FORAGING ECOLOGY OF LACTATING STELLER SEA LIONS (*Eumetopias jubatus*) AT LOVUSHKI ISLAND, RUSSIA

A Dissertation

by

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ABSTRACT

A key objective of the National Marine Fisheries Service recovery plan for Steller sea lions (SSL – *Eumetopias jubatus*) is to protect critical habitats. Doing so relies in part on knowledge of SSL ecology based on time-depth data, at-sea dive locations and post-trip dietary analyses. I used data from animal-borne video and data recorders (VDRs) attached to lactating SSL at Lovushki Island, Russia to improve our knowledge by: 1) classifying dives based on three-dimensional swim paths and foraging success, 2) quantifying rates at which prey were encountered and consumed, and 3) testing whether a giving up rule, shown to be applicable to phocids, could similarly benefit SSL.

I identified five dive types: shallow and deep foraging dives, opportunistic foraging dives, a group of unique dives with no consistent behaviors, and non-foraging dives. I found that discrimination between foraging and non-foraging dives was possible with time-depth data alone, but relied on the assumption that time spent swimming horizontally between the descent and ascent represented swimming at the seabed. I also concluded that SSL at Lovushki were consuming enough prey to satisfy their estimated nutritional requirements.

To determine if lactating SSL at Lovushki Island could improve foraging success by incorporating a giving up rule into their foraging strategy I: 1) identified how dive duration varied according to foraging success and 2) constructed a simulation model to simulate the foraging behaviors and habitats of SSL. SSL did not appear to employ a giving up rule when foraging. This was supported by simulation results which showed that using a giving up rule may not allow SSL to markedly improve foraging success.

My research provided the first descriptions of the submerged foraging behaviors of SSL derived from three-dimensional swim paths and video recorded observations of foraging success. Results improved our knowledge of how SSL utilize the marine resources available to them and demonstrated the benefits of deploying VDRs on SSL. VDR deployments at other locations would increase the geographic resolution at which protection measures could be designed by improving our ability to identify and protect resources based on local foraging behaviors and success rates.

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Thank you to my advisor, Dr. Randall Davis, for your help and guidance through my graduate work and for providing me with numerous opportunities to travel and participate in projects in Alaska, California, Uruguay, and Japan. These experiences had a significant impact on my development as a graduate student and research scientist.

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All of my committee members, fellow graduate students, and my family helped during the preparation of my manuscripts, providing valuable input and advice. Without this, my dissertation could have never reached completion.

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TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

Page

CHAPTER I

INTRODUCTION

Population History

Steller sea lions (SSL – *Eumetopias jubatus*) are the largest of the extant otariids. As adults, SSL males weigh about 700 kg, while females are lighter at about 270 kg (Winship et al. 2001). Historically, SSL occupied a range that extended from California around the North Pacific coastlines to Eastern Russia, and south to Japan. Currently, the majority of the SSL population is located in British Columbia, Alaska and Russia. Within this range, SSL can be found at haul-outs and rookeries that are generally characterized by large rocky outcroppings (Call & Loughlin 2005), but can include beaches or ice. In 1961, published and unpublished data were used to estimate the total SSL population at 240 – 300 thousand SSL (Kenyon & Rice 1961). By 1985, the SSL population inhabiting the Central and Eastern Gulf of Alaska, as well as the Eastern and Central Aleutian Islands had declined by as much as 52% (Merrick 1987). This trend continued with an overall population decline of 78% by 1990 (National Marine Fisheries Service (NMFS) 1992). Similarly, severe population declines were observed in the western (i.e., Russian) part of their range, as populations in the Kuril Islands and along the coast of Kamchatka declined by more than 90% during the twentieth century (Burkanov & Loughlin 2005).

In 1990, SSL were listed as threatened in the US under the Endangered Species Act. The continued decline of the Alaskan SSL population at a rate of approximately

3.2% per year (Sease 2001) as well as the division of the US population into two genetically distinct population segments (east and west of 144^{o} W, Bickham 1996) led to the 1997 listing of the western distinct population segment (WDPS) as endangered and the eastern distinct population segment (EDPS) as threatened. As of 2007, the WDPS was estimated to be either stable or declining slightly, while the EDPS was estimated to be growing at a rate of 3% per year. Most recent population estimates place the WDPS population at 45,000 SSL (2004-2005 survey), the EDPS at 46,000 – 58,000 plus 3% per year (since 2002) and the Russian population at 16,000 SSL (as of 2005) (NMFS 2008). In 1992, NMFS developed a recovery plan designed to identify and mitigate the threats which most likely inhibited the recovery of SSL populations. In addition to protection measures inherent to the listing of SSL as threatened and endangered (i.e., preventing harassment and shooting), this recovery plan sought to, among other things, reduce the impacts of commercial fishing on prey deemed critical to SSL (NMFS 2008). In 2008, the recovery plan was revised to take into consideration the division of SSL into two distinct populations and focused on identifying and managing threats to each population's sustainability separately. Additionally, unique recovery goals were set for each population. Reclassification of the WDPS to threatened, instead of endangered, and de-listing of the EDPS were the new objectives of the NMFS recovery plan.

Reproduction and Maternal Investment

The breeding season is initiated by the arrival of large adult males on rookeries. Females generally arrive on rookeries after males and congregate around the first born pup of the year (Higgins et al. 1998). Pupping begins as early as mid-May and extends as late as mid-July with the majority of pup births occurring during June (Pitcher & Calkins 1981). As females arrive, males establish territories for breeding. Although sexually mature at 3 – 7 years, males are generally not large enough to compete and hold a territory on the rookery until age 9 – 10 when they have reached the upper 87% of their maximum body length (Pitcher & Calkins 1981, Winship et al. 2001). This, in conjunction with a 15 year lifespan, limits the total reproductive life of males to as little as 5 years while females, which may live to an age of 30, are able to reproduce every year after reaching sexual maturity between the ages of 3 – 7 (Pitcher & Calkins 1981).

After giving birth, female SSL spend approximately 7 – 10 days ashore nursing (Milette & Trites 2003). During this perinatal period, females are obligated to fast, relying on energy reserves accumulated prior to parturition. When born, SSL pups weigh approximately 18 kg (female) or 22 kg (male) and grow at a rate of 0.2 to 0.5 kg/day (Higgins et al. 1988, Davis et al. 2006). Following the perinatal period, females begin alternating between foraging at sea and nursing. Foraging trips are usually shorter than one day as pups are incapable of prolonged fasting (Rea et al. 2000, Milette & Trites 2003, Davis et al. 2006). Trip durations ranging from 9-25 hr have been reported for SSL foraging during the summer in Russia, the Aleutian Islands and southeast Alaska (Merrick & Loughlin 1997, Milette & Trites 2003, Davis et al. 2006, Rehberg et al. 2009, Burkanov et al. 2011, Waite et al. 2012b). Over the course of a foraging trip, a SSL must ingest more energy than it expends to remain in positive energy balance for growth and reproduction. Repeated failure to ingest sufficient energy and nutrients would result in reduced body condition, reproductive failure and, for lactating females, increased pup mortality (Trites & Donnelly 2003).

Nutrition and Observed Diet

The energy requirements of SSL have been estimated based on food ingestion in captivity (Kastelein et al. 1990) and modeling (Winship et al. 2002; Winship & Trites 2003). Kastelein et al. (1990) recorded food ingestion for three captive adult SSL over a 15 year period. The diet consisted of mackerel (*Scomber scombrus*), herring (*Clupea herengus*), sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), and squid (*Illex spp.*). On average, SSL consumed 11.5 kg of food per day with pregnant females requiring 30% more than non-pregnant females. Food requirements varied by as much as 20% and reflected annual cycles of fasting or reproduction. A bioenergetics model by Winship & Trites (2003) estimated that during summer months, food requirements for male and female SSL range from 16 ± 2.8 kg to 20 ± 3.6 kg, respectively. Geographic regions with the highest daily food requirements were the central and western Aleutian Islands where SSL are thought to forage more exclusively on either gadids or hexagrammids, respectively, (Merrick et al. 1997) which have lower lipid content (Payne et al. 1999). In the western Aleutian Islands the average length of Atka mackerel consumed is 30 cm (Zeppelin et al. 2004). At this size Atka mackerel are 3 years old and have a mass of 0.4 kg (Lowe et al. 1998). A female SSL would need to capture 40-50 fish per day to satisfy its energy requirements.

Tollit et al. (2006) compared four methods which have been used to identify the prey of SSL: 1) examination of stomach contents, spews and scats, 2) DNA analysis of scat contents, 3) fatty acid signatures in blubber, and 4) stable isotope analysis. Hard parts such as bones, otoliths and scales that have passed through the digestive system can be collected from scats and used to classify prey types. DNA analysis can also be used to identify prey, but with higher taxonomic resolution than by analysis of undigested hard parts (Deagle & Tollit 2007). There are, however, problems with scat sample analysis. For example, scats from a group of non-breeding males are not necessarily indicative of the prey for a nearby population of nursing females as scats taken from males and females cannot be used as analogues for each other (Trites & Calkins 2008). A second problem results from partial or complete digestion of bones and otoliths and the lack thereof in cephalopods. Bowen (2000) notes that partial digestion can result in an inability to classify hard parts into taxonomical groups or to properly estimate prey size, while complete digestion can lead to quantification errors in the number of prey consumed. Some researchers have made efforts to account for the rate at which otoliths and cephalopod beaks are eroded during digestion (see Bowen 2000). Similarly, Cottrell & Trites (2002) and Tollit et al. (2003) note that the number and type of hard parts that can be successfully obtained from SSL scats varies between prey type and individual activity level. Thirdly, defecation at sea results in incomplete records which may not account for all prey consumptions during a foraging trip.

Previous studies have shown that SSL have a diverse diet consisting of cephalopods, flatfish, forage fish, gadids, hexagrammids, and salmon (Merrick et al.

1997). The diversity of prey species consumed by any individual is largely dependent on geographic region. One study showed that female scats taken from rookeries around Forester Island in Southeastern Alaska had remains of primarily forage fish such as herring (*Clupea pallasi*) and sand lance (*Ammodytes hexapterus*) (22%), salmon (*Oncorhynchus spp*.) (28%), gadids such as walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) (13%), rockfish (*Sebastes spp*.), and flatfish (7%). Less than 1% of the prey identified were hexagrammids such as lingcod (*Ophiodon elongatus*) and Atka mackerel (*Pleurogrammus monopterygius*) (Trites & Calkins 2008). An absence of hexagrammids in SSL diets has also been documented at Kodiak Island (McKenzie & Wynne 2008). Western stock SSL, inhabiting the Aleutian Islands, primarily consume walleye pollock, Atka mackerel, salmonids, and Pacific cod (Sinclair & Zeppelin 2002). Studies of SSL diets in the Russian Far East showed that Atka mackerel, walleye pollock and salmon were the most commonly consumed species in the Kuril Islands appearing in 65.7%, 32.4% and 29.9% of scats, respectively (Waite & Burkanov 2006). In general, SSL diet diversity is high in eastern Alaska and low in the Gulf of Alaska, Aleutian Islands, and Russia. This variation in diet diversity has been shown to correlate with the extent of population declines from the Gulf of Alaska to the western Aleutian Islands. Merrick et al. (1997) calculated diet diversity indices for six sub-regions within this range and compared them with measurements of population decline in each region. They found that low diet diversity correlated with larger population declines and vice versa. However, a similar study by Waite & Burkanov

(2006) found no correlation between diet diversity and population decline for SSL populations to the west in Russia.

Diving Constraints

As obligatory air breathers that forage underwater, SSL make round-trip journeys between the surface and the depths where they forage. Dive duration is constrained by their physiological capacity to store oxygen in their lungs, blood and muscle to maintain aerobic metabolism while submerged (Kooyman 1989, Boyd 1997, Davis et al. 2014). Following each dive, SSL must spend a relatively small amount of time replenishing blood and muscle oxygen stores and exhaling carbon-dioxide. Exceeding the aerobic dive limit (ADL) forces SSL to rely on anaerobic metabolism which produces lactate, especially in active muscle, and increases the post-dive recovery period (Kooyman 1989). Most marine mammals, including SSL, typically dive within their ADL (Rehberg et al. 2009). However, exceeding the ADL is not necessarily excluded as a foraging strategy. Australian sea lions (AUSL, *Neophoca cinerea*) and New Zealand sea lions (NZSL, *Phocarctos hookeri*) are two examples of otariids that appear to increase the duration of dives beyond their calculated ADL (cADL) to extend the amount of time at their foraging depth during deeper dives (Gales & Mattlin 1997, Costa & Gales 2000, 2003, Chilvers et al. 2006, Chilvers & Wilkinson 2009). However, this behavior does not correlate with increased surface recovery time, suggesting that the true ADL may vary with swimming mode (i.e., gliding during descent, stroke-and-glide swimming) during a dive (Crocker et al. 2001) as has been documented for other pinniped species (Williams et al. 2000, Davis et al. 2001, Davis & Weihs 2007, Davis et al. 2013).

Based on time-depth records, foraging dives for SSL can be divided into three basic phases: descent, horizontal swimming and ascent. While descending, a SSL swims from the surface to the depth at which it will forage. Although opportunistic foraging may occur along the way, the majority of time spent searching for and handling prey likely occurs between the end of descent and the beginning of ascent. For Weddell seals (WS, *Leptonychotes weddellii*), consumption of small prey usually occurs at the foraging depth, although large prey must be taken to the surface for handling and consumption, preventing further prey searching during that dive (Davis et al. 2003, 2013). Ascent occurs when the SSL returns directly to the surface to reoxygenate its blood and muscles. Although the basic structure of a foraging dive is simple, actual dive paths recorded for WS (Davis et al. 2003, 2013, Fuiman 2007), northern elephant seals (*Mirounga angustirostris*, Davis et al. 2001), bearded seals (*Erignathus barbatus*, Krafft et al. 2000), harbor seals (HS, *Phoca vitulina*, Lesage et al. 1999) and ringed seals (*Pusa hispida*, Simpkins et al. 2001) show variability in depth, duration and swim path tortuosity, suggesting that pinnipeds use different foraging strategies depending on the age, geographic location, season and prey species.

Estimating a cADL for SSL is complicated by a wide range in reported diving metabolic rates (DMR). Crude approximations of published DMR values are 2.41 L O_2 min^{-1} (Hastie et al. 2006), 0.91 L O_2 min^{-1} (Hastie et al. 2007), 1.65 L O_2 min^{-1} (Fahlman et al. 2008), and 2.24 L O_2 min^{-1} (Gerlinksky et al. 2013). As for total body oxygen supplies (TBO), estimates are fairly similar at 38.8 ml O_2 kg^{-1} (Lenfant et al. 1970), 40.4 ml O_2 kg^{-1} (Richmond et al. 2006) and 34.6 ml O_2 kg^{-1} (Gerlinksky et al. 2013). Mean values are 1.6 L O_2 min^{-1} for DMR and 9.5 L O_2 for TBO. Scaling these values by the body masses of study animals ($kg^{0.75}$) allows for the DMR of a 250 kg female to be estimated at 2.05 L O_2 min^{-1}. This translates to a cADL of 4.6 min which exceeds mean dive durations reported for wild SSL, but not for all (Merrick & Loughlin 1997, Loughlin et al. 2003, Rehberg et al. 2009, Waite et al. 2012b). Foraging dives, for example, may require longer durations than transit dives as SSL must descend to a foraging depth, locate prey, pursue prey, capture and handle prey, and then ascend to the surface. Nevertheless, a cADL of 4.6 min provides enough dive time for almost all observed SSL dives, especially if the true ADL can be extended by reductions to DMR by modifications to swimming mode (Williams et al. 2000, Crocker et al. 2001, Davis et al. 2001, Davis & Weihs 2007, Davis et al. 2013).

Unlike AUSL and NZSL, SSL make shallow dives with durations which are usually less than an estimated cADL of 4.6 min and do not appear to be pushing their physiological limits while diving. SSL are able to descend to the seabed, forage, and return to the surface without being forced to extend post-dive surface intervals to flush lactate from their system.

Optimizing Foraging Behavior

Foraging theories predict that diving predators should maximize their catch per unit effort (CPUE) (Emlen 1966, Charnov 1976, Stephens & Krebs 1986) where the benefit is the acquisition of energy from prey capture and the cost results from: 1) swimming to and from foraging areas, 2) searching for, pursuing and capturing prey, and 3) the metabolic cost of digestion and assimilation (Rosen & Trites 1997, Williams et al. 2004). For marine divers, one property of foraging behavior which lends itself to optimization is maximization of CPUE. Three methods to achieve this are: 1) maximizing time spent foraging while at sea, 2) large-scale (i.e., foraging trip) habitat selection and 3) small scale (i.e., dive-to-dive) prey patch selection.

In addition to the metabolic costs of foraging (i.e., cost of transport, digestion etc.), time away from fasting pups is a resource. All time spent travelling, transiting to and from foraging depths and resting at the surface are an investment in the energetic payoff of consuming prey. As such, lactating SSL should maximize their overall foraging trip CPUE by spending as much of that time as possible actively foraging. This comes with the caveat that neither the scope nor density of prey is constant or necessarily known. As a result, SSL may be forced to invest a certain amount of time, which could be used for foraging, into traveling to foraging grounds.

The Optimal Foraging Theory (OFT) states that prey should be selected based on a prey-specific CPUE. One species of fish may have a higher energetic reward than another, but if it takes significantly more time to locate or handle, the overall CPUE may be lower. SSL should select foraging grounds based on both the investment of time to travel to them and the types of prey likely to be available. Travelling far offshore to access foraging grounds with an abundant supply of high energy prey may not be more cost effective (i.e., same or lower CPUE) than foraging near shore on low energy prey.

In addition to modifying large scale (i.e., foraging trip) movements based on travel times, expected prey types and expected prey densities, SSL may also be able to optimize their foraging behavior at the smaller scale of individual dives. The Marginal Value Theorem (MVT) states that, if prey density declines as prey are consumed, the amount of time which should be invested in any one patch (i.e., time spent foraging during a single dive) is proportional to the amount of time required to travel to the next patch (i.e., transit time: sum of ascent, post-dive surface interval and descent durations) and the estimated rate of energetic intake in the current patch (Charnov 1976). Thompson & Fedak (2001) hypothesized that diving phocids could maximize their CPUE during a foraging trip by applying “a simple giving up rule” (GUR) whereby seals would abandon a dive early (i.e., not continuing to search until a diminished oxygen supply necessitated a return to the surface) if prey were not encountered by a certain quitting time (Tq). At the core of this hypothesis was the idea that, by shortening dives which are identified as having poor patch quality, seals could increase the number of dives made to more profitable prey patches during foraging trips. Using early prey success during a dive as a proxy for local prey density and then modifying behavior accordingly would allow a more efficient use of time and an increased overall CPUE. Results conditionally supported the prediction that seals could increase their overall CPUE by abandoning unsuccessful dives, thus increasing the amount of time spent foraging in higher density prey patches. Abandoning unsuccessful shallow dives increased CPUE because transit time was short. For deep dives, longer transit times counteracted the benefit of ending dives early, resulting in no increase to overall CPUE.

To test the GUR proposed and supported by the giving up model (GUM) by Thompson & Fedak (2001), Cornick & Horning (2003) developed an experiment designed to simulate foraging behavior in SSL. This experiment consisted of a variety of scenarios during which SSL searched for and consumed prey in a captive setting. Sparling et al. (2007) also designed an experiment to test the GUR with grey seals (*Halichoerus grypus*). In this experiment, seals swam a course which had a controllable length to simulate varying descent and ascent durations (i.e., dive depths). At the far end of the course, an apparatus provided seals with prey items at rates which varied between trials. Although some results were confounding, which is not unexpected given the complexity of designing and performing an experiment with live animals, both studies obtained data that supported the key conclusions drawn by Thompson & Fedak (2001). In 2014, Heaslip et al. published a study in which researchers sought to test nine predictions of optimal diving theory from a variety of sources. Four of these predictions were derived from Thompson & Fedak (2001) and related to the application of the GUR by diving harbor seals (*Phoca vitulina concolor*). This study was unique in that it not only included data collected from wild, free-roaming pinnipeds, but also that it included quantitative measures of prey capture rates via the inclusion of on-board camera systems which subsampled behavior by recording 10 min of video every 45 min. Heaslip et al. found that seals were shortening dives by spending less time at foraging depths when prey were not encountered. This finding provided additional support for the key component of the GUR: that seals should shorten dives to low prey density patches in order to increase the number of dives to higher prey density patches.

Research Objectives

A key provision of the NMFS Recovery Plan for SSL is that habitats crucial to the sustainability of the SSL population should be protected to ensure the availability of adequate food supplies. Officials and researchers responsible for the development and implementation of protection measures rely on an understanding of where SSL forage, what types of prey are preferred and how many prey are consumed. The primary research question was simple: How could these unique animal-borne video and data recorders (VDRs) be used to better describe the foraging behaviors of SSL? The three objectives were to: 1) classify dives based on three-dimensional swim paths and video recordings of foraging success, 2) quantify the rates at which prey were encountered and consumed during dives and foraging trips, and 3) test how interactions between physiological constraints, behavior and habitat affect foraging success by using simulation modeling to determine if a giving up rule, shown to be applicable to phocids, could similarly benefit SSL.

CHAPTER II

CLASSIFICATION OF STELLER SEA LION DIVE TYPES

Introduction

As central place foragers, lactating SSL are opportunistic marine predators that make numerous trips between the rookery where they nurse their pups and offshore foraging grounds where they feed on fish and cephalopods. Foraging trips are usually shorter than one day as pups are incapable of prolonged fasting (Rea et al. 2000, Milette & Trites 2003, Davis et al. 2006). The average duration of 211 foraging trips made by female SSL during the summer breeding season at Lovushki Island, a rookery in the northern Kuril Islands of Russia and location where this study was performed, was 18.5 ± 12 hr (Waite et al. 2012a). However, median trip durations in 2007 (7.8 hr) and 2008 (10.4 hr) were shorter and similar to estimates (median trip duration: 7 hr) by Burkanov et al. (2011) at Lovushki Island based on visual observations of female attendance patterns. Similar values for mean trip duration (9-25 hr) during the summer have been reported for SSL in the Aleutian Islands and southeast Alaska (Merrick & Loughlin 1997, Milette & Trites 2003, Davis et al. 2006, Rehberg et al. 2009).

Foraging theory predicts that while making foraging trips to sea, SSL should minimize their cost-to-benefit ratio (Emlen 1966, Charnov 1976, Stephens & Krebs 1986) where the benefit is the acquisition of energy from prey captures and costs include: 1) swimming to and from foraging areas, 2) searching for, pursuing and capturing prey, and 3) the metabolic cost of digestion and assimilation (Rosen & Trites

1997, Williams et al. 2004). Over the course of a foraging trip, a SSL must ingest more energy than it expends to remain in positive energy balance for growth and reproduction. Repeated failure to ingest sufficient energy and nutrients would result in reduced body condition, reproductive failure and increased pup mortality (Trites & Donnelly 2003).

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SSL not only act as central place foragers at the large scale of complete foraging trips, but also at the small scale of individual dives. SSL are obligatory air breathers that forage underwater and must repeatedly make round-trip journeys between the surface and depths where prey can be found while foraging at sea. These dives can be divided into three basic phases: descent, horizontal swimming and ascent. While descending, a SSL swims from the surface to the depth at which it will forage. Although opportunistic foraging may occur along the way, the majority of time spent searching for and handling prey likely occurs between the end of descent and the beginning of ascent. For Weddell seals (WS, *Leptonychotes weddellii*), consumption of small prey usually occurs at the foraging depth, although large prey must be taken to the surface for handling and consumption, preventing further prey searching during that dive (Davis et al. 2003, 2013). Ascent occurs when the SSL returns directly to the surface to reoxygenate its blood and muscles. Although the basic structure of a foraging dive is simple, actual dive paths recorded for WS (Davis et al. 2003, 2013, Fuiman 2007), northern elephant seals (*Mirounga angustirostris*, Davis et al. 2001), bearded seals (*Erignathus barbatus*, Krafft et al. 2000), harbor seals (HS, *Phoca vitulina*, Lesage et al. 1999) and ringed seals (*Pusa hispida*, Simpkins et al. 2001) show variability in depth, duration and swim path tortuosity, suggesting that pinnipeds use different foraging strategies depending on the age, geographic location, season and prey species.

Dive duration is constrained by their physiological capacity to store oxygen in their lungs, blood and muscle to maintain aerobic metabolism while submerged (Kooyman 1989, Boyd 1997, Davis et al. 2014). Following each dive, SSL must spend a relatively small amount of time replenishing blood and muscle oxygen stores and exhaling carbon-dioxide. Exceeding the ADL forces SSL to rely on anaerobic metabolism which produces lactate, especially in active muscle, and increases the post-dive recovery period (Kooyman 1989). Most marine mammals, including SSL, typically dive within their ADL (Rehberg et al. 2009). However, exceeding the ADL is not necessarily excluded as a foraging strategy. Australian sea lions (AUSL, *Neophoca cinerea*) and New Zealand sea lions (NZSL, *Phocarctos hookeri*) are two examples of otariids that appear to increase the duration of dives beyond their calculated ADL to extend the amount of time at their foraging depth during deeper dives (Gales & Mattlin 1997, Costa & Gales 2000, 2003, Chilvers et al. 2006, Chilvers & Wilkinson 2009). However, this behavior does not correlate with increased surface recovery time, suggesting that the true ADL may vary with swimming mode (i.e., gliding during descent, stroke-and-glide swimming) during a dive (Crocker et al. 2001) as has been documented for other pinniped species (Williams et al. 2000, Davis et al. 2001, Davis & Weihs 2007, Davis et al. 2013).

As with large scale foraging trips, SSL should minimize their cost-to-benefit ratio at the small scale of individual dives. While costs at this scale include those of large scale foraging trips, they also include: 1) time spent descending to and ascending from the seabed and 2) time spent at the surface between dives while replenishing oxygen stores and, when necessary, flushing lactate from the body. At this scale, the benefit is time spent at the foraging depth and the consequential acquisition of energy from prey captures. While metabolic and respiratory costs of foraging vary according to SSL behavior and physical condition (i.e., pregnant or nursing), the magnitude of energetic benefits derived from prey consumptions varies according to the caloric values of the types of prey consumed.

Identifying the types of prey that SSL consume while at sea is complicated by the inability of researchers to make direct observations of submerged foraging events. Tollit et al. (2006) compared four methods which have been used to identify the prey of SSL: 1) examination of stomach contents, spews and scats, 2) DNA analysis of scat contents, 3) fatty acid signatures in blubber, and 4) stable isotope analysis. Hard parts such as bones, otoliths and scales that have passed through the digestive system can be collected from scats and used to classify prey types. DNA analysis can also be used to identify prey, but with higher taxonomic resolution than by analysis of undigested hard parts (Deagle & Tollit 2007). There are, however, problems with scat sample analysis. For example, scats from a group of non-breeding males are not necessarily indicative of the prey for a nearby population of nursing females as scats taken from males and females cannot be used as analogues for each other (Trites & Calkins 2008). A second problem results from partial or complete digestion of bones and otoliths and the lack thereof in cephalopods. Bowen (2000) notes that partial digestion can result in an inability to classify hard parts into taxonomical groups or to properly estimate prey size, while complete digestion can lead to quantification errors in the number of prey consumed. Some researchers have made efforts to account for the rate at which otoliths and cephalopod beaks are eroded during digestion (see Bowen 2000). Similarly, Cottrell & Trites (2002) and Tollit et al. (2003) note that the number and type of hard parts that can be successfully obtained from SSL scats varies between prey type and individual activity level. Thirdly, defecation at sea results in incomplete records which may not account for all prey consumptions during a foraging trip.

Studies have used these methods to show that SSL have a diverse diet consisting of cephalopods, flatfish, forage fish, gadids, hexagrammids, and salmon (Merrick et al. 1997). The diversity of prey species consumed by any individual is largely dependent on geographic region. One study showed that female scats taken from rookeries around Forester Island in Southeastern Alaska had remains of primarily forage fish such as herring (*Clupea pallasi*) and sand lance (*Ammodytes hexapterus*) (22%), salmon (*Oncorhynchus spp*.) (28%), gadids such as walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) (13%), rockfish (*Sebastes spp*.), and flatfish (7%). Less than 1% of the prey identified were hexagrammids such as lingcod (*Ophiodon elongatus*) and Atka mackerel (*Pleurogrammus monopterygius*) (Trites & Calkins 2008). An absence of hexagrammids in SSL diets has also been documented at Kodiak Island (McKenzie & Wynne 2008). Western stock SSL, inhabiting the Gulf of Alaska and Aleutian islands, primarily consume walleye pollock, Atka mackerel, salmonids, and Pacific cod (Sinclair & Zeppelin 2002). Studies of SSL diets in the Russian Far East showed that Atka mackerel, walleye pollock and salmon were the most commonly consumed species in the Kuril Islands appearing in 65.7%, 32.4% and 29.9% of scats, respectively (Waite & Burkanov 2006).

Our understanding of SSL ecology is based on interpretations of the types of data described above. Time-depth records, GPS derived movements, partial records of at-sea diet, captive studies, and modeling results have all been used to describe where animals forage, how much prey they require, what types of prey are being consumed, etc. These descriptions have served as the foundation on which management policies targeted at protecting the species have been designed. However, this process has relied on a number of assumptions about what animals were actually doing while at sea. Animal-borne VDRs have the capability to provide unprecedented insights into the at-sea behavioral ecology of SSL by recording data which cannot be derived from the types of studies described above. These data have the potential to allow for the recreation of high-resolution 3-dimensional swim paths, quantification of foraging success, qualification of prey preference, description of predator-prey interactions, and an investigation into how all of these relate to each other. The objectives of this study were to: 1) classify and describe the types of dives made by lactating SSL based on an analysis of their three-dimensional movements and video-recorded observations of prey encounters and consumptions, 2) determine if the dive types identified with 3-dimensional data could be identified with time-depth data alone, and 3) quantify the rates at which prey were encountered and consumed during dives and foraging trips. This research would provide new insights into the foraging behaviors of SSL and provide justification for the extraction of additional information regarding foraging behaviors from time-depth data.

Methods

During June of 2008 and 2009, five VDRs (3 in 2008 and 2 in 2009) were deployed on lactating female SSL on Lovushki Island (Figure 1, 48.543° N, 153.876° E) in the Kuril Islands south of Kamchatka, Russia.

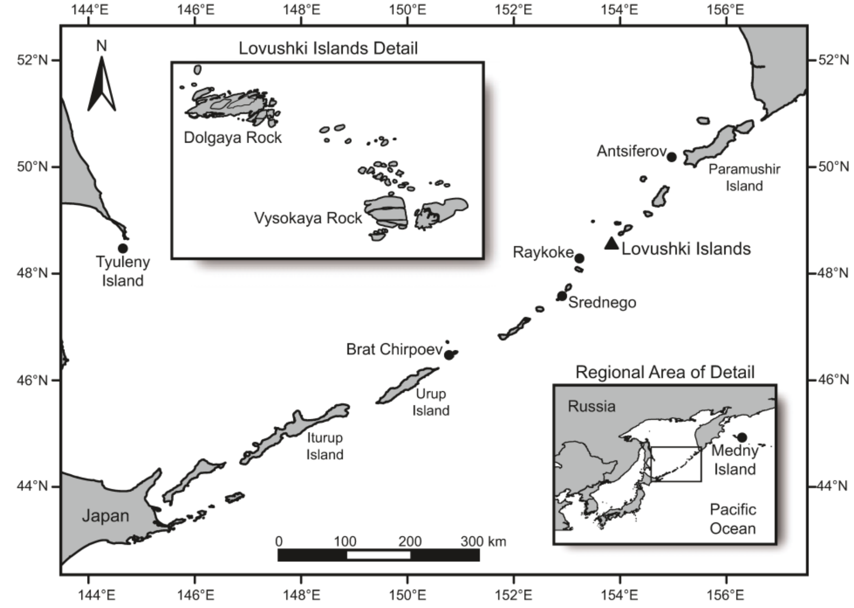

Figure 1. Map of the Kuril Islands and the Lovushki Island complex. The Lovushki Islands are indicated with a triangle and an expanded view is provided in the upper left. (Figure 1 from Waite et al. 2012a and 2012b, Reprinted with permission from Elsevier and © Canadian Science publishing or its licensors: NRC Research Press)

Each VDR consisted of a back-mounted, pressure-resistant housing and a head-mounted video camera. The housing (24 × 9.3 × 7.3 cm; mass 1 kg in water) contained a micro-processor, 2 gigabyte flash memory card (Secure Digital), 20-gigabyte mini-hard drive, and sensors for pressure (depth), swimming speed, compass bearing (3-axis magnetometer, 1Hz), tilt, pitch and roll (3-axis accelerometer, 20Hz). Sound was recorded using a hydrophone with a frequency response of 50 Hz to 16 kHz. Compressed video (approximately one frame every 0.03 s) and audio (12 hr maximum) were stored on the mini-hard drive. Data from the sensors were recorded on the flash memory card. Power was provided by lithium-ion batteries. The camera (8.3 x 5.2 x 5.5 cm) was mounted on the SSL's head and contained near-infrared LEDs as a light source. The low light sensitive, black and white camera provided a view of the SSL's muzzle and the environment immediately in front of it. The camera could image with both visible and near-infrared light. The near-infrared LEDs enabled imaging in total darkness to a maximum distance of about 1 m without disturbing the SSL's behavior. Near-infrared light appears to be invisible to pinnipeds (Levenson et al. 2006) and most marine fishes (Douglas & Hawryshyn 1990). The head-mounted location of the camera and the near-infrared light source enabled recording of foraging behavior, including prey encounters and consumptions.

Head and back-mounted components were attached to thin aluminum plates that were mounted to 1.2 mm thick neoprene patches. Neoprene patches for the main housing were ellipse-shaped with total surface area of 450 cm^2. Camera patches were rectangular with a surface area of 70 cm^2. Neoprene cement was used to glue the head-mounted video camera and the back-mounted housing to the pelage. The back-mounted housing was placed mid-dorsally and posterior to the scapulae. Power and communication cables connecting the video camera to the main housing were secured along the neck with small neoprene patches. A VHF transmitter was also glued to the pelage of each SSL to enable relocation and recovery of instruments onshore.

Female SSL on the rookery were selected for VDR deployments based on five criteria: distance from the water, confirmed presence of a pup, apparent pup health, pup age, and female health. Female and pup health were based on body condition (e.g. no signs of emaciation or disease). Suckling behavior was used to confirm the presence of a pup. Females with older pups were preferred to avoid instrumenting a fasting female during the initial 7-9 day perinatal period (Milette & Trites 2003). This also increased the likelihood that the female was making regular and successful foraging trips. Females were immobilized on the rookery by darting with Zoletil® (2.0 mg kg^{-1}, Tiletamine HCL and Zolazepam HCL, Virbac, France) and atropine (0.02 mg kg^{-1}) based on estimated body mass (Heath et al. 1996). Once females were sedated, they were anesthetized with isoflourine administered with a portable gas anesthesia machine (Heath et al. 1996), and the VDR was attached.

In 2008, VDRs were recovered after one week or less depending entirely on how rapidly VDRs became detached from the pelage. In 2009 VHF radio transceivers connected to VDRs while SSL were onshore and displayed battery voltage and total video recorded during the previous 8 hr of operation. This information aided in determining when to remove VDRs. Deployments lasted approximately one week, depending on the frequency of foraging trips, before the batteries were depleted. At the end of each deployment, the transceiver was used to activate a remote release mechanism that detached the housing and camera from the neoprene patches. Neoprene patches detached when SSL molted.

Dead reckoning was used to calculate three-dimensional paths (at 1Hz) for foraging trips (Bowditch 1837, Davis et al. 2001). A new position was calculated every second while SSL were at sea based on the proceeding position and a vector derived from compass heading (i.e., X and Y direction), body angle (i.e., Z direction) and forward swim speed (magnitude). Foraging trips were then subdivided into individual dives. Only dives deeper than 3 m and longer than 30 sec were included in the analysis. Each dive was then manually subdivided into three phases based on significantly different body angles and validation of SSL behavior from videos: descent, horizontal swimming and ascent. The descent phase was defined as the time between departure from the surface and the point at which negative pitch angle and the change in depth per second rapidly changed from an average value of -50 ± 19° to -1 ± 4° (i.e., SSL assumed a nearly horizontal attitude and stopped increasing depth until the ascent). Based on observations from video, any time between the descent and ascent was considered to be time at the seabed. Ascent was identified as the initiation of a rapid increase in positive pitch angle to an average of 44 ± 20° and simultaneous decrease in depth which continued until the SSL reached the surface.

Video recordings from VDRs were used to identify prey encounters and other behaviors. For every prey encounter, the time of the encounter, prey type and whether the encounter resulted in capture was recorded. Encounters were identified as a prey item entering the field of view of the camera. The field of view was usually limited by available light to a distance of approximately 2 m in front of the SSL, with visibility to either side restricted to approximately 1 m. Because of the cryptic nature of most prey species, increased visibility (>10 m forward distance) at shallow depths during the day did not allow for the identification of prey at greater distances. Each encounter was recorded as: 1) *ignored* if it was not pursued, but drew the attention of the SSL as indicated by redirection of the head, 2) *not seen* if the SSL made no movement to suggest that it saw the prey, 3) *escaped* if the SSL attempted to capture the prey and failed, or 4) *captured* if the prey item was successfully captured and consumed. Prey encounters and other behaviors were synchronized using the real time clock displayed on the video. Minimum prey densities for individual dives were estimated from the total distance swum at the seabed and an assumed visual search area of 1 m^2 (based on video observations of SSL responses to prey presence, SSL were assumed to search up to 0.5 m from either side of the muzzle). The total number of fish, total time spent submerged and total time spent foraging at the seabed were summed for all dives with video. CPUE was calculated by dividing the sum of fish captured by the sum of time spent submerged separately for all dives in each dive type (see below).

Twenty dive and swimming performance variables which did not include information about prey encounters or consumptions were calculated for 221 dives (Table 1) (Krafft et al. 2000, Davis et al. 2001, 2003). Factor analysis (principal factor method) was then performed to reduce the 20 variables to a smaller subset of orthogonal factors according to guidelines presented by Costello and Osborne (2005) and Matsunaga (2010). Prior to factor analysis, all 20 variables were transformed via the Box-Cox transformation (Box & Cox 1964) to be as close to normal as possible. Following varimax rotation of results, variable loadings, Eigenvalues and a scree plot were examined to determine the number of factors to retain for further analysis based on the incidence of under- or over-extraction and the point at which additional factors did not significantly improve the total amount of explained variance. Factor scores were then standardized by range (i.e., min = 0, max = 1, Steinley 2004). Following standardization, case order was randomized and a k-means clustering analysis was performed. Initial cluster seeds were automatically selected to maximize the initial cluster distances. Squared Euclidian distance was selected as the distance measure and v-fold (v = 10, minimum % change = 5%) cross-validation was used to determine the appropriate number of clusters. All data manipulation was performed in MATLAB® R2009b (The MathWorks, Inc. 2009) while Statistica® 12 (StatSoft, Inc. 2013) was used for statistical analyses.

To determine if the dive types identified during the previous analysis could be identified with time-depth data alone, k-means clustering was performed using the six variables which could be derived from TDR data and contributed most to the factors (i.e., largest factor loadings) used in the previous analysis. These six variables were: maximum dive depth, dive duration, duration spent at the seabed (validated for this study with video), the percentage of total dive duration spent at the seabed, and the vertical descent and ascent rates. Identifying benthic foraging as time spent below a threshold percentage of maximum dive depth (i.e., time spent below 80% of maximum depth) may be suitable in the absence of video and where other evidence of benthic foraging exists. Values for each of the variables were calculated from a set of 713 dives that included the 221 dives used in the previous analysis as well as 492 dives for which speed and body orientation data were not available. As with the previous analysis, case order was randomized, values were standardized by range and sample seeds were determined automatically to maximize the initial differences between cluster means. Interpretations of the results from the analysis of 3-dimensional data, described below, suggested that 3 a-priori clusters were appropriate.

Results

Data were recorded for 13 foraging trips (6, 3, 1, 1 and 2 trips each from five SSL) and 713 dives, of which 357 had video recordings. Sixty-six percent of dives were between sunset (approximately 22:00) and sunrise (approximately 06:00), while 83% fell within the 12 hr window between 18:00 and 06:00. SSL dove at an average rate of 6.4 dives hr^{-1} and spent 45% of time at sea submerged during all 13 foraging trips. Sufficient data were available to construct three-dimensional paths (including 221 dives) for four trips (three from one SSL and one from a second, Figure 2). Video was recorded during 154 of the 221 dives. Based on three-dimensional paths, the four foraging trips had a mean duration of 7.0 ± 2.0 hr and average total distance swum of 28.9 ± 10.0 km.

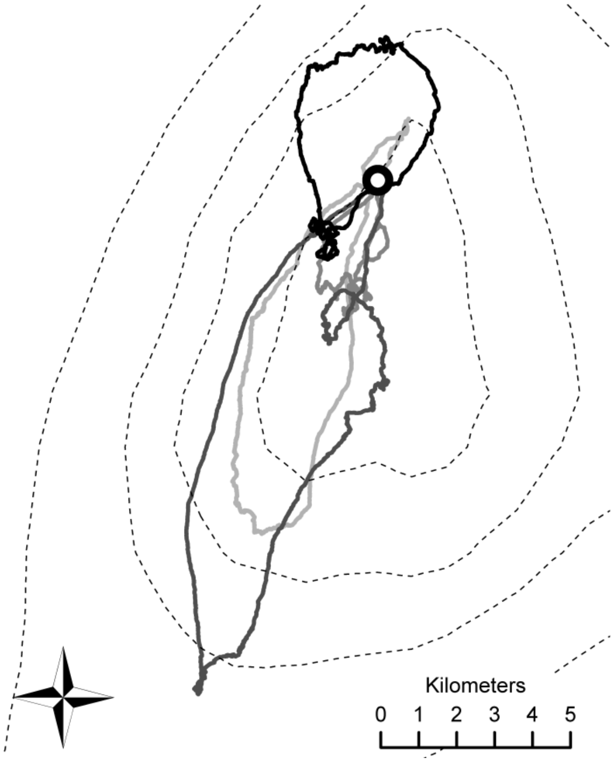

Figure 2. Map of four foraging trips which contained dives used in factor analysis. The three trips in grey were from one SSL, while the trip in black was from a second.

The mean dive duration and mean maximum dive depth for all 713 dives were 3.1 ± 1.2 min (note that dives < 30 s were excluded from the analysis) and 56 ± 44 m, respectively (Figure 3 and 4). Although dive duration was normally distributed, maximum dive depth was not (Shapiro-Wilk test, $p < 0.05$). With a bimodal distribution, the majority (65%) of dives was shallow (< 50 m) while a second group (24%) was deeper (100-150 m) (Figure 4). There was a weak correlation between dive depth and dive duration ($R^2 = 0.28$). However, when dives were binned by maximum dive depth (using 10 m increments), the minimum dive duration in each bin did increase with depth

(R^2 = 0.91, Figure 5). Maximum dive depth did not correlate with either duration at the seabed or the percent of total dive duration spent at the seabed. Excluding dives with no prey encounters, a crude proxy for whether foraging was taking place, increased the strength of the correlation between maximum dive depth and the percentage of total dive duration spent at the seabed (R^2 = 0.54, Fig. 6).

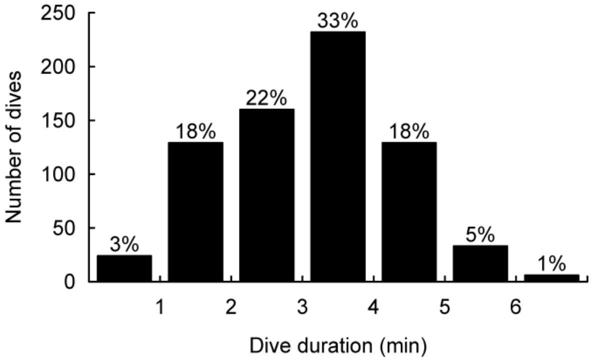

Figure 3. Frequency histogram of dive duration for all dives (n = 713).

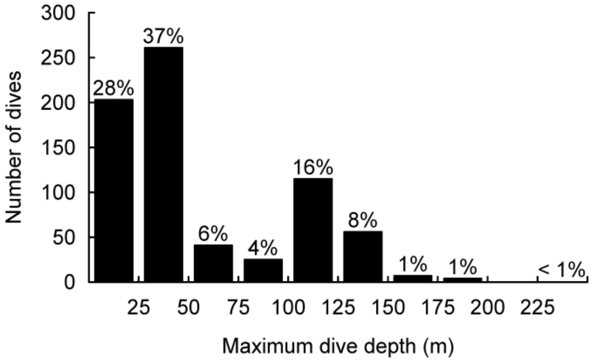

Figure 4. Frequency histogram of maximum dive depth for all dives (n = 713).

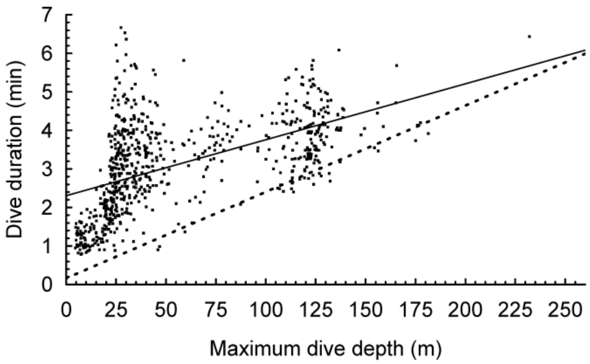

Figure 5. Scatter plot of dive duration vs. maximum dive depth. The solid line represents the linear regression for dive duration and maximum dive depth (n = 713, $R^2 = 0.28$), while the dotted line represents the linear regression for maximum dive depth and minimum dive duration binned into 10 m groups ($R^2 = 0.91$).

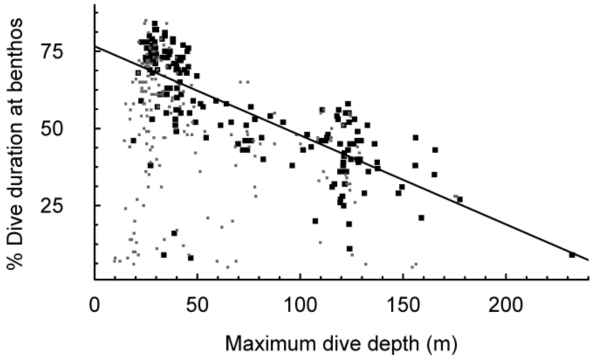

Figure 6. Percent of dive duration at the seabed vs. maximum dive depth. Large black marks indicate dives with at least one prey encounter (n = 173) while smaller gray points indicate dives with no prey encounters (n = 184). The solid line represents the linear regression ($R^2 = 0.54$) for dives with at least one prey encounter.

Of the 713 dives, 50% (357) had accompanying video. During these dives, 495 fish were encountered and 261 consumed. Ninety percent (445) of all encounters and 98% (256) of all captures were Atka mackerel (*Pleurogrammus monopterygius*). Other species encountered were walleye pollock (*Theragra chalcogramma* – 15 encounters, 2 captures), salmon (*Oncorhynchus sp.*- 2 encounters, 2 captures), sculpin (*Cottidae* – 31 encounters, no captures), and 1 capture of a member of the *Bathymaster* genus. Three of the 15 pollock encounters were with large fish that were not pursued. In many of the 31 encounters with sculpin, SSL appeared close enough to identify the presence of the fish (based on proximity to prey during successful captures), but no capture was attempted. Only 18% (92) of all encounters involved a chase longer than 3 sec. Of these, 73% (67) were successful. Vibrissae generally remained in a passive mode (folded against the face) during pursuit, only extending to their maximum forward reach (estimated from video records of yawning SSL) a few seconds prior to prey capture. Vibrissae would generally remain extended while SSL manipulated prey in the mouth.

Factor analysis was performed on the 221 dives for which three-dimensional dive profiles were available as significantly more information could be derived from them than from the remaining dives for which only time-depth data were available (Figure 7).

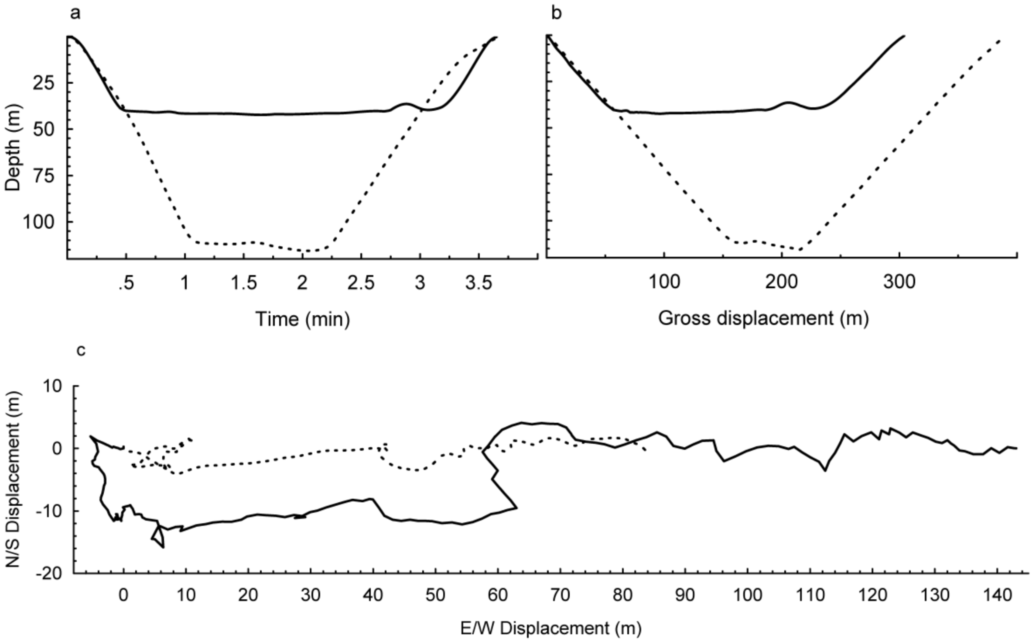

Figure 7. Three representations of the same two shallow (solid line) and deep (dashed line) dives. (a) Depth vs. time: shows how SSL distribute time among different phases of the dive. (b) Depth vs. gross displacement (i.e., distance swum): could be derived from any data set which included swim speed and depth data. Able to provide information describing the distance swum and, if benthic foraging is assumed, area searched at the seabed, an important observation for interpretations of foraging behavior. (c) Horizontal swim path while submerged: shows not only the horizontal displacement, but also gross displacement and the tortuosity of the swim path. This allows for the most detailed descriptions of foraging behavior, especially when combined with video recordings.

Based on these three-dimensional swim paths, factor analysis identified four factors (Table 1). Variables which contributed most to Factor 1 included and co-varied with depth. They were: vertical rate of descent and ascent, descent and ascent pitch, swim speed at the seabed, the difference between descent swim speed and swim speed at the seabed, and the ratio of net to gross displacement for the entire dive. Factor 2 was primarily composed of variables which included and co-varied with the amount of time spent at the seabed. They were: total dive duration, % total dive duration at the seabed, net displacement at the seabed, and gross displacement at the seabed. Factor 3 was derived from descent and ascent speeds, while the ratio of ascent to descent durations and path linearity at the seabed combined to create Factor 4. K-means clustering of factor scores identified five distinct clusters (Figure 8). Each cluster was then designated as a dive type (Types 1, 2, 3, 4 and 5) and described with mean values calculated from the original variables (Table 2).

Variables	**Factor 1:** (39%)	**Factor 2:** (26%)	**Factor 3:** (12%)	**Factor 4:** (6%)
Maximum dive depth	0.902 *	0.067	0.313	0.160
Dive duration	0.591	0.732 *	0.011	0.019
Time at seabed	0.265	0.934 *	0.122	0.131
% of total dive duration at seabed	0.012	0.925 *	0.151	0.196
Net displacement (entire dive)	0.580	0.646	0.191	0.372
Net displacement (at seabed)	0.338	0.898 *	0.057	0.177
Gross displacement (entire dive)	0.429	0.694	0.399	0.177
Gross displacement (at seabed)	0.154	0.964 *	0.015	0.036
Ratio of displacements: Net : Gross (entire dive)	0.877 *	0.181	0.029	0.287
Ratio of displacements: Net : Gross (at seabed)	0.650	0.096	0.085	0.533
Speed (descent)	0.318	0.080	0.807 *	0.008
Speed (at seabed)	0.871 *	0.017	0.216	0.098
Speed (ascent)	0.009	0.002	0.793 *	0.109
Pitch (descent)	0.913 *	0.107	0.091	0.145
Pitch (ascent)	0.884 *	0.122	0.161	0.061
Vertical rate of change (descent)	0.921 *	0.089	0.247	0.128
Vertical rate of change (ascent)	0.837 *	0.144	0.442	0.108
Ratio of speeds: (At seabed) : (Descent)	0.732 *	0.196	0.230	0.179
Ratio of duration: (Ascent) : (Descent)	0.052	0.168	0.470	0.632
Variance of vertical displacement at seabed	0.479	0.304	0.333	0.212

Table 1. Dive and swimming performance variables used for factor analysis. The percentage of total variance explained by each factor is indicated by parentheses. Below are absolute values of factor loadings. Loadings > 0.7 are indicated by *.

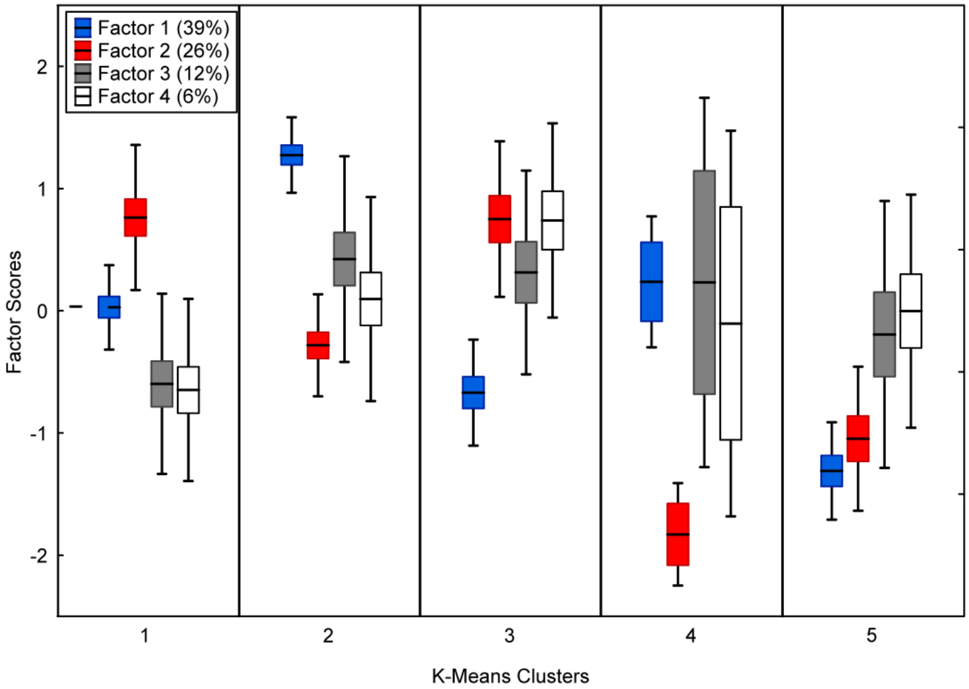

Figure 8. Relationships between factor scores and k-means cluster assignments. The percentage of total variance explained by each factor is shown in the legend.

Variables	**Units**	**All**	**Type 1**	**Type 2**	**Type 3**	**Type 4**	**Type 5**
Dives with video	-	154	59	42	34	9	10
Maximum dive depth	m	60 ± 39	38 ± 7	119 ± 21	38 ± 17	48 ± 14	27 ± 10
Dive duration	min	3.2 ± 0.9	3.5 ± 0.8	3.6 ± 0.5	3.1 ± 0.7	1.5 ± 0.5	1.8 ± 0.4
Duration (at seabed)	s	107 ± 57	147 ± 45	80 ± 27	117 ± 47	15 ± 12	28 ± 18
% of total dive duration at seabed	%	53 ± 21	69 ± 8	36 ± 9	62 ± 13	15 ± 12	25 ± 15
Gross displacement (entire dive)	m	278 ± 75	276 ± 69	311 ± 52	302 ± 61	169 ± 65	167 ± 46
Gross displacement (at seabed)	m	126 ± 85	175 ± 67	53 ± 20	185 ± 70	22 ± 20	45 ± 28
Mean speed	m s^{-1}	1.5 ± 0.3	1.3 ± 0.2	1.4 ± 0.3	1.7 ± 0.2	1.8 ± 0.4	1.5 ± 0.2
Speed (descent)	m s^{-1}	1.7 ± 0.3	1.5 ± 0.2	1.9 ± 0.2	1.8 ± 0.3	1.9 ± 0.4	1.5 ± 0.3
Speed (at seabed)	m s^{-1}	1.2 ± 0.5	1.2 ± 0.3	0.7 ± 0.3	1.6 ± 0.3	1.4 ± 0.5	1.6 ± 0.2
Speed (ascent)	m s^{-1}	1.7 ± 0.3	1.7 ± 0.2	1.8 ± 0.2	1.8 ± 0.3	1.9 ± 0.6	1.6 ± 0.3
Ratio of speeds: (At seabed) : (Descent)	-	0.7 ± 0.3	0.77 ± 0.18	0.36 ± 0.16	0.89 ± 0.15	0.73 ± 0.19	1.10 ± 0.14
Pitch (descent)	degrees	-53 ± 16	-52 ± 12	-72 ± 9	-41 ± 10	-50 ± 13	-32 ± 7
Pitch (ascent)	degrees	48 ± 18	44 ± 12	69 ± 9	35 ± 10	44 ± 22	25 ± 8
Linearity (whole dive)	-	0.44 ± 0.23	0.46 ± 0.13	0.21 ± 0.10	0.71 ± 0.10	0.25 ± 0.24	0.66 ± 0.17
Linearity (at seabed)	-	0.64 ± 0.21	0.59 ± 0.16	0.55 ± 0.21	0.84 ± 0.08	0.41 ± 0.17	0.85 ± 0.07
% successful dives	%	46	59	55	24	33	10
Sum of captures	fish	124	72	36	12	3	1
Sum of encounters	fish	172	101	50	17	3	1
Captures per dive	fish $dive^{-1}$	0.81	1.22	0.86	0.35	0.33	0.10
CPUE (time)	fish min^{-1}	0.25	0.35	0.24	0.12	0.22	0.06
CPUE (distance)	fish m^{-1}	0.003	0.004	0.003	0.001	0.002	0.001
Min prey density	fish m^{-2}	0.009	0.010	0.022	0.003	0.015	0.002

Table 2. Means (± SD) for dives with three-dimensional paths and video.

Type 1 dives (n = 59, Figure 9) had a mean maximum depth of 38 ± 7 m, mean dive duration of 3.5 ± 0.8 min, a mean surface interval of 1.9 ± 1.4 min, and a mean speed of 1.3 ± 0.2 m s^{-1}. SSL descended at a forward speed of 1.5 ± 0.2 m s^{-1} and then swam at 1.2 ± 0.3 m s^{-1} while at the seabed. While making Type 1 dives, SSL spent an average of 69 ± 8% of dive duration at the seabed with the remaining time evenly divided between descent and ascent. A net-to-gross displacement ratio (NGD, a measure of linearity) of 0.59 ± 0.16 (i.e., 0 would be non-linear and 1 perfectly linear) while swimming at the seabed indicated horizontal meandering during prey searching. SSL generally did not swim past the same location more than once (based on three-dimensional dive profiles), but occasionally made small horizontal loops. Type 1 dives were the most successful and accounted for 58% (72) of the 124 prey captures. Sixty-nine percent (41) of Type 1 dives with video had one or more prey encounters, and 59% (35) included one or more captures. These dives had an overall CPUE of 0.35 fish min^{-1} or 1.22 fish $dive^{-1}$. While making Type 1 dives, SSL swam a combined total of 10,328 m at the seabed and encountered 101 prey. Assuming a 1 m^2 search area, the estimated minimum prey density (fish encountered for every meter swum at the seabed) was 0.010 fish m^{-2}.

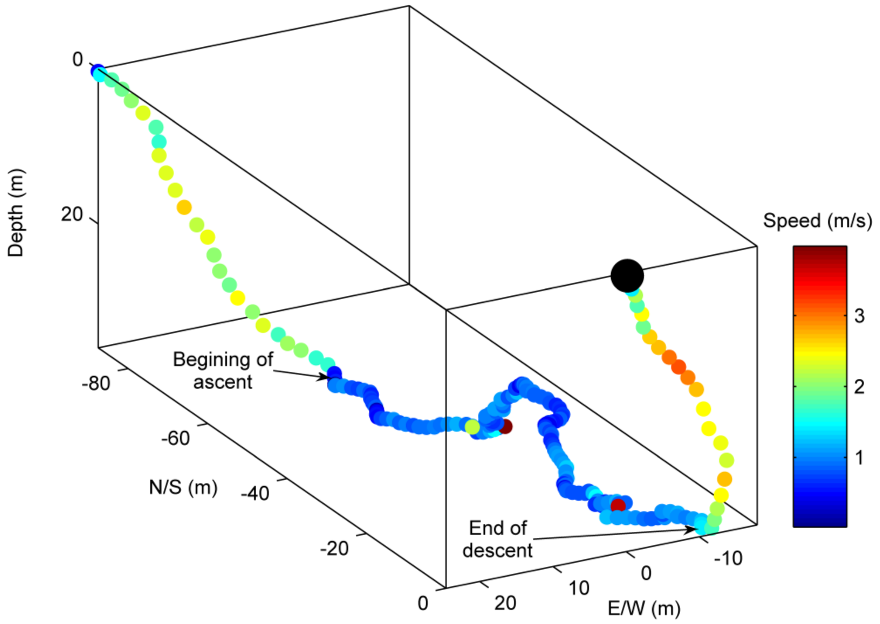

Figure 9. Representative Type 1 dive. The beginning of the dive is indicated by the large black dot.

Type 2 dives (n = 42, Figure 10) had a mean maximum depth of 119 ± 21 m, a mean dive duration of 3.6 ± 0.5 min, a mean surface interval of 2.6 ± 1.6 min, and a mean speed of 1.4 ± 0.3 m s^{-1}. SSL descended at a forward speed of 1.9 ± 0.2 m s^{-1} and swam at 0.7 ± 0.3 m s^{-1} while at the seabed. Type 2 dives were an average of 81 m deeper than Type 1 dives, which resulted in less time (36 ± 9%) spent at the seabed and more time spent descending and ascending. SSL descended and ascended at significantly steeper angles of -72 ± 9° and 69 ± 9°, respectively, compared to Type 1 dives (-52 ± 12° and 44 ± 12°, respectively). These angles were more than 20° steeper than all other dive types. With an NGD at the seabed of 0.55 ± 0.21, these dives exhibited horizontal meandering similar to those of Type 1 dives. Type 2 dives were the second most successful with prey encounters during 62% (26) of dives and prey captures during 55% (23) of dives, resulting in an overall CPUE of 0.24 fish min^{-1} or about 0.9 fish dive^{-1}. SSL swam a combined total of 2,224 m at the seabed and encountered 50 prey for an estimated minimum prey density of 0.022 fish m^{-2}, twice that of Type 1 dives.

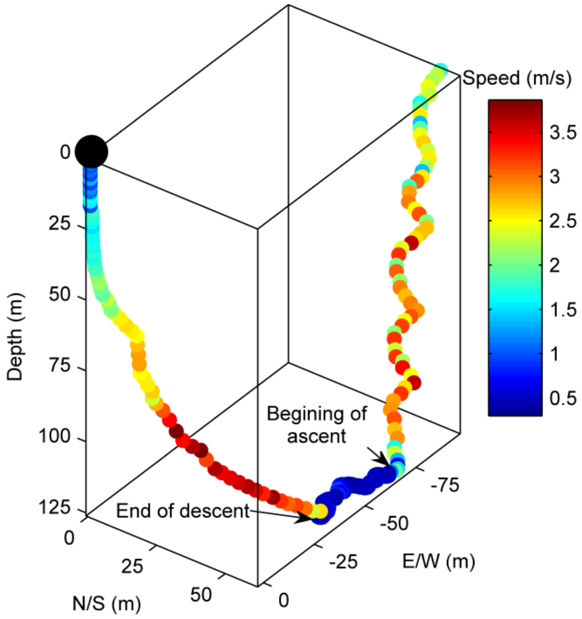

Figure 10. Representative Type 2 dive. The beginning of the dive is indicated by the large black dot.

Type 3 dives (n = 34, Figure 11) were similar to Type 1 dives with a mean maximum dive depth of 38 ± 17 m, a slightly shorter mean duration of 3.1 ± 0.7 min and a mean speed of 1.7 ± 0.2 m s^{-1}. SSL descended at a forward speed of 1.8 ± 0.3 m s^{-1} and swam at 1.6 ± 0.3 m s^{-1} while at the seabed. During Type 3 dives, SSL spent 62 ±

13% of dive time at the seabed and exhibited greater path linearity (NGD = 0.84 ± 0.08) than Types 1 and 2 dives. With 66% and 83% fewer prey encounters than Type 1 or 2 dives, respectively, Type 3 dives had a low overall CPUE of 0.12 fish min^{-1} or 0.3 fish dive^{-1}. SSL swam a combined total of 6,287 m at the seabed and encountered 12 fish for a minimum estimated prey density of 0.003 fish m^{-2}.

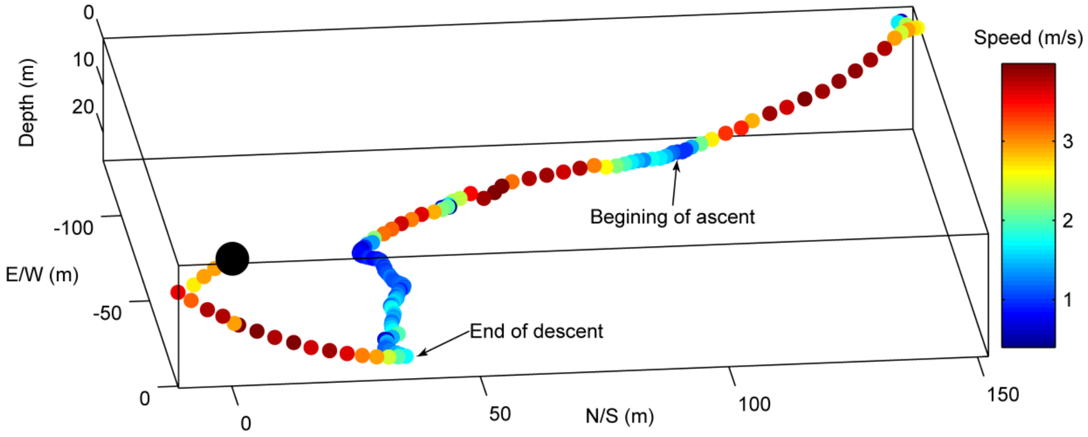

Figure 11. Representative Type 3 dive. The beginning of the dive is indicated by the large black dot.

Type 4 dives (n = 9, Figure 12) were a small group with a mean maximum dive depth of 48 ± 14 m, a mean dive duration of 1.5 ± 0.5 min and a mean speed of 1.8 ± 0.4 m s^{-1}. SSL descended at a forward speed of 1.9 ± 0.4 m s^{-1} and swam at 1.4 ± 0.5 m s^{-1} while at the seabed. Only 15 ± 12% of dive time was spent at the seabed. Despite a relatively high overall CPUE of 0.21 fish min^{-1}, only 3 of the 9 dives included a prey capture. In each of these dives, a single fish was encountered and consumed. The CPUE was high because of the short duration of Type 4 dives and a small sample size. These dives included behaviors not seen in most dives (e.g. opportunistic capture of prey in the water column, swimming near the surface or interaction with other SSL).

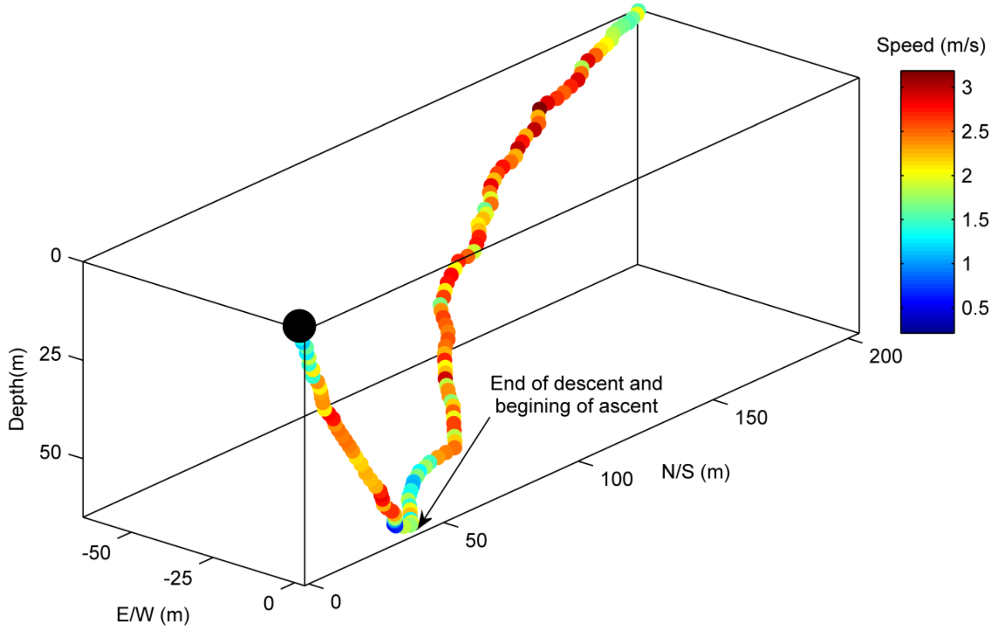

Figure 12. Representative Type 4 dive. The beginning of the dive is indicated by the large black dot.

Type 5 dives (n = 10, Figure 13) were shallow (27 ± 10 m) and short (1.8 ± 0.4 min) with a mean speed of 1.5 ± 0.2 m s^{-1} and a small percentage of time spent at the seabed (25 ± 15%). Type 5 dives were different from other dive types due to the shallow angles at which SSL descended (-32 ± 7°) and ascended (25 ± 8°), which were approximately 10° less than Type 3 dives, 20° less than Type 1 and 4 dives, and 45° less than Type 2 dives. Type 5 dives had a mean swim speed of 1.5 ± 0.2 m s^{-1}. Similar to Type 3 dives, Type 5 dives were relatively linear (NGD: 0.66 ± 0.17). The overall CPUE for Type 5 dives was 0.06 fish min^{-1}. The minimum estimated prey density was 0.002 fish m^{-2}.

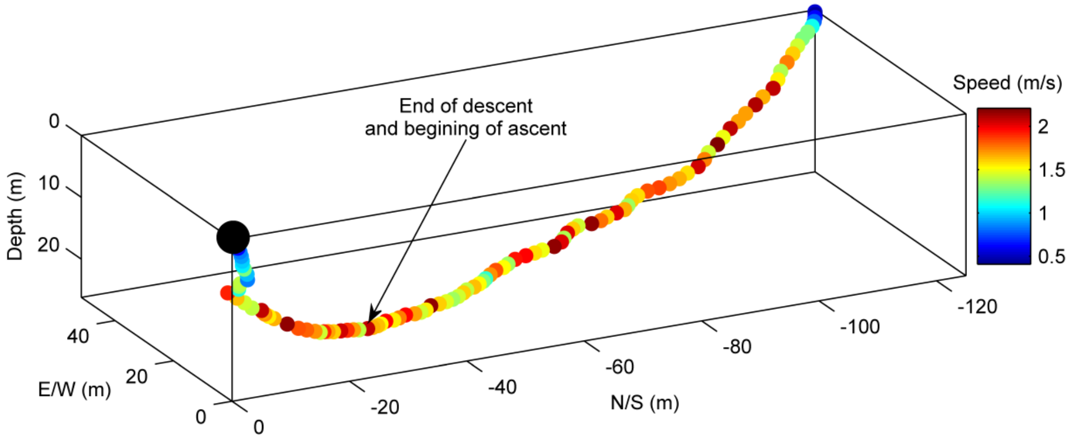

Figure 13. Representative Type 5 dive. The beginning of the dive is indicated by the large black dot.

Clustering analysis using only time-depth data grouped all 713 dives into 3 clusters (TDRC 1 – 3). The majority of Type 1 (97%) and Type 3 (76%) dives were placed together in TDRC 1, while all (100%) of Type 2 dives were placed together in TDRC 2. The remainder of Types 1, 3, 4, and 5 (2%, 18%, 100%, and 85%, respectively) were placed together in TDRC 3. TDRC 1 dives (n = 297) had a mean maximum depth of 34 ± 11 m and mean duration of 3.6 ± 0.9 min. With vertical descent and ascent rates (calculated as the change in depth per second) of 0.96 ± 0.26 and 0.89 ±

0.23 m s^{-1}, SSL spent an average of 68 ± 9% of total dive duration at the seabed. Together, TDRC 1 dives with video (n = 187) had a CPUE of 0.19 fish min^{-1}.

TDRC 2 dives (n = 220) were deeper and longer in duration with a mean maximum dive depth of 117 ± 24 m and mean dive duration of 3.9 ± 0.8 min. SSL descended and ascended at vertical rates of 1.7 ± 0.3 and 1.6 ± 0.3 m s^{-1} and spent an average of 38 ± 13% of dive duration at the seabed. TDRC 2 dives with video (n = 117) had a combined CPUE of 0.30 fish min^{-1}.

TDRC 3 dives (n = 53) were shallow (21 ± 13 m) with short durations (1.7 ± 0.5 min). Vertical descent and ascent rates were 0.6 ± 0.3 and 0.5 ± 0.3 m s^{-1}, respectively, and SSL spent an average of 25 ± 16% of total dive duration at the seabed or swimming horizontally in the water column between the descent and ascent. With only 3 prey consumptions, TDRC 3 dives with video (n = 53) had a total CPUE of 0.03 fish min^{-1}.

Discussion

Classification of Foraging Dives

Types 1 and 2 dives appeared to represent the bulk of SSL foraging efforts as they contributed significantly more than other dive types to total prey encounters and captures. When making foraging dives, SSL maximized the amount of time spent at the seabed by increasing dive duration and descent and ascent angles relative to non-foraging dives. Type 1 dives (Fig. 9) were the most successful (1.22 fish dive-1, 0.35 fish min-1) and accounted for 58% (72) of all prey consumptions. During these shallow

(38 m), long duration (3.5 min) dives, SSL allocated large percentages of dive duration (69%, 2.4 min) to swimming at the seabed (175 m; 63% of gross distance swum). Type 2 dives (Fig. 10) were less successful (0.86 fish dive-1, 0.24 fish min-1), but accounted for the second highest number (29%) of prey captures. Given that the primary difference between Types 1 and 2 dives was maximum dive depth, it is likely that these dives represent two ends of a continuum of a single foraging behavior. During Type 2 dives, SSL were forced to allocate an average of 48% more time (1.2 min) to descent and ascent due to increased dive depth, resulting in a reduction (46%) to the amount of time available for foraging at the seabed. Additionally, 42% slower swim speeds (relative to Type 1 dives) at the seabed reduced the gross displacement (i.e., area searched for prey) at the seabed by 70%. Despite an increase to prey density (2.2 fold) and descent and ascent angles (38 and 57%, respectively), the CPUE for Type 2 dives was 31% smaller than for Type 1 dives.

A study of the foraging behavior of Weddell seals making dives beneath the shore-fast ice in McMurdo Sound, Antarctica used the same VDRs and similar dive variables to identify three dive types (Davis et al. 2013). Most (99%) prey captured were Antarctic silverfish (*Pleuragramma antarcticum*) with 79% of all captures occurring during Weddell seal Type 1 dives (WST 1). WST 1 dives were the deepest (mean maximum depth 324-378 m), longest in duration (15.0-27.0 min), covered the greatest total distance (1,470-2,197 m), and had the steepest dive angles (-30 to 27°). Although much deeper and longer in duration, WST 1 dives were similar (but much deeper) to SSL Types 1 and 2 dives. For both species, reduced path linearity, as well as increased dive depth, duration, and descent and ascent angles were key to discriminating among dive types, specifically between foraging and transit dives (described below).

As Lesage et al. (1999) point out, studies which include swim speed data in addition to time-depth data allow for more detailed interpretations of animal movements. However, the ability to generate three-dimensional dive paths with video recordings of prey encounters and consumptions provides significantly more information about the animal’s behavior. For example, path linearity and prey encounter/capture rates enabled us to distinguish between Type 1 foraging dives and Type 3 opportunistic foraging dives, both of which had flat-bottom time-depth profiles with similar distances swum at the seabed. As with Type 1 dives, Type 3 dives (Figure 11) were shallow (38 m) and long in duration (3.1 min). Type 3 dives were the third most successful (0.35 fish dive^{-1}, 0.12 fish min^{-1}) and appeared to be a variation of Type 1 dives but differed by having: 1) shallower descent and ascent angles, 2) higher swim speeds at the seabed and 3) significantly more linear dive paths (Figure 14). These indicate that horizontal travel was the primary objective of Type 3 dives, and that they may represent opportunistic foraging while transiting through areas with lower prey density.

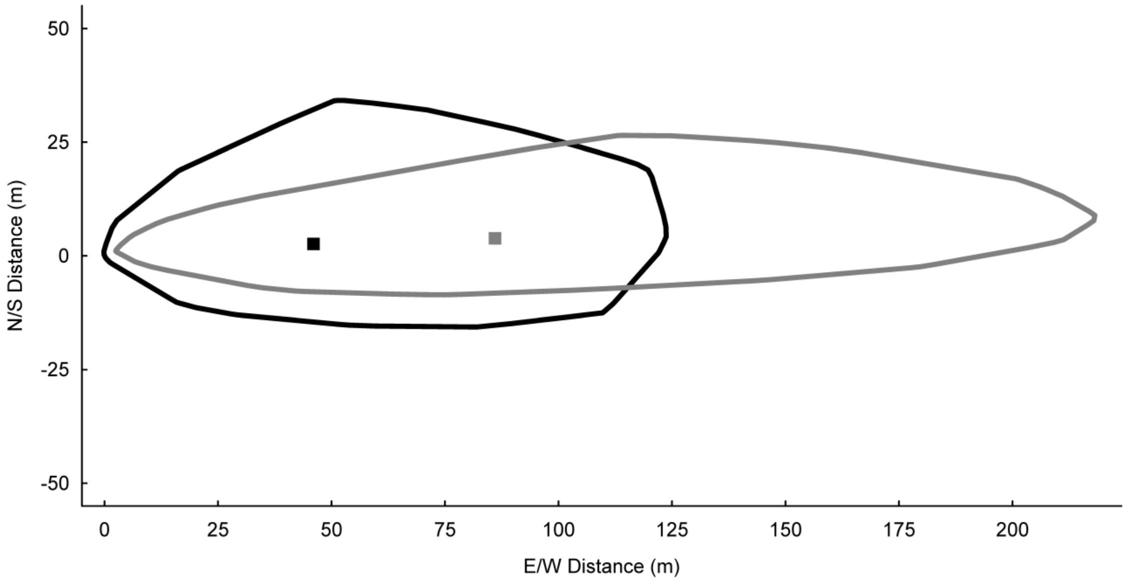

Figure 14. Comparison of path tortuosity for Type 1 (black) and 3 (gray) dives. All dive profiles for Type 1 and 3 dives were oriented from West to East. Bag plots were then generated to represent 50% of all locations for each dive type. Squares represent median locations. Type 1 dives were more tortuous with smaller net displacements (i.e., greater distance between dive start and end locations) while Type 3 dives were more linear and had larger net displacements. The increased net displacement seen in Type 3 dives suggests that horizontal transiting was an important objective.

Lactating SSL with young pups at Lovushki did not travel far from the rookery, spending most of their time within 10 km of shore (Figure 2; Waite et al. 2012b). Had SSL traveled farther offshore, the frequency of Type 3 dives may have been greater. During the breeding season, female South American sea lions (SAMSL, *Otaria flavescens*) exhibit dive patterns similar to SSL, with the majority of dives to depths less than 40 m and shorter than 4 min (Riet-Sapriza et al. 2013). SAMSL that traveled farther from shore during foraging trips did so not by extending trip duration, but instead by increasing swim speed. Type 3 dives may represent a similar strategy, increasing swim speed and path linearity, while still swimming near the seabed to take advantage of opportunistic prey encounters. Unfortunately, discrimination of Type 3 dives from Type 1 dives was heavily reliant on the availability of measurements of path linearity. As such, the identification of these dives in other studies without three-dimensional swim paths may not be possible.

Classification of Non-Foraging Dives

Identification of Type 4 dives (Figure 12) and Type 5 dives (Figure 13) was similarly dependent on path linearity. Although both had V-shaped time-depth profiles, Type 4 dives were deeper (48 m) but shorter in duration (1.5min), duration at the seabed (0.25 min, 15% of dive duration) and distance traveled at the seabed (22 m, 13% of total distance traveled). Type 4 dives appeared not to consist of dives with similar behaviors, but instead of dives that did not group with other dive types. Type 4 dives were highly tortuous, fast and included behaviors not seen in most dives such as opportunistic capture of prey near the surface and interactions with other SSL. Several Type 4 dives appeared to consist of steep descents and ascents with little to no time spent at the seabed. This may represent an exploratory behavior used to identify water depth. WST 2 dives were similar, with short durations (3.6 min) and shallow depths (mean maximum depth 30 m). During these dives, WS remained close to the ice holes used for breathing (farpoint distance 75-130 m) and often engaged in aggressive interactions with other seals targeted at maintaining access to the ice holes for breathing opportunities.

Type 5 dives were shallow (27 m) and short (1.8 min) with little time spent (0.47 min; 28% of dive duration) and short distances travelled (45 m; 27% of total distance traveled) at the seabed. As with Type 1 and 3 dives, Type 4 and Type 5 dives had similar appearances (v-shaped) when compared with time-depth or displacement-depth plots but had significantly different path linearity (Figure 15). Unlike Type 1 and 3 dives, Type 4 and 5 dives did not appear to represent variations on a single behavior (i.e., Type 1 tortuous deliberate foraging vs. Type 3 linear opportunistic foraging). While no specific function was apparent for Type 4 dives, shallow descent and ascent angles, short or non-existent periods of horizontal swimming and highly linear swim paths, suggest that Type 5 dives were associated with transiting.

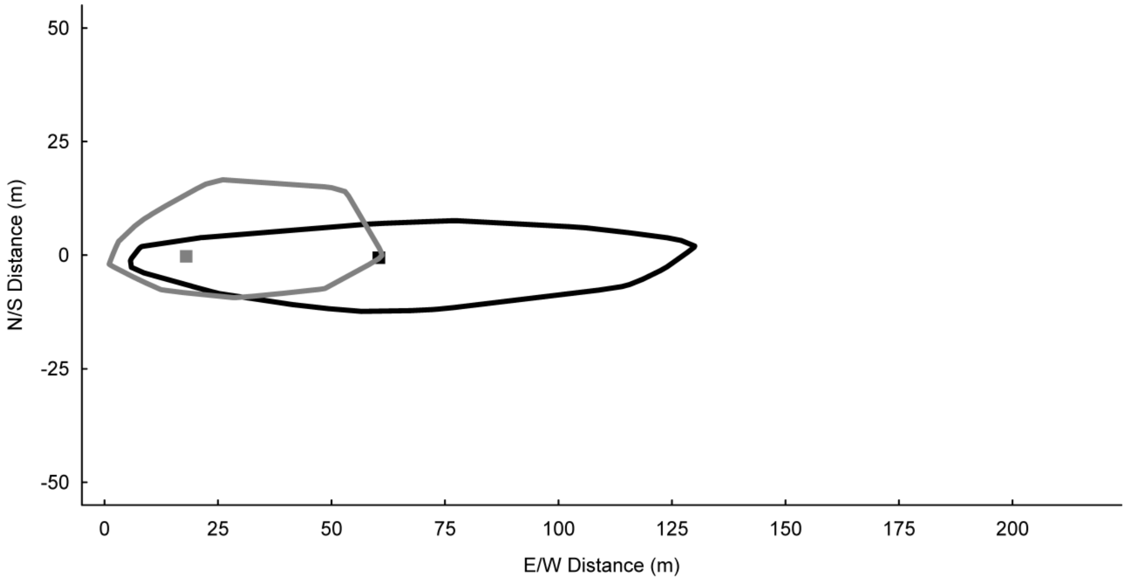

Figure 15. Comparison of path tortuosity for Type 4 (gray) and 5 (black) dives. All dive profiles for Type 4 and 5 dives were oriented from West to East. Bag plots were then generated to represent 50% of all locations for each dive type. Squares represent median locations. Type 4 dives were more tortuous with smaller net displacements (i.e., greater distance between dive start and end locations) while Type 5 dives were more linear and had larger net displacements. As with Type 3 dives, the increased net displacement seen in Type 5 dives suggests that horizontal transiting was an important objective. Axis scales were set to match those of Fig. 14 to allow for direct comparisons.

Although WS are not central place foragers and do not make transit dives to foraging grounds while provisioning a pup as SSL do (female Weddell seals fast during lactation), WST 3 dives (Davis et al. 2013) appear analogous to both SSL Type 3 and 5 dives. WST 3 dives were shallow, relative to foraging dives, with small descent and ascent angles, high path linearity and high swim speeds. Although, WST 3 dives occasionally included foraging behaviors, as did both Type 3 and 5 dives for SSL, Davis et al. (2013) concluded that they likely represented a combination of exploratory dives or dives where seals transited between ice holes.

Classification of Dives with Time-Depth Data

K-means clustering of the six variables which could be derived from time-depth data alone was set a-priori to identify three clusters. This was based on the classification of Types 1 and 3 dives as shallow foraging and opportunistic foraging dives, respectively, and the understanding that, without measurements of speed and path linearity, differentiating between the two would be difficult. The majority of all Types 1 and 3 dives (88%), which collectively represented shallow foraging, were placed together in TDRC 1. With a CPUE of 0.19 fish min^{-1}, this collection of dives was similarly classified as shallow foraging. All Type 2 dives, as well as a handful of Types 1, 3 and 5 dives, were placed together in TDRC 2. With the majority of dives belonging to the deep foraging Type 2 dive classification and a high CPUE of 0.30 fish min^{-1}, TDRC 2 was classified as deep foraging. Finally, TDRC 3 was made up primarily of Types 3 (n = 8), 4 (n = 41) and 5 (n = 11) dives and had a low CPUE of 0.03 fish min^{-1}. These dives were classified as transit dives.

The CPUE for deep foraging (TDRC 2) dives was greater than for shallow foraging (TDRC 1) dives. This conflicted with results from the analysis of 3-dimensional data which showed that shallow foraging dives (Types 1 and 3 combined) had a CPUE which was greater than for deep foraging dives (Type 2). This suggests that the small sample size of dives with both 3-dimensional data and video may have had a significant impact on estimates of minimum prey density and CPUE, preventing direct comparisons between foraging success at the two depths relative to behavioral modifications. However, differences in CPUE values between foraging and non-foraging dives were large in both analyses and likely represent a real distinction in behaviors.

These results suggest that foraging and non-foraging behaviors can be differentiated from one another with time-depth data alone. The key variable in making this distinction was the percentage of total dive duration spent swimming horizontally between the descent and ascent. At shallow (i.e., 30 m) depths, SSL making foraging dives should spent approximately 70% of dive duration in this state. This proportion falls to approximately 40% at a depth of 100 m. Foraging dives were also identified as being longer and were 3.5 – 4 min. SSL making non-foraging dives spent less time submerged (approximately 1.5 min) and allocated a small (25%) proportion of dive time to swimming horizontally at the seabed. Additionally, slower rates of vertical descent and ascent suggest that animals were likely swimming at shallower body angles and covering more horizontal distance than during foraging dives. However, this cannot be confirmed without speed data.

Quantification of Foraging Success

Due to the short duration (< 3 s) of most (82%) prey encounters and consumptions a sampling frequency of 1 Hz resulted in an inability to reliably detect either type of event based on changes in swim speed. Similarly, these events could not be identified from accelerometer data as body orientation was highly variable and could not be reliably associated with unsuccessful encounters, successful consumptions, or maneuvering while searching for prey. As such, only dives which contained video could be used to estimate foraging success. Minimum CPUE values could not be estimated for one of the four foraging trips with 3-dimensional swim paths due to a lack of video during the majority of dives and the inability to detect prey interactions with other data. Minimum CPUE was calculated for the remaining there trips as the ratio between the number of fish consumed and the amount of time spent at sea (fish hr^{-1}). These values represented minimum estimates as several dives in each trip lacked video and prey consumptions could have been inadvertently excluded from total values. With a weighted mean CPUE of 5.2 fish hr^{-1} and median trip duration at Lovushki Island of 7 – 8 hr (Burkanov et al. 2011, Waite et al. 2012b), SSL would be able to capture fish at a rate of 39 fish per foraging trip. As most SSL make one foraging trip per day, this translates to 39 fish per day. With an estimated nutritional requirement of 40 – 50 Atka mackerel per day (Winship & Trites 2003, Zeppelin et al. 2004), lactating SSL at Lovushki appear to be meeting their estimated nutritional requirements.

Conclusion

SSL dives were successfully classified into 5 functional types. Types 1 and 2 dives were shallow and deep dives, respectively, and dedicated to foraging almost exclusively on Atka mackerel. Foraging dives were longer in duration, consisted of steeper descent and ascent angles and included a larger portion of total dive time at the seabed than non-foraging dives. Type 3 dives represented opportunistic foraging while transiting and were distinguished from true foraging dives (Types 1 and 2) by shallower descent and ascent angles, greater speeds at the seabed, and higher path linearity, indicating horizontal movement as the primary objective. Type 4 dives included non-foraging behaviors such as interacting with other SSL, opportunistic prey capture near the surface and exploration of water depth. Finally, Type 5 transiting dives were shallow, short duration dives with shallow descent and ascent angles and little to no time spent at the seabed.

In combination with the successful discrimination between foraging and non-foraging dives with time-depth data alone, results support the idea that foraging dives can be identified in time-depth records as those dives during which animals spend a large proportion (i.e., > 70% at 30 m and > 40% at 100 m) of total dive time swimming horizontally between the descent and ascent. Although this study was able to use animal-borne video to validate that the majority of dives matching this description involved foraging at the seabed and quantify the rates at which prey were consumed during dives and foraging trips, a study which lacked video could not. It is possible, however, that the addition of speed sensors to time-depth recorders could be juxtaposed with fisheries data describing average prey densities to estimate CPUE values without the benefit of animal-borne video. Still, making small scale inferences about individual dives based on large scale fisheries data would be risky. However, using these data to make broader estimates of regional foraging success based on average distances swum at the seabed and average prey densities may be appropriate and would be beneficial to making inferences about the relationships between prey availability and population success.

CHAPTER III

TESTING A PREDICTION FOR OPTIMAL FORAGING IN PHOCIDS ON AN OTARIID, THE STELLER SEA LION

Introduction

Understanding the physiological ecology of marine divers is complicated by a lack of data stemming from the difficulty of making observations of animals diving in their natural habitat. In an effort to resolve this, many studies have been done with wild and/or captive animals to describe how marine divers utilize the submerged resources available to them while adhering to the physiological constraints associated with being air breathers. These studies have relied on the use of a wide variety of sensors and techniques to collect data which describe: where animals travel (horizontal movements), how they dive (vertical movements), prey scope, rates of energetic expenditure and intake, how oxygen is stored and utilized by the body, how body condition fluctuates during foraging trips, etc. Additionally, simulation models have been used to help further explore what types of factors most heavily impact both the physiological constraints imposed on diving animals by their environment and the decisions that animals make to be successful given those limitations.

One such simulation model sought to explore the links between physiological capabilities, habitat and animal behavior by examining the relationship between short-term (i.e., single dive) habitat-dependent decision making and long-term (i.e., foraging trip) success. Thompson & Fedak (2001) hypothesized that diving phocids could maximize their CPUE during a foraging trip by applying “a simple giving up rule” whereby seals would abandon a dive early (i.e., not continuing to search until a diminished oxygen supply necessitated a return to the surface) if prey were not encountered by a certain quitting time (Tq). At the core of this hypothesis was the idea that, by shortening dives which are identified as having poor patch quality, seals could increase the number of dives made to more profitable prey patches during foraging trips. Using early prey success during a dive as a proxy for local prey density and then modifying behavior accordingly would allow a more efficient use of time, and an increased overall CPUE.

To test their prediction by measuring how the GUR might impact foraging trip CPUE values for diving phocids, Thompson & Fedak (2001) developed a model (giving up model, GUM) which simulated a seal diving to a foraging depth and either terminating the dive early or continuing to forage based on whether or not prey was encountered prior to Tq. Whether or not a prey item was encountered was pseudo-randomly determined. Increased prey densities correlated with increased likelihoods of at least one prey capture event occurring prior to Tq. The increase in efficiency (proportional benefit, PB) was calculated as the ratio of control (i.e., never giving up early) CPUE values to treatment (i.e., applying the GUR) CPUE values. To calculate how PB varied in different scenarios, the GUM was sensitive to two variables: 1) the percentage of total dive time spent transiting between the surface and foraging depth (a proxy for depth) and 2) how much time (Tq) should pass before a decision to surface or continue foraging is made. Thompson & Fedak listed 5 assumptions which simplified the GUM: 1) for every dive, all foraging occurred at a constant depth, 2) prey detection only occurred at the established foraging depth, 3) when at depth, seals searched randomly at a constant speed, 4) seals consumed oxygen at a constant rate and departed the foraging depth when ascent time equaled the amount of time required to reach the surface concurrently with complete depletion of oxygen stores, and 5) the area searched during a dive (m^2) could be approximated by twice the product of foraging time (1200 s, less transit time), speed (constant, $m * s^{-1}$) and detection distance (m, not specified).

Results of the GUM favored giving up on dives which were not successful by Tq in some scenarios, but not others. As transit time (i.e., depth) increased, PB decreased, with the greatest PB corresponding to a transit time of 20% total dive time. For these "shallow" dives, giving up when not successful by Tq significantly increased PB for all but the highest prey densities. When transit time increased to 35% total dive time, PB was close to 1 (i.e., little to no benefit) for all prey densities. Similarly, PB increased as Tq became smaller. If Tq became too small, however, PB decreased rapidly. Together, these results conditionally supported the original prediction which stated that seals could increase their overall CPUE by abandoning unsuccessful dives to increase the amount of time spent foraging in higher density prey patches. Abandoning unsuccessful shallow dives increased CPUE because transit time was short. For deep dives, longer transit times counteracted the benefit of ending dives early, resulting in no increase to overall CPUE.

To test the GUR proposed and supported by the GUM by Thompson & Fedak (2001), Cornick & Horning (2003) developed an experiment designed to simulate foraging behavior in SSL. This experiment consisted of a variety of scenarios during which SSL searched for and consumed prey in a captive setting. By varying parameters such as initial search time and the rate at which prey were provided to study animals, researchers investigated the relationships between prey encounter rates and variables such as dive duration, foraging duration, and “search time” (time spent submerged before being presented with prey), a proxy for descent duration. Sparling et al. (2007) also designed an experiment to test the GUR with grey seals (*Halichoerus grypus*). In this experiment, seals swam a course which had a controllable length to simulate varying descent and ascent durations (i.e., dive depths). At the far end of the course, an apparatus provided seals with prey items at rates which varied between trials. Again, the relationship between the rate of prey encounters and variables such as dive duration and foraging duration was examined. Although some results were confounding, which is not unexpected given the complexity of designing and performing an experiment with live animals, both studies were able to present data which helped to validate the key conclusions drawn by Thompson & Fedak (2001).

In 2014, Heaslip et al. published a study in which researchers sought to test several predictions of optimal diving theory from a variety of sources. Four of these predictions were derived from Thompson & Fedak (2001) and related to the application of the GUR by diving harbor seals (*Phoca vitulina concolor*). This study was unique in that it not only included data collected from wild, free-roaming animals, but also that it included quantitative measures of prey capture rates via the inclusion of on-board camera systems which subsampled behavior by recording 10 min of video every 45 min.

Heaslip et al. found that seals were shortening dives by spending less time at foraging depths when prey were not encountered. This finding provided additional support for the key component of the GUR: that seals should shorten dives to low prey density patches in order to increase the number of dives to higher prey density patches. Authors noted that many of their findings were derived from qualitative support for their predictions as statistical models explained little of the variance seen in the data. This was understandably the result of, among other factors, technological limitations and short sampling periods which occurred during the breeding season (Heaslip et al. 2014). Nonetheless, authors provided additional support for utilization of the GUR by foraging phocids to maximize CPUE.

Thus far, the ability of divers to increase CPUE by applying the GUR has been tested by one simulation model, two captive studies, one on SSL and the other on grey seals, and one study using data from free-roaming wild harbor seals. Although all supported the predictions, results were occasionally confounding and relied on a number of assumptions and extrapolations to real-world scenarios. The objective of this study was to further validate the aforementioned conclusions by testing the GUR for wild, free-roaming SSL with high resolution (1 Hz) data and video (continuous, 30 fps) not previously available. Two methods were used to this end: 1) an analysis of three-dimensional foraging dive profiles and their accompanying video recordings, and 2) development of a GUM which accurately simulated SSL foraging dives and prey densities in order to test how implementation of the GUR may impact CPUE values over the course of an entire foraging trip.

Methods

Experimental Design

If SSL employed the GUR while foraging at sea, then dive durations and/or the amount of time spent foraging at the seabed should have been shorter for dives during which prey were not encountered than for dives during which prey were encountered. Two hypotheses were used to test this prediction. Our first null hypothesis, $H_{0,A}$, stated that total dive durations for dives with no prey encounters ($TDUR_{NP}$) should not have been significantly different from total dive durations for dives with 1 or more prey encounters ($TDUR_{YP}$). Conversely, $H_{1,A}$ stated that $TDUR_{NP}$ should have been significantly less than $TDUR_{YP}$. Our second hypothesis stemmed from the consideration that, due to long transit times, abandoning deep dives early may have resulted in only minor changes to overall dive duration, despite significant reductions to benthic search time. $H_{0,B}$ and $H_{1,B}$ were nearly identical to $H_{0,A}$ and $H_{1,A}$ but considered the relationship between benthic foraging duration ($BDUR_{NP}$ and $BDUR_{YP}$), instead of total dive duration, and whether or not prey were encountered. In summary, hypotheses A and B stated that:

$$H_{0,A}: TDUR_{NP} = TDUR_{YP} \text{ and } H_{1,A}: TDUR_{NP} < TDUR_{YP}$$

$$H_{0,B}: BDUR_{NP} = BDUR_{YP} \text{ and } H_{1,B}: BDUR_{NP} < BDURYP$$

A single hypothesis was tested for both shallow and deep dives when using the GUM to examine how applying the GUR to foraging trips impacted CPUE. $H_{0,C}$ stated that, at the scale of a single foraging trip, CPUE values when applying the GUR ($CPUE_{GUR}$) in an environment with variable prey densities should not be significantly different from, or significantly less than, CPUE values when not applying the GUR ($CPUE_{CONT}$). Alternatively, $H_{1,C}$ stated that $CPUE_{GUR}$ should be significantly greater than $CPUE_{CONT}$. A "foraging trip" was defined as the combination of all consecutive dive cycles (dive cycle: dive and surface interval) which could be completed during a 10 hr period. Because an optimum value for Tq (the point in time at which a decision should be made to abandon or continue a dive) was unknown, H_C was tested with Tq values ranging from 10 – 90% of benthic search duration. As a control ($CPUE_{CONT}$), the GUR was disabled by setting Tq to 100%. Hypothesis C stated:

$$H_{0,C}: CPUE_{GUR} \leq CPUE_{CONT} \text{ and } H_{1,C}: CPUE_{GUR} > CPUE_{CONT}$$

The GUM designed for this study was constructed using MATLAB® R2009b (The MathWorks, Inc. 2009) while Statistica® 12 (StatSoft, Inc. 2013) was used to test hypotheses at alpha = 0.01. All mean values were reported ± 1 standard deviation.

Data Acquisition and Analysis

During the summer of 2009, two VDRs were deployed on a pair of lactating female SSL at Lovushki Island, Russia (Figure 1, 48.543^{o} N, 153.876^{o} E), a small outcropping of rocks belonging to the Kuril Island chain. Each VDR was composed of a back-mounted main housing and a head-mounted video camera system. In addition to a micro-processor and storage space (spinning disk for video and solid state disk for data), the main housing of VDRs contained a suit of sensors including a pressure diaphragm (depth), differential swim speed tubes, a 3-axis magnetometer (compass bearing), and a 3-axis accelerometer (tilt, pitch and roll). With the exception of the accelerometer, which sampled at 20 Hz, all sensors sampled at 1 Hz. The low light sensitive camera could image both visible and near infrared light and recorded at 30 fps. A ring of near-infrared LEDs provided a light source invisible to pinnipeds (Levenson et al. 2006) and most marine fishes (Douglas & Hawryshyn 1990) which allowed for observations at a distance of about 1 m in front of the snout when no ambient light was available. Prior to deployment, female SSL were selected as test subjects based on several criteria which described both their apparent health and that of their pups. Selecting healthy individuals maximized the likelihood of instrumenting females which would successfully forage at sea and return to nurse following foraging trips. Once selected, females were immobilized and then sedated according to Heath et al. (1996). While SSL were sedated, neoprene cement was used to glue neoprene patches, to which VDRs were bolted, to the pelage. Main housings were mounted mid-dorsally, posterior to the scapulae. The video camera was mounted in a similar fashion to the top of the head, with the field of view including approximately half of the snout. Following deployments, which generally lasted 1 to 2 weeks, transceivers were used to remotely release both the main housings and cameras from neoprene patches. Neoprene patches fell off on their own within 1 month.

Data were recorded for 1 foraging trip made by one SSL and 3 foraging trips by the second. Dead reckoning (Bowditch 1837) was used to recreate three-dimensional movement paths for each of the foraging trips from depth, heading, pitch, and speed measurements. Foraging trips were then subdivided into individual dives which were then paired with video recordings. Each dive was further subdivided into 3 phases: descent (time between departing the surface and reaching the seabed), benthic foraging (time while swimming at the seabed), and ascent (time between departing the seabed and reaching the surface) (Figure 16).

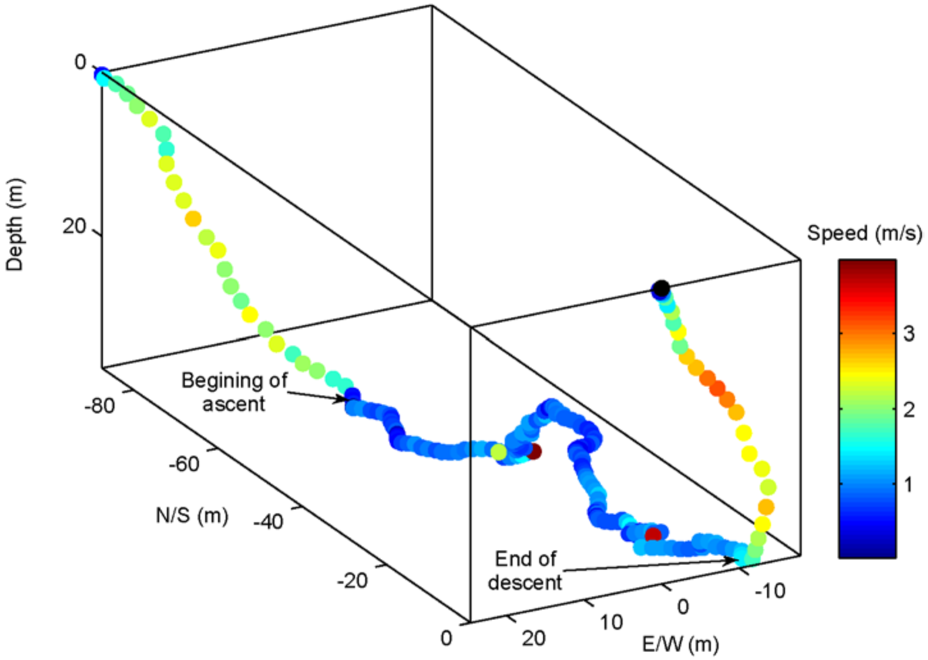

Figure 16. Typical foraging dive. Note the three phases of the dive: Descent (right), benthic foraging (center) and ascent (left).

Twenty variables describing dives were then calculated and used in a statistical analysis which classified dives into 5 dive types. Video recordings of behavior were then used to assign functional roles to each of the 5 dive types (see Chapter II). The descriptors most relevant to this study described the following for shallow and deep foraging dives: duration and percent of total dive duration, mean speed, mean pitch, and maximum depth. When combined with measures of prey encounter and consumption rates and estimates of aerobic dive limits (calculated Aerobic Dive Limit – cADLs), these data provided the information required to test the hypotheses A and B and construct the GUM used to test Hypothesis C.

Model Assumptions

The objective of the GUM was to test hypothesis C, which stated that $CPUE_{GUR}$ should be significantly greater than $CPUE_{CONT}$. In order to accomplish this, the GUM was created to be as simple as possible, including only the information required to address the hypothesis and excluding information which introduced unnecessary complexity to the model and to the interpretation of results. With this philosophy in mind, 4 major assumptions were made. Given their significance to the construction, functionality and validation of the model, justification for each assumption follows.

The first assumption, which simplified the model but reduced the overall accuracy of simulated dives, stated that SSL always maintained a single heading while diving. A 2D prey field and complex, pseudo-random, directionally-biased searching (closest approximation to observed behaviors) could have been incorporated into the model and may have increased the realism of simulated dives. This would have, however, only added an extra level of complexity which did not contribute in any way to testing the hypothesis.

Given that dive duration had a significant impact on the amount of time spent foraging at the seabed, some consideration had to be given to ensuring that varying dive durations for reasons other than application of the GUR did not affect CPUE values. As with the first assumption, a simple solution was used. The second GUM assumption stated that all dives lasted 3.6 min, unless shortened because prey had not been encountered by Tq. Additionally, post-dive surface intervals for shallow and deep dives were 1.9 min and 2.6 min, respectively. Total transit duration for shallow dives was 1.0 min (29% of total dive duration). For deep dives, total transit duration increased to 2.3 min (64% of total dive duration). The maximum amount of time which could be spent at the seabed for shallow and deep dives was 2.5 min (71% of total dive duration) and 1.3 min (36% of total dive duration), respectively. Although the maximum duration for every dive was constant, minimum dive duration decreased as Tq became smaller.

Justification for default dive duration was 2-fold. First, using a set of dives for which all 4 variables (duration, depth, pitch, and speed), as well as video, were available would result in the most accurate possible three-dimensional representation of dive profiles and prey encounter rates. Data used to construct the GUM were derived from shallow (n = 59) and deep (n = 42) foraging dives which had mean dive durations of 3.5 ± 0.8 min and 3.6 ± 0.5 min, respectively. A shorter mean dive duration (1.9 ± 1.4 min) was presented by Waite et al. (2012b) for 14,754 dives, also made by female SSL instrumented during the summer months at Lovushki Island. Although able to provide a more accurate representation of the average duration of summer dives by female SSL at Lovushki, Waite et al. (2012b) could not differentiate between foraging and non-foraging behaviors without corresponding measurements of speed, pitch and depth in conjunction with video recordings of foraging behavior. Although several studies, most relevant to this study being Waite et al. (2012b), have presented shorter average dive durations based on much larger sample sizes, none have discriminated between foraging and non-foraging dives. Because of this, only data from this study was used when parameterizing the GUM.

A second justification for the selected dive durations was based on a crude analysis of body oxygen store (TBO) and diving metabolic rate (DMR) data from several studies (Table 3). A mean TBO of 38 ml $O_2 * kg^{-1}$ and mean DMR, scaled by the body masses of study animals ($kg^{0.75}$), of 2.05 L $O_2 * min^{-1}$ yielded a mean cADL of 4.6 min for a 250 kg female (Kosygin & Kuzin 1979, Richmond et al. 2006). Ninety percent of all dives observed in this study were shorter than 4.6 min. additionally, a value of 4.6 min was approximately 2 standard deviations greater than the mean dive duration (1.9 ± 1.4 min) presented by Waite et al. (2012b) for female SSL at Lovushki Island. A dive duration of 3.6 min allowed for a safety margin (i.e., spare oxygen reserve) of 22% of total body oxygen. As with duration, parameterization of depth, pitch, speed, and post-dive surface interval was based only on the shallow and deep foraging dives described by this study.

Reference	TBO: ($ml\ O_2 * kg^{-1}$)	DMR: ($L\ O_2 * min^{-1}$)	BM: (kg)	Scaled DMR: ($250\ kg^{0.75}$)
Lenfant et al 1970	38.8	n/a	n/a	n/a
Richmond et al 2006	40.40	n/a	n/a	n/a
Hastie et al 2007	n/a	0.91	156	1.30
Fahlman et al 2008	n/a	1.65	177	2.14
Gerlinksky et al 2013	34.60	2.24	193	2.72
Mean	37.93	1.60	175	2.05

Table 3. Data used to estimate a cADL for SSL. Total body oxygen (TBO) and diving metabolic rate (DMR) values scaled for a 250 kg female SSL were 9.5 L O_2 and 2.05 L $O_2 * min^{-1}$, respectively, yielding a cADL of 4.6 min.

The third assumption of the model stated that all dives were to one of two possible depths, 40 m or 120 m. This assumption hinged on the lack of data available describing the foraging behavior and prey densities for dives to intermediate depths. One group of observed foraging dives had a mean depth of 40 m, while the other group had a mean depth of 120 m.

The fourth major assumption was taken directly from the original GUM by Thompson & Fedak (2001). Each dive was assigned one of 3 possible prey patch types (PPT) and occurred entirely within a single patch. The three possible PPT were “High”, “Medium” or “Barren”. For every dive during a foraging trip, a value was pseudo-randomly selected from a uniform distribution and used to select a PPT based on likelihoods derived from the percentage of wild dives with 2^+, 1 or 0 prey encounters, respectively, at each depth. The likelihood of a shallow dive being assigned each of the three PPT was: 49% (“High”), 20% (“Medium”) and 31% (“Barren”). For deep dives, likelihoods were: 33% (“High”), 28% (“Medium”) and 39% (“Barren”). Dives assigned the “High”, “Medium” and “Barren” PPT were assigned prey densities derived from minimum prey density estimates calculated for each depth based on three-dimensional dive profiles and their accompanying video. Patch densities were calculated as the total distance travelled at the seabed divided by the total number of prey encountered at the seabed, assuming a 1 m^2 search area. “High” prey densities for shallow and deep dives were 0.0166 fish m^{-2} and 0.0534 fish m^{-2}, respectively, while “Medium” prey densities were 0.0056 fish m^{-2} and 0.0216 fish m^{-2}. Dives assigned the “Barren” PPT had a prey density of 0.0 fish m^{-2}.

In summary, the four major model assumptions were: 1) a single heading was maintained throughout simulated dives with no search patterns or prey pursuits, 2) dive duration was 3.6 min for all dives, and post-dive surface intervals were 1.9 min, and 2.6 min for shallow and deep dives, respectively, 3) all shallow dives were to a depth of 40 m and all deep dives were to a depth of 120 m, and 4) each dive occurred entirely within a single prey patch which had been pseudo-randomly designated a quality of “High”, “Medium” or “Barren”.

Model Construction

In order to test the hypothesis, the GUM needed to accomplish 3 unique tasks. The first task, and foundation of the GUM, was to accurately simulate a SSL dive in time and space. The second task was to incorporate prey events into the model by assigning prey patch types to dives and by controlling if and when prey were encountered during benthic foraging as well as whether or not prey encountered were successfully consumed. The third task was to implement decision making, responsible for choosing whether or not to abandon dives early based on whether or not prey were encountered within a time limit imposed by Tq.

Four components combined to accomplish these tasks (see Appendix A for a summary of model code). The first model component was the “Tq Selector”. Every foraging trip was assigned a Tq based on which trial was being run. Experimental values of Tq varied from 10% – 90% of benthic foraging time for shallow (40 m, 2.4 min) and deep (120 m, 1.3 min) dives.

The “Prey Density Controller” selected a PPT for each dive based on the likelihoods previously described. The selected PPT was then used as an input for the “Prey Event Trigger” which used the likelihood that prey were encountered during each time step of benthic foraging to identify if and when prey were encountered during dives. For every meter swum at the seabed a number between 0 and 100 was pseudo-randomly selected from a uniform distribution. If that number was less than or equal to the chance, based on the prey density of the assigned PPT, of encountering a prey item in any given meter at the seabed a single prey item was considered as having been encountered. For “Barren” prey patches, a prey density of 0 fish m^2 resulted in no prey encounters. If a prey item was encountered, an additional pseudo-random number generator was used to determine whether or not it was consumed based on a success rate of 72% observed on video for wild SSL. This method approximated the likelihood that a prey item was encountered and, if applicable, consumed during any given meter swum for each of the PPT based on data and video recordings of SSL foraging behavior. The decision to abandon a dive was made if no prey had yet been encountered before the amount of time accrued at the seabed equaled Tq (a percentage) of the maximum benthic foraging time.

The "Dive Controller" acted as the heart of the model, controlling the movement of the SSL along a linear path at the seabed. The ascent, descent and surface intervals were not modeled, but were instead included in every dive as simple time investments. During each dive, SSL swam at a constant speed at the seabed until one of two possible conditions were met: 1) an affirmative decision to abandon a dive had been made, or 2) remaining dive duration, a proxy for oxygen stores, had declined to the point where it was equal to the amount of time required to return to the surface. If either of these conditions were met, the benthic search period was terminated. After each dive, the total amount of time spent in transit between the surface and the seabed, the total amount of time spent at the seabed and the duration of the post-dive surface interval were summed and added to the total foraging trip duration. A new dive was then initialized if an additional complete dive cycle could be completed without exceeding the 10 hr limit on foraging trip durations.

Model Validation

Two aspects of the GUM had to be validated to ensure that the GUM accurately simulated real-world SSL dives: 1) for simulated dives, the amount of time spent swimming and the distance travelled at the seabed should have been similar to the same measures for wild dives and 2) if prey density was constant and equal to estimates from wild dives, prey capture rates for simulated dives should have been similar to those of wild dives. Descriptions of how each was successfully validated follow below.

To test the accuracy of simulated dive profiles, mean values for “time spent foraging at the seabed”, “% of total dive time spent foraging at the seabed” and “gross distance swum at the seabed” for simulated dives were compared with those calculated from foraging dives made by wild SSL. The differences between simulated and wild SSL dives were negligible (< 5%) for all parameters. These results showed that the model was capable of accurately simulating the time spent foraging and area searched during SSL foraging dives. The most significant validation was that the distances swum at the seabed for simulated shallow and deep dives were 181 m and 53 m, while the mean distances swum at the seabed for wild shallow and deep dives were 175 m and 53 m. This was crucial as similar values for distance swum at the seabed allowed for the second necessary validation.

Prey density values used in the GUM were derived from video recordings of SSL foraging in two habitats, shallow and deep water. These values were used as the possible prey patch densities to test the hypothesis by pseudo-randomly assigning PPT to dives while progressively varying Tq between simulations. Validation was achieved by comparing CPUE values from simulated dives where Tq was set to 100% with those of wild dives. Because the amount of time and distance swum at the seabed were identical for simulated and wild dives, model validation could be achieved by confirming that simulated CPUE values were similar to those of the wild SSL for shallow and deep dives. Simulated shallow and deep dives had CPUE values of 0.34 fish min^{-1} and 0.25 fish min^{-1}, respectively. Wild dives had similar CPUE values of 0.35 fish min^{-1} and 0.24 fish min^{-1}, respectively. These results showed that the model was able to accurately simulate the rate at which wild SSL consumed prey while diving to each of the two depths at which H_C was tested.

Model Application

Two trials were used to test H_c: 1) shallow diving (40 m) and 2) deep diving (120 m). The independent variable was Tq, with levels of treatment varying from 10% to 90% at intervals of 10%. As a control "Tq Selector" was set to 100%, with low oxygen stores serving as the only motivation to terminate dives. Ten-thousand replicates each tested one value of Tq for an entire 10 hr foraging trip at either the 40 m or 120 m depth. For control treatments, "Tq Selector" was set to 100% and SSL spent the maximum possible time foraging at the seabed during every dive. The following parameters were calculated for each foraging trip: 1) total number of fish consumed, 2) total amount of time spent at sea and 3) number of fish consumed per minute spent at sea (CPUE). Two-tailed t-tests (alpha = .01) were used to test the hypotheses ($H_{C,\ Shallow}$, $H_{C,\ Deep}$) by comparing CPUE values at each Tq < 100% ($CPUE_{GUR}$) with CPUE values when Tq = 100% ($CPUE_{CONT}$).

Results

Wild SSL Dive Analysis

The mean total dive duration and time spent foraging at the seabed for shallow foraging dives (n = 169) was 3.65 ± 0.83 min. and 2.47 ± 0.85 min., respectively. Shallow foraging dives with no prey encounters (n = 75), had a mean total dive duration of 3.48 ± 0.72 min. while shallow foraging dives with at least 1 prey encounter (n = 94) had a mean total dive duration of 3.79 ± 0.89 min. This difference was not statistically significant (p = 0.016). Benthic dive durations for shallow foraging dives without and with prey encounters were 2.29 ± 0.77 min. and 2.62 ± 0.88 min, respectively. Again, the difference was not statistically significant (p = 0.011).

The mean total dive duration and time spent foraging at the seabed for deep foraging dives (n = 106) was 4.03 ± 0.92 min. and 1.63 ± 0.79 min, respectively. Deep foraging dives with no prey encounters (n = 38), had a mean total dive duration of 3.85 ± 0.95 min. while deep foraging dives with at least 1 prey encounter (n = 68) had a mean total dive duration of 4.12 ± 0.89 min. This difference was not statistically significant (p = 0.141). Benthic dive durations for deep foraging dives without and with prey encounters were 1.48 ± 0.86 min. and 1.72 ± 0.74 min, respectively. Again, the difference was not statistically significant (p = 0.139).

To summarize, total and benthic dive durations did not significantly differ between dives with and without prey encounters for either shallow or deep foraging dives. For both, the null hypotheses ($H_{0,A}$ and $H_{0,B}$) could not be rejected because

$TDUR_{NP} = TDUR_{YP}$ and $BDUR_{NP} = BDUR_{YP}$. Accordingly, alternative hypotheses ($H_{1,A}$ and $H_{1,B}$) could not be accepted as $TDUR_{NP}$ and $BDUR_{NP}$ were not significantly less than $TDUR_{YP}$ and $BDUR_{YP}$, respectively.

Simulated SSL Dive Analysis

The control CPUE ($CPUE_{CONT}$) for shallow foraging trips (Figure 17) was 0.219 ± 0.025 fish min^{-1}. $CPUE_{GUR}$ was significantly less than $CPUE_{CONT}$ for Tq: 10% (0.103 ± 0.022, p = 0.000), 20% (0.159 ± 0.025, p = 0.000), 30% (0.190 ± 0.025, p = 0.000), 40% (0.207 ± 0.026, p = 0.000), and 50% (0.216 ± 0.025, p = 0.000). $CPUE_{GUR}$ was significantly greater than $CPUE_{CONT}$ for Tq: 60% (0.221 ± 0.025, p = 0.000), 70% (0.223 ± 0.026, p = 0.000), 80% (0.223 ± 0.026, p = 0.000), and 90% (0.222 ± 0.025, p = 0.000).

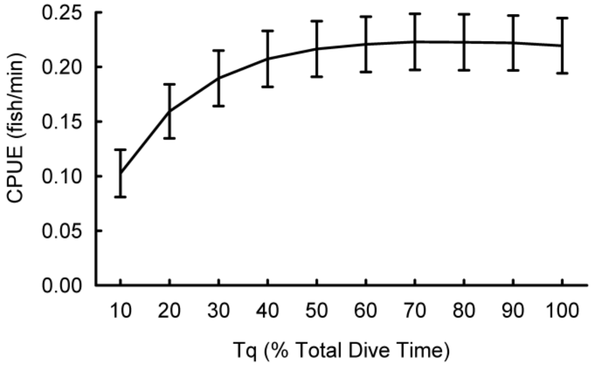

Figure 17. CPUE as a function of Tq for shallow (40 m) dives.

The mean number of fish consumed during control treatments was 132 ± 15. On average, fewer fish were consumed per foraging trip for Tq: 10% (61 ± 13, p = 0.000), 20% (95 ± 15, p = 0.000), 30% (113 ± 15, p = 0.000), 40% (124 ± 15, p = 0.000), and 50% (129 ± 15, p = 0.000). The number of fish consumed was not significantly different from the control when Tq = 60% (132 ± 15, p = 0.216), and was greater for Tq: 70% (133 ± 15, p = 0.000), 80% (133 ± 15, p = 0.000) and 90% (133 ± 15, p = 0.000).

The control CPUE ($CPUE_{CONT}$) for deep foraging trips (Figure 18) was 0.147 ± 0.021 fish min^{-1}. GPU_{GUR} was significantly less than $CPUE_{CONT}$ for Tq: 10% (0.041 ± 0.014, p = 0.000), 20% (0.082 ± 0.019, p = 0.000), 30% (0.104 ± 0.020, p = 0.000), 40% (0.119 ± 0.021, p = 0.000), 50% (0.131 ± 0.021, p = 0.000), 60% (0.137 ± 0.021, p = 0.000), 70% (0.143 ± 0.021, p = 0.000), 80% (0.145 ± 0.021, p = 0.000), and 90% (0.146 ± 0.021, p = 0.007).

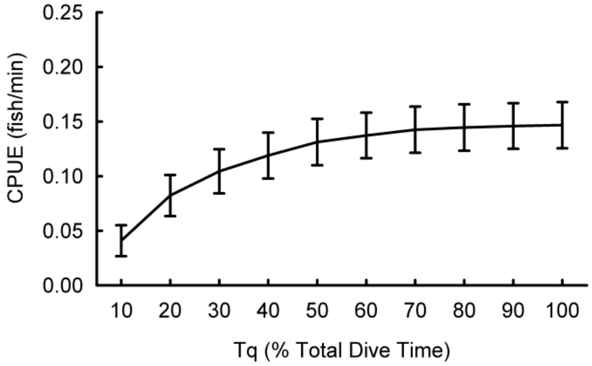

Figure 18. CPUE as a function of Tq for deep (120 m) dives.

The mean number of fish consumed during control treatments was 87 ± 13. On average, fewer fish were consumed per foraging trip for all values of Tq: 10% (24 ± 8, p = 0.000), 20% (49 ± 11, p = 0.000), 30% (62 ± 12, p = 0.000), 40% (71 ± 13, p = 0.000), 50% (78 ± 13, p = 0.000), 60% (82 ± 12, p = 0.000), 70% (85 ± 13, p = 0.000), 80% (86 ± 13, p = 0.000) and 90% (87 ± 12, p = 0.000).

In summary, the null hypothesis ($H_{0,C}$) was rejected and the alternative hypothesis ($H_{1,C}$) was accepted for shallow foraging trips when $Tq \geq 60\%$ as $CPUE_{GUR} > CPUE_{CONT}$. The GUR was optimized when Tq = 70% as the proportional benefit (PB: ratio of treatment CPUE to control CPUE) was maximized at 1.02 (i.e., 2% greater than CPUE). The increased CPUE at Tq = 70% translated to 1 additional fish consumed per 10 hr foraging trip, an increase of less than 1%. The null hypothesis ($H_{0,C}$) could not be rejected for any deep foraging trips, as $CPUE_{GUR} \leq CPUE_{CONT}$.

Discussion

Our hypotheses (H_A and H_B) stated that if SSL were employing a GUR while foraging in the wild, total dive duration and/or benthic foraging duration should be shorter for dives where no prey were encountered than for dives were at least one prey was encountered. Based on the conclusions of Thompson & Fedak (2001), shallow foraging dive durations were expected to reflect the use of a GUR by showing a tendency for unsuccessful dives to be shorter in duration than successful dives, suggesting that SSL abandoned dives early when no prey were encountered. In fact, shallow dives with no prey encounters did not have significantly shorter durations (total and benthic) than dives with at least one prey encounter ($\alpha = 0.01$). Although the differences between means were not significant at $\alpha = 0.01$, they were at $\alpha = 0.05$. Nevertheless, the reduction to dive duration would have corresponded to a Tq of 90%. Both this study and Thompson and Fedak (2001) agreed that, at high values of Tq, PB was negligible.

No differences between duration means for deep foraging dives were expected given that Thompson & Fedak (2001) showed that the GUR was never beneficial to foraging when transit duration was long relative to total dive duration. As with shallow foraging dives, means durations for dives with no prey encounters were shorter than for dives with at least one prey encounter. However, the differences were not statistically significant, even at $\alpha = 0.05$. It is likely that larger sample sizes would help clarify if and by how much these two groups of dives actually differ.

Although evidence of the use of a GUR by wild SSL was confounded by small sample sizes, it was hoped that construction of a simulation model would help to indicate if a GUR could possibly benefit SSL making foraging dives which adhered to physiological constraints, behavioral tendencies and available habitats. As with the analysis of wild dives, it was predicted that when making dives in shallow water, SSL could increase their CPUE by using the GUR as a foraging strategy. Despite the statistically significant increase to CPUE and to the number of fish consumed during foraging trips, the biological significance was negligible. When Tq = 70% of maximum benthic foraging time, the average CPUE and number of fish consumed were statistically greater than the control (i.e., 100%). This resulted in 1 additional fish consumed over the course of an entire foraging trip; an increase of less than 2%. Based on these results, it appears that using the GUM as a foraging strategy may not be beneficial to SSL foraging at Lovushki.

Our GUM was largely based on the original GUM created by Thompson & Fedak (2001). However, there were three key differences. First, all parameter values (i.e., swim speed, descent and ascent pitch, prey density, etc.) were taken from in-situ measurements of wild free-roaming SSL making foraging dives. This resulted in simulated foraging dives and prey fields which closely resembled the wild free-roaming data they were based on and allowed for the determination of whether or not SSL could benefit from utilization of the GUM given the specific constraints of their physiology and habitat. Second, the GUM was developed to simulate prey searching as a continuous stochastic time series instead of as a single statistical probability calculation. During simulated foraging dives prey were encountered randomly at the seabed based on the density-derived likelihood of encountering prey in any given m^2.

One caveat was that calculating a minimum prey density from observations of prey encounters may not have been an accurate way to estimate either prey density or the rate at which SSL could locate prey. The key assumption when making this calculation was that the area searched by SSL was an accurate representation of the immediately surrounding habitat. Even without an obvious search strategy, a foraging path could be biased by any number of factors including: benthic topography (i.e., boulders, crevices, overhangs, etc.), currents (i.e., leeway), presence/absence of other pinnipeds (i.e., social interaction, competition, cooperation, etc.), potential non-visual prey detection (i.e., chemosensory, vibrissal or auditory) etc.

An additional assumption used to calculate minimum prey densities was that prey density did not decline as prey were consumed. When implementing a component into the model which reduced prey density as prey were consumed during dives, initial prey densities had to be increased by 41% to yield the minimum prey density estimate observed in wild SSL. This suggests that there could be substantial errors in prey density estimates. Additional trials were run which incorporated both declining densities and densities with multipliers of 0.5 and 2 in order to test how possible errors in prey density estimate calculations could have impacted model results. Whether or not density declined as prey were consumed did not impact model results as long as the initial prey density was increased by 41% to compensate. When density was reduced by half, the GUR was never advantageous, and when it was doubled the optimum Tq was reduced from 70% to 50%. Even at twice the density, maximum PB was only 1.05. Additionally, doubling prey density resulted in a PB greater than 1 for deep dives when Tq = 70-80%. Nevertheless, PB was only 1.01. Given the range of prey densities tested and the consistency of results throughout that range, the model portrayed the availability of prey to SSL foraging on Atka mackerel near Lovushki Island with enough accuracy to test the hypotheses.

The third important difference between the models was that, in the GUM, post-dive surface interval was not dependent on the proceeding dive duration but instead on depth. This more accurately represented the behavior of the wild SSL on which the model was based. Unlike the original GUM, surface interval was not reduced proportionately to dive duration for dives which had been abandoned early relative to dives which extended to completion. When included in the model this attribute increased the maximum PB to 1.06 and lowered the optimal Tq to 50% for shallow dives. Even still, the mean number of fish consumed during a 10 hr foraging trip only increased by 7. There was a negligible impact on deep dives. Although not included in the core of this study, and despite the minor impact on results when tested, the inclusion of variable surface intervals should be taken into account when considering how the GUM may benefit different species of divers.

Conclusion

Two methods were used to test how the GUR proposed by Thompson & Fedak (2001) might impact SSL foraging behavior: 1) an analysis of data from free-roaming wild SSL, testing how total dive duration and benthic foraging duration fluctuated in response to differences in foraging success and 2) the construction of a model which could simulate the foraging behaviors (i.e., swim speeds, dive durations, surface intervals, descent/ascent pitches) and habitat (i.e., depth ranges, prey densities) of wild SSL making foraging dives around Lovushki Island. SSL could not optimize their foraging by employing a GUR. This was a consequence of: 1) relatively shallow dives which did not exceed their cADL, 2) transit times which were long relative to the original predictions and 3) constant surface intervals which were not shorter for dives which were abandoned early. Additionally, no evidence suggested that SSL were shortening dives in response to low prey encounter rates. Given that dive and surface interval durations are functions of physiological capability while transit times are a function of habitat (i.e., water depth), large scale (i.e., foraging trip) decisions such as where to forage are likely to be more important than small scale (i.e., single dive) behavioral modifications.

CHAPTER IV

SUMMARY

Describing the at-sea behaviors of marine mammals has traditionally been hampered by the inability of researchers to make direct observations of submerged behaviors. Though the deployment of time-depth recorders, accelerometers, swim speed sensors and still cameras has helped to further our understanding of how marine mammals utilize the underwater resources available to them, our understanding of dive behavior is limited. VDRs were used to expand upon this knowledge by recording the first three-dimensional swim paths and first-person video of wild SSL making foraging trips at sea. With this information, dives made by SSL were classified into five types, each dive type was assigned a behavioral role based on direct observations of behavior, and the key attributes which set dive types apart from each other were identified. Types 1 and 2 dives were shallow and deep foraging dives, respectively, during which SSL fed almost exclusively on Atka mackerel (*Pleurogrammus monopterygius*) while Type 3 dives appeared to represent opportunistic foraging while transiting. Type 4 dives had no clear function and included behaviors not seen in other dive types such as interacting with other SSL, opportunistic prey capture near the surface exploration of water depth. Type 5 dives were non-foraging dives used for transiting near the surface. Although individual dive types could not be reliably identified with time-depth data alone, foraging and non-foraging behaviors could be distinguished from each other based primarily on the proportion of total dive time spent swimming between the descent and ascent and maximum dive depth.

After discriminating between foraging and non-foraging dives and quantifying the rates at which SSL encountered and consumed prey, I sought to further explore how characteristics such as total dive duration and benthic foraging duration fluctuated in response to differences in foraging success. I specifically focused on the applicability of a foraging strategy which Thompson & Fedak (2001) showed to benefit foraging phocids. Additionally, I constructed a simulation model which could simulate the foraging behaviors (i.e., swim speeds, dive durations, surface intervals, descent/ascent pitches) and habitat (i.e., depth ranges, prey densities) of wild SSL making foraging dives around Lovushki Island to test how this strategy of abandoning unsuccessful dives early could improve the CPUE for SSL as it might for phocids. I found that SSL could not optimize their foraging by employing a GUR. This was a consequence of: 1) relatively shallow dives which did not exceed their cADL, 2) transit times which were long relative to the original predictions and 3) constant surface intervals which were not shorter for dives which were abandoned early. Additionally, I found no evidence that SSL were shortening dives in response to low prey encounter rates. Given that dive and surface interval durations are functions of physiological capability while transit times are a function of habitat (i.e., water depth), large scale (i.e., foraging trip) decisions such as where to forage are likely to be more important than small scale (i.e., single dive) behavioral modifications. This was supported by the fact that, despite a reduction to CPUE as dive depth increased, SSL did not appear to modify foraging behavior when moving from shallow to deep water. Previous experience and sight fidelity may play an important role in the foraging success of wild SSL.

This study used data from a relatively small number of lactating females at a single rookery in the Kuril Islands of far-east Russia during the summer breeding season. Though it significantly improved upon our knowledge of the foraging behaviors of wild SSL, considerably more work is needed. Future studies should focus on improving sample sizes, collecting data at other rookeries where prey availability and benthic topography differ, deploying instruments on different age classes, and sampling during different seasons. These additional studies may increase the ability to design more effective protection measures capable of targeting individual rookeries and haul-outs based on regionally, seasonally and/or demographically specific needs by: 1) describing specific areas where animals foraging during trips to sea, 2) describing the diversity of potential prey and selection of prey types by SSL and 3) quantifying prey density and the rates at which prey are consumed.

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APPENDIX A

SUMMARY OF FORAGING MODEL CODE

Ten-thousand replicates each tested one value of Tq for an entire 10 hr foraging trip at either the 40 m or 120 m depth. Within each trip, discrete dives were simulated with results (i.e., dive duration, distance swum at the seabed, prey encountered, prey consumed, etc.) added to trip totals. Trip totals were then used to calculate CPUE values which were compared (two-sided t-test) between levels of treatment.

Prior to each dive, the variables which described that dive and the variables which described the likelihoods of that dive being assigned each prey patch type were established. Next, dives were assigned a prey patch type and prey density which corresponded to the assigned patch type. Once dive parameters had been established, benthic foraging was simulated at a time step of 1 Hz. Maximum simulation duration (‘SearchTime’) was ‘TotalDiveDuration’ – ‘TransitDuration’ while the time which could pass before a decision to abandon or continue foraging (‘TimeRemainingToDecision’) was ‘SearchTime’ * ‘Tq’. Each second, ‘TimeRemainingToDecision’ decreased by 1. When ‘TimeRemainingToDecision’ reached 0, dives were abandoned. If prey were encountered at any point in the simulation prior to ‘TimeRemainingToDecision’ reaching 0, ‘TimeRemainingToDecision’ was increased to exceed ‘SearchTime’. When this occurred, the simulation would last for the duration set by ‘SearchTime’.

SSL swam a distance during each time step, according to ‘SpeedAtSeabed’, which cumulatively added to ‘DistanceSwumAtSeabed’. Space was not explicitly modeled but was implicit from the product of speed and time in each time step. When ‘DistanceSwumAtSeabed’ exceeded 1 m, the model used the likelihood that a prey item was encountered during that 1 m (‘FishChancePerMeter’), and the likelihood that a prey item would have been consumed had an encounter taken place (71.5%) to determine if a prey item had been consumed. Though only presented here once, this step was repeated a second time as it was possible for ‘DistanceSwumAtSeabed’ to accrue fractions of meters each time 1 m was sampled and removed from ‘DistanceSwumAtSeabed’. Unless this step was repeated a second time, these fractions would add up to several un-sampled meters by the end of a dive. Three outcomes were possible each time ‘DistanceSwumAtSeabed’ exceeded 1 m: 0 prey encountered and 0 prey consumed, 1 prey encountered and 0 prey consumed, or 1 prey encountered and 1 prey consumed.

At the end of every dive, ‘TimeSwumAtSeabed’, ‘TransitDuration’ and ‘SurfaceInterval’ were added to cumulative values for the current foraging trip. Once all dives in a trip had been simulated, CPUE was calculated for the entire foraging trip as ‘AccruedTripConsumptions’ divided by ‘AccruedTripTime’.

The model was constructed in MATLAB® R2009b (The MathWorks, Inc. 2009) while Statistica® 12 (StatSoft, Inc. 2013) was used for the analyses of results. A summary of the MATLAB code used in the steps described above can be found on the following pages.

Establish variables before every dive.

Units: time (s), distance/depth (m), encounters and consumptions (fish).

```
TotalDiveDuration = 213
Depth = (Set to either 40 m or 120 m depending on the trial)
Tq = (Set as 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, or 1 depending on the trial)
SpeedAtSeabed = -0.00625 * Depth + 1.45
TransitDuration = 0.9375 * Depth + 24.5
SearchTime = TotalDiveDuration – TransitDuration
BarrenMediumThreshold = 0.1 * Depth + 26.7
MediumHighThreshold = (0.1 * Depth + 16.15) + BarrenMediumThreshold
SurfaceInterval = (0.00241 * Depth + 0.4385) * TotalDiveDuration
MaxCycleDuration = TransitDuration + SearchTime + SurfaceInterval
BenthicDistancePosssible = SpeedAtSeabed * SearchTime
TimeRemainingToDecision = Tq * SearchTime
```

Assign patch type (high, medium or barren) before every dive.

```
PatchTypeRandNumber = (RandomNumber from 0 - 100)

if (PatchTypeRandNumber >= 0) & (PatchTypeRandNumber < BarrenMediumThreshold)
    FishChancePerMeter = -999
elseif (PatchTypeRandNumber >= BarrenMediumThreshold) & (PatchTypeRandNumber < (MediumHighThreshold))
    FishChancePerMeter = 100 * (0.0002 * Depth) - 0.00245
elseif (PatchTypeRandNumber >= MediumHighThreshold) & (PatchTypeRandNumber < 100)
    FishChancePerMeter = 100 * (0.00046 * Depth) - 0.00185
end
```

Determine if prey was encountered at 1 m intervals while swimming at the Seabed during individual dives.

```
for Searching = 1 : SearchTime

    if TimeRemainingToDecision >=1
        TimeRemainingToDecision = TimeRemainingToDecision - 1
        TimeSwumAtSeabed = TimeSwumAtSeabed + 1
        DistanceSwumAtSeabed = DistanceSwumAtSeabed + SpeedAtSeabed

        if (DistanceSwumAtSeabed >= 1)
            DistanceSwumAtSeabed = DistanceSwumAtSeabed - 1
            FishEncounterRandNumber = (RandomNumber from 0 - 100)
            FishConsumptionRandNumber = (RandomNumber from 0 - 100)

            if (FishEncounterRandNumber <= FishChancePerMeter)
                YesNoEncounter = 1
                TotalEncounters = TotalEncounters + 1
                TimeRemainingToDecision = 9999
            else
            YesNoEncounter = 0
            end

            if (FishConsumptionRandNumber <= 71.5)
                YesNoConsumptionPossible = 1
            else
                YesNoConsumptionPossible = 0
            end

            if (YesNoEncounter = 1) & (YesNoConsumptionPossible = 1)
                TotalConsumptions = TotalConsumptions + 1
            end
        end
    end
end
```

Following each dive, values were added to totals for current foraging trip.

AccruedTripTime = AccruedTripTime + TimeSwumAtSeabed + TransitDuration + SurfaceInterval

AccruedDistanceSwumAtSeabed = AccruedDistanceSwumAtSeabed + DistanceSwumAtSeabed

AccruedTripEncounters = AccruedTripEncounters + TotalEncounters

AccruedTripConsumptions = AccruedTripConsumptions + TotalConsumptions

Step 5: Calculate CPUE values for total trip.

TripCPUE = AccruedTripConsumptions / (AccruedTripTime / 60)