in the temporal distribution of prey and feeding success, then movement behaviour may largely describe prey distribution over a range of spatial scales (Hooker and Baird 2001). An individual's movement behaviour will reflect their search patterns (Bell 1991), define their home range (Austin *et al.* 2004), determine their energetic costs (Bergman *et al.* 2001) and potentially the prey available to be consumed (Baird *et al.* 1992). An animal can alter its searching behaviour by adjusting turning angles, move lengths and travel speed (Bell 1991). The success of search strategies will depend upon the distribution of prey (patchy vs. random; Zoller and Lima 1999). Hence, by outlining search tactics of foraging top predators, we can make inferences about prey distribution. The integration of movement patterns with diving behaviour may help us understand how search tactics are linked with foraging effort. However, without knowledge of where and when feeding occurs, it will not be possible to fully understand the consequences of different behaviours.

The identification of feeding events in free-ranging grey seals (*Halichoerus grypus*) using stomach temperature telemetry was described in Chapter V. Information on the frequency of foraging success can be combined with time depth recorders (TDRs) and satellite-relay data loggers (SRDLs) to increase our understanding of the temporal and spatial scales of successful foraging in a free-ranging marine predator. Previous studies of diving in grey seals (Beck *et al.* 2003a,b) have indicated sex-specific differences in seasonal diving and bout patterns as well as individual variation in diet (Beck *et al.* submitted). Similarly, evidence for significant individual variation in movement patterns in grey seals (Chapter IV) and in the temporal record of feeding (Chapter V) have been suggested. Therefore, this study sought to integrate data on diving behaviour, movement

and feeding in free-ranging grey seals to better understand the predictors of foraging success. To do this, I investigated diving characteristics in relation to foraging success at two temporal scales. Secondly, I examined the relationship between diving characteristics and movement behaviour, and finally, tested whether movement behaviour was predictive of foraging success.

Methods

Instrument Deployment

The study took place from September 1995 to January 2002 on Sable Island (44°53'N, 60°00'W), a vegetated sand bar approximately 300 km from Halifax, Nova Scotia, Canada. Known-aged, adult grey seals were captured using hand-held nets (Bowen *et al.* 1992) and weighed to the nearest 0.5 kg prior to being anaesthetized with Telazol (equal parts of Tiletamine and Zolazepam). Males and females received 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 the spatial distribution of foraging, animals were instrumented with satellite relay data loggers (SRDLs; Wildlife Computers, Redmond WA or ST-18 - Telonics, Mesa AZ). Instruments were secured to netting and then the netting was attached to the pelage on top of the head or neck of the anaesthetized animals using 5-min epoxy. Each instrument weighed ≤ 650g (<0.6% of body mass). A salinity sensor on the instrument detected whether the animal was wet or dry, and suppressed transmissions when the instrument was wet. To conserve battery power and reduce satellite fees,

satellite transmitters were duty cycled to transmit for 8 h every second day from 1995-1999 h and 8 h every day for deployments from 1999-2001.

In order to examine diving behaviour, each animal was also instrumented with a TDR at the time of deployment. TDRs were secured to the pelage between the shoulders along the dorsal midline of the anesthetized individual using 5-min epoxy. These instruments and their epoxy mounts weighed between 65 and 300 g (< 0.3 % of animal's body mass at deployment) depending on the model used (Mk3e, Mk5, Mk 6 and Mk7 - Wildlife Computers, Richmond, WA). TDRs recorded depth every 20 seconds and a wet/dry sensor was used to determine when the animal was hauled out on land.

Foraging success was determined using stomach temperature telemetry for a subset of animals instrumented from 1999-2001. The stomach temperature telemetry system consisted of two separate instruments: a stomach temperature radio transmitter (STT; 56 x 20 mm, 32 g) placed in the stomach of the seal and a radio receiver with an integrated microprocessor data logger (10 x 50 x 70 mm, 60 g) attached to the seal's pelage along the dorsal midline (next to the TDR) over the stomach using 5-min epoxy (both from Wildlife Computers, Redmond WA, USA). The receiver was programmed to record stomach temperature every 3 s in 1999 and 2000 and every 10 s in 2001. To ensure that the STT remained in the stomach of the animal for an extended sampling period, I devised an assembly that increased the size of the device without endangering the health of the animal. To minimize the potential for rejection of the device, the STT was glued into the center of an oval shaped piece (20 x 15 x 2 cm) of biodegradable ethafoam with 10-min epoxy. The sides of the STT were only slightly reduced by the

ethafoam and therefore remained exposed to gastric fluids and ingested prey in the stomach.

Once the animal was anaesthetized such that the jaw musculature was relaxed, the STT was delivered to the stomach by fastening the assembly to the end of an equine intubation tube. Prior to intubation the STT assembly was compressed with biodegradable paper tape to reduce its cross-sectional area and lubricated. Once in the stomach, the STT assembly was dislodged using a rod inserted through the equine tube. The assembly expanded back to its full size as the paper tape was broken down by stomach acids and peristalsis. Through consultation with veterinarians, the assembly was made large enough to delay passage, but small enough so that as the foam broke down in the stomach over time, it would eventually be passed.

Most instrumented seals returned to Sable Island during the breeding season in December/January, at which point they were re-weighed and the TDR, satellite transmitter and stomach temperature data logger were removed. Instrumented females were not recaptured until several days postpartum to permit females to form a bond with their pup. Similarly, male grey seals were usually captured within several days of appearing on the island in December/January.

Data Processing

Locations of grey seals were determined from data collected by polar orbiting satellites operated by Service Argos. Service Argos provides a location quality index (LQ) for each estimated location. Calibration studies have shown that considerable location errors can occur for all locations, regardless of LQ (Le Boeuf *et al.* 2000, Hull *et al.* 1997). Therefore, all locations for each seal (including auxiliary locations) were

filtered using a three-stage algorithm (Chapter III; Austin *et al.* 2003) to remove

erroneous data. I used these filtered data in subsequent analyses. Mean daily location or

mean bi-daily location (depending on the duty cycle) was determined by taking the mean

latitude and longitude of all locations received within each day.

Upon recovery, TDR data were processed using software supplied by the

manufacturer (Wildlife Computers, Richmond, Washington). Zero-offset correction

(ZOC) software was used to account for shifts in the calibration of the pressure

transducer of the instrument over the data collection period. However, transducer drift

and sea surface conditions introduce noise in depth measurements that cannot be

completely removed by the ZOC program. Hence, I excluded dives < 5 m in depth from

the analysis. Visual inspection of dives that were longer than 30 min indicated that they

generally represented two dives that could not be properly separated by the ZOC

program, and were therefore also excluded from the analysis. These erroneous dives

accounted for < 0.03 % of the total number of dives sampled. Dive analysis software was

then used to analyze the corrected records and provide numerical descriptions of each

individual dive (see Boness *et al.* 1994 for details). For concurrent analyses with stomach

telemetry data, dive records were matched to time periods that coincided with each

animal' concurrent stomach temperature record.

Dive shapes of 95 grey seals were classified by Beck *et al.* (2003a) using a

combination of manual identification and discriminate function analysis (DFA) as

previously described by Schreer and Testa (1996). Discriminate functions were derived

from a subset of 2000 manually classified dives (taken from grey seals deployed between

1995-1999) using the following dive variables: depth, duration, bottom time, bottom

time/depth, rate of descent, rate of ascent and skew (ascent/descent), and the presence or absence of wiggles (vertical movement at depth). Dive profiles were classified as one of five shapes: square, wiggle, V, left-skewed square and right-skewed square (Beck *et al.* 2003a). DFA correctly classified 96.1% of the dives in the subset with a cross-validation error rate of 4.0%. The discriminate functions from Beck *et al.* (2003a) were used to classify the dives in this analysis into the five possible dive shapes.

For each animal, the diving record was examined at two temporal scales. Foraging trips were defined as the period between going from land to sea and returning to land, and represented a larger temporal scale. 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.

Within each foraging trip, I examined clusters of continuous diving, defined as bouts. To determine the temporal organization of diving into bouts, I used a modification of an iterative statistical method presented in Boyd *et al.* (1994) and used by Beck *et al.* (2003b). A bout started when three or more dives occurred within 35 min. This 35-min start window allowed for three dive cycles to be completed based on the mean dive duration and surface interval between dives for grey seals (calculated using data from Beck *et al.* 2003a). 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, $p > 0.05$). If the subsequent surface interval did not meet this criterion, the bout was ended (Beck *et al.* 2003b).

Previous work by Beck *et al.* (2003b) based on a data set with diving records from 87 grey seals suggested that bouts of diving could be classified into four types using cluster analysis (Beck *et al.* 2003b). 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 spent at depth and the percentages of square and V-shape dives/bout). Beck *et al.* (2003b) used a DFA to determine the accuracy of their bout classifications and determined that 97.5% of dive bouts were classified correctly with a cross-validation error rate of 2.5%. Given the success of their clustering analysis, I used the discriminate functions derived from their analysis to classify the dives from the grey seals in this study into four bout types using the same dive and bout characteristics.

Stomach temperature data were downloaded using software provided by the manufacturer Wildlife Computers. The resulting data file was then run through a custom made program (written in Visual Basic within Microsoft Access) designed to identify the timing of individual feeding events, as described in Chapter IV. For each feeding event, the total time associated with that event was calculated. I used total time associated with a feeding event as a proxy for meal size, given the general relationship between meal size and the area under the integral found in other species (as discussed in Chapter IV).

To link the temporal distribution of dives with the locations provided from satellite telemetry, a custom built Visual Basic program assigned a geographic location of each dive based on both the animal's daily location (or mean bi-daily locations 1995-1999), calculated speed of travel and the interpolated distance traveled between satellite-derived locations, depending on satellite duty cycle. For those animals with stomach

telemetry data, feeding events were matched temporally with the corresponding dive and these were linked to an interpolated geographic location. In this way, I linked the three separate behaviours.

<u>Data Analysis</u>

To assess whether significant directionality occurred in the distribution of turning angles between successive moves, mean turning angles were calculated for each seal (ranging from -180° to 180°), and for each trip throughout the stomach temperature pill deployment period using circular statistics (Batschelet 1981). Angular variance, or circular dispersion of turning angles was calculated using the CircStats module (Version 2.0, Lund 2004, http://statweb.calpoly.edu/lund/) in Splus version 6.2 (Copyright 1988, 2003 Insightful Corp.). Additional spatial statistics such as mean distance traveled, total distance traveled and rate of travel were measured using the Animal Movement extension in Arcview. An index of linearity (LI) of each trajectory was calculated as the distance between the first and last point divided by the total distance traveled.

Satellite tracks of grey seals were previously analyzed to determine whether movement patterns could be predicted by a correlated random walk (CRW) model using mean move length, turning angle, and net squared displacement at successive moves (Chapter IV). Animals were described as either fitting the population mean CRW model (correlated random walkers, CRWs), being over-predicted by the model (residents) or being under-predicted by the model (directed movers, DMs) (see Chapter IV). I used these classifications here to provide an overall quantitative measure of movement patterns for individual grey seals with concurrent dive records, such that dive characteristics could be compared between general movement types.

Diving effort was measured using two metrics: cumulative time spent diving/day and accumulated bottom time/day (bottom time calculated as time spent within 85% of the maximum depth obtained during the dive). These two measures of effort were highly correlated to each other, such that they produced similar statistical results when used in statistical testing. Thus I present only the results of accumulated bottom time as grey seals appear to be benthic foragers (Beck *et al.* 2003a). The length of the post-trip haulout period was calculated as the time between consecutive trips.

To compare characteristics of feeding bouts to non-feeding bouts, I used a paired t-test in SPSS version 11.5 (SPSS Inc.). To test for characteristics of both foraging trips and bouts that might be used to predict feeding success, I used a Generalized Linear Mixed Model (GLMM) with Penalized Quasi-Likelihood (PQL) estimation. Two dependent variables were used: total number of feeding events (Poisson model) and total time associated with feeding events (log normal model).

Given that feeding events will be more likely to occur in longer bouts simply because of an increased chance of prey encounter over longer time periods, I also did a second analysis independent of bouts and trips, using intervals of time as the units of measure. To do this, I divided each seals' deployment period into equal blocks of time from start to end of the deployment period and calculated mean depth, bottom time and dive duration, as well as the sum of time spent diving, accumulated bottom time, and the number of each dive shape within each time block. I used a GLMM with number of feeding events as the dependent variable, and examined all possible significant predictors of feeding. To address how predictors of feeding may change with the temporal scale, this analysis was repeated at 3 h, 6 h, 12 h and 24 h time blocks. Given that in this

analysis the structure of the data was such that it was measured at equal time steps, I assumed a continuous auto-regressive correlation structure (CAR1) for the within-subject error terms.

With all GLMMs, all possible models with two-way interactions were examined, and residuals were examined to ensure there was no obvious lack of fit or alternative pattern present. To select the best predictive model, I compared the models with the lowest Akaike's information criteria (AIC). To determine the overall variables that may predict the number of feeding events over the entire deployment period, I used a Generalized Linear Model (GLM). All GLMMs and GLMs were run in Splus version 6.2 (Copyright 1988, 2003 Insightful Corp.). To compare diving behaviour between the three movement types and sex, I used a two- factor MANOVA on four log-transformed parameters (mean depth per bout, mean bout duration, mean accumulated bottom time/d and number of dives per day) in SPSS version 11.5. Where multiple hypothesis testing (i.e., numerous t-tests) was carried out, all p-values were Bonferroni corrected within groups of tests. Means with standard errors are given throughout.

Results

Sixty-four animals were instrumented with satellite transmitters during the 7 yrs of study. Of these, six instruments did not transmit and another six could not be used for this study due to the nature of their duty cycle program. Therefore, I obtained satellite records from 52 seals, 27 of which were not duty cycled, permitting estimates of daily locations to be used for analysis of feeding success. Of these 52 seals, 30 seals also had

concurrent TDR records, and therefore a sample size of n = 30 could be used to compare movement patterns and diving behaviour.

A subset of 32 animals received both TDRs and STTs, however, only 23 of these TDRs returned useable dive data (3 seals did not return, and 6 instruments did not function). Of these 23 animals, only 16 seals had collected valid stomach temperature records. Therefore, to examine the relationship between diving and feeding behaviour, I used a data set of 16 seals (Table 6.1).

The average age of the 16 individuals was 21.4 ± 1.4 years. Mean mass at deployment was 226.7 ± 8.6 kg for males (n=11) and 176.2 ± 8.5 kg for females (n=5). Despite known differences in foraging behaviour between males and females (Chapter IV,V and Beck *et al.* 2003a,b), given this small sample, I was unable to investigate sex differences in this component of the analysis. Similarly, due to small sample sizes, month and year were treated as random variation.

Three out of the remaining 16 animals had concurrent satellite transmitters that failed, leaving a final sample size of 13 individual grey seals for which data on all three behaviours was sampled. Although TDRs and satellites recorded for the entire deployment period from September until January, mean length of time for which the STT remained in the stomach of these individuals was 15.9 ± 2.7 d (Table 6.1). Therefore, for the purpose of examining the distribution of foraging success, both TDR and satellite records were truncated to match the time for which the STT remained in the stomach of each individual animal.

Stomach Telemetry

Table 6.1. Sex (M = male, F = female), age, mass at deployment, deployment length, feeding events/day and total minutes associated with feeding/day for each seal with stomach telemetry, TDR and satellite data (n=16).

Seal id	Sex	Age (yr)	Mass at Deployment (kg)	Pill deployment length (d)	Mean feeding events/day	Total min associated with feeding/day
24	F	27	194.5	29.5	1.3	50.7
3661	M	27	255.0	5.4	2.0	92.4
5108	F	13	195.0	24.5	1.0	44.7
5110	F	13	158.0	13.5	1.2	64.6
5111	M	26	222.0	17.4	0.9	33.0
5112	M	21	194.0	14.4	2.8	273.4
5114	M	21	208.0	30.5	2.7	117.8
5116	M	21	235.0	2.3	0.0	0.0
5684	M	27	226.5	14.8	1.3	40.3
5685	M	15	248.5	0.7	2.9	52.8
5687	M	15	187.0	17.4	1.6	72.4
6116	F	30	178.0	6.3	1.1	59.8
6122	F	14	155.5	32.5	0.3	6.0
6124	M	27	216.0	31.4	2.2	98.7
6125	M	23	215.0	7.2	2.7	144.9
6126	M	23	286.5	7.5	1.1	64.3

A total of 446 feeding events were recorded by the 16 grey seals. The number of feeding events per animal with stomach data over the deployment period was 24.2 ± 5.8, or 1.5 ± 0.2 feeding events per day of deployment. Total amount of time associated with feeding per animal was 1195.8 ± 311.4 min, or 75.4 ± 16.2 min/day (Table 6.1).

TDR Records

A total of 20,568 dives was recorded, an average of 76.0 ± 10.6 dives/day. Mean dive characteristics including depth, duration and bottom time are given in Table 6.2. Over 50% of dives were classified as square shaped, followed by right skewed square dives, wiggle dives, v-shaped dives and finally left skewed square dives (Table 6.3). Mean depth was greatest for square shaped dives, and least for the left skewed square (Table 6.3). Wiggle dives had both the longest duration and the greatest bottom time while V shape dives were the shortest duration, and had almost no bottom time (Table 6.3).
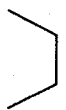
A total of 579 bouts was identified among the 16 animals. Overall, 98.6 ± 0.6 % of dives by individuals were included within dive bouts. Bouts lasted on average 3.4 ± 0.5 h with a mean of 29.6 ± 3.5 dives/bout. The mean number of bouts per day was 3.3 ± 0.6 and the mean post-bout interval was 8.6 ± 1.7 h. Bout type 1 was the predominant type, accounting for 34.0 ± 4.6 % of all bouts across animals. Bouts type 2, 3 and 4 were represented almost equally across all animals (22.3 ± 4.9 %, 21.3 ±3.4 %, 22.1 ± 5.7 %, respectively). General characteristics of each bout type are given in Table 6.4. Type 1 bouts were associated with relatively deep dives, of long duration with the greatest amount of bottom time and mean number of dives. Type 2 bouts were also deep, though somewhat shorter with less bottom time, having the greatest concentration of square

Table 6.2. Mean individual dive characteristics for all study seals with stomach telemetry and TDR data (n=16) with standard errors and the coefficient of variation (CV) during the deployment period.

Dive Characteristics	Mean (n=16)	Standard error	CV (%)
Depth (m)	38.9	5.0	42.7
Duration (min)	6.1	0.5	27.9
Bottom time (min)	3.9	0.4	36.3
Descent (m/s)	0.7	0.05	26.4
Ascent (m/s)	-0.5	0.09	64.8
Time between dives (min)	7.1	2.8	142.5
% bottom time at depth	59.0	3.2	19.4
Accumulated dive time/d (min)	780.6	53.9	88.7
Accumulated bottom time/d (min)	453.9	46.1	86.0
Number of dives/d	185.1	32.5	85.7

Table 6.3. Mean dive shape characteristics ± SE, and the percentage of each shape used by 16 study seals with CV.

Dive Shape	Profile	Depth (m)	Duration (min)	Bottom Time (min)	Descent Rate (m/s)	Ascent Rate (m/s)	Skew Ratio Ascent/Descent	% of dives in study seals	CV (%)
Square		54.9 ±0.2	6.4 ±0.02	4.1 ±0.02	0.81 ±0.003	-0.68 ±0.0030	-0.87 ±0.0037	57.8 ±4.6	31.6
Wiggle		51.8 ±0.4	7.8 ±0.07	5.1 ±0.1	0.70 ±0.008	-0.46 ±0.0098	-0.70 ±0.025	11.0 ±3.5	127.1
V shape		31.5 ±0.9	4.2 ±0.1	0.4 ±0.01	0.35 ±0.012	-0.42 ±0.015	-2.22 ±0.12	7.3 ±1.6	89.4
Left skewed square		25.1 ±0.8	6.2 ±0.07	3.97 ±0.1	0.28 ±0.0054	-0.86 ±0.017	-3.83 ±0.11	7.7 ±2.0	103.2
Right skewed square		38.0 ±0.6	6.1 ±0.05	4.0 ±0.05	1.12 ±0.022	-0.42 ±0.0059	-0.41 ±0.0045	16.2 ±2.5	61.9

Table 6.4. Characteristics of four bout types identified from 16 grey seals. Values are means ± SE.

Bout Characteristic	Type 1	Type 2	Type 3	Type 4
Mean depth (m)	51.2 ± 1.4	57.3 ± 1.4	21.1 ± 1.2	18.0 ± 1.6
Mean dive duration (min)	6.7 ± 0.1	5.6 ± 0.1	5.1 ± 1.2	3.6 ±0.2
Mean bottom time (min)	4.2 ± 0.1	3.0 ± 0.1	3.1 ± 0.2	1.2 ± 0.1
Mean number of dives	63.6 ± 2.8	10.2 ± 0.4	13.4 ± 1.0	6.0 ± 0.4
% square shape dives	68.0 ±1.4	78.7 ± 1.3	36.0 ± 1.9	20.5 ± 2.5
% V shape dives	5.1 ± 0.6	22.5 ± 2.0	25.9 ± 2.6	46.5 ± 3.0
Mean bout duration (h)	7.9 ± 0.4	8.2 ± 0.1	1.3 ± 0.1	0.4 ± 0.0
Mean post-bout interval (h)	4.3 ± 0.8	0.6 ± 0.1	9.4 ± 1.9	9.6 ± 0.1

shape dives, and also a greater number of V shape dives than Type 1 bouts. Type 3 bouts were considerably shallower and shorter than Type 1 and 2 bouts, but with comparable dive duration and bottom time as Type 2 bouts. Finally, Type 4 bouts were the shortest, shallowest, and have the least number of dives, with minimal bottom time (Table 6.4).

In total, 79 trips were identified among the 16 grey seals with an average of 4.9 ± 1.1 trips per seal and lasting an average of 3.2 ± 0.9 d. Seals spent an average of 60.7 ± 6.2 % of their time at sea. Post-trip duration was on average 2.7 ± 0.5 d. Each trip averaged 5.4 ± 0.8 bouts, 364.4 ± 268.2 dives, for an average of 140.0 ± 16.2 dives per d.

Satellite Locations

A total of 808 locations were received from the 13 animals with SRDLs and STTs, an average of 3.8 ± 0.4 locations/seal per d. The filtering algorithm removed 160 erroneous locations (18.9 ± 3.7%), leaving 648 locations, or 3.1 ± 0.3 per seal/d for analysis. Most locations were within approximately100 km of Sable Island, with a large number of locations distributed over the Sable/Western Banks. Of the 13 individuals, nine were CRWs, two were Residents and two were DMs. Sample size was too small for analysis by movement type to be conducted here. Thus I address this question below with the larger sample of animals with only satellite and TDR data. Seal 5685 was excluded from analysis of movement given that only a single location was received. Movement characteristics were highly variable among seals, reflecting considerable individual variation (Table 6.5). The mean turning angles of most seals were centered near 90° or 270 ° (Figure 6.1), indicating frequent reversals in direction. Mean angular dispersion was 0.55 ± 0.073, suggesting that angles were moderately dispersed (completely random = 1, completely concentrated = 0; Table 6.5).

Table 6.5. Mean movement characteristics across individual seals (n=13) with SE and CV.

Movement Characteristic	Mean	±SE	CV (%)
Total distance traveled (km)	191.3	48.5	91.4
Distance traveled/d (km)	12.3	2.7	79.1
Travel rate (km/h)	1.4	0.3	67.7
Linearity Index	0.40	0.069	59.6
Angular variance	0.55	0.073	46.5
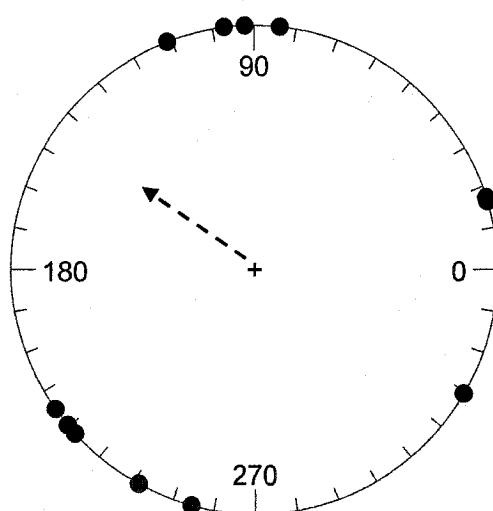
Figure 6.1. Mean turning angles of individual grey seals (n =13). Dashed line is mean angle (154.6°).

Feeding and characteristics of bouts and trips

About 84% or 375 feeding events occurred within bouts of diving. The remaining 71 events were associated with dives either not belonging to a bout (n = 64), or dives that were < 5 m or longer than 30 min and had been deleted in initial data processing (n = 6). Successful foraging occurred in 200 or 27.2% of bouts. Bouts in which feeding occurred had greater mean depth, longer dive duration and mean bottom time, and had significantly longer mean accumulated bottom time and bout duration compared to non-feeding bouts (Table 6.6). There were no differences in the percentage of dive shapes between feeding and non-feeding bouts, with the exception that the percentage of V shaped dives was significantly less in non-feeding bouts (Table 6.6).

Using the number of feeding events within a bout as dependent variable, the best predictor variables were mean depth per bout (value = 0.02, P <0.0001) and mean bottom time per h of bout (b = 0.02, P = 0.0001, DF= 717, observ = 735 and groups = 16). Mean dive duration, percent square shaped dives, percent V shaped dives, bout length and post bout interval were also added to the model, but did not improve model fit. To determine if there were any significant independent variables that may predict the time associated with feeding, I used another GLMM with percentage of time associated with feeding per bout as the dependent variable. Significant predictors were mean depth (b = 0.246, P = 0.003, DF = 724, observ = 743, groups = 16) and %V shape dives (b = -0.23, P = 0.02). The greatest number of feeding events occurred during type 1 bouts (78.1%), followed by type 2 bouts (13.9%), type 3 bouts (6.4%) and type 4 bouts (1.6%). However, considering the difference in average bout duration associated with each bout type (Table 6.4), the

Table 6.6. Comparison of characteristics of dive bouts in which feeding occurred and bouts in which feeding did not occur. Means are given with SE. Results of paired t-test with t statistic and P value given in brackets.

Bout characteristics	Feeding bouts (n=200)	Non-feeding bouts (n=536)	t	(P)
Mean depth (m)	39.3 ± 5.1	31.8 ± 4.0		-1.5 (0.3)
Mean dive duration (min)	6.3 ± 0.3	5.2 ± 0.4		-2.1 (0.04)
Mean bottom time (min)	4.0 ± 0.3	3.0 ± 0.3		-2.3 (0.03)
Accumulated bottom time (min)*	260.2 ± 43.0	73.5 ± 14.7		-4.2 (<0.001)
Number of dives*	58.1 ± 7.9	18.8 ± 2.3		-4.8 (<0.001)
Bout length (h)*	7.4 ± 1.2	2.1 ± 0.3		-4.6 (<0.001)
Accumulated bottom time (min/h)	33.9 ± 1.8	29.5 ± 1.8		-2.2 (0.04)
Number of dives/h*	9.5 ± 0.9	12.5 ± 0.9		5.7 (<0.001)
Post bout interval (h)	9.9 ± 5.0	8.2 ± 1.7		-0.3 (0.7)
% square shaped dives	53.8 ± 6.0	41.7 ± 5.2		-1.5 (0.1)
% wiggle dives	10.2 ± 3.4	10.2 ± 3.3		0.002 (0.9)
% V shaped dives*	4.6 ± 1.1	15.2 ± 2.8		3.6 (0.002)
% Left skewed square	8.8± 3.0	9.2 ± 2.6		0.1 (0.9)
% Right skewed square	20.6 ± 5.9	18.1 ± 2.3		-0.4 (0.7)

*indicates significance at P <0.004 (Bonferroni corrected p value)

percentage of time associated with feeding across bout types is greater in type 2 bouts, followed by type 1, 3 and 4 (Figure 6.2).

Feeding occurred on 46 of 79 trips (58%). Using total time associated with feeding per trip as a dependent variable, the best predictive model was one which included trip duration (GLMM; b = 0.45, P <0.0001) and accumulated bottom time per day (b = 0.003, P = 0.0045, DF = 58, observ = 75, groups = 15). Thus, trip duration was best predictor of feeding during a trip, with longer trips more likely to result in greater time associated with feeding. Post trip duration was not a significant factor in predicting the time associated with feeding during the previous foraging trip.

To examine how the distribution of feeding events within a trip might predict the length of a trip, I calculated: the time from the start of the trip to the first feeding event within each trip (mean = 11.0 ± 3.6 h), the length of time from that first feeding event to the end of the trip (mean = 4.0 ± 1.1 d), and the length from the last feeding event to the end of the trip (mean = 18.3± 3.6 h). Time to the first feeding event did not predict the duration from the first feeding event to the end of trip (GLMM; b = 0.42, P = 0.2, DF = 27, observ = 44, groups = 15). To determine if characteristics of the trip itself provided insight into the post-haulout duration, I tested total time spent associated with feeding, trip duration and accumulated bottom time per day as predictor variables against post-trip haulout duration. Trip duration was the best predictor of post trip haulout (GLMM; b = - 4.5, P < 0.0001, DF = 59, observ = 75, groups = 15), with longer trips resulting in shorter post trip haulouts.

Predictors of feeding over time intervals

At all 4 temporal scales of investigation, the overall most important factor in
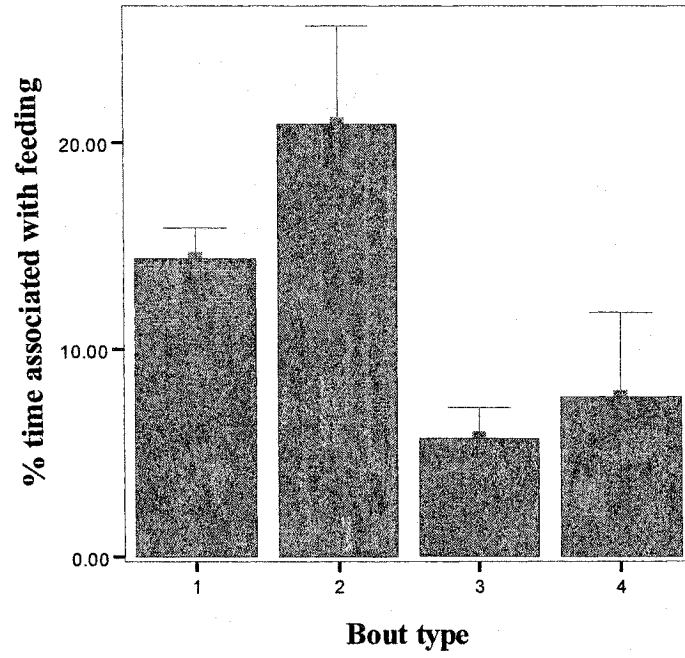
Figure 6.2. Percent of time associated with feeding for each bout type (n=16) with ±SE.

predicting the number of feeding events for the 16 seals and the best fit to the GLMM model was the total time spent diving in each time interval (3 h: b = 0.006, $P < 0.0001$, DF = 1003, obs = 1021; 6 h: b = 0.009, $P < 0.0001$, DF = 550, obs = 568; 12 h: b = 0.003, $P < 0.0001$, DF = 333, obs = 351; 24 h: b = 0.001, $P < 0.0001$, DF = 207, obs = 224). Given that this is a relatively obvious outcome resulting from a greater chance of prey encounter with longer time spent diving, I next removed this predictor from the model, and tested the remaining variables to determine their significance in predicting feeding. There was a significant interaction with total time spent diving and accumulated bottom time, at the 24 hour time interval (b = -0.0001, $P = 0.383$). Accumulated bottom time was significantly correlated to total time spent diving, and this correlation increased with longer time intervals (Pearsons: 3h, 0.86, $P < 0.0001$; 6h, 0.90, $P < 0.0001$; 12h, 0.94, $P < 0.0001$; 24h, 0.96, $P < 0.0001$). For these reasons I did not consider accumulated bottom time together with sum of time spent diving together in the same model. In all four time intervals, accumulated bottom time was the most significant predictor of feeding after total time spent diving. Mean dive depth was also significant at the 3 h and 12 h time intervals (Table 6.7).

Spatial Distribution of Feeding

Most feeding occurred within approximately 100 km of Sable Island, on Sable/Western Banks and Banquereau Bank (Figure 6.3). Individual locations tended to be clustered between the 50 m and 100 m isobaths on the offshore bank areas. Examples of the longest tracks from eight individuals with successful feeding locations are given in Figure 6.4. The track of Seal 5114 was quite tortuous, often reversing direction, with the majority of feeding locations to the southwest of Sable Island, but with a small number of

Table 6.7: Significant predictors of feeding by time interval resulting from best fit to a GLMM model for 16 seals

Time interval (h)	Observations	DF	Predictor variables	B (slope)	*P* value
3	1021	1003	Mean depth	0.009	0.001
			Accumulated bottom time	0.01	<0.0001
6	568	550	Accumulated bottom time	0.008	<0.0001
12	351	333	Mean depth	0.01	0.004
			Accumulated bottom time	0.004	<0.0001
24	224	207	Accumulated bottom time	0.003	<0.0001
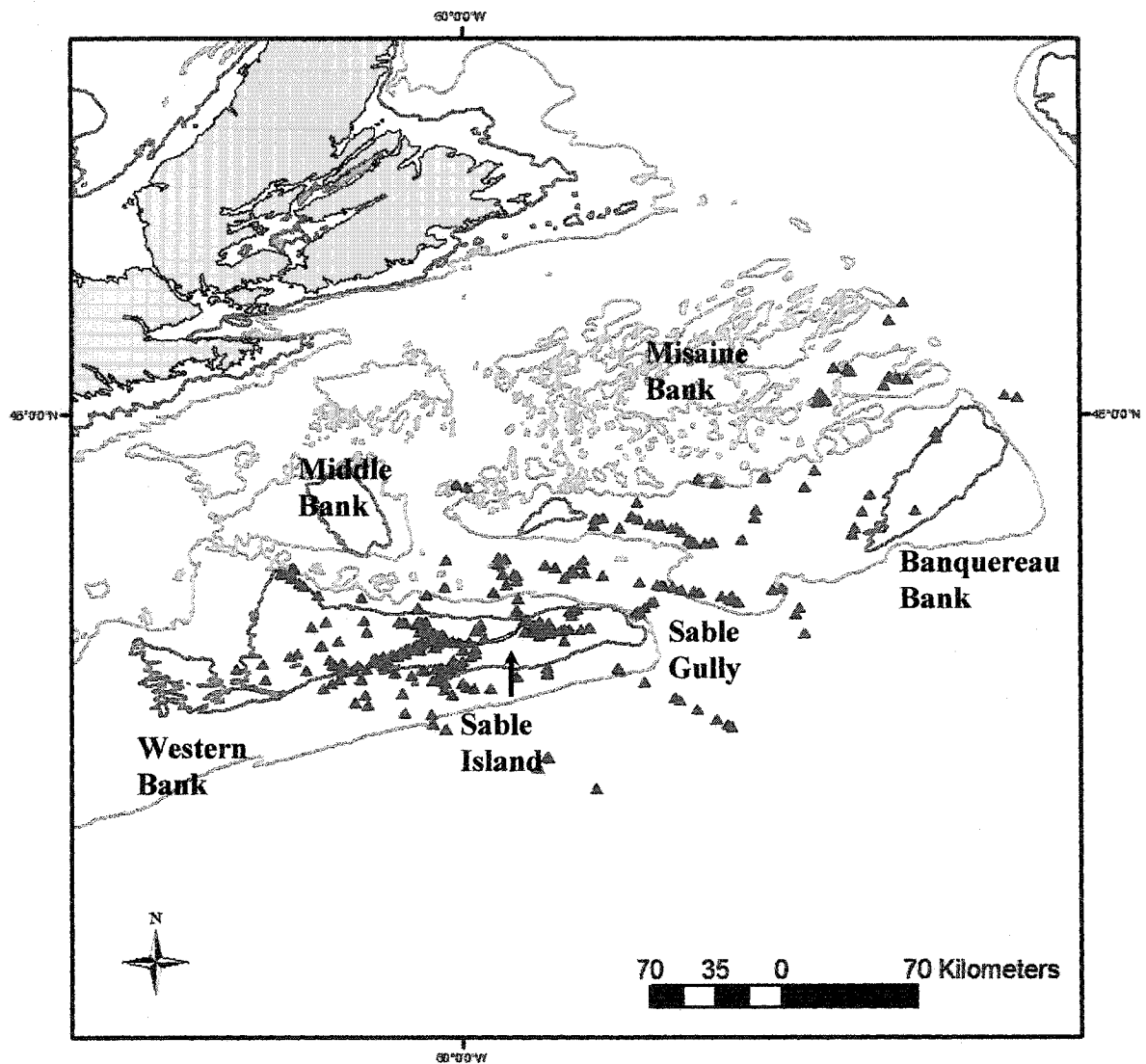
Figure 6.3. Distribution of successful feeding of 13 grey seals. Triangles indicate locations at which foraging occurred. Light coloured lines are the 100 m isobath, darker lines are the 50 m isobath.
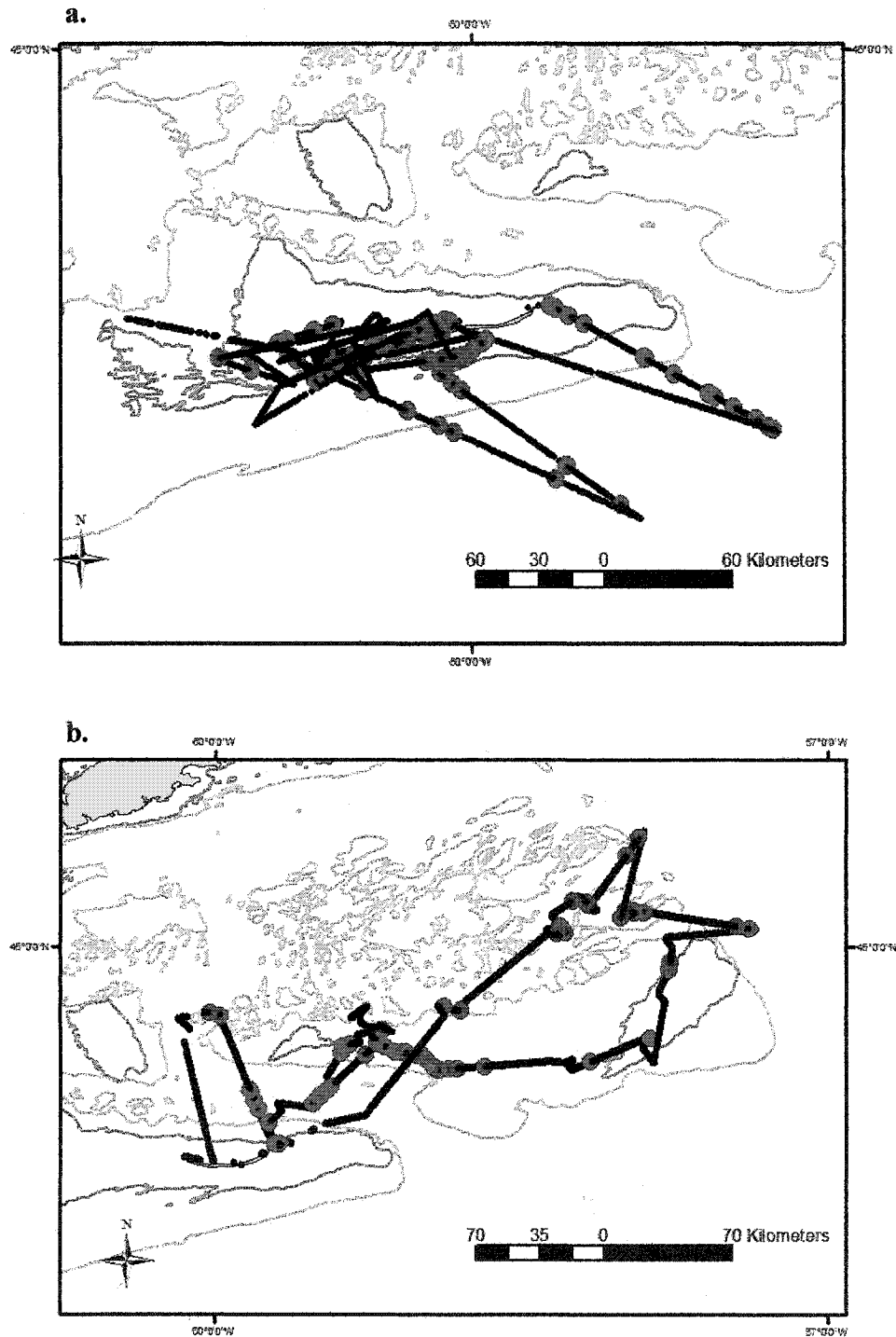
Figure 6.4. Satellite locations of grey seals with locations of foraging success demarcated by circles. Light coloured line is the 100 m isobath, darker line is the 50 m isobath. **a.** Seal 5114, n = 30.5 d **b.** Seal 6124, n = 31.4 d.
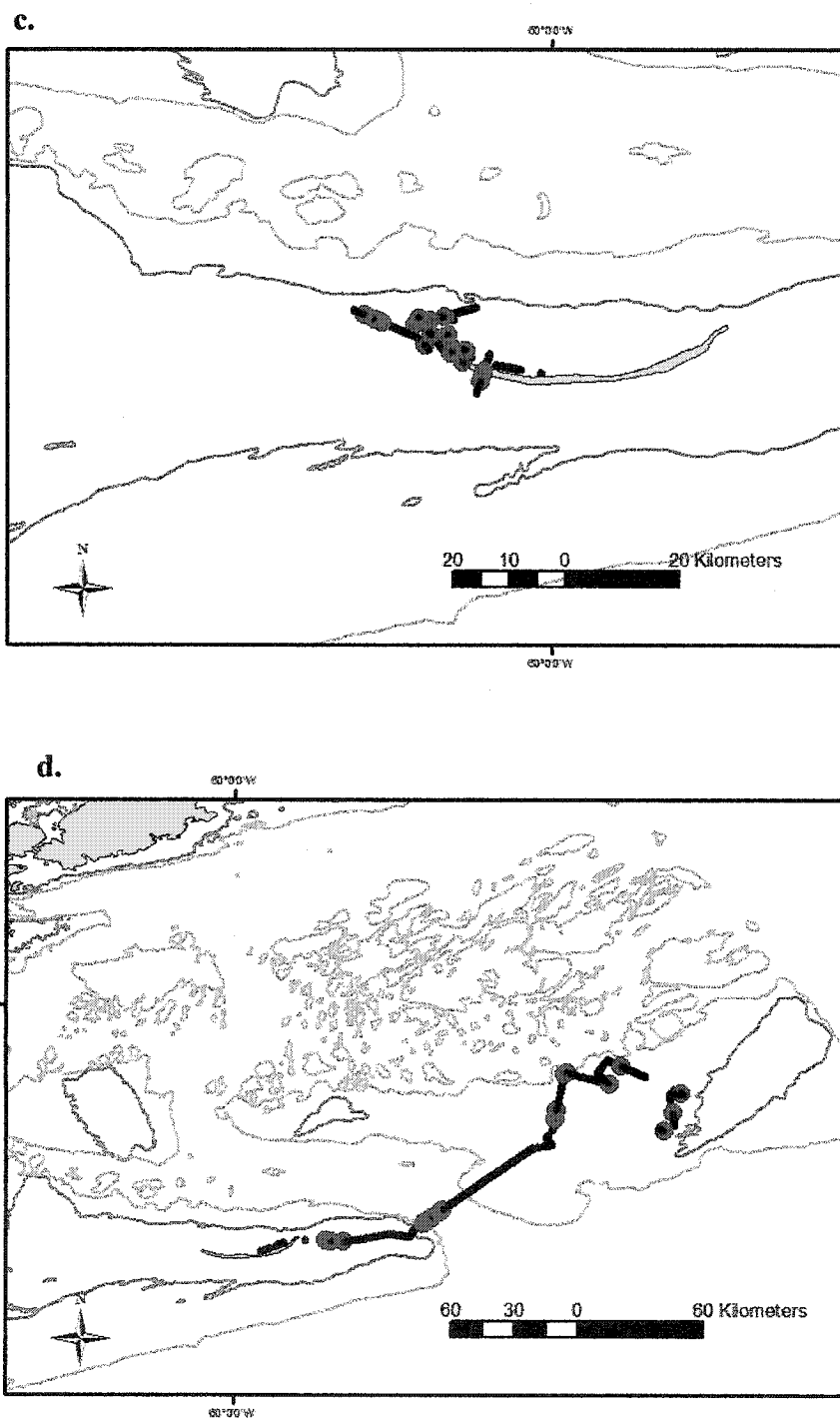
Figure 6.4. (continued) **c.** Seal 5687, n = 17.4 d, **d.** Seal 6125, n = 7.2 d.

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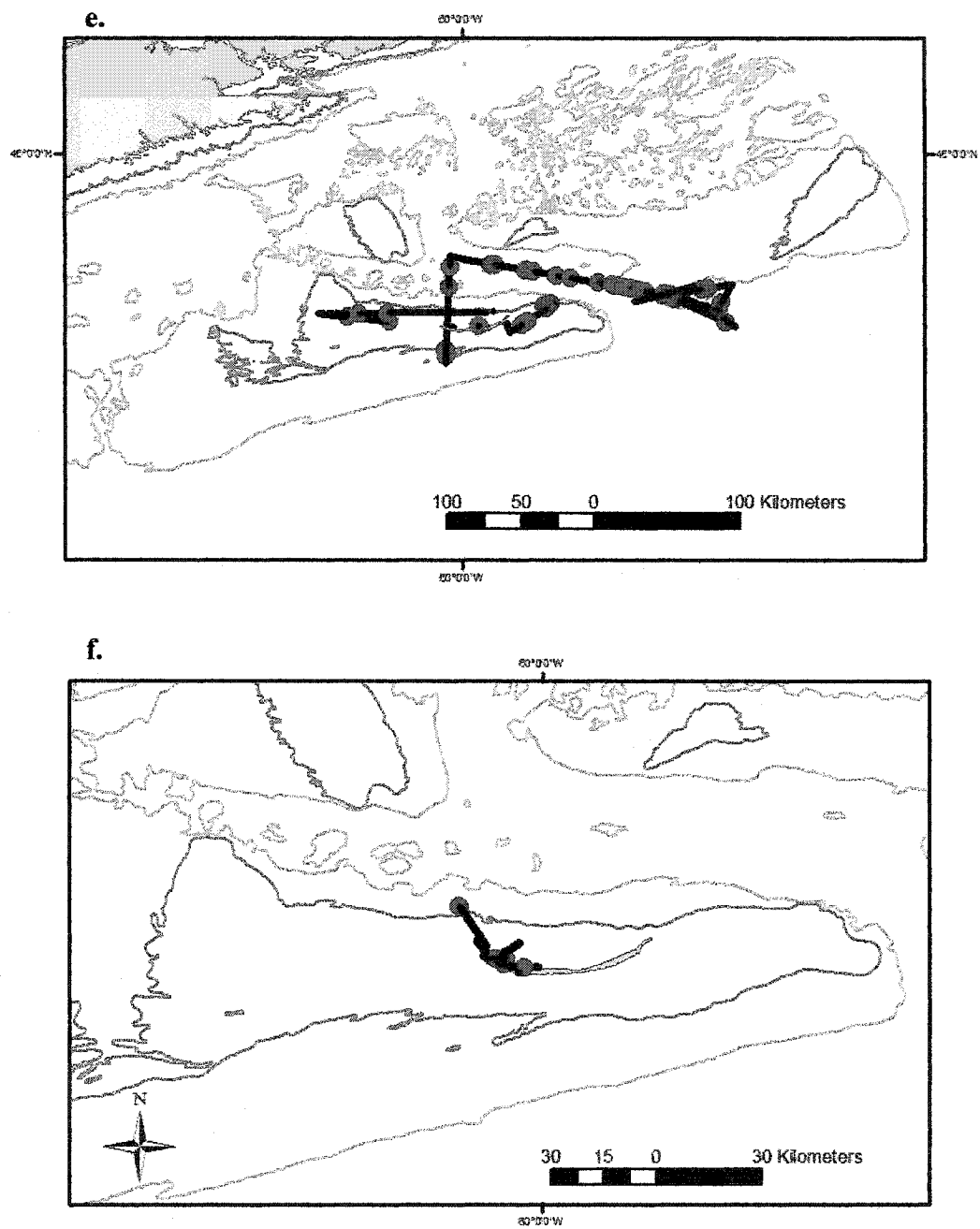
Figure 6.4. e. Seal 24, n = 30 d. **f.** Seal 6122, n = 32.5 d.
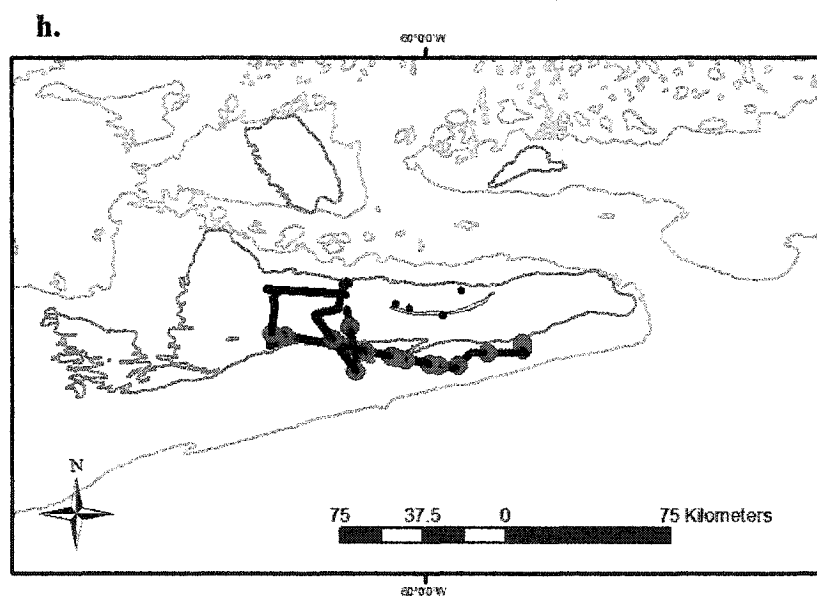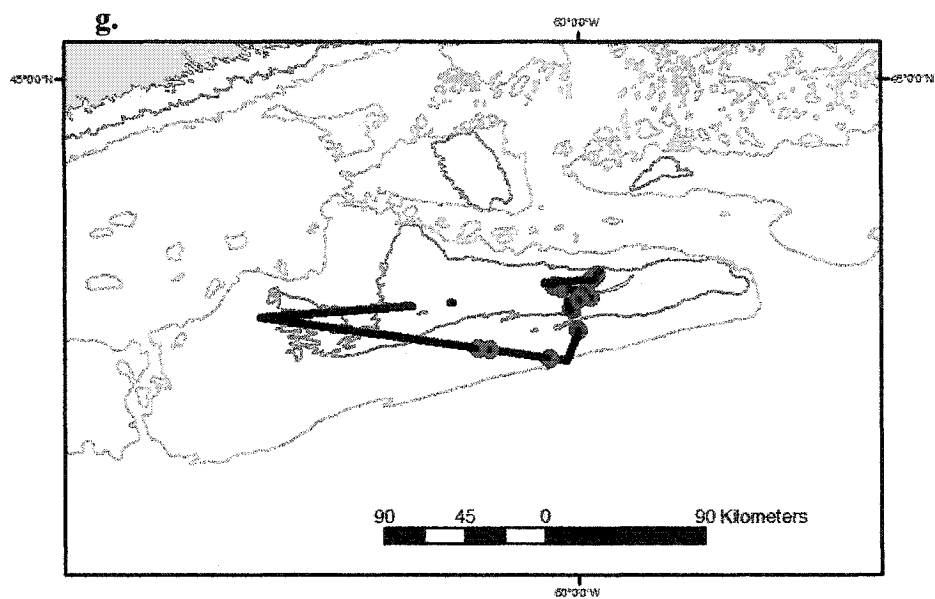
Figure 6.4. g. Seal 5110, n = 13.5 d. **h.** Seal 5684, n = 15.0 d.

locations apparently off the continental shelf (Figure 6.4a). Seal 6124 departed the island

and moved rather directly towards the banks northeast of Sable Island (namely

Banquereau and Misaine Banks), before looping back towards the island again in a

circular track, apparently feeding mostly over bank areas (Figure 6.4b). More spatially

constrained movement was exhibited by Seal 5687 (Figure 6.4c). She remained in a small

area, with an extremely tortuous track and turning angles approaching 180°. Seal 6124

departed the island heading directly northeast in a near straight line, with foraging

clustered over these northeastern bank areas (Figure 6.4d). Seal 24 exhibited feeding in

both the area around Sable, and along the edge of the continental shelf, on the north side

of the Sable Gully. Seal 6122 had one of the longest records of stomach temperature, and

yet traveled only short distances off the western side of Sable Island. Seal 5110 remained

in close proximity to Sable Island for the first portion of the deployment, before heading

directly southeast, where she was also successful. Seal 5684 was unsuccessful during the

first part of the deployment but had considerable success along the 50m isobath for the

remainder of her trip. Most feeding events were clustered both along portions of the track

that are highly tortuous (e.g., Seal 5687 and 6122) and also along relatively straight

sections of track (e.g., Seal 5114 and Seal 24).

Feeding and Movement

Among the 13 seals, angular variance was greater in successful feeding trips (0.52

± 0.04) compared to non-feeding trips (0.17 ± 0.52; $t = 5.01$, $P = 0.04$), indicating greater

tortuosity during feeding trips. The mean travel rate was significantly greater in

successful feeding trips (0.3 ± 0.08 m/s) vs non-feeding trips (0.07 ± 0.02 m/s; $t = -2.7$, P

$= 0.023$). This, combined with the longer duration of feeding trips, resulted in

significantly greater distance traveled/d in feeding trips (24.5 ± 4.8 km) compared to non-feeding trips (11.1 ± 1.3 km; t = -3.4, P = 0.015). Significant predictors of the number of feeding events per trip were angular variance (GLMM; b = 2.2, P = 0.03) and distance traveled per d (b = 0.03, P = 0.009 DF = 15, observ = 30, groups = 12).

To determine the best overall predictors of the total number of feeding events per seal over the entire deployment period, I used a GLM with independent factors: accumulated bottom time/d, mean depth of dives, % square shaped dives, % V shaped dives, % bout type, mean angular variance, distance traveled/d and overall linearity. Accumulated bottom time/d (t_{11}= 2.1, P = 0.034), angular variance (t_{11}= 2.86, P = 0.004) and mean distance traveled per day (t_{11}= 1.2, P = 0.25) provided best model fit, with both angular variance and accumulated bottom time being significant predictors of the total number of feeding events.

Diving and Movement

Satellite locations and simultaneous diving records were available for 30 seals, 16 males and 14 females, with a mean age of 19 ±1.2 years. Average deployment length was 134.2 ± 10.6 d. Amongst these 30 animals, 17 individuals were CRWs, 6 were residents and another 7 were DMs (Chapter IV). There was a total of 11,851 bouts across all seals, a mean of 10,353 ± 887 dives per seal. Diving behaviour differed significantly among movement types (MANOVA Pillai's Trace, $F_{2,29}$ = 2.6, P = 0.02), but not between sexes (Pillai's Trace, F = 0.29, P = 0.12). Based on Tukey's *post hoc* tests, residents had the longest bout duration (F = 4.7, P = 0.02, R^2 = 0.27; Table 6.8). As a result, accumulated bottom time was also higher in the residents (F = 5.8, P = 0.008, R^2 = 0.30) than either the CRWs or DMs, but, mean accumulated bottom time per day did not

Table 6.8. Mean bout characteristics ± SE demonstrated by three movement types. Significance determined from Tukey's *post hoc* tests.

Mean bout characteristics	CRWs (n =17)	Residents (n =6)	Directed movers (n =7)
Number of dives	39.8 ± 7.9[a]	79.7 ± 28.3[b,c]	19.8 ± 0.9[a]
Number of bouts/d	3.6 ± 0.7	1.5 ± 0.6	4.3 ± 1.3
Bout duration (min)	237.8 ± 45.6	493.7 ± 185.2[c]	133.1 ± 8.4[a]
Depth (m)	53.4 ± 2.8[a]	38.1 ± 3.4[b,c]	55.8 ± 6.4[a]
Bottom time per dive (min)	2.8 ± 0.1	3.1 ± 0.3	3.1 ± 0.2
Accumulated bottom time (min)	122.8 ± 22.9[a]	291.8 ± 115.4[b,c]	64.8 ± 5.9[a]
Bottom time/d (min)	309.2 ± 48.5	258.4 ± 59.6	244.25 ± 57.2
Dive duration (min)	5.1 ± 0.1	5.1 ± 0.4	5.3 ± 0.2

[a] significantly different from Residents at p ≤ 0.05

[b] significantly different from Directed Movers at p ≤ 0.05

[c] significantly different from CRWs at p ≤ 0.05

differ between the three movement types (F = 0.02, P = 0.98, R^2 = 0.001). Dive depth was significantly less for residents (F = 4.2, P = 0.03, R^2 = 0.24). Mean dive duration and mean bottom time per dive did not show much difference between the three movement types (Table 6.8). Percentage of dive shapes used by individuals does not appear to differ between movement types, in all three groups, the most common dive shape was square (Figure 6.5). However, there was considerable variation in the bout types used between the DMs and the other two movement types (Figure 6.6). DMs use exclusively Type 2 bout types, whereas the other two groups of seals use all four bout types, primarily type2, followed by type 4, type 1 and type 3.

Discussion

This is the first study to have simultaneously recorded movement (i.e., displacement or ranging), diving and feeding in a free-ranging marine mammal. There were a number of limitations to this study, mainly due to the difficulty in keeping the STT in the stomachs of the study animals. Nevertheless, the length of time that the STT was maintained in the stomach was significantly greater than in previous attempts (e.g., Bjørge *et al.* 1995, Lesage *et al.* 1999), and long enough to conduct a quantitative analysis of feeding and foraging behaviour. Instrument failures, particularly TDRs, further reduced sample size. Still, this study tested a number of hypotheses about the aspects of diving behaviour and movement patterns that may be related to feeding. I was able to identify locations where feeding occurred and to describe the behaviour that was associated with success. Findings indicate that the probability of feeding can be predicted by examining changes in diving behaviour and movement. Furthermore, this study has
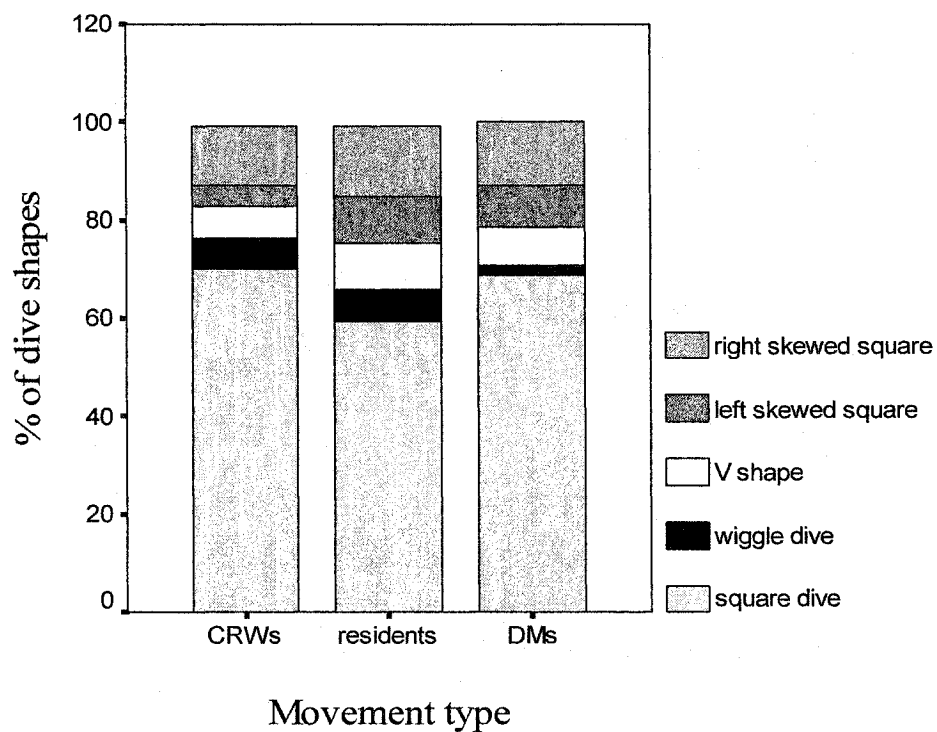
Figure 6.5. Percent of dive shapes demonstrated by seals belonging to the three different movement categories (n = 30).
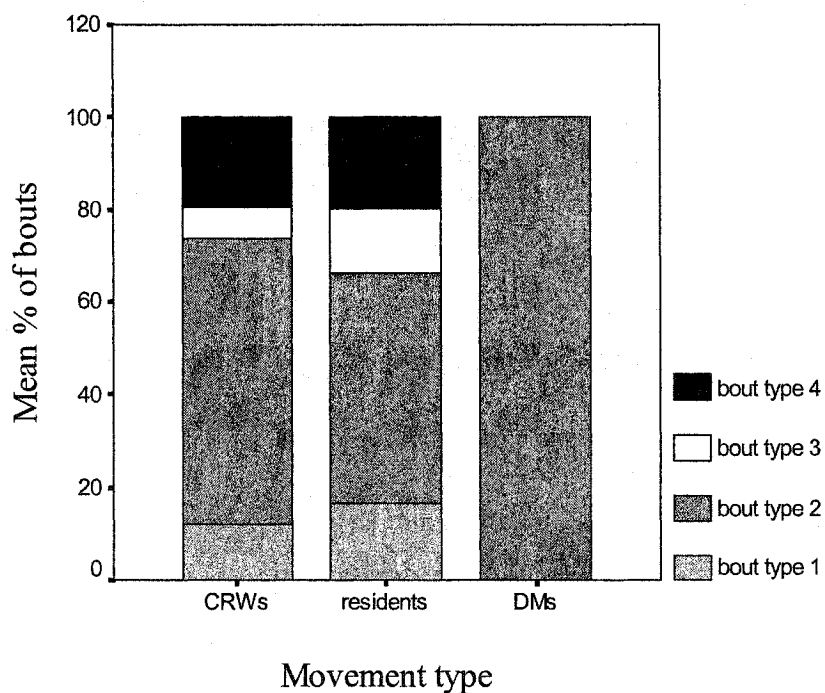
Figure 6.6. Mean percent of dive bout types demonstrated by grey seals in the three movement categories (n =30).

provided additional supporting evidence for the functional classification of dive shapes and bouts. Finally, my results demonstrate that diving and movement behaviours interact in complex ways in this species, indicating the value of simultaneously recording multiple types of information to better understanding foraging behaviour.

<u>Diving variables as predictors of feeding</u>

Using bouts as the unit of study, a number of dive characteristics appear to be important predictors of both the number of feeding events, and the duration of time spent feeding. Deeper dives with greater accumulated bottom time were significant predictors of the number of feeding events, whereas the total time associated with feeding was best predicted by increased bout duration, longer mean bottom time per dive, and fewer V-shaped dives. In this study, feeding bouts were 3 times longer than non-feeding bouts. There are two potential reasons for this. If feeding occurred randomly in time, longer bouts would always have a higher probability of feeding. Alternatively, perhaps bouts are longer because feeding occurred; therefore animals are modifying their behaviour to remain in the bout longer, providing evidence that increased foraging success may increase bout length. It has been suggested that the duration of a dive bout may be an indication of the time a seal spends in a prey patch. Consequently, bout duration should also be related to patch quality (Mori 1998, Harcourt *et al.* 2002). If so, we would expect bout duration to increase if foraging was successful. Notably, feeding bouts have significantly less dives/h; suggesting that although bouts are longer when feeding occurs, animals are in fact diving less often, spending longer at the bottom of the dive.

Accumulated bottom time per day has previously been used as a measure of dive effort in benthic feeding pinnipeds (Beck *et al.* 2003a, Lidgard *et al.* 2003). In this study,

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the longer seals spent at the bottom of the dive (and hence the fewer V shaped dives), the more likely they were to feed, suggesting that this index may contain more information than previously thought. Food intake in harbour seals (*Phoca vitulina*) has also been shown to be positively correlated with the proportion of dives with bottom time (essentially non-V shape dives) (Lesage *et al.* 1999, Beachler *et al.* 2002). Increased dive depth has also been shown to be an important factor in predicting feeding in this study. Grey seals are relatively shallow divers given their body size (Beck *et al.* 2003b), but results herein demonstrate that most feeding occurs as diving depths increase. This may be in part due to the fact that V-shaped dives, considered to be representative of travelling, are typically shallower, and as predicted, little or no feeding is taking place during these dives.

At a longer temporal scale (days), trip duration and accumulated bottom time per day were the best predictors of feeding, but trip duration was the most important predictor. Since time at sea and total number of dives are positively related, the more time spent at sea increased the chances of encountering prey and feeding. Predators require time to find prey patches, and the time spent searching for patches can be predicted to be a function of their availability (Stephens and Krebs 1986). In addition, it is conceivable that grey seals may extend foraging trip duration if they have found profitable prey patches, and hence are successful at foraging. Surprisingly, post trip duration actually decreased with longer trip duration, suggesting that fatigue is not an important factor affecting trip duration.

Movement and foraging success

Both an increase in angular variance and in distance traveled per day were significant predictors of successful foraging. Variable directional changes are often associated with foraging behaviour (termed area-restricted searching); as an animal's path increases in tortuosity, it is better able to optimally sample a prey patch (Turchin 1998). However, Zollner and Lima (1999) proposed that an animal using straighter tracks (without actually being perfectly straight), can potentially search a larger area. Thus for longer travel, such as that between patches, observations suggest that straight movements are most common for a number of species including moose (*Alces alces*, Pastor *et al.* 1997), narwhals (*Monodon monoceros*, Laidre *et al.* 2004) and red foxes (*Vulpes vulpes,* Phillips *et al.* 2004) because they enable a greater distance to be covered and searched. Hence, it appears that during successful foraging trips, grey seals may exhibit a combination of directed travel during which time they are able to search large areas, interspersed with periods of high angular variance upon finding a valuable patch. Zollner and Lima (1999) suggest that when food patches are clumped, the optimal angular variance does not matter, provided the trajectory is neither perfectly straight nor random. Assuming a non-random distribution of prey on the Scotian Shelf, perhaps this is the search tactic used by grey seals in this study.

Functional classification of dives and bouts

Dive shape analysis has become a popular approach for inferring behaviour associated with individual dives. In the past decade, researchers have used dive shape analysis in pinnipeds, (Northern Elephant Seals, *Mirounga angustirostris*, Le Boeuf *et al.* 1988, 1992, 2000, Asaga *et al.* 1994; southern elephant seals *Mirounga leonina*, Hindell *et al.* 1991; crabeater seals, *Lobodon carcinophagus*, Bengston and Stewart 1992;

Weddell seals *Leptonychotes weddelli*, Schreer and Testa 1996, Davis *et al.* 2003;

harbour seals, *Phoca vitulina,* Lesage *et al.* 1999, Beachler *et al.* 2002; grey seals Beck *et al.* 2003a, Lidgard *et al.* 2003), belugas (*Dephinapterus leucas*, Martin *et al.* 1998), gentoo penguins (*Pygoscelis papua,* Wilson *et al.* 1996) and green turtles (*Chelonia mydas*, Hochsfield *et al.* 1999). Overall consensus across species and studies suggests that two dive shapes in particular, square and V-shaped dives, likely represent foraging and traveling, respectively (Schreer *et al.* 2001). The remaining shapes are viewed as variations of these forms that differ in skewness (the ratio of rates of ascent and descent), the presence of wiggles or the mean depth or duration of the dive (Schreer *et al.* 2001, Beachler *et al.* 2002).

Square shaped dives have been consistently attributed to feeding, particularly in animals that are known to feed on benthic prey (e.g., Le Boeuf *et al.* 1992, Beachler *et al.* 2002, Beck *et al.* 2003a). I did not attempt to link feeding events to single dives given that there were almost certainly some discrepancy between the times of the two instruments (data-logger and TDR) due to perhaps minutes of drift in the independent clocks (R. Hill, Wildlife Computers, pers. comm.). Therefore, I was not able to confirm if feeding occurred only in square shaped dives. However, at the level of bouts, given that most feeding occurred in bouts with a high proportion of accumulated bottom-time, it seems reasonable to conclude that feeding was largely associated with such dives in grey seals as in other species.

Grey seals were not successful in every bout, in fact only about a quarter of all bouts had evidence of feeding. According to Boyd *et al.* (1994), differing bout types in the Antarctic fur seal (*Arctocephalus gazella*) are assumed to represent different

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behaviours. However, the functional interpretation of bout types in phocid seals is more challenging since telemetry data reveals that most phocids do not travel at the surface of the water (Thompson *et al.* 1991, Le Boeuf *et al.* 2000). Nevertheless, Beck *et al.* (2003b) speculated that most foraging in grey seals was associated mainly with their bout types 1, 2 and 3. My results indicate that this was a reasonable assumption as most feeding events were recorded in these bout types, although the greatest proportion was in bout type 2.

Distribution of foraging success

Feeding locations were somewhat clustered in the area surrounding Sable Island within the 50 m to 100 m depths. Past studies of diving behaviour in grey seals indicate that most dives were within this depth range (96% of dives < 120 m; Beck *et al.* 2003a). These areas of continental shelf tend to be areas of high productivity (Zwanenburg *et al.* 2002). Two feeding locations of seal 5114 were apparently off the continental shelf, in an area in which grey seals are seldom associated. It is likely that these locations are erroneous locations that passed through the filtering algorithm. However, given that there is more than one location in this vicinity, and given that they both belong to the same animal and are only separated by 4 days, I cannot exclude the possibility that grey seals occasionally feed over deep water.

Estimates of diet based on fecal analysis (Bowen and Harrison 1994) and quantitative fatty acid signature analysis (QFASA, Beck *et al.* submitted) suggest that important grey seal prey in the area around Sable Island include capelin (*Mallotus villosus*), sandlance (*Ammodytes dubius*), redfish (*Sebastes* sp.) and several species of gadoids and flounders. Evidence from the Department of Fisheries and Oceans summer

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trawl surveys indicate that capelin occurred mainly on the Banquereau-Misaine Banks

from 1999-2001, an area that was used by a number of animals in this study. Redfish are

frequently caught along the continental shelf edge and over the Sable Gully. Sandlance

are more difficult to sample via trawl surveys, but are distributed mainly over the sandy

substrate in the banks immediately surrounding Sable Island and Western Bank.

Diving and Movement Patterns

Preliminary analysis of bout types in grey seals by Beck *et al.* (2003b) suggested

that bout type 4 may be associated with travel in grey seals. However, in this study I

found that the DMs, which travel significantly more than all movement types, in fact do

not use bout type 4. Instead they use exclusively type 2 bouts, consisting of a distinct

combination of only square and V-shaped dives. These bouts are relatively short in

length, with very short bout intervals, indicating perhaps, that these animals are almost

constantly within a dive bout and spend very little time hauled out. Potentially it reflects a

combined foraging/traveling tactic in which these animals are continuously traveling,

searching and foraging en route. Similarly, Jaquet and Whitehead (1999) suggested that

foraging and migratory behaviour are not distinct in sperm whales (*Physeter*

macrocephalus), instead animals forage as they travel.

Residents illustrate one of the most striking differences in bout characteristics

among seals exhibiting different movement types. These seals had a mean bout duration

that was twice as long as CRWs and three times as long as DMs. Accumulated bottom

time per bout followed the same pattern, with more than twice that of the CRWs and

almost 4 times that of the DMs, though mean accumulated bottom time/d did not differ.

At the same time, residents dove to significantly shallower depths than the other two

groups, which may be simply be a reflection of the relatively shallow waters surrounding Sable Island. Given that there is no significant difference in the mass gained over the deployment period between all three movement types (Chapter IV), why then are these animals spending so much more time in bouts? There are a number of possible explanations. Dietary composition of grey seals on Sable Island as determined using fecal analysis by Bowen and Harrison (1994) indicates that perhaps the most important prey item in the area around Sable Island is sandlance. Sandlance can be both a cryptic prey, when in the bottom substrate, and a conspicuous schooling prey (Bowen *et al.* 2002). Evidence from animal borne video recordings of foraging harbour seals reveals that although pursuit and handling time for sandlance is low, search time for cryptic sandlance is much higher than other prey. Thus, one might surmise that longer bouts may be associated with searching for prey. In addition, sandlance distribution tends to be quite heterogeneous (Groundfish Survey Database, Department of Fisheries and Oceans, Canada) and therefore when a seal finds a patch it may be most cost-efficient to spent time there as long as they are being successful. Another potential explanation is that the area around Sable Island is one that is heavily used by grey seals, in fact, the Island is the largest breeding colony of grey seals in the world and many seals use the Island throughout the remainder of the year as a haul out site. Although there is still no overall evidence for food being limited in grey seals (Bowen *et al.* 2003), prey depletion in the vicinity of Sable Island may reduce foraging efficiency. For example, longer foraging trip duration has been related to increasing colony size in seabirds (Lewis *et al.* 2001). Thus, perhaps it is a question of tradeoffs. By remaining close to Sable, these animals have the benefit of a nearby haulout site for rest and predator avoidance, and since these animals

are not expending large amounts of energy to travel to distant foraging areas, they can afford to expend more energy foraging to sufficiently meet energetic demands.

The results presented in this study indicate that individual variation in movement patterns (as previously observed in Chapter IV) may also be important for structuring diving behaviour. Sex differences are also known to be implicated in grey seal diving behaviour (Beck *et al.* 2003a,b), and movement (Chapter IV). However, in this particular data set, I found that sex was not a significant factor. Of course, sample size in this study is considerably less than in Beck *et al.* 2003a,b, and hence may suffer from reduced power. Instead, type of movement was more important in predicting diving behaviour. These findings suggest that perhaps grey seals diving patterns may in part result from their ranging behaviour. Beck *et al.* (2003a) found that females have greater accumulated bottom time and dive to shallower depths than males throughout the year. Residents also have greater accumulated bottom time and dive to shallower depths (this study). In Chapter IV, using a larger dataset (n = 52) I determined that females are more likely to be residents.

Another potential explanation for why diving patterns vary with movement behaviour may be that seals are using different habitats. Studies with seabirds (e.g, Grémillet *et al.* 1999), seals (Le Boeuf *et al.* 2000) and whales (e.g., Martin and Smith 1999, Laidre *et al.* 2004) have all demonstrated that diving in these animals covaries with habitat. For example, long and deep dives in narwhals have been linked with bathymetry and distance from shore. Further study of habitat selection in grey seals, including such oceanographic features as bottom temperature, substrate type, and bathymetry will allow

a greater understanding of whether habitat features may be linked to diving behaviour in this species.

Still, features of the habitat only serve as proxies for prey availability, and behavioural variation may ultimately be linked to characteristics of prey (e.g., Benoit-Bird and Au 2003). Using quantitative fatty acid signature analysis (QFASA) as an indicator of diet, (Beck *et al.* submitted) suggested that there is considerable individual variation in prey eaten by grey seals. Searching behaviour and movement at the bottom of a dive both vary depending on the prey species (e.g., Bowen *et al.* 2002, Estes *et al.* 2003). Individual variation in prey selection can vary along a continuum, ranging from extreme individual specialization (e.g., Estes *et al.* 2003) or simply change in prey selection in response to environmental (Dellinger and Trillmich 1999), seasonal (e.g., Hall *et al.* 1998, Lake *et al.* 2003) or intrinsic factors (e.g., Beauplet *et al.* 2004). Therefore, it will be interesting to determine if individual variation in movement and diving behaviour in grey seals can be causally linked to dietary selection, and if so, to determine if these responses are related to extrinsic factors (e.g., season, oceanographic changes) or intrinsic factors (e.g., ontogeny, reproductive status, time away from the breeding/moulting seasons).

Conclusions

Although difficult, the simultaneous recording of multiple sources of information holds great promise. Despite a small sample size, this study has both tested and generated new hypotheses about the characteristics of diving behaviour and movement patterns that may be related to successful feeding. Thus, there is potential extend my findings (e.g., predictors such as angular variance, accumulated bottom time) to a much larger sample of

grey seals from which both movement and diving behaviour have been obtained in the past, and thereby extract additional information about foraging. Future studies with improved instruments will enable us to extend our analysis to habitat selection models and spatially explicit predator-prey models which will benefit from the ability to predict locations and behaviour associated with feeding success.

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