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SANTA CRUZ

**MEASURING AT SEA FEEDING TO UNDERSTAND THE FORAGING
BEHAVIOR OF PINNIPEDS**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Carey Elizabeth Kuhn

June 2006

The Dissertation of Carey Elizabeth Kuhn
is approved:

Professor Daniel P. Costa, Chair

Professor Daniel E. Crocker

Professor James A. Estes

Professor Terrie M. Williams

Lisa C. Sloan
Vice Provost and Dean of Graduate Studies

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MEASURING AT SEA FEEDING TO UNDERSTAND THE FORAGING BEHAVIOR OF PINNIPEDS

Carey Elizabeth Kuhn

Abstract

Pinniped have evolved a range of reproductive and foraging patterns to deal with the constraint of terrestrial parturition and marine feeding. To understand the link between these constraints it is necessary to understand both reproductive periods on land and foraging at sea. I examined the foraging behavior of a phocid (northern elephant seal, *Mirounga angustirostris*) and otariid (California sea lion, *Zalophus californianus*) species to provide insight into the divergent life histories of these families. To understand foraging behavior it is necessary to know when and where animals find prey. Using stomach temperature telemetry, I conducted rigorous feeding experiments with both species to determine whether measures of stomach temperature can be used to identify and quantify prey consumption. Feedings were identified with high accuracy and the equations to estimate mass consumed were not significantly different between species.

Until recently, studies on the foraging behavior of marine predators have relied on indirect measures of feeding, such as changes in diving behavior or movement patterns. When combined with measures of at sea behavior, stomach temperature telemetry can provide information about when and where animals

successfully capture prey. I deployed stomach temperature telemeters along with time-depth recorders and satellite transmitters to examine the foraging behavior of northern elephant seals. This resulted in the first measures of feeding behavior and foraging success in elephant seals, as well as provided a validation of indirect indices of foraging behavior.

Finally, I examined the foraging behavior of free-ranging California sea lions and documented how their behavior changed annually in response to environmental variation that occurred over three years. Although stomach temperature telemeters were deployed on sea lions, I was only able to maintain the telemeters in the animals for long enough to measure at sea feeding in one female. Therefore, foraging behavior was examined based on indirect measures of feeding, such as diving behavior and at sea distribution. I found females alter movement patterns in response to even modest environmental variation. Such detailed information on the foraging behavior of these species will make it possible to examine the link between reproductive pattern and at sea foraging behavior.

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Introduction

Life-history patterns are often the response to trade-offs that result from conflicting requirements between the acquisition and allocation of maternal resources. Pinnipeds are an ideal group to examine this conflict because of the separation of two fundamental components of life, terrestrial parturition and marine feeding. During the evolution of pinnipedia, the outcome of this conflict resulted in a wide range of reproductive patterns incorporating varying time spent on land suckling a pup and at sea foraging (Bonner, 1984; Boyd, 1998, 2000; Costa, 1993; Kovacs & Lavigne, 1986; Oftedal, Boness & Tedman, 1987). In order to examine the relationship between reproductive strategy and foraging behavior it is crucial to understand both time on land and time at sea.

The reproductive strategies of pinnipeds fall along a continuum between income and capital breeding (Boyd, 2000; Costa, 1993; Drent & Daan, 1980; Gentry & Kooyman, 1986; Trillmich, 1996; Trillmich & Weissing, 2006). Income breeding, considered the energetically expensive breeding strategy, is displayed by otariid seals (sea lions and fur seals). For example, to meet the high cost of lactation, northern fur seal females (*Callorhinus ursinus*) increase food consumption by 80% over non-lactating females (Perez & Mooney, 1986). This strategy is described by an extended lactation period (4 months to 3 years) where females alternate time on land suckling a pup with time at sea foraging (Costa, 1991; Gentry *et al.*, 1986). Resources required for reproduction are obtained during short foraging trips (1 to 7

days), making females highly dependant on local resources (Costa, 1993; Gentry *et al.*, 1986). As otariid at sea metabolic rates are 4.8-7.3 times basal (Costa, Thorson & Kretzmann, 1989; Costa, Antonelis & Delong, 1991; Costa, Croxall & Duck, 1989; Costa & Gales, 2003; Costa & Gentry, 1986a; Trillmich & Kooyman, 2001), females expend high amounts of energy during foraging and must acquire energy at a high rate while at sea.

In contrast, capital breeding is considered the slow and conservative reproductive strategy and is employed by phocid (true) seals (Boyd, 2000; Costa, 1991; Trillmich, 1996). Resources for reproduction are obtained prior to parturition and females fast during a short lactation (4 days up to 7 weeks), supporting themselves and a pup with only stored resources. With this reproductive strategy females have an extended period after lactation to replenish resources and prepare for the following seasons reproduction. To accomplish this, pregnant northern elephant seals (*Mirounga angustirostris*) only have to increase daily food intake by 12% during the foraging trip versus non-pregnant females (Costa *et al.*, 1986b). Northern elephant seals, and phocids in general, expend energy at a lower rate than otariid females and acquire energy at a lower rate (Costa, 1993; Le Boeuf *et al.*, 1988), making this a more economical reproductive strategy.

California sea lions (*Zalophus californianus*) and northern elephant seals offer an ideal study system to investigate the trade-off between foraging and reproduction in an income breeding otariid and a capital breeding phocid (Melin,

2002; Oftedal *et al.*, 1987; Ono, 1991; Sydeman & Nur, 1994). California seal lions as income breeders, alternate short foraging trips with periods on land suckling (Feldkamp, Delong & Antonelis, 1989; Melin, 2002; Melin *et al.*, 2000; Ono, 1991). Females have high at sea metabolic rates (Costa *et al.*, 1991), requiring high rates of energy acquisition. Northern elephant seals as capital breeders, prepare for lactation by feeding over two extended foraging trips (Le Boeuf *et al.*, 2000; Stewart & Delong, 1995). Females fast during a short lactation period (28 days) and abruptly wean the pup before starting the post breeding foraging migration.

Although information is available on the reproductive strategies of these species, to accurately examine the link between reproduction and foraging it is necessary to also understand foraging behavior. However, studying the foraging behavior of marine predators is challenging, as most feeding occurs underwater and often outside the scope of observational studies. With the development of time-depth recorders and satellite telemetry numerous studies have been conducted on the diving and movement patterns of free-ranging marine mammals (Boyd & Croxall, 1996; Costa, 1993; Kooyman, 1965, 1989; Shaffer & Costa, 2006). By examining changes in diving and at sea movements, these studies have attempted to understand foraging behavior. However, the use of these tools requires researchers to make assumptions about when and where animals are successfully finding prey. To truly understand foraging behavior it is necessary to identify the frequency and location of prey consumption.

The goal of this dissertation research was to examine the foraging behavior of these two species (northern elephant seals and California sea lions) with the objective of identifying potential differences in foraging efficiency that may arise from the very different foraging patterns of income versus capital breeding. In order to measure feeding behavior I utilized stomach temperature telemetry to quantify foraging rates and success. The first step was to rigorously validate the use of stomach temperature telemetry, a tool to measure feeding behavior. Since marine mammals feed on ectothermic prey, the prey is colder than the predators' core body temperature. This results in a drop in stomach temperature with consumption. Chapter one examines the use of characteristic changes in stomach temperature to identify feeding events and quantify prey consumption. In addition, this chapter examines how these measures differ between species.

The second objective was to use measures of at sea feeding events to characterize the foraging behavior of adult female northern elephant seals. For this species, a large amount of information exists on their at sea behavior through the use of satellite telemetry and time-depth recorders (Crocker *et al.*, 2006; Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000; Le Boeuf *et al.*, 1992). These studies have relied primarily on indirect measures to identify foraging, using changes in dive shape and decreases in transit rate, to identify feeding periods. However, the direct link between feeding and dive shape and changes in transit rate has not yet been made and the inability to directly measure at sea feeding events limits our understanding of

elephant seal foraging ecology. In chapter two, I combined records from time-depth recorders, satellite transmitters, and stomach temperature recorders to identify when and where females are successfully capturing prey. In addition, I compared feeding behavior between females and examined the validity of indirect measures (dive shape and transit rate) as indicators of feeding behavior.

The final objective of the study was to examine the at sea feeding behavior of free-ranging California sea lions. Although stomach temperature telemeters were deployed on sea lions, I was unable to maintain telemeters in the animals for long enough to measure at sea feeding in all but one female. Therefore, in chapter three, foraging behavior was examined based on indirect measures of feeding, such as diving behavior and at sea distributions. This chapter for the first time describes in detail the diving behavior and at sea distributions of adult female California sea lions on San Nicolas Island.

References

- Bonner, W.N. (1984). Lactation strategies in pinnipeds: Problems for a marine mammalian group. In *Physiological strategies in lactation* (eds M. Peaker, R.G. Vernon & C.H. Knight), pp. 253-272. Academic Press, London.
- Boyd, I.L. (1998) Time and energy constraints in pinniped lactation. *American Naturalist*, **152**, 717-728.
- Boyd, I.L. (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Functional Ecology*, **14**, 623-630.

- Boyd, I.L. & Croxall, J.P. (1996) Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **74**, 1696-1705.
- Costa, D., Thorson, P., & Kretzmann, M.B. (1989) Diving and foraging energetics of the Australian sea lion, *Neophoca cinerea*. *American Zoologist*, **29**, 71A.
- Costa, D.P. (1991). Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In *The behaviour of pinnipeds* (ed D. Renouf), pp. 300-344. Chapman and Hall, London.
- Costa, D.P. (1993). The relationship between reproductive and foraging energetics and the evolution of Pinnipedia. In *Recent advances in marine mammal science* (ed I. Boyd), Symposium Zoological Society of London No. 66, pp. 293-314. Oxford University Press, Oxford.
- Costa, D.P., Antonelis, G.A., & DeLong, R. (1991). Effects of El Niño on the foraging energetics of the California sea lion. In *Pinnipeds and El Niño: Responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 156-165. Springer-Verlag, Berlin.
- Costa, D.P., Croxall, J.P., & Duck, C.D. (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, **70**, 596-606.
- Costa, D.P. & Gales, N.J. (2003) Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs*, **73**, 27-43.
- Costa, D.P. & Gentry, R. (1986a). Free-ranging energetics of northern fur seals. In *Fur seals: maternal strategies on land and at sea* (eds R. Gentry & G.L. Kooyman), pp. 79-101. Princeton University Press, Princeton.
- Costa, D.P., Le Boeuf, B.J., Huntley, A.C., & Ortiz, C.L. (1986b) The energetics of lactation in the northern elephant seal *Mirounga angustirostris*. *Journal of Zoology*, **Series A 209**, 21-34.
- Crocker, D., Costa, D., Le Boeuf, B.J., Webb, P.M., & Houser, D.S. (2006) Impact of El Niño on the foraging behavior of northern elephant seals. *Marine Ecology-Progress Series*, **309**, 1-10.
- Drent, R. & Daan, S. (1980) The prudent parent. *Ardea*, **68**, 225-252.

- Feldkamp, S.D., DeLong, R.L., & Antonelis, G.A. (1989) Diving patterns of California sea lions, *Zalophus californianus*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **67**, 872-883.
- Gentry, R. & Kooyman, G.L. (1986) *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton.
- Kooyman, G.L. (1965) Techniques used in measuring diving capacities of Weddell seals. *Polar Record*, **12**, 391-394.
- Kooyman, G.L. (1989) *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin.
- Kovacs, K.M. & Lavigne, D.M. (1986) Maternal investment and neonatal growth in phocid seals. *Journal of Animal Ecology*, **55**, 1035-1051.
- Le Boeuf, B.J., Costa, D.P., Huntley, A.C., & Feldkamp, S. (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **66**, 446-458.
- Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., & Houser, D.S. (2000) Foraging ecology of northern elephant seals. *Ecological Monographs*, **70**, 353-382.
- Le Boeuf, B.J., Naito, Y., Asaga, T., Crocker, D., & Costa, D.P. (1992) Swim speed in a female northern elephant seal - Metabolic and foraging implications. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **70**, 786-795.
- Melin, S.R. (2002) *The foraging ecology and reproduction of California sea lions (Zalophus californianus)*. PhD, University of Minnesota.
- Melin, S.R., DeLong, R.L., Thomason, J.R., & VanBlaricom, G.R. (2000) Attendance patterns of California sea lion (*Zalophus californianus*) females and pups during the non-breeding season at San Miguel Island. *Marine Mammal Science*, **16**, 169-185.
- Oftedal, O.T., Boness, D.J., & Tedman, R.A. (1987) The behavior, physiology, and anatomy of lactation in the Pinnipedia. *Current Mammalogy*, **1**, 175-245.
- Ono, K.A. (1991). Introductory remarks and the natural history of the California sea lion. In *Pinnipeds and El Nino: responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 109-111. Springer-Verlag, Berlin.

- Perez, M.A. & Mooney, E.E. (1986) Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus*. *Fisheries Bulletin*, **84**, 371-381.
- Shaffer, S.A. & Costa, D.P. (2006) A database for the study of marine mammal behavior: gap analysis, data standardization, and future directions. *Journal of Oceanic Engineering*, **31** (1).
- Stewart, B.S. & DeLong, R. (1995) Double migrations of the northern elephant seal, *Mirounga angustirostris*. *Journal of Mammalogy*, **76**, 196-205.
- Sydeman, W.J. & Nur, N. (1994). Life history strategies of female northern elephant seals. In *Elephant seals: population ecology, behavior, and physiology* (eds B.J. Le Boeuf & R.M. Laws), pp. 121-136. University of California Press, Berkeley.
- Trillmich, F. (1996) Parental investment in pinnipeds. *Advance Study of Behavior*, **25**, 533-577.
- Trillmich, F. & Kooyman, G.L. (2001) Field metabolic rate of lactating Galapagos fur seals (*Arctocephalus galapagoensis*): the influence of offspring age and environment. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, **129**, 741-749.
- Trillmich, F. & Weissing, F.J. (2006) Lactation patterns in pinnipeds are not explained by optimization of maternal energy delivery rates. *Behavioral Ecology and Sociobiology*, **59**, 1-13.

Chapter 1: Identifying and quantifying prey consumption using stomach temperature change in pinnipeds

Summary

For many marine predators, knowledge of foraging behavior is limited to inferences based on changes in diving behavior or movement patterns at sea. This results in an incomplete and potentially inaccurate view of the foraging ecology of a species. This study examined the use of stomach temperature telemetry to identify and quantify prey consumption in both a phocid (northern elephant seal, *Mirounga angustirostris*) and an otariid (California sea lion, *Zalophus californianus*) species. In addition, I used opportunistic water consumption by northern elephant seals to test a method to distinguish between prey and water ingestion. Over 96% of feedings were identified based on a decline in stomach temperature, even when meals were separated by as little as 70 minutes. Water consumption was distinguishable from prey consumption, as the rate of recovery in stomach temperature was significantly faster for water ($F_{1,142}=79.2$, $p<0.01$). However, the overlap in recovery rates between prey and water resulted in 30.6% of water ingestion events being misclassified as prey ingestion. For both species, the area above the curve created by the decline in stomach temperature could be used to estimate mass consumed, when adjusted for the temperature difference between the prey and core body temperature. For California sea lions, there was a significant effect of individual on the ability to quantify prey consumed, which was not related to sea lion mass or sex. Although

many factors may influence the ability to use stomach temperature change to identify and quantify prey consumed, this study demonstrated that stomach temperature can accurately identify prey consumption and provide an estimate of meal mass, allowing for a greater understanding of the feeding behavior of pinnipeds.

Introduction

Knowledge of when and where predators forage is critical for understanding their role in the ecosystem and their impact on other species. With the development of time-depth recorders and satellite tracking transmitters, at sea diving and movement patterns have been used to infer the foraging behavior of a variety of marine predators, including seabirds (Bost *et al.*, 1997; Prince *et al.*, 1992; Wilson *et al.*, 2002), fish (Block, 2005; Gunn & Block, 2001; Metcalfe & Arnold, 1997), turtles (Morreale *et al.*, 1996; Polovina *et al.*, 2000; Renaud & Carpenter, 1994) and marine mammals (Boyd & Croxall, 1996; Costa, 1993b; Kooyman, 1965, 1989; Shaffer & Costa, 2006). Previous studies examined changes in behavior, such as transit rate (Le Boeuf *et al.*, 2000; McConnell *et al.*, 1999), dive shape (Hindell, Slip & Burton, 1991; Lesage, Hammill & Kovacs, 1999; Simeone & Wilson, 2003), and swim velocity (Le Boeuf *et al.*, 1992; Lesage *et al.*, 1999) to identify foraging. However, time-depth recorders and satellite transmitters cannot provide information about when and where prey are captured. Instead, these instruments can only be used to identify putative foraging behavior. To obtain a complete picture of a species

foraging behavior it is necessary to combine direct measures of prey ingestion with data collected on at sea diving behavior and movement patterns.

To examine at sea feeding behavior, stomach temperature technology has been used with a variety of marine predators, such as seabirds (Catry *et al.*, 2004; Gremillet & Plos, 1994; Weimerskirch, Gault & Cherel, 2005; Weimerskirch & Wilson, 1992; Wilson, Cooper & Plotz, 1992), sharks (Klimley *et al.*, 2001; Sepulveda *et al.*, 2004), turtles (Tanaka *et al.*, 1995), and marine mammals (Andrews, 1998; Austin *et al.*, 2006; Hedd, Gales & Renouf, 1995; Lesage *et al.*, 1999). This technology is based on the assumption that the ectothermic prey of marine endotherms are colder than the predators' core body temperature. Therefore, prey consumption results in a rapid decline in stomach temperature (Figure 1.1).

Stomach temperature telemetry has been tested with captive validations on a variety of seabird species (Ancel, Horning & Kooyman, 1997; Catry *et al.*, 2004; Gremillet *et al.*, 1994; Ropert-Coudert *et al.*, 2000; Wilson *et al.*, 1992; Wilson *et al.*, 1995). These studies have demonstrated that identifying both prey and water consumption is possible; however the method of quantifying prey consumption differed among species. Although, these instruments have been used on free-ranging marine mammals (Andrews, 1998; Austin *et al.*, 2006; Hedd *et al.*, 1995; Lesage *et al.*, 1999), only limited effort has been made to validate the technique (Bekkby & Bjorge, 1998; Gales & Renouf, 1993; Hedd, Gales & Renouf, 1996). Due to the complicated nature of interpreting stomach temperature data, including the potential

need to distinguish between prey and water ingestion, studies of feeding behavior can be misinterpreted in the absence of validation (Catry *et al.*, 2004; Gremillet *et al.*, 1994; Wilson *et al.*, 1995).

Previous validation studies with marine mammals have been limited by small numbers of study subjects or small numbers of experiments per animal. Nonetheless, changes in stomach temperature were able to identify and differentiate between the ingestion of fish, ice, snow, and free water in four harp seals (*Phoca groenlandica*; Gales *et al.*, 1993). Using only 11 feedings, Gales *et al.* (1993) found a significant linear relationship between meal mass and the time it took for stomach temperature to recover to pre-ingestion temperature. Bekkby and Bjorge (1998) investigated the effects of meal size, fish temperature, and fish size on changes in stomach temperature in two harbor seals (*Phoca vitulina*). The response in stomach temperature was significantly different between these individuals and data from each animal had to be treated independently, further limiting sample size. Finally, a study re-examining the use of stomach temperature telemetry with harp seals (N=7), demonstrated that prey and water consumption could be identified and distinguished based on changes in stomach temperature (Hedd *et al.*, 1996). However, the authors found problems with using this technique to quantify prey consumed as mass only accounted for 27% of the variance measured in the changes in stomach temperature.

While the previous studies examined the efficacy of both identifying and quantifying prey consumed, they have all been limited to phocid seals (true seals).

To date, I am unaware of published research that has validated the use of stomach temperature records to identify and quantify prey consumed in an otariid seal (fur seals and sea lions). Given the significant differences in body size, metabolic rate, and core body temperature between pinniped families, differences may exist in the relationship between prey ingestion and changes in stomach temperature between these groups (Bartholomew, 1954; Bartholomew & Wilke, 1956; Costa, 1993a; Nagy, 1987).

This study tested the accuracy of stomach temperature telemeters in identifying prey consumption in both a phocid (northern elephant seal, *Mirounga angustirostris*) and an otariid (California sea lion, *Zalophus californianus*) species. In addition, I examined changes in stomach temperature to determine if the mass of prey consumed could be estimated and whether these estimates differed between species. Based on previous captive studies (Gales *et al.*, 1993; Hedd *et al.*, 1996), I hypothesized that meal mass would result in a significant difference in the area above the curve created by the stomach temperature deflection (Figure 1.1). In addition, based on the physics of heat transfer, the rate of the warming of stomach contents should be related to the temperature difference between the predator and the prey (Wilson *et al.*, 1995). Therefore, I hypothesized that meal mass would also result in a significant difference in the area above the curve, adjusted for temperature difference between the prey and core body temperature (Ancel *et al.*, 1997). Finally, due to opportunistic water consumption by northern elephant seals, I hypothesized

that water consumption could be distinguished from prey consumption based on the rate of recovery of stomach temperature (Catry *et al.*, 2004). By examining changes in stomach temperature in a controlled environment, it will be possible to better interpret similar data collected on free-ranging animals.

Materials and Methods

Study subjects and instrumentation

Stomach temperature was measured using a stomach temperature recorder and stomach temperature telemeter (Wildlife Computers, Redmond, WA). The stomach temperature recorder (10 x 50 x 70 mm) was attached to the dorsal pelage and stored stomach temperatures at four or ten second intervals. The stomach temperature telemeter (63 x 21.5 mm diameter) was placed in the stomach, via a stomach tube or hidden in a fish. The titanium cover of the telemeter conducted temperature changes to one or four thermistors within the telemeter. The telemeter then transmitted a pulse at a rate that varied with temperature. The inter-pulse interval was measured by the recorder and converted to temperature ($\pm 0.2^{\circ}\text{C}$). During laboratory calibrations, Lesage *et al.* (1999) found that these sensors differed from water temperature by $0.7 \pm 0.6^{\circ}\text{C}$ and response times averaged 6.0 ± 0.6 seconds.

In some animals, I attempted to increase retention time by increasing the size of the telemeter by attaching an oval foam mount (northern elephant seals 12 x 16 x

1.0 cm, California sea lions 8 x 12 x 1.0 cm, Austin *et al.*, 2006). In order to minimize influence on the telemeter, the foam mount covered less than 30% of the region of the telemeter that conducted heat to the internal thermistors. When stomach temperature telemeters were expelled, they were immediately re-administered following the methods described above.

Northern elephant seals (N=13) were transported from Año Nuevo State Reserve (CA) to Long Marine Laboratory (LML, University of California, Santa Cruz, CA). Sub-adult male and female elephant seals (approximately 2 – 3 years of age) were chosen after completion of the annual molt in May - June of 2003, 2004 and 2005. Seals were chosen based on condition, as thin seals with longer new hair growth were more likely to depart for the foraging migration and would potentially be more willing to eat while in captivity. Seals were housed individually in pens with access to haulout areas and saltwater pools (2.3 x 2.3 x 1.1 m or 4.6 x 2.3 x 1.1 m). Pool temperature ranged from 10.9 to 17.8°C, with an average of $14.6 \pm 0.1^\circ\text{C}$.

For transport and to attach recording equipment, seals were sedated with an initial intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA) at 1.0 mg kg^{-1} based on a visual estimate of mass. Sedation was maintained with intravenous doses of ketamine hydrochloride when necessary (Fort Dodge Animal Health, Fort Dodge, IA). Upon completion of the study, temperature recorders were removed and animals were released at Año Nuevo State Reserve.

California sea lions (N=15) were rehabilitation animals from The Marine Mammal Center (TMMC, Sausalito, CA). All animals had completed treatment and were deemed releasable by TMMC staff veterinarians prior to the start of the study. Animals were held at either TMMC or LML. Adult females or sub-adult males of comparable body mass were selected for the study. Sea lions were sedated using gas anesthesia to attach stomach temperature recorders. Sea lions held at LML were returned to the care of TMMC for release or further treatment if necessary. Sea lions were housed individually with a haulout area and either a fresh (TMMC, range 2.2 x 0.8 m to 3.1 x 0.8 m) or salt water pool (LML, 2.3 x 2.3 x 1.1 m or 4.6 x 2.3 x 1.1 m). Pool temperature ranged from 9.5 to 26.2°C, with an average of $17.5 \pm 0.2^\circ\text{C}$.

Feeding protocols

All animals were fed whole herring (*Clupea harengus harengus*), and to mimic natural feeding, fish were warmed to pool temperature as determined by inserting a temperature probe into every fish ($\pm 0.1^\circ\text{C}$, Physitemp Instruments, NJ). Trials were conducted between 0700 and 2330. Animals were fed in the water and had to consume all fish within 8 minutes for a trial to be considered successful. Most feedings were completed in less than 2 minutes. For each feeding, the times of first and last fish consumption were recorded. Animals were fed quantities of 0.5, 1.0, 2.0, 3.0, and 4.0 kg (± 0.05 kg). Time to next feeding ranged from a minimum of 70 minutes to a minimum of 6 hours, depending on meal size. Thus, I assumed that each feeding event was independent from previous feeding events (Kuhn, Hurley, and

Costa unpublished data). Number of feedings per day for northern elephant seals ranged from 1 to 6, with an average of 2.2 ± 0.9 . Sea lions were fed on average 2.9 ± 0.1 meals per day (range 1-6). Animals were not given access to food outside of feeding experiments.

Stomach temperature analysis

Stomach temperature changes were analyzed using Sable Systems DataCan V software (Sable Systems, NV). For each drop in stomach temperature, a group of variables were defined for analysis (Figure 1.1). Initial temperature was defined as the baseline temperature preceding the sharp decline resulting from feeding or drinking. Minimum temperature was identified and time to minimum was calculated as the interval between time at first fish consumption and the time at minimum temperature. Temperature difference (ΔT) was calculated as the difference between initial temperature and fish (water) temperature. Recovery in the stomach temperature was determined when temperature became stable over a 10 min period ($\pm 0.1^\circ\text{C}$). Time at recovery was then defined as the first temperature reading in the 10 min period. The area above the curve created by the decline in stomach temperature (Area) was calculated using the Sable Systems software based on a trapezoidal integration algorithm from the initial temperature to the recovery temperature. When the initial and recovery temperatures were different, area was calculated based on the methods of Wilson *et al.* (1995). Essentially, area was

calculated based on the lowest temperature (initial or recovery) and added to one half of the area above this curve (Figure 1.2).

A general linear mixed model was used to test the hypotheses that mass consumed can be estimated by 1) Area or 2) Area/ ΔT . To assess the influence of individuals, I tested a random factor (individual) to examine whether this improved the models. Models with and without the random factor were compared using a log-likelihood ratio test. The model with the lowest AIC (Akaike's information criterion) was selected as the best model, unless there was no significant difference between models based on the likelihood ratio test (Burnham & Anderson, 2002). When no impact of individual was found, r-squared values were used to compare Area and Area/ ΔT to determine which showed the stronger relationship to meal mass. In addition, when the random factor was considered significant I tested mass and sex as fixed factors.

To determine whether water and prey consumption could be distinguished from one another I followed the methods of Catry *et al.* (2004), using the equation:

$$I = t_{0.5} / (T_{\text{initial}} - T_{\text{minimum}})$$

where I is an index of the rate of stomach temperature recovery (lower I corresponds with faster recovery) and $t_{0.5}$ is the time (seconds) from the start of the temperature decline to the half way point of temperature recovery. Catry *et al.* (2004) found that I values for liquid consumption were significantly lower than for prey consumption

and I values of less than $30 \text{ s } ^\circ\text{C}^{-1}$ always denoted water ingestion. I values were calculated for all water ingestion events and a subsample of 100 feeding events.

Summary data are reported as mean \pm SE. Statistical analysis was conducted using SYSTAT 10 (SPSS Inc. 2000) or R2.2.1 (R. Gentleman and R. Ihaka, <http://www.r-project.org>). All data were tested for normality and homogeneity of variance. Data that were non-normal or displayed unequal variances were \log_{10} or square root transformed. Contrasts were considered significantly different at $p < 0.05$.

Results

Study subjects

Eight male and 5 female northern elephant seals were obtained for the study. Three of the females continued to fast for over 10 days while in captivity and were released. The remaining 10 animals ranged in mass from 132 to 218 kg (average 183.3 ± 7.6 kg), and length from 192 to 277 cm (average 210.5 ± 4.5 cm). There was no significant difference between sexes for mass or length. Seals retained stomach temperature telemeters for 7.1 ± 1.3 days (range 1 – greater than 22 days).

Eleven adult female and 4 sub-adult male California sea lions were used for the feeding study. Two females that were initially deemed healthy showed signs of health problems (lack of interest in food or unusual behavior), and were immediately removed from the study. Sea lions ranged in mass from 63.0 to 102 kg (average 80.1

± 2.6 kg). Sub-adult males were significantly larger than females ($F_{1,12}=21.6$, $p=0.01$), however these animals were within the range of free-ranging adult females. Therefore, I assumed the difference was not biologically significant for the study. Sea lions retained stomach temperature telemeters for 11.8 ± 2.5 days (range 1 – 53 days).

Core body temperatures, in the absence of feeding or water ingestions, were variable for both species. Northern elephant seals had an average core body temperature of $36.8 \pm 0.04^{\circ}\text{C}$, with a range of $35.4 - 40.2^{\circ}\text{C}$. California sea lions had an average core body temperature of $38.0 \pm 0.03^{\circ}\text{C}$, with a range of $36.8 - 40.0^{\circ}\text{C}$. Core body temperatures were significantly different between individuals for both elephant seals and sea lions ($F_{9,395}=32.4$, $p<0.01$, $F_{12,317}=38.4$, $p<0.01$, respectively) and significantly different between species ($F_{1,733}=578.9$, $p<0.01$). However, these statistical difference may be a result of large number of temperatures recorded and not biologically significant as temperatures differed by less than 4.0°C between individuals and only 1.2°C between species.

Identifying feeding events

For the 10 northern elephant seals, 432 feeding events were recorded. Data from 17 feedings (4.0%) were deemed unusable due to missed data points, erroneous values, or instrument failure. Nine feedings (2.1%) showed no change in stomach temperature (range 0 – 7.3% per animal, $N=6$ individuals). Of the feedings that showed no change in temperature, six were 0.5 kg and the largest meal with no

change in temperature was 2.0 kg (N=2). Missed feedings occurred after 1 or 2 prior feedings (average 1.2 ± 0.1), however multiple feedings per day were often easily identified (Figure 1.3). This resulted in a total of 40.5 ± 0.86 feedings analyzed per animal (range 36 – 46).

For the 13 California sea lions, 497 feeding events were recorded. Data from 149 feedings (30.0%) were deemed unusable due to missed data points, erroneous values, or instrument failure. Thirteen feedings (3.8%) showed no change in stomach temperature (range 0 – 25%, per animal, N=3 individuals). Eight of the feeds that showed no change in stomach temperature were from one individual. Of the feedings that showed no change, seven were 0.5 kg and 11 were 1.0 kg or less. The largest meal size that did not result in a change in temperature was 2.0 kg (N=2). Feedings that showed no change in stomach temperature occurred after 1 to 3 prior feedings (average 1.9 ± 0.2 meals). This resulted in a total of 38.2 ± 2.4 feedings analyzed per animal (range 7 – 43).

Water consumption

Since sea lions were held at a rehabilitation facility, employing numerous volunteers with access to the animals, I cannot be completely certain whether additional drops in stomach temperature were due to water ingestion or extra feedings by volunteers. These drops in stomach temperature only occurred 5 times for all animals in the 133 days of experiments. Conversely, access to northern elephant seals was limited, and all drops in stomach temperature outside of feeding

experiments were assumed to be water consumption (N=49, Figure 1.3). One northern elephant seal showed no sign of water ingestion, while the other nine animals consumed water on average 5.8 ± 1.3 times during the study (range 2 – 13). Water consumption occurred on 9.1 to 43.8% of the days in captivity (average $20.0 \pm 4.6\%$). When animals consumed water, it occurred 1.4 ± 0.1 times per day (range 1 – 6 ingestions per day) and $70.1 \pm 8.2\%$ of the time in the morning prior to the first feed (range for individuals 33.3 – 100%).

Water consumption (N= 49) resulted in significantly lower I values than fish consumption (N= 97, $F_{1,142} = 79.2$, $p < 0.01$). I values for fish ranged from 55.1 to $4380.0 \text{ s } ^\circ\text{C}^{-1}$ and water ranged from 37.8 to $764.0 \text{ s } ^\circ\text{C}^{-1}$. To distinguish between fish and water consumption I used a threshold of $250 \text{ s } ^\circ\text{C}^{-1}$. This resulted in the lowest error rate with fish consumption being accurately identified 83.5% (N= 81) of the time, and water misidentified as fish 30.6% of the time (N= 15). There was no relationship between meal size and misclassification ($\chi^2 = 3.4$, $p = 0.50$). Water ingestions showed a faster overall recovery time and smaller area than the smallest meal consumed (0.5 kg, Table 1.1).

Quantifying feeding events

Feeding events resulted in an average drop in temperature of $4.7 \pm 0.1^\circ\text{C}$ and $4.4 \pm 0.1^\circ\text{C}$, for northern elephant seals and sea lions, respectively. Quantity consumed resulted in differences in all of the variables measured for both species (Table 1.1).

For northern elephant seals, there was a relationship between meal mass and both $\sqrt{\text{Area}}$ and $\sqrt{\text{Area}/\Delta T}$ (Table 1.2). There was no significant effect of individual for these relationships ($\sqrt{\text{Area}}$: log-likelihood ratio= 1.92, df=1, p=0.17, $\sqrt{\text{Area}/\Delta T}$: log-likelihood ratio= 0.88, df=1, p=0.35). Based on r-squared values, $\sqrt{\text{Area}/\Delta T}$ showed a slightly stronger relationship with meal size ($\sqrt{\text{Area}}$: $r^2=0.29$, $\sqrt{\text{Area}/\Delta T}$: $r^2=0.30$, Figure 1.4). Therefore, the best equation to estimate quantity consumed is: $\text{Quantity} = 0.57(\sqrt{\text{Area}/\Delta T}) - 0.12$.

For California sea lions, both $\sqrt{\text{Area}}$ and $\sqrt{\text{Area}/\Delta T}$ were also related to meal mass. Unlike northern elephant seals, there was a significant effect of individual for both models ($\sqrt{\text{Area}}$: log-likelihood ratio= 131.9, df=1, p<0.01, $\sqrt{\text{Area}/\Delta T}$: log-likelihood ratio= 53.0, df=1, p<0.01). The impact of individual was not a result of animal mass or sex as these parameters resulted in higher AIC values. Since it was not possible to account for the impact of individual, the two best equations that explain quantity consumed are: $\text{Quantity} = 0.028(\sqrt{\text{Area}}) - 0.13$ and $\text{Quantity} = 0.67(\sqrt{\text{Area}/\Delta T}) - 0.54$. The equation based on area adjusted for temperature ($\sqrt{\text{Area}/\Delta T}$) was not significantly different from the equation calculated for the northern elephant seals (Figure 1.4; 95% confidence intervals: slope 0.56 – 0.79, constant - 1.02 – -0.06).

Discussion

Through the use of captive validations I have demonstrated stomach temperature technology can accurately identify feeding events and can be used to estimate mass consumed in both a phocid and otariid species. Although stomach temperature telemeters have been used in the lab and field with phocids (Austin *et al.*, 2006; Bekkby *et al.*, 1998; Gales *et al.*, 1993; Hedd *et al.*, 1995, 1996; Lesage *et al.*, 1999), only one study used this technology with otariid seals (Andrews, 1998). Previous studies using stomach temperature technology to measure feeding have described its challenges in detail (Ancel *et al.*, 1997; Gremillet *et al.*, 1994; Wilson *et al.*, 1992; Wilson *et al.*, 1995). Among these are retention of the stomach temperature telemeter in the animal and identification of feeding as the stomach fills (Ancel *et al.*, 1997; Austin *et al.*, 2006; Gremillet *et al.*, 1994; Wilson *et al.*, 1995). In the present study, retention times for the stomach temperature telemeter averaged 7 days for elephant seals and 12 days for sea lions. Retention time varied among individuals as some regularly lost telemeters in 1 to 3 days, while others retained telemeters for the length of the study (greater than 22 days). Therefore, the successful use of stomach temperature telemetry in free-ranging animals requires further study to find a reliable method of increasing retention time.

The process of identifying and quantifying prey consumed could also be influenced by many factors such as the location of the telemeter in the stomach, the amount of stomach mixing, and the animals' activity level (Wilson *et al.*, 1995). In addition, the prey species, and more specifically the composition of the prey is likely

to influence the warming process in the stomach (see Wilson *et al.* 1995). For consistency all animals in the present study were fed the same fish species (herring), which has a body composition similar to other prey species found within the diet of northern elephant seals (Antonelis *et al.*, 1987; Condit & Le Boeuf, 1984) and California sea lions (Antonelis, Fiscus & DeLong, 1984; Lowry & Carretta, 1999; Lowry *et al.*, 1991).

Despite the limitations of stomach temperature technology, its use can still provide valuable information about the foraging behavior of free-ranging seals and sea lions that is currently not available for many species (Andrews, 1998; Austin *et al.*, 2006; Hedd *et al.*, 1995; Lesage *et al.*, 1999).

Identifying consumption

For both species, the identification of feeding occurred with high accuracy (97.9% northern elephant seals, 96.2% California sea lions). Feedings that were not identified tended to be small meals of 1.0 kg or less. Although it is not known what a 'normal' meal size is for either species in the wild, it appears that stomach temperature telemetry can accurately be used to identify prey consumed when feeding events are separated in time. Interestingly, the ability to identify ingestion appears to differ among individuals, as one sea lion had a much greater number of unidentified feedings than the others. In addition, although feeding regimes were similar for all animals, 4 elephant seals and 7 sea lions did not have any unidentified

feedings. It is not known whether this variation was a result of differences in activity level between individuals or other factors not measured in this study.

In addition to identifying feeding events, it was possible to distinguish between prey and water consumption with a relatively high accuracy in northern elephant seals. Catry *et al.* (2004) created an index of the rate of recovery of stomach temperature (*I*) to distinguish between prey and water ingestion, with 100% accuracy, in grey-headed albatross (*Thalassarche chrysostoma*). However, with the small sample size measured (N=6 water, N=8 feeding), the authors may not have measured the full variation in recovery rates. Although the accuracy in this study was not as high (16.5% of fish ingestion and 30.6% water ingestion misclassified), previous research suggests that free-ranging phocids can maintain water balance without free water consumption (Costa 2001; Depocas, Hart & Fisher, 1971; Ortiz, 2004). Studies with northern elephant seals during both molt and lactation have also found that animals do not consume water during these fasting periods on land (Costa *et al.*, 1986; Ortiz, Costa & Le Boeuf, 1978; Worthy *et al.*, 1992). Therefore, the misidentification of water consumption as prey may not be a problem when interpreting northern elephant seal stomach temperature data from free-ranging animals.

Quantifying consumption

Previous research with seabirds and marine mammals have used a variety of factors to quantify prey consumption, such as recovery time, total area created by the

deflection, and area for only the recovery phase (Figure 1.1, B-C; Ancel *et al.*, 1997; Bekkby *et al.*, 1998; Catry *et al.*, 2004; Gales *et al.*, 1993; Gremillet *et al.*, 1994; Hedd *et al.*, 1996; Putz *et al.*, 1998). Ancel *et al.* (1997) found a significant relationship when the difference between prey temperature and body temperature was incorporated in the estimate of meal mass ($\text{Area} = \text{Mass} * \Delta \text{Temp}$). For elephant seals this equation provided the best fit model for estimating mass consumed [$\text{Quantity} = 0.57(\sqrt{\text{Area} / \Delta T}) - 0.12$]. Given that it is possible to measure environmental temperature when dive recorders are used in conjunction with stomach temperature recorders, and fish temperature is similar to the temperature of the environment, all necessary parameters can be acquired to estimate quantity consumed.

As observed for northern elephant seals, both the area under the curve created by the change in stomach temperature and the area adjusted for temperature difference, were related to mass consumed for sea lions. However, unlike elephant seals, there was a significant effect of individual for both models (Table 1.2). This difference between individuals was not related to mass or sex, but could be a result of variables not measured in this study, including differences in metabolic rate or activity level. For sea lions, the equation using area corrected for temperature difference was not significantly different from that for the northern elephant seals. Therefore, I suggest using area corrected for temperature to estimate meal mass. Although the added uncertainty of individual differences makes the estimate of meal

mass more variable, the similar relationship between stomach temperature change and quantity fed for both species provides support for the general applicability of this technology to estimate mass consumed in free-ranging pinnipeds.

As previously stated, the goal of this study was to examine independent feeding events to determine a method of estimating mass consumed. Additional research with California sea lions found both the ability to identify ingestion events and estimate mass consumed can become obscured as animals ingest multiple meals within a smaller range of time (Kuhn and Costa, unpublished data). Therefore, the nature of feeding behavior in the wild may influence the ability to detect and quantify prey consumed.

Both northern elephant seals and California sea lions show bout structure in their diving behavior, suggesting prey consumption occurs within distinct windows of time (Feldkamp, DeLong & Antonelis, 1989; Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 1992). To estimate mass consumed using the equations presented in this study it is necessary to identify the time to recovery (Figure 1.1C) as this is used to calculate area above the curve (Figure 1.1). If animals feed during the recovery period this disrupts the recovery curve and could influence the ability to estimate mass consumed. By comparing recovery times with the diving behavior measured in free-ranging animals it is possible to examine the extent of feeding that might occur during the recovery period.

For northern elephant seals, dive times average 20.1 ± 0.5 min (Kuhn, Chapter 2). Therefore, for the range of meal sizes examined in this study, free-ranging animals would have to feed only once every four dives for the recovery period to be unaltered by further feedings. Although foraging success rates are not known for northern elephant seals, Austin *et al.* (2006) found grey seals feed on average just 2 times per day. For California sea lions dive times average just 2.2 ± 0.2 minutes (Kuhn, Chapter 3). In order to measure full recovery periods unaltered by additional feeding events, feedings for this species would have to be separated by 25 to 45 dives. Since females average 54 dives in a foraging bout (Feldkamp *et al.*, 1989), it is unlikely females would only successfully capture prey on one or two dives while foraging. Therefore, while consecutive feeding events may be identified, it is necessary to consider the impacts of bout feeding when estimating quantity consumed for California sea lions.

Recent data from stomach temperature telemeters in free-ranging animals of both species show feeding does occur in bouts, but animals also display single feeding events separated in time by further consumption (Kuhn Chapter 2; Kuhn and Costa unpublished). For these single feeding events the application of the equations presented here would provide a reasonable estimate of quantity consumed. For bout feeding periods, additional models are required if researchers are interested in estimating mass consumed (Kuhn and Costa, unpublished data; Wilson *et al.* 1995).

Without the ability to identify when and where an animal feeds it is difficult to truly understand foraging behavior. By using instruments to measure feeding events, it is possible to not only fill these gaps, but also test the validity of the indirect methods currently used to examine foraging behavior, such as changes in dive shape or transit rate. For northern elephant seals, a great deal of information has been gathered on at sea behavior through the use of time-depth recorders and satellite telemetry (Crocker *et al.*, 2006; Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000; Le Boeuf & Laws, 1994). Using specific changes in behavior, ‘focal’ foraging areas have been identified during foraging migrations (Le Boeuf *et al.*, 2000). To date, it is not known the extent of feeding within these ‘focal’ areas versus outside these areas and direct measures of feeding behavior can help provide the answer.

Due to the variability in stomach temperature change (Figure 1.4), I suggest using these data as a tool to compare meal sizes, rather than to calculate exact quantities consumed for both northern elephant seals and California sea lions. For instance, Austin *et al.* (2006) used stomach temperature change in grey seals (*Halichoerus grypus*) to examine sex differences in both feeding frequency and estimated meal size. This type of analysis provides a unique tool for comparing feeding behavior between sexes, individuals, seasons, or years. In addition to addressing questions of foraging in the species of interest, measures of feeding behavior have also been used to examine prey distribution and behavior (Austin *et al.*, 2006; Fuiman, Davis & Williams, 2002; Hennenke & Culik, 2005; Weimerskirch

et al., 2005), providing greater insight into the behavior of both marine predators and their prey.

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References

- Ancel, A., Horning, M., & Kooyman, G.L. (1997) Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *Journal of Experimental Biology*, **200**, 149-154.
- Andrews, R.D. (1998) Remotely releasable instruments for monitoring the foraging behaviour of pinnipeds. *Marine Ecology-Progress Series*, **175**, 289-294.
- Antonelis, G.A., Fiscus, C.H., & DeLong, R.L. (1984) Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978-79. *Fishery Bulletin*, **82**, 67-76.
- Antonelis, G.A., Lowry, M.S., Demaster, D.P., & Fiscus, C.H. (1987) Assessing northern elephant seal feeding-habits by stomach lavage. *Marine Mammal Science*, **3**, 308-322.
- Austin, D., Bowen, W.D., McMillan, J.I., & Boness, D.J. (2006) Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology*, **75**, 408-420.
- Bartholomew, G. (1954) Body temperature and respiratory heart rates in the northern elephant seal. *Journal of Mammalogy*, **35**, 211-218.
- Bartholomew, G. & Wilke, F. (1956) Body temperature in the northern fur seal, *Callorhinus ursinus*. *Journal of Mammalogy*, **37**, 327-337.
- Bekkby, T. & Bjorge, A. (1998) Variation in stomach temperature as indicator of meal size in harbor seals, *Phoca vitulina*. *Marine Mammal Science*, **14**, 627-637.
- Block, B.A. (2005) Physiological Ecology in the 21st century: Advancements in biologging sciences. *Integrative and Comparative Biology*, **45**, 305-320.
- Bost, C.A., Georges, J.Y., Guinet, C., Cherel, Y., Putz, K., Charrassin, J.B., Handrich, Y., Zorn, T., Lage, J., & LeMaho, Y. (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology-Progress Series*, **150**, 21-33.
- Boyd, I.L. & Croxall, J.P. (1996) Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **74**, 1696-1705.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: A practical information-theoretic approach*. Springer, New York.

- Catry, P., Phillips, R.A., Phalan, B., Silk, J.R.D., & Croxall, J.P. (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Marine Ecology-Progress Series*, **280**, 261-273.
- Condit, R. & Le Boeuf, B.J. (1984) Feeding-habits and feeding grounds of the northern elephant seal. *Journal of Mammalogy*, **65**, 281-290.
- Costa, D.P. (1993a). The relationship between reproductive and foraging energetics and the evolution of Pinnipedia. In *Recent advances in marine mammal science* (ed I. Boyd), Symposium Zoological Society of London No. 66, pp. 293-314. Oxford University Press, Oxford.
- Costa, D.P. (1993b) The secret life of marine mammals: Novel tools for studying their behavior and biology at sea. *Oceanography*, **6**, 120-128.
- Costa, D.P. (2001) Osmoregulation. In *Encyclopedia of Marine Mammals* (eds W.F. Perrin, J.G.M. Thewissen & B. Wursig), pp. 337-342. Academic Press.
- Costa, D.P., Le Boeuf, B.J., Huntley, A.C., & Ortiz, C.L. (1986) The energetics of lactation in the northern elephant seal *Mirounga angustirostris*. *Journal of Zoology*, **Series A 209**, 21-34.
- Crocker, D., Costa, D., Le Boeuf, B.J., Webb, P.M., & Houser, D.S. (2006) Impact of El Niño on the foraging behavior of northern elephant seals. *Marine Ecology-Progress Series*, **309**, 1-10.
- Depocas, F., Hart, J., & Fisher, H.D. (1971) Seawater drinking and water flux in starved and fed harbor seals, *Phoca vitulina*. *Canadian Journal of Physiological Pharmacology*, **49**, 53-62.
- Feldkamp, S.D., DeLong, R.L., & Antonelis, G.A. (1989) Diving patterns of California sea lions, *Zalophus californianus*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **67**, 872-883.
- Fuiman, L.A., Davis, R.W., & Williams, T.M. (2002) Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology*, **140**, 815-822.
- Gales, R. & Renouf, D. (1993) Detecting and measuring food and water-intake in captive seals using temperature telemetry. *Journal of Wildlife Management*, **57**, 514-519.

- Gremillet, D.J.H. & Plos, A.L. (1994) The use of stomach temperature records for the calculation of daily food-intake in cormorants. *Journal of Experimental Biology*, **189**, 105-115.
- Gunn, J. & Block, B.A. (2001). Acoustic, archival and pop-up satellite tagging of tunas. In *Tuna: Ecological physiology and evolution. Fish Physiology* (eds B.A. Block & E.D. Stevens), Vol. 19, pp. 167-224. Academic Press, San Diego, CA.
- Hedd, A., Gales, R., & Renouf, D. (1995) Use of temperature telemetry to monitor ingestion by a harbor seal mother and her pup throughout lactation. *Polar Biology*, **15**, 155-160.
- Hedd, A., Gales, R., & Renouf, D. (1996) Can stomach temperature telemetry be used to quantify prey consumption by seals? A re-examination. *Polar Biology*, **16**, 261-270.
- Hennicke, J.C. & Culik, B.M. (2005) Foraging performance and reproductive success of Humboldt penguins in relation to prey availability. *Marine Ecology-Progress Series*, **296**, 173-181.
- Hindell, M.A., Slip, D.J., & Burton, H.R. (1991) The diving behavior of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia, Phocidae). *Australian Journal of Zoology*, **39**, 595-619.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S., & Kelly, J.T. (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology*, **138**, 617-636.
- Kooyman, G.L. (1965) Techniques used in measuring diving capacities of Weddell seals. *Polar Record*, **12**, 391-394.
- Kooyman, G.L. (1989) *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin.
- Le Boeuf, B.J., Costa, D.P., Huntley, A.C., & Feldkamp, S. (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **66**, 446-458.
- Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., & Houser, D.S. (2000) Foraging ecology of northern elephant seals. *Ecological Monographs*, **70**, 353-382.

- Le Boeuf, B.J. & Laws, R.M. (1994) *Elephant seals: Population ecology, behavior and physiology*. University of California Press, Berkeley, USA.
- Le Boeuf, B.J., Naito, Y., Asaga, T., Crocker, D., & Costa, D.P. (1992) Swim speed in a female northern elephant seal - Metabolic and foraging implications. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **70**, 786-795.
- Lesage, V., Hammill, M.O., & Kovacs, K.M. (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **77**, 74-87.
- Lowry, M.S. & Carretta, J.V. (1999) Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in Southern California (1981-1995). *CalCOFI Reports*, **40**, 196-207.
- Lowry, M.S., Stewart, B.S., Heath, C.B., Yochem, P.K., & Francis, J.M. (1991) Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981-86. *Fishery Bulletin*, **89**, 331-336.
- McConnell, B.J., Fedak, M.A., Lovell, P., & Hammond, P.S. (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, **36**, 573-590.
- Metcalf, J.D. & Arnold, G.P. (1997) Tracking fish with electronic tags. *Nature*, **38**, 665-666.
- Morreale, S.J., Standora, E.A., Spotila, J.R., & Paladino, F.V. (1996) Migration corridor for sea turtles. *Nature*, **384**, 319-320.
- Nagy, K.A. (1987) Field metabolic-rate and food requirement scaling in mammals and birds. *Ecological Monographs*, **57**, 111-128.
- Ortiz, R.M. (2004) Osmoregulation of marine mammals. *Journal of Experimental Biology*, **204**, 1831-1844.
- Ortiz, C.L., D. Costa, & B.J. Le Boeuf. (1978) Water and energy flux in elephant seal pups fasting under natural conditions. *Physiological Zoology* **51**: 166-178.
- Polovina, J.J., Kobayashi, D.R., Ellis, D.M., Seki, M.P., & Balasz, G.H. (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along

- oceanic fronts in the central North Pacific. *Fisheries Oceanography*, **9**, 71-82.
- Prince, P.A., Barton, A.G., Wood, T., & Croxall, J. (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*, **4**, 31-36.
- Putz, K., Wilson, R.P., Charrassin, J.B., Raclot, T., Lage, J., Le Maho, Y., Kierspel, M.A.M., Culik, B.M., & Adelung, D. (1998) Foraging strategy of king penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology*, **79**, 1905-1921.
- Renaud, M.L. & Carpenter, J.A. (1994) Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bulletin of Marine Science*, **55**, 1-15.
- Ropert-Coudert, Y., Baudat, J., Kurita, M., Bost, C.A., Kato, A., Le Maho, Y., & Naito, Y. (2000) Validation of oesophagus temperature recording for detection of prey ingestion on captive Adelie penguins (*Pygoscelis adeliae*). *Marine Biology*, **137**, 1105-1110.
- Sepulveda, C.A., Kohin, S., Chan, C., Vetter, R., & Graham, J.B. (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Marine Biology*, **145**, 191-199.
- Shaffer, S.A. & Costa, D.P. (2006) A database for the study of marine mammal behavior: gap analysis, data standardization, and future directions. *Journal of Oceanic Engineering*, **31** (1).
- Simeone, A. & Wilson, R.P. (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Marine Biology*, **143**, 825-831.
- Tanaka, H., Sato, K., Matsuzawa, Y., Sakamoto, W., Naito, Y., & Kuroyanagi, K. (1995) Analysis of possibility of feeding of loggerhead turtles during interesting periods based on stomach temperature-measurements. *Nippon Suisan Gakkaishi*, **61**, 339-345.
- Weimerskirch, H., Gault, A., & Cherel, Y. (2005) Prey distribution and patchiness: Factors in foraging success and efficiency of wandering albatrosses. *Ecology*, **86**, 2611-2622.

- Weimerskirch, H. & Wilson, R.P. (1992) When do wandering albatrosses *Diomedea exulans* forage. *Marine Ecology-Progress Series*, **86**, 297-300.
- Wilson, R., Gremillet, D., Syder, J., Kierspel, M., Garthe, S., & Weimerskirch, H. (2002) Remote-sensing systems and sea-birds: Their use, abuse and potential for measuring marine environmental variables. *Marine Ecology-Progress Series*, **130**, 559-566.
- Wilson, R.P., Cooper, J., & Plotz, J. (1992) Can we determine when marine endotherms feed - a case-study with seabirds. *Journal of Experimental Biology*, **167**, 267-275.
- Wilson, R.P., Putz, K., Gremillet, D., Culik, B.M., Kierspel, M., Regel, J., Bost, C.A., Lage, J., & Cooper, J. (1995) Reliability of stomach temperature-changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology*, **198**, 1115-1135.
- Worthy, G.A., Morris, P.A., Costa, D.P., & Le Boeuf, B.J. (1992) Moulting energetics of the northern elephant seal *Mirounga angustirostris*. *Journal of Zoology*, **227**, 257-265.

Tables:

Table 1.1: Summary of stomach temperature change variables for northern elephant seals (N=10) and California sea lions (N=13) for each quantity fed. Means are presented (\pm SE). Due to opportunistic water consumption by elephant seals, stomach temperature change for water ingestion was included. Change in temperature was the difference between initial body temperature and minimum temperature. Time to minimum was the difference between time at minimum and the time of first fish consumption. Recovery was the time for stomach temperature to return to stable body temperature. Area was calculated based on the temperature change as depicted in Figures 1.1 and 1.2.

		0.5kg	1.0kg	2.0kg	3.0kg	4.0kg	Water
Elephant seals	Minimum temp (°C)	33.6 (0.3)	32.8 (0.2)	31.9 (0.3)	31.6 (0.2)	30.4 (0.2)	32.9 (0.6)
	Change in temp (°C)	3.2 (0.3)	3.9 (0.2)	4.8 (0.2)	5.2 (0.2)	6.4 (0.2)	4.1 (0.5)
	Time to minimum (min)	12.2 (0.7)	11.0 (0.7)	13.2 (0.9)	12.5 (0.6)	11.8 (0.4)	----
	Recovery time (min)	61.7 (1.9)	69.8 (2.2)	77.7 (2.6)	87.2 (2.3)	88.1 (2.4)	35.2 (2.2)
	Area (s °C)	5105 (507)	6429 (473)	7957 (579)	9779 (406)	11099 (464)	2843 (375)
Sea lions	Minimum temp (°C)	34.3 (0.3)	34.0 (0.3)	33.4 (0.3)	33.5 (0.3)	32.8 (0.3)	----
	Change in temp (°C)	3.7 (0.2)	4.0 (0.2)	4.6 (0.2)	4.6 (0.2)	5.2 (0.2)	----
	Time to minimum (min)	10.0 (1.1)	12.3 (1.5)	10.1 (0.8)	14.3 (1.3)	10.9 (0.9)	----
	Recovery time (min)	55.2 (2.4)	73.1 (4.5)	81.2 (3.7)	95.2 (5.4)	93.4 (5.2)	----
	Area (s °C)	4288 (225)	5657 (282)	7310 (383)	8513 (480)	9255 (458)	----

Table 1.2: Factors affecting the estimate of quantity consumed for each species. The lowest AIC value was used to determine the best fitting model (indicated in bold), except when models were not significantly different (*). Included for each model is the Akaike weight (AICW), which can be viewed as the probability that a model is the best, given the set of models and K, the number of model parameters.

Model = $\sqrt{\text{AREA}}$		K	AIC	Δ AIC	AICW
Elephant seals (N=10)	Quantity*	5	3695.2	3.7	0.14
	Quantity + Individual*	15	3691.5	0.0	0.86
Sea lions (N=13)	Quantity	5	2893.3	133.3	>0.01
	Quantity + Individual	18	2760.0	0.0	0.99
Model = $\sqrt{\text{AREA}} / \Delta T$			AIC	Δ AIC	AICW
Elephant seals	Quantity*	5	1174.2	0.0	0.99
	Quantity + Individual*	15	1184.1	9.8	0.01
Sea lions	Quantity	5	827.4	41.9	>0.01
	Quantity + Individual	18	785.4	0.0	0.99

Figures:

Figure 1.1: Characteristic change in stomach temperature as a result of feeding (solid line). Data from a sub-adult male northern elephant seal fed 1.0 kg of herring at 8:12am (denoted by arrow). Variables used to analyze stomach temperature change were A= initial temperature ($^{\circ}\text{C}$), B= minimum temperature ($^{\circ}\text{C}$), C= recovery (min). Area ($\text{s } ^{\circ}\text{C}$) was calculated from the dashed line to the stomach temperature curve.

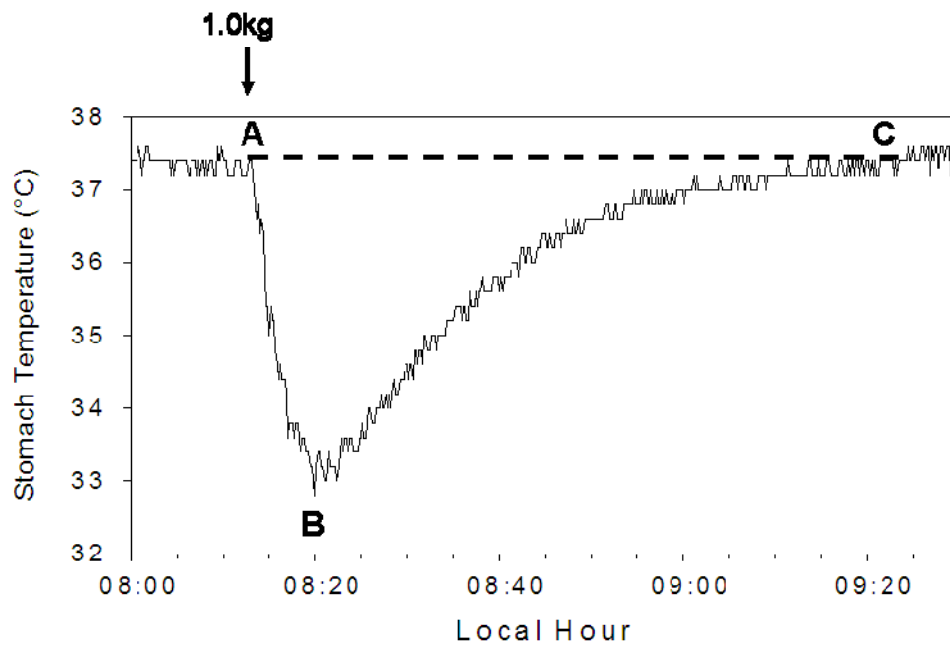


Figure 1.2: Method to calculate area above the curve created by the drop in stomach temperature when initial temperature and recovery temperature are not equal. Following the methods of Wilson *et al.* (1995), area was calculated based on the lower temperature (initial or recovery) and added to 1/2 the area between the lower and higher temperature [INT=(X/2) + Y]. A) Recovery temperature was greater than initial temperature. B) Recovery temperature was lower than initial temperature.

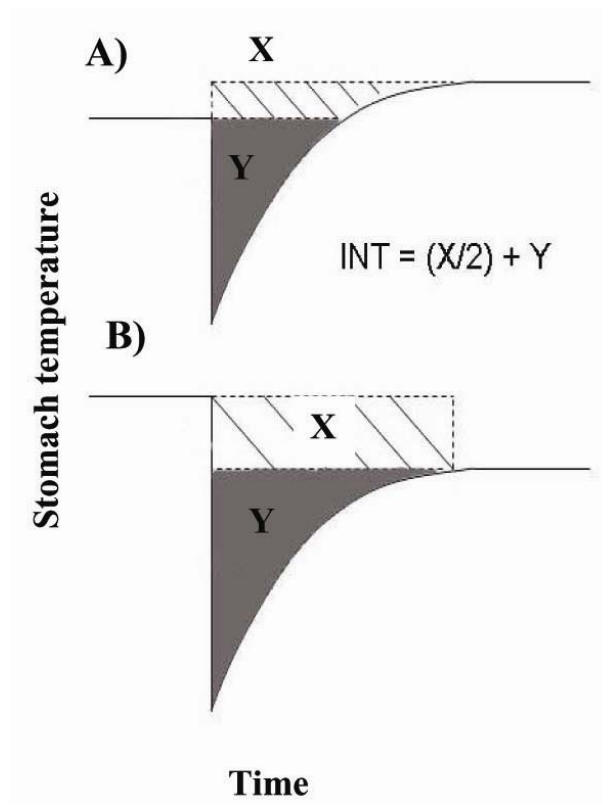


Figure 1.3: Stomach temperature record for a sub-adult male northern elephant seal fed 4 meals (0.5 kg, 1.0 kg, 0.5 kg, and 3.0 kg, denoted by arrows). First decline in stomach temperature was a result of water ingestion.

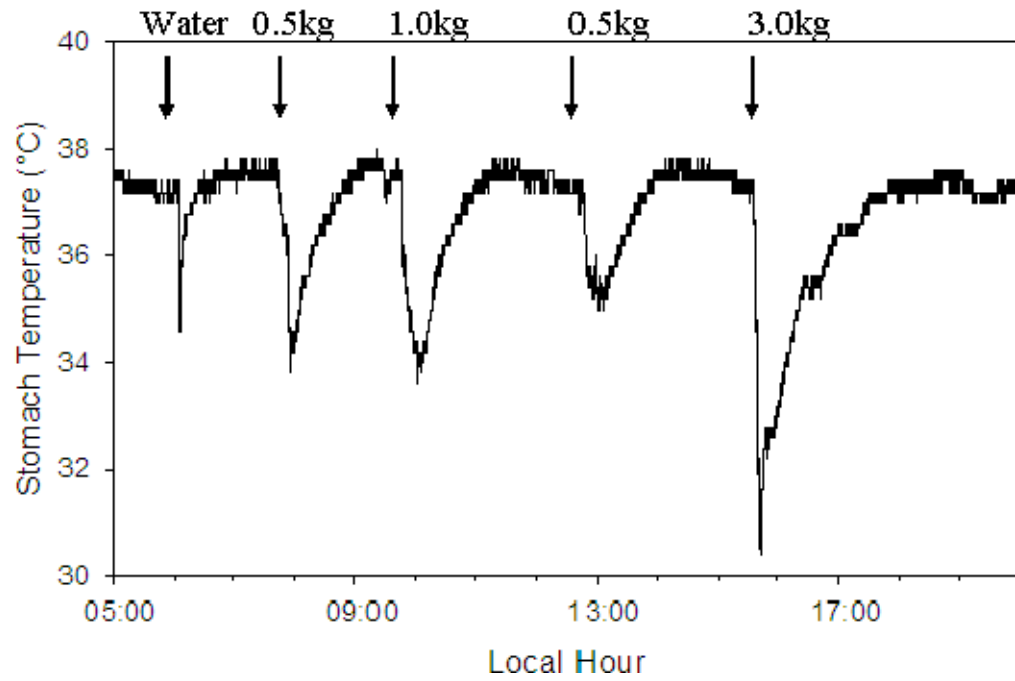
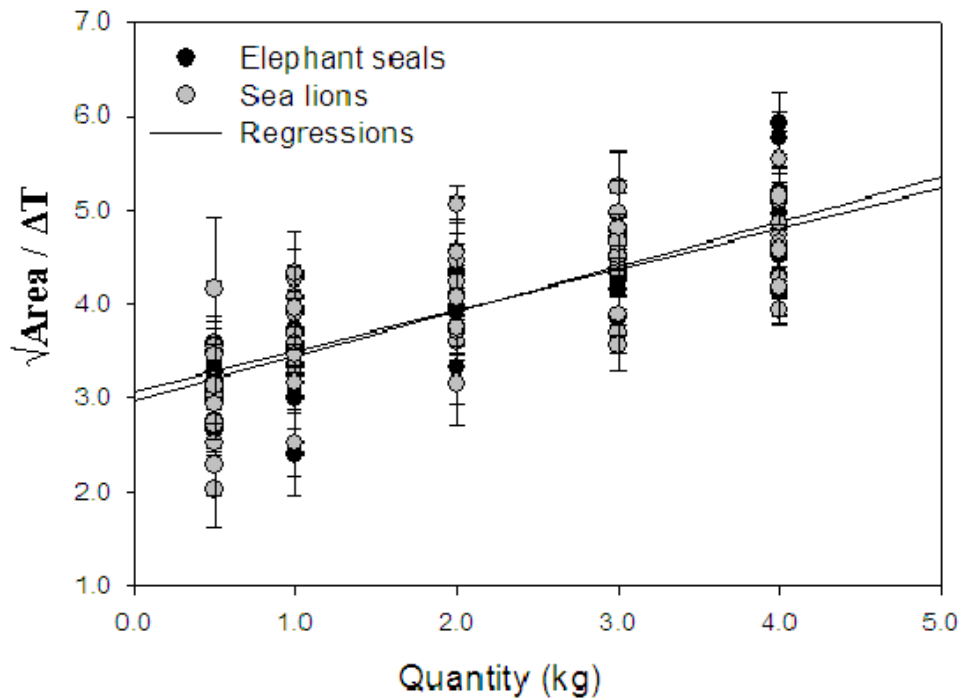


Figure 1.4: Relationship between mass consumed and area above the curve created by the decline in stomach temperature, adjusted for temperature difference between animals' core body temperature and fish (ΔT). The regression lines for both species are not significantly different (Elephant seals: $\sqrt{\text{Area}} / \Delta T = 0.52 * \text{Quantity} + 2.9$, California sea lions: $\sqrt{\text{Area}} / \Delta T = 0.41 * \text{Quantity} + 3.1$). Black circles denote mean values for each individual northern elephant seal (N=10), while grey circles represent the mean values for individual California sea lions (N=13).



Chapter 2: Time to eat: Understanding the feeding behavior of a large marine predator, the northern elephant seal (*Mirounga angustirostris*)

Summary

I examined the at sea feeding behavior of thirteen adult female northern elephant seals in 2004 and 2005 by utilizing satellite transmitters, time-depth recorders, and stomach temperature recorders, to directly measure feeding behavior. The first feeding events occurred early and close to the rookery (4.0 ± 1.5 hours and 58.6 ± 21.9 km, respectively), but these feedings were followed by extended periods without feeding (14.5 ± 2.5 hours). Continuous (bout) feeding did not occur until on average 7.5 ± 1.8 days after the females left the rookery. Females fed more during daylight hours than at night, which could result from higher capture success when vertically migrating prey are clumped at depth during the day. There were no significant differences between females for feeding bout length (6.7 ± 1.2 hours, $F_{2,32}=0.27$, $p=0.76$), feedings per bout (8.4 ± 1.0 feedings, $F_{2,32}=0.01$, $p=0.38$), and number of feeding bouts per day (1.5 ± 0.6). Females showed significant differences in the feeding rate while feeding in a bout (range 1.3 – 2.1 feeding events/hour, $F_{2,32}=5.27$, $p=0.01$). In addition, stomach temperature telemetry allowed for the validation of indirect measures of foraging behavior previously used with this species, such as decreases in transit rate and changes in dive shape. There was a significant negative relationship between transit rate and feeding events ($R^2=0.73$, $p<0.01$) and feeding occurred most often during the foraging type (D) dive shape

(74.2%). If foraging type (D) dives signify actual feeding attempts, then females are only successfully catching prey 18 – 24% of the time during foraging. This study shows females not only feed extensively during the early migration, but also shows individual variation in foraging locations and foraging success.

Introduction

Marine predators have evolved to find prey resources in a dynamic, heterogeneous environment. Knowledge of the foraging behavior of marine predators can provide insight into the spatial and temporal variation in prey (Georges, Bonadonna & Guinet, 2000; McConnell, Chambers & Fedak, 1992; Weimerskirch, Doncaster & Cuenotchaillet, 1994), as well as how animals deal with changes in prey abundance and distribution (Boyd *et al.*, 1994; Crocker *et al.*, 2006; Hennenke & Culik, 2005). However, studying the foraging behavior of marine predators is challenging, as most feeding occurs underwater and often outside the scope of observational studies. With the development of time-depth recorders and satellite telemetry, information on the diving behavior and movement patterns of free-ranging marine mammals and seabirds has become available (Boyd & Croxall, 1996; Costa, 1993; Kooyman, 1965, 1989; Shaffer & Costa, 2006; Weimerskirch *et al.*, 1994). By examining changes in at sea behavior, these instruments have been used to assess foraging behavior and foraging locations. However, the use of these tools requires researchers to make assumptions about when and where animals are

successfully finding prey. To truly understand foraging behavior it is necessary to directly measure prey consumption.

Foraging behavior can be measured directly, either visually or through the use of physical changes known to occur with feeding, such as beak/jaw movement, stomach temperature changes, or changes in stomach pH (Papastamatiou & Lowe, 2004; Weimerskirch *et al.*, 1994; Wilson, Cooper & Plotz, 1992; Wilson *et al.*, 2002). Foraging behavior can also be indirectly measured by examining changes in behavior thought to be associated with feeding. For most marine predators visual observation of feeding is difficult or impossible and therefore indirect measures of feeding are used extensively. Indirect measures associate feeding with changes in a variety of behaviors. These can include changes in transit rate (Le Boeuf *et al.*, 2000; McConnell *et al.*, 1999; Robinson *et al.*, In press), dive shape (Hindell, Slip & Burton, 1991; Le Boeuf *et al.* 1988; Lesage, Hammill & Kovacs, 1999; Simeone & Wilson, 2003), swim velocity (Hassrick *et al.*, In press; Le Boeuf *et al.*, 1992; Lesage *et al.*, 1999), and landings in seabirds (Shaffer, Costa & Weimerskirch, 2001; Weimerskirch *et al.*, 1994; Weimerskirch *et al.*, 2000).

For relatively few species of marine predators feeding behavior can be directly measured by observing prey consumption. For sea otters (*Enhydra lutris*), which bring prey to the surface for consumption, visual observations of feeding make it possible to examine preferences in prey species and size, foraging duration, and foraging success (Estes, Jameson & Rhode, 1982; Estes *et al.*, 2003; Ostfeld,

1982). An alternative approach to visualizing foraging behavior is the use of animal mounted cameras (Davis *et al.*, 1999; Marshall, 1998; Parrish *et al.*, 2005).

Another direct method used to identify feeding is the use of stomach temperature telemetry. Many studies have used this technology to identify when, where, and how often free-ranging marine birds feed (Catry *et al.*, 2004; Gremillet & Plos, 1994; Putz & Bost, 1994; Weimerskirch, Gault & Cherel, 2005; Wilson *et al.*, 1992; Wilson *et al.*, 1995). The technique has also been used to measure feeding behavior in sharks (Klimley *et al.*, 2001; Papastamatiou *et al.*, 2004; Sepulveda *et al.*, 2004) and turtles (Southwood *et al.*, 2005; Tanaka *et al.*, 1995). In addition a few studies have used stomach temperature telemetry in free-ranging marine mammals (Andrews, 1998; Austin *et al.*, 2006; Bjorge *et al.*, 1995; Hedd, Gales & Renouf, 1995; Lesage *et al.*, 1999). However, for many species studies of foraging behavior still rely on indirect measures of feeding. Yet, many indirect indicators of feeding have not been validated and may in fact be inaccurate.

For northern elephant seals (*Mirounga angustirostris*), a large amount of information has been gathered on at sea behavior through the use of satellite telemetry and time-depth recorders. For this species, researchers have relied extensively on indirect measures to identify foraging. These animals exhibit dives that vary in two-dimensional shape as a result of changes in descent rate, bottom time, and/or ascent rate. It has been speculated that these dive shapes reflect a variety of behaviors such as transit, foraging, and food processing (Crocker, Le Boeuf &

Costa, 1997; Hindell *et al.*, 1991; Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 1992).

Using dive shapes and decreases in transit rate, predictions have been made about foraging behavior in northern elephant seals (Crocker *et al.*, 2006; Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000; Le Boeuf *et al.*, 1992).

Specifically for northern elephant seals, there has been considerable support for the functionality of the putative foraging (D) type dive shape as an indicator of feeding behavior. This dive shape shows a marked diel pattern (Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000) and often includes extensive bursts in swim speed during the bottom segment (Hassrick *et al.*, In press; Le Boeuf *et al.*, 1992), suggesting pursuit of vertically migrating prey. Type D dives have high descent and ascent rates (Hassrick *et al.*, In press; Le Boeuf *et al.*, 1992) and increase significantly during periods of slow horizontal transit, indicating seals have possibly located and may be exploiting prey patches (Le Boeuf *et al.*, 2000). Finally, there is a positive relationship between the occurrence of D dives and rates of mass gain for females (Crocker *et al.*, 2006; Le Boeuf *et al.*, 2000). However, the direct link between feeding and dive shape has not been made and the inability to directly measure at sea feeding events limits our understanding of elephant seal foraging ecology.

This study directly measured feeding events in northern elephant seals through the use of stomach temperature telemetry. Since elephant seals feed on ectothermic prey, the prey is colder than the seals' core body temperature. This

results in a drop in stomach temperature with the consumption of prey (Figure 2.1). Captive feeding experiments conducted with northern elephant seals have shown that this technique accurately identifies prey consumption (97.9% of the time) and can be a valuable tool to measure at sea feeding in free-ranging animals (Kuhn, Chapter 1). When used in conjunction with time-depth recorders and satellite transmitters, it is possible to identify when and where animals successfully capture prey.

The aim of this study was to examine the foraging ecology of northern elephant seals through direct measures of feeding behavior. Specific objectives were to identify when and where feeding occurs, compare feeding behavior between individuals, and examine the validity of the indirect measures of feeding previously used with this species. As northern elephant seals spend 67 to 83% of the year in the pelagic environment (Le Boeuf & Laws, 1994), remote recording instruments are essential to advance our understanding of their at sea behavior.

Materials and Methods

Animal handling

Adult female northern elephant seals at Año Nuevo State Reserve (37.116°W, 122.332°N) were equipped during their annual breeding haulout. After females give birth (December – February), they nurse a pup for an average of 28 days before departing on a post-breeding foraging migration. Research was conducted on seven seals in February 2004 and eight in February 2005. All animals

were selected based on healthy appearance, accessibility, and proximity to other individuals. Animals were sedated with an initial intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA) at 1.0 mg kg^{-1} based on a visual estimate of mass. Sedation was maintained with intravenous doses of ketamine hydrochloride (Fort Dodge Animal Health, Fort Dodge, IA).

Instrumentation

Each seal was equipped with a satellite tracking transmitter (PTT; Telonics, Mesa, AZ or Wildlife Computers, Redmond, WA) and time-depth recorder (TDR; Mk7 or Mk9; Wildlife Computers, Redmond, WA). In addition, a VHF transmitter (Telonics, Mesa, AZ) was attached to locate seals on land after the migration (approximately 70 days, Le Boeuf *et al.*, 2000). Stomach temperature was measured using a stomach temperature recorder (HTR) and stomach temperature telemeter (STT; Wildlife Computers, Redmond, WA). Recording instruments (PTT, TDR, HTR) were wrapped in rubber splicing tape, to facilitate removal when the animals returned for the annual molt. The instruments were attached to high tension, nylon mesh netting using cable ties, and glued to the pelage using 5 minute quick set epoxy (LoctiteTM and DevconTM epoxy). The STT was modified to increase retention time in the stomach following the methods of Austin *et al.* (2006) and was placed in the stomach via a stomach tube.

PTTs were programmed to transmit at a frequency of 34 or 45 seconds while on the surface. At sea satellite locations were obtained using the Argos satellite system (Service Argos, Toulouse, France). TDRs and HTRs sampled at four second intervals. For instrument recovery, females were sedated following the methods described above. Recording instruments were removed by cutting through the splicing tape and it was assumed, based on stomach temperature records, that the STT was expelled during the foraging migration. The epoxy mounts remained after tag removal and fell off during the subsequent molt.

Data processing and analysis

Erroneous satellite locations were filtered following the methods outlined in Tremblay *et al.* (2006) based on a maximum transit rate of 10 km hr⁻¹ and a minimum time between satellite locations of 10 minutes. All Z quality satellite locations were removed and the remaining location qualities (3-0, A, B) were used in the filtering algorithm. Tracks were interpolated using a Bezier curve ($\mu=0.1$) based on the methods described in Tremblay *et al.* (2006). This allowed each dive and feeding event to be associated with a location along the track. Maximum and total distances travelled were calculated for each female. Maximum distance was defined as the straight line distance from the rookery to the farthest location. Total distance was defined as the sum of distances travelled between satellite locations along the migration route.

Dive data were processed using a custom made zero-offset correction algorithm and analysis program (IKNOS toolbox, Y. Tremblay unpublished). A dive was defined as a minimum depth of four meters and minimum duration of 16 seconds. The analysis program calculated basic parameters for each dive such as maximum depth, dive duration, and surface interval. Bottom time was calculated at 95% of the maximum dive depth. Percent time diving was the percent of time at sea for which a seal was at depths greater than 4.0 m.

Dive records from previous studies were typed visually using the categories described by Le Boeuf *et al.* (1988, Figure 2.2). Dive parameters from each category were then used to create discriminant functions that were applied to the dive records in this study (Hassrick *et al.*, In press). Dives assigned to the A category were assumed to represent transit dives as they displayed little to no bottom time. C type (drift) dives were considered putative food processing dives (Crocker *et al.*, 1997) and D dives, defined by vertical excursions in the bottom phase (wiggles), were considered putative foraging dives. Benthic dives, used for either traveling along the continental shelf or benthic foraging, were assigned to the E category. Short, shallow dives (< 100 m) that did not fall into the previous categories were defined as I dives. This dive type occurred most often at the beginning and end of the migration as animals transited over the continental shelf, and made up only $5.3 \pm 0.9\%$ of the total dive records (N=12).

To analyze stomach temperature records, the methods from Lesage *et al.* (1999) were modified based on data collected from laboratory feeding experiments with northern elephant seals (Kuhn, Chapter 1). Feeding was defined simply as ingestion of prey and could include consumption of one or more prey items. A feeding event was identified when stomach temperature dropped by a minimum of 1.0 °C and was followed by a warming of a minimum of 0.4 °C within a 10 minute period (Figure 2.1). This allowed for the elimination of long term declines in core body temperature that may not be related to feeding (Hill *et al.*, 1987). Using time between ingestion, feeding events were divided into single feeding events and bout (continuous) feeding. A minimum of 4 feeding events each separated by less than 1 hour was considered bout feeding. The ending criterion for a feeding bout was determined following the methods of Gentry and Kooyman (1986) based on time between feedings. All other feedings were defined as single feeding events (Figure 2.1).

Previous research found a diel cycle in the dive depths of female northern elephant seals hypothesized to be driven by vertically migrating prey, such as epi- and meso-pelagic squid and fish (Antonelis *et al.*, 1987; Antonelis *et al.*, 1994; Condit & Le Boeuf, 1984). To assess differences in foraging success due to the behavior of vertically migrating prey, I examined the number of feeding events by hour. Local sunrise and sunset times were used to determine differences in day and night behavior.

Indirect measures of feeding

To investigate the relationship between successful feeding and indirect measures of foraging, such as transit rate and dive shape, satellite tracks and dive records were examined for the duration of time stomach temperature records were available. Le Boeuf *et al.* (2000) used a two day average transit rate of less than 0.4 m s^{-1} to define ‘focal foraging areas’ for female northern elephant seals. Two day average transit rate was calculated following the methods of Le Boeuf *et al.* (2000) to examine if seals showed decreased transit rates while feeding. However, two day average transit rate may obscure animal movements on a smaller temporal scale. Therefore, transit rates were also calculated between interpolated satellite locations. Each feeding event was associated with a transit rate, making it possible to examine the relationship between short-term transit rates and feeding events. Additionally, to examine the relationship between dive types and feeding behavior, I calculated the proportion of feeding events associated with each dive type.

Statistical analysis

Summary data are reported as mean \pm SE. Statistical analysis was conducted using SYSTAT 10 (SPSS Inc. 2000). Comparisons between females were conducted using an ANOVA. Relationships between transit rate and feeding events were tested using least-squares linear regression analysis. All data sets were tested for normality and homogeneity of variances. When data were non-normal or displayed unequal

variances, they were \log_{10} transformed. Differences were considered significant at $p < 0.05$.

Results

At sea behavior

Of the fifteen females tagged, instruments were recovered from thirteen: twelve from Año Nuevo and one from San Miguel Island (34.023°W, 120.308°N). Ten females had complete satellite tracks, two had tracks that lasted into the return phase of the migration, and one female's satellite transmitter failed early along the migration. Of the 13 dive recorders recovered, one instrument failed to record any dive data. There were 12 stomach temperature records that recorded data after the females left for the migration. This resulted in eight females with all three records (satellite, dive, stomach temperature), while the remaining females had some combination of two records.

There were no significant differences between diving parameters (depth: $t_{10} = -1.68$, $p = 0.12$; duration: $t_{10} = 0.38$, $p = 0.71$; bottom time: $t_{10} = 1.64$, $p = 0.13$; surface interval: $t_{10} = -0.04$, $p = 0.97$; percent time diving: $t_{10} = -0.31$, $p = 0.76$) or movement parameters (maximum distance travelled: $t_9 = 0.38$, $p = 0.72$; total distance travelled: $t_9 = 1.1$, $p = 0.30$; trip duration: $t_{11} = 0.73$, $p = 0.48$) between years, so years were combined for analysis. The post breeding migration lasted 83.3 ± 2.5 days (range 68.3 – 105.4 days). Both maximum distance and total distance travelled spanned a

large range for the females (1267 km – 4145 km, 4777 – 11,072 km, respectively). This was reflected in the differing habitats used by females as some stayed near the continental shelf and others displayed the more typical pelagic foraging pattern (Figure 2.3A).

Females displayed diving patterns similar to those previously described for this species (Table 2.1; Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000; Le Boeuf *et al.*, 1989; Naito *et al.*, 1989). Females spent $87.5 \pm 0.01\%$ of the time at sea diving with surface intervals of 2.4 ± 0.09 minutes. Based on dive shape, during the period of time when stomach temperature records were available, females spent over 43% of the time traveling and only 23.4% of the time foraging (Figure 2.2). As this analysis was only conducted for the duration of stomach temperature records, type I (shallow) dives represented a larger proportion of the dive types than when compared to the entire trip records (21.7% vs. 5.3%).

Feeding behavior

STTs remained in the stomach for 7.8 ± 1.9 days (range 2.2 to 21 days, N=12). The median number of feedings per record was 5.5 (range 0 to 191). The first feeding occurred early and close to the rookery for all but one female. On average the first feeding occurred 4 hours after females left the beach and 58.6 km from the rookery (Table 2.2). One female consumed her first prey 48.8 hours after leaving the beach. First feedings were usually single feeding events (1.4 ± 0.3 feeding events) and were followed by extended periods without feeding (14.5 ± 2.5 hours).

Three females retained STTs into areas where continuous (bout) feeding occurred. The feeding bout ending criterion was determined to be 105 minutes, meaning a bout was considered over when a female did not show additional feeding within this amount of time. Feeding bout duration was calculated from the first to the last feeding event. The first feeding bout occurred on average 7.5 ± 1.8 days after leaving the rookery, at an average distance of 610 km. Feeding bout duration did not differ significantly among females (6.7 ± 1.2 hours, $F_{2,32}=0.27$, $p=0.76$). On average, females displayed 1.5 feeding bouts per day. There was no significant difference in the number of feeding events per bout, with females feeding on average less than 9 times per bout ($F_{2,32}=0.01$, $p=0.38$). There was a significant difference among the 3 females in feeding rate when bout feeding (1.3 ± 0.5 , 1.5 ± 0.5 , 2.1 ± 0.6 feeding events/hour, $F_{2,32}=5.27$, $p=0.01$).

For the three females that displayed bout feeding, there was a diel pattern in feeding behavior (Figure 2.4). Females had increased feeding events just after local sunrise which continued until sunset. For all females, only 35.0% of feeding events occurred during the night (range 25 – 39%). Greater number of feeding events during the day was not a result of increased dive frequency as females displayed a significantly greater number of dives during the night than during the day ($t_{22}=-9.1$, $p<0.01$).

Indirect measures of feeding

During the period of stomach temperature records, females displayed an average interpolated transit rate of $1.43 \pm 0.01 \text{ m s}^{-1}$. Females exhibited feeding behavior at all transit rates measured (Figure 2.5). For the three females that displayed bout feeding there was a significant negative relationship between two day average transit rate and daily number of feeding events (Figure 2.6A, $r^2=0.33$, $p<0.01$). When interpolated transit rate was used, the relationship with number of feeding events was highly significant (Figure 2.6B, $r^2=0.73$, $p<0.01$). Two day average transit rate did not identify any areas of ‘focal foraging’ for the three females that displayed bout foraging behavior because transit rate did not fall below 0.4 m s^{-1} .

Females displayed D (putative foraging) type dives 24% of the time when stomach temperature was recorded (Figure 2.2). Although feeding is most strongly associated with D dives (74.2%), the stomach temperature records indicated that feeding also occurs with all dive types (Figure 2.7). Type A (transit) dives account for the second highest dive type associated with feeding at 16.4%. When all D dives for the length of the stomach temperature record were examined, feeding only occurred for 18.5% of the dives. This relationship improved to 23.5% when only the two bout feeding females with matching dive records were examined.

Discussion

By directly measuring the feeding behavior of northern elephant seals this study was able to identify when and where feeding occurs, calculate foraging success, and show the extent of feeding during the early part of the foraging migration. In addition, I found relationships between feeding events and indirect measures of foraging behavior, such as changes in transit rate and dive shape.

Feeding behavior

For all but one female, the first feeding events occurred early and close to the rookery (Table 2.2). Given that females travel over 4,000 km from the rookery during a foraging migration (Le Boeuf *et al.* 2000; this study), this suggests either the prey quality or quantity in the area close to the rookery is not sufficient to meet the energetic requirements of female northern elephant seals after their extended breeding fast. Early feedings were often single feeding events and were possibly opportunistic prey captures as females migrated to more productive foraging grounds in the North Pacific. In grey seals (*Halichoerus grypus*), where feeding behavior has been examined in detail using stomach temperature telemetry, feeding also began as early as one day after leaving the beach (Austin *et al.*, 2006). However, depending on the foraging strategy used, the main foraging grounds of grey seals can be as close as 39 km from the rookery or up to 259 km away (Austin, Bowen & McMillan, 2004). This is in contrast to northern elephant seal females, which travel much greater distances from the rookery. For other pelagic predators such as wandering (*Diomedea exulans*) and grey-headed albatross (*Thalassarche chrysostoma*)

opportunistic feeding has also been identified, as animals were found to consume single, potentially low quality prey items in between bout feeding (Catry *et al.*, 2004; Weimerskirch *et al.*, 1994; Weimerskirch *et al.*, 2005).

In this study, continuous (bout) feeding did not begin until females travelled on average over 600 km from the rookery (Table 2.2). This extended travel time resulted in the post-breeding fast lasting an additional week for some females. For one female, the stomach temperature record lasted 13 days at sea with only two, single feeding events occurring. For this female the breeding fast essentially lasted at least 43 days. This previously unknown fasting at sea represents an increase in the length of this female's breeding fast by 39%. Females lose on average 36% of their body reserve while on land during the lactation period and this unmeasured fasting time could drastically change our understanding of the breeding and foraging energetics of northern elephant seals (Crocker *et al.*, 2001).

As with other studies examining foraging behavior of marine predators, this study found individual variation in the timing, frequency, and locations of feeding events (Figure 2.3B; Putz *et al.*, 1994; Weimerskirch, Wilson & Lys, 1997). Austin *et al.* (2006) found individual variation when examining the temporal distribution of feeding and intervals between feeding in grey seals. Although female northern elephant seals showed some similarities in feeding bout duration and number of bouts per day, there was a significant difference among females in feeding events per hour while feeding in a bout. Due to the limited sample size it is difficult to draw

relationships between differences in success and other variables such as age, mass or foraging location. However, these differences in bout foraging success may help explain the variation in mass gain as measured when females return to the beach for the annual molt (Crocker *et al.*, 2006; Le Boeuf & Crocker, 2005; Le Boeuf *et al.*, 2000).

Although differences between females exist, some patterns remain consistent. Based on diving behavior, it was previously hypothesized that female northern elephant seals foraged throughout the day (Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000). Dive depths varied with time of day, suggesting females followed the vertical migrating layer; and D type (putative foraging) dives were displayed throughout the day and night, lasting up to several days (Le Boeuf *et al.*, 1988; Le Boeuf *et al.*, 2000). The present study found not only did females display diel differences in diving behavior, but there was also a difference in number of feeding events based on time of day (Figure 2.4). All three females who reached areas of bout feeding before stomach temperature telemeters were lost showed an increase in the number of feeding events during the daylight hours (Figure 2.4). This is in contrast to some species that show a diel pattern in foraging behavior where foraging increases during the night when it is hypothesized that vertically migrating prey move to the surface and are easily captured (such as for northern fur seals, *Callorhinus ursinus*, Gentry *et al.*, 1986; and Antarctic fur seals, *Arctocephalus gazella*, Boyd, Lunn & Barton, 1991).

Studies with king penguins (*Aptenodytes patagonicus*), New Zealand fur seals (*Arctocephalus forsteri*) and crabeater seals (*Lobodon carcinophaga*) found that the behavior of vertically migrating prey may influence the timing of foraging (Burns *et al.*, 2004; Harcourt *et al.*, 2002; Putz *et al.*, 1998). For these species, vertically migrating prey is only profitable when clumped at depth during the daylight hours. Putz *et al.* (1998) hypothesized the decrease in foraging efficiency of king penguins during the night was a combination of the lack of light and the dispersion of prey as it moves to the surface. For crabeater seals, daytime hunting was more profitable, not only because of the clumping behavior, but also because the prey moved to the sea floor. The use of this bottom barrier may have increased prey capture efficiency for the crabeater seals (Burns *et al.*, 2004). The assistance of bottom topography is not available to female northern elephant seals as they forage over deep pelagic waters, but clumping of prey could explain the increase of foraging success during the day.

Alternatively, the increase in feeding rate during the day could be a result of switching prey type or prey size during periods of darkness, decreasing the need to consume as many prey items. Currently, stomach temperature telemetry does not allow for the discrimination of prey types during foraging or the distinction between many small or few, large prey consumed at one time. With additional controlled experiments, the nuances in stomach temperature records or the use of stomach

temperature technology in combination with other tools may help answer these questions.

Indirect measures of feeding

Feeding events measured by stomach temperature telemetry provide an opportunity to validate the use of indirect measures of feeding behavior in northern elephant seals. Le Boeuf *et al.* (2000) used a two day average transit rate of less than 0.4 m s^{-1} to identify ‘focal foraging areas’ for northern elephant seals. No females in this study displayed a two day transit rate of less than 0.4 m s^{-1} during the period of stomach temperature records (Figure 2.6A). This is not surprising as stomach temperature was only measured for the first 12 - 27% of the migration and females in the Le Boeuf *et al.* (2000) study showed slow transit rates (less than 0.4 m s^{-1}) for only 25% of the entire migration. Since no ‘focal foraging areas’ were identified, it is not possible to determine if feeding increases in these areas. However, it is clear extensive feeding occurs outside of ‘focal foraging areas’ and the early part of the migration is an important foraging period for female elephant seals.

Le Boeuf *et al.* (2000) also found mass gain over the period at sea increased as the percent of time at slow transit rates increased. This was supported by the stomach temperature records as both two day average transit rate and interpolated transit rate showed a significant relationship with feeding events (Figure 2.6A and B). Both measures of transit rate indicated that a greater amount of successful feeding occurred at slower speeds. This supports the use of slow transit rates to

identify important foraging areas, but the amount of successful feeding within and outside these areas can not be determined by transit rate alone.

A second foraging proxy used extensively with northern elephant seals is changes in dive shape. The D type dive, distinguished by vertical excursions (wiggles) during the bottom phase, has been hypothesized as pursuit of prey (Le Boeuf *et al.*, 1988). The present study found that of the four described dive types, feeding is highly associated with D type dives (Figure 2.7). However, over 25% of feedings occur during other dive shapes, with transit (A type) dives accounting for 16% of feedings. This means a potentially significant proportion of feeding events may be missed when using solely D type dives to examine foraging behavior. In addition, as the relative proportion of dive shapes change, such as during El Niño years (Crocker *et al.*, 2006), the proportion of feeding events associated with each dive type may also change. Therefore, care must be taken when attributing feeding behavior to various dive shapes.

When using type D dives as a proxy for feeding behavior, D dives appear to overestimate successful feeding. However, since D type dives are defined as foraging dives it is important to consider the ultimate differences between feeding (consumption of prey) and foraging behavior. Foraging encompasses many other behaviors such as searching or unsuccessfully pursuing prey. Stomach temperature measurements can only provide information about when animals successfully capture prey. Therefore, if dive behavior and specifically D type dives are used to

identify all aspects of foraging (searching, pursuing, and capture) then females on average are successfully capturing prey between 18 and 24% of the time during foraging periods. By using stomach temperature telemetry in conjunction with time-depth recorders, it is now possible to quantify the foraging success of northern elephant seal females. Further research will help elucidate how this success changes in response to environmental variation.

Previous studies using stomach temperature technology have described in detail the limitations of this technology, not the least of which is retention of the stomach telemeter in the stomach (Austin *et al.*, 2006; Bjorge *et al.*, 1995; Lesage *et al.*, 1999; Wilson *et al.*, 1995). In addition to this limitation, stomach filling may reduce the ability to identify sequential feeding events as the telemeter may become buried under undigested prey items (Ancel, Horning & Kooyman, 1997; Gremillet *et al.*, 1994). If feedings were obscured, this analysis represents at the very least a conservative estimate of the feeding behavior of northern elephant seals. However, captive feeding experiments validating the use of stomach temperature telemetry with northern elephant seals showed multiple feedings within a day could be identified, so this may not be a problem for this species (Kuhn, Chapter 1).

Conclusions

Since this research recorded stomach temperature during the early phase of the foraging migration (maximum 21 days of a 78 day trip, range 12 – 27% of total trip), this limits our ability to extrapolate the data obtained through the entire post-

breeding migration. Le Boeuf *et al.* (2000) found diving behavior changes when animals reach ‘focal foraging areas’ in the North Pacific. When dive shape distributions are compared for the two females with long stomach temperature records and matching dive records, it is clear the distributions differ between the early migration and the full migration (Figure 2.8). Interestingly, each female displayed differing distributions of dive types both during the period of stomach temperature measurements and the overall migration. The first female had a greater percentage of foraging (D) dives over the entire migration than during the early phase. This corresponded with a lower percentage of both shallow (I) and transit (A) dives over the entire migration. In contrast, the second female showed a similar increase in percentage of foraging dives but the same percentage of transit dives throughout the migration. As the distribution of dive types change during the middle and later phases of the migration, this may alter the associations between feeding and dive type. In addition, changes in the distribution of dive types may also influence the number of feeding bouts per day, length of feeding bouts, and/or number of feeding events per bout. However, it is also important to consider that intake rates may be influenced by feeding motivation (Tolkamp *et al.*, 1998). Early in the migration, I expect feeding motivation to be high as female elephant seals are recovering from the breeding fast that lasts over one month. As the migration progresses it is unknown how feeding motivation changes and how this impacts feeding rates.

To examine whether the feeding rates measured in the early migration would be appropriate to explain mass gain over the migration, a simple calculation was conducted based on diet data from Antonelis *et al.* (1987, 1994). If each female continued feeding based on the maximum feeding rates measured, the rates of mass gain could easily be explained. Assuming females ate exclusively Gonatid squid (*Gonatopsis borealis*) with a mean body size of 249 g, based on average feeding rates (7.9 – 13.4 feeding events per day) females would have to consume between 0.6 to 2.5 squid per feeding event. If females continued to feed at the maximum feeding rates they would have to eat only 0.3 to 1.1 squid per feeding event. Given that the diet of female northern elephant seals includes other species and dive behavior changes when females reach ‘focal foraging areas’, this exercise suggests the feeding behavior measured in the early part of the foraging migration could reflect feeding behavior throughout the migration.

By directly measuring the feeding behavior of northern elephant seal females it is now possible to gain greater insight into their at sea behavior. Further investigations examining the environmental variables associated with feeding will help elucidate how these animals locate prey in the dynamic marine environment. In addition, with the ability to quantify foraging success it is now possible to measure the direct impacts of environmental change on the foraging behavior of this large marine predator.

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References

- Ancel, A., Horning, M., & Kooyman, G.L. (1997) Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *Journal of Experimental Biology*, **200**, 149-154.
- Andrews, R.D. (1998) Remotely releasable instruments for monitoring the foraging behaviour of pinnipeds. *Marine Ecology-Progress Series*, **175**, 289-294.
- Antonelis, G.A., Lowry, M.S., Demaster, D.P., & Fiscus, C.H. (1987) Assessing northern elephant seal feeding-habits by stomach lavage. *Marine Mammal Science*, **3**, 308-322.
- Antonelis, G.A., Lowry, M.S., Fiscus, C.H., Stewart, B.S., & DeLong, R. (1994). Diet of the northern elephant seal. In *Elephant seals: population ecology, behavior, and physiology* (eds B.J. Le Boeuf & R.M. Laws), pp. 211-223. University of California Press, Berkeley.

- Austin, D., Bowen, W.D., & McMillan, J.I. (2004) Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos*, **105**, 15-30.
- Austin, D., Bowen, W.D., McMillan, J.I., & Boness, D.J. (2006) Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology*, **75**, 408-420.
- Bjorge, A., Thompson, D., Hammond, P., Fedak, M., Bryant, E., Aareford, H., Roen, R., & Olsen, M. (1995). Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In *Whales, seals, fish and man* (eds A.S. Blix, L. Walloe & O. Ulltange), pp. 211-223. Elsevier, Amsterdam.
- Boyd, I.L., Arnould, J.P.Y., Barton, T., & Croxall, J.P. (1994) Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology*, **63**, 703-713.
- Boyd, I.L. & Croxall, J.P. (1996) Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **74**, 1696-1705.
- Boyd, I.L., Lunn, N.J., & Barton, T. (1991) Time budgets and foraging characteristics of lactating Antarctic fur seals. *Journal of Animal Ecology*, **60**, 577-592.
- Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J.A., Gales, N.J., McDonald, B., Trumble, S.J., & Crocker, D.E. (2004) Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. *Deep-Sea Research Part II*, **51**, 2279-2303.
- Catry, P., Phillips, R.A., Phalan, B., Silk, J.R.D., & Croxall, J.P. (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Marine Ecology-Progress Series*, **280**, 261-273.
- Condit, R. & Le Boeuf, B.J. (1984) Feeding-habits and feeding grounds of the northern elephant seal. *Journal of Mammalogy*, **65**, 281-290.
- Costa, D.P. (1993) The secret life of marine mammals: Novel tools for studying their behavior and biology at sea. *Oceanography*, **6**, 120-128.

- Crocker, D., Costa, D., Le Boeuf, B.J., Webb, P.M., & Houser, D.S. (2006) Impact of El Niño on the foraging behavior of northern elephant seals. *Marine Ecology-Progress Series*, **309**, 1-10.
- Crocker, D.E., Le Boeuf, B.J., & Costa, D.P. (1997) Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **75**, 27-39.
- Crocker, D.E., Williams, J.D., Costa, D.P., & Le Boeuf, B.J. (2001) Maternal traits and reproductive effort in northern elephant seals. *Ecology*, **82**, 3541-3555.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Collier, S.O., Hagey, W.P., Kanatous, S.B., Kohin, S., & Horning, M. (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science*, **283**, 993-996.
- Estes, J.A., Jameson, R.J., & Rhode, E.B. (1982) Activity and prey election in the sea otter - Influence of population status on community structure. *American Naturalist*, **120**, 242-258.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., & Lyon, B.E. (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology*, **72**, 144-155.
- Gentry, R. & Kooyman, G.L. (1986) *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton.
- Georges, J.Y., Bonadonna, F., & Guinet, C. (2000) Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Marine Ecology-Progress Series*, **196**, 291-304.
- Gremillet, D.J.H. & Plos, A.L. (1994) The use of stomach temperature records for the calculation of daily food-intake in cormorants. *Journal of Experimental Biology*, **189**, 105-115.
- Harcourt, R.G., Bradshaw, C.J.A., Dickson, K., & Davis, L.S. (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology-Progress Series*, **227**, 11-24.
- Hassrick, J.L., Crocker, D.E., Zeno, R.L., Blackwell, S.B., Costa, D.P., & Le Boeuf, B.J. (In press) Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II*.

- Hedd, A., Gales, R., & Renouf, D. (1995) Use of temperature telemetry to monitor ingestion by a harbor seal mother and her pup throughout lactation. *Polar Biology*, **15**, 155-160.
- Hennicke, J.C. & Culik, B.M. (2005) Foraging performance and reproductive success of Humboldt penguins in relation to prey availability. *Marine Ecology-Progress Series*, **296**, 173-181.
- Hill, R.D., Schneider, R.C., Liggins, G.C., Schuette, A.H., Elliott, R.L., Guppy, M., Hochachka, P.W., Qvist, J., Falke, K.J., & Zapol, W.M. (1987) Heart-rate and body-temperature during free diving of Weddell seals. *American Journal of Physiology*, **253**, R344-R351.
- Hindell, M.A., Slip, D.J., & Burton, H.R. (1991) The diving behavior of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia, Phocidae). *Australian Journal of Zoology*, **39**, 595-619.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S., & Kelly, J.T. (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology*, **138**, 617-636.
- Kooyman, G.L. (1965) Techniques used in measuring diving capacities of Weddell seals. *Polar Record*, **12**, 391-394.
- Kooyman, G.L. (1989) *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin.
- Le Boeuf, B.J., Costa, D.P., Huntley, A.C., & Feldkamp, S. (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **66**, 446-458.
- Le Boeuf, B.J. & Crocker, D.E. (2005) Ocean climate and seal condition. *BMC Biology*, **3**, 9.
- Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., & Houser, D.S. (2000) Foraging ecology of northern elephant seals. *Ecological Monographs*, **70**, 353-382.
- Le Boeuf, B.J. & Laws, R.M. (1994) *Elephant seals: Population ecology, behavior and physiology*. University of California Press, Berkeley, USA.

- Le Boeuf, B.J., Naito, Y., Asaga, T., Crocker, D., & Costa, D.P. (1992) Swim speed in a female northern elephant seal - Metabolic and foraging implications. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **70**, 786-795.
- Le Boeuf, B.J., Naito, Y., Huntley, A.C., & Asaga, T. (1989) Prolonged, continuous, deep diving by northern elephant seals. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **67**, 2514-2519.
- Lesage, V., Hammill, M.O., & Kovacs, K.M. (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **77**, 74-87.
- Marshall, G.J. (1998) CRITTERCAM: An animal-borne imaging and data logging system. *Marine Technology Society Journal*, **32**, 11-17.
- McConnell, B.J., Chambers, C., & Fedak, M.A. (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern-Ocean. *Antarctic Science*, **4**, 393-398.
- McConnell, B.J., Fedak, M.A., Lovell, P., & Hammond, P.S. (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, **36**, 573-590.
- Naito, Y., Le Boeuf, B.J., Asaga, T., & Huntley, A.C. (1989) Long-term diving record of an adult female northern elephant seal. *Antarctic Record*, **33**, 1-9.
- Ostfeld, R.S. (1982) Foraging strategies and prey switching in the California sea otter. *Oecologia*, **53**, 170-178.
- Papastamatiou, Y.P. & Lowe, C.G. (2004) Postprandial response of gastric pH in leopard sharks (*Triakis semifasciata*) and its use to study foraging ecology. *Journal of Experimental Biology*, **207**, 225-232.
- Parrish, F.A., Marshall, G.J., Littnan, C.L., Heithaus, M., Canja, S., Becker, B., Braun, R., & Antonelis, G.A. (2005) Foraging of juvenile monk seals at French Frigate Shoals, Hawaii. *Marine Mammal Science*, **21**, 93-107.
- Putz, K. & Bost, C.A. (1994) Feeding-behavior of free-ranging king penguins (*Aptenodytes patagonicus*). *Ecology*, **75**, 489-497.
- Putz, K., Wilson, R.P., Charrassin, J.B., Raclot, T., Lage, J., Le Maho, Y., Kierspel, M.A.M., Culik, B.M., & Adelung, D. (1998) Foraging strategy of king

- penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology*, **79**, 1905-1921.
- Robinson, P.W., Tremblay, Y., Antolos, M., Crocker, D.E., Kuhn, C.E., Shaffer, S.A., Simmons, S.E., & Costa, D.P. (In press) A comparison of indirect measures of foraging behavior based on ARGOS tracking data. *Deep-Sea Research Part II*.
- Sepulveda, C.A., Kohin, S., Chan, C., Vetter, R., & Graham, J.B. (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Marine Biology*, **145**, 191-199.
- Shaffer, S.A. & Costa, D.P. (2006) A database for the study of marine mammal behavior: gap analysis, data standardization, and future directions. *Journal of Oceanic Engineering*, **31** (1).
- Shaffer, S.A., Costa, D.P., & Weimerskirch, H. (2001) Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology*, **70**, 864-874.
- Simeone, A. & Wilson, R.P. (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Marine Biology*, **143**, 825-831.
- Southwood, A.L., Andrews, R.D., Paladino, F.V., & Jones, D.R. (2005) Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiological and Biochemical Zoology*, **78**, 285-297.
- Tanaka, H., Sato, K., Matsuzawa, Y., Sakamoto, W., Naito, Y., & Kuroyanagi, K. (1995) Analysis of possibility of feeding of loggerhead turtles during interesting periods based on stomach temperature-measurements. *Nippon Suisan Gakkaishi*, **61**, 339-345.
- Tolkamp, B.J., Allcroft, D.J., Austin, E.J., Nielsen, B.L., & Kyriazakis, I. (1998) Satiety splits feeding behaviour into bouts. *Journal of Theoretical Biology*, **194**, 235-250.
- Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C.A., Weimerskirch, H., Crocker, D.E., Goebel, M.E., & Costa, D.R. (2006) Interpolation of animal tracking data in a fluid environment. *Journal of Experimental Biology*, **209**, 128-140.

- Weimerskirch, H., Doncaster, C.P., & Cuenotchaillet, F. (1994) Pelagic seabirds and the marine-environment - Foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **255**, 91-97.
- Weimerskirch, H., Gault, A., & Cherel, Y. (2005) Prey distribution and patchiness: Factors in foraging success and efficiency of wandering albatrosses. *Ecology*, **86**, 2611-2622.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A., & Costa, D.P. (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 1869-1874.
- Weimerskirch, H., Wilson, R.P., & Lys, P. (1997) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology-Progress Series*, **151**, 245-254.
- Wilson, R.P., Cooper, J., & Plotz, J. (1992) Can we determine when marine endotherms feed - a case-study with seabirds. *Journal of Experimental Biology*, **167**, 267-275.
- Wilson, R.P., Putz, K., Gremillet, D., Culik, B.M., Kierspel, M., Regel, J., Bost, C.A., Lage, J., & Cooper, J. (1995) Reliability of stomach temperature-changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology*, **198**, 1115-1135.
- Wilson, R.P., Steinfurth, A., Ropert-Coudert, Y., Kato, A., & Kurita, M. (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology*, **140**, 17-27.

Tables

2.1: Summary of dive parameters for 12 adult female northern elephant seals during the post breeding migration. Ranges provided are the minimum and maximum means for all females. Bottom time was defined as the period when the animal was at 95% of the maximum dive depth. Percent time diving was the period at sea during which the females were below 4.0 m.

	Mean (SE)	Range
Dive depth (m)	466.4 (23.2)	304.9 – 613.9
Dive duration (min)	20.1 (0.5)	17.8 – 22.9
Bottom time (min)	8.6 (0.4)	7.0 – 10.4
Surface interval (min)	2.4 (0.09)	2.0 – 3.3
% time diving	87.5 (0.008)	85.8 – 91.0

2.2: Summary of stomach temperature records and feeding events for 12 adult female northern elephant seals during the post breeding migration. Where N = 3 all values are presented instead of the range.

	N	Mean (SE)	Range
Stomach temperature record length (days)	12	7.8 (1.9)	2.3 – 21.1
Number of feedings	12	43.2 (21.1)	0 - 191
Time to first feeding (hours)	11	4.0 (1.5)	0.8 – 48.8
Time to bout feedings (days)	3	7.5 (1.8)	4.1, 8.1, 10.3
Distance to first feeding (km)	11	58.6 (21.9)	2 - 180
Distance to bout feeding (km)	3	610 (167)	281, 728, 821

Figures:

Figure 2.1: Plot of stomach temperature (red) and dive depth (blue) against time (Greenwich Mean Time) from a free-ranging female northern elephant seal. Stomach temperature record shows two single feeding events denoted by sharp declines in temperature, as indicated by arrows.

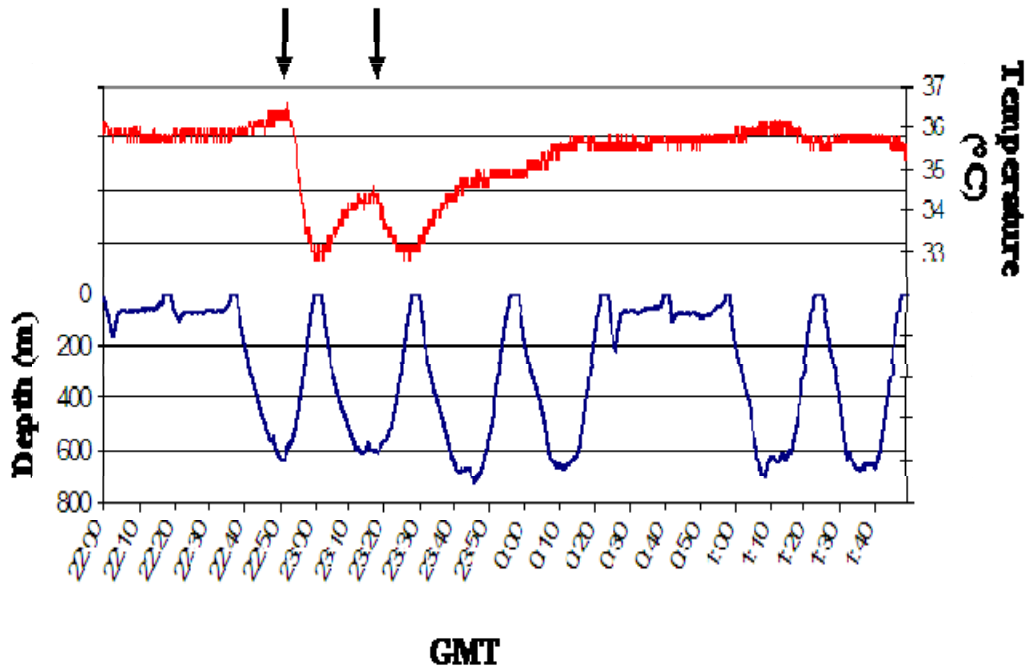


Figure 2.2: Distribution of dive types for the period of matching stomach temperature records in northern elephant seal females (N=10). A schematic of each dive type and putative function is presented for each category. Females displayed A (transit) dives most frequently, followed by D (putative foraging) dives. Percent of each dive type is presented above each bar.

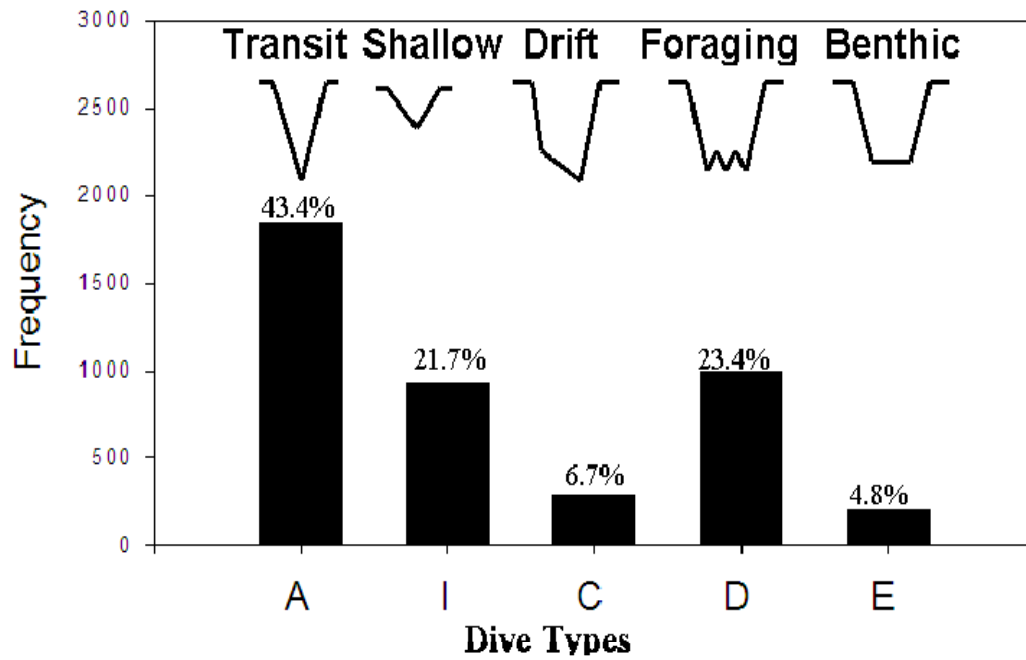


Figure 2.3A: Satellite tracks from four representative female northern elephant seals, displaying the differing foraging habitats or strategies used during the post breeding migration. Red tracks show females foraging in coastal areas or near the continental shelf, while grey tracks show females using pelagic habitats. Note one red track does not continue through the return to Año Nuevo.

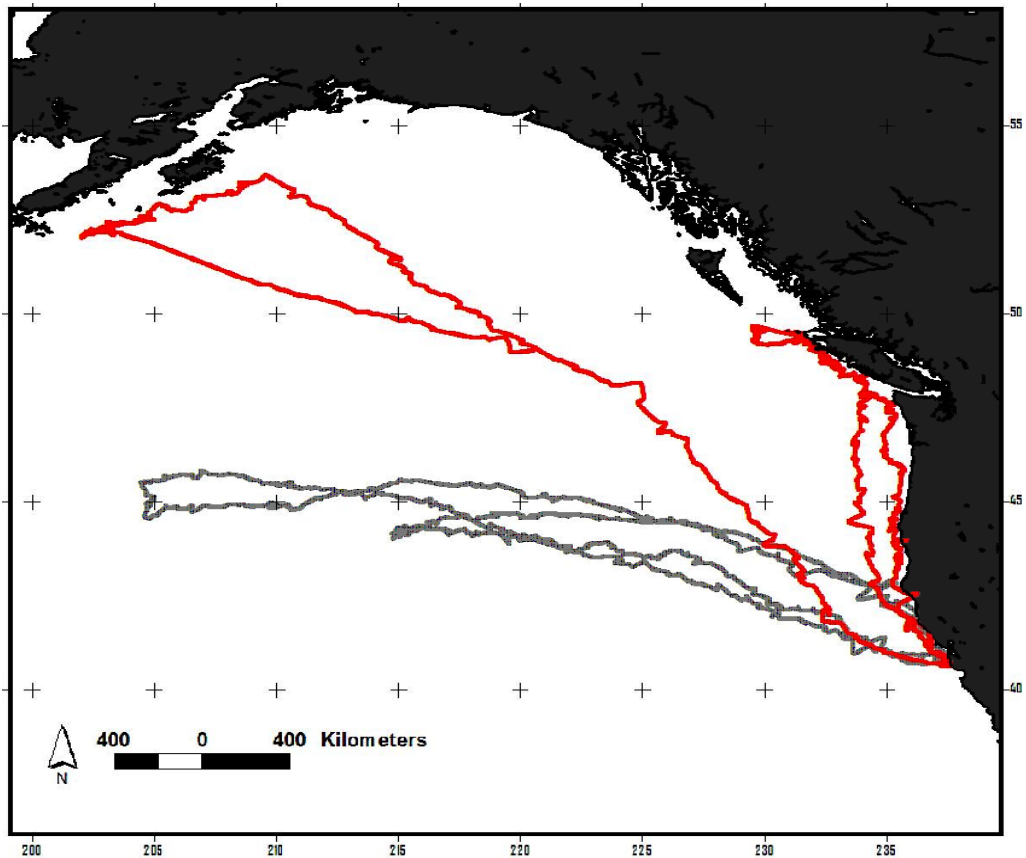


Figure 2.3B: Satellite tracks for two females with feeding areas highlighted to show the spatial and temporal differences in feeding between individuals. Tracks are plotted for the duration of the stomach temperature records (Female A: 12.1 days, Female B: 10.3 days). Grey circles (Female A) and triangles (Female B) represent feeding events for each female. Female B fed 191 times during the length of the stomach temperature record while female A fed only 2 times.

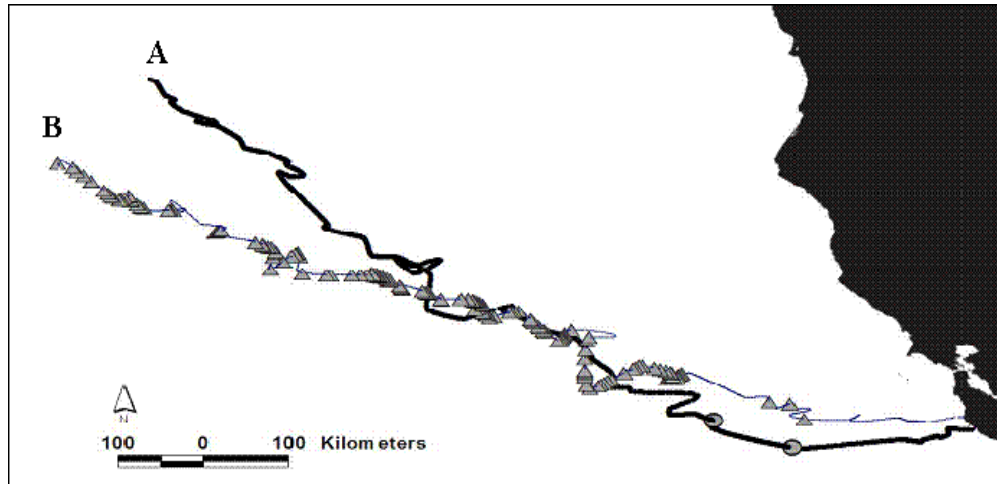


Figure 2.4: Top: Distribution of feeding events by hour for female northern elephant seals that displayed bout feeding behavior (N=3). Note feeding occurs at all hours. Bottom: Diel cycle in dive depths for the same females with matching dive records (N=2). Error bars are SE. Shaded area indicates period of night. Feeding rate increases just after sunrise and drops sharply after sunset.

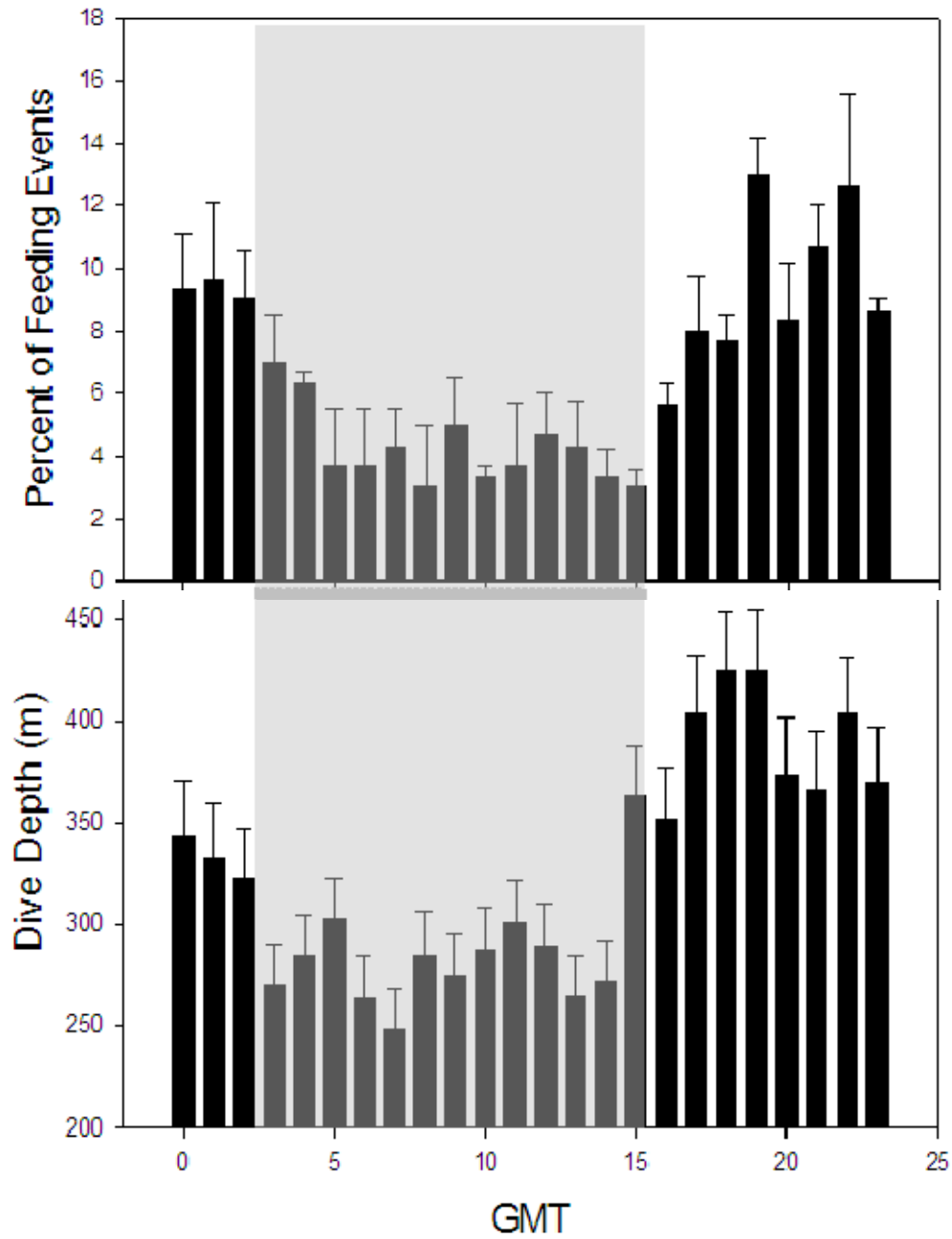


Figure 2.5: Distribution of transit rates (m s^{-1}) displayed by female northern elephant seals for the length of time of the stomach temperature records ($N=10$). Transit rates were calculated between interpolated satellite positions (Tremblay *et al.*, 2006). Grey areas indicate the proportion of each transit rate associated with feeding events.

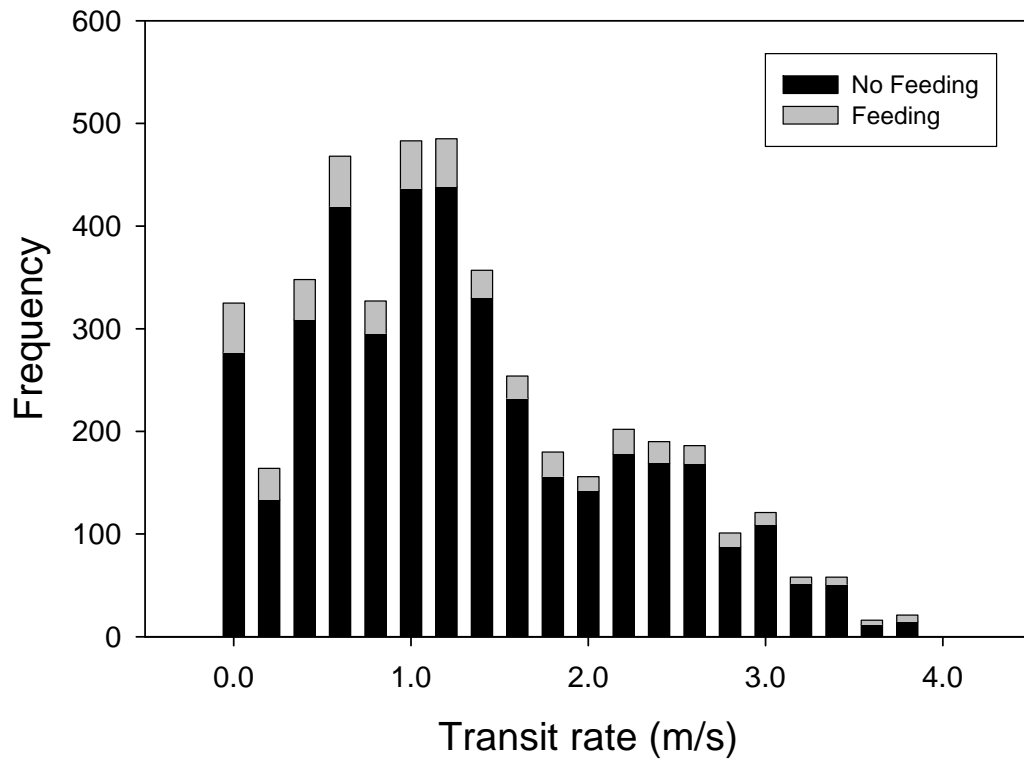


Figure 2.6A: Relationship between two day average transit rate (m s^{-1}) and number of feedings per day for female northern elephant seals displaying bout feeding behavior ($N=3$). As the two day average transit rate decreases the number of feedings per day increases ($r^2=0.33$, $p<0.01$). Dashed line represents cutoff used by Le Boeuf *et al.* (2000) to identify ‘focal foraging areas’ based on a transit rate of less than 0.4 m s^{-1} .

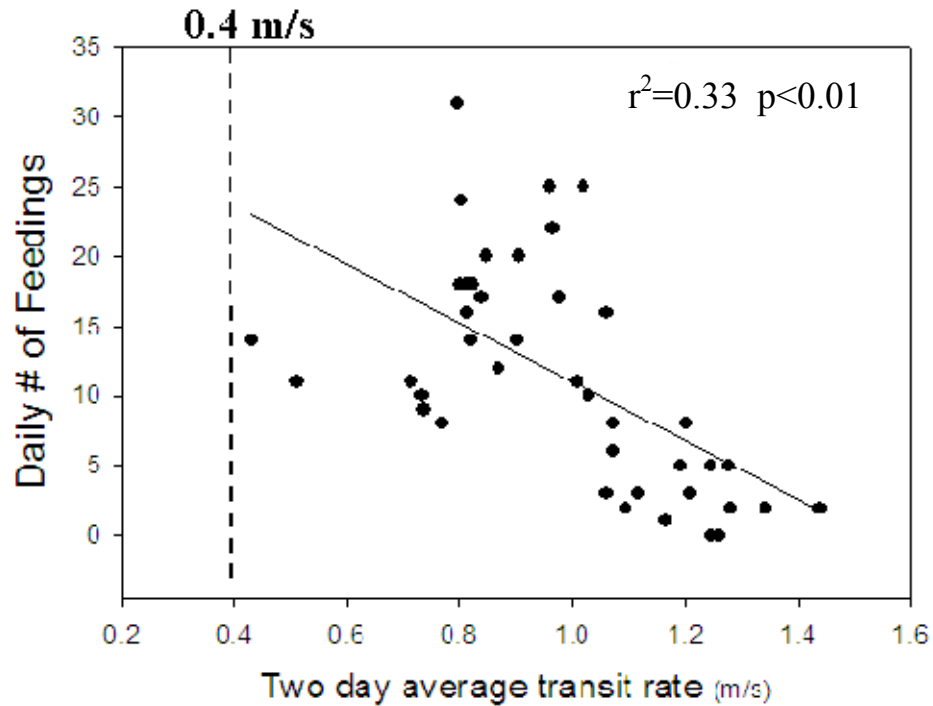


Figure 2.6B: Relationship between interpolated transit rate (m s^{-1}) and number of feedings for all females ($N=10$, $r^2=0.73$, $p<0.01$). The relationship is also similar for the three females that displayed bout feeding behavior.

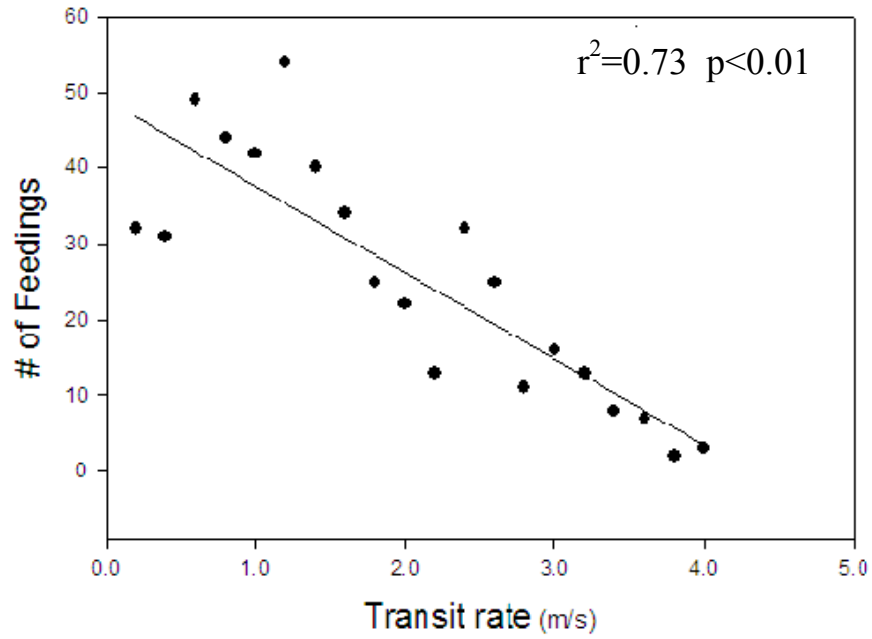


Figure 2.7: Distribution of dive types associated with successful feeding events based on stomach temperature records in female northern elephant seals (N=10). A schematic of each dive type and putative function is presented in Figure 2.2. Most feeding is associated with D type (putative foraging) dives; however 16% of the time feeding occurs with A (transit) dives. Percent of feeding events associated with the dive type is given above each the category.

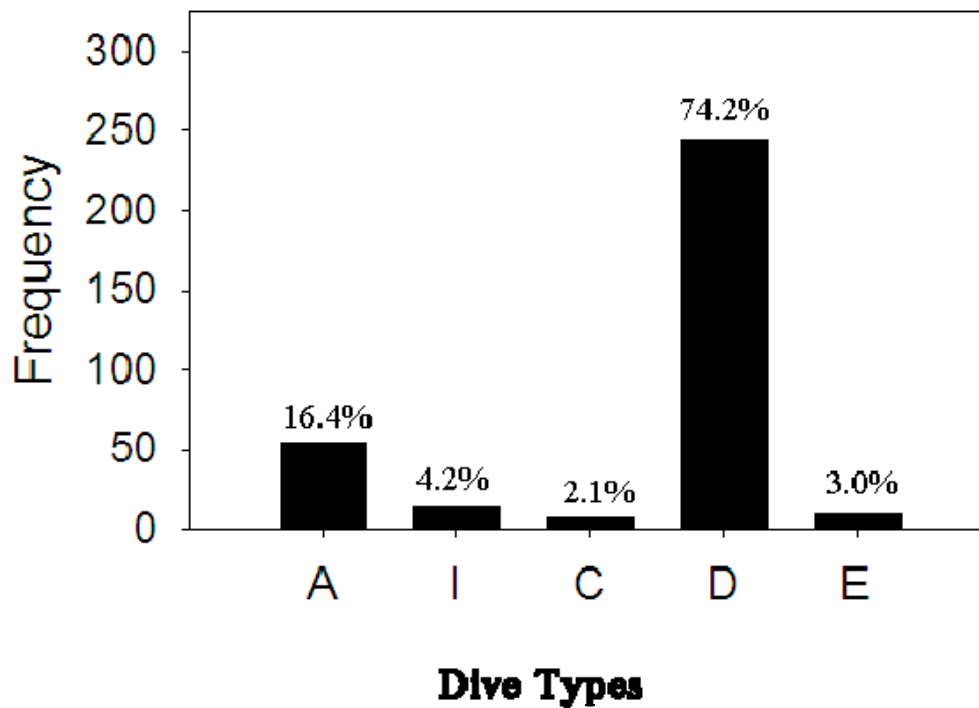
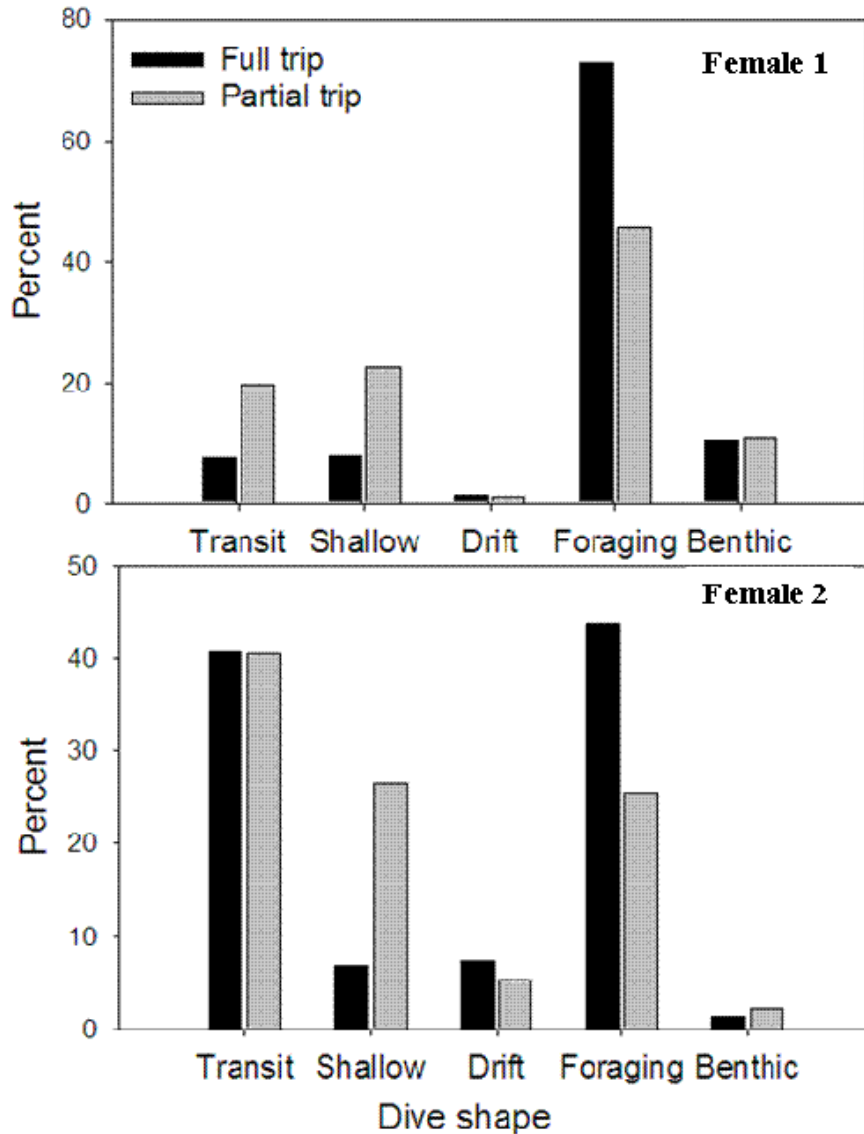


Figure 2.8: Distribution of dive types for the 2 female northern elephant seals (1 and 2) that displayed bout feeding and had matching dive records. Full trip (black bars) is the distribution for the female’s complete migration and partial trip (gray bars) is for only the period of the length of the stomach temperature record (8.1 and 10.3 days, respectively). Both females displayed a greater percent of foraging dives over the entire migration than measured in the early phase (partial trip). In addition, distributions for the early phase and full migration differed between individuals.



Chapter 3: Interannual variation in the at sea behavior of adult female California sea lions (*Zalophus californianus*): habitat utilization and diving behavior

Summary

I examined the winter foraging behavior of 30 adult female California sea lions (*Zalophus californianus*) over 3 years (2003, 2004, and 2005). Satellite transmitters and time-depth recorders were deployed to characterize foraging behavior and examine interannual changes in behavior in relation to environmental variation. Females travelled on average 66.3 ± 11.0 km from the rookery during foraging trips that lasted 47.9 ± 2.0 hours. Of the $67.1 \pm 1.3\%$ of time at sea, females spent $41.5 \pm 1.5\%$ of their time diving and displayed short, shallow dives (2.1 ± 0.2 minutes and 58.2 ± 8.4 m, respectively). Individual variation, which was similar among years, was found for all diving and movement parameters. Among years, there were significant differences in movement parameters (transit rate: $F_{2,23}=11.0$, $p<0.01$; trip duration: $F_{2,23}=5.2$, $p<0.01$; total distance travelled: $F_{2,23}=5.6$, $p=0.01$; percent time at sea: $F_{2,23}=5.8$, $p<0.01$), but no significant differences in dive behavior. Females had significantly longer trip durations in 2004 and 2005, but travelled further from the rookery in 2004 (up to 445 km). Time spent in transit, diving and haulout varied among years with the greatest amount of time in transit occurring in 2004 ($43.1 \pm 2.6\%$). The differences in movement patterns among years correlated with increased sea surface temperatures and decreased upwelling in 2004 and 2005. The flexibility

in at sea behavior in response to environmental variation displayed by California sea lions may be linked to the continuing growth of sea lion populations.

Introduction

The foraging behavior of marine predators is shaped in part by the distribution and abundance of prey in the dynamic and patchy marine environment. Predators must be able to cope with environmental variation in order to obtain sufficient resources for survival, growth, and reproduction. Thus, the study of marine predator foraging behavior can provide insight into the spatial and temporal variation in prey resources (Burns *et al.*, 2004; Croll *et al.*, 2005; Georges, Tremblay & Guinet, 2000b; Goebel *et al.*, 1991; Hindell, Slip & Burton, 1991; McConnell, Chambers & Fedak, 1992; Weimerskirch, Doncaster & Cuenotchaillet, 1994), as well as strategies animals use to deal with changes in prey abundance and distribution (Boyd *et al.*, 1994; Costa, Croxall & Duck, 1989; Crocker *et al.*, 2006; Goebel, 1998; Hennicke & Culik, 2005; Trillmich *et al.*, 1991b).

Otariid seals (sea lions and fur seals), as central place foragers, are dependent upon local resources and respond to environmental variation by altering at sea behavior. Adult females are constrained to pup rearing sites during lactation, alternating between foraging trips at sea (1 to 14 days) and periods on land (1 to 3 days) suckling a pup, for periods that range from 4 months to 3 years (Costa, 1991; Trillmich & Weissing, 2006). Due to the close link between female otariids and the

local environment, changes in at sea behavior have been observed in response to environmental variation both seasonally and interannually (Boyd, 1999; Boyd *et al.*, 1994; Costa, Croxall, & Duck, 1989; Costa & Gales, 2003; Georges, Bonadonna & Guinet, 2000a; Goebel, 1998; Mattlin, Gales & Costa, 1998; McCafferty *et al.*, 1998). Previous research with fur seals and sea lions has demonstrated that females can cope with environmental variability by altering foraging locations and dive behavior (Beauplet *et al.*, 2004; Boyd *et al.*, 1994; Costa *et al.*, 2003; Feldkamp, Delong, & Antonelis, 1991; Georges *et al.*, 2000b; Goebel, 1998; Mattlin *et al.*, 1998; Merrick & Loughlin, 1997), as well as increasing trip durations during period of low prey availability (Beauplet *et al.*, 2004; Boyd *et al.*, 1994; Costa *et al.*, 1989; Merrick *et al.*, 1997; Trillmich & Ono, 1991a).

However, there is a limit to this plasticity in foraging behavior as time at sea is constrained by a pup fasting on the beach. A female must find a way to balance time at sea acquiring resources with time on land nursing her pup. This balance can be disrupted if females are forced to travel further or spend more time searching in response to changes in prey distribution or abundance (Trillmich *et al.*, 1991a). As prey resources become less available, females will eventually abandon their pups for their own survival (Francis & Heath, 1991; Soto, Trites & Arias-Schreiber, 2004). Therefore, examining the foraging behavior of otariids can provide insight into not only how animals allocate time between foraging and reproduction, but also the strategies animals use to deal with environmental variation in foraging areas.

California sea lions (*Zalophus californianus*) are an ideal species with which to examine the link between environmental variation and changes in at sea behavior. California sea lions are an abundant otariid species that occur along the west coast of North America from southern Canada to Mexico (Caretta, Barlow & Forney, 2001). Populations have increased markedly since the end of commercial hunting in the 1940's, and following the passage of the Marine Mammal Protection Act (1972). Since 1972, populations have grown at an annual rate up to 6.2% (Caretta *et al.*, 2001). With increasing population size, there is escalating competition between California sea lions and almost all commercial and recreational fisheries in California (Beeson & Hanan, 1996; NMFS, 1997). Therefore, obtaining information on the foraging behavior and habitat use of California sea lions can contribute to a better understanding of these fisheries conflicts.

Despite the growing population, increasing competition, relative accessibility, and need for data on the foraging behavior of California sea lions, there are surprisingly few published reports on at sea behavior. These studies focused on adult females from one breeding rookery (San Miguel Island) and found that dive times averaged 1.5 to 2.8 minutes and mean dive depths ranged between 20 and 98 m (Feldkamp, DeLong & Antonelis, 1989, 1991). Although dive behavior has been measured, at sea distributions are less understood. Antonelis *et al.* (1990), using VHF tags and aerial surveys, were able to locate ten animals at sea, providing data on the habitats used by these females. While this study provided insight on where

females are found at sea, information linking at sea distributions with dive behavior is still lacking.

Previous research has shown the significant impacts of El Niño events on the energetics, foraging trip durations, and pup survival of California sea lions (Costa, Antonelis & DeLong, 1991; Feldkamp *et al.* 1991, Francis *et al.*, 1991; Heath *et al.*, 1991). These studies have demonstrated the impact of extreme environmental change (Trillmich *et al.*, 1991b), however, there is still little known about these animals respond to more typical small scale environmental variation. The aim of this research was to characterize the foraging behavior of California sea lions, by measuring at sea distributions, dive behavior, and habitat use of adult female sea lions. In addition, this study examined how behavior changed in association with interannual environmental variation in foraging areas.

Materials and Methods

Animal handling

Research was conducted at San Nicolas Island, CA (33.275°N, 119.576°W) in winter of 2003, 2004, and 2005. San Nicolas Island is the most westerly of the southern Channel Islands and is one of the two major rookeries of California sea lions in this region (Figure 3.1). Instruments were deployed in October (2004) and November (2003 and 2005) and recovered in December (2003 and 2004) and January (2006). A total of thirty two adult female California sea lions were

instrumented: eight in 2003, and twelve in both 2004 and 2005. Sea lions were captured using custom-made hoop nets (Fuhrman Diversified, TX). Only lactating females (determined by ability to express milk from mammary gland) were instrumented. Animals were sedated using gas anesthesia (Isoflurane) administered with oxygen via a field portable vaporizer (Gales & Mattlin, 1998), and weighed using a hanging digital scale (± 0.1 kg, Dynalink, Measurement Systems Inc., WA).

Measuring at sea behavior

Each animal was equipped with a satellite tracking transmitter (PTT, Sirtrack, New Zealand or Wildlife Computers, WA) and a time-depth recorder (TDR, MK8 or MK9, Wildlife Computers, WA). To facilitate instrument recovery, each female was also equipped with a VHF tag (Sirtrack, New Zealand). Instruments were mounted on a neoprene base, attached to high tension mesh netting using cable ties, and glued to the dorsal pelage with quick set epoxy (Loctite™ or Devcon™ 5-minute epoxy).

PTTs transmitted at a frequency of 34 or 45 seconds while on the surface. Satellite locations were obtained using the Argos satellite system (Service Argos, Toulouse, France). TDRs sampled depth at four second intervals. Females were recaptured and physically restrained while instruments were removed by cutting through the neoprene base. The remaining epoxy mounts fell off during the subsequent molt.

Data processing and analysis

Using satellite location qualities defined by Argos, locations qualities of 3-0, A, and B, were filtered following the methods of Tremblay *et al.* (2006), based on a maximum transit rate of 9 km hr⁻¹ and a minimum time between locations of 10 minutes. As I was primarily interested in regions where sea lions were actively foraging, I limited the analysis to only locations that were associated with diving behavior. This assured the home ranges measured focused on putative foraging areas and excluded transit to and from the rookery. Maximum distance travelled was calculated for each foraging trip as the straight line distance from the rookery to the farthest satellite location. Mean distance was calculated as the average of all locations during a foraging trip. The sum of distances between each satellite location was used to calculate total distance travelled. Total distance was divided by time at sea to get mean transit rate. Differences in spatial distributions among years were examined using Kernel home range analysis (Animal Movement Extension, Arcview GIS). This analysis created a fixed kernel home range based on a crossed validation smoothing parameter. Satellite tracks were either sub-sampled or interpolated (Tremblay *et al.*, 2006) to ensure each female contributed equally to the home range analysis within a year and that each year had an equal number of locations. The 95% and 50% kernels were chosen for comparison between individuals within a year and density contours with decreasing 5% increments were used to examine interannual differences in foraging areas.

Dive data were processed using a custom made zero-offset correction algorithm and analysis program (IKNOS toolbox, Y. Tremblay unpublished). Dives were defined by a minimum depth of four meters and duration of 16 seconds. Maximum dive depth, dive duration, and surface interval were calculated for each dive. Bottom time was calculated as the time between the first and last inflection points at greater than 70% of the maximum depth. Time at sea was calculated from TDR records as the time the animal left the rookery to the time it returned. Percent time diving was the percent of time at sea for which an animal was at depths greater than 4.0 meters. Dive rate was the number of dives per hour at sea. Behavior was divided into three categories: diving, transit, and haulout to examine changes in behavior among years. Transit was defined as time at sea not spent diving and could also include rest periods when no swimming occurs. However, Feldkamp *et al.* (1991) found female California sea lions rest a minimal amount of time while at sea (1.6 to 4.1%).

Environmental variation

Sea surface temperature (SST) and a local upwelling index were used as indices of changes in the environment. The SSTs for 2003 and 2004 were a monthly average from AVHRR Pathfinder V5 Global area coverage (0.05 degree resolution, <http://las.pfeg.noaa.gov/oceanwatch.html>). Sea surface temperatures for 2005 were from AVHRR Global Area Coverage (11 km resolution). Monthly upwelling index was derived by the Environmental Research Division of the National Marine

Fisheries Services. This index used wind stress to calculate the extent of Ekman transport, which brings cold, nutrient rich waters to the surface. The cold water promotes high primary productivity, which can support larger predators, including fish, birds, and marine mammals (Barber & Smith, 1981; Croll *et al.*, 2005; Hutchings *et al.*, 1995). The upwelling index location of 33°N, 119°W was approximately 55km southeast of San Nicolas Island, and 120km from the mid point of the major foraging grounds identified in the present study.

Statistical analysis

Summary data are reported as mean \pm SE. Statistical analysis was conducted using SYSTAT 10 (SPSS Inc. 2000). Ranges presented are the minimum and maximum of the female averages. Comparisons among years were conducted using an ANOVA with a Tukey post-hoc test to determine which years were significantly different. Bartlett's homogeneity of variances test was used to compare variances among years. Relationships between mass and dive and movement parameters were tested using least-squares linear regression analysis. Due to multiple regression analyses with mass, a Bonferroni procedure was used to control type I error rates. Therefore, linear regressions were considered significant at $p < 0.005$. Data that were non-normal were \log_{10} transformed. Percent data were arcsine transformed. All other contrasts were considered significantly different at $p < 0.05$.

Results

In 2003, satellite tracks were obtained from seven females and dive records from six females. Five animals had a matching satellite track and dive record. In 2004, satellite tracks were recorded for eight females and dive records recovered from eight females. Six animals had a matching satellite track and dive record. In 2005, matching satellite tracks and dive records were recovered from 11 females.

Females ranged in mass from 61.8 – 109.0 kg and standard length from 149 – 177 cm. There was no significant difference in female mass or standard length among years ($F_{2,22}=1.02$, $p=0.38$, $F_{2,22}=0.32$, $p=0.73$, respectively). There were no relationships between mass and any of the dive parameters (dive depth: $r^2=0.04$, $p=0.33$, duration: $r^2=0.10$, $p=0.12$, bottom time: $r^2=0.20$, $p=0.025$, dive rate: $r^2=0.16$, $p=0.048$, surface interval: $r^2=0.19$, $p=0.03$; percent time diving: $r^2=0.22$, $p=0.017$) or movement parameters (percent time at sea: $r^2=0.01$, $p=0.94$, maximum distance travelled: $r^2=0.01$, $p=0.67$, average distance travelled: $r^2=0.02$, $p=0.057$, and total distance travelled: $r^2=0.01$, $p=0.77$).

Characterization of at sea behavior

For all years combined, trip durations averaged 47.9 ± 2.0 hours (range 15.7 – 96.5 hours) and females travelled an average distance of 66.3 ± 11.0 km from the rookery (range 8.3 – 291.4 km, Table 3.1). Average transit rate was 0.84 ± 0.1 m s⁻¹ (range 0.5 – 1.6 m s⁻¹). Concentrated foraging occurred in an area 60 km northwest of San Nicolas, south of the northern Channel Islands (Figure 3.1). Females also dispersed eastward to the coast, and north of the Channel Islands towards Monterey

Bay. Most satellite locations were along the continental shelf within the 500 m isobath (Figure 3.1).

Foraging locations and the size of foraging areas used varied between individuals in all years (Figure 3.2 A, B). The individual 95% kernel home ranges varied from 337 to 38,293 km² and the 50% kernel home ranges varied from 24 to 4011 km² (Table 3.1). The individual variation measured in home range size was similar across all years (Bartlett's $k^2=0.27$, $df=2$, $p=0.87$). Although the majority of females travelled northwest to foraging grounds located south of the northern Channel Islands (58%), two other patterns in foraging locations were identified (Figure 3.2 A, B). Twenty three percent of the females travelled northeast to forage near the mainland coast and 15% travelled further north, foraging along the mainland coast beyond the northern Channel Islands. One female in 2003, did not travel beyond 31 km from the island, foraging on average just 8 km from San Nicolas (Table 3.1).

On average females displayed short, shallow dives (Table 3.2). The maximum dive depth was 482 m and maximum dive duration was 14.7 minutes. As was the case for home ranges, individual females showed differences in diving behavior, with average dive depths ranging from 14 to 171 m (Table 3.2). The variation in individual dive depths was similar across all years (Bartlett's $k^2=1.5$, $df=2$, $p=0.46$). As found with dive depths, individuals showed large variation in all dive parameters and this variation was similar across years (Table 3.2).

Females spent $67.1 \pm 1.3\%$ of their time at sea (range 51.0 – 75.7%, Table 3.2). Of the time at sea, $41.5 \pm 1.6\%$ was spent diving (range 24.5 – 53.8%), with an average of 13.2 ± 1.0 dives per hour (range 3.4 – 22.2 dives hour⁻¹). There was a significant negative relationship between dive rate (dives hour⁻¹) and average dive depth (Depth = $-0.11 * \text{Dive rate} + 19.56$, $r^2 = 0.80$, $p < 0.001$).

Interannual variation in behavior

Movement parameters were significantly different among years (Table 3.3). Transit rate was significantly lower in 2005 than 2003 ($F_{2,23} = 11.0$, $p < 0.01$, Tukey post hoc test $p < 0.01$) and 2004 (Tukey post hoc test $p < 0.01$, Table 3.3). Percent time at sea was also significantly different among years ($F_{2,22} = 5.82$, $p = 0.009$; 2003 = $60.5 \pm 3.2\%$, 2004 = $70.2 \pm 1.4\%$, 2005 = $68.6 \pm 1.4\%$), with females in 2003 spending the least amount of time at sea (Tukey post hoc test 2003 and 2004 $p = 0.01$, 2003 and 2005 $p = 0.03$). This was a result of significantly shorter trip durations in 2003 ($F_{2,22} = 5.25$, $p = 0.001$; Tukey post hoc test 2003 and 2004 $p = 0.03$, 2003 and 2005 $p = 0.02$) and was visible in the differing distribution of time between transit, haul-out, and diving among years (Figure 3.3).

There was a trend for greater mean and maximum distance travelled by females in 2004 ($F_{2,23} = 2.6$, $p = 0.09$, $F_{2,23} = 2.6$, $p = 0.09$, respectively). In addition, total distance travelled was significantly different among years ($F_{2,23} = 5.6$, $p = 0.01$). Females in 2004 travelled a significantly greater total distance during foraging trips than in 2005 (Tukey post hoc test $p < 0.001$). Not only was total distance different

between years, but females in 2004 also showed significantly greater variation in total distance travelled (Bartlett's $k^2=35.6$, $df=2$, $p<0.01$). Although foraging was concentrated in similar areas in all three years (Figure 3.2B), the 95% kernel home range for all females in 2004 was 2.3 times larger than in 2003 and 2.1 times larger than in 2005 (Figure 3.4, 13,743km², 5,865 km², and 6,445km², respectively). Similarly, the 50% kernel home range for all females in 2004 was 2.1 and 3.1 times larger than in 2003 and 2005, respectively (Figure 3.4, 1,198km², 570 km², and 380km², respectively).

Dive depth, dive duration, and surface interval did not differ significantly among years ($F_{2,22}=0.53$, $p=0.60$; $F_{2,22}=0.52$, $p=0.60$; $F_{2,22}=0.20$, $p=0.82$; respectively). There was also no significant difference among years for dive rate ($F_{2,22}=0.74$, $p=0.49$) or percent time diving ($F_{2,22}=1.10$, $p=0.35$). There was a trend for longer bottom times in 2004, than 2003 and 2005 ($F_{2,22}=3.33$, $p=0.055$; Tukey post hoc 2004 and 2003 $p=0.07$, 2004 and 2005 $p=0.02$).

Environmental variation

Differences among years were found for both sea surface temperature and regional upwelling. In the area where females concentrated foraging, sea surface temperatures were up to 2.0°C warmer in 2004 and 2005, compared to 2003 (Figure 3.5). While regional upwelling did not differ among years during the months of tracking (November – January), the upwelling index was considerably lower earlier in the year for both 2004 and 2005 (Figure 3.6). In June of 2004 and 2005, the

upwelling index was 218 and 239 m³/s/100 m coastline, respectively. Maximum upwelling in 2004 and 2005 were similar at only 65% of the average maximum and 55% of the maximum in 2003 (Figure 3.6).

Discussion

Characterization of at sea behavior

The time at sea and movement patterns of lactating female California sea lions are ultimately constrained by the need to return to the rookery to nurse their pups. This study provides the first data on the at sea distribution of California sea lions on San Nicolas Island. Previous research conducted at San Miguel Island (Figure 3.1), found females travelled primarily northwest to foraging grounds 54 km from the rookery (Antonelis, Stewart & Perryman, 1990), during foraging trips of approximately 73 hours. If San Nicolas sea lions were using the same foraging grounds (northwest of San Miguel), they would have to travel over 150 km to reach the foraging areas. Instead, females from San Nicolas travelled on average only 66 km to foraging grounds directly south of the northern Channel Islands (Figure 3.1). By using foraging grounds closer to the island females were able to maintain average trip durations of less than 2 days, which are similar to other otariid species (Costa, 1991).

Interestingly, the foraging grounds used by females breeding on San Nicolas Island were less than 60 km from San Miguel Island. Observed differences in

primary foraging grounds between the two rookeries may be attributable to the fact that research was conducted in different years and seasons (San Miguel: 1985 July-August, this study: 2003-2005 October-November). In addition, separation of foraging grounds may be a strategy to decrease intra-specific competition. In the Pribilof Islands, northern fur seals (*Callorhinus ursinus*) from different rookeries, both on the same island and different islands, showed segregation of foraging grounds (Robson *et al.*, 2004). However, there is still overlap as some females from San Nicolas (15%) travelled to the foraging areas used by San Miguel females. As these females were observed suckling pups in December, it appears that females from San Nicolas can reach the same foraging grounds used by San Miguel females (by making longer trips) and maintain pups, although the pup condition was unknown. Simultaneous measurements of the at sea distribution of sea lions from both islands (San Nicolas and San Miguel) are necessary to directly examine if foraging location differences are a result of studies conducted in differing years or seasons, or if they indeed represent spatial segregation of foraging grounds between breeding rookeries.

Although population level descriptions of the at sea distribution of California sea lions provides much needed information on the species, with the large sample size examined it was also possible to assess variation in distribution patterns among individual females. Marked individual variation was seen in all of the movement parameters measured (Table 3.1). Individual differences in both maximum and

average distance from the island were over 370 and 283 km, respectively. In addition, even females that travelled similar distances from the island differed in the total amount of traveling during foraging trips. For example, two females that differed by only 0.4 km in average distance travelled (SNI1-03, SNI7-04) had a two fold variation in the total distance travelled (Table 3.1). This suggests dissimilarity in foraging success between females which could be a result of individual foraging strategies or environmental variation between years. By comparing data collected across multiple years, this study found the variation measured between individuals in at sea distributions and movement patterns was similar across all years. The only movement parameter that showed differing variability among years was total distance travelled, which is discussed below in relation to environmental variation.

Female California sea lions have previously been described as shallow water divers that feed on a variety of epipelagic species (Antonelis, Fiscus & Delong, 1984; Feldkamp *et al.*, 1989; Lowry & Carretta, 1999; Lowry *et al.*, 1991). The diving behavior of sea lions from San Nicolas Island supports this description, as females spent a large amount of time at relatively shallow depths (Table 3.2). Average dive depths and durations were similar to those measured at San Miguel Island (Feldkamp *et al.*, 1991; Feldkamp *et al.*, 1989). However, the percent of time spent diving for females at San Nicolas Island was significantly greater than reported by Feldkamp *et al.* (1989) at San Miguel Island (Feldkamp $32.7 \pm 1.6\%$, present study $41.5 \pm 1.6\%$, $t_{24} = 5.7$, $p = 0.001$). Nevertheless, both sets of measurements were

within the range reported for other sea lion species (32.5 – 60.7%; Costa *et al.*, 2003; Crocker, Gales & Costa, 2001).

This study also measured extensive variation in dive behavior among female California sea lions (Table 3.2). This variation was similar in all three years, with some females diving on average under 30 m and others diving on average over 100 m. Individual differences were also observed in dive duration, bottom time, and dive rate (Table 3.2). Based on diet studies, California sea lions have been described as plastic specialists, feeding on a variety of prey species (Antonelis *et al.*, 1984; Lowry *et al.*, 1991). This variation in dive behavior may be indicative of flexibility in foraging behavior that results from females targeting prey found at a variety of depths. Conversely, this variation could result from more stable individual foraging strategies, such as found in other marine mammal species (Boyd *et al.*, 1994; Estes *et al.*, 2003; Goebel *et al.*, 1991; Harcourt, Bradshaw & Davis, 2001; Harcourt *et al.*, 2002).

Interannual behavioral and environmental variation

While extensive variability was found among individuals for at sea distribution, movements, and diving behavior, there were still significant differences in at sea behavior among years. It appears that California sea lions are able to respond to environmental variability by changing foraging locations and increasing time at sea. The strategy of increasing trip duration or time at sea to deal with seasonal and interannual variation has been documented in both fur seals (Beauplet

et al., 2004; Boyd *et al.*, 1994; Costa *et al.* 1998; Goebel, 1998) and sea lions (Costa *et al.*, 2003; Feldkamp *et al.* 1991; Merrick *et al.*, 1997). Beuplet *et al.* (2004) suggested that female subantarctic fur seals (*Arctocephalus tropicalis*) increased foraging trip duration and travelled further to foraging grounds during the winter due to low prey availability. Boyd (1999) found that female Antarctic fur seals (*Arctocephalus gazella*) almost doubled the length of foraging trips during 1993-1994, a year of low krill availability. Conversely, two years later when krill was abundant (20 times greater biomass than 1993) females spent significantly less time at sea.

In addition to differences in foraging locations and time at sea, females also spent more time in transit and travelled more extensively during foraging trips in 2004 (Figure 3.2, 3.3). Harcourt *et al.* (2002) found female New Zealand fur seals (*Arctocephalus forsteri*) spent greater time swimming between prey patches in winter when prey availability was lower. Both the increase in total distance travelled and the increase in the proportion of time spent in transit suggests in 2004 females were foraging in an environment with decreased prey availability, as compared to 2003 and 2005. In addition to the significant differences among years, females in 2004 also showed the greatest variability in total distance travelled suggesting the decreased prey availability impacted individual females differently.

In contrast to the changes in movement patterns, there were no significant differences in dive behavior among years. Studies with other otariid species have

found females change dive behavior in response to environmental variation (Costa *et al.*, 2003; Goebel, 1998; Merrick *et al.*, 1997). New Zealand fur seals respond to seasonal variation by switching from epipelagic to benthic prey species, which results in a drastic change in dive behavior (Mattlin *et al.* 1998). Georges *et al.* (2000) found that subantarctic fur seals dive deeper and longer during winter as a result of the movement of the oceanic mixed layer depth. In addition to seasonal changes, otariids change dive behavior in response to interannual variation (Boyd *et al.*, 1994; Costa *et al.*, 2003; Goebel, 1998). Boyd *et al.* (1994) found female Antarctic fur seals during periods of low prey availability increase dive rate (vertical depth/ minute) and time spent in foraging bouts. The large amount of variation between individuals in the present study may have obscured the ability to measure interannual differences in dive behavior. However, the extent of behavioral change should be considered with respect to the intensity of the environmental variation.

Previous research has shown the significant impacts of El Niño events on the energetics, foraging trip durations, diving behavior, and pup survival of California sea lions (Costa *et al.*, 1991; Feldkamp *et al.*, 1991; Francis *et al.*, 1991; Heath *et al.*, 1991). However, the response of animals to more typical interannual variation has not been examined. In late 2004 continuing into 2005, there were notable changes to oceanographic features in the eastern Pacific. Although signals are mixed, the Climate Prediction Center at the National Centers for Environmental Predictions described late 2004 and early 2005 as weak warm episode conditions defined by an

increase in water temperature and decrease in upwelling (Figures 3.5 and 3.6; <http://www.cpc.ncep.noaa.gov>). Sea surface temperatures in the Channel Islands region were up to 2.0°C warmer in 2004 and 2005, as compared to 2003 (Figure 3.5). In addition, while upwelling appears consistent among years in November and December, decreased upwelling in 2004 and 2005 was noted earlier in the year (June and July). Since upwelling is directly linked to an increase in primary productivity, I would expect a delayed impact on sea lion foraging behavior as sea lions consume prey farther up the food chain (Antonelis *et al.*, 1984; Lowry *et al.*, 1999; Lowry *et al.*, 1991). Croll *et al.* (2005) found that the abundance of blue whales (*Balaenoptera musculus*) in Monterey Bay lagged behind increases in primary productivity by 3 to 4 months. Although the relationship between blue whales, their prey, and environmental change in Monterey Bay is well understood, less is known about how environmental change impacts sea lions and their prey in the Channel Islands region.

To more accurately determine the impacts of varying ocean conditions on sea lions, it is necessary to understand the influence of environmental change on their prey species. Fisheries catch data can provide an index of the distributions and abundances of prey species. Diet studies have shown that market squid (*Loligo opalescens*), sardine (*Sardinops sagax*), and anchovy (*Engraulis mordax*) are top prey items of California sea lions in the Channel Islands (Antonelis *et al.*, 1984; Lowry *et al.*, 1999; Lowry *et al.*, 1991). A proxy of prey availability can be derived from a comparison of fishery catches for these species in the Channel Islands region

for November and December 2003 and 2004 (2005 is not yet available). Average catches for both sardine and squid were lower in 2004 (95% and 91% of 2003 catches, respectively, California Dept. of Fish and Game, Commercial landings 2003 and 2004). Additionally, the average catch for anchovy in 2004 was only 1.8% of that in 2003. Although fisheries catch data may not be an accurate measure of prey abundance, previous research examining the diet of California sea lions through scat analysis found that the occurrence of Market squid in the diet of sea lions is positively correlated with fishery catches (Lowry *et al.*, 1999). Therefore, the possible change in anchovy availability and the decrease in catches of all species in this region, may be linked to the animals expanding their foraging areas or traveling more extensively.

Overall it appears 2003 was the most productive year, based on both environmental data and sea lion behavior. In 2003, there was above average upwelling, which results in increased nutrients for primary producers, and likely more prey for large predators, such as California sea lions (Barber *et al.*, 1981; Croll *et al.*, 2005; Hutchings *et al.*, 1995). Females in 2003 spent the least amount of time at sea and the greatest amount of time on land (Figure 3.3). In 2004 and 2005, sea surface temperatures warmed, upwelling decreased, and in 2004 prey resources may have been less available. During these years, females spent a significantly greater amount of time at sea and in 2004, females travelled more extensively, spending the greatest amount of time in transit and making foraging trips to much further

destinations (Figure 3.2A, 3.3). This suggests that female California sea lions are able to alter their foraging behavior annually in order to find sufficient prey resources to support both themselves and their pups.

Conclusions

This study provided a detailed characterization of the diving and at sea movement patterns of California sea lions at San Nicolas Island. Although knowledge of population patterns in behavior provides much needed information on this species, the identification of individual differences in both movement patterns and diving behavior is also informative. Examination of individual female diving and movement patterns demonstrates that not all females display the same 'average' foraging behavior, and instead females display a range of behaviors.

Even with variation in foraging behavior among individuals, modest interannual changes in the environment resulted in significant differences in the at sea behavior of California sea lions. The individual variation measured in at sea behavior may aid females in their ability to respond to environmental change. Although it is not known if the individual variation is a result of plasticity within individuals or more prolonged individual specialization, both may serve as a buffer that helps this species cope with environmental variability. Ultimately, this flexibility in foraging behavior may be linked to the continuing success of the growing California sea lion populations.

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References

Antonelis, G.A., Fiscus, C.H., & DeLong, R.L. (1984) Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978-79. *Fishery Bulletin*, **82**, 67-76.

- Antonelis, G.A., Stewart, B.S., & Perryman, W.F. (1990) Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **68**, 150-158.
- Barber, R.T. & Smith, R.L. (1981). Coastal upwelling ecosystems. In *Analysis of marine ecosystems* (ed A. Longhurst), pp. 31-68. Academic Press, New York.
- Beauplet, G., Dubrocal, L., Guinet, C., Cherel, Y., Dabin, W., Gagnel, C., & Hindell, M.A. (2004) Foraging ecology of subantarctic fur seals (*Arctocephalus tropicalis*) breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Marine Ecology-Progress Series*, 211-225.
- Beeson, M.J. & Hanan, D.A. (1996). An evaluation of pinniped-fisheries interactions in California. Report to the Pacific States Marine Fisheries Commission, pp. 46.
- Boyd, I. (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behavioral Ecology*, **10**, 198-208.
- Boyd, I.L., Arnould, J.P.Y., Barton, T., & Croxall, J.P. (1994) Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology*, **63**, 703-713.
- Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J.A., Gales, N.J., McDonald, B., Trumble, S.J., & Crocker, D.E. (2004) Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. *Deep-Sea Research Part II*, **51**, 2279-2303.
- Caretta, J.V., Barlow, J., & Forney, K.A. (2001) U.S. Pacific marine mammal stock assessments. U.S. Department of Commerce NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-317, pp. 284.
- Costa, D.P. (1991). Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In *The behaviour of pinnipeds* (ed D. Renouf), pp. 300-344. Chapman and Hall, London.
- Costa, D.P., Antonelis, G.A., & DeLong, R. (1991). Effects of El Niño on the foraging energetics of the California sea lion. In *Pinnipeds and El Niño: Responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 156-165. Springer-Verlag, Berlin.

- Costa, D.P., Croxall, J.P., & Duck, C.D. (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, **70**, 596-606.
- Costa, D.P. & Gales, N.J. (2003) Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs*, **73**, 27-43.
- Crocker, D., Costa, D., Le Boeuf, B.J., Webb, P.M., & Houser, D.S. (2006) Impact of El Niño on the foraging behavior of northern elephant seals. *Marine Ecology-Progress Series*, **309**, 1-10.
- Crocker, D.E., Gales, N.J., & Costa, D.P. (2001) Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology*, **254**, 267-277.
- Croll, D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., Ternullo, R., & Tershy, B.R. (2005) From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology-Progress Series*, **289**, 117-130.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., & Lyon, B.E. (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology*, **72**, 144-155.
- Feldkamp, S.D., Delong, R.L., & Antonelis, G.A. (1989) Diving patterns of California sea lions, *Zalophus californianus*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **67**, 872-883.
- Feldkamp, S.D., Delong, R.L., & Antonelis, G.A. (1991). Effects of El Niño 1983 on the foraging patterns of California sea lions (*Zalophus californianus*) near San Miguel Island, California. In *Pinnipeds and El Niño: Responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 146-155. Springer-Verlag, Berlin.
- Francis, J.M. & Heath, C.B. (1991). The effects of El Niño on the frequency and sex ratio of suckling yearlings in the California sea lion. In *Pinnipeds and El Niño: Responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 192-201. Springer-Verlag, Berlin.
- Gales, N. & Mattlin, R.H. (1998) Fast, safe, field-portable gas anesthesia for otariids. *Marine Mammal Science*, **14**, 355-361.
- Georges, J.Y., Bonadonna, F., & Guinet, C. (2000a) Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface

- temperatures at Amsterdam Island. *Marine Ecology-Progress Series*, **196**, 291-304.
- Georges, J.Y., Tremblay, Y., & Guinet, C. (2000b) Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. *Polar Biology*, **23**, 59-69.
- Goebel, M.E. (1998). Female foraging behavior: Inter- and intra-annual variation in individuals. In *Behavior and ecology of the northern fur seal* (ed R. Gentry), pp. 243-259. Princeton University Press, Princeton.
- Goebel, M.E., Bengtson, J.L., DeLong, R.L., Gentry, R.L., & Loughlin, T.R. (1991) Diving patterns and foraging locations of female northern fur seals. *Fishery Bulletin*, **89**, 171-179.
- Harcourt, R.G., Bradshaw, C.J.A., & Davis, L.S. (2001) Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). *Wildlife Research*, **28**, 599-606.
- Harcourt, R.G., Bradshaw, C.J.A., Dickson, K., & Davis, L.S. (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology-Progress Series*, **227**, 11-24.
- Heath, C.B., Ono, K.A., Boness, D.J., & Francis, J.M. (1991). The influence of El Niño on female attendance patterns in California sea lions. In *Pinnipeds and El Niño: Responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 138-145. Springer-Verlag, Berlin.
- Hennicke, J.C. & Culik, B.M. (2005) Foraging performance and reproductive success of Humboldt penguins in relation to prey availability. *Marine Ecology-Progress Series*, **296**, 173-181.
- Hindell, M.A., Slip, D.J., & Burton, H.R. (1991) The diving behavior of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia, Phocidae). *Australian Journal of Zoology*, **39**, 595-619.
- Hutchings, L., Pitcher, G.C., Probyn, T.A., & Bailey, G.W. (1995). The chemical and biological consequences of coastal upwelling. In *Upwelling in the ocean: modern processes and ancient records* (eds C.P. Summerhaes, K.C. Emeis, M.V. Angel, R.L. Smith & B. Zeitzschel), pp. 64-81. Wiley and Sons, New York.

- Lowry, M.S. & Carretta, J.V. (1999) Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in Southern California (1981-1995). *CalCOFI Reports*, **40**, 196-207.
- Lowry, M.S., Stewart, B.S., Heath, C.B., Yochem, P.K., & Francis, J.M. (1991) Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981-86. *Fishery Bulletin*, **89**, 331-336.
- Mattlin, R.H., Gales, N.J., & Costa, D.P. (1998) Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **76**, 350-360.
- McCafferty, D.J., Boyd, I.L., Walker, T.R., & Taylor, R.I. (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Marine Ecology-Progress Series*, **166**, 285-299.
- McConnell, B.J., Chambers, C., & Fedak, M.A. (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern-Ocean. *Antarctic Science*, **4**, 393-398.
- Merrick, R.L. & Loughlin, T.R. (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **75**, 776-786.
- NMFS (1997) Impacts of California sea lions and Pacific harbor seals on salmonids and the coastal ecosystems of Washington, Oregon, and California., pp. 16. NOAA Tech. Report. NMFS circular 420.
- Robson, B.W., Goebel, M.E., Baker, J.D., Ream, R.R., Loughlin, T.R., Francis, R.C., Antonelis, G.A., & Costa, D.P. (2004) Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **82**, 20-29.
- Soto, K.H., Trites, A.W., & Arias-Schreiber, M. (2004) The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *Journal of Zoology*, **264**, 419-428.
- Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C.A., Weimerskirch, H., Crocker, D.E., Goebel, M.E., & Costa, D.R. (2006) Interpolation of animal tracking data in a fluid environment. *Journal of Experimental Biology*, **209**, 128-140.

- Trillmich, F. & Ono, K.A. (1991a) *Pinnipeds and El Nino: responses to environmental stress*. Springer-Verlag, Berlin.
- Trillmich, F., Ono, K.A., Costa, D., DeLong, R., Feldkamp, S., Francis, J.M., Gentry, R., Heath, C.B., Le Boeuf, B.J., Majluf, P., & York, A.E. (1991b). The effects of El Niño on pinniped populations in the Eastern Pacific. In *Pinnipeds and El Niño: responses to environmental stress* (eds F. Trillmich & K.A. Ono), pp. 247-270. Springer-Verlag, Berlin.
- Trillmich, F. & Weissing, F.J. (2006) Lactation patterns in pinnipeds are not explained by optimization of maternal energy delivery rates. *Behavioral Ecology and Sociobiology*, **59**, 1-13.
- Weimerskirch, H., Doncaster, C.P., & Cuenotchaillet, F. (1994) Pelagic seabirds and the marine-environment - Foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **255**, 91-97.

Table 3.1: Summary of mean movement parameters for 26 adult female California sea lions from 2003-2005. Last two digits in animal ID represent the year of study. ‘All females’ is the mean of the mean values for each individual. Percent deviation from the overall mean is presented for each dive parameter. Statistical differences between years are summarized in Table 3.3.

Animal ID	Max. distance (km)	% dev	Mean distance (km)	% dev	Total distance (km)	% dev	Transit rate (m/s)	% dev	Home range 95% (km ²)	% dev	Home range 50% (km ²)	% dev
SN11-03	97	-3.2	61.6	-7.1	301	-30.1	1.10	30.5	1726	-79.4	82	-91.1
SN12-03	37	-63.3	22.9	-65.5	174	-59.6	0.96	13.5	11551	37.7	1123	22.4
SN13-03	105	4.7	60.9	-8.1	722	67.3	0.95	12.4	2711	-67.7	249	-72.9
SN15-03	73	-27.1	42.2	-36.4	428	-0.8	0.98	15.9	1521	-81.9	160	-82.5
SN16-03	31	-69.7	8.3	-87.4	409	-5.2	0.96	13.5	408	-95.1	24	-97.3
SN18-03	119	17.9	82.9	25.0	505	17.1	1.17	38.7	4618	-45.0	373	-59.3
SN19-03	85	-15.6	59.8	-9.9	316	-26.6	0.79	-6.7	1121	-86.6	221	-75.9
SN11-04	96	-4.4	76.3	15.0	1875	334.9	0.66	-21.3	38293	356.3	3952	330.9
SN13-04	401	297.9	291.4	339.3	1301	201.6	1.08	28.1	1653	-80.3	233	-74.6
SN16-04	74	-26.9	48.9	-26.3	348	-19.2	0.85	0.8	5546	-33.9	538	-41.3
SN17-04	112	11.2	61.2	-7.7	642	48.8	0.90	6.4	12976	54.6	984	7.3
SN18-04	249	147.5	157.7	137.8	567	31.5	0.88	3.9	2067	-75.4	246	-73.1
SN110-04	81	-19.4	46.1	-30.5	400	-7.2	0.73	-12.8	1554	-81.5	141	-84.6
SN111-04	54	-46.5	39.7	-40.1	155	-64.0	1.57	85.8	1574	-81.2	205	-77.7
SN112-04	126	25.6	96.3	45.2	474	10.0	1.03	22.3	767	-90.9	84	-90.9
SN1100-05	55	-45.9	30.4	-54.1	155	-64.1	0.53	-37.5	2673	-68.1	145	-84.2
SN1101-05	94	-6.2	56.3	-15.1	273	-36.7	0.55	-35.3	20046	138.9	4011	337.4
SN1102-05	180	79.1	112.9	70.3	457	6.0	0.88	4.2	12420	48.0	864	-5.8
SN1104-05	64	-36.9	39.6	-40.3	206	-52.1	0.60	-28.3	2280	-72.8	333	-63.7
SN1105-05	57	-43.0	38.9	-41.4	167	-61.4	0.55	-34.8	671	-92.0	69	-92.5
SN1107-05	63	-37.9	44.9	-32.4	200	-53.7	0.55	-34.5	3213	-61.7	348	-62.0
SN1108-05	68	-32.5	39.1	-41.1	199	-53.9	0.63	-25.5	337	-96.0	61	-93.3
SN1109-05	126	24.9	95.0	43.2	340	-21.1	0.75	-11.0	1716	-79.5	188	-79.5
SN1110-05	37	-63.0	23.2	-65.1	124	-71.2	0.83	-1.9	2127	-74.7	364	-60.3
SN1111-05	92	-8.8	61.8	-6.8	334	-22.4	0.65	-22.8	1160	-86.2	131	-85.7
SN1140-05	42	-58.6	26.1	-60.6	139	-67.7	0.81	-3.8	1476	-82.4	194	-78.8
All females	101 (15)		66 (11)		431 (75)		0.84 (0.1)		5239 (1628)		589 (203)	

Table 3.2: Summary of dive parameters for 25 adult female California sea lions from 2003-2005 [Mean (SE)]. Last two digits in animal ID represent the year of study. ‘All females’ is the mean of the mean values for each individual. There were no significant differences among years for all dive parameters and there were no significant differences in individual variation between years. Percent deviation from the overall mean is presented for each dive parameter.

Animal ID	Mass (kg)	Depth (m)	% dev	Duration (min)	% dev	Bottom time (min)	% dev	Surface interval (min)	% dev	Time at sea (%)	% dev	Percent diving	% dev	Dive rate (dives/hr)	% dev
SNI1-03	96.0	31.4 (0.4)	-46.0	1.9 (0.02)	-11.0	0.8 (0.01)	33.1	4.9 (0.9)	16.9	51	-24.0	53.8	29.4	16.5	24.6
SNI2-03	73.2	26.2 (0.3)	-55.0	1.4 (0.01)	-36.9	0.4 (0.01)	-7.2	4.0 (0.7)	-48.3	61.2	-8.8	41.6	0.1	18.4	38.9
SNI4-03	87.8	103.7 (2.5)	78.3	2.9 (0.05)	33.7	0.6 (0.01)	-33.9	8.8 (1.8)	-11.2	66	-1.7	37.0	-10.9	7.7	-41.7
SNI6-03	85.4	17.1 (0.2)	-70.7	1.3 (0.02)	-41.7	0.6 (0.01)	110.6	4.0 (0.7)	-18.6	52.7	-21.5	44.5	7.1	21.3	60.9
SNI8-03	83.8	34.1 (0.4)	-41.5	1.8 (0.01)	-14.5	0.9 (0.01)	20.2	3.6 (0.6)	22.7	71.7	6.7	47.3	14.0	15.4	16.6
SNI9-03	87.0	54.6 (1.0)	-6.2	2.0 (0.02)	-7.8	0.6 (0.01)	-23.7	5.3 (1.0)	-22.4	60.1	-10.4	45.2	8.8	13.0	-1.7
SNI1-04	82.2	35.4 (0.5)	-39.3	2.0 (0.02)	-7.5	1.0 (0.01)	24.5	6.6 (0.9)	37.7	64.8	-3.4	37.2	10.4	11.2	-15.2
SNI2-04	90.6	114.3 (2.3)	96.4	3.7 (0.05)	71.2	1.1 (0.02)	-30.6	12.6 (2.6)	55.6	74.5	11.0	29.4	29.2	4.8	-63.9
SNI4-04	87.0	13.6 (0.1)	-76.7	1.3 (0.01)	-38.5	0.6 (0.01)	62.5	2.5 (0.3)	-9.3	70.6	5.2	48.9	17.7	22.2	67.4
SNI7-04	61.8	53.9 (0.7)	-7.3	2.0 (0.02)	-8.0	0.7 (0.01)	-1.5	4.2 (0.6)	-6.1	63.9	-4.8	48.2	16.1	14.6	10.4
SNI8-04	109.0	42.4 (0.4)	-27.2	1.8 (0.01)	-17.0	0.7 (0.01)	8.5	5.3 (1.0)	-4.2	67.5	0.5	36.4	-12.3	12.2	-7.5
SNI9-04	88.2	32.5 (0.3)	-44.2	1.6 (0.01)	-23.9	0.6 (0.01)	13.8	3.9 (0.6)	-15.7	74.4	10.8	38.4	-7.5	14.1	6.3
SNI11-04	94.2	171.3 (2.2)	194.4	4.3 (0.04)	98.4	1.3 (0.02)	-31.9	18.8 (2.4)	87.6	71.7	6.7	24.4	-41.1	3.4	-74.0
SNI12-04	94.8	32.0 (0.2)	-45.0	2.0 (0.01)	-8.7	1.0 (0.01)	-14.2	3.7 (0.6)	49.1	74.3	10.7	46.5	12.1	14.2	7.4

Table 3.2: Continued

Animal ID	Mass (kg)	Depth (m)	% dev	Duration (min)	% dev	Bottom time (min)	% dev	Surface interval (min)	% dev	Time at sea (%)	% dev	Percent diving	% dev	Dive rate (dives/hr)	% dev
SNI100-05	69.4	40.1 (0.2)	-30.4	1.7 (0.01)	-21.8	0.5 (0.01)	-11.8	3.0 (0.3)	-31.4	70.2	4.5	51.3	23.6	18.3	38.4
SNI101-05	86.4	30.1 (0.3)	-48.3	1.6 (0.01)	-25.3	0.5 (0.01)	3.4	4.0 (0.5)	-29.5	62.1	-7.5	45.9	10.4	17.1	29.4
SNI102-05	73.6	31.8 (0.2)	-45.4	1.7 (0.01)	-20.7	0.5 (0.01)	-4.9	3.0 (0.4)	-22.5	70.6	5.1	50.5	21.5	17.8	34.1
SNI104-05	86.2	33.1 (0.4)	-43.1	1.6 (0.01)	-25.0	0.5 (0.01)	14.9	4.1 (0.5)	-30.3	66.8	0.5	41.7	0.3	15.5	17.1
SNI105-05	91.4	63.3 (0.9)	8.8	2.1 (0.02)	-1.7	0.5 (0.01)	-28.5	7.5 (0.8)	-30.2	70.0	3.8	30.5	-26.5	8.7	-34.5
SNI107-05	96.0	133.1 (1.3)	128.7	3.7 (0.03)	73.8	1.2 (0.01)	-12.8	12.1 (1.1)	71.8	75.7	12.7	30.8	-25.8	5.0	62.6
SNI108-05	72.0	56.7 (0.4)	-2.6	1.9 (0.01)	-11.3	0.4 (0.01)	-42.5	3.2 (0.3)	-49.2	75.6	12.6	48.4	16.5	15.2	15.0
SNI109-05	78.6	23.0 (0.1)	-60.6	1.5 (0.01)	-30.7	0.6 (0.01)	17.4	4.2 (0.5)	-10.8	65.7	-2.2	39.4	-5.0	15.9	19.9
SNI110-05	90.0	135.3 (1.6)	132.5	3.4 (0.03)	56.5	0.7 (0.01)	-33.0	9.3 (1.1)	6.5	60.1	-9.3	42.5	2.3	7.6	-42.8
SNI111-05	63.6	54.0 (0.5)	-7.2	2.1 (0.01)	-3.9	0.7 (0.01)	-2.3	4.1 (0.4)	-4.6	69.5	3.5	47.2	13.7	13.7	3.6
SNI140-05	87.4	91.8 (1.3)	57.7	2.6 (0.02)	22.3	0.7 (0.01)	-29.9	9.8 (1.2)	-3.5	67.4	0.4	31.2	-24.9	7.1	-46.2
All females	84.6 (2.2)	58.2 (8.4)		2.2 (0.2)		0.7 (0.05)		6.0 (0.8)		67.1 (1.3)		41.5 (1.6)		13.2 (1.0)	

Table 3.3: Summary of movement parameters by year for 26 adult female California sea lions in 2003 (N=7), 2004 (N=8), 2005 (N=11). Trip duration is for 25 females (2003, N=6). Means are presented \pm SE, NS= not significantly different.

	2003	2004	2005	Significant differences	
Maximum distance (km)	78.2 (12.7)	149.2 (41.7)	79.8 (12.7)	Trend: 2004 > 2003=2005	$F_{2,23}=2.6$ $p=0.09$
Mean distance (km)	48.4 (9.7)	102.2 (30.2)	51.6 (8.6)	Trend: 2004 > 2003=2005	$F_{2,23}=2.6$ $p=0.09$
Total distance traveled (km)	407.9 (65.9)	720.3 (203.6)	235.9 (31.3)	2004 > 2005	$F_{2,23}=5.6$ $p=0.01$
Mean transit rate (m/s)	0.98 (0.04)	0.96 (0.10)	0.67 (0.04)	2005 < 2004=2003	$F_{2,23}=11.0$ $p<0.01$
Trip duration (hours)	27.5 (3.2)	53.9 (1.5)	54.7 (1.4)	2003 < 2004=2005	$F_{2,22}=5.2$ $p=0.01$
Home range area 95% (km²)	3379 (1454)	8054 (4549)	4375 (1858)	NS	--
Home range area 50% (km²)	319 (140)	798 (462)	610 (347)	NS	--

Figures:

Figure 3.1: Distribution of all filtered at sea satellite locations for 26 adult female California sea lions from San Nicolas Island (SNI). Most locations were along the continental shelf within the 500 m isobath. Females concentrated foraging to the northwest of the island and along the mainland coast to the northeast. Previous research examining California sea lion at sea behavior was conducted at San Miguel Island (SMI).

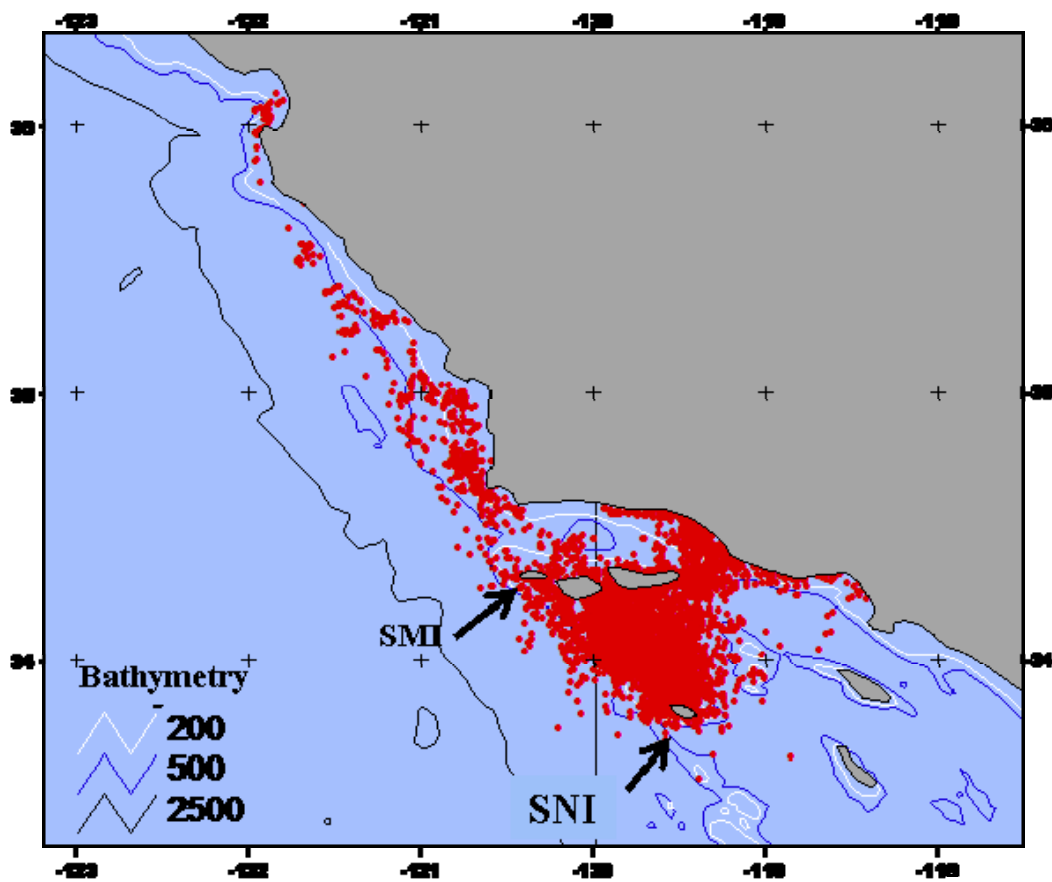


Figure 3.2 A) 95% kernel home ranges for each individual by year. Home range was calculated using only satellite locations associated with diving. Each color represents a different female and the grey shaded area is the kernel for all females combined in each year. To help visualize each female, two panels are presented for each year and distance scales differ between years. Differences between females' home range area varied up to 37,956 km². Variation between individual home ranges was similar among years.

Figure 3.2A:

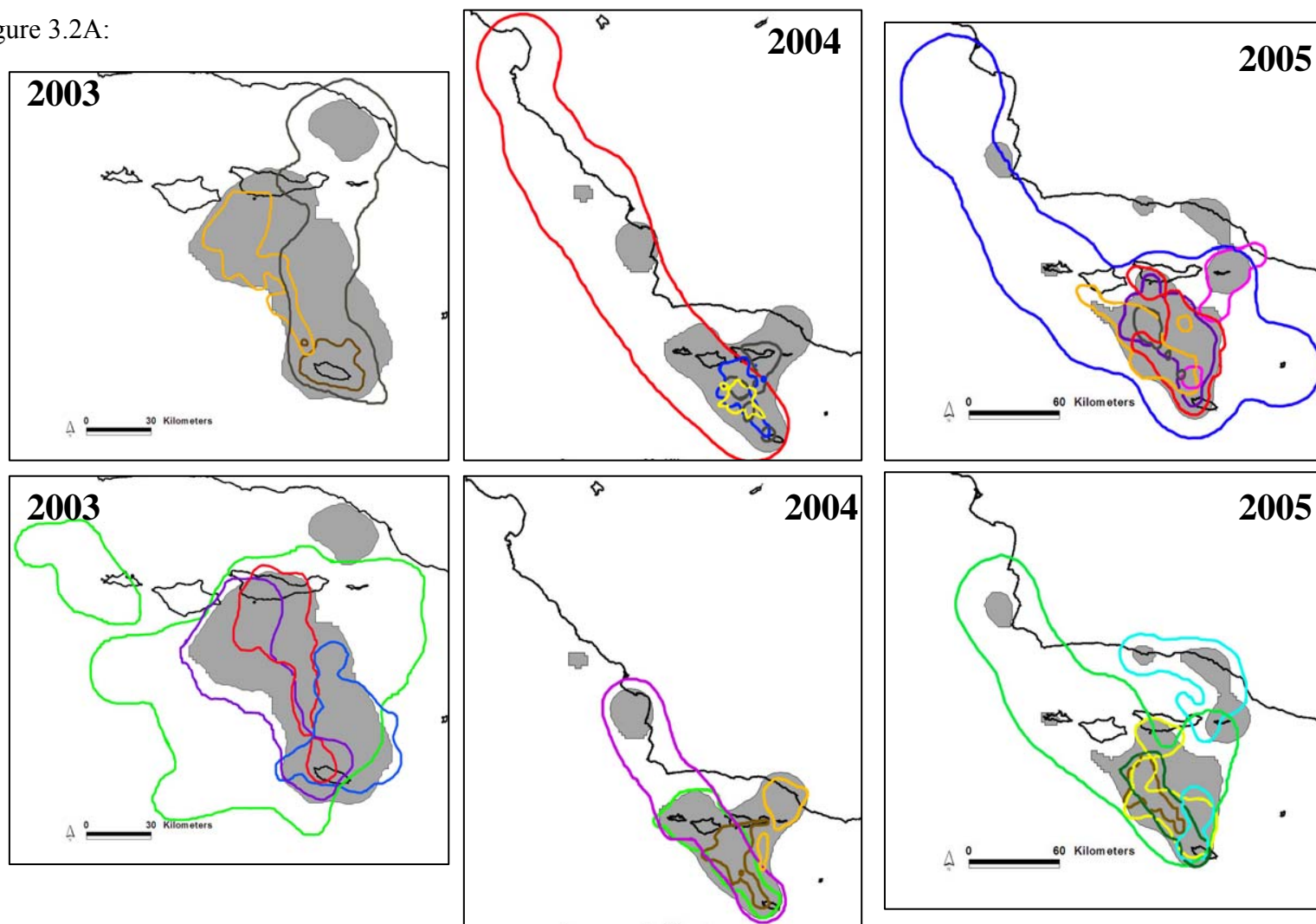


Figure 3.2 B) 50% and kernel home ranges for each individual by year. Home range was calculated using only satellite locations associated with diving. Each color represents a different female and the grey shaded area is the kernel for all females combined in each year. To help visualize each female, two panels are presented for each year and distance scales differ between years. Differences between females' home range area varied up to 37,956 km². Variation between individual home ranges was similar among years.

Figure 3.2B:

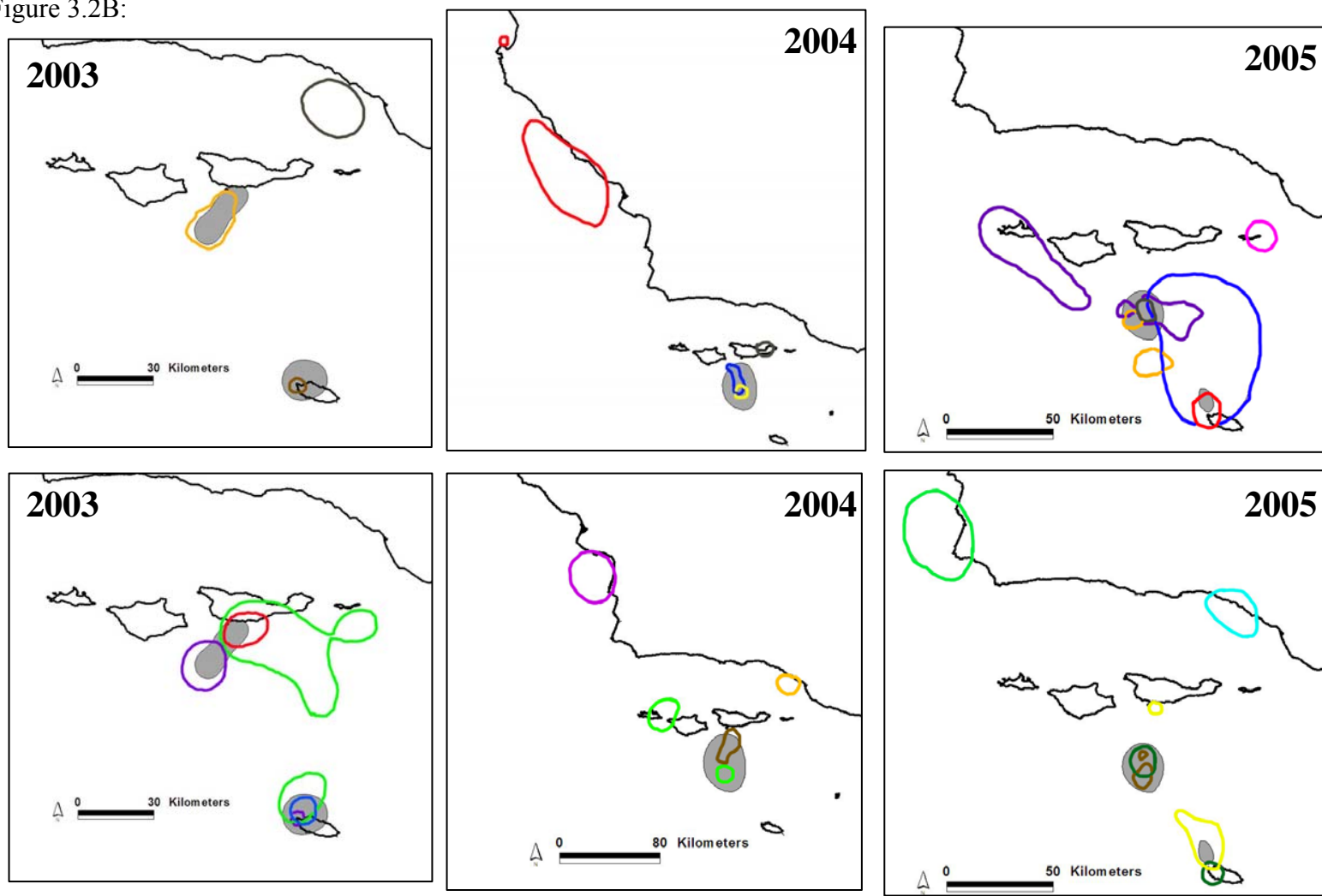


Figure 3.3: Distribution of time spent between diving, transit (or rest), and haulout for female California sea lions in 2003, 2004, and 2005 (N=25, Mean \pm SE). In both 2004 and 2005 females spent more time in transit. Note percent of time diving is similar among years.

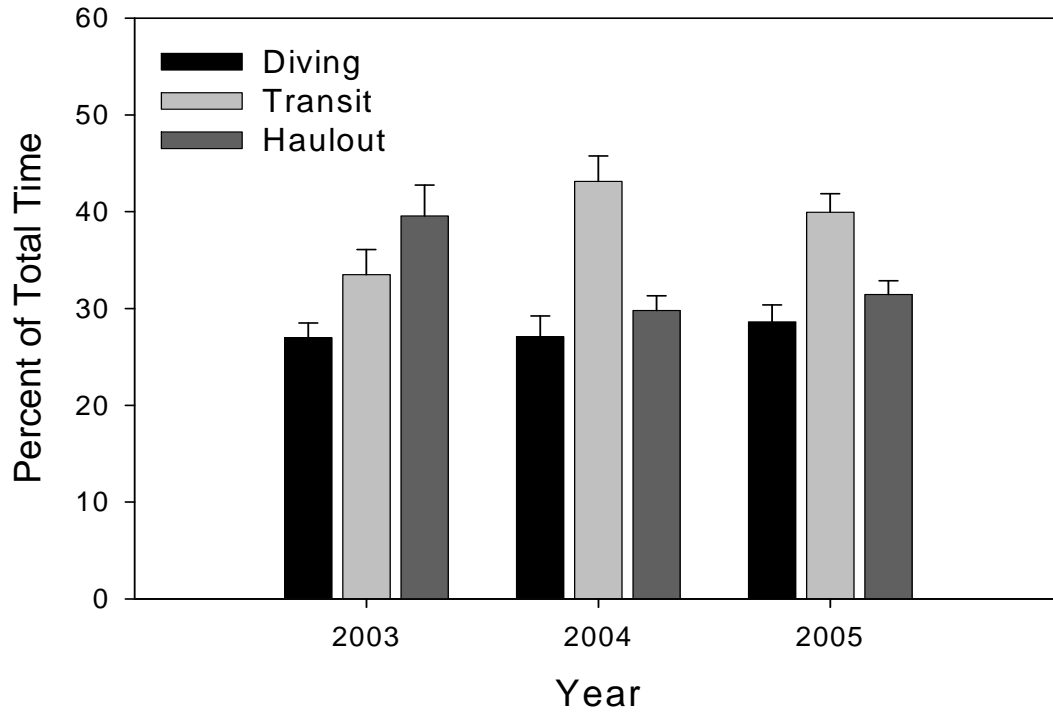


Figure 3.4: Kernel home range contours for all females within each deployment year (2003-2005). Home range was calculated using only satellite locations associated with diving. In 2004 (N=8), the 95% home range was 2.3 and 2.1 times larger than 2003 (N=7) and 2005 (N=11).

Figure 3.4:

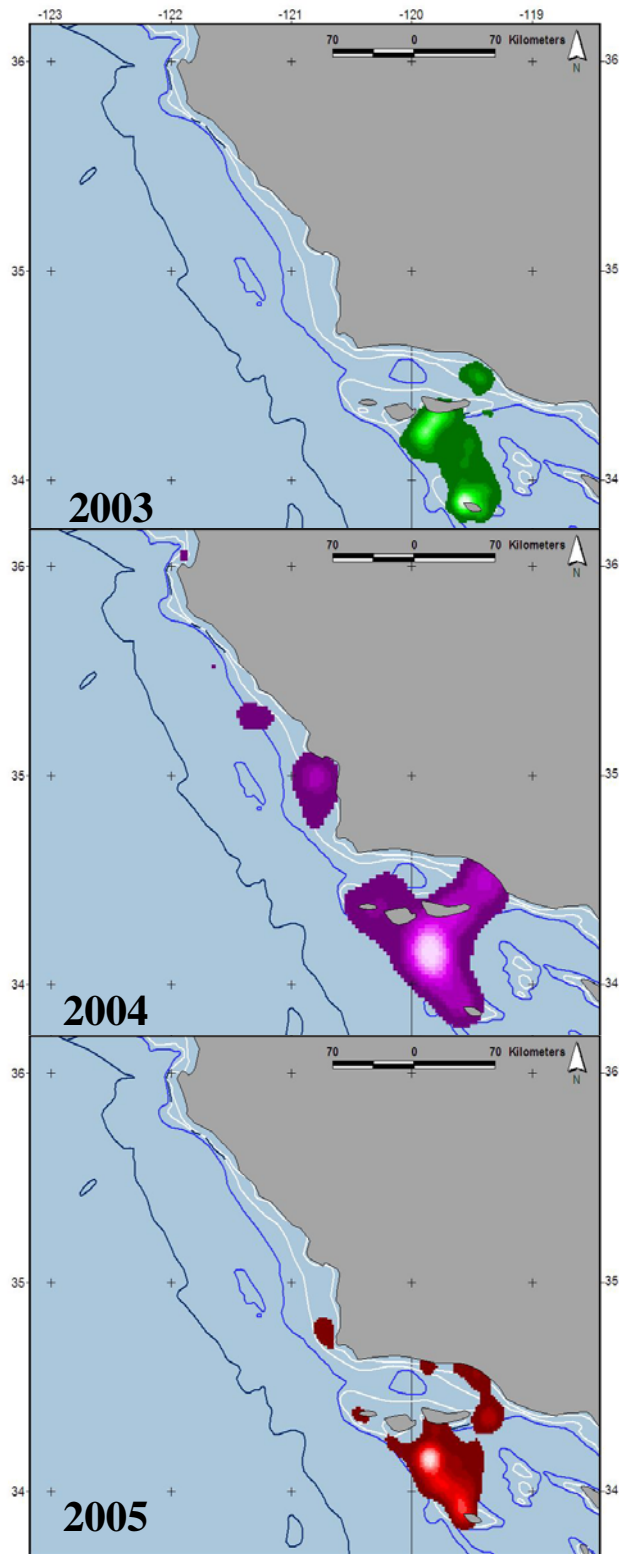


Figure 3.5: Sea surface temperatures (°C) for 2003-2005 with kernel home ranges plotted to show distribution of females during each year (95% black line, 50% white line). Home range was calculated using only satellite locations associated with diving. Sea surface temperatures were up to 2.0° C warmer in 2004 and 2005, than 2003.

Figure 3.5:

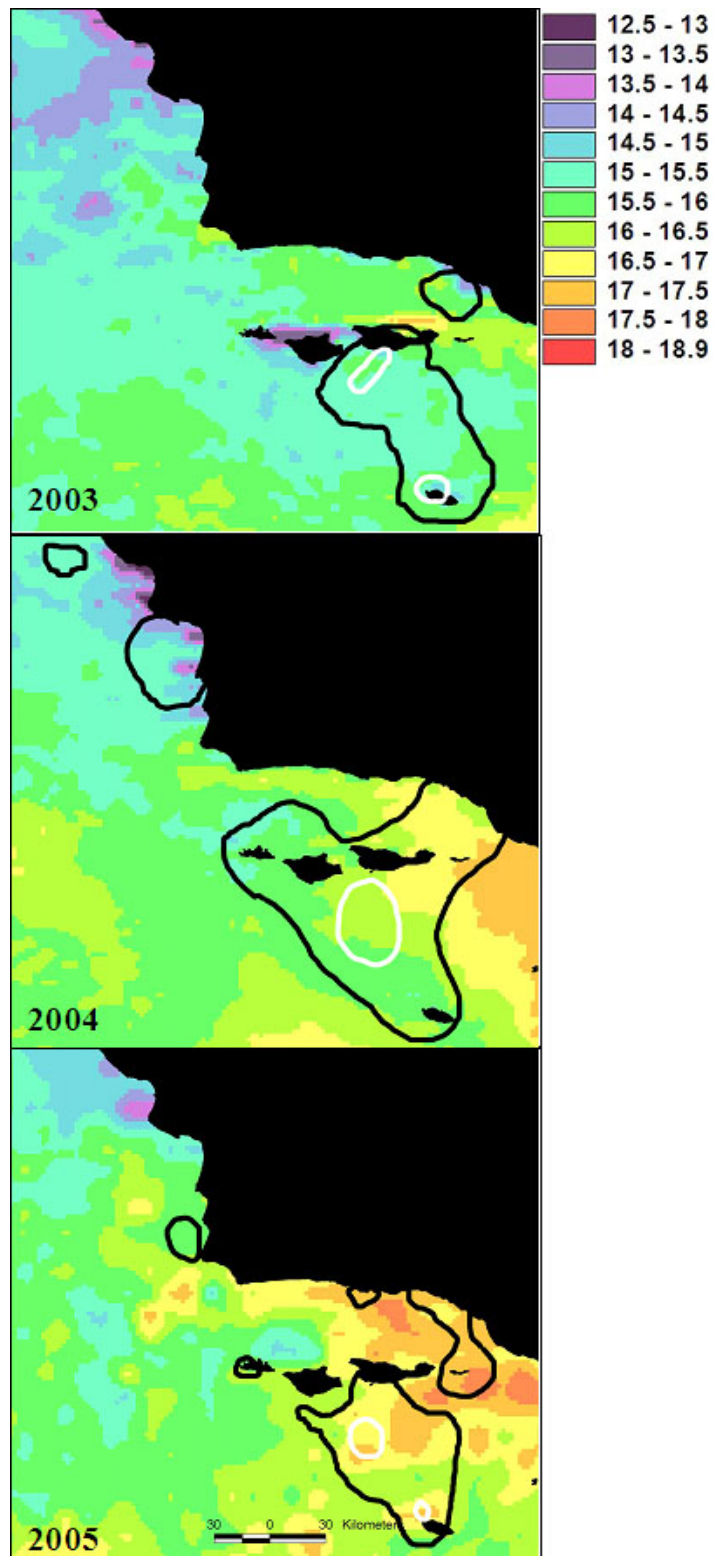


Figure 3.6: Upwelling index for 33°N, 119°W derived by the Environmental Research Division of the National Marine Fisheries Service. Both 2004 and 2005 show a decrease in peak upwelling for the year compared to average (1946-2005) and 2003.

