A BIOENERGETIC MODEL FOR SEA OTTERS: EXPLORING INTERACTIONS BETWEEN ENERGY REQUIREMENTS AND DIETARY CHOICES

by

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Abstract

Sea otters (*Enhydra lutris*) are keystone predators with voracious appetites that impose immense predation pressure on their prey, thereby significantly altering the structure of local ecosystems. To better understand how much food sea otters must consume to meet their energy needs and impacts of predation, I developed bioenergetic models for sea otters. These models infer how the energy expenditures of individual sea otters vary under changing conditions, while accounting for sex, age, and reproductive status. I created three models— females without a pup, females with a pup, and males— using peer-reviewed, published data on sea otter ecology, physiology, and behaviour.

The models demonstrated that females caring for a pup have the highest total energy expenditures when compared to adult males (3-10% less on average) and females without pups (33% less). Sensitivity analyses showed that the body mass parameter had the largest effects on model outcomes, due to many input values being mass-specific. The second variable affecting model outcomes was metabolic rate, which helps inform which types of data should be collected to improve model accuracy.

The amount of food sea otters require to satisfy their energy expenditures depends on complex relationships between the energy density, digestive value, and foraging costs of obtaining different prey items. I converted the energy expenditure estimates generated by the models into ingested food mass (IFM) and biomass removed to investigate the effects of diet and prey availability on prey consumed by sea otters. I chose five diet scenarios to compare: one general otter diet and four specialist diets. Otters that prefer more energy dense prey species (e.g., abalone) had lower IFM than otters consuming less dense prey (e.g., urchins). The amount of food required by mothers with pups on a low energy diet may present a significant challenge. I further explored how changes in food availability affect otters' foraging efficiency and found that as foraging efficiency decreases, foraging time and energy expenditure both increase. Therefore, prey selection by sea otters has critical energetic consequences effecting their overall energy balance, and may contribute to limiting range expansion or population growth of sea otters in certain areas.

Lay Summary

I developed a bioenergetic model (mathematical representation of the costs of living) of sea otters to estimate energy expenditures while accounting for differences in sex, age, and reproductive status using published data. I found that female otters with a pup require slightly more energy than males and significantly more than females without pups. I then converted energy expenditure into food mass and compared five diet scenarios to investigate how specialized diets may affect the energy needs of sea otters. Otters that consume high-calorie prey need to consume less prey than those consuming low-calorie prey. Additionally, when food is less available, the efficiency of foraging decreases, thereby increasing both the time spent foraging and overall amount of energy expended. I found that prey selection by sea otters has energetic consequences effecting their overall energy balance, potentially contributing to limits on population growth in certain areas.

Preface

This thesis and the research presented within it is my original work. Under the guidance of Dr. David A.S. Rosen, I developed the research questions, model structure and mechanics, parameterized the model, conducted the data analyses, and summarized my findings in writing. Feedback from my committee members, Dr. Nicole M. Thometz-Tomoleoni and Dr. Andrew W. Trites, was incorporated into the model design and final thesis draft. I obtained the data used in the model from peer-reviewed, published literature, which is cited properly throughout the document. Chapter 2 was written and formatted as a manuscript for submission to peer-reviewed journals. Generative AI was not used as a part of this research nor in the drafting and preparation of this thesis.

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%	Percent
A	Non-foraging activity
BMR	Basal metabolic rate
C	Cost
C_B	Cost of behaviour *i*
AC_F	Additional cost of foraging
d	Day
EE_P	Partial energy expenditure (non-foraging costs)
ELS	End-lactation syndrome
F	Actual cost of foraging
FMR	Field metabolic rate
g	Grams
g g^{-1}	Gram per gram
g kJ^{-1}	Grams per kilojoule
G	Growth
GEI	Gross energy intake
GFI	Gross food intake
HIF	Heat increment of feeding
IFM	Ingested food mass
kJ	Kilojoules
kJ d^{-1}	Kilojoules per day
kJ g^{-1}	Kilojoules per gram
kJ kg^{-1}	Kilojoules per kilogram
kJ min^{-1}	Kilojoules per minute
m	Body mass
m_i	Average body mass of age *i*
MJ d^{-1}	Megajoules per day
MR_{Bi}	Metabolic rate of behaviour *i*

NE	Net energy
P	Cost of caring for a pup
r_F	Rate of foraging (mass-specific)
r_R	Rate of resting (mass-specific)
R	Cost of resting
RMR	Resting metabolic rate
ROR_N	Net rate of return
ROR_G	Gross rate of return
SD	Standard deviation
SDA	Specific dynamic action
t_A	Time spent in non-foraging activity (minutes)
t_F	Time spent foraging (minutes)
t_{iB}	Time spent in Behaviour *i* (minutes)
t_R	Time spent resting (minutes)
TEE	Total energy expenditure

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Wild Geese

You do not have to be good.
You do not have to walk on your knees
for a hundred miles through the desert, repenting.
You only have to let the soft animal of your body
love what it loves.
Tell me about despair, yours, and I will tell you mine.
Meanwhile the world goes on.
Meanwhile the sun and the clear pebbles of the rain
are moving across the landscapes,
over the prairies and the deep trees,
the mountains and the rivers.
Meanwhile the wild geese, high in the clean blue air,
are heading home again.
Whoever you are, no matter how lonely,
the world offers itself to your imagination,
calls to you like the wild geese, harsh and exciting–
over and over announcing your place
in the family of things.

-Mary Oliver

To Artie, Wallie, future niblings, and future kiddos
in the hopes that your oceans are full of otters

To my parents, Steve and Tara,
for your endless love and support

To Otter 841,
for your contributions to research
and being a menace to society

Chapter 1: Introduction

Sea otters (*Enhydra lutris*) are the largest and heaviest member of the Mustelidae family, a grouping of carnivores that includes species such as weasels, badgers, and wolverines (Riedman & Estes, 1990). Sea otters are the best adapted of all mustelid species for aquatic living, thus spending the majority of their lives in marine environments, such as intertidal, coastal, and estuarine habitats as opposed to riverine or terrestrial habitats (Kenyon, 1969; Riedman & Estes, 1990). Despite their status as the largest mustelid, sea otters are recognized as the smallest marine mammal (Kenyon, 1969).

1.1 Distribution

Historically, sea otter populations were distributed across North Pacific coastlines from Baja California, Mexico all the way westward to northern Japan (Figure 1.1) and numbered around 300,000 individuals (Davis et al., 2019). As a result of the maritime fur trade in the late 1700's through the 1800's, those populations were reduced to fewer than 2,000 animals across their entire historic range, before they were eventually protected in 1911 within the international North Pacific Fur Seal Convention (Davis et al., 2019).

There are three recognized extant subspecies of sea otters: the Russian or Asian sea otter, *Enhydra lutris lutris*, the northern sea otter, *E. lutris kenyoni*, and the southern sea otter, *E. lutris nereis* (Wilson et al., 1991). There are some recorded physical differences between subspecies, populations, and sexes, such as differences in body size and skull, nasal, and tooth sizes (Wilson et al., 1991). Sea otters are sexually dimorphic, with males often weighing 34% more than females and measuring 8% longer (Kenyon, 1969). Southern sea otters are the smallest of the subspecies, with the smallest body, skull, and tooth sizes, shortest mandible length, and the longest nasal length of the three (Wilson et al., 1991). Southern sea otter males weigh on average 29 kg compared to females weighing ~20 kg. Males are an average length of 129 cm and females are 120 cm (Riedman & Estes, 1990). In Alaskan populations with high population density, male otters weigh an average of 28 kg (mean length 135 cm) and female otters weigh 21 kg (125 cm long), similar to measurements of southern sea otters (Riedman & Estes, 1990). Animals are larger in low density populations, where males weigh an average of

40 kg (141 cm long) and females weighed an average of 25 kg (130 cm long) (Riedman & Estes, 1990).

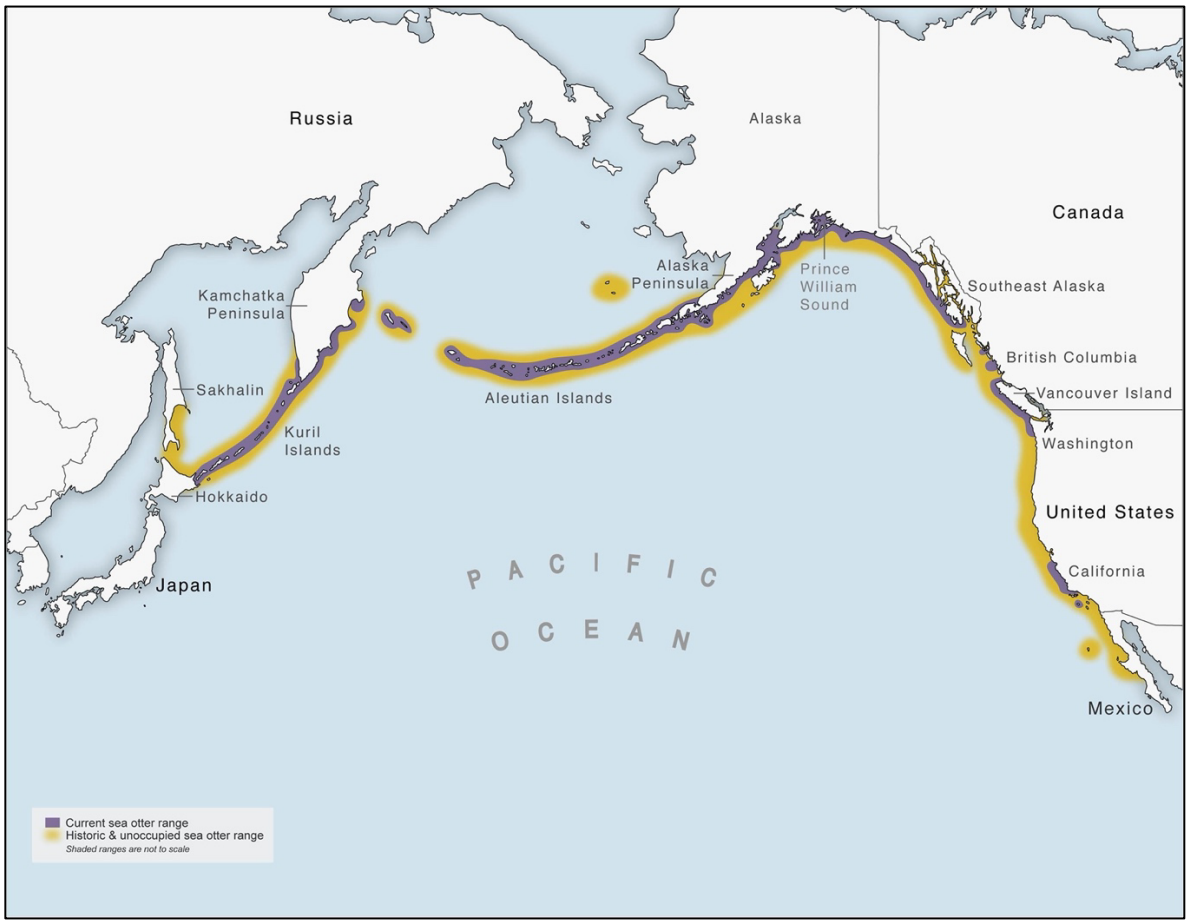


Figure 1.1: Current (purple) and historic (yellow) distribution of sea otters. Figure from Davis et al., (2019).

At the time of the North Pacific Fur Seal Convention, sea otters were extirpated from much of their current range. Populations were reestablished by relocating otters from Amchitka Island, Alaska to other areas across Alaska, Washington, Oregon and British Columbia, Canada between 1965–1972 (Riedman & Estes, 1990). A number of southern sea otters were also relocated to different habitats within California in 1969 and later from mainland California to San Nicolas Island between 1987–1989 (Riedman & Estes, 1990). Despite these efforts, the current distribution of sea otters remains very reduced compared to their historic ranges, and populations have never returned to their pre-fur trade numbers (Bodkin, 2015). However, in all four countries where current sea otter populations exist — Japan, Russia, Canada, and the

United States — there are laws in place protecting these marine mammals, and overall population trends are increasing (Davis et al., 2019).

Northern sea otters are found in Canada around northern Vancouver Island and the northern coast of British Columbia, whose population estimate was over 8,000 otters in 2017 and steadily increasing (Nichol et al., 2020). In the United States, northern sea otters are found in Alaska (~100,000 otters in 2023) (Schuette et al., 2023; U.S. Fish and Wildlife Service, 2023a, 2023b) and Washington State (~1,700 otters in 2021) (Hale et al., 2022). There are not currently northern sea otters south of Washington State, however, Central California is home to ~3,000 southern sea otters (Hatfield et al., 2019). Northern California and the Oregon Coast were never repopulated after the fur trade, despite relocation efforts in the 1970's (Davis et al., 2019).

Despite some recovery after the fur trade, populations of sea otters in both Alaska and California have struggled to expand. Some factors limiting population expansion of sea otters are prey availability (particularly in high density populations) and predation by white sharks (*Carcharodon carcharias*), killer whales (*Orcinus orca*), and even wolves (*Canis lupus*) in some parts of Alaska (Lyon et al., 2024; Roffler et al., 2023). In California, an additional factor that may be limiting population range expansion is the geography of California's coastline (Davis et al., 2019; Lyon et al., 2024). Compared to the coastlines of Alaska and British Columbia, where there are many islands, fjords, inlets, and more overall complexity, California's coastline has a "linear nature" (Davis et al., 2019), limiting available habitat for sea otters and their prey bases.

1.2 Habitat and Diet

Sea otters inhabit nearshore, coastal habitats that are typically rocky areas characterized by kelp forests, or in soft-sediment and estuarine areas characterized by seagrass beds and salt marshes (Hughes et al., 2024; Kenyon, 1969). Otters rely on these rocky areas near the coastline as well as estuaries to haul out in order to rest or for females to leave their pups while foraging (Kenyon, 1969). Sea otters are rarely seen in waters deeper than 50 meters (Kenyon, 1969).

Sea otters have a generalist diet, and consume a large variety of benthic macroinvertebrate species that inhabit their intertidal, littoral, and estuarine habitats (Davis, 2019; Kenyon, 1969). The majority of the prey that otters have been observed eating are sessile or slow-moving organisms such as bivalves, echinoderms, snails, crab species, etc. (Davis, 2019; Kenyon, 1969; Oftedal et al., 2007; Tinker, 2004). Since many of their preferred prey species are hard shelled, some sea otters have adapted to using tools to break apart shells to forage more efficiently (Fujii et al., 2017; Law et al., 2024). Additionally, otters will shift their diets and consume large proportions of the next most abundant or preferred prey species when preferred prey become less available in population dense areas (Estes et al., 2003; Fujii et al., 2017; Law et al., 2024; Lyon et al., 2024; Newsome et al., 2009; Oftedal et al., 2007; Smith et al., 2015; Tinker, 2004; Tinker et al., 2007, 2008).

As occupation time in a habitat increases, the overall diet diversity of individual otters increases while energy intake rates simultaneously decrease (Lyon et al., 2024; Tinker et al., 2019). Females in general, but especially those caring for pups, appear to diversify their diets more often than male otters, leading to lower food intake rates (Staedler, 2011). Sea otter population sizes appear to be limited by prey availability— as seen at Año Nuevo in Central California— where the population dynamics of its low-density population is akin to that of high-density populations in other regions (Lyon et al., 2024). Low prey availability has contributed to the stagnation of range expansion of this population of otters, which is the northernmost population on the periphery of the southern sea otter habitat range, in addition to lack of kelp cover north of this area and increasing predation from white sharks (Lyon et al., 2024).

1.3 Reproduction

Sea otters exhibit a polygynous mating structure, where males mate with many females, and are often territorial in preventing other males from mating with nearby females (Davis & Pagano, 2021; Kenyon, 1969). Male otters can reach physical sexual maturity as early as 3 years old (Hutchinson et al., 2015), however on average they reach maturity at five and six years old, but often do not begin mating until they are a few years older when they can defend a territory

and gain access to females (Davis & Pagano, 2021; Estes, 1989). Aside from mating, male sea otters do not participate in pup rearing.

Females can reproduce as early as two years old, but more commonly breed for the first time between three and four years old (Jameson & Johnson, 1993). The reproductive cycle of female otters is about one year in duration split into three phases, with females typically giving birth to one pup. The first phase of the cycle begins with the female entering estrus, followed by copulation and delayed implantation (Chinn et al., 2016; Jameson & Johnson, 1993). Delayed implantation is a strategy utilized by many species of marine mammal females to increase the odds of a successful pregnancy and pup survival by waiting to implant the fertilized egg until there are more favorable conditions, either environmental or biological (Chinn et al., 2016). In many other species, delayed implantation also acts to synchronize the seasonal reproductive cycle, but otters do not have a strict breeding season (Davis & Pagano, 2021). After implantation occurs, there is a period of ~5 months of gestation before giving birth (Chinn et al., 2016; Jameson & Johnson, 1993). The last phase of the sea otter reproductive cycle is pup care, which includes both lactation and supplemental feeding until weaning after about six months (Chinn et al., 2016; Jameson & Johnson, 1993; Thometz et al., 2014). Female sea otters expend considerable energy caring for their pups during lactation and rearing (Thometz et al., 2014). Sea otters are considered income breeders, meaning females give birth with little to no additional energy reserves, necessitating foraging during lactation to support their offspring (Thometz et al., 2014).

Sea otter pups can be classified into distinct stages of development determined by their pelage, the amount of time nursing versus foraging, and changes in the pups' diving abilities (Payne & Jameson, 1984; Thometz et al., 2014). Newborn pups are unable to dive, swim, or feed themselves and have their natal fur coat (Thometz et al., 2014). At about six weeks, the pup will begin to molt its natal pelage and learn to swim and make shallow dives. While the pup is still fed entirely by its mother at this stage, the pup begins to eat more solid foods to supplement its nursing (Payne & Jameson, 1984; Thometz et al., 2014). A post-molt pup (~3–4.5 months postpartum) has its "adult" fur and is a stronger swimmer and diver at this point in

its development and doesn't need its mother to carry it. However, it still cannot forage successfully for itself (Payne & Jameson, 1984; Thometz et al., 2014).

A sea otter pup is considered a dependent, immature otter when it has full adult pelage and is able to forage for itself a large portion of the time and doesn't nurse very often. This developmental stage is from roughly 4.5 to 6 months (Payne & Jameson, 1984; Thometz et al., 2014). When a pup is fully weaned from milk and self-sufficient— typically just after reaching 6 months old— it is considered a juvenile (Thometz et al., 2014).

As with all marine mammal species, females are the sole caregiver for their offspring. Female sea otters' energy demands more than double during parts of their reproductive cycle in order to produce milk for their pup, groom herself and her pup, and forage enough food for herself and increasingly for the pup as it reaches weaning age (Thometz et al., 2014; Thometz, Kendall, et al., 2016). Sea otters have very little fat to use as energy storage, and females must therefore employ physiological and behavioural strategies to cope with these high energy demands. Physiologically, females reduce their resting metabolic rate (RMR) during the last months of gestation, seemingly to increase and build fat storage prior to parturition (Thometz, Kendall, et al., 2016). Higher levels of fat deposition contribute to improved body condition prior to the physically demanding period of pup rearing (Chinn et al., 2016; Thometz, Kendall, et al., 2016). Behaviourally, female otters have adapted to utilizing tools more often than males to consume hard-shelled prey items more easily, thereby increasing foraging efficiency and allowing them greater access to larger prey with harder shells (Fujii et al., 2017; Law et al., 2024).

Despite the adaptations female sea otters use for successful reproduction, the energetic costs placed on mothers caring for pups, especially during the last 60-90 days of lactation and pup rearing prior to weaning, are so significant that she often experiences a prolonged period of energy deficit (Chinn et al., 2016; Thometz, Kendall, et al., 2016). Extended energy deficits lead to emaciation, higher susceptibility to other health conditions, and even death. Mortality in female otters associated with this period of high energy demands at the end of pup rearing and lactation is called end-lactation syndrome and has been widely studied in California's populations of southern sea otters (Chinn et al., 2016).

1.4 Physiology

Sea otters are unique in their physiology compared to their marine mammal relatives, with metabolic rates roughly 2.5 times the rate of a terrestrial mammal of the same size (Costa & Kooyman, 1982; Kleiber, 1975; Noren & Rosen, 2023). Most other marine mammals have thick layers of vascularized fat called blubber, that serve vital roles in energy storage and thermoregulation (Davis, 2019). However, sea otters lack blubber, but boast the thickest fur in the animal kingdom (Costa & Kooyman, 1982).

Sea otters have developed a number of strategies to cope with a lack of blubber and maintain thermal homeostasis in marine environments. First, they spend a large amount of their day grooming and maintaining their immensely thick fur, blowing air from their nostrils into the fur and trapping it, which provides insulation (Costa & Kooyman, 1982; Davis, 2019). Additionally, sea otters also use the energy released during and after the digestion of food, called the heat increment of feeding (HIF) or specific dynamic action (SDA), to help maintain homeostasis (Costa & Kooyman, 1984). The short but significant increase in basal metabolic rate (BMR) (54% average increase at its peak) associated with digestion helps with thermoregulation and replaces heat lost during periods of rest in addition to allowing for more extended rest periods between bouts of feeding and activity (Costa & Kooyman, 1984). Staying active also helps sea otters to maintain their internal body temperature through the heat generated from muscular activity (Costa & Kooyman, 1984).

1.5 Ecological role of sea otters

It is widely accepted that sea otters play vital roles in the stability of the marine ecosystems that they inhabit (Estes & Palmisano, 1974; Hughes et al., 2024). They are often referred to as keystone species, meaning that they have a disproportionate effect on their community diversity, composition, and ecology compared to other species present (Paine, 1969). A classic example of sea otters as a keystone species and ecosystem engineer is seen in the comparison of kelp forest and seagrass communities with and without sea otters present (Estes & Palmisano, 1974).

Sea otter consumption of macrograzer species, especially sea urchin (*Strongylocentrotus* species), acts as a top-down pressure to limit the predation of urchins on the species of kelp and grasses growing in these areas (Estes & Palmisano, 1974). In areas without otters, urchins are able to consume young kelp unchecked, leading to the disappearance of these important macroalgae species (Estes & Palmisano, 1974). In areas with otters, the flourishing of kelp forests, seagrass beds, and salt marshes provide marine habitats that are critical nursery and reproductive grounds for many commercially important fish and invertebrate species, leading to increases in biomass, biodiversity, and carbon sequestering. In central California, the influence of sea otter predation can also be seen in coastal salt marshes, where sea otter predation on burrowing crab species has greatly reduced the rates of erosion of these marine habitats (Hughes et al., 2024). Salt marshes are essential for protecting shorelines, providing habitat, and storing carbon (Estes & Palmisano, 1974; Hughes et al., 2024).

The prominent effects that sea otters have on their ecosystems via predation are driven not just by their aforementioned high energy requirements due to the unique physiological challenges they face as small mammals living in aquatic habitats, but also by the diets that they consume (Costa & Kooyman, 1984; Estes & Palmisano, 1974). Many of these marine invertebrate species tend to be high in protein and lower in fats, and therefore have relatively lower energy density. In comparison, the majority of other marine mammal species consume diets of primarily fish or crustaceans (i.e., krill, genus *Euphausia*) high in lipids and fats. The lower prey energy density consumed by otters requires greater levels of food intake to meet energy requirements. The very high protein content magnifies the differences in energy density, as almost 30% of protein consumed by sea otters is lost via digestion and as nitrogenous waste (excreted as urea) (Oftedal et al., 2007). The overall digestive efficiency of sea otters has been measured at 82% (i.e., 18% of all nutrients are lost during digestion as feces and urine), which is considered a low value for a mammal, but may be partly explained by their rapid food passage rate of only three hours (Costa, 1982).

The combination of having a small body size, high maintenance costs associated with their fur, and consuming diets high in protein and electrolytes explains the high daily metabolic rates of sea otters when compared to other marine mammals (Costa, 1982; Costa & Kooyman,

1984; Noren & Rosen, 2023). Maintaining energy balance and homeostasis with high metabolic rates while consuming relatively low energy-yielding prey necessitates sea otters having to eat large amounts and forage for large proportions of the day, driving the predation pressure exerted on their prey bases. Daily food consumption is estimated to be between 20–25% of a sea otter's body mass (Costa, 1982; Costa & Kooyman, 1984; Iskandar et al., 2023). However, females caring for pups may require 29–39% of body mass (Cortez et al., 2016).

1.6 Importance of understanding prey requirements

Since at least the 1960s, there has been conflict between commercial shellfish fisheries and sea otters, generally due to the large amounts of prey they consume daily to sustain their high metabolic rates (Davis et al., 2019). This ongoing competition for resources is further complicated by concerns that sea otters, especially southern sea otters in California, may be experiencing range stagnation, with some populations likely reaching the limits of their current habitats' capacity to support them, including in some peripheral populations that have been unable to expand into new areas (Lyon et al., 2024). These issues beg the questions: 1) What are the prey requirements of sea otters and 2) How do prey and/or habitat limitations on sea otter populations affect their food requirements and predation rates on their prey bases?

It is important to understand how differences in diets will affect food intake requirements of otters given that the prey species being consumed by sea otters do not have the same energy densities across species, or even within species depending on their size and reproductive status. Having estimates of food intake based on multiple prey species can provide insights into current limitations on sea otter population expansion—and can be used to estimate future limitations on existing populations, as well as aid in potential reintroduction efforts by ensuring that the prey bases in new areas are of sufficient size and composition to support sea otters. Additionally, understanding links between prey availability and energy requirements and subsequently on food intake requirements of sea otters is important for understanding population dynamics.

Introductions of new populations of otters, such as those being discussed in northern California and along the Oregon Coast, will likely create conflicts with commercial fisheries.

Similar conflicts occurred in the 1960's – 1980's after reintroducing northern sea otters in British Columbia, parts of Alaska, Washington, and Oregon—and relocating southern sea otters to different locations in central California. Possible conflict mitigation strategies include furthering research on sea otter diets and patterns of prey consumption in order to anticipate locations of potential conflict with commercial fisheries (Davis et al. 2019). Having estimates of food and energy requirements, and the amount of biomass removed from the ecosystem by sea otters, can help in these conflict mitigation efforts.

1.7 Research Gap

Given the complexities of sea otters' biology and physiological adaptations for life at sea, it can be difficult to estimate the overall energy requirements of an individual sea otter and, by extension, the entire population. Previous studies have investigated the adaptations of sea otters over the years to better understand their energetics, life histories, and influence on their ecosystems via their diets (Estes et al., 2003; Fujii et al., 2017; Oftedal et al., 2007; Tinker, 2004; Tinker et al., 2007, 2008; Yeates et al., 2007). Much of the energetics research has been focused on diving and foraging behaviour. While these studies provide a wealth of important knowledge, they can be limited by short study durations, and are often focused only on one sex or age group. Additionally, for some of the dietary studies, it is often difficult to identify the sex and age of the focal otters.

Despite the large body of energetic, physiological, and ecological peer-reviewed research about sea otters, important questions still remain (Griffen et al., 2024). These largely encompass questions of sea otter food intake and energy requirements and how they differ by age, sex, and reproductive status. Addressing these knowledge gaps represent important steps in the process of informing ongoing conservation efforts with the goal of increasing sea otter population ranges, aiding in potential future relocation efforts, and mitigating conflict between otters and humans.

1.8 Using models to estimate food requirements

A popular method used by researchers to investigate how much food an organism needs to eat to survive is estimating energy expenditure as a proxy for food and energy requirements (note that — as explained later — energy expenditure is not the same as food energy requirements, as digestive costs must be accounted for in the latter). One common tool used to estimate these values is a bioenergetic model. Bioenergetic models are essentially frameworks or statistics used to estimate energy budgets or food requirements for individuals while incorporating a variety of both environmental and biological factors (Booth et al., 2023; Pirotta, 2022).

There are two main types of bioenergetic models that are most often used to investigate energy needs: accounting models and dynamic models (Pirotta, 2022). Accounting models are commonly built to represent an individual organism's total energy requirements or prey consumption under "typical" conditions, by summing estimates of individual costs in an individual's energy budget. These final estimates can then be scaled to a population level (as seen in Figure 1.2) (Pirotta, 2022). These models include individual parameters such as: costs of tissue growth, reproductive costs (including lactation), costs of various behaviours and activities, and general maintenance costs (essentially, the cost of existing). They may also incorporate energy densities of the organisms' diet choices and any associated metabolic losses to estimate food intake.

Dynamic models are similar to accounting models and generally use the same parameters to explore energy needs. However, dynamic models also estimate how these may change in response to environmental changes, age transitions, or reproductive status (Pirotta, 2022).

Understanding an animal's energy and food requirements and how they change under various conditions is a crucial piece of information that is required to generate successful management and conservation plans, particularly for many endangered or vulnerable species. Both dynamic and accounting models can be used to contribute essential data to these efforts by predicting how an organism or population of organisms may respond to changes in their environment such as habitat disturbance, climate change, or human competition for resources

that often lead to changes in prey availability and ultimately affect population dynamics (Booth et al., 2023).

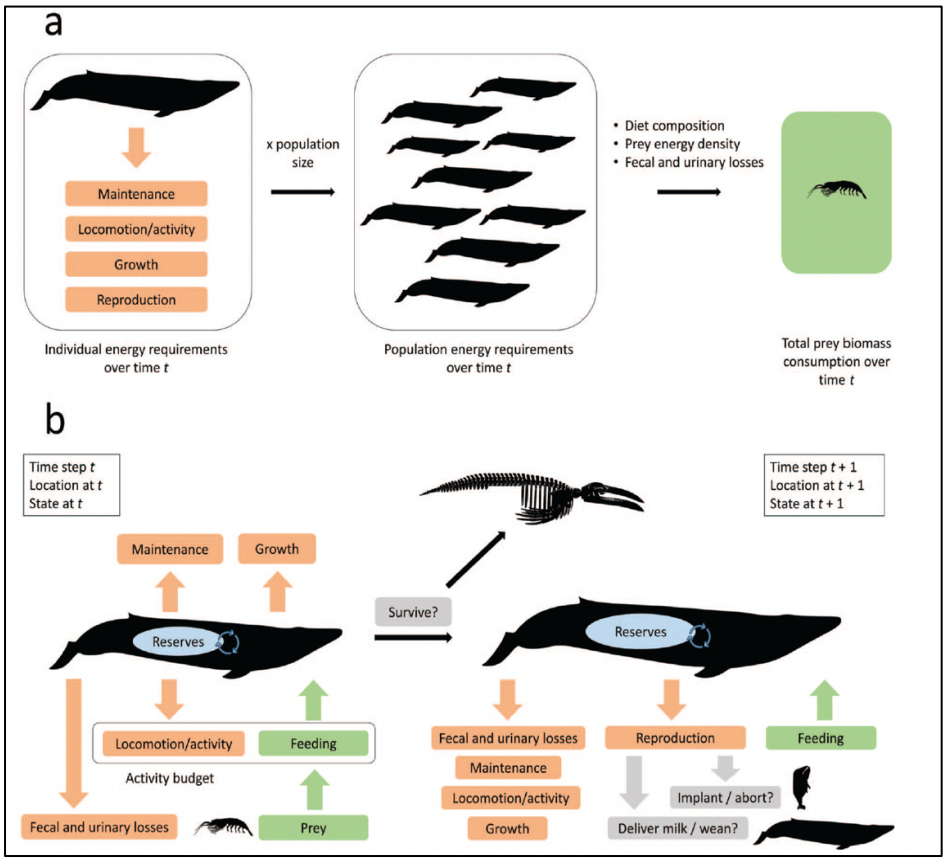


Figure 1.2*:* A schematic demonstrating the differences between an accounting bioenergetic model (a) and a dynamic bioenergetic model (b). Orange boxes represent energy costs, green boxes show energy intake, blue bubbles signify energy reserves, and grey boxes (in dynamic models only) show possible variations at each time step being modelled (Pirotta, 2022).

1.9 Existing bioenergetic models for marine mammals

There are a number of accounting-type bioenergetic models that currently exist for pinnipeds and cetaceans to investigate marine mammal ecology and physiology. These use a variety of methods depending on what types of data are available about the species in question. Metabolic rates under different activity states form the foundation of most models, but direct measurements are rarely, if ever, available. Some models use allometric comparisons from Kleiber's (1975) inter-specific scaling equation to estimate basal metabolic rates, and then estimate how they change under different activities. Such models include Winship et al.'s (2002) model for Steller sea lions (*Eumetopias jubatus*) and Noren's (2011) model for resident

killer whales (*Orcinus orca ater*). Other accounting models use empirical measures of average field metabolic rates (FMR) or respiration rates from both captive and wild animals that have been estimated from combining metabolic rates of observed behaviours, like Fortune et al.'s (2013) model for North Atlantic Right whales (*Eubalaena glacialis*) and McHuron et al.'s (2020) bioenergetic model for northern fur seals (*Callorhinus ursinus*).

These calculations provide estimates of total energy expenditure, but to translate these into estimates of food requirements means accounting for digestive efficiency (urinary and fecal losses) (Agbayani, 2022; Bejarano et al., 2017; Fortune et al., 2013; McHuron et al., 2020; S. Noren et al., 2012; Rechsteiner et al., 2013; Winship et al., 2001). Depending on the source and nature of the metabolic expenditure estimates, translations into food requirements may also have to account for the heat increment of feeding. Again, species-specific empirical data may be missing.

Although bioenergetic models already exist for several species of marine mammals, there is no bioenergetic model to estimate the energy expenditures of the smallest species of marine mammal: the sea otter. None of the existing marine mammal bioenergetic models suffice for estimating sea otter energy expenditures because of the major differences in comparison to cetaceans and pinnipeds in sea otters' body size, prey base energy densities, preferred habitats, and especially in their physiology. For example, the energy density of prey species for otters in one study listed that urchins had an energy density of 1,610 kJ kg^{-1}, butter clams' energy density was 2,610 kJ kg^{-1}, and *Cancer* crabs energy density was measured at 3,320 kJ kg^{-1} (Oftedal et al., 2007). However, fish species like salmon and pollock that many other marine mammals consume had higher energy densities (7,250 kJ kg^{-1} and 4,260 kJ kg^{-1}, respectively) (Iskandar et al., 2023).

As mentioned earlier (see: *Physiology*), sea otters' metabolic rates are strongly affected by their small body size and lack of blubber; a stark contrast to almost all other marine mammals that use blubber to maintain homeostasis. This physiological distinction necessitates using a distinct model to assess the energy expenditures of sea otters. Fortunately, abundant metabolic and dietary data exist to tailor a bioenergetic model for sea otters.

1.10 Research Goals

The aim of my research was to create an accounting bioenergetic model to investigate sea otter energy expenditures. I wanted to answer four general questions:

1. *What are the energy expenditures and food requirements of sea otters?*
2. *How does this differ by sex, age, and reproductive status?*
3. *How does diet affect food intake requirements?*
4. *How do energy expenditures change with prey quality and abundance?*

I addressed these four questions by constructing three individual bioenergetic models: one for males, one for non-reproductive females, and one for females caring for a pup. Model parameters included body mass, tissue growth, resting metabolic rates, foraging metabolic rates, activity budgets, as well as the additional cost of caring for a pup. Using Monte Carlo simulations, I investigated which of these input parameters had the greatest effect on model outcomes.

Additionally, I aimed to demonstrate various applications of this new bioenergetic model for sea otters that could ultimately contribute to species conservation. I conducted an analysis of specialist diets observed in sea otters and modeled how their energetic expenditures change accordingly, in addition to showing the amount of biomass removed from the environment by diet and how many prey items must be consumed based on preferred diets. I also estimated changes in foraging efficiency due to scenarios like decreased prey abundance or increased competition and how those changes would affect energy expenditures of sea otters.

Chapter 2: Building a Bioenergetic Model for Sea Otters

2.1 Summary

Bioenergetic models are a valuable tool to quantify food requirements, explore how diet affects a species overall energy balance, and predict the effects of a changing environment on an organism's physiological demands. I constructed a bioenergetic model for sea otters to investigate how energy expenditure and food intake requirements change with sex, age, and reproductive status. Three separate models were constructed— one for females with a pup, one for females without a pup, and one for males— using published energetic, physiological, and behavioural data. The models estimate total energetic expenditures in kilojoules of energy expended per day. Results showed that adult female otters with a pup have the highest daily energy expenditures; requirements for much larger adult males were 3-10% lower depending on year class, while females without pups expend an average 33% less energy. On a mass-specific basis, the energy expended by adult females with pups was 30% higher than adult males. I also conducted sensitivity analyses to test which parameters of the model had the largest effect on the model results. Body mass was the most sensitive parameter due to the use of mass-specific values throughout the model. After body mass, the parameter with the greatest effect on energy expenditure estimates was metabolic rate, highlighting the need for more data to improve model precision. Overall, these models can be utilized in further analyses to increase our understanding of potential energetic limitations placed on sea otters due to their dietary choices and the ultimate implications that this constraint may have on sea otter population dynamics, range expansion, and conservation.

2.2 Introduction

Sea otters contend with a number of physiological challenges in order to thrive in the marine environments they inhabit, resulting in them having high energy demands and consequently high food intake requirements. Factors contributing to their energy requirements include their small body size (Iversen & Krog, 1973), reliance on fur for thermoregulation instead of blubber like most marine mammals (Costa & Kooyman, 1984), and inherently high basal metabolic rate (BMR), which is an average of 2.54 times the predicted value for terrestrial mammals (Costa,

1982; Kleiber, 1975; S. Noren & Rosen, 2023). To satisfy their significant energetic demands, adult sea otters ingest an estimated 20%-25% of their body mass every day, typically consuming the invertebrate species most abundant in their immediate environment (Costa & Kooyman, 1984; Hughes et al., 2024; Morrison et al., 1974; Tinker et al., 2008). Otters consume sessile invertebrates at such a rapid rate that their prey fields often incur significant predation pressure, and can be significantly reduced in habitats they occupy (Kenyon, 1969; Laidre & Jameson, 2006; Ostfeld, 1982).

Predation pressure is the mechanism by which sea otters fulfill their well-known ecological role of keystone species (Paine, 1969), where their presence has a large effect on the stability, diversity, and community structure within the ecosystem they inhabit (Estes & Palmisano, 1974). In a classic example, sea otter predation on invertebrate macrograzer species like sea urchin and abalone have helped kelp forests to recover in areas where kelp was greatly depleted by these avid grazers, thereby increasing the abundance and diversity of many commercially important fish species that rely on these forested areas as nursery habitat (Estes & Palmisano, 1974). Additionally, sea otter predation can reduce and prevent shoreline erosion of critical salt marsh and seagrass habitats by removing burrowing prey (Hughes et al., 2024).

High food intake requirements paired with a lack of built-in energy storage (i.e., lipid reserves) can pose a challenge for sea otters to maintain energy balance. These pressures are especially felt by reproductive females, whose energy requirements increase by 110% during the later stages of pup rearing, when they are still lactating and feeding themselves along with an almost adult-sized pup (Chinn et al., 2016; Thometz, Kendall, et al., 2016). Many female otters struggle to survive this difficult period, often developing end-lactation syndrome (ELS), where mother otters experience prolonged periods of caloric deficits, leading to higher rates of infections, illness, and emaciation, often leading to mortality (Chinn et al., 2016). For example, 80% of reproductive females necropsied between 2005-2012 in California were diagnosed with ELS as the contributing cause of death (Chinn et al., 2016). Also of note, there were higher rates of female otter deaths due to ELS in areas with higher otter densities reported, leading to concerns about prey availability in some populations at or nearing carrying capacity.

On a larger scale, these high food intake requirements may determine a population's carrying capacity. Studies in Alaska on northern sea otters (*Enhydra lutris kenyoni*) have shown a negative association between the number of years otters have been present in an area and the population growth rate (Tinker et al., 2019). Surveys and models of newly populated areas in Alaska show them reaching carrying capacity very quickly because of the high rate at which prey bases are consumed by growing otter populations (Tinker et al., 2019).

Given the complexities of sea otters' biology and physiological adaptations for life at sea, it can be very difficult to estimate the overall energy requirements of an individual sea otter and, by extension, entire populations. As described in Chapter 1, numerous peer-reviewed studies have explored the energetic adaptations of sea otters to better understand their energy use, life history traits, and their influences on local ecology through their diets (Estes et al., 2003; Estes & Palmisano, 1974; Fujii et al., 2017; Lyon et al., 2024; Tinker et al., 2007, 2008). While these studies have provided an abundance of data about sea otters, many of them are limited by a narrow focus of diving and foraging behaviours, short study durations, or challenges in identifying the age and sex of observed otters. Despite the abundance of data and observations, important questions remain. Many can be addressed through further explorations of sea otter energetics and their links to age, sex, reproductive status, and diet.

Marine mammal energetics are often difficult to measure accurately in the wild due to the animals' inherent marine nature and often protected status. Bioenergetic models are a common tool in marine mammal ecology and physiology utilized to estimate energy budgets for individuals or populations based on multiple biological and environmental factors (Booth et al., 2023; Pirotta, 2022). A number of models have been produced to estimate food and energy requirements of cetacean and pinniped species, including bottlenose dolphins (*Tursiops t17runcatus*) (Bejarano et al., 2017), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Rechsteiner et al., 2013), harbour porpoises (*Phocoena phocoena*) (Gallagher et al., 2018), North Atlantic right whales (*Eubalaena glacialis)* (Fortune et al., 2013), Steller sea lions (*Eumetopias jubatus*) (Winship et al., 2002), and Pacific walrus (*Odobenus rosmarus divergens*) (Noren et al., 2012). However, there is no bioenergetic model currently available to estimate the energy expenditures of the smallest species of marine mammal: the sea otter.

Bioenergetic models not only serve as an important tool for researchers to use to improve their understanding of the energetics of marine mammal species, but these models can also be used to investigate the effects of environmental disturbances. Temperature changes or variations in prey availability can be measured by estimating how the energy or food requirements of otters will be impacted by such factors; thereby providing information crucial to the species' conservation and effective management. To determine how much energy a sea otter expends, I used an accounting bioenergetic modelling framework to investigate how energetic and behavioural costs interact with each other and ultimately affect the energy balance of individual sea otters, while accounting for sex, age, and reproductive status. In this chapter I hope to answer the first two research questions stated in Chapter 1:

I. *What are the energy expenditures and food requirements of sea otters?*
II. *How does this differ by sex and reproductive status?*

To address these questions, I constructed three individual models: one for males, one for non-reproductive females, and one for females caring for a pup. In addition to producing age- and sex-specific estimates of energy requirements, I investigated which model parameters make the greatest contribution to total otter energy expenditure and which affect the precision of model outcomes the most.

2.3 Methodology

2.3.1 Base model description

I constructed a model of sea otter energy expenditures using previously published energetics data, predominantly collected from southern sea otters in California, United States, both in the wild and under human care. The model was built using Microsoft Excel (Version 16.78) and rStudio (rStudio 2022.07.1+554). The base bioenergetic model was built using an energy balance equation similar to other accounting models (Pirotta, 2022) to estimate the total energy expenditure (TEE) of male and female sea otters at different ages and reproductive states (Agbayani, 2022; Bejarano et al., 2017; Winship et al., 2002). These models assume that

the animal is in a "steady physiological state" (i.e., that all energy expenditures are being satisfied, such that the terms "energy expenditure" and "energy requirements" can be considered synonymous). The total energy requirements of an organism can be assessed by estimating individual energy costs within a set of conditions, including costs incurred for resting metabolism, lactation, tissue growth, activity, cellular maintenance, digestion, thermoregulation, etc. The sum of these energy costs is assumed to represent the total energy expenditure of the organism and costs are independent of each other. Modelling using energy balance equations is a useful means to show how total energy expenditure of the organism changes under different life history conditions (e.g., age, sex, reproductive status).

To account for differences due to sex and reproductive status, I created three separate models: one for females with a pup, one for females without a pup, and one for males. The models calculated total energy expenditure for each year up to 20 years old. The model's age range was based on studies finding that sea otters have been able to live to 24 years old under human care, although wild otters often only live to 13- 17 years (Nicholson et al., 2020).

2.3.2 Age Class

Determining specific age classes was important to the construction of the models because published metabolic rates and behavioural activity budgets are specific to a given age class (vs. year): pups, juveniles, subadults, and adults (Table 2.1). For wild otters, the age class "pups" is assigned to animals from birth to 6 months old, while "juveniles" are 6 months to 2 years (Thometz et al., 2014, 2015). "Subadults" is used to describe male otters only, and is defined as males from 2-3 years old. Female otters are considered "adult" in the models based on when they reach physical sexual maturity, which is as early as 2 years old for females (Jameson & Johnson, 1993) and 3 years old for males (Hutchinson et al., 2015). After 3 years of age, all otters were considered adults.

The base model was structured to provide total energy expenditure estimates for entire year classes. This necessitated combining parameters for some portions of the model from multiple age classes within a given year class (age) due to overlap or averaging male and female values from data. For example, in Year class 1 (1-2 years old) the model used juvenile values for

both females and males. Year 2 (2-3 years old) was considered the subadult age class for males, and used averages of juvenile and adult values. Females in Year 2 and onwards were considered to be at reproductive age and adult values were used. Similarly, Year 3 (3-4 years old) is when males were considered reproductive adults. The pup age class, referred to as Year 0, represents birth to 6 months old, the period of time that otter pups are still dependent on their mother before being an independent juvenile. The values used were calculated as the weighted average from days spent within different developmental stages of immature sea otters (pre-molt pup, molting pup, post-molt pup, dependent immature) (Payne & Jameson, 1984).

Table 2.1 Age classification details used for the sea otter bioenergetic model. Data are presented separately for male and female otter models, and detail how age-class specific data was incorporated in the Year class structure of the model.

Females

Calendar Age	Year Class in Model	Age Class	Details
Birth to 6 months	0	Pup	This age class only accounts for the months when a pup is dependent on its mother and still nursing. Source: (Payne & Jameson, 1984)
6 months-2 years	1	Juvenile	Source: (Payne & Jameson, 1984)
2+ years	2-20	Adult	Source: (Payne & Jameson, 1984)

Males

Calendar Age	Year Class in Model	Age Class	Details
Birth to 6 months	0	Pup	This age class only accounts for the months when a pup is dependent on its mother and still nursing. Source: (Payne & Jameson, 1984)
6 months-2 years	1	Juvenile	Source: (Payne & Jameson, 1984)
2-3 years	2	Subadult	Average of juvenile and adult values Source: (Payne & Jameson, 1984)
3+ years	3-20	Adult	Source: (Payne & Jameson, 1984)

2.3.3 Model Parameters

The energy balance equation parameters incorporated into the base models calculating total energy expenditure were: growth (cost of somatic tissue growth), resting metabolism (the basic amount of energy needed to be alive and at rest; cost of resting), non-foraging activity (the energy to engage in behaviour such as swimming, grooming, etc., not including energy needed

to forage), foraging activity (the energy expended diving, foraging for prey, and handling food; i.e., breaking open mussels), and the cost of reproduction.

The cost of reproduction differs between the two sexes. In males, the cost of reproduction was accounted for only as changes in non-foraging activity within published activity budgets. For females, reproductive costs were accounted for via both the behavioural changes in non-foraging activity and the cost of caring for a pup. The cost of caring for a pup reflected the portion of the energy requirements of the pup that are provided by the mother, either from milk or foraging for food. The costs of gestation and lactation were not explicitly accounted for in this model, as they were incorporated into the resting metabolic rates (RMR) of females while pregnant and throughout lactation (Thometz, Kendall, et al., 2016). In the model for female otters without a pup, the cost of caring for a pup were assigned a value of zero.

Total energy expenditure (TEE) was calculated for male and female otters using:

Male: $$TEE = G + R + F + A$$

Female: $$TEE = G + R + F + A + P$$

Where *TEE* is total energy expenditure, *G* is cost of growth, *R* is cost of resting, *F* is the cost of foraging, *A* is cost of non-foraging activity, *P* is the pup cost. TEE and all inherent costs were expressed in kilojoules per day (kJ d^{-1}).

As noted earlier, TEE is considered equivalent to net energy intake requirements from food. However, the model outputs were subsequently used to calculate gross energy intake (GEI; i.e., food energy intake) requirements under specific dietary conditions. This transformation requires accounting for digestive losses, as detailed in *Converting TEE to GEI***.** Changes in GEI due to differences in diet were calculated as a separate component of the model overall (see Chapter 3).

2.3.4 Body Mass

Body mass was used to calculate the cost of growth and to scale mass-specific energy expenditure parameters. Data were acquired from published growth curves for southern sea otters in California (Fig. 39, Tinker et al., 2019). The predicted average mass values used in the original growth curves were presented in 1/10 of a year increments. These incremental data were used to calculate an average mass per year in kilograms (kg) and used to represent the associated year class (Table 2.1). For pups (birth to 6 months), only the first 5/10 values were used for Year 0. Average masses were calculated separately for male and female otters from 0 (birth) to 20 years.

2.3.5 Growth

The cost of tissue growth in kJ d^{-1} for age class *i* was estimated in two steps. First, the difference in average mass between one year class (*i*) and the previous year class (*i*-1) was calculated from the body mass raw data. The resulting value was then multiplied by the estimated caloric density of sea otters. A peer-reviewed study investigating killer whale diets estimated the average caloric content of a sea otter was 1.81 ± 0.04 kcal g^{-1} by utilizing adiabatic bomb calorimetry (Estes et al., 1998), which was converted into kJ kg^{-1} ($7{,}573 \pm 167.36$ kJ kg^{-1}).

(3) $$Growth_i = (Mass_i - Mass_{i-1}) * 7{,}573\ kJ\ kg^{-1}$$

This calculation accounts for annual changes in mass, but does not account for any annual or seasonal changes in body composition, which are assumed to be minimal in this species due to lack of seasonal lipid storage (Costa & Kooyman, 1982). Additionally, this cost of growth estimate accounts only for the cost of tissue growth, not the deposition of tissues (i.e., the heat increment of growth). The latter is accounted for in the resting metabolic rates.

2.3.6 Pup Cost

"Pup cost" accounted for the additional energy that the mother otter must expend in order to care for her pup on top of her own energetic needs. This includes both changes in non-foraging activity (such as grooming the pup) and expending energy to meet the pup's own metabolic needs in the form of milk or food (Figure 2.1, "female to pup" band). Data accounting for the energy expenditure of females caring for a pup were collected by Thometz, Kendall, et al. (2016) using wild, pregnant female otters maintained under human care. These estimates of the additional costs of caring for a pup do not account for the indirect costs of milk production (i.e., heat increment of lactation) or the additional costs of foraging, which are accounted for in the "female to self" band. Specifically, indirect milk production costs are included in the estimates of RMR and foraging costs are accounted for in the appropriate behavioural budgets (Thometz, Kendall, et al., 2016). I calculated a weighted average of the cost of caring for a pup over the 180-day period of parental care from the estimates provided by Thometz, Kendall, et al. (2016) and incorporated them into the model as additional costs added into the female's energy expenditures. The weighted average was calculated as 3,931 kJ d^{-1}. This additional cost was added into the TEE for the females with a pup model (Year classes 2 and up) (Table 2.2).

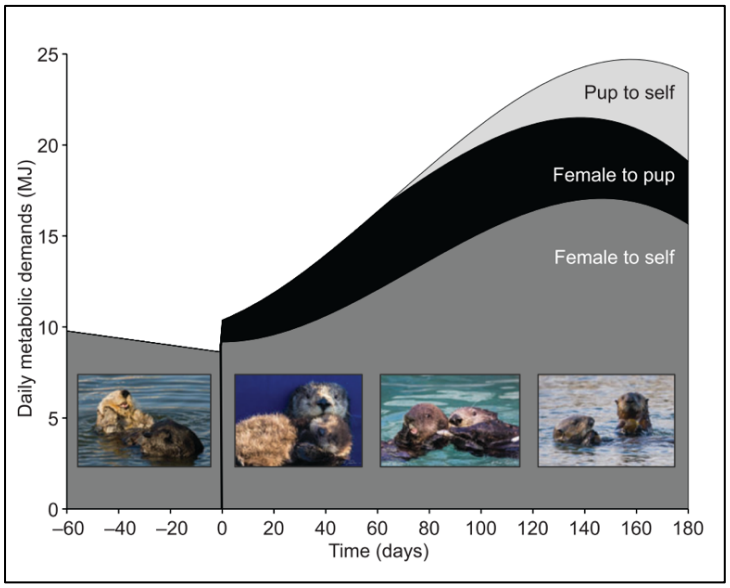


Figure 2.1: Estimates of the energy demands of female sea otters caring for a pup via lactation and providing foraged food. "Female to self" accounts for the mother otter's own energy demands, "Female to pup" is additional energy expended by the mother to care for her pup, (e.g., milk or food delivered to pup) and "Pup to self" is energy expended by the pup to groom and forage for itself (not added to female model). Figure taken from Thometz, Kendall, et al., 2016**.**

Table 2.2: Energetic cost estimates of "Female to pup" with pup age used to calculate overall "pup cost". The data describe the black band on Figure 2.1, with pup age in days (Thometz, Kendall, et al., 2016). At 200 days pups are weaned and are considered juveniles. Note that the peak in energy expenditure from the mother to the pup is 4.8 MJ d^{-1} (4,800 kJ d^{-1}) at ~100 days.

Pup Age (days)	Metabolic costs (kJ d^{-1})	Weighted Metabolic Costs (kJ d^{-1})	
1-21	1,800	189	
22-49	3,600	882	
50-200	4,400	2,860	
		3,931	**Total**

2.3.7 Cost of different activities

Published behavioural activity budgets (accounting for the percent time spent in specific behaviours and/or behavioural categories per day) in combination with activity-specific metabolic rates were used to estimate the daily cost incurred by different types of behaviours (Table 2.3). Adapting published activity budgets (Thometz et al., 2014; Thometz, Staedler, et al., 2016; Yeates et al., 2007), my three models used six different activity budgets specific to different age, reproductive, and age classes: pups, juveniles, male subadults, adult females with a pup, adult females without a pup, and adult. Both pup and juvenile activity budgets were the same for male and female otters. For this study, I divided all behaviours into three mutually-exclusive categories: resting, foraging, and non-foraging activities, consistent with groupings used in many published studies (Staedler, 2011; Thometz et al., 2014; Yeates et al., 2007). When necessary, the behaviours reported in the original activity budgets were recategorized. Specifically, "active" refers to any behaviours which are neither resting nor foraging. Previously listed behaviours that I condensed into "active" included: swimming, active grooming, as well as "other" (Staedler, 2011; Thometz et al., 2014; Yeates et al., 2007). I then converted the percent time spent in specific behaviour categories into minutes per day (min day^{-1}).

To determine the daily cost of each of these behaviours at different age classes, the published (or extracted) mass-specific metabolic rate of an activity was multiplied by the average mass of the animal in that age class and then multiplied by the total minutes per day spent in each activity:

(4) $$C_B = (MR_{iB} * m_i) * t_{iB}$$

where C_B is cost of behaviour B, MR_{iB} is the metabolic rate of behaviour B for age class *i*, m_i is the average mass of age class *i*, and t_{iB} is minutes per day spent in behaviour B for age class *i*.

Table 2.3: Behavioural activity budgets of each sea otter age class with mass-specific metabolic rates calculated from activity rates and percent time published in literature. When necessary, mass-specific metabolic rates were calculated from absolute rates in the original sources using the average mass of each age class given in the publications.

Pups

Behaviour	Proportion of day	Time (min day^{-1})	Metabolic rate (kJ min^{-1})	Mass specific metabolic rate (kJ kg^{-1} min^{-1})	Sources
Resting	64.1%	923.4	2.17	0.29	Thometz et al., 2014
Active	15.5%	223.2	7.45	1.00	
Foraging	20.3%	292.7	5.25	0.70	

Juveniles

Behaviour	Proportion of day	Time (min day^{-1})	Metabolic rate (kJ min^{-1})	Mass specific metabolic rate (kJ kg^{-1} min^{-1})	Sources
Resting	30.5%	439.2	3.76	0.26	Thometz et al., 2014; Yeates et al., 2007
Active	28.1%	404.6	7.27	0.50	
Foraging	41.4%	596.2	6.68	0.46	

Subadult males

Behaviour	Proportion of day	Time (min day^{-1})	Metabolic rate (kJ min^{-1})	Mass specific metabolic rate (kJ kg^{-1} min^{-1})	Sources
Resting	35.3%	507.6	5.96	0.26	Thometz et al., 2014; Yeates et al., 2007
Active	26.1%	375.1	12.06	0.53	
Foraging	38.7%	557.3	10.07	0.45	

Adult females without a pup

Behaviour	Proportion of day	Time (min day^{-1})	Metabolic rate (ml O_2 kg^{-1} min^{-1})	Mass specific metabolic rate (kJ kg^{-1} min^{-1})	Sources
Resting	51.6%	743.0	13.50	0.27	Thometz et al., 2014; Thometz, Kendall, et al., 2016; Yeates et al., 2007
Active	8.7%	125.3	24.74	0.50	
Foraging	39.7%	571.7	23.58	0.47	

Adult females with a pup

Behaviour	Proportion of day	Time (min day^{-1})	Metabolic rate (ml O_2 kg^{-1} min^{-1})	Mass specific metabolic rate (kJ kg^{-1} min^{-1})	Sources
Resting	50.4%	725.8	13.88	0.28	Thometz et al., 2014; Thometz, Kendall, et al., 2016; Thometz, Staedler, et al., 2016; Yeates et al., 2007
Active	6.4%	92.4	30.25	0.61	
Foraging	43.2%	621.8	28.83	0.58	

Adult males

Behaviour	Proportion of day	Time (min day^{-1})	Metabolic rate (ml O_2 kg^{-1} min^{-1})	Mass specific metabolic rate (kJ kg^{-1} min^{-1})	Sources
Resting	40.0%	576.0	13.30	0.27	Yeates et al., 2007
Active	24.0%	345.6	27.80	0.56	
Foraging	36.0%	518.4	21.60	0.43	

2.3.8 Adjusting metabolic rates for females with a pup

The metabolic rates used in the behaviour budgets for female otters with a pup were adjusted based on methods from Thometz, Kendall, et al. (2016). The study recorded large differences in the RMR of reproductive females throughout different phases of pregnancy, immediately pre- and post-parturition, during lactation, and after weaning pups. They found that the RMR of a post-weaning, non-reproductive female was much lower than a lactating otter, and calculated the percent differences in the mother's RMR at each pup developmental stage relative to non-reproductive females. They applied those calculated percent changes in RMR to the metabolic rates for other behaviours (foraging and non-foraging activity). Using the same method, I calculated a weighted average of those percent changes in RMR throughout lactation (the period of caring for a pup) and applied it to the metabolic rates for foraging and non-foraging activity.

2.3.9 Altering behaviour budgets

The original published behaviour budgets were applicable to a specific (empirically measured) age, sex, and reproductive class (Thometz et al., 2014; Thometz, Kendall, et al., 2016; Thometz, Staedler, et al., 2016; Yeates et al., 2007). It would be inappropriate to uniformly apply a constant activity budget to all animals in that group, regardless of mass, age, and diet. I

therefore used mass-specific (rather than absolute) rates of energy expenditure to account for the physiological impact of the change in body mass as otters grow. However, this meant that remained constant. This effectively meant that either (i) animals would have to become more efficient foragers if they maintained the same percent time foraging as TEE increased or (ii) changes in foraging time that account for changes in TEE would have to be integrated into the model. I chose the latter option, and the process for adjusting foraging times are detailed below.

2.3.10 Adjusting foraging time

The cost of foraging accounts for the energy expended by sea otters while foraging for food, including behaviours such as diving, searching for, capturing, and physically processing their prey items (e.g., deshelling). A basic assumption of the model is that the energy gained from foraging, and therefore the time spent foraging, functions to offset all non-foraging costs. A second assumption is that time not spent foraging or active (non-foraging activity) would be spent resting. Therefore, I adjusted behavioural budgets to account for changes in foraging time so that the time spent "active" remained constant within the activity budget, and that any time not spent foraging would be spent resting (i.e., increases in foraging activity would lead to decreases in resting behaviour).

My approach entailed calculating the foraging time needed (t_F) to meet the non-foraging costs (partial energy expenditure, EE_P) for each age and sex class in the model. The amount of time required to forage (t_F) to meet EE_P depends upon the net rate of energy gained from foraging (the net rate of return (ROR_N)), so that an otter can offset its energetic needs:

(5)
$$t_F = \frac{EE_P}{ROR_N}$$

ROR_N is itself dependent upon two factors. The first is the rate at which an otter can capture and ingest biologically useful food energy (kJ min^{-1}). This measure of foraging efficiency is denoted as gross rate of return (ROR_G). The second factor is the additional cost of foraging compared to resting. In other words, it is the additional energetic expenditure required to

"switch" from resting to foraging behaviour in order to satisfy EE_P. It is calculated as the difference between metabolic rate when foraging (r_F) and the rate of energy expenditure when resting (r_R), such that:

(6) $$ROR_N = ROR_G - (r_F - r_R)$$

ROR_G is assumed to remain constant within an age class; i.e., individuals do not increase or decrease their foraging efficiency as TEE goes up or down within the same age class. Therefore, ROR_G was calculated from "model" sea otters for each age, sex, and reproductive class based on the energy costs and behavioural budgets found in the literature for that specific otter class. More specifically, ROR_G was calculated for specific age, sex, and reproductive classes using the activity-specific energy costs, behaviour budgets, and body mass in the literature, and adding in additional calculated costs of growth and reproduction, when appropriate, as detailed previously. Male and female values were averaged to calculate the ROR_G for the "model" otters of the juvenile age class. There was no calculation done for the pup age class based on the assumption that they are still dependent on their mother for food, so their foraging efficiency is irrelevant. This provided an estimate of total energy expenditure, which was divided by the foraging time reported for the specific age and sex class.

(7) Males: $$ROR_G = \frac{G+R+A+F}{t_F}$$

(8) Females: $$ROR_G = \frac{G+R+A+F+P}{t_F}$$

Where *G* is cost of growth, *R* is cost of resting, *A* is cost of (non-foraging) activity, *F* is the cost of foraging, *P* is the pup cost, and t_F is minutes reported spent foraging. ROR_G was expressed in kilojoules per minute (kJ min^{-1}).

This process is demonstrated below using data from the literature for an 18.38 kg, 2-year-old (adult) female otter without a pup that served as the "model organism" for those sex and reproductive classes. We then demonstrate how we applied the calculated ROR_G representing female adults without a pup to a 21.28 kg, 8-year-old female without a pup to determine the required foraging time and subsequently the TEE.

1. Calculate ROR_G for each "model" age class by adding costs of *G*, *R*, *A*, *F*, and *P* as seen above in Equation 8. These are based on appropriate published values of body mass, time spent foraging, and calculated energy costs. Time in each activity and activity-specific metabolic rates are provided in Table 2.3, and growth cost is calculated on the published growth curve as previously described.

   Example:

   (8) Females: $$ROR_G = \frac{G+R+A+F+P}{t_F}$$

$$ROR_G = \frac{38.32 + 3{,}701.54 + 1{,}143.72 + 4{,}974.32 + 0\ kJ}{571.68\ min}$$

$$ROR_G = 17.24\ kJ\ min^{-1}$$

2. As per Equation 6, calculate the ROR_N for the 8-year-old female age class by subtracting the additional cost of foraging from the ROR_G calculated for the appropriate "model otter." Additional cost of foraging is calculated by taking the rate of energy expenditure when foraging (r_F, kJ min^{-1}); based upon reported average body mass (21.279 kg) and mass-specific rate of energy expenditure minus r_R (the mass-specific rate of energy expenditure when resting).

$$ROR_N = ROR_G - (r_F - r_R)$$

   Example:

$$ROR_N = 17.24 - (21.28 * [0.47 - 0.27])$$

$$ROR_N = 12.98\ kJ\ min^{-1}$$

3. Calculate the total non-foraging costs (EE_P) for the 8-year-old otter. For this step, the time (in minutes per day) spent active (non-foraging activity; A) is set by the original time budget, with the remainder of the time allocated to resting (R).

   (9) Males: $$EE_P = G + R + A$$

(10) Females: $$EE_P = G + R + A + P$$

Example:

$$EE_P = 1.65 + (21.28 * [743.04 + 571.68] * 0.27) + (21.28 * 125.28 * 0.50) + 0$$

$$EE_P = 1.65 + 7{,}553.86 + 1{,}332.98 + 0$$

$$EE_P = 8{,}888.49\ kJ$$

4. Calculate total foraging time required to meet the EE_P using Equation 5 in minutes per day and percent of day.

   Example:

$$t_F = \frac{EE_P}{ROR_N}$$

$$t_F = \frac{8{,}888.49\ kJ}{12.98\ kJ\ min^{-1}}$$

$$t_F = 684.78\ min$$

$$\%t_F = \frac{684.78\ min}{1{,}440\ min/day}$$

$$\%t_F = 0.48$$

5. Keeping original non-foraging activity, recalculate the time spent resting in percent of day and minutes per day.

(11) $$\%t_R = 1 - (\%t_F + \%t_A)$$

$$\%t_R = 1 - (0.48 + 0.09)$$

$$\%t_R = 0.43$$

$$t_R = 0.43 * 1440\ min$$

$$t_R = 619.20\ min$$

6. Recalculate the TEE (as the sum of the costs of growth, resting, active, foraging, and reproduction) using the new behavioural budgets and the appropriate mass-specific metabolic rates for each behaviour.
   Example:

$$TEE = 1.65 + (21.28 * 619.20 * 0.27) + (21.28 * 125.28 * 0.50) + (21.28 * 684.78 * 0.48) + 0$$

$$TEE = 1.65 + 3557.68 + 1332.98 + 6994.62 + 0$$

$$TEE = 11{,}886.93\ kJ\ d^{-1}$$

2.3.11 Sensitivity Analysis

I evaluated model sensitivity in two ways, both designed to determine how the level of uncertainty in parameter estimates affects the precision of the final model output and which parameter had the greatest effect on the overall outcome of the model (i.e., affected the total energy expenditure (TEE) the most). The analyses involved performing Monte Carlo simulations of the model with 10,000 iterations using values generated from a randomized population for each parameter. These values were created with means corresponding to the original parameters of the base model, and random sampling was performed from normal distributions with a pre-defined standard deviation (detailed below). The parameters varied were: body mass, cost of tissue growth, percent time spent in each behaviour category, mass-specific metabolic rate of each behaviour, and the cost of caring for a pup. The simulations were run in sets of 10,000 iterations, varying only one parameter at a time, for each of these parameters.

To evaluate which parameter was the most "sensitive", I took the 10,000 replicates of the model, and calculated the mean, standard deviation, confidence intervals, and standard error of the estimate of TEE from the replicate runs. I then compared the standard deviations between the different model runs. The higher the standard deviations were, the more sensitive the parameter was, thereby having a greater impact on the TEE model outputs.

The first set of iterations looked at overall sensitivity of the model. Specifically, I wanted to ascertain which model parameter, given the same amount of variation, has the greatest effect on the model outcome (TEE). Three scenarios were used, where the standard deviation of the underlying population for each parameter was set at 5%, 10%, or 20% of the parameter mean.

An additional set of model runs was done to examine how the current state of scientific knowledge affected the TEE estimates. These tests were similar to those previously described; except they used the variation given in the source literature. They tested the effect of the same set of parameters, except for pup costs, and were all varied one at a time for 10,000 repetitions. The costs of caring for a pup were not included in this literature analysis because there was no error available in the source literature used for this estimate.

2.3.12 Estimated error on model predictions

To account for variation in my model outputs, I did an additional Monte Carlo simulation with 10,000 repetitions where I allowed all of the parameters to vary simultaneously, using the error taken from literature values (see Appendix B for these values). The same five parameters from the sensitivity analysis were used: mass, growth, percent time spent in each behaviour category, metabolic rate of each behaviour, and the additional cost of caring for a pup. I assumed that all parameters were normally distributed, and did not allow for the selection of negative values when generating random values. I then calculated the standard deviation from the mean of the 10,000 TEE values within each year class as well as. Those standard deviation values were then utilized as variation estimates for my model outputs for TEE.

2.3.13 Important model assumptions

There were a few assumptions made in the construction of the base model. Firstly, I assumed that the metabolic costs of a sea otter scale to their body mass, and that they otherwise remain constant within an age and sex group. A second important assumption was that changes in a sea otter's foraging time only affected the time spent resting and that non-foraging activity stayed constant. Lastly, I assumed that the efficiency of foraging (the rate at which otters obtain and ingest prey energy) within age classes, among sexes and reproductive status remains independent of energy requirements. Additional investigations into how energy requirements change with diet are described in Chapter 3.

2.4 Results

2.4.1 "Rate of Return"

Gross rate of return (ROR_G) describes the rate of food energy (in kJ) acquired per minute foraging. It is calculated from "model" published activity budgets based upon Equations 7 and 8, and therefore remains constant within age classes, among sexes and reproductive status (Table 2.4). It is consequently used to calculate net rate of return (ROR_N), the net energy profit gained via foraging, which is ultimately used to calculate the foraging time needed to sustain all non-foraging activities.

Table 2.4: The ROR_G values used to calculate the foraging times for each age class in each of the three models - males, females without a pup, and females with a pup. The juvenile ROR_G was based on average costs (growth, resting, foraging, etc.) from 6 months old to 2 years old. The same energy budget was used for all juveniles. The Year 2 energy budget for subadult males was an average of juvenile and adult male energy budgets and metabolic rates. All values are presented in kJ min^{-1}. There are no values given for pups due to the assumption that pups (up to 6 months) are not foraging to gain energy while dependent on their mother for milk and solid food.

Age Class	Female without a pup	Female with a pup	Male
Pup	--	--	--
Juvenile	17.74	--	17.74
Subadult	--	--	23.64
Adult	17.24	24.66	28.34

The calculated ROR_G of juveniles (17.74) and adult females without a pup (17.24) were close in value to one another meaning they must intake essentially the same amount of energy per minute to satisfy their non-foraging energy needs. The ROR_G value for adult females with a pup is 25 kJ min^{-1}, which is 30% higher than an adult female without a pup. This means that a female otter caring for a pup must maintain a higher rate of foraging efficiency per minute than one without a pup in her care, in addition to any differences in foraging time. Adult males have the highest ROR_G values, where they acquire 28 kJ min^{-1}, 40% more than a female without a pup. The ROR_G of subadult males (Year 2) was intermediate to adult males and juveniles (23.64).

2.4.2 Behaviour budgets

Calculating the net rate of return (ROR_N) for each year class by subtracting the additional cost of foraging from ROR_G (Equation 6), allowed me to calculate the time necessary to satisfy the energy requirements for non-foraging behaviours. This, in turn, directly affected the amount of time per day spent resting. The newly calculated behavioural budgets were used to calculate TEE for each year class in all three models.

It is important to note that, while a single ROR_G was applied to each age, sex, and reproductive class (Table 2.4), ROR_N and the resulting behavioural budgets were affected by age-specific foraging metabolic costs and age- and sex-specific differences in body mass. For example, although the same ROR_G was used for male and female juveniles, the calculated activity budgets (Figures 2.2 & 2.3) differed due to differences in body mass between males and females.

The calculated behavioural budgets show that male otters spend the most time foraging during the juvenile age class, at 47% of the day, compared to other age classes (40% as a subadult, and 42% as an adult) (Figure 2.2). For male otters, time spent active increased between pup and juvenile age classes- from 16% in pups to 28% in juveniles, but then decreased to 24% in adults. The amount of time male otters spent active as subadults and adults (27% and 24%, respectively) are substantially greater than the amount of time adult female otters spent on non-foraging activity, either with (6%) or without (9%) a pup. Instead,

adult females with and without pups spent more time resting (44% for both) and more time foraging (49% and 47%, respectively) compared to adult males (34% resting, 42% foraging) (Figure 2.3). Females with pups spent almost the same amount of time foraging and resting as females without pups, offsetting the costs associated with pup provisioning through a higher ROR_G.

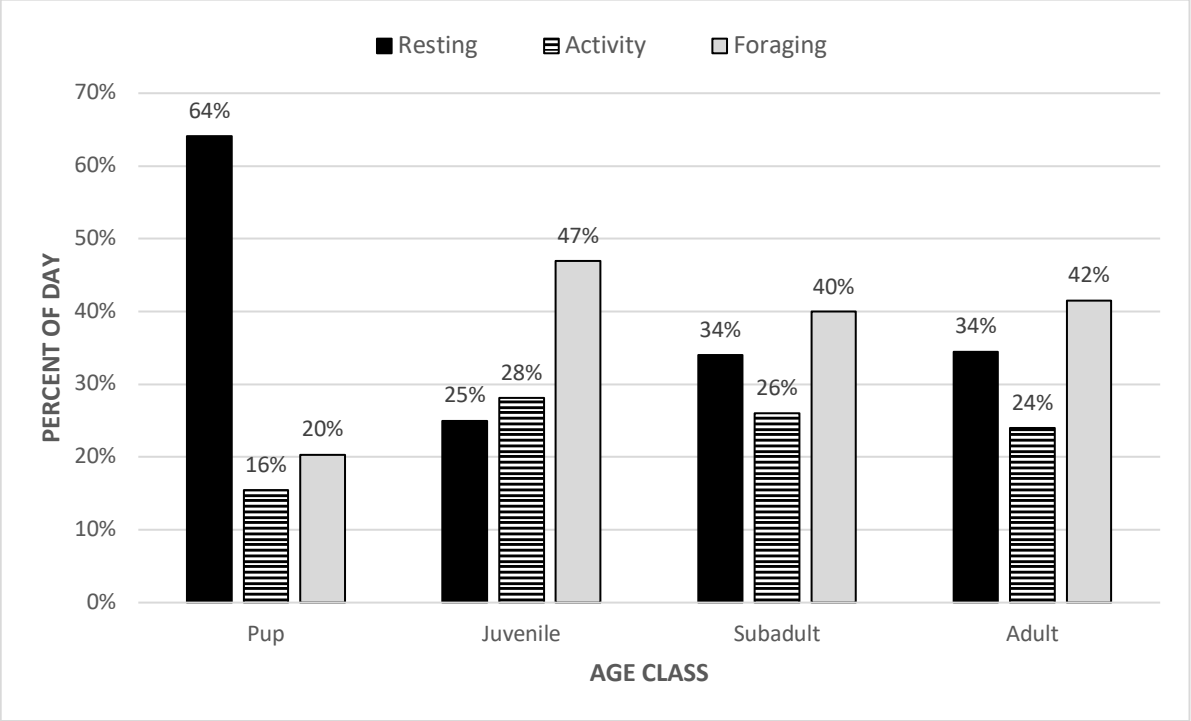


Figure 2.2: Behavioural budgets used to calculate total energy expenditure for each age class of male otters. The adult behavioural budget in this figure represents an average of the values for all years within the adult age class, although separate budgets were calculated for each Year class in the actual model.

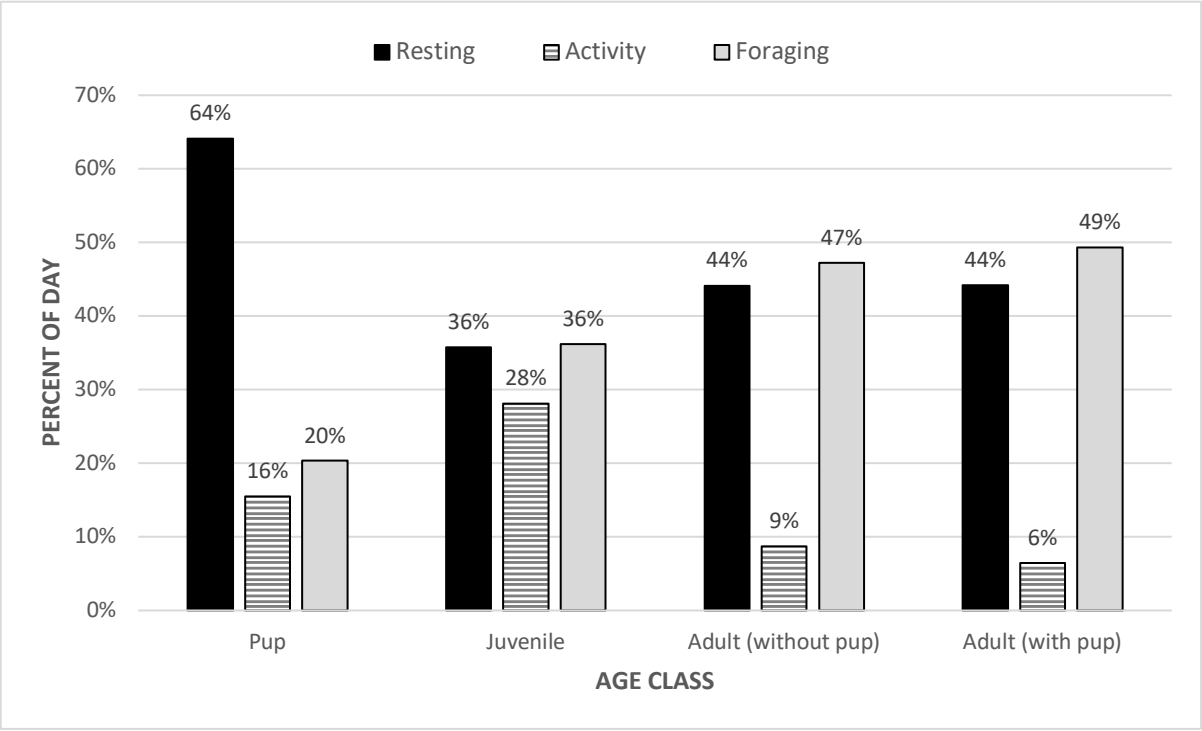


Figure 2.3: Behavioural budgets used to calculate total energy expenditure for each age class of female otters. Budgets for both adult females with and without a pup are represented. This figure shows the average percent of day spent in each behavioural category for all years in the adult age class, although separate budgets were calculated for each Year class in the actual model.

2.4.3 Total energy expenditure

As expected, total energy expenditure (TEE) rises rapidly with age for young otters, with the rate of annual changes in TEE decreasing as the animals mature. In the early adult years, large increases in TEE occur between Years 2 and 3 in both female models (~900 kJ day^{-1} difference between years for females without a pup and ~1,000 kJ day^{-1} for females with a pup). Total energy expenditures for male otters largely stabilize at Year 10 compared to a plateau at Year 7 and Year 8 for females without a pup and females with a pup, respectively (Figure 2.4). In the pup and juvenile age classes, male otters have higher energy expenditures than females due to differences in body mass. More specifically, in the pup age class, males TEE was 18% higher than female pups. Similarly, within the juvenile age class, females require 19% less energy than males. In Year 2, females are in the adult age class and able to reproduce while males are still in the subadult age class and not yet reproductive (Table 2.1). Subadult males have a higher TEE

than adult females without a pup by 28%; however, in Year 2, adult females caring for a pup have higher TEE than males by a margin of 11% (Table 2.5).

Table 2.5: Total energy expenditure (TEE) calculations of sea otters at all age and Year classes (means ± sd). All values are presented in kJ day^{-1}. Note that females in Year classes 0 and 1 do not have pups and only 2-year-old males are considered subadults. Standard deviation (sd) values were derived from the sensitivity analysis using literature error with all parameters varying simultaneously.

Age Class	Year Class	Female without a pup	Female with a pup	Male
Pup	0	7,567.86 ± 22,492.90	---	9,347.06 ± 52882.83
Juvenile	1	9,487.96 ± 2,705.66	---	11,679.16 ± 3,422.77
Subadult	2	---	---	13,637.35 ± 1,930.75
Adult	2	9,853.84 ± 1,485.73	15,339.42 ± 1,108.49	---
Adult	3	10,739.73 ± 1,724.11	16,381.27 ± 1,204.32	14,689.62 ± 1,020.11
Adult	4	11,235.76 ± 1,863.17	16,965.37 ± 1,246.16	15,665.27 ± 1,061.20
Adult	5	11,520.57 ± 1,947.82	17,300.93 ± 1,280.21	16,283.68 ± 1,103.91
Adult	6	11,693.55 ± 2,003.32	17,504.78 ± 1,301.57	16,682.18 ± 1,128.75
Adult	7	11,795.13 ± 2,036.65	17,624.52 ± 1,314.69	16,931.15 ± 1,144.78
Adult	8	11,868.22 ± 2,060.99	17,710.64 ± 1,325.30	17,090.93 ± 1,156.67
Adult	9	11,912.18 ± 2,075.24	17,762.44 ± 1,331.41	17,195.46 ± 1,164.64
Adult	10	11,949.01 ± 2,087.85	17,805.82 ± 1,336.61	17,258.23 ± 1,169.59
Adult	11	11,978.57 ± 2,097.83	17,840.64 ± 1,340.78	17,300.15 ± 1,172.78
Adult	12	11,993.32 ± 2,102.76	17,858.02 ± 1,342.90	17,328.14 ± 1,174.84
Adult	13	12,008.13 ± 2,107.73	17,875.46 ± 1,344.96	17,349.18 ± 1,176.66
Adult	14	12,022.98 ± 2,112.92	17,892.95 ± 1,347.23	17,363.22 ± 1,177.71
Adult	15	12,037.87 ± 2,117.90	17,910.47 ± 1,349.28	17,370.21 ± 1,178.18
Adult	16	12,045.29 ± 2,120.45	17,919.22 ± 1,350.38	17,377.25 ± 1,178.77
Adult	17	12,052.73 ± 2,123.02	17,927.98 ± 1,351.38	17,377.20 ± 1,178.76
Adult	18	12,060.18 ± 2,125.53	17,936.75 ± 1,352.44	17,377.16 ± 1,178.76
Adult	19	12,060.15 ± 2,125.57	17,936.72 ± 1,352.47	17,384.26 ± 1,179.32

In Year class 3, both males and females are considered reproductive adults. Across all the adult age class, female otters caring for a pup have higher TEE than males, who have a greater TEE than females without a pup (Table 2.5). In Year 3, females with a pup have a TEE 34% greater than Year 3 adult females without a pup and 10% higher energy expenditure than

adult male otters. By Year 10, TEE values have plateaued in both females and males. While females with a pup still expend 33% more energy than females without a pup, the TEE of females with a pup is only 3% higher than that of males. This is the smallest difference in TEE between reproductive females and males.

Overall, adult females with a pup have 33% higher TEEs than those without, an average difference of 5800 kJ day^{-1} (Figure 2.4). The majority of this difference is directly attributable to the additional cost of caring for a pup that is placed on the mother otter, designated "pup cost" in the model, which accounts for a constant 3931 kJ day^{-1}. The remaining average 1873 kJ day^{-1} is due to variation in the behavioural budgets between reproductive and non-reproductive adult female otters. Additional tables from model outputs can be reviewed in Appendix A.

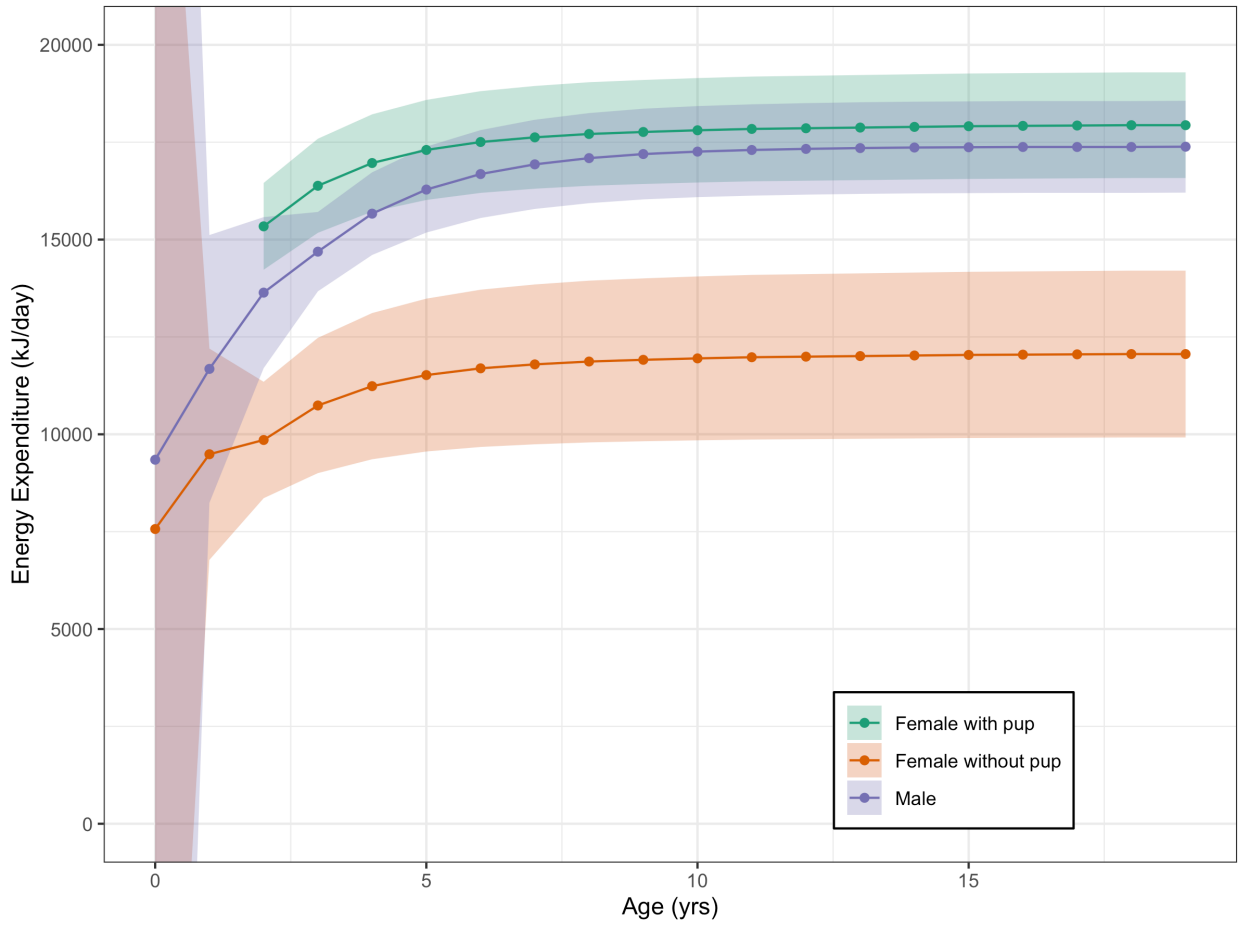


Figure 2.4: Model output describing total energy expenditure in kJ day^{-1} by age. This shows the outputs of the three models (Male, Female without Pup, Female with Pup). The shading around the lines illustrates ± 1 standard deviation from the mean of 10,000 runs of the model with all parameters varied simultaneously, using error taken from source literature (values in Table 2.5).

While the scale of the mass-specific differences between females with and without pups is the same as calculated on absolute TEE, it does allow us to calculate the mass-specific cost of pup rearing. Specifically, the additional cost imposed by reproduction is on average 276 kJ kg^{-1} day^{-1} for mature female otters.

Table 2.6: Mass specific total energy expenditure (TEE) calculations of "model" sea otters at different age classes (means ± sd). All values presented in kJ kg^{-1} day^{-1}. Again, note that females in year classes 0 and 1 do not have pups and only 2-year-old males are considered subadults.

Age Class	Year Class	Female without a pup	Female with a pup	Male
Pup	0	706.62	---	705.97
Juvenile	1	599.37	---	599.85
Subadult	2	---	---	585.80
Adult	2	536.12	834.57	573.14
Adult	3	545.44	831.96	578.27
Adult	4	550.77	831.64	581.56
Adult	5	553.87	831.78	583.70
Adult	6	555.78	831.98	585.04
Adult	7	556.90	832.13	585.91
Adult	8	557.72	832.27	586.48
Adult	9	558.21	832.35	586.82
Adult	10	558.63	832.44	587.04
Adult	11	558.96	832.51	587.20
Adult	12	559.13	832.54	587.31
Adult	13	559.30	832.58	587.39
Adult	14	559.47	832.62	587.43
Adult	15	559.64	832.66	587.47
Adult	16	559.73	832.68	587.46
Adult	17	559.81	832.70	587.46
Adult	18	559.90	832.72	587.50
Adult	19	559.90	832.72	587.50

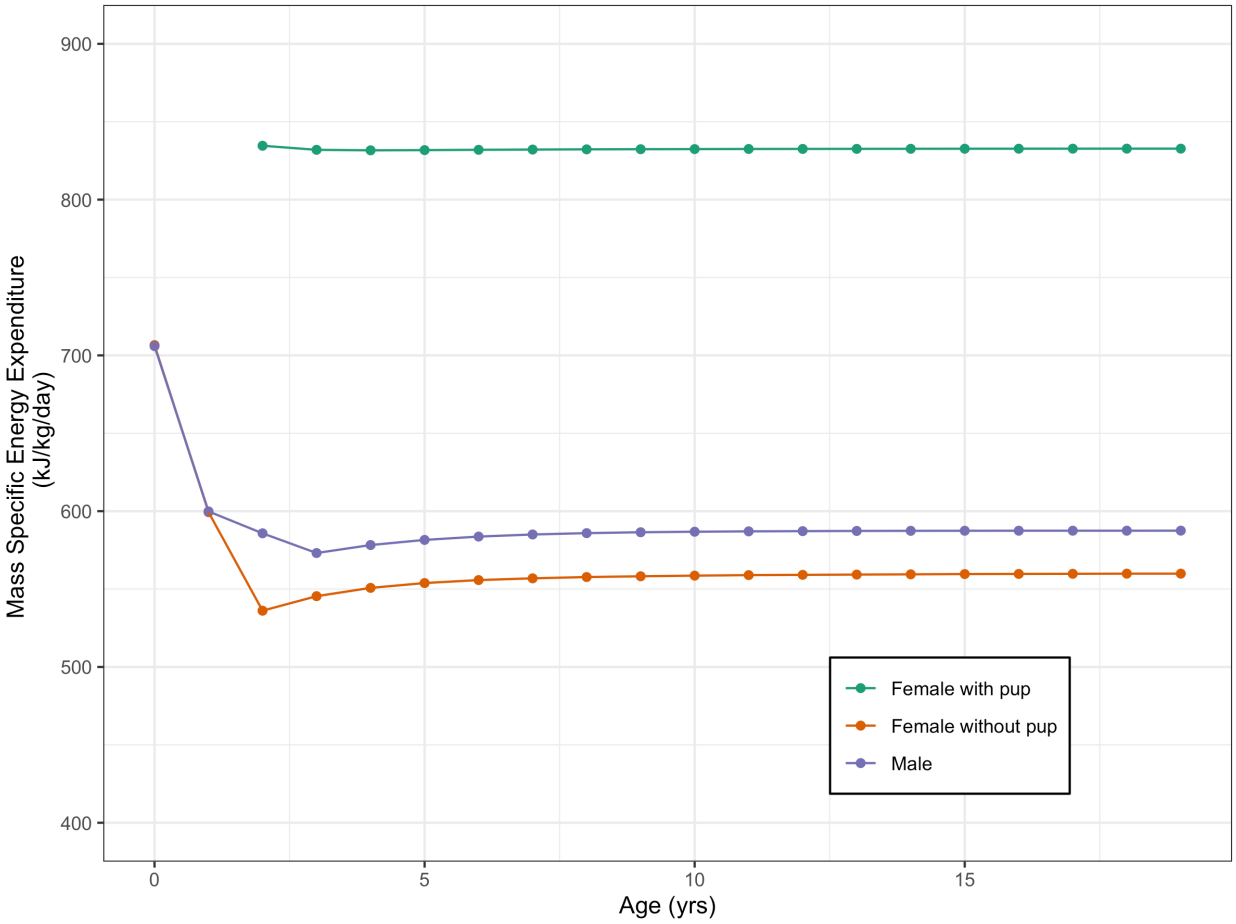
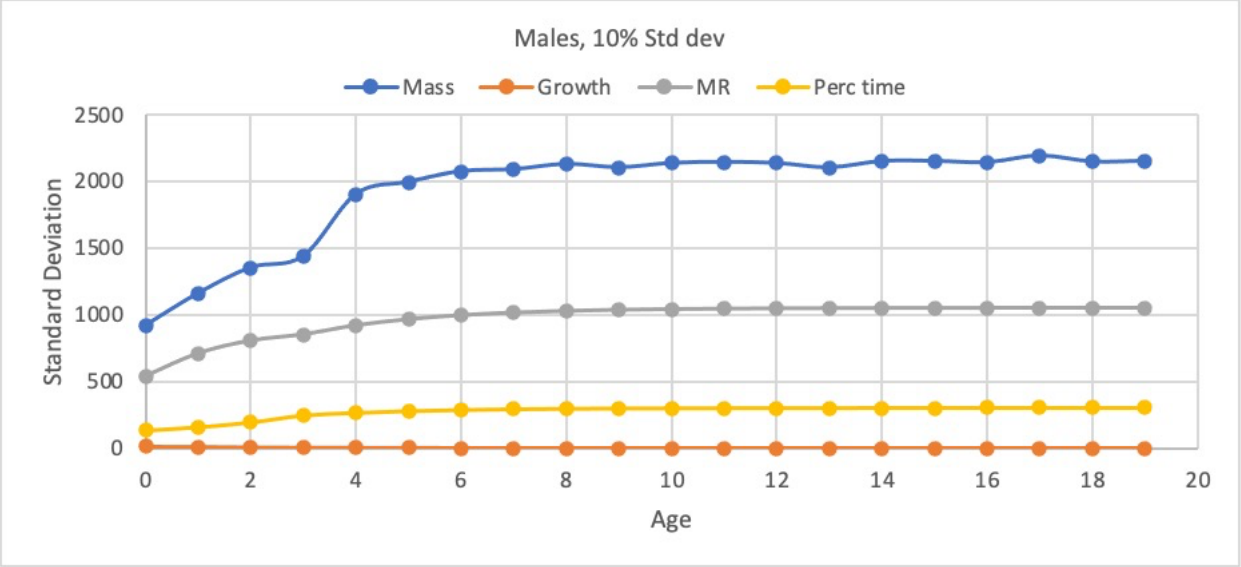


Figure 2.5: Mass-specific TEE estimates of the three models (Male, Female without Pup, Female with Pup) in kJ kg^{-1} d^{-1}.

2.4.4 Sensitivity analysis

The first sensitivity analysis was run to ascertain which model parameter, given the same amount of variation, has the greatest effect on the model outcome (the total energy expenditure (TEE)). By measuring the standard deviation of the randomly sampled TEE outputs and comparing these values between parameters, I found that body mass was the parameter that resulted in the highest amount of variation, and therefore has the greatest effect on the model outcomes across all three models, followed by metabolic rate. The comparison of parameter variation at 10% standard deviation from the mean can be seen in Figure 2.6. Additional figures of 5% and 20% standard deviation can be seen in Appendix B.


Males, 10% Std dev
Mass
Growth
MR
Perc time
Standard Deviation
2500
2000
1500
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0
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2
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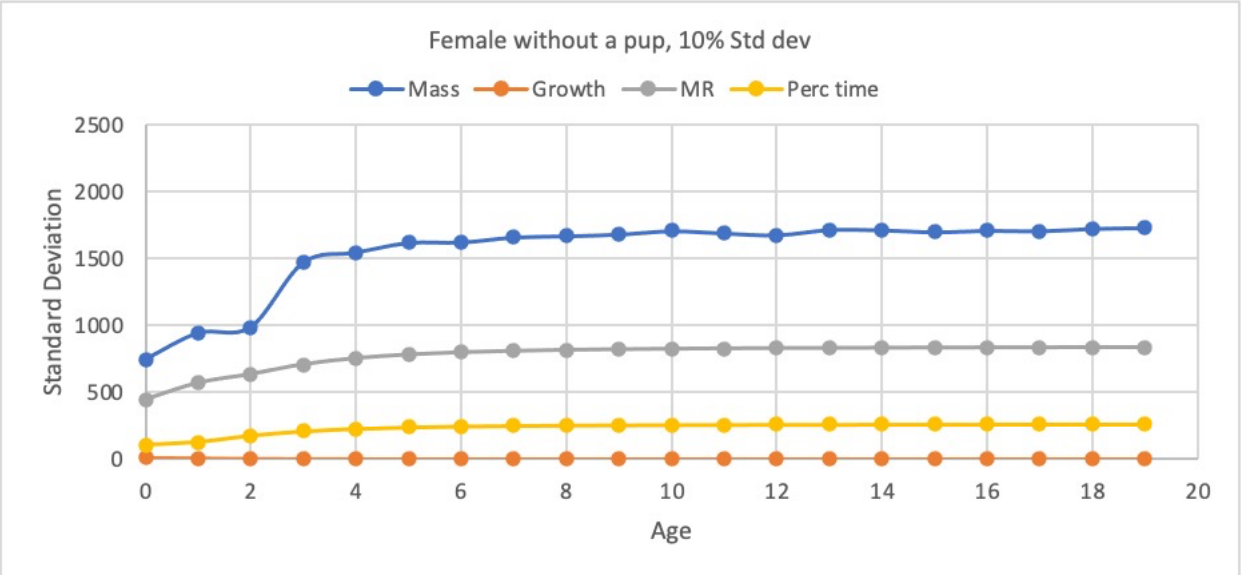
Age


Female without a pup, 10% Std dev
Mass
Growth
MR
Perc time
Standard Deviation
2500
2000
1500
1000
500
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Age

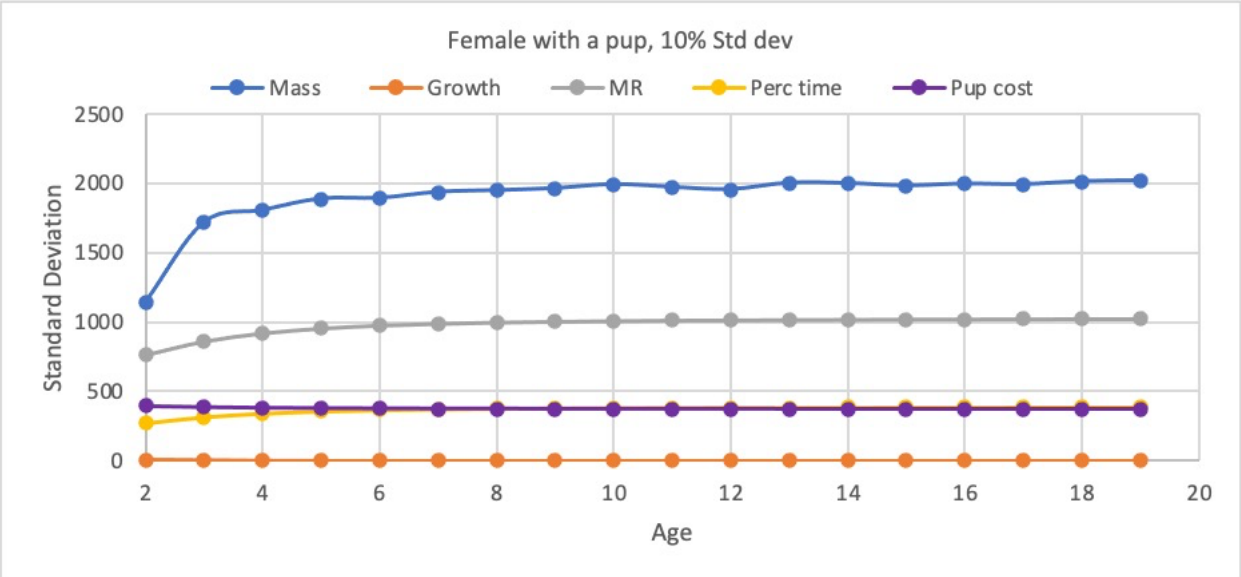


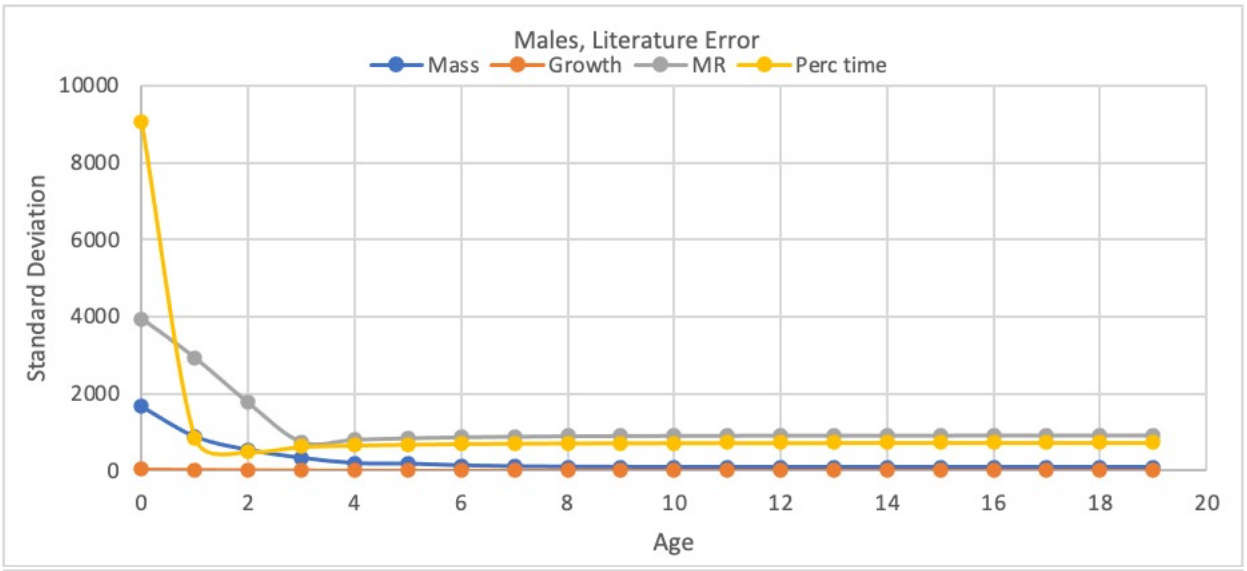
Figure 2.6: Comparisons of the standard deviation from the mean measured by varying each model parameter (mass, growth, metabolic rate, percent of day spent in each behaviour, and cost of caring for a pup) by a set amount for each of the three models (Male, Female without Pup, Female with Pup). In this case, the underlying sampled population had a standard deviation equal to 10% of the mean. These results were obtained from 10,000 runs of each model. All SD values in kJ day^{-1}.

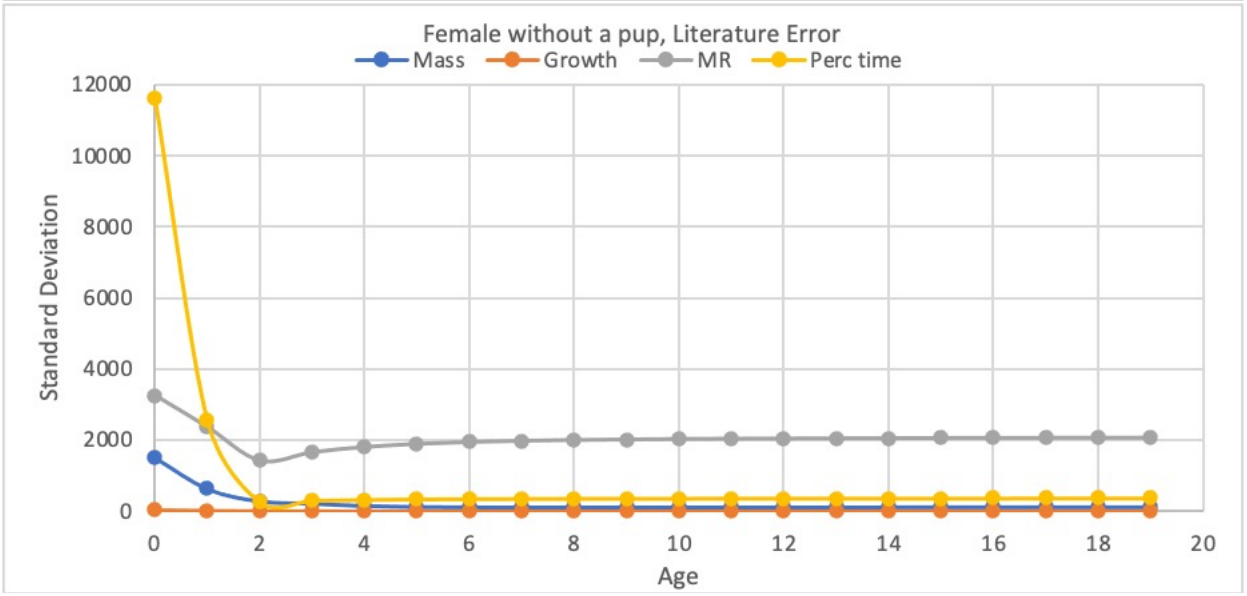
An additional sensitivity analysis using known variation obtained from the literature yielded different results, where the most sensitive parameter varied depending on the age class (Figure 2.7). Comparing the standard deviations resulting from varying each parameter, the parameter with the greatest effect on a pup's energy expenditure was percent time spent in a behaviour (activity budgets) by a massive margin: a standard deviation of 11,600 kJ day^{-1} for females and 9,000 kJ day^{-1} for males compared to standard deviations corresponding to metabolic rates estimated at 3,000 kJ day^{-1} for female pups and 4,000 kJ day^{-1} males. Percent of time spent in a behaviour was also the highest for female juveniles, while variation from metabolic rate was the highest for male juveniles. Conversely, in the subadult and adult age classes across all models, metabolic rate was the most sensitive parameter, having the greatest effect on model outcomes.

2.4.5 Estimated error on model outcomes

When providing estimates of precision around our output estimates, repeatedly running the model with randomized input values for all parameters simultaneously based on distributions

from literature showed Year classes 0, 1, and 2 had the largest error with their associated energy requirements (seen as in the shading on Figure 2.4). These first two Year classes (0 & 1) represent pups and juveniles, while Year class 2 represents subadults in males and adults in females. Pups had especially high standard deviations compared to the other age classes due to the data sources used for pups having high variation as well, especially evident in measures of percent time spent in a behaviour throughout the published activity budgets.





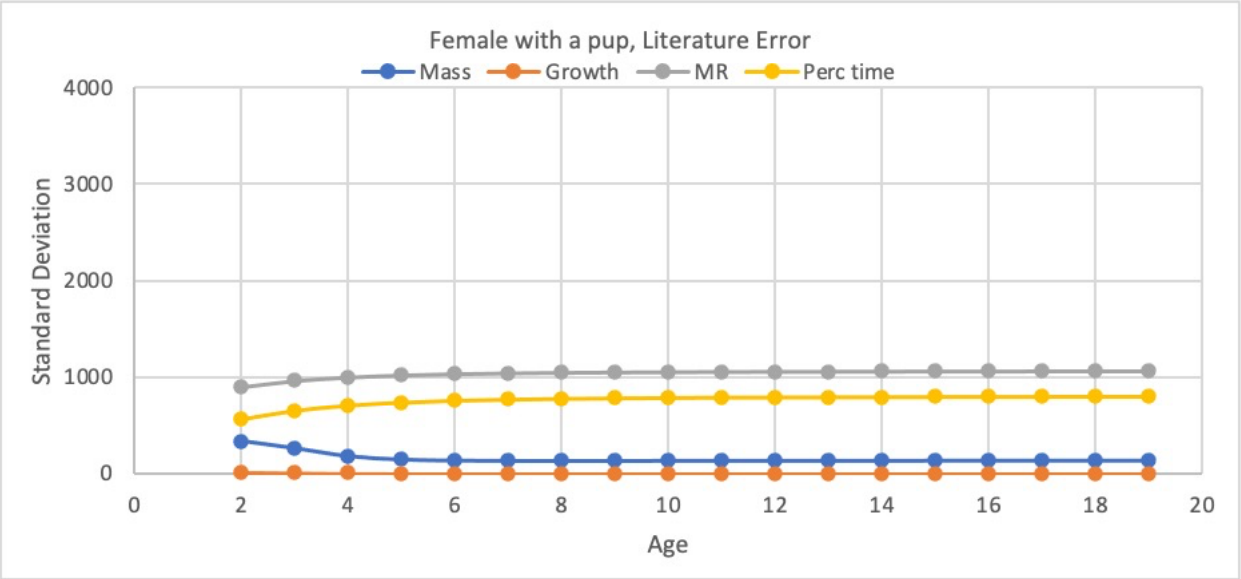


Figure 2.7: Comparisons of the standard deviation measured by varying each model parameter (mass, growth, metabolic rate, percent of day spent in each behaviour, and cost of caring for a pup) by error values taken from the literature for each of the three models (Male, Female without Pup, Female with Pup). These results were measured after 10,000 runs of each model. All sd values in kJ day^{-1}.

2.5 Discussion

This bioenergetic model is a version of an accounting model as described by Pirotta (2022), and was built using an energy balance equation for an individual sea otter to determine the rate of total energy expenditure (TEE). The resultant TEE values vary by age, sex, and reproductive conditions, providing insight into changes in the rate of energy expenditure and food requirements over the lifespan of sea otters.

There were three separate models created: males, females without a pup, and females with a pup. Adult females with a pup had the highest overall energy expenditure, which was 4% higher on average than adult males and 33% higher than adult non-reproductive females. The TEE values calculated by my models were similar to those reported in the literature using other methods, providing confidence in the ability of our model to estimate energy expenditure. For example, for an adult female without a pup, Thometz et al. (2014) estimated TEE of 10,370 kJ day^{-1} (mass = 19.89 kg), where our model estimates 10,740 $\pm$ 1,724 kJ day^{-1} at 19.69 kg mass. Additionally, a study by Yeates et al. (2007) estimated TEE of a 27.7 kg captive male sea otter as 16,090 kJ day^{-1} and for a 28.5 kg wild male otter 15,570 kJ day^{-1}. The average energy

expenditure value from this study was 16,283 $\pm$ 1,104 kJ day^{-1} for an otter with an average mass of 28 kg. My model also was consistent with previous TEE estimates for younger otters. For example, one study estimated juvenile female otter energy expenditure (14.4 kg mass) at 8,560 kJ day^{-1} (Thometz et al., 2014) while my model showed a TEE of 9,488 $\pm$ 2,704 kJ day^{-1} for a juvenile otter at 15.8 kg.

A clear developmental trend was seen in model outputs for non-reproductive females and males: a steep increase in energy expenditure across the pup, juvenile, and subadult (for males only) age classes. TEE values plateau in adult age classes between Year classes 7 and 8 for females with and without a pup, respectively, and Year class 10 for males. The TEE values of male sea otters were consistently higher than for female otters, even within the pup and juvenile age classes (Year classes 0 and 1). When females reach the adult age class at Year 2 (the first year they are able to reproduce), females with a pup have the highest TEE which is substantially greater than males. There are a few biological and behavioural factors that account for these trends seen in energy expenditures.

2.5.1 Contributions to differences in TEE

One important factor that drives the changes in total energy expenditures (TEE) over the sea otter's lifespan is changes in body mass. The steep increase in TEE over the pup, juvenile, and male subadult age classes, Year classes 0-3, are consistent with the observed rates of physical growth (Figure 2.4 & Table 2.5) (Tinker et al., 2019). Similarly, the plateau in TEE values seen beginning at adult Year classes 7, 8, and 10 for all three models are consistent with a plateau in tissue growth as animals mature. The plateau occurs not only due to decreased growth rates, but also because of the model's assumption that sea otters do not increase their foraging efficiency throughout their entire lives (see *Important aspects of model design*).

However, the direct energetic cost of growth – that is the cost of tissue growth – is relatively minor. The largest growth rates are seen in the pup age class between Year 0 and Year 1 with parallel significant increases in TEE in both male and female models. However, the direct costs of growth are only 125 kJ day^{-1} for males and 108 kJ day^{-1} for females, which accounts for a very small proportion of the increase in TEE of 1,920 kJ day^{-1} in the female model

and 2,340 kJ day^{-1} in the male model over the same period. The direct costs of growth become even less significant as animals mature, with costs falling below 10 kJ day^{-1} starting in Year 6 in males and Year 5 in females.

Rather, changes in body mass have a large effect on the TEE values calculated by our model because of the allometric relationship between mass and metabolic rates (Kleiber, 1975; McNab, 2008; S. Noren & Rosen, 2023). Changes in body mass with age and differences in body mass between sexes result in differences in TEE given the assumptions that (i) metabolic rate is scaled to body mass and (ii) that these rates remain constant for the two sexes within different age classes (i.e., pups, juveniles, adults). Hence, as body mass increases, TEE will increase as well, especially in the early year classes, a trend observed in all three models. Further, as male sea otters have larger body masses than females, they are expected to have higher energy expenditures than females, all other factors being equal. This is supported by the model outputs for male and non-reproductive females (within all age and year classes) where males have higher TEE values than females by an average of 29%.

An additional factor that affects the energy expenditure of male versus female otters is behavioural differences exhibited between the sexes. These are particularly impactful when accounting for the amount of time spent engaged in more active, energetically expensive behaviours. As seen in Figures 2.2 and 2.3, the model shows that adult females and males forage for a similar amount of time daily (42% males, 47% non-reproductive females, 49% females with a pup); however, there is a large difference between the amount of the day spent resting versus in non-foraging active behaviours. Females rest about 45% of the day while males only rest 34%. Non-foraging activities (such as swimming and active grooming) account for 24% of the day's behaviours for males, whereas it only accounts for 6% or 9% for females without a pup and with a pup, respectively. This is an important difference as metabolic rates were highest for non-foraging active behaviours for males and females alike (Thometz et al., 2014; Williams, 1989; Yeates et al., 2007). Together, the higher metabolic rates (given greater mass) and higher percent of the day spent partaking in more energetically expensive behaviours, result in the observation that males would have higher energy expenditures than

non-reproductive females. The differences attributed to reproduction within females are discussed later.

The percentages generated in my model are consistent with activity budgets observed in areas that have limited prey resources (Staedler, 2011; Thometz et al., 2014, Thometz, Kendall et al., 2016). This is not surprising seeing as much of the sourced data were from studies of populations in California, often in areas of high otter density. This fact, plus the assumption of a direct trade-off between foraging activity and resting used in the modelling mechanics, means these activity budgets might be a considered a worst-case scenario (further discussed in *Important aspects of model design*).

The fact that not all of the developmental differences in TEE are due to changes in body mass can be seen through changes and differences in mass-specific TEE values (Figure 2.5 & Table 2.6). Mass-specific energy expenditure is greatest for pups, and declines steadily as they mature, a trend typical of most mammals. These patterns primarily reflect the developmental changes in the cost of tissue growth. The same pattern was seen in otters under human care, where the mass-specific gross energy intake (GEI) was highest in the otters in their first year, from birth to 12 months of age (Iskandar et al., 2023). The higher mass-specific TEE of male adult otters compared to females without a pup is due to the aforementioned differences in behaviour, particularly the greater amount of time males spend being active.

2.5.2 The cost of reproduction

The additional cost of caring for a pup is apparent in both absolute and mass-specific TEE for reproductive females. Adult females with pups have the highest rates of energy expenditure, on average 33% greater than non-reproductive females. As stated, because pups and juvenile otters are not able to reproduce, those age classes were not included in the model for females with a pup which begins at Year class 2. The TEE of reproductive females is slightly greater (4% on average) than the much larger male otters at all age classes. This difference is particularly evident in the observation that the mass-specific TEE of reproductive females is 30% greater than males at Year 10.

Comparing the two female models shows that, on average, adult females with a pup expend 33% (~5,800 kJ day^{-1}) more energy than non-reproductive females. There are a few factors that contribute to that difference in energy expenditure. The primary factor leading to differences in energy expenditure between the two female models is the additional cost of caring for a pup. I calculated the average additional cost of caring for a pup incurred by a mother otter as an estimated 3,931 kJ day^{-1}, which accounts for the majority of the 5,800 kJ day^{-1} difference between reproductive and non-reproductive female otters. This value includes the direct costs of lactation, the behavioural costs of grooming the pup, as well as the additional foraging efforts undertaken to feed the pup.

Another factor contributing to the difference between the female models is differences in metabolic rates. Thometz, Kendall et al. (2016) measured the resting metabolic rates (RMR) of a pregnant otter repeatedly throughout the end of gestation, before and after parturition, and throughout lactation until weaning. They also tracked the development of the pup alongside the mother to inform how RMR values coincide with the age and size of the pup. In my model, as well as in the Thometz, Kendall et al. (2016) study, the metabolic rates for resting and non-foraging behaviour were adjusted by the same percent changes to reflect overall metabolic expenditures. Therefore, the adjusted metabolic rates of lactating otters were higher than non-reproductive otter metabolic rates, contributing to the higher TEE estimates (Table 2.3). Surprisingly, one factor that had minimal impact on differences in energy expenditure between the two female models was disparity in behaviour budgets. The average activity budgets for females with and without a pup estimated by the model were very similar. Females with a pup spent only 2% more of their day foraging, with minimal increases in time resting (~1%) and slightly less time (~3%) in non-foraging behaviour. These differences in behaviour would contribute little to the large difference in energy expenditure. It is also important to note that these behavioral budgets are based upon direct observations and only slightly modified by the model itself (See *Cost of different activities*). An additional consideration is that the activity budgets for females with a pup were averaged over the entire period of pup rearing for use in the model, however, there is significant variation in the activity budgets of mother otters throughout the period of pup dependency depending on the developmental phase of the pups.

As previously stated, male sea otters do not participate in pup rearing, therefore their energy expenditure related to reproduction is largely behavioural via competing to find and mate with females (Thometz, Staedler, et al., 2016). Because there is not significant seasonal variation in the reproductive cycle of sea otters, these changes in male behaviour related to mating are accounted for in the activity budgets utilized in the model (Thometz, Staedler, et al., 2016; Yeates et al., 2007).

2.5.3 Implications of reproductive status and associated cost

For female sea otters, reproduction is extremely energetically taxing, especially during the 6 months of pup dependence and lactation (Chinn et al., 2016; Staedler, 2011; Thometz et al., 2014; Thometz, Kendall, et al., 2016; Thometz, Staedler, et al., 2016). Both elevated metabolic rates and the direct costs of caring for a pup contribute to the higher energy expenditures in reproductive female sea otters compared to a non-reproductive female otter. However, it is important to consider that the activity budget used for females with a pup in the model is a weighted average across the whole pup rearing period. On a finer scale, there are substantial differences in behaviour throughout different pup development stages. For example, from birth to when the pup is 45 days old, females spend 72% of the day resting and 22% foraging, compared to 45% resting and 49% foraging when the pup is 136-180 days old and nearing independence (Thometz et al., 2014). These may have short-term implications on energy requirements in wild otters that are not reflected in the model.

In the 3 months prior to parturition, female otters decrease their body temperature and resting metabolic rates (RMR), assumedly to allow them to build fat stores in preparation for lactation and increased energy expenditure while caring for their pup (Chinn et al., 2016; Esslinger et al., 2014; Thometz, Kendall, et al., 2016). Directly after parturition, the amount of time spent foraging temporarily decreases at the same time that lactation begins, leading to an almost immediate energetic deficit for the mother otter (Chinn et al., 2016; Esslinger et al., 2014). This physiological stress often continues throughout pup rearing. One study by Thometz, Kendall, et al. (2016) found that female sea otters' energy requirements can be 85-110% higher during their last 3 months of lactation than when they are non-reproductive. This increase in

energy demand can cause female otters to live under an energy deficit for a prolonged period before their pups are independent. This can result in end-lactation syndrome (ELS) (Chinn et al., 2016; Thometz, Kendall, et al., 2016), where many female otters are not able to recover after weaning a dependent pup, ultimately leading to mortality.

While the bioenergetics of reproduction in female otters are complicated, the outcomes of our model for reproductive females are consistent with the previous research on the metabolic and behavioural costs of caring for an otter pup. These costs were accounted for in multiple aspects in my model. Thometz, Kendall, et al. (2016) divided these costs into "female to self" and "female to pup" (See Figure 2.1). The former includes costs required for the female to support herself while caring for a pup, and is based upon activity-specific metabolic rates and activity budgets. The heat increment of lactation (i.e., the metabolic effect of being in a lactating state) is accounted for in the higher resting metabolic rate of the female otter. As previously described, Thometz, Kendall, et al. (2016) measured RMR in females throughout multiple stages of pup growth and calculated the percent change in RMR in each stage compared to RMR of a non-reproductive female. Based on the calculations in that study, my model applied similar increases to metabolic rates for foraging and non-foraging activity during lactation and pup rearing.

Thometz, Kendall, et al. (2016) also calculated additional energy expenditure attributable to aspects of pup care ("female to pup"). In my model, the parameter "pup cost" represents these additional energetic costs placed on females caring for a pup that are necessary to fulfill the pup's food and energetic needs. These costs are met in a number of ways by the mother, including food in the form of milk and additional foraging for food provided directly to the pup, as well as extra grooming.

It is important to note that this model for a female sea otter with a pup represents the daily TEE only over the 6-month period of lactation and actively caring for a dependent pup, and are not averaged over an entire reproductive cycle of a female sea otter with a pup (gestation, parturition, and post-weaning). An annual estimate of energy expenditure for a female otter can be easily calculated by averaging the TEE of a female during the 3 months of post-pup energy expenditure using the non-reproductive female model and behavioural

budgets, and then adjusting metabolic costs using the methods of Thometz, Kendall, et al. (2016) to add the TEE values for the second half of gestation when females decrease their body temperature and RMR to improve body condition and retain fat reserves for 3 months (Thometz, Kendall, et al., 2016). After averaging the TEE of those 6 months (3 months pre-parturition and 3 months post-weaning and in early stages of pregnancy) with the TEE of a reproductive female sea otter during lactation and caring for a pup (6 months), the average annual energy expenditure for a 5-year-old female sea otter is 13,978.79 kJ day^{-1}.

2.5.4 Important aspects of model design

My model incorporated several key assumptions and mechanisms. Understanding these was important for interpreting the output of the models. One important mechanism was the way in which we adjusted activity budgets. First, we assumed otters foraged just long enough to fulfill non-foraging energetic needs. This allowed us to alter activity budgets to account for changes in non-foraging energy expenditures. Foraging time was based upon the estimated rate that an otter is able to acquire biologically useful energy, which we called the rate of return (ROR). This metric of foraging efficiency was calculated from "model" published activity budgets, and was used to recalculate activity budgets for the three models (males, non-reproductive females, and reproductive females) across all age classes. In other words, my model employed changes in behaviour rather than foraging efficiency to account for changes in TEE.

Another mechanism of the model was that, when recalculating activity budgets for "non-model" ages, we assumed that non-foraging activity (i.e., swimming, grooming, etc.) remained at the same percentage of overall activity throughout the day. This leads to a direct tradeoff between time foraging and time resting instead of an increase in foraging effecting both resting and non-foraging activity times. This assumption can be considered a worst-case scenario for sea otter in terms of energetic expenditure as increases in expensive foraging time negatively impact time in low-cost resting behaviour. The mechanism whereby foraging efficiency stays constant partly reflect biological and physiological limits to how efficient at foraging an otter can be, such as stomach capacity, diving time, handling time, etc. However, it

does not preclude the option for otters to switch prey species or foraging locations to be more successful at foraging, but these scenarios are beyond the designs of this model.

As previously noted, my model calculated required foraging time to adjust behavioural budgets based upon published values for specific "models". As a result, overall adult male otters in my model were estimated to forage for more of the day (42%) and rest less time (34%) than estimates in the literature (foraging = 36%, resting = 40%) (Yeates et al., 2007). Both reproductive and non-reproductive adult female models have similar activity budgets to those in the literature, although with slightly higher levels of foraging and lower levels of resting. Non-reproductive females modelled behavioural budgets estimate 44% of the day resting and 47% foraging, as compared to 52% resting and 40% foraging in literature (Thometz et al., 2014). Otters caring for a pup had different modelled daily budgets of 44% resting, 49% foraging, compared to in the literature (51% resting, 43% foraging) (Thometz et al., 2014).

The activity budgets were strongly affected by the calculated rates of return (ROR), the rate of food energy that needs to be acquired per minute spent foraging, based again upon published "model" animals. The calculated values can also provide insight about the foraging requirements for different sexes and age classes (Table 2.4). The highest ROR value is that of adult males (28 kJ min^{-1}), which is not necessarily surprising given their larger body mass and more time spent in expensive, active behaviours throughout the day as compared to females. Despite their larger size, adult females without a pup had a slightly lower ROR than juveniles (female = 17.24 kJ min^{-1}, juvenile = 17.74 kJ min^{-1}), due to the latter's higher costs of growth and greater level of energetically-expensive, non-foraging activities (30% vs. 9%).

There is a substantial difference between the necessary foraging efficiency of reproductive and non-reproductive females. Reproductive females have an ROR of 25 kJ min^{-1} versus non-reproductive females' ROR of 17 kJ min^{-1}. This means that a female otter caring for a pup must maintain a higher rate of foraging efficiency per minute than one not caring for a pup in order to meet her energetic needs. According to my models, females with a pup only forage for an estimated 2% (~29 minutes) more per day than a female without a pup. This may be due to the fact that a female is limited in her ability to reduce the time spent resting or engaged in non-foraging activities. This may be another factor that contributes to female otters with pups

existing at or near their physiological limit potentially leading to ELS and/or mortality (Chinn et al., 2016). Again, it is worth consideration that the difference in minutes per day spent foraging between reproductive and non-reproductive otters seems small because of the weighted average of the pup rearing stages. There would likely be larger differences when comparing activity budget of a female with a small pup versus with a larger pup. It is also important to note that my model did not account for any changes in foraging efficiency that might occur in tandem with increased energy demands for reproductive females, and this is an avenue for potential future research.

It is also important to note that my model did not specifically account for separate thermoregulatory costs. Unlike most other marine mammals, sea otters do not have a vascularized blubber layer to aid in thermoregulation, and rely on their extremely dense fur to trap air and keep them warm (Costa & Kooyman, 1984; Davis, 2019; Lavigne et al., 1986). Despite their dense fur, it has been suggested that sea otters are in a constant state of heat loss while in water due to their small size and resulting high surface area to volume ratio (Davis, 2019; Yeates et al., 2007). However, sea otters may utilize both the heat generated during foraging activity as well as the heat increment of feeding (HIF; the energy given off by the process of digestion) to reduce the amount of time necessary to generate heat via activity (Costa & Kooyman, 1984). Additionally, as my model was based on metabolic measurements taken under ambient water conditions, I assumed that any additional thermoregulatory costs were already incorporated into these estimates.

Finally, it should be noted that this model is parameterized by data collected on southern sea otters in California, USA, as opposed to northern otters found in Alaska, Washington State, and British Columbia, Canada. Literature focused on Alaskan otters varies in many significant aspects to that published on Californian otters such as behavioural budgets and mass values. Despite the differences, the model could easily be repopulated with data from northern sea otters to ascertain more precise estimates of their energy expenditures.

2.5.5 Ecological implications

The ecological impact of a particular animal on its environment is partly based upon its food requirements. Otters have often been considered to have high food requirements, compared to both their terrestrial and marine mammal counterparts. When compared to other terrestrial mammal species, sea otters have resting metabolic rates at least 2.5 times higher (Costa & Kooyman, 1984; Morrison et al., 1974). However, when compared allometrically to other species of marine mammals, sea otter resting and field metabolic rates are higher than some groups (e.g., phocid seals) but equal to or lower than others (e.g., otariid seals) (S. Noren & Rosen, 2023). Our modelled levels of energy expenditure were similar to other estimates for otters (Thometz et al., 2014; Williams, 1989; Yeates et al., 2007).

In the subsequent chapter, Chapter 3, I used these models to convert the total energy expenditures into estimated food intake requirements by incorporating assumed levels of digestive losses and a diet of average nutritional quality (Costa, 1982; Costa & Kooyman, 1984; Oftedal et al., 2007). Based on a general sea otter diet (Tinker, 2004), the daily food intake of juvenile otters would be the equivalent of 34% of their body mass, decreasing slightly to 33% in adult male otters and 31% in adult non-reproductive female otters. Of course, females with a pup had higher intake levels of 46%. In comparison, both adult males and non-reproductive female otters under human care have a food intake equivalent to 19% of body mass (Iskandar et al., 2023). These levels of food intake calculated in my model and observed in captive otters are much higher than reported for other wild or captive marine mammals (Innes et al., 1987; Perez et al., 1990), partly as they consume high-protein, less energy-rich prey. The effects of differences in specific otter diets on intake are explored more fully in Chapter 3.

2.5.6 Sensitivity analysis and estimating error

Bioenergetic models can provide a point estimate of energy expenditures for a given age and sex class. However, it is important to not only consider the variability inherent in these estimates but also use a sensitivity analysis to understand which model parameter (body mass, tissue growth, metabolic rate, percent of the day spent exhibiting different behaviours, and the cost of caring for a pup) has the greatest effect on the model outcomes. When variation was

held constant at different levels (SD = 5%, 10%, and 20% of parameter mean) the parameter with the greatest effect on model outcome was body mass, followed by metabolic rate. The dominating effect of body mass on energy expenditure estimates from the model is not surprising given that all metabolic rates used were scaled to mass.

This analysis highlights the relative effect of variation in different input parameters given equal levels of uncertainty. However, I also examined the effect of scientific uncertainty on TEE estimates. In the second sensitivity analysis, I used the standard deviation ranges provided in the scientific literature. For the pup age class and for juvenile females, percent time spent in a behaviour was the parameter with the greatest effect, by a margin of thousands of kJ per day. For male juveniles, subadult males, and all adults, metabolic rate was the parameter with the greatest effect on model outcomes. One surprising aspect of the sensitivity analysis results was the low effect of pup cost, especially considering its effect on reproductive female otters when calculating TEE. This could be explained by the fact that much of the energy necessary to care for a pup are accounted for in the metabolic rates and their associated costs of different behaviours. The finding that for adult otters, the uncertainty in our estimates of metabolic rates had the greatest effect on final estimates of TEE suggests that greater knowledge of additional research about metabolic rates will be most beneficial for finetuning of the model results.

Running the model with literature values for all parameters at once generated quantifiable measures of variation ($\pm$ 1 standard deviation) for my TEE point estimates (Figure 2.4). This provides a measure of relative confidence in our model outputs. The largest variation was seen in the first three Year classes: Years 0, 1, and 2, but significantly larger in Year 0, the pup age class. This can potentially be explained by delving further into the data used to populate the model parameters for the pup age classes (Thometz et al., 2014). Some of the values used had standard deviations that are larger than the mean, or values very close to the mean which accounts for large amounts of variation within the model's outputs (See Appendix B).

This variation may also be due to the methods used to homogenize the year classes as described in the methods section (See *Age Class*). Combining parameter values for adults and

juveniles in Year 2 (for males only), may have contributed to the larger standard deviation. Additionally, for Year 1, mass-specific metabolic rates that were used in the juvenile activity budget were calculated from one average value of mass taken from Thometz et al.'s paper (2014), and not from the raw data for masses, and the sex was not specified. This may be the source of high variation for Year 1. In other words, the high levels of variation in some cases were due to grouping natural changes in parameter values within an age class rather than lack of scientific certainty.

2.5.7 Future directions and use of the model

Bioenergetic models are very useful tools for estimating energy or food requirements for a variety of species. This particular model fills a knowledge gap by providing a means to determine energy expenditure of sea otters under varying conditions. There have been decades of extensive research conducted studying many aspects of sea otter energetics, but they have not been combined to provide comprehensive estimates of energy expenditure until now. These models help to increase our understanding of potential energetic limitations placed on sea otters due to their dietary choices, and helps us understand the ultimate implications that this constraint may have on sea otter population dynamics, range expansion, and conservation.

Knowing which parameter has the greatest effect on the model can help direct future research efforts, especially under the assumption that the parameter that effects the energy expenditure estimates will have the same effect on otters' energetics in the wild. While mass was the parameter with the highest variation in the first analysis, at this juncture, researchers are very adept at measuring mass with precision. However, the sensitivity analysis also highlighted the inordinate effect that metabolic data had on model predictions. Unfortunately, the data are too sparse (particularly for reproductive females throughout phases of pup rearing) to determine whether the observed uncertainty is due to small sample sizes or natural variation. Regardless, my analysis highlights that additional research concerning metabolic rates would be beneficial to improving the accuracy of the model and understanding sea otter energy expenditures.

Additionally, the very high energy expenditure estimates of reproductive female otters and the ecological implications of females that do not survive post-weaning their pups is very concerning for southern sea otter populations in California. The model estimates support previous research highlighting the need for robust conservation measures to protect the struggling southern sea otters, their habitats, and their prey bases (Chinn et al., 2016; Thometz et al., 2014; Thometz, Kendall, et al., 2016; Thometz, Staedler, et al., 2016).

This bioenergetic model can be used to support conservation efforts and ascertain information about how energy balance may be affected by different dietary preferences or availability. In Chapter 3, I translate energy expenditure into food intake and look closer and how much food is required to meet energy needs under different diet scenarios. Using the model in this way is incredibly useful in understanding any constraints on sea otter populations that may be caused by prey availability, especially for populations that exhibit dietary specializations. Additionally, in the context of efforts to repopulate the Oregon Coast with sea otters, this model can estimate energy expenditures of individuals or populations and can subsequently convert that energy to the amount of prey items needed given local conditions. This information can be used in concert with habitat suitability studies to determine areas that may be suitable for recolonization.

Chapter 3: Investigating the Effects of Diet and Prey Availability on Energy Expenditure in Sea Otters

3.1 Summary

This chapter investigates the consequences of diet specializations and prey availability in sea otters across age, sex, and reproductive status. Using the energy expenditure outputs of the bioenergetic models developed in Chapter 2, I compared the ingested food mass, total biomass removed from the ecosystem, and the total biomass ingested between five diet scenarios. Overall, the results showed that sea otters with preferences for diets that consist predominantly of *Cancer* species of crab and abalone have lower ingested food masses than otters that prefer lower energy dense prey like urchins. Additionally, between sex, age, and reproductive status, females with a pup, which have the highest energy demands, must consume near between 43% and 50% of their body mass daily depending on their diet. Further, I explored the energetic effects of decreased foraging efficiency due to changes in food availability. These results showed that when prey is limited— such as in otter populations with high densities— decreases in foraging efficiency cause a rise in both foraging time and total energy requirements. The findings in this chapter enhance our understanding of different diets and prey availability on sea otters and may provide further insight into habitat suitability that will support the design of conservation strategies for successful management.

3.2 Introduction

Sea otters occupy nearshore, rocky coastal ecosystems that are home to many species that can serve as potential prey items for their consumption. There have been a multitude of studies investigating sea otter foraging behaviour and food preferences (Bodkin et al., 2004; Esslinger et al., 2014; Fujii et al., 2017; Kvitek & Staedler, 1993; Laidre & Jameson, 2006; Newsome et al., 2009; Oftedal et al., 2007; Tinker, 2004; Tinker et al., 2007, 2008). Many of these are observational studies, where researchers watch diving bouts and record what prey species the otters return with to the surface. In general, sea otters are consumers of a wide variety of

species including bivalves, crabs, echinoderms, worms, snails, abalone, and more (Oftedal et al., 2007; Tinker, 2004).

Not all otters consume the same prey items. On a population level, diet can be affected by the prey that is available due to environmental factors such as substrate types and local oceanography. For example, sea otters can be sustained long term by clam species they dig up in muddy and soft sediment habitats that are common in southern Alaska (Kvitek & Staedler, 1993; Oftedal et al., 2007), whereas they more commonly consume urchin, various crab species, and snails in California's more rocky coasts (Oftedal et al., 2007).

However, prey availability — and its effect on diet — can also be affected by the otters themselves due to factors such as population density, how long a population has been established in a habitat, and how close it is to carrying capacity (Tinker, Gill, et al., 2019). In areas experiencing high population density and potentially nearing their carrying capacity, individual sea otters can have "preferences" for specific prey species (Estes et al., 2003; Lyon et al., 2024), and have been observed consuming diets of 50% or more of just one species (Fujii et al., 2017; Newsome et al., 2009; Tinker et al., 2008). Otters in population dense areas have also been observed switching from one targeted species to another as the preferred prey base is exhausted (Fujii et al., 2017; Tinker, 2004; Tinker et al., 2008; Tinker, Gill, et al., 2019).

Not all species are created equal when it comes to their nutritional value, however. When sea otters are forced to switch their diet to prey items with lower energy density, they may have to spend more time foraging to meet their energetic needs and/or suffer from energetic limitations. Decreases in foraging efficiency— the amount of energy ingested per time (minutes) spent foraging— can also result from decreases in effective prey density (either from decreases in number of prey items or increased competition to acquire them). For example, in southeast Alaska, northern sea otters in recently colonized populations had higher food energy intake rates than at more established population sites where prey was limited (LaRoche et al., 2023; Tinker, Gill, et al., 2019).

All of these changes may result in "sub-optimal" diets that can have critical energetic consequences, both at the individual and population level. For example, in southeast Alaska, female northern sea otters with pups consumed the highest diversity of species, but had the

lowest energy intake rate compared to males and females without pups (LaRoche et al., 2023). In southern sea otters, females nearing the end of pup rearing develop end-lactation syndrome (ELS) due to prolonged periods spent in an energy deficit, often leading to emaciation, higher risk of co-morbidities, and mortality (Chinn et al., 2016). ELS was more likely to contribute to or to be the cause of death for female otters from areas with high population density (therefore low energy intake rates) (Chinn et al., 2016).

The effect of prey availability at the population level can also be seen in southern sea otters at the fringes of their ranges. In one study from central California, a well-established population on the edge of sea otters' range was assumed to be resource abundant because of its small size. However, new research shows that in actuality, the long-term occupation of this site has diminished the overall prey availability, thereby limiting the potential for the recovery and expansion of this population (Lyon et al., 2024). This habitat's limited prey abundance and long-term occupation by otters is causing "range stagnation" and hindering the population's northward expansion to new areas (Lyon et al., 2024).

I investigated the energetic implications of two specific types of changes in sea otter prey. First, I used the bioenergetics models created in Chapter 2 to examine the energetic implication of changes in diet composition. Specifically, I compared the average diet energy density, required ingested food mass, and total biomass removed from the environment under five dietary scenarios (4 species specialists and 1 general sea otter diet). A second analysis explored the effects of changes in prey availability. I examined how changes in an otter's foraging efficiency affected the total amount of foraging time needed to fulfill their energetic requirements and, consequently, total energy expenditure. Together, these analyses can further our understanding of the energetic consequences of prey specialization in densely populated areas, and can help to estimate the energetic costs of changes in foraging efficiency and how they may vary between age, sex, and reproductive status.

3.3 Methodology

As noted in the previous chapter, the bioenergetic model I constructed assumes that total energy expenditure (TEE) is equivalent to net energy (NE) intake requirements from food (i.e.,

the individual is assumed to be in energetic homeostasis with no compensatory energetic changes). The difference between net energy intake and gross energy intake (GEI; food energy intake) is the energetic loss attributable to digestion and assimilation. In this first analysis, estimates of total energy expenditure derived from Chapter 2 model outputs (Figure 2.4) were utilized to calculate food intake requirements based upon the gross energy requirements as they relate to prey species ingested. This allowed me to calculate both the ingested and the captured food biomass (the mass of prey removed from the ecosystem) for each age and sex class of otter under five different dietary conditions.

3.3.1 Diet scenario selection

Using previously published data, I selected five sea otter diet scenarios observed in wild otters to compare with each other: four specialist diets and one general diet (Table 3.1). These included:

- Diet 1 for otters that specialize in large, energy dense species like *Cancer* species of crabs and abalone (*Haliotis* spp.) (Tinker et al. 2007).
- Diet 2 is for otters that prefer marine snails, especially turban snails (*Tegula* spp.) (Tinker et al. 2007).
- Diet 3 represents a preference for kelp crabs (*Pugettia producta*) and small to intermediate-sized bivalves and molluscs (Tinker et al. 2007).
- Diet 4 reflects a diet preference for sea urchins (*Strongylocentrotus* spp.) and was based upon a study where over 60% of the observed prey biomass consumed was urchin species (Fujii et al., 2017).
- Diet 5 represents a general sea otter diet as observed from past studies (Tinker, 2004).

All published diets on which my analysis was based originally included a proportion of the diet listed as "other", which always represented less than 15%. For my study, I recalculated the diet scenarios without the "other" category and adjusted the proportion of each species accordingly. This meant there were seven common species represented throughout the different diet scenarios, detailed in Table 3.2.

Table 3.1: Proportional breakdown of various specialist diets observed *in situ*. Adapted from data in Tinker et al. (2007) (Diets 1-3), Fujii et al. (2017) (Diet 4), and Tinker (2004) (Diet 5). The proportion of diet is based on relative number of food items observed to be ingested by otters. This was converted into the proportional ingested biomass, which is the mass of each prey item per gram of total prey ingested by the otter. The contribution to total energy density represents the energy contributed by each prey item to the total energy intake per gram of ingested prey mass, which is also used to calculate the average total energy density of the diet. The captured biomass represents the mass of the prey items removed from the ecosystem (both edible and inedible portion) to provide 1 kJ GEI in the specific diet.

Diet 1: *Cancer* Crab

Species	Proportion of diet	Proportion ingested biomass	Contribution to total energy density (kJ g^{-1})	Captured biomass (g kJ^{-1})
Abalone	0.06	0.05	0.23	0.09
Cancer crab	0.64	0.88	2.77	1.19
Kelp crab	0.19	0.06	0.18	0.06
Urchin	0.04	0.00	0.01	0.01
Clam	0.02	0.00	0.00	0.00
Mussel	0.02	0.00	0.00	0.00
Turban snail	0.03	0.00	0.00	0.00

Diet 2: Marine Snails

Species	Proportion of diet	Proportion ingested biomass	Contribution to total energy density (kJ g^{-1})	Captured biomass (g kJ^{-1})
Abalone	0.00	0.00	0.00	0.00
Cancer crab	0.14	0.72	2.26	0.97
Kelp crab	0.22	0.26	0.79	0.28
Urchin	0.00	0.00	0.00	0.00
Clam	0.03	0.01	0.02	0.02
Mussel	0.00	0.00	0.00	0.00
Turban snail	0.61	0.02	0.06	0.05

Diet 3: Kelp Crab and Bivalves

Species	Proportion of diet	Proportion ingested biomass	Contribution to total energy density (kJ g^{-1})	Captured biomass (g kJ^{-1})
Abalone	0.00	0.00	0.00	0.00
Cancer crab	0.34	0.79	2.48	1.06
Kelp crab	0.34	0.18	0.55	0.19
Urchin	0.04	0.01	0.01	0.02
Clam	0.17	0.02	0.03	0.04
Mussel	0.11	0.01	0.03	0.04
Turban snail	0.00	0.00	0.00	0.00

Diet 4: Urchin

Species	Proportion of diet	Proportion ingested biomass	Contribution to total energy density (kJ g^{-1})	Captured biomass (g kJ^{-1})
Abalone	0.00	0.00	0.00	0.00
Cancer crab	0.12	0.61	1.92	0.82
Kelp crab	0.13	0.15	0.46	0.16
Urchin	0.71	0.24	0.39	0.65
Clam	0.00	0.00	0.00	0.00
Mussel	0.01	0.00	0.01	0.01
Turban snail	0.03	0.00	0.00	0.00

Diet 5: General Diet

Species	Proportion of diet	Proportion ingested biomass	Contribution to total energy density (kJ g^{-1})	Captured biomass (g kJ^{-1})
Abalone	0.02	0.08	0.34	0.14
Cancer crab	0.11	0.62	1.94	0.83
Kelp crab	0.10	0.13	0.40	0.14
Urchin	0.20	0.07	0.12	0.20
Clam	0.14	0.03	0.06	0.07
Mussel	0.22	0.06	0.14	0.18
Turban snail	0.21	0.01	0.02	0.02

It is important to note that the reported "proportion of diet" in the published diets was calculated from the relative number of individual prey items observed to be eaten by the otters, and not the biomass. Therefore, I first calculated the proportional ingested biomass for each prey item in each diet. This was defined as the diet-specific mass (wet weight) of each prey type per gram of total prey mass ingested (g g^{-1}) (Table 3.1). This was calculated from the proportion of each prey (by number) in the diet and the average total mass of the edible portions of each species (e.g., a clam without its shell) within that diet (g), using values from Oftedal et al. (2007) (Table 3.2). Nutritional information from Oftedal et al. (2007) was also used to convert the proportional ingested biomass into the energetic contribution (in kJ) of each prey item to GEI per gram of total ingested biomass (kJ g^{-1}), as well as the average energy density of each diet (the sum of the contribution of each individual prey type) (kJ g^{-1}). I also calculated the biomass removed from the environment, or captured biomass (both per prey item and in total per diet), per GEI ingested in grams per kilojoule (g kJ^{-1}), by, again, incorporating data on the proportion of each prey item that was edible (Oftedal et al., 2007).

These calculations can ultimately be used to calculate not only the biomass ingested or removed from the ecosystem, but the corresponding number of items of each prey species removed for each age/sex class as well.

Table 3.2: Most common prey species represented in sea otter diets. Edible portion represents the proportion of the prey that is consumed by sea otters. For example, 61% of abalone is edible, and the remaining 39% is the shell, which otters will not eat. Data from Oftedal et al. (2007) and presented as mean ± standard error of the mean.

Species	Edible portion (1 =100%)	Ave mass of edible portion (g)	Energy density (kJ g^{-1})
Abalone	0.61 ± 0.01	142.38 ± 20.96	4.17 ± 0.17
Cancer crab	0.74 ± 0.01	224.45 ± 20.96	3.15 ± 0.21
Kelp crab	0.94 ± 0.01	51.30 ± 4.71	3.05 ± 0.14
Urchin	0.36 ± 0.03	14.43 ± 3.17	1.64 ± 0.15
Clam	0.43 ± 0.02	8.63 ± 1.83	2.22 ± 0.11
Mussel	0.36 ± 0.01	11.62 ± 1.99	2.29 ± 0.17
Turban snail	0.33 ± 0.03	1.12 ± 0.06	3.80 ± 0.26

3.3.2 Converting TEE to GFI

After running the model detailed in Chapter 2, I used the resulting total energy expenditure (TEE) estimates to calculate gross energy intake (GEI). I also used the GEI values to calculate food mass intake (kg) required to satisfy the TEE estimates. First, to convert the TEE to the GEI, I incorporated estimates of digestive losses from previously published studies of sea otters. I assumed ~40% energy losses within the model otters based on publications addressing the heat increment of feeding (HIF) (~10%) (Costa & Kooyman, 1984) and digestive losses via urine (~10%) and feces (~18% lost, i.e., 82% assimilation efficiency) (Costa, 1982). Using this overall estimate, I converted TEE values into estimate gross energy intake requirements as:

(12)
$$GEI = \frac{TEE}{0.60}$$

I then used the resulting estimates of GEI to calculate the gross food intake (GFI) and mass of individual food items required to satisfy the TEE estimates at each age class. The energy density of the individual prey items and overall average diet density were used to calculate the GFI from GEI. This provided an estimate of how many grams of food (total intake) were

required for each diet scenario at each age and year class for each sex and at different reproductive statuses. The GFI and the proportional ingested mass were used to calculate the amount of each prey type consumed to meet GEI. The captured biomass per GEI ingested was used to calculate the total and prey-specific biomass removed from the environment for each diet scenario. Finally, I used the total biomass removed for each species consumed to calculate the number of prey items removed for each diet. This also allowed me to calculate the ecological ratio, the proportion of total captured biomass to ingested biomass of prey within each diet scenario.

3.3.3 Effects of foraging efficiency on TEE and foraging time

Foraging efficiency — defined in terms of the amount of energy ingested per time spent foraging — can vary due to a number of factors, including difference in prey type and changes in relative resource abundance. I investigated the consequences of how changes in foraging efficiency affected total energy expenditure (TEE) via changes in required foraging time to meet energetic demands. Foraging efficiency in the model was operationalized as the gross rate of return (ROR_G), the rate of food energy ingested per unit foraging time. In the basic model (see Chapter 2: *Adjusting foraging time*), ROR_G was calculated for each sex and age class based on field observations of activity budgets, but remained constant within that class (i.e., all pups, all juveniles, and all adults had the same ROR_G, although adult values differed by sex and reproductive class). ROR_G is ultimately used to calculate the net rate of return (ROR_N), which is the net energy profit gained through foraging in order to fulfill all non-foraging energy requirements.

To simulate changes in foraging efficiency, I decreased the ROR_G by varying amounts — 5%, 10% and 20% — in order to represent conditions where 5, 10 and 20% less food was available. I then recalculated the ROR_N to determine the foraging time required under these conditions, and then re-ran each model to recalculate the TEE to account for increased foraging costs associated with these decreased foraging efficiencies.

3.4 Results

3.4.1 Diet energy density

Of the five diet scenarios tested, Diet 1 (*Cancer* crabs) had the highest energy density (3.19 kJ g^{-1}; Table 3.3), meaning that, with all other things being equal, otters would need to ingest the least amount of prey biomass to meet their TEE requirements. This was closely followed by Diet 2, with only a slightly lower energy density (3.13 kJ g^{-1}). Although this diet is dominated by high energy snails by number, the larger *Cancer* crabs again make the largest contribution to the overall energy density of the diet. Diet 4 had the lowest energy density (2.78 kJ g^{-1}), and was dominated in numbers by relatively low energy density urchins, although the small proportion of crabs actually made the largest energetic contribution.

Table 3.3: Gross energy density, ingested biomass, captured biomass, and ecological ratio between diet scenarios. Gross energy density is based on the relative proportion (by number) of each prey item ingested, the average edible mass for each item, and its energy density. Ecological ratio is the proportion of total captured biomass to ingested biomass of prey within each diet scenario.

Diet Scenario	Average gross energy density (kJ g^{-1})	Ecological Ratio (Captured: Ingested)	Captured mass per 100 kJ intake (g)	Ingested mass per 100 kJ intake (g)
Diet 1 *Cancer* crab & Abalone	3.19	1.36: 1	42.6	31.3
Diet 2 Marine snails	3.13	1.31: 1	41.9	32.0
Diet 3 Kelp crab & Bivalves	3.10	1.34: 1	43.3	32.3
Diet 4 Urchin	2.78	1.65: 1	59.3	36.0
Diet 5 General diet	3.04	1.57: 1	51.6	32.9

3.4.2 Gross food intake

The required IFM (ingested food mass) differed substantially between diets. Given the energy density of the diets, sea otters that have preferences for sea urchins (Diet 4) have the highest predicted IFM compared to the other specialist diets as well as compared to the general diet (Diet 5) across all sexes, ages, and reproductive statuses (Figure 3.1; Table 3.4). Reproductive

females have the highest estimated TEE and therefore the highest daily IFM for any given diet scenario. On Diet 4, where sea urchins represent 71% of ingested items, females caring for a pup consume an estimated 10,500 g per day compared to males (10,200 g per day) and non-reproductive females (7,000 g per day) when consuming this diet.

Table 3.4: The average ingested food mass that must be consumed daily in order to satisfy the average total energy expenditure of adult sea otters. Values are averaged across year classes 2-19 for females and 3-19 for males, and differentiated by sex and reproductive status. Data for each age, sex, and reproductive class available in Appendix C.

Diet Scenario	Females with a pup Ingested food mass (g)	Females without a pup Ingested food mass (g)	Males Ingested food mass (g)
Diet 1 *Cancer* crab & Abalone	9,150	6,120	8,844
Diet 2 Marine snails	9,338	6,245	9,026
Diet 3 Kelp crab & Bivalves	9,430	6,307	9,115
Diet 4 Urchin	10,515	7,032	10,164
Diet 5 General diet	9,620	6,434	9,298

The diet scenario with the highest energy density and therefore the lowest required IFM was Diet 1, which represents a sea otter specialist that prefers large, energy-dense prey like *Cancer* crab species and abalone. For example, the required IFM of otters on Diet 1 (*Cancer* crabs and abalone) is 13% lower compared to those on Diet 4 (Urchin diet) to satisfy the same energy expenditure. For 10-year-old otters, this translates into IFM of 9,300 g on Diet 1 for females caring for a pup compared to 10,700 g on Diet 4. Similar differences in IFM between Diet 1 and Diet 4 are predicted for 10-yr old females without a pup (6,200 g vs 7,200 g) and for 10-yr old males on Diet 1 versus Diet 4 (9,000 g vs 10,400 g) (Figure 3.1).

Daily food intake can also be expressed as a percentage of body mass. Based on my model TEE outputs, on a general diet (Diet 5), sea otters must consume between 29% to 46% of their body mass depending on sex, age, and reproductive status (Table 3.5). Averaged across all diet scenarios, females caring for a pup must consume the highest percentage of their body mass, at 46%. Juveniles in Year 1 consume a higher percentage of their body mass (34%) than

both adult females without pups (31%) and adult males (33%). As noted in Chapter 2, when otters are considered juveniles in Year 1, they have higher mass-specific total energy expenditures than in their first year in the adult year classes (Year 2 or 3 for females and males, respectively), partly explained by the fact they also exhibit the highest rate of tissue growth during this time.

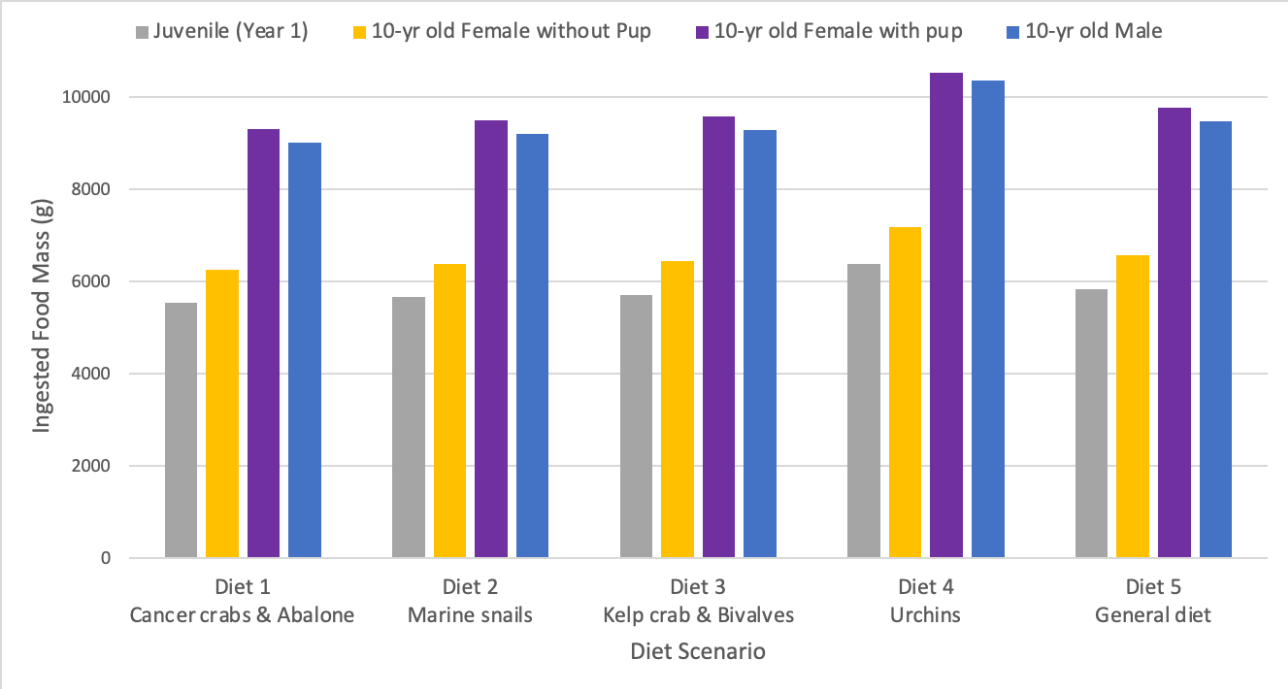


Figure 3.1: Comparison of ingested food mass (IFM) of 4 different modelled otters: a 10-yr old male, 10-yr old female with a pup, 10-yr old female without a pup and a juvenile otter ~1 year old.

While the average IFM of females with pups is not significantly higher than males, they must consume a much larger percentage of their body mass per day than males due to females having a smaller mass. When averaged across all of the diets in this study, reproductive females must consume food mass equal to approximately 46% of their body mass daily. In comparison, non-reproductive females need to eat the equivalent of 31% of their body mass daily, males must consume 32%, and juveniles 33%.

Table 3.5: Required ingested food mass per diet expressed as percentage of body mass. The average percent of body mass that must be consumed daily based on ingested food mass (g) estimates in order to satisfy the average total energy expenditure of juvenile sea otters (both sexes) and adults averaged across all adult year classes (2-19 for females and 3-19 for males) divided by sex and reproductive status. Data for each age, sex, and reproductive class available in Appendix C.

Diet Scenario	Juveniles (Year 1) Average % body mass	Females with a pup Average % body mass	Females without a pup Average % body mass	Males Average % body mass
Diet 1 *Cancer* crab & Abalone	31.3	43.5	29.1	30.6
Diet 2 Marine snails	32.0	44.4	29.6	31.2
Diet 3 Kelp crab & Bivalves	32.3	44.8	30.0	31.5
Diet 4 Urchin	36.0	49.9	33.4	35.1
Diet 5 General diet	32.9	45.7	30.5	32.1

As with absolute intake, these estimates of relative ingested food mass will also differ by diet due to differences in energy density. Hence, ingested food mass as a proportion of body mass is lowest for Diet 1 (*Cancer* crabs and abalone) and highest for Diet 4 (sea urchins). In the latter case, reproductive females (averaged across all adult ages) must consume the equivalent of half their body mass (50%) on a daily basis while caring for a pup. Non-reproductive females consume an average of 33% of their body mass and males 35% on Diet 4 (Table 3.5).

3.4.3 Captured food mass

As expected, based on the aforementioned estimates of IFM requirements, reproductive females will remove the most biomass from their environments on a given diet. In comparison, males are estimated to remove only 3% less per day than reproductive females, compared to non-reproductive females who remove an estimated 33% less per day. However, the exact biomass removed from the environment under each diet scenario is dependent upon both the energy density of the ingested components of the prey items as well as the proportion of the entire prey item that is edible (Table 3.6).

Similar to the trends seen in IFM requirements, otters on Diet 4 (sea urchin specialists) show the highest average captured prey mass removed from the environment (Figure 3.2) for any given age or sex class, while otters on Diet 2 (marine snails) had the lowest average biomass removed from the environment for any model. Our model predicts that adult females

with a pup on Diet 4 will remove 17,300 g of prey per day. This includes ~12,300 g of urchins, which represents 171 individuals consumed daily.

Table 3.6: The average captured prey mass or total biomass that is removed from the environment by an adult sea otter to satisfy daily energy expenditures across all adult age classes. Data for each age, sex, and reproductive class available in Appendix C.

Diet Scenario	**Females without a pup** Average captured biomass (g)	**Females with a pup** Average captured biomass (g)	**Males** Average captured biomass (g)
Diet 1 *Cancer* crab & Abalone	8,316	12,435	12,019
Diet 2 Marine snails	8,184	12,237	11,828
Diet 3 Kelp crab & Bivalves	8,461	12,651	12,228
Diet 4 Urchin	11,592	17,333	16,754
Diet 5 General diet	10,081	15,073	14,569

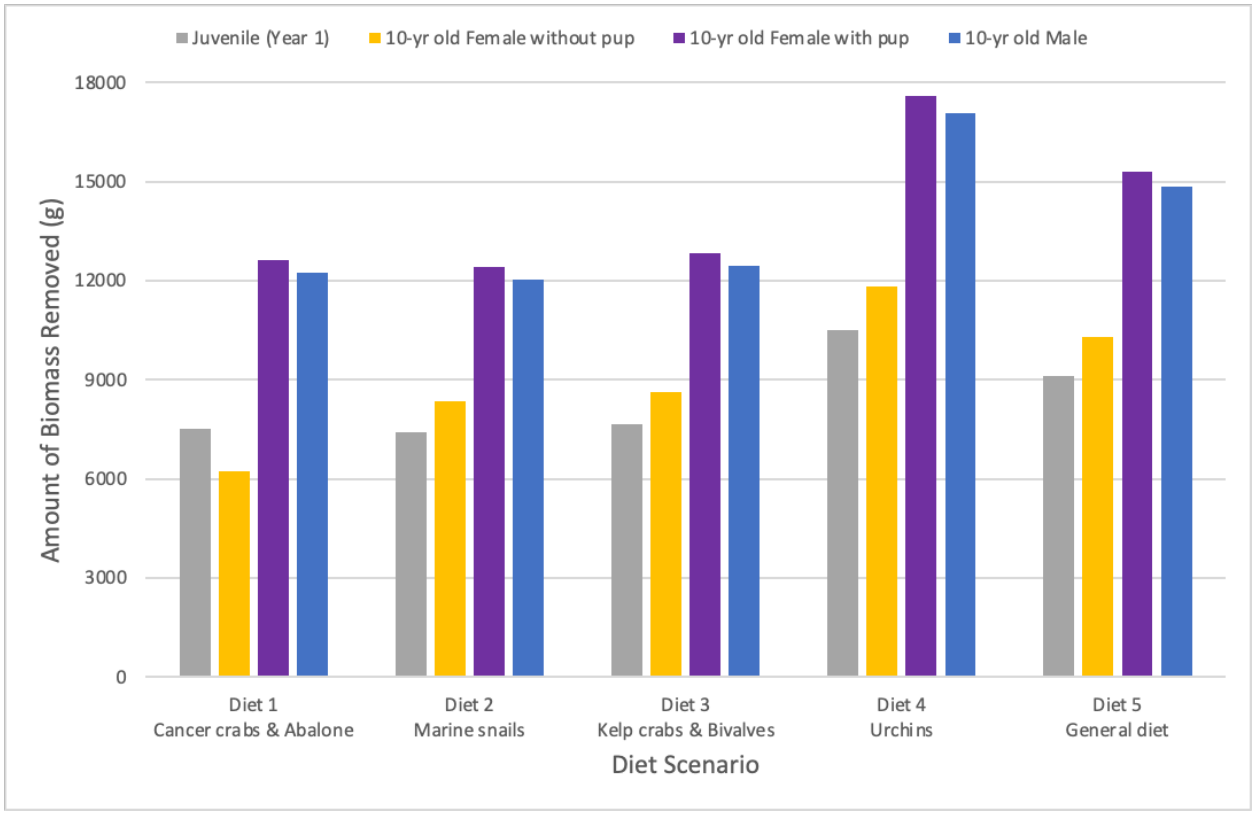
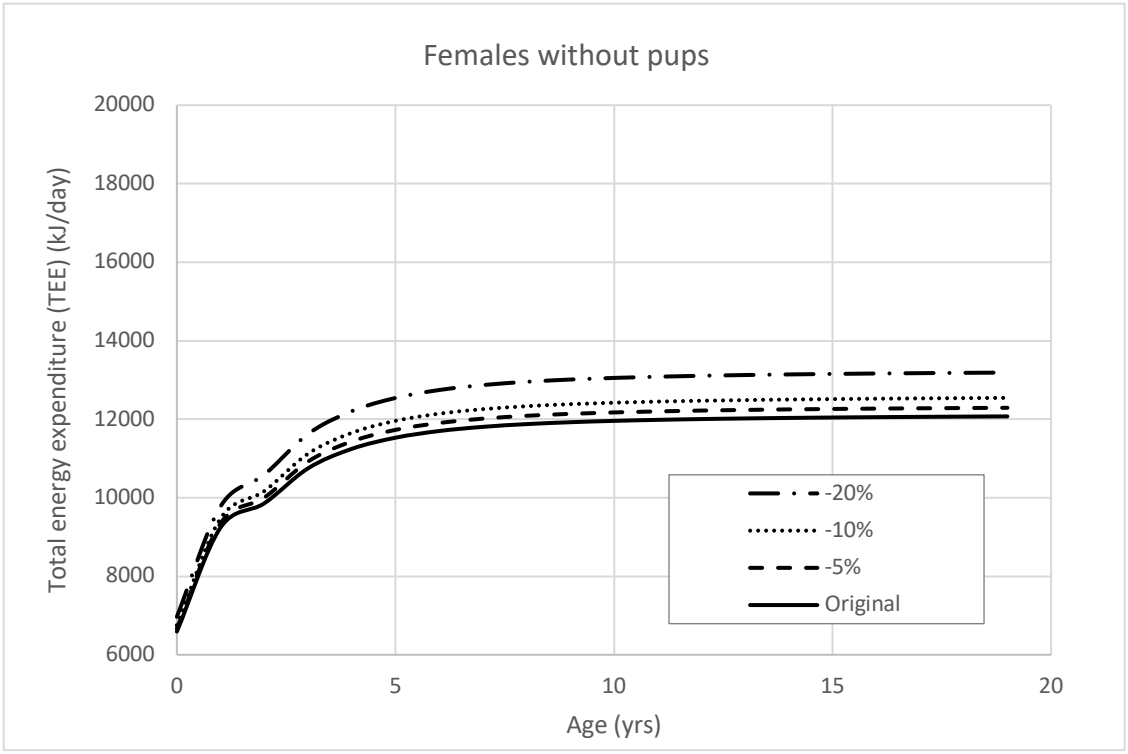


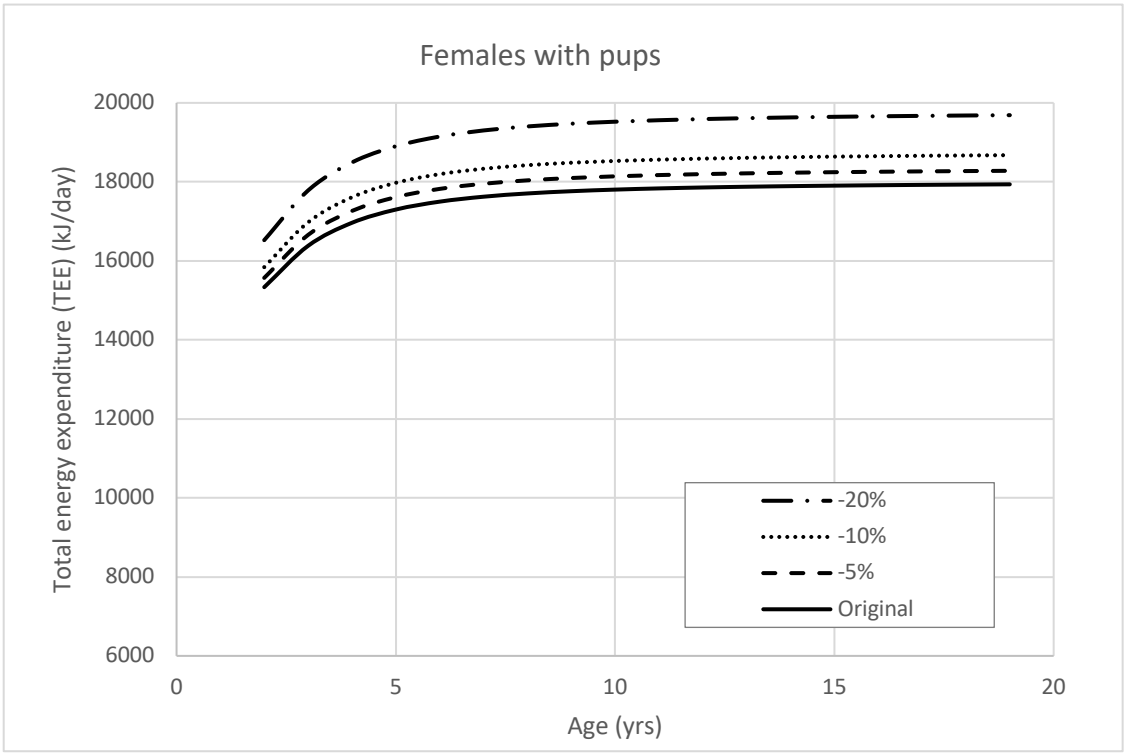
Figure 3.2: Graph showing the average biomass removed from the environment across diet scenarios for 4 individual otters: 10-yr old male, 10-yr old female without a pup, 10-yr old female with a pup, and a ~1-yr old Juvenile.

The differences in captured prey mass between Diets 1, 2, and 3 are much smaller than the differences seen in ingested food mass due to differences in the ratio of captured to ingested biomass. Diet 2 had the lowest ratio of captured to ingested biomass. Still, an adult female otter with a pup is predicted to remove 12,200 g of prey daily, of which 7,500 g is composed of 134 snails.

3.4.4 Effect of foraging efficiency on TEE and foraging time

In my analysis investigating the effect of foraging efficiency, I decreased the gross rate of return (ROR_G) from my baseline model, thereby changing the net rate of return, to represent scenarios of varying prey availability. As expected, when the ROR_G is decreased by 5%, 10%, and 20%, the total energy expenditures increase across all sexes and ages (Figure 3.3). Decreasing available food (ROR_G) decreases ROR_N (amount of energy gained per minute foraging) which increases the amount of time during the day required for foraging. However, the relationship between decreases in ROR_G and resulting total energy expenditure (TEE) is not 1:1. Not surprisingly, the 20% decrease in foraging efficiency shows the highest increase in energy expenditures, with an average 9% increase in TEE for reproductive females, 11% for non-reproductive adult females, and 10% for adult males. This is the result of increased foraging times of 262 minutes (37% increase) and 246 minutes (36% increase) for reproductive and non-reproductive females, respectively, and 190 minutes (32% increase) for males. With a 10% decrease in foraging efficiency, TEE increases 4% on average for reproductive females, 7% for both adult females without a pup and adult males. As expected, decreasing ROR_G by 5% results in the smallest percent change in average TEE, predicted to be only 2% difference in TEE for females with pups, 5% for non-reproducing females, and 6% for males.


Females without pups
Total energy expenditure (TEE) (kJ/day)
20000
18000
16000
14000
12000
10000
8000
6000
0
5
10
15
20
Age (yrs)
-20%
-10%
-5%
Original


Females with pups
Total energy expenditure (TEE) (kJ/day)
20000
18000
16000
14000
12000
10000
8000
6000
0
5
10
15
20
Age (yrs)
-20%
-10%
-5%
Original

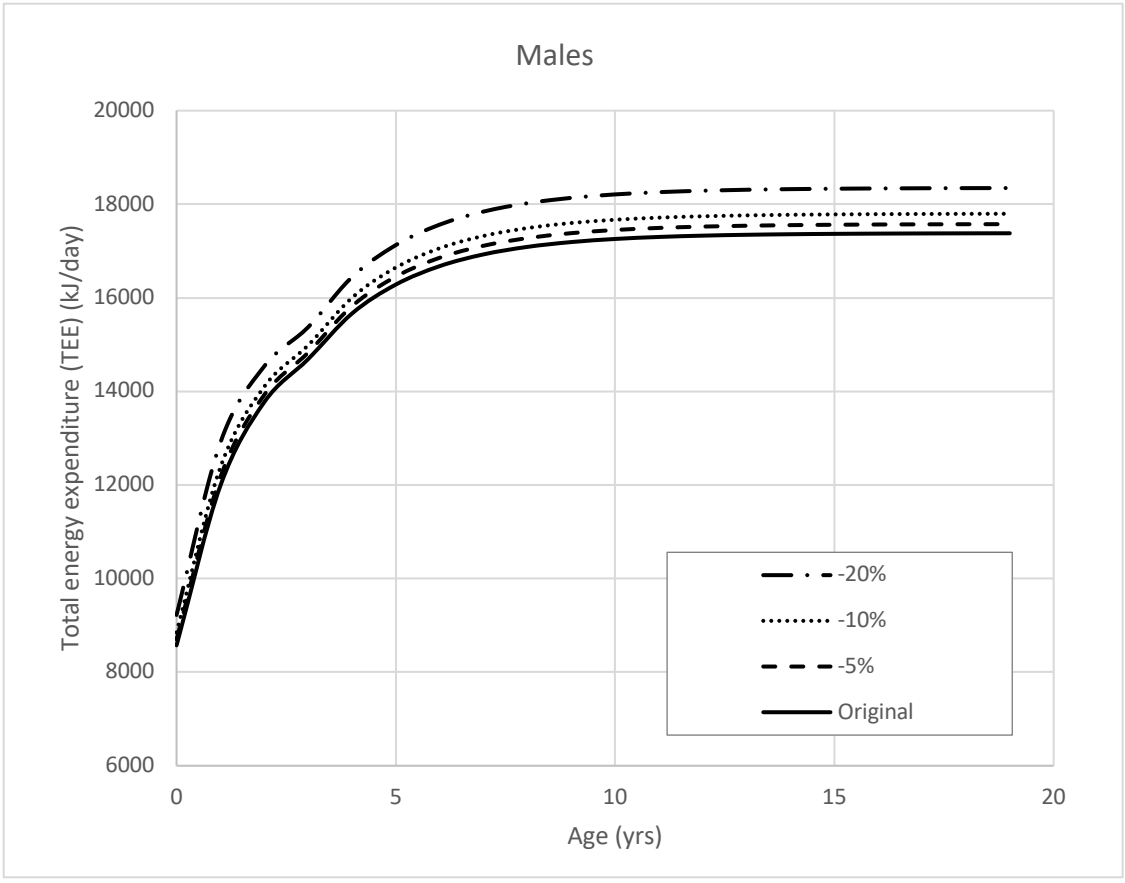


Figure 3.3: Changes in total energy expenditure (TEE) when foraging efficiency (gross rate of return, ROR_G) is decreased by 5%, 10%, and 20% compared to the original model. The imposed changes in foraging efficiency represent factors such as decreases in food availability in the environment or increased competition. Separate figures are given for females without a pup (top), females with a pup (middle), and males (bottom) across all modelled ages.

3.5 Discussion

Observational studies of sea otters' diets have shown they consume a wide variety of prey items, that can vary for different reasons. Sea otter diets can differ due to habitat substrate types and oceanographic conditions, as seen with otters in muddy substrates in Alaska consuming predominantly clams versus otters in rocky areas focusing on consuming crabs and urchins (Kvitek & Staedler, 1993; Oftedal et al., 2007). Diets may also vary depending on population density and the amount of time a population has been established. Studies have shown that the diversity of prey items consumed by sea otters increases within high-density populations that have occupied its habitat for prolonged periods. On the contrary, however, sea otters living in these populations are often observed specializing their diets, thereby decreasing

the diversity in their diets at an individual level (Fujii et al., 2017; Law et al., 2024; Oftedal et al., 2007; Tinker, 2004; Tinker et al., 2007, 2008). These same conditions have also been linked to decreases in their overall energy intake rate.

When established populations have low energy intake rates, they may have difficulties expanding their ranges, as has been seen in northern edges of southern sea otters' habitats which have experienced long term range stagnation, despite its relatively small size (Lyon et al., 2024). The relationship between low energy intake rates and population and range stagnation may be specifically tied to difficulties experienced by reproductive females whose energy requirements can nearly double during pup rearing (Thometz et al., 2014). In highly density areas in central California, deceased southern sea otter females recovered for necropsy have a higher probability of having died from conditions related to ELS than ones recovered from areas of low population density (Chinn et al., 2016; Thometz, Kendall, et al., 2016).

Due to the potential role of diet quality affecting sea otter populations, it is important to explore how different diets may affect the necessary ingested food mass (IFM), time spent foraging, and the potential resultant ecological impacts. Additionally, it is important to investigate how changes in resource availability can affect sea otter energy expenditures. This information is ultimately critical to ensure proper management and conservation steps are taken to expand population ranges of these critical keystone species.

To address the aforementioned concerns, my study sought to quantify how food requirements change with sex, age, and reproductive status across a variety of diet specialization scenarios using the energy expenditure results from the models described in Chapter 2. Additionally, changes in foraging efficiency as a reflection of fluctuations in resource availability were also modelled, showing the estimated energetic consequences of low food intake rates.

3.5.1 Ingested food mass

Sea otters predominantly forage on prey bases that are high in protein and have lower levels of fat, including a variety of crustaceans, bivalves, echinoderms, and gastropods (Oftedal et al., 2007). This means that sea otter prey is going to be of lower energy density than that of

piscivorous marine mammals. In addition, protein has a higher rate of digestive losses than fats, with around 30% of ingested energy typically lost to digestion and excreted as waste (Oftedal et al., 2007). The lower energy density of prey items, the higher proportion of energy lost from digestion, coupled with the otter's higher rate of metabolism, all drive up the ingested food mass necessary to satisfy energy needs.

I explored the effect of five different diets (Table 3.1) on sea otter ingested food mass (IFM). Not surprisingly, IFM was inversely proportional to energy density of the diets. Hence, IFM from diets associated with *Cancer* crab and abalone specialists, kelp crab and bivalve specialists, and marine snail specialists were all very similar. However, according to the models, adult otters that consume a diet with a preference for urchins are predicted to have the highest ingested food mass requirements across sexes and reproductive status. Additionally, urchin specialists are also predicted to remove the highest amount of biomass from the marine system. This is not just due to the lower energy density of the diet, but also because only 36% of each urchin is edible by sea otters (Oftedal et al., 2007). Based upon field observations, our scenario for urchin specialists assumed that 71% of the diet was urchin, and the remaining 28% of the diet consisted of *Cancer* crab (12%), kelp crab (13%), and turban snails (3%) — all moderate to high energy dense prey items— and the remaining 1% was low density mussels (Fujii et al., 2017; Oftedal et al., 2007). However, these proportions are based upon number of prey items. When examined as relative amount of ingested biomass, *Cancer* crabs contribute 2.5x the ingested biomass and ~5x the energy intake. Hence, the 28% of energy dense prey items in this scenario serve to shield the potential negative effect of consuming an urchin-focused diet.

Despite sea otters classically being associated with consuming sea urchin species in their role of keystone species (Paine, 1969), my model shows that they are a difficult food source to survive off of, requiring more time spent foraging to fulfill the same energy requirements when compared to other, more energy dense food items. However, not all urchins are nutritionally identical and their energy density will depend on their size, species, and reproductive status and my conclusion is based upon the specific type of urchin I used to model the diets. In comparison, according to Oftedal et al. (2007), in Monterey Bay National Marine Sanctuary

(MBNMS), a diet of 40% urchin and 33% mussels was shown to have the highest levels of both fat (% of dry mass) and energy (kcal g^{-1}) among the observed diet types. However, the nutritional values for the urchins represented in that calculation were a combination of red and purple urchins. In my model, I only use values corresponding to purple urchins because they had the largest sample size in the Oftedal et al. (2007) publication by a large margin. Red urchins collected in MBNMS have much higher levels of fat (18%) than purple urchins (6%) (Oftedal et al., 2007).

The value of a particular prey item is also based upon availability. In areas with well-established populations that have long occupied an area, readily available urchins are seldom seen throughout the habitat (Estes et al., 2003; Kvitek & Staedler, 1993; Lyon et al., 2024). In newly colonized habitats, urchins are rapidly depleted as a food source before otters switch to other prey items (Kvitek & Staedler, 1993), suggesting that sea otters prioritize the most readily available food item, regardless of the energy density of that prey species. In one study, foraging observations made from the same location, but across four separate blocks of time within three years, showed urchins were the most common prey item in the first two blocks of time, and were then essentially nonexistent in the otters' diets for the last two periods (Ostfeld, 1982).

3.5.2 Percent body mass consumed

The amount of food consumed each day is often presented as a percentage of an organism's body mass (g). This is partly because there is an assumed physiological capacity for prey ingestion (e.g., digestive capacity) that is related to body mass. In my study, the percentage of body mass consumed varied not only between diet scenarios (due to differences in the ingested food mass), but also by sex and age class. The differences in relative ingested food mass among most otter age and sex classes were relatively minor. On an average diet, juvenile otters (Year 1) must consume a higher body mass percentage (34%) than adult males (33%) and females without pups (31%) to meet their daily energy requirements. My model's estimates align with estimates from literature predicting juveniles consume up to 30% of the body mass (Kenyon, 1969).

However, mothers caring for a pup must consume the highest body mass percentage, at an average of 46% across diets, which is 15% more than non-reproductive females and 13% more than males. For comparison, observational studies of mothers with pups in Simpson Bay, Alaska, concluded that 20kg females must consume 24% of their body mass daily (Cortez et al., 2016). This increases to 29% for females with a one-month-old pup, and to 39% of her body mass while caring for a 3-month-old pup (Cortez et al., 2016). My model estimates that on a general diet, a female sea otter must consume the equivalent of roughly 46% of her body mass every day over the course of six months of caring for a pup.

Caring for a pup between three and four months old is when energy demands are the highest for a female otter (Thometz, Kendall, et al., 2016) — and would require her to consume more than 55% of her body mass on a general diet during that time according to my models. The 3–4-month mark is a point in a pup's development when pups begin to consume solid food along with milk, while the female must continue to feed herself and produce milk for her pup lactating (Thometz, Kendall, et al., 2016).

Consuming 46%-55% of their body mass may not be feasible for many female sea otters for a number of reasons. For example, an otter may not have enough time to consume that much food, especially since otters with pups already spend more than 40% of their day foraging (Thometz et al., 2014). Otters also need periods of rest to digest food (Costa & Kooyman, 1984). Additionally, it may not be physically feasible for otters to consume 55% of their body mass every day due to constraints of digestion rates and potentially the size of their stomachs. Otters have limited lipid storage capacity to offset these periods of high food intake requirements. These challenges will be further amplified for otters in population dense areas where available food may be limited and require additional foraging effort, further increasing energetic needs.

Reproductive female otters that are unable to consume enough food for themselves and their pups may be more likely to develop ELS, leading to potential mortality that can significantly limit sea otter population growth. It is important to consider that the estimated quantities of prey consumed by females caring for a pup previously noted are based on weighted averages over the entire 6 months of pup rearing. The amount of care otter pups need fluctuate greatly over their time as a pup, requiring differing amounts and types of care

during their developmental phases. Mother otters' metabolic rates and activity budgets associated with the pup's development are lower during the phase nearest parturition, where pups rest 91% of the day and do not eat solid food, compared to last phase, when pups have grown to juvenile size, are still being nursed, groomed, and fed solid food by their mothers, requiring extra foraging energy. Thus, the time required for female otters to consume the equivalent of 55% or more of their body mass every day may not be prolonged, and may only be the reality for the last phase of pup development before pups become independent juveniles.

According to my model, non-reproductive adult sea otters on a general diet (Diet 5) consume between 31%-33% of their body mass. This is higher than the widely used estimates from Costa's (1982) study that sea otters must consume between 20-23% of their body mass. The higher numbers generated by my model compared to Costa's estimates are due to a number of factors. First, the energy density of the diets fed to otters in the Costa study were significantly higher than any of the calculated energy densities of diets compared in my study (4.8 kJ d^{-1} vs. 3.1 kJ d^{-1}, respectively) (Costa, 1982). In Costa's study, two of the prey species fed to the otters were not typical or widely consumed by wild sea otters in California and had higher energy densities than the other prey items: Atlantic surf clams (*Spissula solidissima*) and Pacific Coast squid (*Loligo opalescens*) (Costa, 1982).

My models used diets observed in wild otters throughout California and did not include Atlantic surf clams or Pacific Coast squid. In addition, the urchins used in Costa's research were red urchins, while I used purple urchins for my analyses, which have lower energy densities than red urchins (Oftedal et al., 2007). Additionally, two of the five otters in Costa's study were under long-term human care. It is therefore noteworthy that another study based on otters under human care also consumed around 20% of their body mass consistent with Costa's study—although their body masses were greater than those of an average wild otter of the same age (Iskandar et al., 2023). Hence, I believe my estimates of percent body mass consumed by adult otters on a general diet better reflect the diet and energy expenditure of wild otters.

This high intake requirements of sea otters (46–55% of body mass) is partly facilitated by the speed with which sea otters can digest their food (a 3-hour "food passage rate" from

end to end when fed clams or squid) (Costa & Kooyman, 1984). However, the specific amount of ingested food mass (IFM) required to satisfy a given otter's energy requirement will change depending on what species they consume.

When comparing specialist diets, Diet 1 (*Cancer* crab) requires the lowest body mass percentage consumed, while the relative amount an otter must consume on Diets 2 (marine snails) and 3 (kelp crab and bivalves) are all within 1% of each other. Juveniles must consume 32% of their body mass, while adult females without pups need 30% of their body mass and adult males need 31% for both Diet 2 and Diet 3. Females with pups need to consume 44.4% (Diet 2) and 44.8% (Diet 3) of their body mass. In contrast, the sea urchin specialist diet (Diet 4) requires sea otters to consume the highest percentage of their body mass across sex and age classes (36% for juveniles, 50% for females with a pup, 33% for adult females without pups, 35% for adult males) (Table 3.5). As discussed previously, this level of intake may be challenging for reproductive females to sustain, and could jeopardize their reproductive success and survival.

It was initially surprising that Diets 2 and 3 were so close in the body mass percentage estimates considering Diet 2 is more than 60% marine snails and Diet 3 is more than 60% kelp crabs and bivalves. However, comparing the remaining proportions of the diets (Table 3.1) shows that *Cancer* crabs are present in both scenarios and kelp crabs are also consumed in the snail diet, adding to the overall energy density and biomass consumed. Additionally, turban snails have the second highest average energy density of the prey items despite their small sizes (Table 3.2).

3.5.3 Effect of foraging efficiency on TEE and foraging time

Changes in prey type and prey availability will affect the foraging efficiency of sea otters (in terms of rate of energy intake) which will also affect energy expenditure through increased foraging time. This was accounted for in my model via changes in ROR (used as a proxy for foraging efficiency). Sea otter diets increase in diversity as populations become well established within a geographic area. Otters tend to meet their energetic needs in well-established areas by consuming prey species that are less nutritionally dense, but easier to

access (Fujii et al., 2017; Laidre & Jameson, 2006; Tinker, 2004; Tinker et al., 2008). Otters consuming more diverse diets also have a lower rate of energy intake (LaRoche et al., 2023). The time required by an otter to dive, catch, and process their food, including removal of shells, exoskeletons, and any further processing, varies between prey species (Yeates et al., 2007).

Overall, the results of my analysis using my bioenergetic models show that if the rate of return (ROR) of foraging (foraging efficiency) decreases—simulating a decrease in prey availability, or increases in search or handling time—the estimated energy expenditures increase, regardless of sex, age, or reproductive status. This is directly related to the increased foraging time required to meet energy expenditures. More time spent foraging will have an effect on energetic expenditure. My model is somewhat unique with its feedback loop wherein the increased foraging time decreases resting time, and further contributes to TEE. My model predicted that— with no other forms of compensation —a 20% decrease in available prey will increase energy expenditures by 11% for females without a pup, 9% for females with a pup, and 10% for males. Increased energy expenditures translate into an increase of in the time spent foraging to meet energy needs on a daily basis by 18% for adult females and 13% for adult males. While these percentages seem insignificant, 18% of the day is an additional 4.3 hours (260 minutes) per day females would spend foraging, and 3.2 hours (190 minutes) for adult males.

The effects of additional foraging time are most likely to affect female sea otters caring for pups, that are already contending with much higher metabolic rates and energy demands. Caring for a large pup during the last three months of lactation increase energy expenditures by an estimated 85-110% compared to during non-reproductive periods (Thometz et al., 2014; Thometz, Kendall, et al., 2016). Having to forage an increased 260+ minutes per day—time that is detracted from that spent resting, grooming, or caring for their pup—may simply not be feasible. As a result, conditions that lead to decreases in foraging efficiency have the potential to add further strain on the energy demands of reproductive females—potentially leading to the development of end-lactation syndrome (Chinn et al., 2016).

Of course, there are a number of behavioural adaptations that can be employed to offset the effects of decreased prey availability. In multiple studies, female otters with pups

often consume more diverse diets, opting for prey with lower nutritional density, but more readily accessible, such as marine snails (Fujii et al., 2017; LaRoche et al., 2023; Law et al., 2024; Tinker et al., 2007, 2008) In addition to diet specialization in population dense areas, sea otters exhibit increased tool use in areas of dense population where prey resources are likely to be more limited (Fujii et al., 2017; Law et al., 2024). Using rocks and other found objects to process prey items was seen more frequently in female otters and was shown to increase their foraging success, allowing for consumption of much larger and harder shelled prey items (Law et al., 2024). Hence, tool use by female otters increases foraging intake and efficiency, and is an important adaptation for supporting their high energy requirements.

3.5.4 Ecological impacts of diet specialization in sea otters

Driven by high metabolic rates, energy expenditures, and food requirements, sea otters have long been known to have strong impacts on their local nearshore marine ecosystems, whether by limiting grazing pressure on kelp by consuming urchins or preventing coastal erosion damage by predating on burrowing crab species (Estes & Palmisano, 1974; Hughes et al., 2024). However, the amount of actual biomass removed by sea otters from their environment on a daily basis is not often considered when discussing sea otter diets. For example, if a reproductive female sea otter must consume 50% of her body mass on an urchin specialist diet (Diet 4), how many urchins is she removing from the system daily?

Based on the mass and energy densities of prey species, the model predicts that a 10-yr old female caring for a pup would consume 171 purple urchins daily on the urchin-preferred Diet 4, but only 48 on a more general diet (Figure 3.4). Comparing the number of prey items consumed on a general diet across age, sex, and reproductive status (Figure 3.5) shows that this same otter would consume a similar number of *Cancer* crabs, regardless of diet scenario, as seen in Figure 3.4.

Integrating the proportion of edible biomass sheds further light into the source of the nutritional value of different diets that may not be apparent when comparing frequency of ingested prey items (which is how otter diets are commonly reported). For example, kelp crabs and bivalves comprise the largest proportion of Diet 3 by items (62%), however, 34% of the diet

is *Cancer* crabs (Table 3.1). Not only do *Cancer* species of crabs have a higher energy density (3.15 kJ g^{-1}) than kelp crabs (3.05 kJ g^{-1}), but there is also a significant difference in the average mass of the edible portion of these crabs, where kelp crabs' average edible mass is 51g compared to 225g for *Cancer* species (Table 3.2) (Oftedal et al., 2007). Hence, when translating into the proportion of ingested biomass within the diet (g g^{-1}), 79% of the biomass from Diet 3 is *Cancer* crab, despite only representing 34% of species consumed in this scenario. Similarly in Diet 2, 61% of items are turban snails (*Tegula* spp.), but 14% are *Cancer* crabs and 22% are kelp crabs.

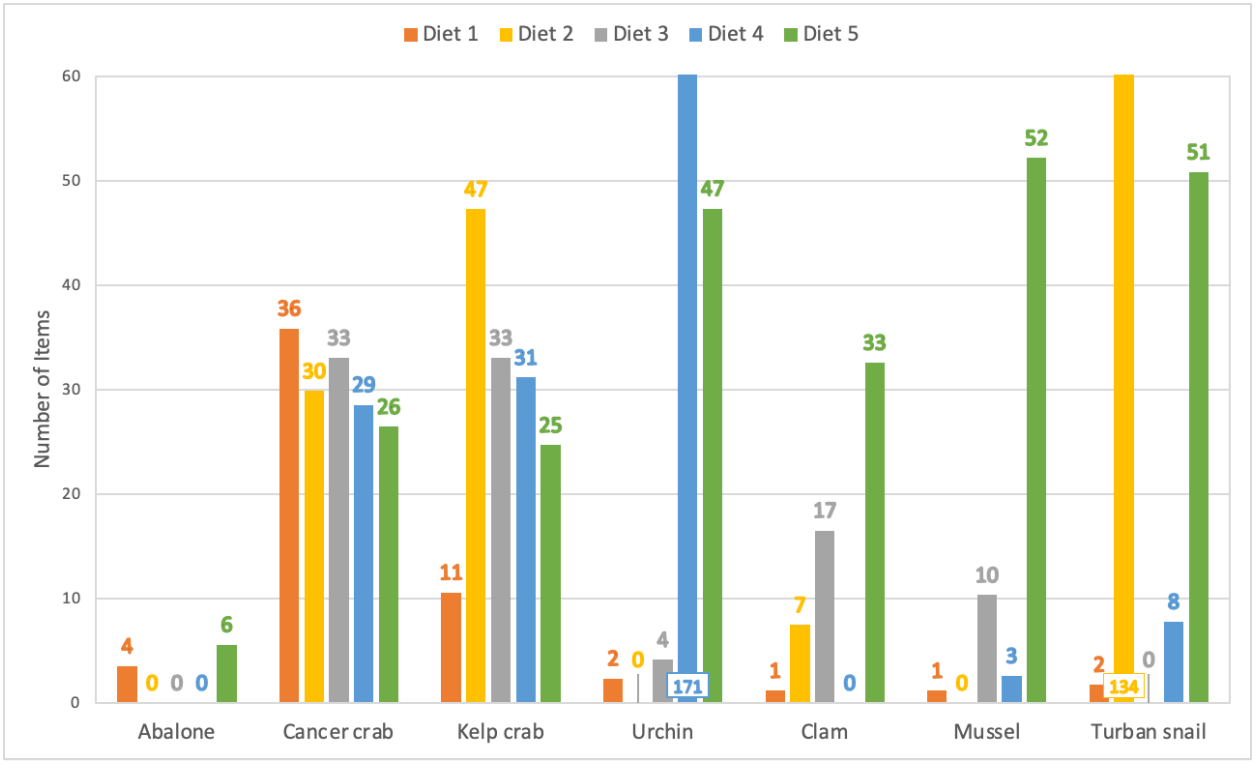


Figure 3.4: Five diet scenarios broken down into the average number of prey items consumed by a "model" 10-year-old female otter caring for a pup. Diet 1 is *Cancer* crab and abalone specialists, Diet 2 is turban snail specialists, Diet 3 is kelp crab and bivalve specialists, Diet 4 is urchin specialists, and Diet 5 is a general otter diet.

Surprisingly, turban snails have a higher energy density than both species of crabs (3.80 kJ g^{-1}) (Table 3.2). However, in terms of ingested biomass (g g^{-1}), they only represent 2% of biomass compared to 72% for *Cancer* crabs (despite representing only 14% of items consumed) (Table 3.1). Despite their high energy density and contributing to 61% of the diet consumed, the edible portion of turban snails has a small average mass (1.12g) and only makes a minor contribution (0.06 kJ g^{-1}) to the overall energy density of Diet 2. Comparing the biomass

consumed and energy density of prey items, even in specialist diets, highlights how important the availability of higher-density prey species with a high edible biomass like *Cancer* crabs are to sea otter populations—even in small quantities.

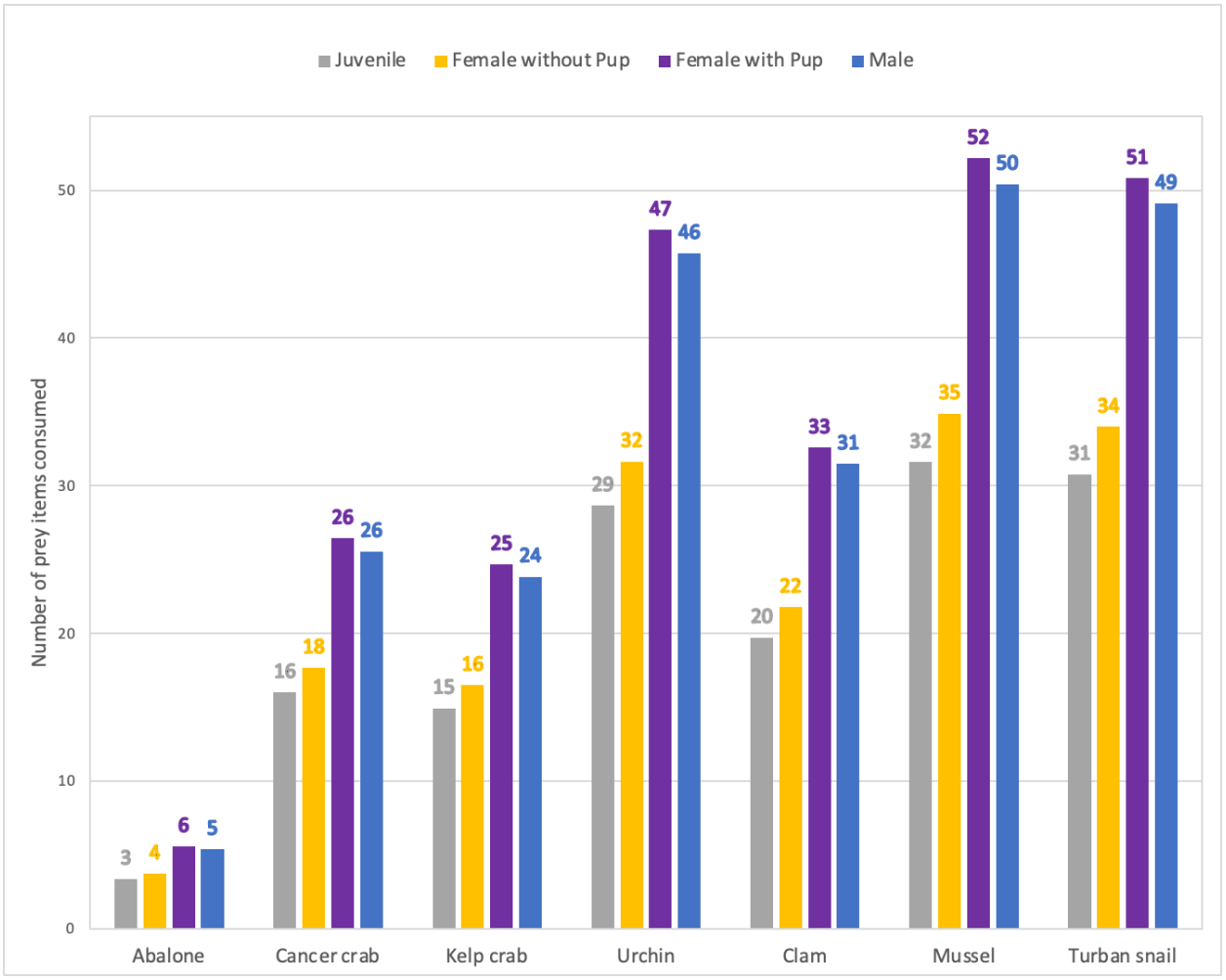


Figure 3.5: Breakdown of a generalized sea otter diet (Diet 5) into the average number of prey items consumed across sex, age, and reproductive status.

The diet specialization of sea otters has ecological effects in occupied habitats, often altering the community composition over time. Additionally, the prevalence of observed specializations in sea otter diets can be a metric for understanding local population dynamics. Urchins and other easily visible and sessile invertebrate species (like abalone) are often the first choice for consumption by sea otters in newly colonized areas (Kvitek & Staedler, 1993; Ostfeld, 1982).

Once the most easily seen (and accessed) prey species have been depleted, otters begin consuming the next available species, often leading to diversity among otters' diets over time as prey base populations are consumed (Estes & Palmisano, 1974; Kvitek & Staedler, 1993; Ostfeld, 1982). This change in prey base consumption also drives a trophic cascade, increasing long-term kelp growth in these areas as grazers are eliminated from the local ecosystem (Estes & Palmisano, 1974; Laidre & Jameson, 2006). As sea otter populations become well established and near their carrying capacity, individuals are increasingly pushed to specialize their diets in order to consume enough to satisfy their energy requirements (Estes et al., 2003; Law et al., 2024; Lyon et al., 2024). This is reflected in the diet scenarios used in my study, which were based on observations made in central California in densely populated areas (Fujii et al., 2017; Tinker, 2004; Tinker et al., 2008).

Reproductive female otters caring for pups have the highest energy requirements, and are therefore more likely to alter their typical diets to meet their energy needs, such as specializing their diets to meet their food needs, by occasionally sacrificing more nutritionally dense food items for less dense but more easily foraged prey items (like marine snails) (Fujii et al., 2017; Kvitek & Staedler, 1993; Law et al., 2024; Tinker et al., 2008). However, it should be noted that similar to mother otters' activity budgets and metabolic rates that vary throughout pup development, female otters will adjust their diets based on the stage of pup dependency as well. For example, females that have been observed as specialists will broaden their prey bases shortly after giving birth, in order to forage in areas that are safer and better suited for new pups (Staedler, 2011).

3.5.5 Considerations and Limitations

While the bioenergetic model framework created can be a valuable tool for scientists and conservation managers concerned about sea otter populations, there are a few things to consider when using it. One consideration is that the model was built to be a worst-case scenario (as discussed in Chapter 2: *Important aspects of model design*) in terms of the premise that rest and foraging are direct tradeoffs. One of the unique features of my model is that

foraging time can be increased in response to decreases in effective prey availability, a mechanism that potentially increases food intake estimates.

That being said, all of the diet scenarios presented in this analysis were from observational studies conducted in known study sites containing dense populations of southern sea otters. High population density in otter populations is what drives specialization in diets in both male and female otters alike due to limited availability of preferred prey species, which are often exhausted first (Fujii et al., 2017; Law et al., 2024; Tinker, 2004; Tinker et al., 2008). Additionally, as discussed in Chapter 2 (*Contributions to Differences in TEE*), the proposed activity budgets based on the model outputs are similar to those observed in areas with low prey availability (Thometz, Staedler, et al., 2016). Both of these factors could also increase my intake and foraging efficiency estimates.

An additional consideration for my analysis it that not all prey species are created equal. For example, *Strongylocentrotus* species of sea urchins have a relatively low energy density, but their overall nutritional content will vary based on size and reproductive status, seeing as gravid urchins have a much higher energy density (Kenyon, 1969). The energy density values used in my modelling were taken from Oftedal et al. (2007) that contained averages calculated from samples of multiple individuals, and so represents a potential snapshot of actual nutritional values. To improve the accuracy of my analysis, an updated energy and nutritional density study on prey species would be extremely useful. Additionally, differences in geographic locations from where samples come from can affect the outcome of this analysis and should be considered, particularly for modelling specific otter populations.

Another factor to consider within the model is that the foraging efficiency (including handling time) is kept constant between prey species, and therefore total energy expenditure is kept constant when comparing diet scenarios. This chapter's analysis does not address differences in the time and effort necessary to process food items, which can vary drastically by species; for example, comparing the efficiency of eating snails to eating clams, where the clamshell needs to be cracked or pried open to consume its contents. These efforts in food handling do have ecological effects on sea otter foraging and diving times (Yeates et al., 2007).

Incorporating differences in handling time, dive time, and overall foraging efforts between prey species is a future potential addition to the model.

3.5.6 Concluding thoughts and future directions

The physiological adaptations required to live in marine environments by species such as sea otters that do not have fat reserves or vascularized blubber to keep them warm are the main drivers behind the ecological impacts and therefore the designation of sea otters as a keystone species (Paine, 1969), especially exerting strong predation pressure on grazing invertebrate species (Estes & Palmisano, 1974). The large amounts of food otters consume pose a number of challenges for the long-term establishment of sea otter populations. One concern is how rapidly sea otter populations can deplete a prey base. In one study, a rapidly growing, but small population of otters (where observations of otters numbered less than four otter sightings per day on average over the two-year study period) consumed the vast majority of sea urchins at Santa Cruz Point in one year (Ostfeld, 1982). In the first two observation periods, urchins accounted for 24% and 31% of the prey consumed, which dropped to only 1.3% in the subsequent observation periods one calendar year later (Ostfeld, 1982). Similar trends have been seen in northern sea otters in both Alaska and Washington, where abundant abalone and urchin populations were widely absent after the expansion of nearby otter populations to new areas (Kvitek & Staedler, 1993; Laidre & Jameson, 2006).

If prey bases are diminished by otters over short periods, the prey species may not be able to reproduce quickly enough to support the otter populations at sustainable rates, thereby increasing overall competition for resources and moving populations towards their carrying capacities. If sea otter populations are unable to expand and begin to recolonize their historic ranges, increased intraspecific competition for resources is most likely to negatively affect females caring for a pup, who are already pushed to their physiological limits during pup rearing (Thometz, Kendall, et al., 2016). With these consequences in mind, sea otters require additional habitat to expand into to ensure their long-term ecosystem services to nearshore coastal ecosystems, including kelp forests and the commercially important species that rely on them.

When discussing and planning the expansion or reintroduction of sea otter populations, however, interspecific competition should be considered— especially direct competition with humans. Many commercial shellfish fisheries will experience negative financial effects due to sea otters expanding into new areas, consuming fishers' livelihoods, and removing substantial biomass from the ecosystem (Gregr et al., 2020). Despite the short-term losses that are likely to be experienced by commercial fisheries, the benefits— both economic and ecological— to be gained long-term by the introduction of sea otters are estimated to far outweigh those potential losses (Gregr et al., 2020). Having comprehensive management plans in place prior to introducing otters is an important step in minimizing fisheries conflicts, as suggested by Davis et al., (2019).

Ensuring that all necessary stakeholders are involved in management decisions and plans is crucial to successful sea otter introductions. Canadian First Nations and Native American tribal governments have historically been left out of these conservation conversations (Salomon et al., 2015). Archaeological evidence from coastal First Nations territories have provided evidence that shellfish were managed sustainably throughout pre-contact history using clam gardens, despite the presence of sea otters in the same locations (Salomon et al., 2015). Incorporating Indigenous voices and alternative ways of knowing (Reid et al., 2021) into management plans will strengthen them, hopefully helping to continue harvesting shellfish commercially while expanding sea otter habitat ranges while minimizing negative impacts.

My bioenergetic model is tool can be used to further investigate how many of each prey item are consumed by otters on a particular diet at different age classes, reproductive statuses, and between sexes to fulfill their unique energy needs. By converting energy requirements into actual food items, my model can ultimately be used to measure habitat suitability and aid in sea otter conservation. This metric can also help determine what size population a potential reintroduction site could support. By extrapolating food items consumed by individual otters at all life stages to a population level, managers can use this to estimate how much food must be available to successfully support a sea otter population for the long term.

Chapter 4: Conclusion

4.1 Summary of findings

The presence of sea otters in nearshore, coastal habitats greatly impacts the physical and biological profiles of marine ecosystems across the northeastern Pacific. Most notably, sea otters disproportionately impact their prey bases compared to other species within their biological communities. There are a number of factors that cause this pressure, including their reliance on high protein diets, fast rates of digestion, and high metabolic rates. As a result, predation pressure from sea otters aids in keeping macro-grazers in check, which reduces consumption rates on macroalgae (*Macrocystis* & *Nereocystis* spp.) by urchin and abalone, decreases predation on mesograzers that prevent epiphytic algal growth in seagrass communities by consuming their predators, and reduces coastal erosion rates in salt marshes by consuming burrowing crab species (Estes & Palmisano, 1974; Hessing-Lewis et al., 2018; Hughes et al., 2024).

Despite the reputation of sea otters as dominant consumers, there have been no reliable tools to explore food intake requirements under different life history and ecological conditions. Chapter 2 described the development of a bioenergetic model to estimate sea otter energy and food requirements. Using published data, I quantified the energetic costs across sex, age, and reproductive state. This resulted in three separate models: one for males, one for females caring for a pup, and one for non-reproductive females. The model outputs were total energy expenditure in kilojoules of energy expended per day for each year of life. The results of the models were consistent with previous estimates from the literature. The total energy requirements for adult females caring for a pup are higher than for adult males by 3%, and 33% higher compared to adult females without a pup. The higher energy expenditure of males was largely due to sexual dimorphism, even in the pup and juvenile age classes. However, some differences were accounted for by time spent in different observed behaviours.

When comparing mass-specific total energy expenditure between the three models, the differences between males and females without a pup was very slight. Further, the differences remained the same between females, with 33% more energy needed when caring for pup. Comparisons between males and females with a pup showed that females with a pup require

30% more energy per kilogram of body mass per day than similarly-aged males. Pups had the highest total energy expenditure per kilogram followed by juveniles, largely due to the rapid amount of tissue growth that occurs during these two age classes.

In Chapter 3, I used the model outputs from Chapter 2 to convert the estimated total energy expenditure of sea otters into food requirements under various dietary conditions. I selected five different diet scenarios from publications detailing observed prey species consumed in wild otters. I chose four specialist diets, where more than 60% of the diet was one category of prey: large prey such as *Cancer* crab and abalone (Diet 1), a preference for marine snails (Diet 2), moderate-sized prey represented by kelp crabs and bivalves (Diet 3), and lastly, a preference for urchins (Diet 4) (Fujii et al., 2017; Tinker et al., 2007). The fifth diet scenario was a "general" sea otter diet (Diet 5) (Tinker, 2004).

Diet 1 (*Cancer* crab and abalone) had the highest average gross energy density, and therefore the lowest estimated ingested food mass necessary to satisfy energy requirements. Diet 4 (urchins) had the lowest energy density and subsequently the highest ingested food mass needed to meet energy requirements. Not surprisingly, in line with differences in total energy expenditure, females caring for a pup had the highest food requirements across all five diets compared to males and females without a pup, needing to consume 46% of her body mass per day on the generalist Diet 5, compared to 33% (males) and 31% (females without a pup). Juveniles had higher ingested food mass estimates as a percent of body mass than adult males and non-reproductive females, requiring them to consume the equivalent of 34% of their body mass in prey to satisfy energy needs.

Chapter 3 also investigated the effects of changes in foraging efficiency as a result of changes in food availability. Decreasing the gross rate of return (ROR_G) calculated in Chapter 2 for "model" otters by set percentages (5%, 10%, and 20%) simulated 5, 10, and 20% less food available (or more difficult to obtain). This exercise in decreased foraging efficiency estimated not only increases in the necessary time spent on foraging daily, but also the overall energy expended per day. The increase in energy expenditures were not proportional. For example, a 20% decrease in available food caused an increase between 9-11% in energy expenditures across the three models, due to a 32% (males) to 36% (reproductive females) increase in the

minutes per day needed to be spent foraging. These increases in both energy expenditure and foraging time can lead to significant challenges in meeting energy requirements, especially for females caring for a pup who are responsible not only feeding pups via lactation, but also foraging for solid food items for their pup, in addition to foraging for themselves. The last stage of pup development, when the large pups are nearing independence but still demand food from their mothers is often the most physiologically challenging for mother otters, which are often operating under an energy deficit, causing negative health effects that can lead to a condition called end-lactation syndrome (Chinn et al., 2016). Further increases in time spent foraging for mother sea otters due to decreased food availability and foraging efficiency may ultimately inhibit population expansion due to high mortality rates of reproductive females.

4.2 Model applications and implications

Quantifying the energy and food requirements of predators is important for understanding their ecological impact, and understanding how these change under different ecological scenarios. I developed a bioenergetic model for sea otters to produce such estimates and to understand the inter-relationship between physiology, behaviour, and ecology.

My research is not the first to investigate the energy and food requirements of sea otters. However, many past studies investigating energy expenditures of sea otters were often focused on only one population or one sex and/or age class. My model is the first comprehensive bioenergetics model for sea otters to account for changes in energy requirements across a wide age range, both sexes, and multiple age classes and reproductive statuses within the same framework. The model thus represents a significant improvement on previous point estimates of energy or food requirements of otters.

An additional strength of my research is that I built the basic model in a highly transparent way so that it can serve as a tool that can be easily used by other researchers, providing the opportunity to investigate different scenarios. Specifically, the mechanics of the model allow for the input variables — both in terms of energy expenditure and diet characteristics — to be easily changed for more specific investigations. For example, the majority of the data I used in the model was collected on southern sea otters across

populations in California. However, values for parameters such as mass or activity budgets can readily be replaced with input data collected from northern sea otters from Alaska instead. The structure of the diet analyses as seen in Chapter 3 also provided a lot of flexibility, such that different diet scenarios could be easily substituted for more relevant ones depending on location or prey species involved, such as more clam-heavy diets seen in Alaskan populations.

An additional consideration of my study is that I used single energetic values per prey item (partly due to data availability). Additional investigations could investigate the effect of potential differences in energy densities across habitats and sizes (likely requiring additional energy density studies on prey species).

Models are inherently limited not just by the requirements to parameterize it according to a specific set of conditions, but also by the availability of data and decisions on underlying structure. However, both of these limitations represent potential directions for future research. In my base model, I condensed and averaged values from the literature for a few parameters, such that the precision and applicability of the model can be increased by expanding the mechanics of the model for those parameters. For example, one could separate out the stages of pup development and the associated metabolic rates and activity budgets of the female otters caring for the pups at each development stage instead of doing an overall weighted average. This could be easily done to better understand how the energy and food requirements at each pup developmental stage change for females, especially given how strenuous the last months before weaning are for mother otters.

My model could also be expanded by fleshing out each behaviour category in the activity budgets. Non-foraging activity metabolic rates and time spent per day was often an average of values from multiple behaviours, such as grooming and swimming. By separating out each behaviour, the model inputs will be more precise, as well as allowing energy expenditures associated with increased time spent in certain behaviours to be further investigated. While adding many of these details was beyond the scope of my study, I constructed the model in a way that they can be accounted for by altering the model inputs.

Finally, the precision of the estimates of any model are also determined by internal mechanics as well as the variability in input estimates. These are often investigated by

sensitivity analyses, but the results of these are often discarded or underplayed in interpreting the results of the model. In my model, body mass most greatly affected the model's results (with all other things being equal) because most input values were mass-specific. Since measuring body mass is easily done in research, this is not where efforts should be focused. The next most sensitive parameter that had a significant effect on model outputs were the metabolic rates. Focusing future research on additional studies measuring metabolic rates of otters under various conditions, especially reproductive females across pup developmental stages, will help improve the model's precision and therefore energy expenditure estimates as well.

4.3 Broader value of this study

I developed this bioenergetic model for sea otters to obtain comprehensive estimates of their energy requirements across age from birth to 20 years old, between males and females, and under reproductive and non-reproductive states. Using the model's energy expenditure estimates, I made further inferences into the amount of food required to satisfy those energetic needs across different diet scenarios and prey species observed.

As mentioned previously, a strength of my model is that it was structured to be applied to otters living under different circumstances, despite being based on a number of specific physiological and biological assumptions. My bioenergetic model is therefore a tool that can be used by current and future researchers to delve deeper into understanding sea otter energy and food requirements, and how they change under various conditions. This information is vital to support sea otter conservation and management objectives.

Populations of sea otters have not reached their pre-fur trade numbers, and some populations have reached the carrying capacity of their current locations and are struggling to expand into areas of their former ranges (Lyon et al., 2024). The presence of otters in coastal habitats like kelp forests, salt marshes, and seagrass meadows, creates many long-term ecological benefits as well as economic ones (Gregr et al., 2020). In recent years there have been discussions among various stakeholders about aiding sea otter populations in their expansion, and beginning to plan for reintroductions in Northern California and the Oregon

coast. My bioenergetic model and subsequent dietary analyses are tools that can be utilized in preparation for these reintroduction efforts in concert with other conservation and management projects working to support current and future populations of sea otters.

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Appendices

Appendix A

Additional tables of detailed inputs and outputs of basic bioenergetic models.

Table A.1: Mass and growth values used for all Year classes of sea otters.

Females			Males		
Year Class	Average Mass (kg)	Growth (kJ day^{-1})	Year Class	Average Mass (kg)	Growth (kJ day^{-1})
0	10.71	133.41	0	13.24	147.28
1	15.83	75.58	1	19.47	102.46
2	18.38	38.32	2	23.28	62.93
3	19.69	20.20	3	25.63	38.93
4	20.40	11.12	4	27.09	24.25
5	20.80	6.41	5	28.00	15.21
6	21.04	3.88	6	28.58	9.59
7	21.18	2.47	7	28.94	6.09
8	21.28	1.65	8	29.17	3.89
9	21.34	1.16	9	29.32	2.49
10	21.39	0.85	10	29.41	1.61
11	21.43	0.64	11	29.47	1.04
12	21.45	0.50	12	29.51	0.68
13	21.47	0.40	13	29.54	0.44
14	21.49	0.33	14	29.56	0.29
15	21.51	0.27	15	29.57	0.19
16	21.52	0.23	16	29.58	0.13
17	21.53	0.20	17	29.58	0.09
18	21.54	0.17	18	29.58	0.06
19	21.54	0.14	19	29.59	0.04

Table A.2: ROR values for each year class. The gross rate of return (ROR_G) values were different for each age class (pup, juvenile, subadult, and adult) and the value for adults (different for males and females) repeats for every year in that age class. The net rate of return (ROR_N) was used to calculate the time (in minutes) needed to satisfy the energy expenditure of non-foraging behaviours (resting and non-foraging activity). Each year had a different value to because it is calculated as the ROR_G minus the additional cost of foraging (vs resting) which is a mass-specific value.

	Females without a pup		Females with a pup		Males	
Year Class	**ROR_G**	**ROR_N**	**ROR_G**	**ROR_N**	**ROR_G**	**ROR_N**
0	--	--	--	--	--	--
1	17.74	14.54	17.74	14.54	17.74	13.80
2	17.24	13.52	24.66	19.14	23.64	19.53
3	17.24	13.26	24.66	18.75	28.34	24.06
4	17.24	13.11	24.66	18.54	28.34	23.82
5	17.24	13.03	24.66	18.42	28.34	23.67
6	17.24	12.99	24.66	18.34	28.34	23.57
7	17.24	12.96	24.66	18.30	28.34	23.51
8	17.24	12.94	24.66	18.27	28.34	23.47
9	17.24	12.92	24.66	18.25	28.34	23.45
10	17.24	12.91	24.66	18.24	28.34	23.43
11	17.24	12.91	24.66	18.23	28.34	23.42
12	17.24	12.90	24.66	18.22	28.34	23.42
13	17.24	12.90	24.66	18.21	28.34	23.41
14	17.24	12.89	24.66	18.21	28.34	23.41
15	17.24	12.89	24.66	18.20	28.34	23.41
16	17.24	12.89	24.66	18.20	28.34	23.41
17	17.24	12.89	24.66	18.20	28.34	23.41
18	17.24	12.88	24.66	18.19	28.34	23.41
19	17.24	12.88	24.66	18.19	28.34	23.41

Table A.3: Model output values from the base model for females without a pup. The parameters that are shaded in lighter grey are energy costs that are added across each Year class to calculate the total energy expenditure. The parameters that are shaded in darker grey are the daily behaviour/activity budgets (percent of each day spent in each behaviour) that have been recalculated within the model to account for changes in energy expenditure.

Year Class	Age Class	Growth (kJ day^{-1})	Activity (% Time)	Activity (min day^{-1})	Activity Actual Costs (kJ day^{-1})	Foraging (% Time)	Foraging (min day^{-1})	Foraging Costs (kJ day^{-1})	Resting (% Time)	Resting (min day^{-1})	Resting Costs (kJ day^{-1})	Pup Cost (kJ day^{-1})	Total Energy Expenditure (kJ day^{-1})
0	pup	107.92	16%	223.20	2380.91	20%	292.32	2197.78	64%	924.48	2881.24	0.00	7567.86
1	juvenile	75.58	28%	404.64	3228.35	41%	596.16	4369.43	31%	439.20	1814.61	0.00	9487.96
2	adult	38.32	9%	125.28	1144.42	40%	571.68	4970.04	52%	743.04	3701.07	0.00	9853.84
3	adult	20.20	9%	125.28	1225.98	43%	623.08	5802.93	48%	691.64	3690.61	0.00	10739.73
4	adult	11.12	9%	125.28	1270.19	45%	651.85	6289.87	46%	662.87	3664.59	0.00	11235.76
5	adult	6.41	9%	125.28	1295.09	46%	668.38	6575.76	45%	646.34	3643.31	0.00	11520.57
6	adult	3.88	9%	125.28	1310.04	47%	678.41	6751.51	44%	636.31	3628.12	0.00	11693.55
7	adult	2.47	9%	125.28	1318.75	48%	684.31	6855.47	44%	630.41	3618.44	0.00	11795.13
8	adult	1.65	9%	125.28	1324.98	48%	688.55	6930.52	43%	626.17	3611.07	0.00	11868.22
9	adult	1.16	9%	125.28	1328.72	48%	691.10	6975.81	43%	623.62	3606.50	0.00	11912.18
10	adult	0.85	9%	125.28	1331.83	48%	693.23	7013.77	43%	621.49	3602.57	0.00	11949.01
11	adult	0.64	9%	125.28	1334.32	48%	694.95	7044.27	43%	619.77	3599.34	0.00	11978.57
12	adult	0.50	9%	125.28	1335.57	48%	695.80	7059.52	43%	618.92	3597.73	0.00	11993.32
13	adult	0.40	9%	125.28	1336.81	48%	696.66	7074.83	43%	618.06	3596.08	0.00	12008.13
14	adult	0.33	9%	125.28	1338.06	48%	697.52	7090.18	43%	617.20	3594.42	0.00	12022.98
15	adult	0.27	9%	125.28	1339.30	48%	698.39	7105.56	43%	616.33	3592.73	0.00	12037.87
16	adult	0.23	9%	125.28	1339.92	49%	698.82	7113.25	43%	615.90	3591.88	0.00	12045.29
17	adult	0.20	9%	125.28	1340.55	49%	699.25	7120.95	43%	615.47	3591.03	0.00	12052.73
18	adult	0.17	9%	125.28	1341.17	49%	699.68	7128.67	43%	615.04	3590.18	0.00	12060.18
19	adult	0.15	9%	125.28	1341.17	49%	699.68	7128.65	43%	615.04	3590.19	0.00	12060.15

Table A.4: Model output values from the base model for adult females with a pup. The parameters that are shaded in lighter grey are energy costs that are added across each Year class to calculate the total energy expenditure. The parameters that are shaded in darker grey are the daily behaviour/activity budgets (percent of each day spent in each behaviour) that have been recalculated within the model to account for changes in energy expenditure.

Year Class	Growth (kJ day^{-1})	Activity (% Time)	Activity (min day^{-1})	Activity Actual Costs (kJ day^{-1})	Foraging (% Time)	Foraging (min day^{-1})	Foraging Costs (kJ day^{-1})	Resting (% Time)	Resting (min day^{-1})	Resting Costs (kJ day^{-1})	Pup Cost (kJ day^{-1})	Total Energy Expenditure (kJ day^{-1})
2	38.32	6%	92.16	1028.20	43%	622.08	6620.19	50%	725.76	3721.71	3931	15339.42
3	20.20	6%	92.16	1101.48	46%	664.33	7573.73	47%	683.51	3754.85	3931	16381.27
4	11.12	6%	92.16	1141.20	48%	688.02	8126.62	46%	659.82	3755.43	3931	16965.37
5	6.41	6%	92.16	1163.58	49%	701.63	8449.86	45%	646.21	3750.09	3931	17300.93
6	3.88	6%	92.16	1177.00	49%	709.90	8648.07	44%	637.94	3744.83	3931	17504.78
7	2.47	6%	92.16	1184.83	50%	714.75	8765.16	44%	633.09	3741.06	3931	17624.52
8	1.65	6%	92.16	1190.43	50%	718.24	8849.57	44%	629.60	3737.99	3931	17710.64
9	1.16	6%	92.16	1193.78	50%	720.35	8900.48	44%	627.49	3736.02	3931	17762.44
10	0.85	6%	92.16	1196.58	50%	722.10	8943.13	43%	625.74	3734.27	3931	17805.82
11	0.64	6%	92.16	1198.82	50%	723.52	8977.37	43%	624.32	3732.81	3931	17840.64
12	0.50	6%	92.16	1199.94	50%	724.22	8994.50	43%	623.62	3732.08	3931	17858.02
13	0.40	6%	92.16	1201.06	50%	724.93	9011.68	43%	622.91	3731.32	3931	17875.46
14	0.33	6%	92.16	1202.17	50%	725.64	9028.90	43%	622.20	3730.55	3931	17892.95
15	0.27	6%	92.16	1203.29	50%	726.35	9046.15	43%	621.49	3729.75	3931	17910.47
16	0.23	6%	92.16	1203.85	50%	726.70	9054.78	43%	621.14	3729.36	3931	17919.22
17	0.20	6%	92.16	1204.41	50%	727.06	9063.41	43%	620.78	3728.96	3931	17927.98
18	0.17	6%	92.16	1204.97	51%	727.41	9072.06	43%	620.43	3728.55	3931	17936.75
19	0.15	6%	92.16	1204.97	51%	727.41	9072.04	43%	620.43	3728.56	3931	17936.72

Table A.5: Model output values from the base model for males. The parameters that are shaded in lighter grey are energy costs that are added across each Year class to calculate the total energy expenditure. The parameters that are shaded in darker grey are the daily behaviour/activity budgets (percent of each day spent in each behaviour) that have been recalculated within the model to account for changes in energy expenditure.

Year Class	Age Class	Growth (kJ day^{-1})	Activity (% Time)	Activity (min day^{-1})	Activity Actual Costs (kJ day^{-1})	Foraging (% Time)	Foraging (min day^{-1})	Foraging Costs (kJ day^{-1})	Resting (% Time)	Resting (min day^{-1})	Resting Costs (kJ day^{-1})	Pup Cost (kJ day^{-1})	Total Energy Expenditure (kJ day^{-1})
0	pup	124.88	16%	223.20	2942.35	20%	292.32	2716.96	64%	624.48	3561.87	0.00	9347.06
1	juvenile	102.46	28%	404.64	3970.68	41%	596.16	5374.15	31%	439.20	2231.87	0.00	11679.16
2	subadult	63.98	26%	375.84	4646.01	39%	557.28	5812.12	35%	506.88	3115.24	0.00	13637.35
3	adult	38.94	24%	345.60	4942.61	36%	518.40	5766.38	40%	576.00	3941.69	0.00	14689.62
4	adult	24.25	24%	345.60	5224.17	38%	552.83	6499.67	38%	541.57	3917.18	0.00	15665.27
5	adult	15.21	24%	345.60	5399.65	40%	574.65	6983.21	36%	519.75	3885.61	0.00	16283.68
6	adult	9.59	24%	345.60	5511.50	41%	588.72	7302.29	35%	505.68	3858.79	0.00	16682.18
7	adult	6.09	24%	345.60	5580.93	41%	597.50	7504.63	35%	496.90	3839.50	0.00	16931.15
8	adult	3.89	24%	345.60	5625.28	42%	603.14	7635.65	34%	491.26	3826.10	0.00	17090.93
9	adult	2.49	24%	345.60	5654.21	42%	606.83	7721.86	34%	487.57	3816.90	0.00	17195.46
10	adult	1.61	24%	345.60	5671.57	42%	609.05	7773.84	34%	485.35	3811.22	0.00	17258.23
11	adult	1.04	24%	345.60	5683.14	42%	610.53	7808.62	34%	483.87	3807.35	0.00	17300.15
12	adult	0.68	24%	345.60	5690.85	42%	611.51	7831.87	34%	482.89	3804.74	0.00	17328.14
13	adult	0.45	24%	345.60	5696.64	43%	612.26	7849.35	33%	482.14	3802.75	0.00	17349.18
14	adult	0.29	24%	345.60	5700.49	43%	612.75	7861.02	33%	481.65	3801.42	0.00	17363.22
15	adult	0.19	24%	345.60	5702.42	43%	613.00	7866.85	33%	481.40	3800.75	0.00	17370.21
16	adult	0.13	24%	345.60	5704.35	43%	613.25	7872.70	33%	481.15	3800.08	0.00	17377.25
17	adult	0.09	24%	345.60	5704.35	43%	613.25	7872.67	33%	481.15	3800.09	0.00	17377.20
18	adult	0.06	24%	345.60	5704.35	43%	613.24	7872.66	33%	481.16	3800.10	0.00	17377.16
19	adult	0.04	24%	345.60	5706.28	43%	613.49	7878.53	33%	480.91	3799.41	0.00	17384.26

Appendix B

Appendix B shows the original mean values and their standard deviations that were used in the model, or in weighted averages. As described in the Chapter 2 Methodology sections, I estimated weighted averages using published data to calculate the model input values. For all parameters except for “pup cost” input into the model, there were individual measurements of variation in the published data. To properly account for variation within the weighted averages, I generated 10,000 random values using Monte Carlo simulations for each mean value within its reported standard deviation. I did this for each original value added into the weighted average (i.e., 4 original values to calculate a weighted average generated 40,000 total new values). I then used the standard deviation and mean of those 40,000 generated means as values in the model.

Table B.1: Values of variation in mass used in the second sensitivity analysis used to examine the effects of variation from current scientific publications on model outcomes. Raw data used to calculate these estimates from Tinker et al., (2019). Standard deviations listed as "0.00" in the table were values < 0.01.

Females			Males		
Year Class	**Average Mass (kg)**	**Standard Deviation (kg)**	**Year Class**	**Average Mass (kg)**	**Standard Deviation (kg)**
0	10.71	2.16	0	13.24	2.39
1	15.83	1.06	1	19.47	1.46
2	18.38	0.54	2	23.28	0.89
3	19.69	0.29	3	25.63	0.55
4	20.40	0.16	4	27.09	0.25
5	20.80	0.09	5	28.00	0.22
6	21.04	0.06	6	28.58	0.14
7	21.18	0.04	7	28.94	0.09
8	21.28	0.02	8	29.17	0.06
9	21.34	0.02	9	29.32	0.04
10	21.39	0.01	10	29.41	0.02
11	21.43	0.01	11	29.47	0.02
12	21.45	0.01	12	29.51	0.01
13	21.47	0.01	13	29.54	0.01
14	21.49	0.01	14	29.56	0.00
15	21.51	0.00	15	29.57	0.00
16	21.52	0.00	16	29.58	0.00
17	21.53	0.00	17	29.58	0.00
18	21.54	0.00	18	29.58	0.00
19	21.54	0.00	19	29.59	0.00

Table B.2: Values of variation in cost of tissue growth used in the second sensitivity analysis used to examine the effects of variation from current scientific publications on model outcomes. Raw data used to calculate these estimates from Tinker et al., (2019).

Females			Males		
Year Class	**Growth (kJ day^{-1})**	**Standard Deviation (kJ day^{-1})**	**Year Class**	**Growth (kJ day^{-1})**	**Standard Deviation (kJ day^{-1})**
0	133.41	29.47	0	147.28	22.31
1	75.58	15.87	1	102.46	15.20
2	38.32	7.62	2	62.93	9.20
3	20.20	3.77	3	38.93	5.61
4	11.12	1.93	4	24.25	3.44
5	6.41	1.02	5	15.21	2.13
6	3.88	0.56	6	9.59	1.33
7	2.47	0.32	7	6.09	0.83
8	1.65	0.19	8	3.89	0.52
9	1.16	0.12	9	2.49	0.33
10	0.85	0.08	10	1.61	0.21
11	0.64	0.05	11	1.04	0.14
12	0.50	0.04	12	0.68	0.09
13	0.40	0.03	13	0.44	0.57
14	0.33	0.02	14	0.29	0.04
15	0.27	0.01	15	0.19	0.02
16	0.23	0.01	16	0.13	0.02
17	0.20	0.01	17	0.09	0.01
18	0.17	0.01	18	0.06	0.01
19	0.14	0.01	19	0.04	0.01

Table B.3: Values of metabolic rates and associated variation used in the second sensitivity analysis used to examine the effects of variation from current scientific publications on model outcomes. Some sources had additional behaviours listed and they were categorized into one of the three main behaviour types and were averaged for use in the model. Values of metabolic rates and SD are in the original units reported in source literature.

Pups

Behaviour	Metabolic rate ($MJ\ day^{-1}$)	Standard Deviation ($MJ\ day^{-1}$)	Source
Resting	1.22	1.01	
Active	0.86	0.82	Thometz et al., 2014
Foraging	1.54	1.87	

Juveniles

Behaviour	Metabolic rate ($MJ\ day^{-1}$)	Standard Deviation ($MJ\ day^{-1}$)	Source
Resting	1.67	0.97	
Active	1.21	0.75	Thometz et al., 2014
Foraging	3.99	1.79	

Adult females without a pup

Behaviour	Metabolic rate ($ml\ O_2\ kg^{-1}\ min^{-1}$)	Standard Deviation ($ml\ O_2\ kg^{-1}\ min^{-1}$)	Source
Resting	13.50	1.80	
Active	24.74	5.38	Williams, 1989
Foraging	23.55	6.26	

Adult females with a pup

Behaviour	Metabolic rate ($ml\ O_2\ kg^{-1}\ min^{-1}$)	Standard Deviation ($ml\ O_2\ kg^{-1}\ min^{-1}$)	Source
Resting	14.06	2.55	Thometz, Kendall, et al., 2016

Adult males

Behaviour	Metabolic rate ($ml\ O_2\ kg^{-1}\ min^{-1}$)	Standard Deviation ($ml\ O_2\ kg^{-1}\ min^{-1}$)	Source
Resting	13.30	0.90	
Active	27.84	2.95	Yeates et al., 2007
Foraging	21.60	1.70	

Table B.4: Values of variation in behaviour budgets used in the second sensitivity analysis used to examine the effects of variation from current scientific publications on model outcomes.. All values are proportions representing how much of the day is spent in a given behaviour. There were three categories: Resting, Active, and Foraging. Some sources had additional behaviours listed within the daily activity budgets. For use in the model, they were categorized into one of the three main behaviour types. For sections with more than the three categories, the darker shade of grey is all behaviours categorized into "Resting". The lighter grey is behaviours categorized into "Active" which represents non-foraging activity. Foraging behaviours are in white. In the tables with values for pups, juveniles, and adult males, bolded rows denote the values used as model inputs.

Pups

Behaviour	Percent of day	Standard Deviation
Resting on mother	9.45	16.94
Resting on water	29.31	21.77
Nursing on mother	5.52	8.51
Nursing in water	8.48	10.06
Groomed by mother	8.58	10.37
Passive Grooming	2.97	3.77
Total Resting	**64.31**	**28.50**
Active Grooming	5.94	6.15
Swimming	8.14	11.62
Other	1.40	2.79
Total Active	**15.50**	**10.90**
Foraging	**20.36**	**22.34**

Source: Thometz et al., 2014

Juveniles

Behaviour	Percent of day	Standard Deviation
Resting in water	28.90	16.60
Passive Grooming	1.60	2.60
Total Resting	**30.50**	**15.30**
Active Grooming	7.00	5.20
Swimming	16.00	7.50
Other	5.00	5.00
Total Active	**28.00**	**9.30**
Foraging	**41.40**	**17.40**

Source: Thometz et al., 2014

Adult females without a pup

Behaviour	Percent of day	Standard Deviation
Resting	51.60	4.90
Active	8.70	3.80
Foraging	39.70	6.60

Source: (Staedler, 2011; Thometz et al., 2014)

Adult females with a pup

Behaviour	Percent of day	Standard Deviation
Resting	52.04	11.00
Active	6.44	1.68
Foraging	44.78	7.89
	Source: (Staedler, 2011; Thometz et al., 2014)	

Adult males

Behaviour	Percent of day	Standard Deviation
Resting	**39.68**	**7.81**
Swimming	8.38	6.71
Grooming	8.97	1.87
Other	7.20	5.72
Total Active	**24.51**	**7.60**
Foraging	**35.83**	**7.37**
	Source: Yeates et al., 2007	

Table B.5: Sensitivity analysis results for total energy expenditure for females without a pup. For this analysis, all model parameters were varied at once using variation from publications. All values are in kJ day^{-1}.

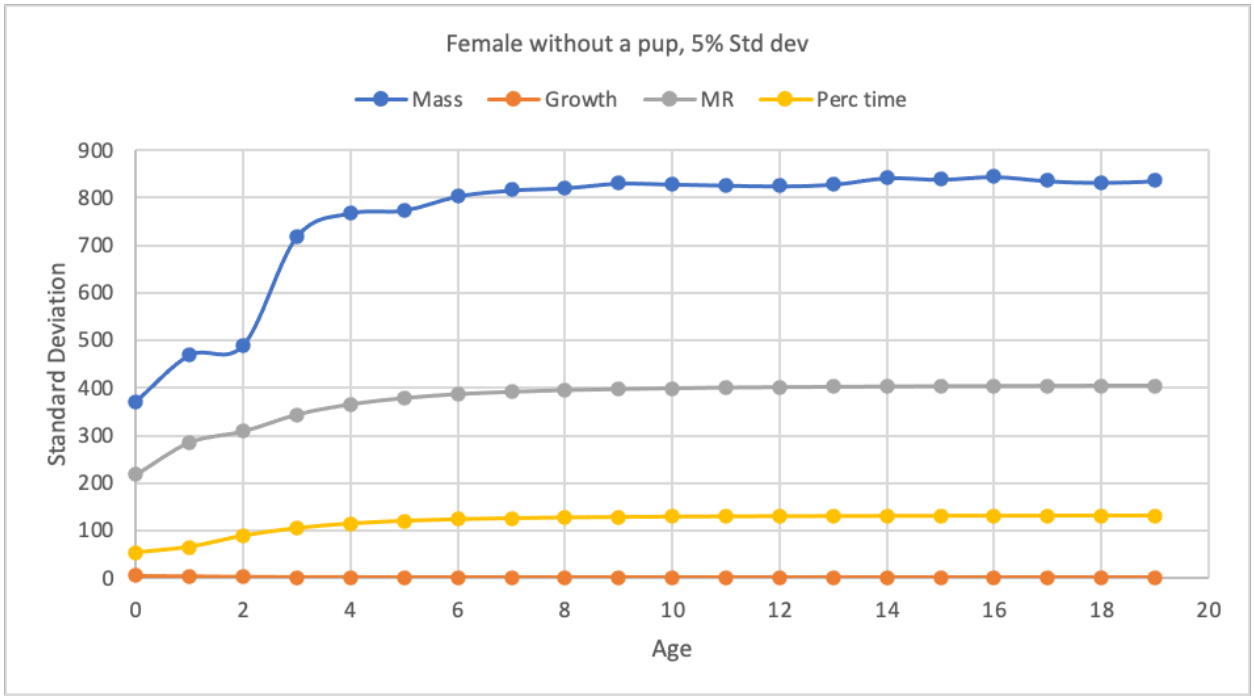
Year Class	Age Class	Mean Value	Standard Deviation	Standard Error	Lower Confidence interval	Upper Confidence Interval
0	pup	7914.35	24385.77	243.86	7436.34	8392.36
1	juvenile	9492.22	2711.07	27.11	9439.08	9545.36
2	adult	9834.47	1494.03	14.94	9805.18	9863.75
3	adult	10749.04	1736.14	17.36	10715.01	10783.07
4	adult	11262.72	1876.43	18.76	11225.94	11299.51
5	adult	11555.82	1962.22	19.62	11517.35	11594.28
6	adult	11737.36	2018.29	20.18	11697.80	11776.93
7	adult	11843.48	2051.86	20.52	11803.26	11883.70
8	adult	11919.93	2076.39	20.76	11879.23	11960.64
9	adult	11965.81	2090.86	20.91	11924.82	12006.79
10	adult	12004.50	2103.68	21.04	11963.26	12045.73
11	adult	12035.35	2113.74	21.14	11993.92	12076.78
12	adult	12050.90	2118.70	21.19	12009.37	12092.43
13	adult	12066.33	2123.72	21.24	12024.70	12107.96
14	adult	12081.94	2128.96	21.29	12040.21	12123.67
15	adult	12097.57	2134.01	21.34	12055.74	12139.40
16	adult	12105.38	2136.56	21.37	12063.50	12147.27
17	adult	12113.20	2139.18	21.39	12071.27	12155.13
18	adult	12120.99	2141.71	21.42	12079.00	12162.97
19	adult	12120.97	2141.74	21.42	12078.99	12162.95

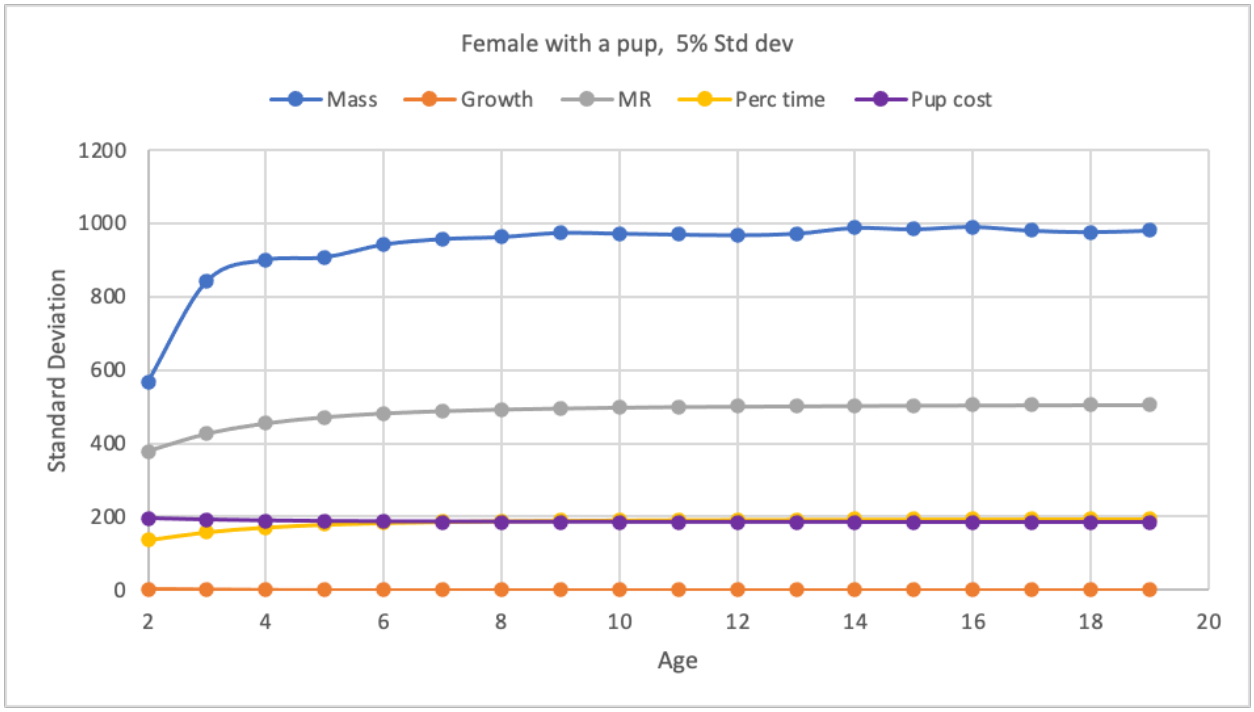
Table B.6: Sensitivity analysis results for total energy expenditure for females with a pup. For this analysis, all model parameters were varied at once using variation from publications. All values are in kJ day^{-1}.

Year Class	Age Class	Mean Value	Standard Deviation	Standard Error	Lower Confidence interval	Upper Confidence Interval
2	adult	15363.88	1113.81	11.14	15342.04	15385.71
3	adult	16419.98	1207.20	12.07	16396.32	16443.65
4	adult	17012.58	1249.24	12.49	16988.09	17037.07
5	adult	17350.45	1284.09	12.84	17325.28	17375.62
6	adult	17558.42	1305.37	13.05	17532.84	17584.01
7	adult	17679.97	1318.55	13.19	17654.13	17705.82
8	adult	17767.66	1329.05	13.29	17741.61	17793.71
9	adult	17820.25	1335.26	13.35	17794.07	17846.42
10	adult	17864.41	1340.41	13.40	17838.13	17890.68
11	adult	17899.70	1344.55	13.45	17873.34	17926.05
12	adult	17917.51	1346.70	13.47	17891.11	17943.91
13	adult	17935.16	1348.78	13.49	17908.72	17961.60
14	adult	17952.97	1351.03	13.51	17926.49	17979.45
15	adult	17970.84	1353.10	13.53	17944.32	17997.36
16	adult	17979.78	1354.19	13.54	17953.24	18006.33
17	adult	17988.68	1355.20	13.55	17962.12	18015.25
18	adult	17997.59	1356.26	13.56	17971.01	18024.18
19	adult	17997.56	1356.29	13.56	17970.98	18024.15

Table B.7: Sensitivity analysis results for total energy expenditure for males. For this analysis, all model parameters were varied at once using variation from publications. All values are in kJ day^{-1}.

Year Class	Age Class	Mean Value	Standard Deviation	Standard Error	Lower Confidence interval	Upper Confidence Interval
0	pup	8601.73	41749.30	417.49	7783.36	9420.10
1	juvenile	11753.28	3436.36	34.36	11685.92	11820.63
2	subadult	13672.03	1938.36	19.38	13634.03	13710.02
3	adult	14675.75	1018.46	10.18	14655.79	14695.71
4	adult	15659.74	1060.64	10.61	15638.94	15680.53
5	adult	16281.33	1103.25	11.03	16259.70	16302.96
6	adult	16680.48	1128.11	11.28	16658.37	16702.60
7	adult	16931.70	1144.23	11.44	16909.27	16954.12
8	adult	17092.70	1155.89	11.56	17070.04	17115.35
9	adult	17197.54	1163.88	11.64	17174.73	17220.35
10	adult	17260.36	1168.87	11.69	17237.45	17283.27
11	adult	17302.75	1172.11	11.72	17279.77	17325.72
12	adult	17330.87	1174.14	11.74	17307.86	17353.89
13	adult	17352.04	1175.96	11.76	17328.99	17375.09
14	adult	17366.21	1177.00	11.77	17343.14	17389.28
15	adult	17373.19	1177.47	11.77	17350.11	17396.27
16	adult	17380.27	1178.06	11.78	17357.18	17403.37
17	adult	17380.22	1178.04	11.78	17357.13	17403.31
18	adult	17380.19	1178.05	11.78	17357.10	17403.28
19	adult	17387.31	1178.61	11.79	17364.21	17410.42


Female without a pup, 5% Std dev
Mass
Growth
MR
Perc time
Standard Deviation
900
800
700
600
500
400
300
200
100
0
0
2
4
6
8
10
12
14
16
18
20
Age


Female with a pup, 5% Std dev
Mass
Growth
MR
Perc time
Pup cost
Standard Deviation
1200
1000
800
600
400
200
0
2
4
6
8
10
12
14
16
18
20
Age

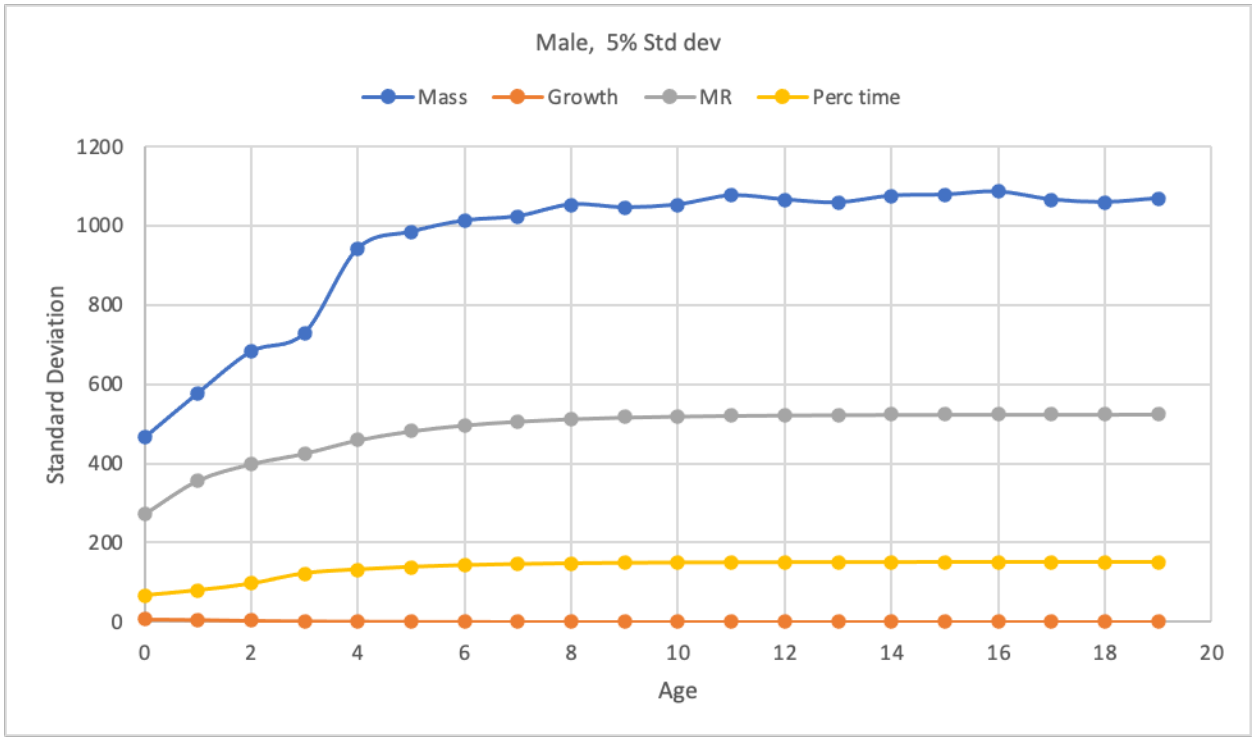
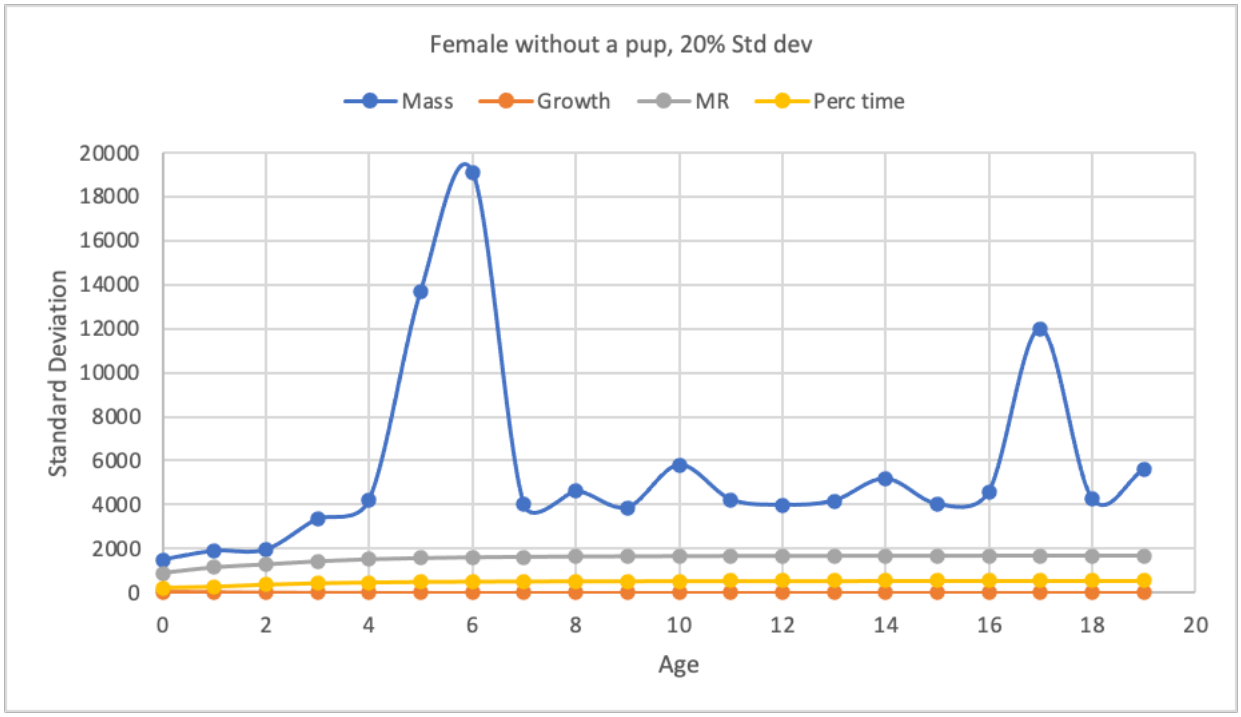
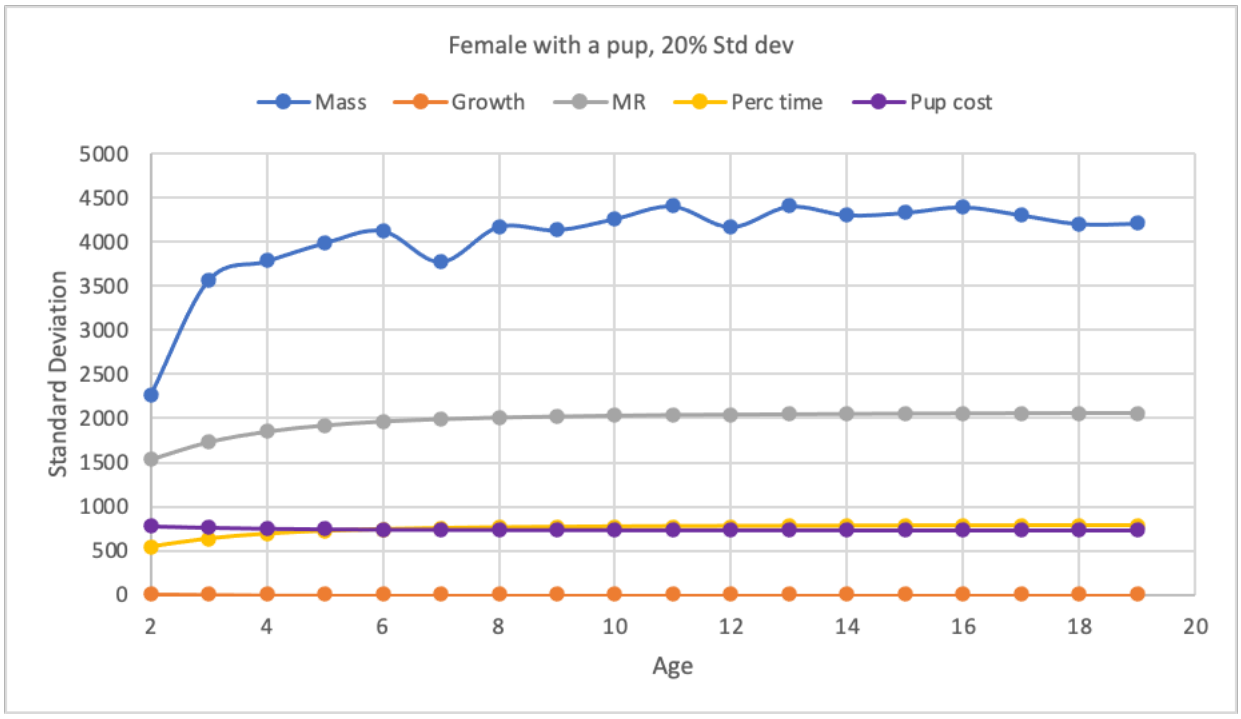


Figure B.1: Overall variation in model output when all parameters varied by 5% of mean. Comparisons of the standard deviation from the mean measured by varying each model parameter (mass, growth, metabolic rate, percent of day spent in each behaviour, and cost of caring for a pup) by a set amount for each of the three models (Male, Female without Pup, Female with Pup). These results were obtained from 10,000 runs of each model. All SD values in kJ day^{-1}.


Female without a pup, 20% Std dev
Mass
Growth
MR
Perc time
Standard Deviation
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
0
2
4
6
8
10
12
14
16
18
20
Age


Female with a pup, 20% Std dev
Mass
Growth
MR
Perc time
Pup cost
Standard Deviation
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
2
4
6
8
10
12
14
16
18
20
Age

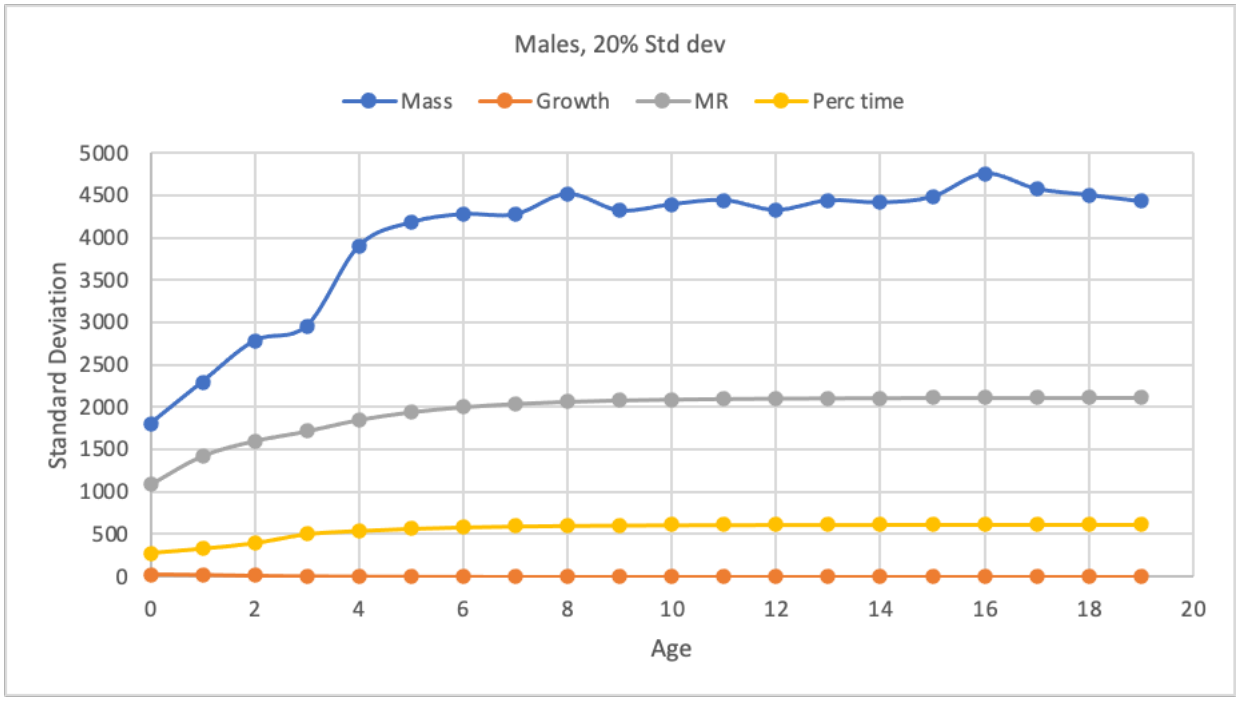


Figure B.2: Overall variation in model output when all parameters varied by 20% of mean. Comparisons of the standard deviation from the mean measured by varying each model parameter (mass, growth, metabolic rate, percent of day spent in each behaviour, and cost of caring for a pup) by a set amount for each of the three models (Male, Female without Pup, Female with Pup). These results were obtained from 10,000 runs of each model. All SD values in kJ day^{-1}.

Appendix C

Additional tables for Chapter 3.

Table C.1: Ingested food mass and captured biomass associated with Diet 1 (*Cancer* crab and abalone). Values were calculated from the energy expenditures calculated by the model in Chapter 2 and converted using energy density of the prey items in each diet and edible proportion of prey (Oftedal et al., 2007). Diet proportions adapted from Tinker et al (2007).

Year Class	Females without a pup		Females with a pup		Males	
	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)
0	3869.18	5258.06	--	--	4987.26	6777.48
1	4825.31	6557.40	--	--	6257.62	8503.86
2	5146.77	6994.25	8006.22	10880.13	7159.95	9730.08
3	5612.09	7626.60	8552.87	11623.01	7669.17	10422.10
4	5870.93	7978.35	8857.33	12036.76	8178.00	11113.58
5	6019.46	8180.21	9032.15	12274.33	8501.42	11553.09
6	6108.25	8300.86	9136.68	12416.37	8707.03	11832.51
7	6163.83	8376.39	9202.10	12505.29	8838.03	12010.53
8	6200.33	8426.00	9245.07	12563.68	8921.77	12124.33
9	6225.46	8460.15	9274.65	12603.88	8975.52	12197.38
10	6243.53	8484.71	9295.92	12632.78	9010.17	12244.46
11	6257.05	8503.07	9311.82	12654.39	9032.61	12274.95
12	6267.49	8517.26	9324.10	12671.08	9047.21	12294.79
13	6275.78	8528.53	9333.85	12684.33	9056.75	12307.75
14	6282.50	8537.67	9341.77	12695.09	9063.01	12316.26
15	6288.06	8545.22	9348.30	12703.97	9067.14	12321.88
16	6292.72	8551.55	9353.78	12711.41	9069.87	12325.59
17	6296.66	8556.91	9358.42	12717.71	9071.69	12328.06
18	6300.03	8561.49	9362.38	12723.10	9072.91	12329.72
19	6302.93	8565.43	9365.79	12727.74	9073.72	12330.82

Table C.2: Ingested food mass and captured biomass associated with Diet 2 (*Tegula* marine snails). Values were calculated from the energy expenditures calculated by the model in Chapter 2 and converted using energy density of the prey items in each diet and edible proportion of prey (Oftedal et al., 2007). Diet proportions adapted from Tinker et al (2007).

Year Class	Females without a pup		Females with a pup		Males	
	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)
0	3948.55	5174.46	--	--	5089.56	6669.72
1	4924.28	6453.14	--	--	6385.98	8368.64
2	5252.34	6883.04	8170.44	10707.13	7306.81	9575.37
3	5727.20	7505.34	8728.31	11438.20	7826.48	10256.38
4	5991.35	7851.50	9039.02	11845.37	8345.75	10936.87
5	6142.93	8050.14	9217.42	12079.17	8675.80	11369.39
6	6233.54	8168.88	9324.09	12218.95	8885.63	11644.36
7	6290.26	8243.21	9390.86	12306.45	9019.32	11819.56
8	6327.51	8292.02	9434.71	12363.92	9104.78	11931.55
9	6353.16	8325.63	9464.89	12403.47	9159.63	12003.43
10	6371.60	8349.80	9486.60	12431.92	9194.99	12049.77
11	6385.39	8367.87	9502.82	12453.18	9217.89	12079.78
12	6396.04	8381.84	9515.36	12469.61	9232.78	12099.30
13	6404.50	8392.92	9525.31	12482.65	9242.52	12112.06
14	6411.37	8401.92	9533.38	12493.23	9248.91	12120.43
15	6417.04	8409.35	9540.06	12501.97	9253.12	12125.95
16	6421.79	8415.58	9545.64	12509.30	9255.91	12129.61
17	6425.82	8420.85	9550.38	12515.50	9257.77	12132.04
18	6429.26	8425.36	9554.42	12520.80	9259.01	12133.67
19	6432.22	8429.24	9557.90	12525.36	9259.84	12134.76

Table C.3: Ingested food mass and captured biomass associated with Diet 3 (Kelp crabs and bivalves). Values were calculated from the energy expenditures calculated by the model in Chapter 2 and converted using energy density of the prey items in each diet and edible proportion of prey (Oftedal et al., 2007). Diet proportions adapted from Tinker et al (2007).

Year Class	Females without a pup		Females with a pup		Males	
	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)
0	3987.55	5349.57	--	--	5139.83	6895.43
1	4972.93	6671.52	--	--	6449.06	8651.85
2	5304.23	7115.98	8251.15	11069.47	7378.99	9899.41
3	5783.78	7759.33	8814.53	11825.28	7903.80	10603.47
4	6050.54	8117.20	9128.31	12246.24	8428.19	11306.99
5	6203.62	8322.57	9308.48	12487.95	8761.51	11754.15
6	6295.12	8445.33	9416.20	12632.46	8973.41	12038.43
7	6352.40	8522.17	9483.63	12722.92	9108.41	12219.55
8	6390.02	8572.64	9527.91	12782.33	9194.72	12335.33
9	6415.92	8607.38	9558.39	12823.22	9250.11	12409.65
10	6434.54	8632.37	9580.31	12852.63	9285.82	12457.55
11	6448.47	8651.05	9596.70	12874.61	9308.95	12488.58
12	6459.23	8665.49	9609.36	12891.60	9323.99	12508.76
13	6467.77	8676.95	9619.41	12905.08	9333.82	12521.95
14	6474.71	8686.25	9627.56	12916.02	9340.27	12530.60
15	6480.43	8693.93	9634.30	12925.06	9344.53	12536.31
16	6485.23	8700.37	9639.94	12932.63	9347.35	12540.10
17	6489.29	8705.82	9644.72	12939.04	9349.22	12542.61
18	6492.77	8710.48	9648.81	12944.52	9350.48	12544.29
19	6495.76	8714.49	9652.32	12949.24	9351.32	12545.42

Table C.4: Ingested food mass and captured biomass associated with Diet 4 (Urchin). Values were calculated from the energy expenditures calculated by the model in Chapter 2 and converted using energy density of the prey items in each diet and edible proportion of prey (Oftedal et al., 2007). Diet proportions adapted from Fujii et al (2017).

Year Class	Females without a pup		Females with a pup		Males	
	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)
0	4446.22	7329.26	--	--	5731.04	9447.20
1	5544.94	9140.42	--	--	7190.86	11853.61
2	5914.35	9749.36	9200.24	15165.91	8227.76	13562.85
3	6449.06	10630.80	9828.42	16201.42	8812.93	14527.46
4	6746.50	11121.10	10178.29	16778.16	9397.65	15491.32
5	6917.19	11402.47	10379.18	17109.31	9769.30	16103.96
6	7019.22	11570.65	10499.29	17307.30	10005.57	16493.44
7	7083.08	11675.93	10574.48	17431.24	10156.11	16741.59
8	7125.03	11745.08	10623.86	17512.64	10252.34	16900.22
9	7153.91	11792.68	10657.85	17568.67	10314.11	17002.04
10	7174.68	11826.92	10682.29	17608.96	10353.92	17067.67
11	7190.20	11852.52	10700.56	17639.07	10379.71	17110.18
12	7202.20	11872.29	10714.67	17662.34	10396.48	17137.83
13	7211.73	11887.99	10725.88	17680.81	10407.44	17155.90
14	7219.46	11900.74	10734.97	17695.80	10414.64	17167.76
15	7225.84	11911.27	10742.48	17708.19	10419.38	17175.58
16	7231.19	11920.09	10748.78	17718.56	10422.53	17180.76
17	7235.73	11927.56	10754.11	17727.34	10424.62	17184.21
18	7239.60	11933.94	10758.66	17734.85	10426.01	17186.51
19	7242.93	11939.43	10762.58	17741.31	10426.95	17188.05

Table C.5: Ingested food mass and captured biomass associated with Diet 5, a general sea otter diet. Values were calculated from the energy expenditures calculated by the model in Chapter 2 and converted using energy density of the prey items in each diet and edible proportion of prey (Oftedal et al., 2007). Diet proportions adapted from Tinker (2004).

Year Class	Females without a pup		Females with a pup		Males	
	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)	Ingested Food Mass (g)	Total Captured Biomass (g)
0	4067.78	6373.49	--	--	5243.25	8215.24
1	5072.99	7948.47	--	--	6578.82	10307.84
2	5410.95	8477.99	8417.17	13188.20	7527.46	11794.18
3	5900.15	9244.49	8991.88	14088.67	8062.83	12633.01
4	6172.28	9670.86	9311.98	14590.20	8597.78	13471.17
5	6328.44	9915.53	9495.77	14878.17	8937.79	14003.92
6	6421.78	10061.78	9605.66	15050.34	9153.96	14342.61
7	6480.21	10153.33	9674.44	15158.12	9291.68	14558.40
8	6518.59	10213.46	9719.62	15228.90	9379.72	14696.35
9	6545.01	10254.86	9750.71	15277.62	9436.23	14784.89
10	6564.01	10284.63	9773.07	15312.66	9472.66	14841.96
11	6578.22	10306.89	9789.79	15338.85	9496.25	14878.92
12	6589.19	10324.09	9802.70	15359.08	9511.60	14902.97
13	6597.91	10337.74	9812.95	15375.14	9521.62	14918.68
14	6604.98	10348.82	9821.27	15388.18	9528.21	14929.00
15	6610.82	10357.98	9828.15	15398.95	9532.55	14935.80
16	6615.72	10365.65	9833.90	15407.97	9535.42	14940.30
17	6619.86	10372.14	9838.78	15415.61	9537.34	14943.30
18	6623.41	10377.69	9842.95	15422.14	9538.61	14945.30
19	6626.46	10382.47	9846.53	15427.76	9539.47	14946.64

Table C.6: Number of prey items by species that a female sea otter needs to consume per day based on a general otter diet (Diet 5). Data provided for each Year class, as well as for mean across adult Year classes (2-19).

Female without a pup								Female with a pup							
Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails	Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails
0	2.4	11.2	10.4	20.0	13.8	22.1	21.5	0	--	--	--	--	--	--	--
1	2.9	13.9	13.0	25.0	17.2	27.5	26.8	1	--	--	--	--	--	--	--
2	3.1	14.9	13.9	26.6	18.3	29.3	28.6	2	4.9	23.1	21.6	41.4	28.5	45.6	44.5
3	3.4	16.2	15.1	29.0	20.0	32.0	31.2	3	5.2	24.7	23.1	44.2	30.4	48.8	47.5
4	3.6	17.0	15.8	30.4	20.9	33.5	32.6	4	5.4	25.6	23.9	45.8	31.5	50.5	49.2
5	3.7	17.4	16.2	31.1	21.4	34.3	33.4	5	5.5	26.1	24.4	46.7	32.2	51.5	50.2
6	3.7	17.6	16.5	31.6	21.7	34.8	33.9	6	5.6	26.4	24.6	47.2	32.5	52.1	50.7
7	3.8	17.8	16.6	31.9	21.9	35.1	34.2	7	5.6	26.6	24.8	47.6	32.8	52.5	51.1
8	3.8	17.9	16.7	32.1	22.1	35.3	34.4	8	5.6	26.7	24.9	47.8	32.9	52.7	51.3
9	3.8	18.0	16.8	32.2	22.2	35.5	34.6	9	5.7	26.8	25.0	48.0	33.0	52.9	51.5
10	3.8	18.0	16.8	32.3	22.2	35.6	34.7	10	5.7	26.9	25.1	48.1	33.1	53.0	51.6
11	3.8	18.1	16.9	32.4	22.3	35.7	34.7	11	5.7	26.9	25.1	48.2	33.1	53.1	51.7
12	3.8	18.1	16.9	32.4	22.3	35.7	34.8	12	5.7	26.9	25.1	48.2	33.2	53.2	51.8
13	3.8	18.1	16.9	32.5	22.3	35.8	34.8	13	5.7	27.0	25.2	48.3	33.2	53.2	51.8
14	3.8	18.1	16.9	32.5	22.4	35.8	34.9	14	5.7	27.0	25.2	48.3	33.3	53.3	51.9
15	3.8	18.2	17.0	32.5	22.4	35.8	34.9	15	5.7	27.0	25.2	48.3	33.3	53.3	51.9
16	3.8	18.2	17.0	32.5	22.4	35.9	34.9	16	5.7	27.0	25.2	48.4	33.3	53.3	51.9
17	3.8	18.2	17.0	32.6	22.4	35.9	35.0	17	5.7	27.0	25.2	48.4	33.3	53.3	52.0
18	3.8	18.2	17.0	32.6	22.4	35.9	35.0	18	5.7	27.0	25.2	48.4	33.3	53.4	52.0
19	3.8	18.2	17.0	32.6	22.4	35.9	35.0	19	5.7	27.1	25.3	48.4	33.3	53.4	52.0
Adult mean	**3.7**	**17.7**	**16.5**	**31.6**	**21.8**	**34.9**	**34.0**	**Adult mean**	**5.6**	**26.4**	**24.7**	**47.3**	**32.6**	**52.2**	**50.8**

Table C.7: Number of prey items by species that a male sea otter needs to consume per day based on a general otter diet (Diet 5). Data provided for each Year class, as well as for mean across adult Year classes (3-19).

Males

Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails
0	3.0	14.4	13.4	25.8	17.8	28.4	27.7
1	3.8	18.1	16.9	32.4	22.3	35.7	34.7
2	4.4	20.7	19.3	37.0	25.5	40.8	39.8
3	4.7	22.2	20.7	39.7	27.3	43.7	42.6
4	5.0	23.6	22.0	42.3	29.1	46.6	45.4
5	5.2	24.6	22.9	44.0	30.3	48.5	47.2
6	5.3	25.2	23.5	45.0	31.0	49.6	48.3
7	5.4	25.5	23.8	45.7	31.5	50.4	49.1
8	5.4	25.8	24.1	46.1	31.8	50.9	49.5
9	5.5	25.9	24.2	46.4	31.9	51.2	49.8
10	5.5	26.0	24.3	46.6	32.1	51.4	50.0
11	5.5	26.1	24.4	46.7	32.2	51.5	50.2
12	5.5	26.1	24.4	46.8	32.2	51.6	50.2
13	5.5	26.2	24.4	46.8	32.2	51.6	50.3
14	5.5	26.2	24.4	46.9	32.3	51.7	50.3
15	5.5	26.2	24.4	46.9	32.3	51.7	50.3
16	5.5	26.2	24.5	46.9	32.3	51.7	50.4
17	5.5	26.2	24.5	46.9	32.3	51.7	50.4
18	5.5	26.2	24.5	46.9	32.3	51.7	50.4
19	5.5	26.2	24.5	46.9	32.3	51.7	50.4
Adult mean	**5.4**	**25.5**	**23.8**	**45.7**	**31.5**	**50.4**	**49.1**

Table C.8: Number of prey items by species that a female sea otter needs to consume per day based on Diet 1, a specialist diet that prefers abalone and *Cancer* crabs. Data provided for each Year class, as well as for mean across adult Year classes (2-19).

Female without a pup								Female with a pup							
Year Class	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**	**Year Class**	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**
0	1.5	15.2	4.5	1.0	0.5	0.5	0.7	0	--	--	--	--	--	--	--
1	1.9	18.9	5.6	1.2	0.6	0.6	0.9	1	--	--	--	--	--	--	--
2	2.0	20.2	5.9	1.3	0.7	0.7	1.0	2	3.1	31.4	9.3	2.1	1.0	1.0	1.5
3	2.2	22.0	6.5	1.4	0.7	0.7	1.1	3	3.3	33.5	9.9	2.2	1.1	1.1	1.6
4	2.3	23.0	6.8	1.5	0.8	0.8	1.1	4	3.4	34.7	10.2	2.3	1.1	1.1	1.7
5	2.3	23.6	7.0	1.5	0.8	0.8	1.2	5	3.5	35.4	10.4	2.3	1.2	1.2	1.7
6	2.4	23.9	7.1	1.6	0.8	0.8	1.2	6	3.5	35.8	10.6	2.3	1.2	1.2	1.8
7	2.4	24.1	7.1	1.6	0.8	0.8	1.2	7	3.5	36.1	10.6	2.4	1.2	1.2	1.8
8	2.4	24.3	7.2	1.6	0.8	0.8	1.2	8	3.6	36.2	10.7	2.4	1.2	1.2	1.8
9	2.4	24.4	7.2	1.6	0.8	0.8	1.2	9	3.6	36.3	10.7	2.4	1.2	1.2	1.8
10	2.4	24.5	7.2	1.6	0.8	0.8	1.2	10	3.6	36.4	10.7	2.4	1.2	1.2	1.8
11	2.4	24.5	7.2	1.6	0.8	0.8	1.2	11	3.6	36.5	10.8	2.4	1.2	1.2	1.8
12	2.4	24.6	7.2	1.6	0.8	0.8	1.2	12	3.6	36.5	10.8	2.4	1.2	1.2	1.8
13	2.4	24.6	7.3	1.6	0.8	0.8	1.2	13	3.6	36.6	10.8	2.4	1.2	1.2	1.8
14	2.4	24.6	7.3	1.6	0.8	0.8	1.2	14	3.6	36.6	10.8	2.4	1.2	1.2	1.8
15	2.4	24.6	7.3	1.6	0.8	0.8	1.2	15	3.6	36.6	10.8	2.4	1.2	1.2	1.8
16	2.4	24.7	7.3	1.6	0.8	0.8	1.2	16	3.6	36.6	10.8	2.4	1.2	1.2	1.8
17	2.4	24.7	7.3	1.6	0.8	0.8	1.2	17	3.6	36.7	10.8	2.4	1.2	1.2	1.8
18	2.4	24.7	7.3	1.6	0.8	0.8	1.2	18	3.6	36.7	10.8	2.4	1.2	1.2	1.8
19	2.4	24.7	7.3	1.6	0.8	0.8	1.2	19	3.6	36.7	10.8	2.4	1.2	1.2	1.8
Adult mean	**2.4**	**24.0**	**7.1**	**1.6**	**0.8**	**0.8**	**2.4**	**Adult mean**	**3.5**	**35.8**	**10.6**	**2.4**	**1.2**	**1.2**	**1.8**

Table C.9: Number of prey items by species that a male sea otter needs to consume per day based on Diet 1, a specialist diet that prefers abalone and *Cancer* crabs. Data provided for each Year class, as well as for mean across adult Year classes (3-19).

Males

Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails
0	1.9	19.5	5.8	1.3	0.6	0.6	1.0
1	2.4	24.5	7.2	1.6	0.8	0.8	1.2
2	2.8	28.0	8.3	1.8	0.9	0.9	1.4
3	3.0	30.0	8.9	2.0	1.0	1.0	1.5
4	3.2	32.0	9.5	2.1	1.1	1.1	1.6
5	3.3	33.3	9.8	2.2	1.1	1.1	1.6
6	3.4	34.1	10.1	2.2	1.1	1.1	1.7
7	3.4	34.6	10.2	2.3	1.1	1.1	1.7
8	3.4	35.0	10.3	2.3	1.1	1.1	1.7
9	3.5	35.2	10.4	2.3	1.2	1.2	1.7
10	3.5	35.3	10.4	2.3	1.2	1.2	1.7
11	3.5	35.4	10.4	2.3	1.2	1.2	1.7
12	3.5	35.4	10.5	2.3	1.2	1.2	1.7
13	3.5	35.5	10.5	2.3	1.2	1.2	1.7
14	3.5	35.5	10.5	2.3	1.2	1.2	1.7
15	3.5	35.5	10.5	2.3	1.2	1.2	1.7
16	3.5	35.5	10.5	2.3	1.2	1.2	1.7
17	3.5	35.5	10.5	2.3	1.2	1.2	1.7
18	3.5	35.5	10.5	2.3	1.2	1.2	1.7
19	3.5	35.5	10.5	2.3	1.2	1.2	1.7
Adult mean	**3.4**	**34.6**	**10.2**	**2.3**	**1.1**	**1.1**	**1.7**

Table C.10: Number of prey items by species that a female sea otter needs to consume per day based on Diet 2, a specialist diet that prefers marine snails. Data provided for each Year class, as well as for mean across adult Year classes (2-19).

Female without a pup								Female with a pup							
Year Class	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**	**Year Class**	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**
0	0.0	12.6	20.0	0.0	3.2	0.0	56.8	0	--	--	--	--	--	--	--
1	0.0	15.7	24.9	0.0	3.9	0.0	70.8	1	--	--	--	--	--	--	--
2	0.0	16.8	26.6	0.0	4.2	0.0	75.5	2	0.0	26.1	41.3	0.0	6.5	0.0	117.5
3	0.0	18.3	29.0	0.0	4.6	0.0	82.4	3	0.0	27.9	44.2	0.0	7.0	0.0	125.5
4	0.0	19.1	30.3	0.0	4.8	0.0	86.2	4	0.0	28.9	45.7	0.0	7.2	0.0	130.0
5	0.0	19.6	31.1	0.0	4.9	0.0	88.4	5	0.0	29.5	46.6	0.0	7.4	0.0	132.6
6	0.0	19.9	31.5	0.0	5.0	0.0	89.7	6	0.0	29.8	47.2	0.0	7.5	0.0	134.1
7	0.0	20.1	31.8	0.0	5.0	0.0	90.5	7	0.0	30.0	47.5	0.0	7.5	0.0	135.1
8	0.0	20.2	32.0	0.0	5.1	0.0	91.0	8	0.0	30.2	47.7	0.0	7.5	0.0	135.7
9	0.0	20.3	32.2	0.0	5.1	0.0	91.4	9	0.0	30.3	47.9	0.0	7.6	0.0	136.1
10	0.0	20.4	32.2	0.0	5.1	0.0	91.6	10	0.0	30.3	48.0	0.0	7.6	0.0	136.4
11	0.0	20.4	32.3	0.0	5.1	0.0	91.8	11	0.0	30.4	48.1	0.0	7.6	0.0	136.7
12	0.0	20.4	32.4	0.0	5.1	0.0	92.0	12	0.0	30.4	48.2	0.0	7.6	0.0	136.9
13	0.0	20.5	32.4	0.0	5.1	0.0	92.1	13	0.0	30.4	48.2	0.0	7.6	0.0	137.0
14	0.0	20.5	32.4	0.0	5.1	0.0	92.2	14	0.0	30.5	48.2	0.0	7.6	0.0	137.1
15	0.0	20.5	32.5	0.0	5.1	0.0	92.3	15	0.0	30.5	48.3	0.0	7.6	0.0	137.2
16	0.0	20.5	32.5	0.0	5.1	0.0	92.4	16	0.0	30.5	48.3	0.0	7.6	0.0	137.3
17	0.0	20.5	32.5	0.0	5.1	0.0	92.4	17	0.0	30.5	48.3	0.0	7.6	0.0	137.4
18	0.0	20.5	32.5	0.0	5.1	0.0	92.5	18	0.0	30.5	48.4	0.0	7.6	0.0	137.4
19	0.0	20.6	32.6	0.0	5.1	0.0	92.5	19	0.0	30.5	48.4	0.0	7.6	0.0	137.5
Adult mean	**0.0**	**20.0**	**31.6**	**0.0**	**5.0**	**0.0**	**89.8**	**Adult mean**	**0.0**	**29.8**	**47.3**	**0.0**	**7.5**	**0.0**	**134.3**

Table C.11: Number of prey items by species that a male sea otter needs to consume per day based on Diet 2 a specialist diet that prefers marine snails. Data provided for each Year class, as well as for mean across adult Year classes (3-19).

Males

Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails
0	0.0	16.3	25.8	0.0	4.1	0.0	73.2
1	0.0	20.4	32.3	0.0	5.1	0.0	91.8
2	0.0	23.4	37.0	0.0	5.8	0.0	105.1
3	0.0	25.0	39.6	0.0	6.3	0.0	112.6
4	0.0	26.7	42.2	0.0	6.7	0.0	120.0
5	0.0	27.7	43.9	0.0	6.9	0.0	124.8
6	0.0	28.4	45.0	0.0	7.1	0.0	127.8
7	0.0	28.8	45.6	0.0	7.2	0.0	129.7
8	0.0	29.1	46.1	0.0	7.3	0.0	131.0
9	0.0	29.3	46.4	0.0	7.3	0.0	131.7
10	0.0	29.4	46.5	0.0	7.3	0.0	132.3
11	0.0	29.5	46.6	0.0	7.4	0.0	132.6
12	0.0	29.5	46.7	0.0	7.4	0.0	132.8
13	0.0	29.5	46.8	0.0	7.4	0.0	132.9
14	0.0	29.6	46.8	0.0	7.4	0.0	133.0
15	0.0	29.6	46.8	0.0	7.4	0.0	133.1
16	0.0	29.6	46.8	0.0	7.4	0.0	133.1
17	0.0	29.6	46.9	0.0	7.4	0.0	133.2
18	0.0	29.6	46.9	0.0	7.4	0.0	133.2
19	0.0	29.6	46.9	0.0	7.4	0.0	133.2
Adult mean	**0.0**	**28.8**	**45.7**	**0.0**	**7.2**	**0.0**	**129.8**

Table C.12: Number of prey items by species that a female sea otter needs to consume per day based on Diet 3, a specialist diet that prefers kelp crabs and bivalves. Data provided for each Year class, as well as for mean across adult Year classes (2-19).

Female without a pup								Female with a pup							
Year Class	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**	**Year Class**	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**
0	0.0	14.0	14.0	1.7	7.0	4.4	0.0	0	--	--	--	--	--	--	--
1	0.0	17.4	17.4	2.2	8.7	5.4	0.0	1	--	--	--	--	--	--	--
2	0.0	18.6	18.6	2.3	9.3	5.8	0.0	2	0.0	28.9	28.9	3.6	14.5	9.0	0.0
3	0.0	20.3	20.3	2.5	10.1	6.3	0.0	3	0.0	30.9	30.9	3.9	15.4	9.6	0.0
4	0.0	21.2	21.2	2.6	10.6	6.6	0.0	4	0.0	32.0	32.0	4.0	16.0	10.0	0.0
5	0.0	21.7	21.7	2.7	10.9	6.8	0.0	5	0.0	32.6	32.6	4.1	16.3	10.2	0.0
6	0.0	22.0	22.0	2.8	11.0	6.9	0.0	6	0.0	33.0	33.0	4.1	16.5	10.3	0.0
7	0.0	22.3	22.3	2.8	11.1	7.0	0.0	7	0.0	33.2	33.2	4.2	16.6	10.4	0.0
8	0.0	22.4	22.4	2.8	11.2	7.0	0.0	8	0.0	33.4	33.4	4.2	16.7	10.4	0.0
9	0.0	22.5	22.5	2.8	11.2	7.0	0.0	9	0.0	33.5	33.5	4.2	16.7	10.5	0.0
10	0.0	22.5	22.5	2.8	11.3	7.0	0.0	10	0.0	33.6	33.6	4.2	16.8	10.5	0.0
11	0.0	22.6	22.6	2.8	11.3	7.1	0.0	11	0.0	33.6	33.6	4.2	16.8	10.5	0.0
12	0.0	22.6	22.6	2.8	11.3	7.1	0.0	12	0.0	33.7	33.7	4.2	16.8	10.5	0.0
13	0.0	22.7	22.7	2.8	11.3	7.1	0.0	13	0.0	33.7	33.7	4.2	16.8	10.5	0.0
14	0.0	22.7	22.7	2.8	11.3	7.1	0.0	14	0.0	33.7	33.7	4.2	16.9	10.5	0.0
15	0.0	22.7	22.7	2.8	11.3	7.1	0.0	15	0.0	33.7	33.7	4.2	16.9	10.5	0.0
16	0.0	22.7	22.7	2.8	11.4	7.1	0.0	16	0.0	33.8	33.8	4.2	16.9	10.6	0.0
17	0.0	22.7	22.7	2.8	11.4	7.1	0.0	17	0.0	33.8	33.8	4.2	16.9	10.6	0.0
18	0.0	22.7	22.7	2.8	11.4	7.1	0.0	18	0.0	33.8	33.8	4.2	16.9	10.6	0.0
19	0.0	22.8	22.8	2.8	11.4	7.1	0.0	19	0.0	33.8	33.8	4.2	16.9	10.6	0.0
Adult mean	**0.0**	**22.1**	**22.1**	**2.8**	**11.0**	**6.9**	**0.0**	**Adult mean**	**0.0**	**33.0**	**33.0**	**4.1**	**16.5**	**10.3**	**0.0**

Table C.13: Number of prey items by species that a male sea otter needs to consume per day based on Diet 3, a specialist diet that prefers kelp crabs and bivalves. Data provided for each Year class, as well as for mean across adult Year classes (3-19).

Males

Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails
0	0.0	18.0	18.0	2.3	9.0	5.6	0.0
1	0.0	22.6	22.6	2.8	11.3	7.1	0.0
2	0.0	25.8	25.8	3.2	12.9	8.1	0.0
3	0.0	27.7	27.7	3.5	13.8	8.7	0.0
4	0.0	29.5	29.5	3.7	14.8	9.2	0.0
5	0.0	30.7	30.7	3.8	15.3	9.6	0.0
6	0.0	31.4	31.4	3.9	15.7	9.8	0.0
7	0.0	31.9	31.9	4.0	16.0	10.0	0.0
8	0.0	32.2	32.2	4.0	16.1	10.1	0.0
9	0.0	32.4	32.4	4.0	16.2	10.1	0.0
10	0.0	32.5	32.5	4.1	16.3	10.2	0.0
11	0.0	32.6	32.6	4.1	16.3	10.2	0.0
12	0.0	32.7	32.7	4.1	16.3	10.2	0.0
13	0.0	32.7	32.7	4.1	16.3	10.2	0.0
14	0.0	32.7	32.7	4.1	16.4	10.2	0.0
15	0.0	32.7	32.7	4.1	16.4	10.2	0.0
16	0.0	32.7	32.7	4.1	16.4	10.2	0.0
17	0.0	32.7	32.7	4.1	16.4	10.2	0.0
18	0.0	32.8	32.8	4.1	16.4	10.2	0.0
19	0.0	32.8	32.8	4.1	16.4	10.2	0.0
Adult mean	**0.0**	**31.9**	**31.9**	**4.0**	**16.0**	**10.0**	**0.0**

Table C.14: Number of prey items by species that a female sea otter needs to consume per day based on Diet 4, an urchin specialist diet. Data provided for each Year class, as well as for mean across adult Year classes (2-19).

Female without a pup								Female with a pup							
Year Class	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**	**Year Class**	**# of Abalone**	**# of *Cancer* crabs**	**# of Kelp crabs**	**# of Urchins**	**# of Clams**	**# of Mussel**	**# of Snails**
0	0.0	12.1	13.2	72.4	0.0	1.1	3.3	0	--	--	--	--	--	--	--
1	0.0	15.1	16.4	90.3	0.0	1.4	4.1	1	--	--	--	--	--	--	--
2	0.0	16.1	17.5	96.3	0.0	1.5	4.4	2	0.0	25.0	27.2	149.9	0.0	2.3	6.8
3	0.0	17.5	19.1	105.0	0.0	1.6	4.8	3	0.0	26.7	29.1	160.1	0.0	2.4	7.3
4	0.0	18.3	20.0	109.9	0.0	1.7	5.0	4	0.0	27.6	30.1	165.8	0.0	2.5	7.5
5	0.0	18.8	20.5	112.7	0.0	1.7	5.1	5	0.0	28.2	30.7	169.1	0.0	2.6	7.7
6	0.0	19.1	20.8	114.3	0.0	1.7	5.2	6	0.0	28.5	31.1	171.0	0.0	2.6	7.8
7	0.0	19.2	21.0	115.4	0.0	1.7	5.2	7	0.0	28.7	31.3	172.2	0.0	2.6	7.8
8	0.0	19.3	21.1	116.1	0.0	1.8	5.3	8	0.0	28.8	31.5	173.0	0.0	2.6	7.9
9	0.0	19.4	21.2	116.5	0.0	1.8	5.3	9	0.0	28.9	31.6	173.6	0.0	2.6	7.9
10	0.0	19.5	21.2	116.9	0.0	1.8	5.3	10	0.0	29.0	31.6	174.0	0.0	2.6	7.9
11	0.0	19.5	21.3	117.1	0.0	1.8	5.3	11	0.0	29.0	31.7	174.3	0.0	2.6	7.9
12	0.0	19.6	21.3	117.3	0.0	1.8	5.3	12	0.0	29.1	31.7	174.5	0.0	2.6	7.9
13	0.0	19.6	21.4	117.5	0.0	1.8	5.3	13	0.0	29.1	31.8	174.7	0.0	2.6	7.9
14	0.0	19.6	21.4	117.6	0.0	1.8	5.3	14	0.0	29.1	31.8	174.9	0.0	2.6	7.9
15	0.0	19.6	21.4	117.7	0.0	1.8	5.3	15	0.0	29.2	31.8	175.0	0.0	2.7	8.0
16	0.0	19.6	21.4	117.8	0.0	1.8	5.4	16	0.0	29.2	31.8	175.1	0.0	2.7	8.0
17	0.0	19.6	21.4	117.9	0.0	1.8	5.4	17	0.0	29.2	31.8	175.2	0.0	2.7	8.0
18	0.0	19.7	21.4	117.9	0.0	1.8	5.4	18	0.0	29.2	31.9	175.2	0.0	2.7	8.0
19	0.0	19.7	21.5	118.0	0.0	1.8	5.4	19	0.0	29.2	31.9	175.3	0.0	2.7	8.0
Adult mean	**0.0**	**19.1**	**20.8**	**114.5**	**0.0**	**1.7**	**5.2**	**Adult mean**	**0.0**	**28.5**	**31.1**	**171.3**	**0.0**	**2.6**	**7.8**

Table C.15: Number of prey items by species that a male sea otter needs to consume per day based on Diet 4, an urchin specialist diet. Data provided for each Year class, as well as for mean across adult Year classes (3-19).

Males

Year Class	# of Abalone	# of *Cancer* crabs	# of Kelp crabs	# of Urchins	# of Clams	# of Mussel	# of Snails
0	0.0	15.6	17.0	93.4	0.0	1.4	4.2
1	0.0	19.5	21.3	117.1	0.0	1.8	5.3
2	0.0	22.3	24.4	134.0	0.0	2.0	6.1
3	0.0	23.9	26.1	143.6	0.0	2.2	6.5
4	0.0	25.5	27.8	153.1	0.0	2.3	7.0
5	0.0	26.5	28.9	159.1	0.0	2.4	7.2
6	0.0	27.2	29.6	163.0	0.0	2.5	7.4
7	0.0	27.6	30.1	165.4	0.0	2.5	7.5
8	0.0	27.8	30.4	167.0	0.0	2.5	7.6
9	0.0	28.0	30.5	168.0	0.0	2.5	7.6
10	0.0	28.1	30.7	168.7	0.0	2.6	7.7
11	0.0	28.2	30.7	169.1	0.0	2.6	7.7
12	0.0	28.2	30.8	169.3	0.0	2.6	7.7
13	0.0	28.3	30.8	169.5	0.0	2.6	7.7
14	0.0	28.3	30.8	169.6	0.0	2.6	7.7
15	0.0	28.3	30.9	169.7	0.0	2.6	7.7
16	0.0	28.3	30.9	169.8	0.0	2.6	7.7
17	0.0	28.3	30.9	169.8	0.0	2.6	7.7
18	0.0	28.3	30.9	169.8	0.0	2.6	7.7
19	0.0	28.3	30.9	169.8	0.0	2.6	7.7
Adult mean	**0.0**	**27.6**	**30.1**	**165.5**	**0.0**	**2.5**	**7.5**

Table C.16: Ingested food mass (IFM) as a percentage of body mass on different diets. Results are presented for each age, sex, and reproductive status.

	Females without a pup					Females with a pup					Males				
Year Class	**Diet 1** (*Cancer* crab /Abalone)	**Diet 2** (Snails)	**Diet 3** (Kelp crab/ Bivalves)	**Diet 4** (Urchin)	**Diet 5** (General)	**Diet 1** (*Cancer* crab /Abalone)	**Diet 2** (Snails)	**Diet 3** (Kelp crab/ Bivalves)	**Diet 4** (Urchin)	**Diet 5** (General)	**Diet 1** (*Cancer* crab /Abalone)	**Diet 2** (Snails)	**Diet 3** (Kelp crab/ Bivalves)	**Diet 4** (Urchin)	**Diet 5** (General)
0	36.1	36.9	37.2	41.5	38.0	--	--	--	--	--	37.7	38.4	38.8	43.3	39.6
1	30.5	31.1	31.4	35.0	32.0	--	--	--	--	--	32.1	32.8	33.1	36.9	33.8
2	28.0	28.6	28.9	32.2	29.4	43.6	44.5	44.9	50.1	45.8	30.8	31.4	31.7	35.3	32.3
3	28.5	29.1	29.4	32.7	30.0	43.4	44.3	44.8	49.9	45.7	29.9	30.5	30.8	34.4	31.5
4	28.8	29.4	29.7	33.1	30.3	43.4	44.3	44.7	49.9	45.6	30.2	30.8	31.1	34.7	31.7
5	28.9	29.5	29.8	33.3	30.4	43.4	44.3	44.8	49.9	45.7	30.4	31.0	31.3	34.9	31.9
6	29.0	29.6	29.9	33.4	30.5	43.4	44.3	44.8	49.9	45.7	30.5	31.1	31.4	35.0	32.0
7	29.1	29.7	30.0	33.4	30.6	43.4	44.3	44.8	49.9	45.7	30.5	31.2	31.5	35.1	32.1
8	29.1	29.7	30.0	33.5	30.6	43.4	44.3	44.8	49.9	45.7	30.6	31.2	31.5	35.1	32.2
9	29.2	29.8	30.1	33.5	30.7	43.5	44.3	44.8	49.9	45.7	30.6	31.2	31.6	35.2	32.2
10	29.2	29.8	30.1	33.5	30.7	43.5	44.3	44.8	49.9	45.7	30.6	31.3	31.6	35.2	32.2
11	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	49.9	45.7	30.6	31.3	31.6	35.2	32.2
12	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	49.9	45.7	30.7	31.3	31.6	35.2	32.2
13	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	49.9	45.7	30.7	31.3	31.6	35.2	32.2
14	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	49.9	45.7	30.7	31.3	31.6	35.2	32.2
15	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	50.0	45.7	30.7	31.3	31.6	35.2	32.2
16	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	50.0	45.7	30.7	31.3	31.6	35.2	32.2
17	29.2	29.8	30.1	33.6	30.7	43.5	44.4	44.8	50.0	45.7	30.7	31.3	31.6	35.2	32.2
18	29.3	29.9	30.1	33.6	30.8	43.5	44.4	44.8	50.0	45.7	30.7	31.3	31.6	35.2	32.2
19	29.3	29.9	30.2	33.6	30.8	43.5	44.4	44.8	50.0	45.7	30.7	31.3	31.6	35.2	32.2
Adult Mean	**29.1**	**29.6**	**29.9**	**33.4**	**30.5**	**43.5**	**44.4**	**44.8**	**49.9**	**45.7**	**30.5**	**31.2**	**31.5**	**35.1**	**32.1**