UNIVERSITY OF CALIFORNIA, SANTA CRUZ

Department Physical & Biological Sciences,

Ecology & Evolutionary Biology

ENERGY DENSITIES OF FORAGE FISH FROM THE MESOPELAGIC ZONE OF THE NORTH PACIFIC OCEAN AND ITS IMPLICATIONS FOR A HIGH-LEVEL MARINE PREDATOR, THE NORTHERN ELEPHANT SEAL (*MIROUNGA ANGUSTIROSTRIS*)

A senior thesis submitted for the degree of

BACHELOR OF SCIENCES

in

MARINE BIOLOGY

by

Xochitl Clare

April 2016

The thesis of Xochitl Clare is approved by:

Distinguished Professor Daniel P. Costa

Postdoctoral Researcher Jennifer L. Maresh, Ph.D.

Ph.D. Candidate Chandra Goetsch

Table of Contents

Tables and Figures

Tables

Figures

Appendix

See pages 30-31*

Appendix 1. Tables

Appendix 2. Figures

ABSTRACT

Mesopelagic fish are primary prey for marine predators such as the northern elephant seal (*Mirounga angustirostris*). Modern tracking technology has provided unprecedented insight into the long-distance foraging migrations of elephant seals, revealing dives into the mesopelagic zone (200-1,000 m) averaging 517 m in depth, with some dives exceeding 1,761 m. While the extreme foraging behaviors of these animals are well-documented, the factors driving them remain unclear. Hypotheses include the targeting of energy-rich prey species according to the predictions of Optimal Foraging Theory. To understand the energetic benefit associated with these foraging migrations we used bomb calorimetry to determine the energy densities of potential prey species. We collected individuals that collectively represent 55 forage species from the mesopelagic zone via mid-water trawls that spatially and temporally correlated with seals foraging in the north Pacific Ocean. Preliminary energy density data from eleven species shows the show the Northern pearleye (*Benthalbella dentata*), found from 98 to 3,4000 m, with the highest energy density output of 10,787 kJ kg $^{-1}$ compared to the average energy density of 7, 119 kJ kg $^{-1}$. Mesopelagic forage fish were observed to have a higher average energy density (7,119 kJ kg $^{-1}$) than the average energy density commonly reported in literature for marine mammal prey at shallower depths (5,450 kJ kg $^{-1}$). The energy densities for two species that were shown in in elephant seal diet, Garman's lanternfish (*Diaphus gigas*) and the Electric lanternfish (*Electrona risso*) were 7,367 kJ kg $^{-1}$ and 5,155 kJ kg $^{-1}$. Both species occur at the shallow end of the mesopelagic zone, indicating that prey choice is partly determined by prey behavior. These data suggest that elephant seals employ a foraging strategy that targets small, energy-dense species, and represent an important step toward understanding the bioenergetics of foraging in this high-level predator.

Keywords: marine predators, bioenergetics, optimal foraging theory, northern elephant seal, mesopelagic, accelerometry, laternfish

INTRODUCTION

Background

The absence of apex predators results in massive cascading events in marine, terrestrial, and freshwater ecosystems. Apex predators serve as a top-down ecosystem structural component and have the ability to maintain the integrity of trophic relations [1]. Marine apex predators play an essential role in pelagic ecosystems because of their ability to influence landscape-level community dynamics across a variety of overlapping food webs on many trophic levels [2,3]. Recent declines in marine predator species have motivated many research programs to further investigate the distribution, foraging behaviors and habitat use of marine predators to better inform management efforts aimed at recovering depleted populations [1,2]. While biological and physiological information on marine predators can inform management strategies, this information is difficult to obtain due to the logistical limitations of directly observing organisms that forage at sea. Thus, very little is understood about the foraging behavior of marine predators, including fundamental information on diet and prey consumption rates.

Modern tracking technology has provided unprecedented insight into the extreme foraging behaviors of otherwise cryptic, highly mobile marine predators such as sea turtles, sharks, seabirds, and tunas [4]. Observations made from developing marine predator tagging programs provide an excellent tool to begin understanding factors that influence marine mammal foraging behavior (Fig. 1). As a continuation of the work of various marine mammal tagging and tracking programs, the Tagging of Pacific Predators (TOPP) program is a data-sharing consortium of marine scientists that includes the National Oceanic and Atmospheric Administration, the Center for Ocean Health and Long Marine Laboratory at UC Santa Cruz, and the Hopkins Marine Lab at Stanford University. TOPP has used advancements in archival tagging instrumentation and 3-axis accelerometry and magnetometry to study an unprecedented 23 species over 10 years [3], providing a continuous study of predator foraging throughout the north Pacific Ocean.

These studies have allowed researchers to observe marine predator foraging at a finer scale than ever before. These tools have been used to uncover the extreme foraging behaviors of northern elephant seals, (*Mirounga angustirostris*), revealing long-distance migrations of 3-8 months that range thousands of kilometers into the north Pacific Ocean [5]. Elephant seals have also been discovered to conduct deep dives into the mesopelagic zone (200-1,000 m), an important foraging habitat for many predators [3]. Mesopelagic prey are found in higher density patches and present a richer food source once located by divers [6]. Female northern elephant seals continuously foraging across the northeast Pacific Ocean to exploit the mesopelagic zone during their migrations represent an ideal species to explore how energy value of prey affects foraging behavior in marine mammal predators.

Mesopelagic fish remain one of the least studied aspects of pelagic ecosystems. The magnitude of mesopelagic biomass has been widely underestimated. Recent studies suggest that the mesopelagic fish biomass of over 1,000 million tons, far exceeding past estimates [7]. This serves as an alarm to the significant role mesopelagic fishes play in marine ecosystems. It is well

Figure 1. Map of migration tracking data of female northern elephant seals. This map shows migration tracking data of 209 female northern elephant seals from 2004-2010 during their foraging migrations into the north Pacific Ocean [3]. This map includes 195 tracks (white) from Año Nuevo, CA, USA colonies and the Islas San Benito, B.C., Mexico colony (red dots) [3].

established that mesopelagic prey are important resources for marine predators, yet little is known about their nutritional value due to the fact that they are also difficult to access. According to the predictions of Optimal Foraging Theory (OFT), the potentially high costs associated with accessing prey at mesopelagic depths should be offset by a relatively high energy payoff for this strategy to be successful.

Optimal Foraging Theory

OFT is a widely-used framework that incorporates energy as a ‘currency’ to predict the foraging decisions of organisms. Energy intake rate is once such currency, whereby organisms are predicted to maximize energy intake and minimize energy output during foraging events [2, 6, 8]. OFT has been tested in captive environments in both terrestrial and marine organisms, but support for this form of energy balancing has rarely been observed in the wild [9]. In addition, the development of optimal foraging models in diving air-breathers is complicated by the limitations imposed on them by the spatial separation of two critical resources: prey at depth and oxygen at the surface. To account for this complication, OFT is termed “optimal diving theory” (ODT) in air-breathing, aquatic animals (divers such as seabirds, seals, whales, and turtles).

ODT predicts that divers optimize foraging costs between oxygen use and energy gain, pointing to oxygen use as the most important factor to prioritize during foraging events for air-breathing divers [9]. It has been shown that for deep-diving pinnipeds (seals, sea lions, fur seals and walruses), the relationship between dive duration and prey availability is very complex [9]. The complexity of this relationship is illustrated by the foraging events of female northern elephant seals. It is clear that foraging events are influenced by both physiological (metabolic) and ecological factors (prey patch size, value, availability).

Recent studies have identified the energy value of prey patches (energetics) to be a missing component in ODT modeling [9], however, this has not been rigorously tested because of the difficulty in measuring the quality of prey targeted by free-ranging animals [9]. ODT investigations have shown that prey type influences foraging in unexpected ways left unidentified due to the little information targeted prey at the mesopelagic zone [9].

Bioenergetics in Marine Predators

High lipid energy prey can be beneficial to diving predators (seabirds and marine mammals) when recovering from fasting or during reproduction [10]. This study focuses on energy gained from potential elephant seal prey as an important ‘currency’ factor driving elephant seal foraging behavior. Previous work indicates that elephant seals have a catholic diet dominated by a variety of small fish and squid species from mesopelagic depths [11, 12]. The exact diet composition as well as variability between individual seals is currently under investigation [13].

In this study we build off current questions of ODT in elephant seals using bioenergetics modeling. Specifically, we determine the caloric value of potential prey of adult female northern elephant seals using bomb calorimetry by creating a prey energy library for this species. In addition, we compare the caloric value of individual prey items to the depths where they were caught to better understand the energetic benefit-to-cost ratio associated with these deep foraging dives. In this study we are testing against the null hypothesis—there is no direct relation between energy density and depth, i.e. energy density of prey does not increase with depth. We expect to experimental results to be contingent with the alternative hypothesis: There is a positive correlation between the caloric value (energy benefit) of prey and the depths at which they are found, i.e., prey found at deeper depths (higher cost) should provide a higher caloric benefit (higher payoff) (Fig. 2). This energetics component will provide the essential link between what is known about the diet of elephant seals and their foraging behavior. Further, this will contribute to the quantification of the prey consumption rates and bioenergetics of foraging in northern elephant seals, facilitating the understanding of the role these high-level predators play in their ecosystems.

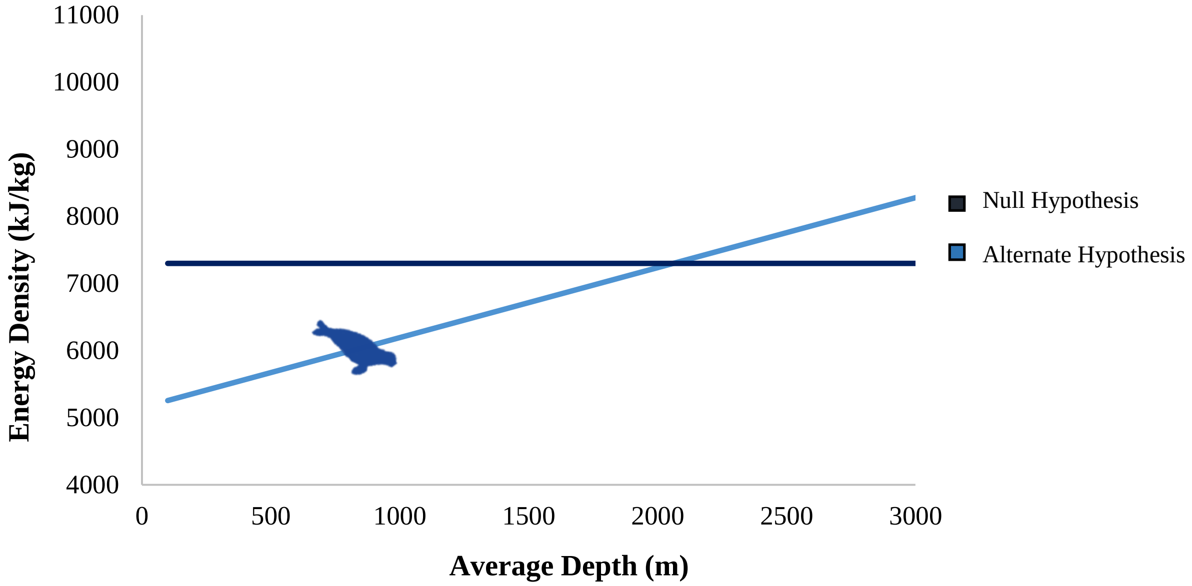
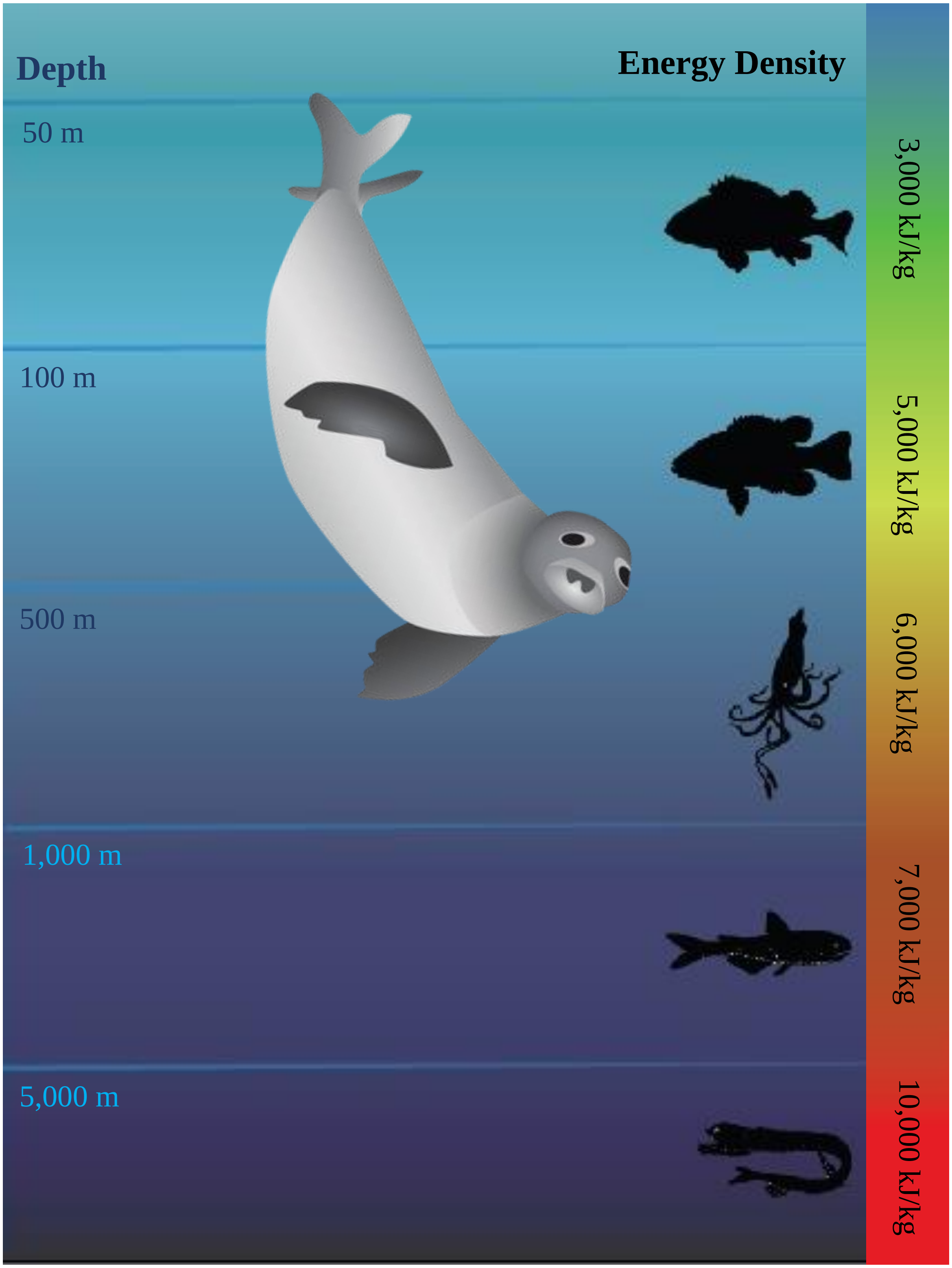


Figure 2. Energy density dependent elephant seal foraging hypothesis. This study tests against the null hypothesis that there is energy density does not increase with depth. Energy densities of mesopelagic forage fish were determined to test the alternate hypothesis: prey species found at deeper depths (higher cost) should provide a higher caloric benefit (higher payoff). See Appendix 2 for graphic sources.

Figure 3. Energy density dependent elephant seal foraging hypothesis. Energy densities of mesopelagic forage fish were determined to test the alternate hypothesis: prey species found at deeper depths (higher cost) should provide a higher caloric benefit (higher payoff). See Appendix 2 for graphic sources.



Project Relevance

This project bridges the mesopelagic zone trophic levels, an area little understanding, into the greater picture of optimal foraging in marine mammal predators. Findings from this project can potentially explain behaviors that were previously entirely unobserved at such high resolution. This study answers the call across marine predator ODT studies to begin to integrate other aspects of the foraging process (e.g. diet and prey value) into foraging behavior modeling [9]. This study steps forward in expanding the scope of optimal foraging modeling for other top predators that rely on mesopelagic prey. Information on the energy densities of northern elephant seal prey will inform the limited understanding of foraging constraints of other pelagic predators. The trophic level dynamics at the mesopelagic zone are the backbone that supports and sustains top predator distribution. Further investigating the importance of the mesopelagic zone will help provide effective management strategies for pelagic top predators [3].

MATERIALS AND METHODS

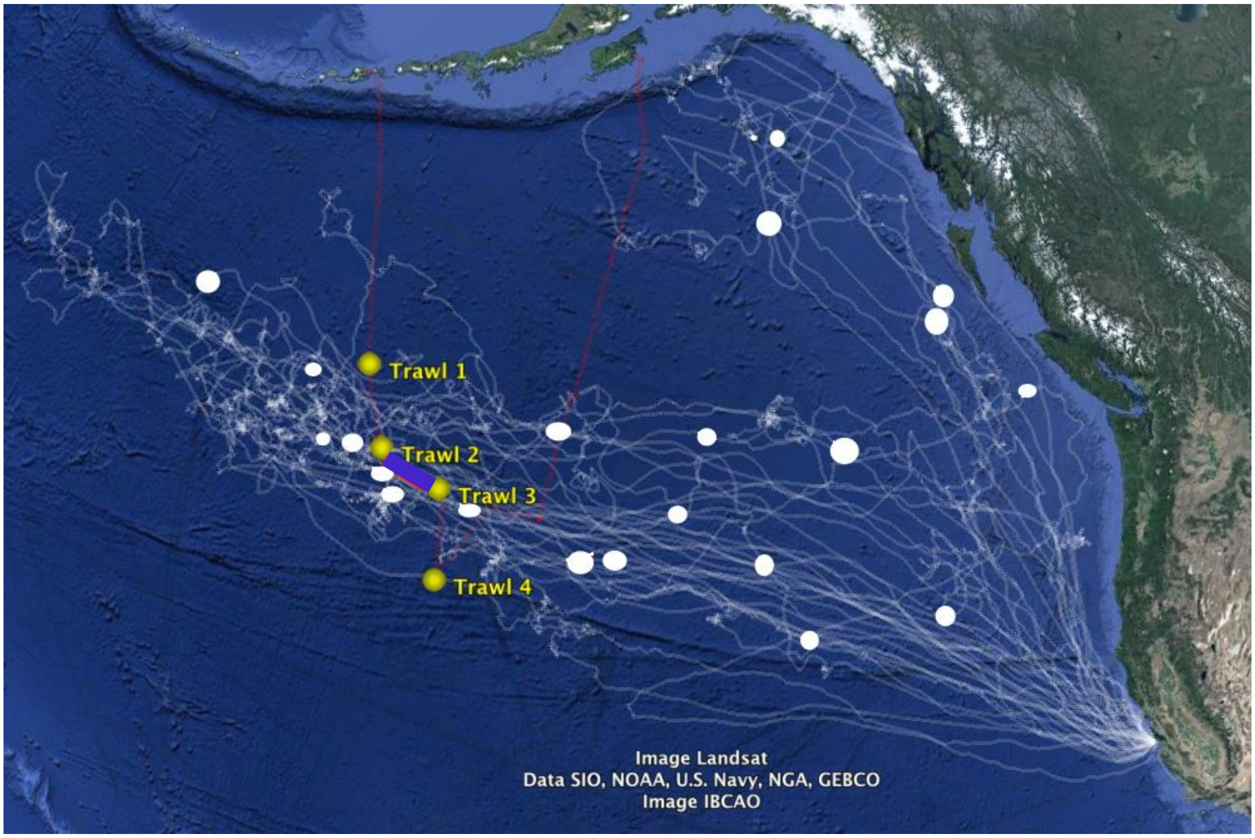


Figure 4. Map of mid-water trawling sites. Trawling sites (yellow) relative to the foraging activities of adult female northern elephant seals. The white lines show the individual tracks of 20 elephant seals during their eight-month-long post-molt foraging migration, while the white dots show the point locations of each seal at the time of sample collection. Fine red lines show the travel route of the research vessel [13].

Overview

To investigate northern elephant seal optimal foraging strategies, we measured the caloric value of potential prey samples collected via mid-water trawls in the mesopelagic zone (200 to 1,000 m) of the north Pacific Ocean (Fig. 4). Prey items were homogenized, freeze-dried, pressed into pellets, and combusted in triplicate via bomb calorimetry. Species caloric averages were incorporated into a prey-energy library.

Sample Collection and Processing

Trawling locations were chosen based on the satellite tracks of female northern elephant seals from previous studies [3,13] (Fig. 4), so that samples overlapped spatially and temporally with seal foraging behavior. Deep-sea prey were collected from multiple locations using four midwater trawls and automated squid jigs on the research ship *Oshoro-maru* (Hokkaido University, Japan). Samples were collected in collaboration with the Dr. Yoko Mitani Cruise from July 1-19, 2012 from Dutch Harbor, Alaska to Kodiak, Alaska through the Transition Zone. Two trawls were conducted at night at about 650 m. An additional two trawls were conducted during the day at 850 m where female seals were known to have foraged in previous field seasons [3]. (For details of collection procedures see: [13]). Fifty-five species were collected for determination of energy density, including twelve species of squid and forty-three species of fish (Table 1). All samples were of whole fish and collected in accordance with collection and animal ethics permits issued to the collector in each instance.

In the laboratory, samples were kept frozen at -20°C and identified down to the species level with the assistance of the National Marine Mammal Laboratory, Seattle, WA [21]. Items were then each homogenized using a combination of food processor and scalpel blades, until the item was of uniform consistency. Individual homogenates consisted of one large individual or multiple small individuals of the same species, depending on the resulting mass of the homogenate, as a minimum of 2 g dry weight is required for bomb calorimetry of samples. Samples were then freeze-dried for 72 hours and stored in a desiccator until combusted via bomb calorimetry.

Table 1. **Mesopelagic forage species collected via mid-water trawls.** Species that were collected via mid-water trawls temporally and spatially correlated with northern female elephant seal foraging. "Depth" refers to the range where these species are known to inhabit. Bolded species are represented in elephant seal diet (Fig. 5) [13]. Species bolded and marked with an asterisk are species that are represented in elephant seal diet and have been processed for energy density via bomb calorimetry. Blank spaces indicate where information is not found. Species that were not found were represented by a depth range of another species with close taxonomic relations (within the same family, order, genus). See Appendix 1 for depth sources for individual species noted as: *a, b, c, d, e*.

Species Name	Common Name	Depth (m)
Abraliopsus spp.		*500-900* [a]
Anoplogaster cornuta	Common fangtooth	*2-4,992* [b]
Aphanopus carbo	Black scabbardfish	*200-1,700* [b]
Aristostomias scintillans	**Shiny loosejaw**	***0-1,219*** [b]
Avocettina infans	Avocet snipe-eel	*785-4,580* [b]
Bathylagus pacificus	**Slender blacksmelt**	***772-7,700*** [b]
Benthalbella dentata	Northern pearleye	*98-3,400* [b]
Berryteuthis anonychus	**Minimal armhook squid**	***0-1,500*** [a]
Chauliodus macouni	Pacific viperfish	*25-4,390* [b]
Cololabis saira	Pacific saury	*0-230* [b]
Diaphus gigas*	**Laternfish**	***100-839*** [b]
Diaphus perspicillatus	**Transparent laternfish**	***0-1,500*** [b]
Diaphus theta	California headlightfish	*258-3,400* [b]
Diplospinus multistriatus	Striped escolar	*50-1,000* [b]
Electrona risso*	**Electric lanternfish**	***90-820*** [b]
Galiteuthis phyllura	**Cockatoo squid**	***1,000-1,300*** [a]
Gonatopsis borealis	Boreopacific armhook squid	*366-4,500* [a]
Gonatus berryi	Berry armhook squid	*200-1,080* [a]
Histioteuthis	Cock-eyed squid	*200-1,000* [c]
Howella sherborni	Sherborn's pelagic bass	*26-950* [b]
Icosteus aenigmaticus	Ragfish	*18-732* [b]
Lampadena yaquinea		
Lampanyctus jordani	Brokeline laternfish	*588-3,400* [b]
Lipolagus ochotensis		
Macropinna microstoma	**Barreleye fish**	***16-1,267*** [b]
Melamphes lugubris	**Ridgehead**	***200-2,000*** [b]
Melanonus zugmayeria		*900-5,100* [d]
Nannobrachium fernae	Black lanternfish	*0-750* [b]
Nannobrachium regale	Pinpoint lampfish	*772-3,400* [b]

Table 1. continued. See Appendix 1 for depth sources for individual species. Sources are noted as: *a, b, c, d, e*.

Species Name	Common Name	Depth (m)
Octopoteuthis spp.		*500-600* [e]
Ommastrephes bartramii	Neon flying squid	
Onychoteuthis borealijapinica		
Opostomias mitsuii	**Pitgum lanternfish**	***60-1,366*** [b]
Poromitra crassiceps	Crested bigscale	*164-2,730* [b]
Pseudobathylagus milleri	Stout blacksmelt	*772-6,600* [b]
Sagamichthys abei	**Shining tubeshoulder**	***37-1,500*** [b]
Stemonosudis rothschildi	**Rothschild's barracuda**	***0-532*** [b]
Stenobrachius leucopsarus	Nothern lampfish	*785-3,400* [b]
Stenobrachius nannochir	Garnet lanternfish	*441-3,400* [b]
Tactostoma macropus	**Longfin dragonfish**	***30-2,000*** [b]
Taonius belone		*400-700* [b]
Tarletonbeania taylori	**Northern pacific lanternfish**	***0-1,500*** [b]
Winteria telescopa	**Binocular fish**	***400-2,500*** [b]

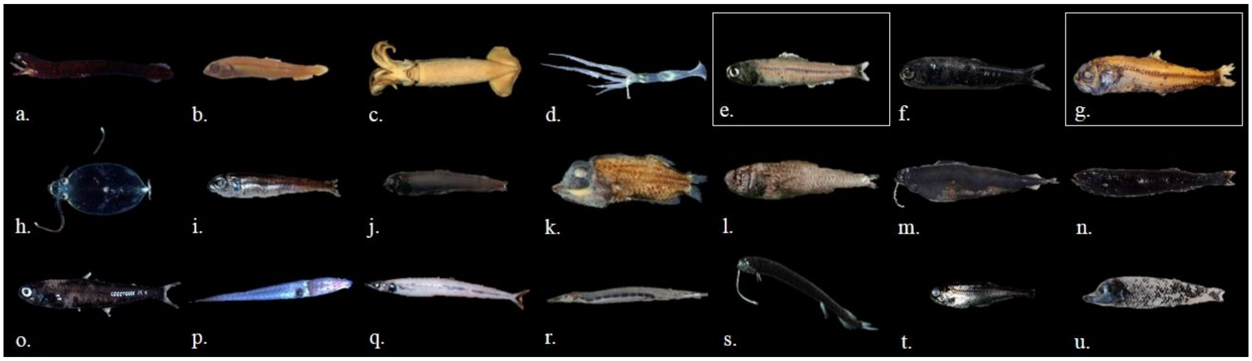


Figure 5. Mesopelagic forage fish that represent elephant seal diet. A subset of forage species collected from the mesopelagic zone of the north Pacific Ocean that have been shown in elephant seal diet as a result of stable isotope analysis [13]. The energy densities of both *e. Electrona risso* and *g. Diaphus gigas*(outlined) have been determined in this study. See Appendix 2 for photo sources for individual species noted as: *a-u.* Species that were not found were represented by a photograph of another species with close taxonomic relations (within the same family, order, genus), see Appendix 2 for more information.

Bomb Calorimetry

Energy density was determined for 11 out of the 55 species collected via bomb calorimetry. A subset of mesopelagic forage species collected via mid-water trawls have been shown in elephant seal diet via stable isotope analysis. These species include: *Aristostomias scintillans*, *Bathylagus pacificus*, *Berryteuthis anonychus*, *Chiroteuthis spp.*, *Diaphus gigas*, *Diaphus perspicillatus*, *Electrona risso*, *Galiteuthis phyllura*, *Lipolagus ochotensis*, *Melanolagus bericoides*, *Macropinna microstoma*, *Melamphes lugubris*, *Opostomias mitsuii*, *Sagamichthys abei*, *Syngnathus californiensis*, *Stigmatoteuthis dolfleni*, *Scopelosaurus harryi*, *Stemonosudis rothschildi*, *Tactostoma macropus*, *Tarletonbeania taylori*, *Winteria telescopa* (Fig. 5) [13]. Out of the species listed as a part of elephant seal diet, in this study the energy densities were determined for Garman's lanternfish (*D. gigas*) and the Electric lanternfish (*E. risso)* (Fig. 5). The energy densities were also determined for nine other mesopelagic forage fish collected: *Anoplogaster cornuta*, *Avocettina infans*, *Benthalbella dentata*, *Chauliodis macouni*, *Diaphus* *theta*, *Diplospinus multistratus*, *Icosteus aenigmaticus*, *Lampadena yaquinae*, and *Lampanyctus jordanii* (Table 1).

The caloric value of each species was determined in triplicate, and only values within 2% of the average value were used in analyses. For combustion, freeze-dried samples were mashed to an even consistency and then pressed into pellets using a pellet press. We determined the energy density for a .4-.6 g dried homogenate using an adiabatic bomb calorimeter (Model 1341, Parr Instruments, Moline, IL, USA) calibrated with pre-weighed benzoic acid tablets [37]. Corrections were made for the energy equivalents of fuse wire combustions and acid byproducts. Pellets were pressed 3-5 times to yield pellets of appropriate size for the process. Pellets were loaded into the bomb vessel and connected to the ignition wires via 10 cm of fuse wire prior to the vessel being filled with 35 atm of oxygen and 1 mL of deionized (DI) water. We then set the bomb vessel into the calorimeter bucket of 2,000 (+/-.05) g of DI water at room temperature. Once the bomb vessel was sealed and loaded into the covered bomb jacket encasing the calorimeter bucket the sample was combusted by a spark sent through the fuse wire by the calorimeter device. The heat released from the combustion reaction the calorimeter raised the temperature of the water bath and was then converted into calories. Benzoic acid standards, which we used to calibrate the machine ensured that the machine read each degree of temperature rise equals as a number of calories released [12].

In order to ensure results included only the heat released from the sample, we accounted for the fuse wire burned during combustion and the nitric acid formed as a byproduct. Bomb washings of 25 mL were titrated using sodium hydroxide (.0709 N) and a phenolphthalein indicator. The portion of the nitric acid in the bomb washings results from nitrogen in the air that gets trapped in the calorimeter and is then burned at high pressure.

Wet Weight Conversions

Energy densities for the 11 species in this study were found by converting the gross heat in dry weight (cal g^{-1}) to wet weight (kJ kg $^{-1}$). This conversion from wet to dry weight allowed for an analysis of consumption of the entire fish and its wet mass. This was done by averaging the gross heat (cal g^{-1}) from each trial of comb calorimetry and adjusting for the percentage of water weight initially present in each sample vial using a wet-to-dry conversion factor.

RESULTS

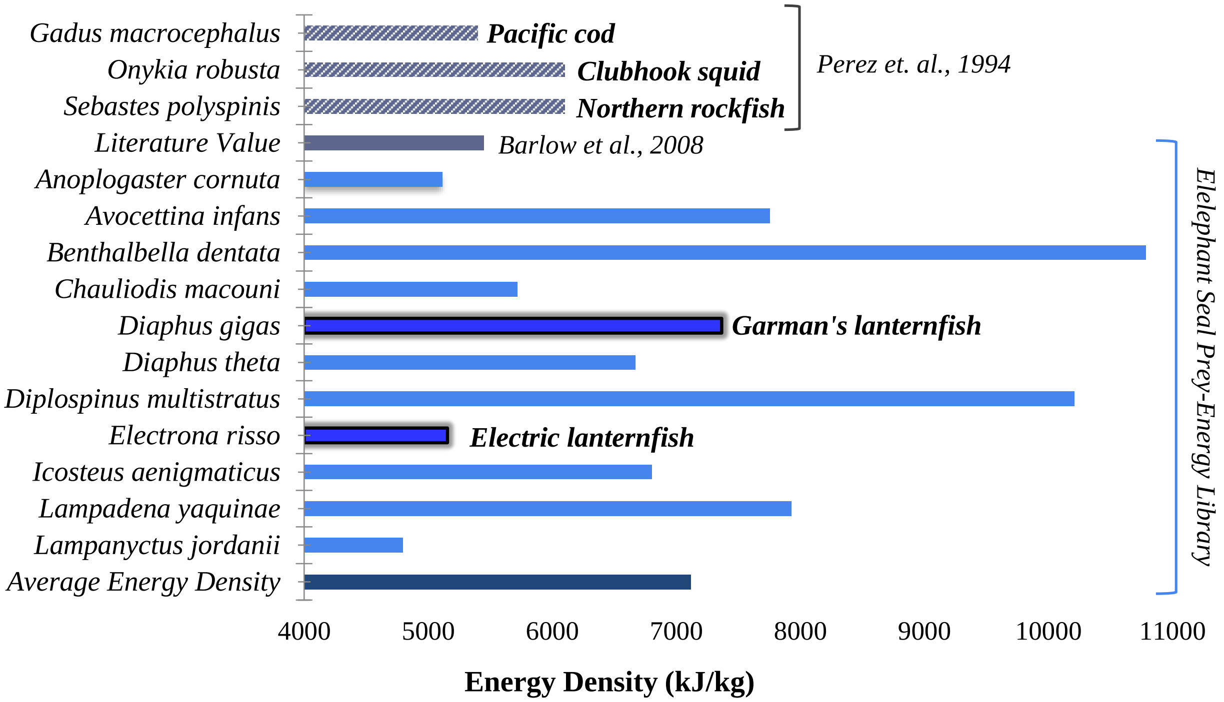


Figure 6. Energy densities of forage species. Energy density of mesopelagic forage species determined in this study (light blue bars) were compared with species known to be targeted by marine mammals at shallower depths (dashed grey bars) [38]. The solid grey bar represents the common energy value used in prey consumption models where fish and squid are the primary diet [39]. The dark blue bar at the bottom of the graph represents the average energy density of mesopelagic fish and squid from this study. The energy densities were determined for the two species in this study that were shown in elephant seal diet (bolded blue bars) [13].

Energy densities determined for 11 out of the 55 mesopelagic species collected (Table 2, Fig. 6) show the Northern pearleye (*B. dentata*), found from 98 to 3,4000 m, with the highest energy density output of 10,787 kJ kg $^{-1}$ compared to the average energy density of 7, 119 kJ kg $^{-1}$ (Fig.6). Energy densities of marine mammal prey found at more shallow depths, such as Pacific cod (*Gadus macrocephalus*), Northern rockfish (*Sebastes polyspinis*) and Clubhook squid (*Onykia robusta*) [38] were compared to mesopelagic prey (Fig. 6). Mesopelagic forage fish were observed to have a higher average energy density (7,119 kJ kg $^{-1}$) than the average energy density commonly reported in literature for marine mammal prey at shallower depths (5,450 kJ kg $^{-1}$) [39]**.** The energy densities were determined for the two species in this study that were shown in in elephant seal diet. *D. gigas* was determined to have an energy density output of 7,367 kJ kg $^{-1}$ and *E. risso* to have an output of 5,155 kJ kg $^{-1}$ (Table 2, Fig. 6). *D. gigas* and *E. risso* were found at more shallow depths in comparison to other species in this study (470 and 455 m respectively). The percentage of water of the wet weight was also determined for the 11 species in this study.

Table 2. Energy densities, wet weight and depth range of mesopelagic forage species. The energy densities of mesopelagic forage species determined via bomb calorimetry alongside the percentage of water of each prey species. Average depths where species may be found are also listed. Bolded species are represented in elephant seal diet [13]. Species that were not found were represented by a depth range of another species with close taxonomic relations (within the same family, order, genus). See Appendix 1 for depth sources for individual species (same as **Table 1**).

Species Name	Energy Density (kJ/kg)	Percent Water	Average Depth (m)
Anoplogaster cornuta	*5,113*	80%	*2,497* [a]
Avocettina infans	*7,754*	73%	*2,683* [b]
Benthalbella dentata	*10,787*	62%	*1,749* [b]
Chauliodis macouni	*5,721*	78%	*2,208* [b]
Diaphus gigas	***7,367***	**70%**	***470*** [b]
Diaphus theta	*6,670*	74%	*1,829* [b]
Diplospinus multistratus	*10,210*	66%	*950* [b]
Electrona risso	***5,155***	**77%**	***455*** [b]
Icosteus aenigmaticus	*6,804*	75%	*375* [b]
Lampadena yaquinae	*7,928*	72%	
Lampanyctus jordanii	*4,795*	79%	*1,994* [b]

DISCUSSION

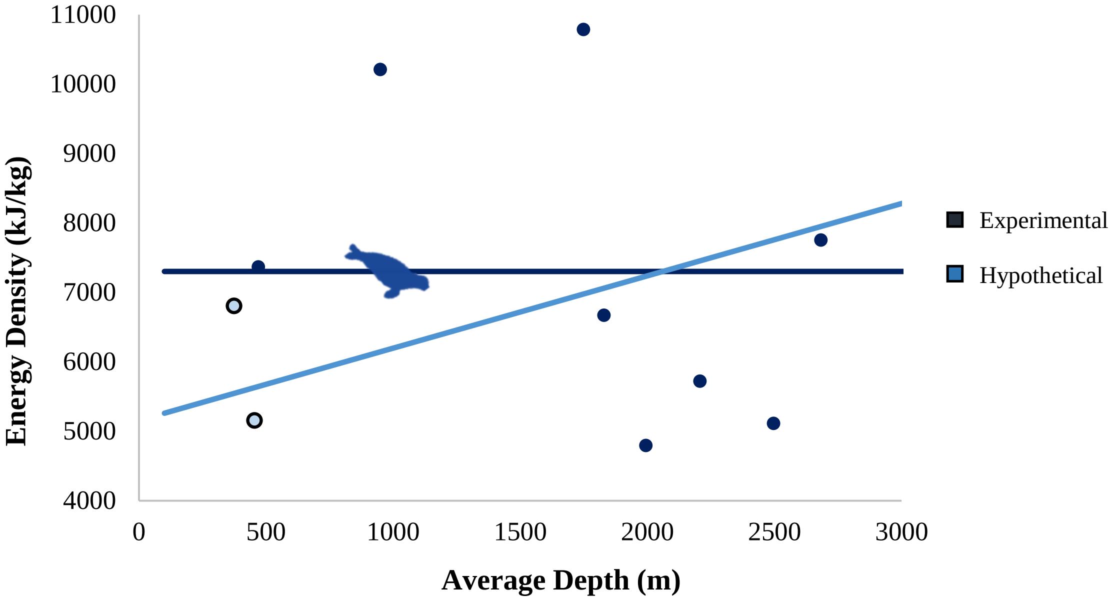


Figure 7. Relationship between energy density and foraging depth. Experimental results confirm the null hypothesis (Fig. 2) that energy density of prey does not increase with depth. The two bolded and lighter points mark prey that have been represented in elephant seal diet (*D. gigas* and *E. risso*) [13]. See Appendix 2 for graphic sources.

Prey Energy Density and Foraging Depth

Energy densities of mesopelagic forage fish determined via bomb calorimetry did not increase with depth (Fig. 7). These results support the null hypothesis (Fig. 2) that there is no direct relationship between depth and energy density. Therefore, there must be other factors outside of energy density that influence mesopelagic foraging in elephant seals.

From this study we are able to gather information about elephant seal foraging behavior that may have not otherwise been apparent. The preliminary data are indicating that elephant seals target mesopelagic prey that are energy-rich and more accessible. This is supported by the fact that species that represent elephant seal diet (*D.* gigas and *E. risso*, Table 2, Fig. 7) are found at more shallow depths in comparison to other species in this study. This behavior can be explained by ODT which holds that energy gain must offset the energetic costs of foraging. As a result, elephant seals should not spend energy foraging at deeper depths if the same amount of energy is available at shallower depths as supported by these data. While this behavior is in accordance with ODT, this piece of information alone fails to explain the reasons behind deep sea foraging behavior.

This is shown in this individual case: *E. risso*, targeted by elephant seals at the shallower end of the mesopelagic zone, has an average energy density (5,157 kJ kg $^{-1}$) that is not higher than the energy density of forage fish reported in literature (5,450 kJ kg $^{-1}$) [39]. This information would lead to the conclusion that elephant seals are not targeting energy-rich mesopelagic prey. However, on average, mesopelagic prey available to elephant seals has a higher energy density (7, 119 kJ kg $^{-1}$) than that prey found at shallower depths (5,450 kJ kg $^{-1}$), making the mesopelagic zone a valuable energy source to elephant seals overall.

Future Steps

To further test the concept that elephant seals target mesopelagic prey that are energy-rich and more accessible (found at the shallower end of the mesopelagic zone) I will prioritize energy density determination (bomb calorimetry) of the remaining species that have been shown in elephant seal diet. I expect to find that species that are shown in elephant seal diet will be species that are both energy-rich and tending to occur at more shallow average depths in contingence with OFT.

Potential discrepancies in this analysis will be resolved as additional energy densities of species that are representative of elephant seal diet are determined. Furthermore, the usage of a range of depth for each species allows us to asses where the species may occur but not where elephant seals are precisely capturing them. Obtaining the exact depths of which prey are captured for future studies will expand the scope of this analysis. This study raises the notion that

that prey choice is partly determined by prey behavior due to the fact that many of the fish shown as significant in elephant seal diet are small schooling fish [13]. The effect of mesopelagic fish behavior and ecology on elephant seal foraging is a major component that cannot be ignored in future investigations.

Conclusion

Conclusive findings from this study were that mesopelagic prey species tend to be small-bodied but have a higher energy density on average (7, 119 kJ kg $^{-1}$) than the standard energy density (5450 kJ kg^{-1}) used in studies on marine mammal prey consumption rates for species primarily targeting fish and squid [37, 38, 39]. These data suggest that elephant seals employ a foraging strategy that targets small, energy-dense species, and represent an important step toward understanding the bioenergetics of foraging in this high-level predator.

While this study merely points to potential aspects of elephant seal foraging behavior, this information will inform critical questions about how elephant seals prioritize foraging costs or ‘currency’ when targeting mesopelagic prey. Studies such as this are necessary components in larger investigations on how the value (energy density) of prey can provide great insight on the behavior of apex predators, such as the northern elephant seal.

AKNOWLEDGMENTS

University of California, Santa Cruz
Division of Physical and Biological Sciences,
Department of Ecology and Evolutionary Biology

UCSC Long Marine Laboratory and Center for Ocean Health
Daniel P. Costa Laboratory
Researchers and Faculty:
Jennifer L. Maresh, Ph.D., Postdoctoral Researcher
Chandra Goetsch, Ph.D. Candidate
Patrick Robinson, Ph.D., Ano Nuevo Reserve Director and Researcher
Distinguished Professor Daniel P. Costa, Ph.D.

Hokkaido University, Japan
Dr. Yoko Mitani Cruise, *Oshoro-maru*

National Marine Mammal Laboratory, Seattle
William Walker, Ph.D., Mesopelagic prey sample identification

UCSC Institute for Marine Science

Friends of Long Marine Laboratory (FLML)
Student Research and Education Award (SREA)

California Alliance for Minority Participation (CAMP)
Undergraduate Research Stipend

UCSC STEM Diversity Program
Yulianna Ortega, UCSC STEM Diversity Programs Director
Sigolene Ortega, UCSC STEM Diversity Programs Assistant

Senior Thesis Seminar (BME 194F)
Zia Isola, Ph.D.

Undergraduate Research in Ecology and Evolutionary Biology (EEB) – Writing (BIOE 183W)
Grant Pogson, Ph.D.

A special thanks to the Costa Laboratory bomb calorimetry volunteers, Daphne Mark and Sarah Simon-Contreras, for their time and dedication to this project. I would like to thank Sara Sherine Ebadi for taking the initial steps to push this project along. I extend my gratitude to Chandra Goetsch, Ph.D. candidate, for sharing her unpublished dissertation. This project could not have been made possible without my faculty mentor, Daniel P. Costa, Ph. D. and the guidance of my mentor and role model, Jennifer L. Maresh, Ph.D. I am forever grateful to my friends and family for their endless support.

LITERATURE CITED

1. Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Marquis, R. J. (2011). Trophic downgrading of planet Earth. *science*, *333*(6040), 301-306.
2. Maresh, J. L., Adachi, T., Takahashi, A., Naito, Y., Crocker, D. E., Horning, M., ... & Costa, D. P. (2015). Summing the strokes: energy economy in northern elephant seals during large-scale foraging migrations. *Movement ecology*, *3*(1), 1-16.
3. Robinson, P. W., Costa, D. P., Crocker, D. E., Gallo-Reynoso, J. P., Champagne, C. D., Fowler, M. A., ... & Kuhn, C. E. (2012). Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PloS one*, *7*(5), e36728.
4. Block, Barbara A., et al. "Revealing pelagic habitat use: the tagging of Pacific pelagics program." *Oceanologica Acta* 25.5 (2002): 255-266.
5. Stephens, T. (2012, May 15). Elephant seal tracking reveals hidden lives of deep-diving animals. Retrieved October 29, 2015, from *http://news.ucsc.edu* (accessed October 2015).
6. Foo, D., Semmens, J. M., Arnould, J. P., Dorville, N., Hoskins, A. J., Abernathy, K., ... & Hindell, M. A. (2016). Testing optimal foraging theory models on benthic divers. *Animal Behaviour*, *112*, 127-138.
7. Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., ... & Agusti, S. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature communications, 5*.

8. Adachi T, Maresh JL, Robinson PW, Peterson SH, Costa DP, Naito Y, Watanabe YY, Takahashi A. 2014. The foraging benefits of being fat in a highly migratory marine mammal. *Proc. R. Soc.* B 281: 20142120.
9. Hazen, E. L., Friedlaender, A. S., & Goldbogen, J. A. (2015). Blue whales (Balaenoptera musculus) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science advances*, *1*(9), e1500469.
10. Lenky C, Eisert R, Oftedal OT, Metcalf V. 2011. Proximate composition and energy density of notothenioid and myctophid fish in McMurdo Sound and the Ross Sea, Antarctica. *Polar Biol* (2012) 35:717-724.
11. Condit, R., & Le Boeuf, B. J. (1984). Feeding habits and feeding grounds of the northern elephant seal. *Journal of Mammalogy*, *65*(2), 281-290.
12. Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M., & Takahashi, A. (2013). Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Functional Ecology*, *27*(3), 710-717.
13. Goetsch, C. (2016). [Ph.D. Thesis]. Unpublished
14. 4x6. (2013). *Seals in action [*JPEG]. Retrieved from http://www.istockphoto.com/vector/seals-in-action-gm165694428-11343601.
15. Woerner, J. (2001). *Illustration of a Hawaiian monk seal (Monachus Schauinslandi)* [Vector Image]. Retrieved from http://ian.umces.edu/imagelibrary/displayimage-6646.html.
16. DeWitt, G. (2012). *Rockfish 3* [Vector Image]. Retrieved from https://www.signtorch.com/vector/Fish-Vector-Art-fish-Catalog.html.

17. Pam’s Clipart. (2015). *Clipart illustration of silhouette of a clownfish* [JPEG]. Retrieved from http://doodlekidz.com/design/clip-art-image-of-a-clown-fish-silhouette-by-pams-clipart-73.
18. Clipart Panda. (2014). *Free Squid Clip Art* [PNG]. Retrieved from http://www.clipartpanda.com/clipart_images/free-squid-clip-art-squid-5511200.
19. Sea and Sky. (2016). *Laternfish* [JPEG]. Retrieved from http://www.seasky.org/deep-sea/lanternfish.html.
20. Denny Manufacturing. (2016). *Viperfish Cutout Magnet/Sculpture Photo Cutout* [JPEG]. Retrieved from http://www.zazzle.com/viperfish_cutout_magnet_sculpture_photo_cutout-153073190557902698.
21. IUCN 2015. *The IUCN Red List of Threatened Species. Version 2015-4.*
22. Walker, W. (2012). National Marine Mammal Laboratory, Seattle, WA.
23. Froese, R. and D. Pauly. Editors. 2015. FishBase.
24. Tu, C. (2015, June 23). Picture of the Week: Cock-Eyed Squid. Retrieved March 31, 2016, Retrieved from http://www.sciencefriday.com/articles/picture-of-the-week-cock-eyed-squid/.
25. Henriques, M., Murta, A. G., & Cabral, H. N. (2001). Melanonus zugmayeri Norman, 1930, captured off Portugal. A review of the current knowledge on this species. *Scientia Marina, 65*(1), 43-46.
26. Korte, T. (2012, August 1). Squid Detaches Arms In Self-Defense, Octopoteuthis Deletron VIDEO Shows. Retrieved March 31, 2016, Retrieved from

http://www.huffingtonpost.com/2012/07/31/squid-detach-arms-octopoteuthis_n_1725772.html.

27. Gilbert (Photographer). (1890). *Bathylagus pacificus [digital image]. Retrieved from* http://coleccion.cicimar.ipn.mx/Coleccion/paginas/desp_ejemplares.php?idEspecie=1125
28. Maddison, D. R. and K.-S. Schulz (eds.) 2007. The Tree of Life Web Project. Retrieved from http://tolweb.org.
29. Senou, H. (Photographer). (1996, May). *Diaphus gigas Gilbert, 1914 [Myctophidae]* [digital image]. Retrieved from http://fishpix.kahaku.go.jp/fishimage-e/detail?START=43874&FAMILY=&SPECIES=&LOCALITY=&.
30. Pulptastic (Website). (2014). *Cranchiidae sp.* [digital image]. Retrieved from http://www.tinmoi.vn/ngam-ve-dep-ky-la-cua-muc-ong-thuy-tinh-trong-suot-011371805.html.
31. Saito, H. (Publisher). [digital images]. Retrieved from http://tnfri.fra.affrc.go.jp/personal/HP/gallary1.html.
32. Digital Fish Library (Image library). (2009). *Macropinna microstoma* [digital image]. Retrieved from http://www.digitalfishlibrary.org/cached/0x0_2809Macropinna%20microstoma%2088-60-10%20-%20MRI%2087mm.jpg.
33. McGrouther, M. (Photographer). Obese *Dragonfish, Opostomias micripnus* [digital image]. Retrieved from URL http://australianmuseum.net.au/obese-dragonfish-opostomias-micripnus-guumlnther-1878#sthash.U52SJBJ7.dpuf.

34. Bray, D.J. (Photographer). (2016, March). *Rothschild's Barracudina, Stemonosudis rothschildi, from off northwestern Western Australia, Australian National Fish Collection* [digital image]. Retrieved from http://www.fishesofaustralia.net.au/Home/family/269.
35. Floon, H. (2015, April 7). Tag: Dragonfish. Retrieved February 04, 2016, from https://hilaryandheruniverse.wordpress.com/tag/dragonfish/.
36. Pogonoski, J. (Photographer). (2011 March). *Binocular Fish, Winteria telescopa* [digital image]. Retrieved from http://www.fishesofaustralia.net.au/home/species/3632.
37. Parr Instrument Company (2008). Parr Operating Manual No. 204M, 1341 Oxygen Bomb Calorimeter Operating Instruction Manual. Parr Instrument Company, Moline IL, USA.
38. Perez, M. A. (1994). *Calorimetry measurements of energy value of some Alaskan fishes and squids*. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center.
39. Barlow, J., Kahru, M., & Mitchell, B. G. (2008). Cetacean biomass, prey consumption, and primary production requirements in the California Current ecosystem. *Marine Ecology Progress Series*, *371*, 285-295.
40. Tamura, T., & Ohsumi, S. (2000). Regional assessments of prey consumption by marine cetaceans in the world. *Publication no. SC/52 E, 6.*

APPENDIX

Appendix 1. Tables

Table 1. Mesopelagic forage species collected via mid-water trawls **14-15**

Depth sources*:

a. IUCN Red List of Threatened Species [21]

b. FishBase [23]

c. [24]

d. [25]

e. [26]

Species that were not found were represented by a depth ranges of another species with close taxonomic relations (within the same family, order, genus).

Table 2. Energy densities, wet weight and depth range of mesopelagic forage species **20**

Same depth sources as Table 1*

Species that were not found were represented by a depth ranges of another species with close taxonomic relations (within the same family, order, genus).

Appendix 2. Figures

Figure 2. Energy density dependent elephant seal foraging hypothesis graph **9**

Elephant seal silhouette graphic [14]

Figure 3. Energy density dependent elephant seal foraging hypothesis illustration **10**

Elephant seal graphic [5]

Prey silhouette graphics (from top to bottom) [16, 17, 18, 19, 20]

Figure 5. Mesopelagic forage fish that represent elephant seal diet **16**

Photo sources:

FishBase [23]: *a, f, g, j, l, n, q*

APPENDIX

Appendix 2. Figures continued

Figure 5. Mesopelagic forage fish that represent elephant seal diet

Photo sources

Centro Interdisciplinario de Ciencias Marinas del Instituto Politécnico Nacional [27]: *b*

Tree of Life Web Project [28]: *c, d, p*

FishPix [29]: *e*

Marine Ecosystem for Sustainable Utilization of Biological Resources [31]: *i, o, t*

Digital Fish Library [32]: *k*

Australian Museum [33]: *m*

Australian National Fish Collection [34]: *r*

[30]: *h*.

[35]: *s*

[36]: *u*

Species that were not found were represented by a photograph of another species with close taxonomic relations (within the same family, order, genus):

a. A. scintillans: Fish photographed is in the same Subfamily, Malacosteinae

l. M. lugubris: Fish photographed is in the same genus, Melamphaes (Ridgeheads)

m. O. mitsuii: Fish photographed is the same genus, Opostomias

n. T. macropus: Fish photographed is a part of the same family (Dragonfishes)

Figure 7. Relationship between energy density and foraging depth

Elephant seal silhouette graphic [14]