Title

Growth, Body Size, and Fitness in Marine Mammals

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Abstract

Growth, body size, and fitness in marine mammals

by

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Understanding the interplay between growth, body size, and fitness in individuals positions us to link population body size trajectories to population success. Individuals allocate excess energy from ingestion to growth. Thus, differences in energy availability can influence individual growth and body size at maturity. Body size is a critical determinant of reproductive success and survival, thereby influencing the overall fitness of an individual. However, quantifying how individuals allocate resources to growth, trade-offs between attaining large body size and prioritizing early reproduction or survivorship, and the direct fitness consequences of body size trajectories are difficult in wild populations, especially those that live in the marine environment, limiting access to data collection. My dissertation addresses these data gaps by investigating how marine mammals allocate energy to growth, the benefits and costs of attaining large body size, and the direct fitness associated with different body size trajectories.

First, I conducted a comprehensive literature review of how marine mammals grow and how they allocate energy to growth, as well as provided an empirical estimate of the cost of growth in marine mammals (Chapter 1). I then focused on the potential life history benefits of attaining large body size, and the potential energetic and life history constraints placed on changing size trajectories (Chapter 2). I used stochastic dynamic programming to model three populations of North Sea harbor porpoises (*Phocoena phocoena*) of different size classes. Finally, I used empirical data from northern elephant seals (*Mirounga angustirostris*) to directly measure the annual and lifetime fitness consequences of deviating from expected body size (Chapter 3). Overall, this dissertation contributes a new biologically relevant understanding of the fitness consequences of investing in growth in marine mammals. Expanding our understanding of fitness consequences of variability in body size is critical in an environment that is experiencing rapid changes due to anthropogenic and natural stressors, often influencing the resources available to individuals to allocate to growth. Observations of shifting body size trajectories in response to environmental change have been documented in marine mammals, and understanding the individual fitness consequences and down-stream population consequences of these shifting size trajectories can aid in the management and conservation of these species.

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The text of this dissertation includes reprints of the previously published material:

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Introduction

Body size is an important driver of individual survival and fitness and contributes to a species' life history strategy (Blueweiss et al., 1978; Craig and Ragen 1999; Crocker et al., 2001; Fokidis et al., 2007). Small animals often employ a "live fast, die young" life history strategy and have high reproductive rates. In contrast, large animals are known to "live slow, die old" and have lower reproductive rates but greater lifetime reproductive success due to their long lifespans. On an individual scale within a lifetime, large body size confers numerous benefits, including decreased metabolic costs, increased energy storage capabilities, and increased fasting endurance (Schmidt-Nielsen, 1972; Kleiber 1975; McNab et al., 1980; Lindstedt and Boyce, 1985; Millar and Hickling, 1990; Williams, 1999; Molnár et al., 2009; Gunnlaugsson et al., 2020). However, attaining large body size requires more absolute energy, which may not be supported by the environment or by certain foraging strategies, and likely requires higher overall metabolic costs of somatic growth (Goldbogen 2018; Adamczak et al., 2023). Therefore, the fitness benefits of large body size should outweigh the costs associated with increased investment in growth despite. Despite these benefits, there often exists variability in individual size within a population, yielding variation in individual fitness which can have downstream impacts on population demography. As such, a detailed look at the confluence of growth, body size, and fitness consequences is critical to our understanding of evolutionary size trajectories and how changes to these trajectories can have population-level consequences.

Interspecific trends in body size assert that small species will have high reproductive rates, and high mortality for young individuals (Sibly and Brown, 2007). The high reproductive rates of smaller species allow their population sizes to be greater than that of larger species, despite the high mortality of individuals (Pianka, 1970). It is theorized that small species may be less sensitive to climate- and anthropogenically-mediated disturbance due to the ability of females to reproduce rapidly (Rytwinski et al., 2017; Keen et al., 2021). Further, the long generation times of larger species (Sibly and Brown, 2007) may yield longer recovery times following disturbance, making them more sensitive to disturbance.

Despite the slow life history strategy of large species which may increase sensitivity to disturbance, intraspecific trends point to the benefits of large body size. Individuals that attain large body size have lower mass-specific metabolic costs when compared to conspecifics, but may face resource limitation due to their high overall metabolic demands (Kleiber, 1975). To balance the high total metabolic demands of larger bodies they often have improved foraging capabilities and foraging success. For example, large individuals have a higher fasting endurance, allowing them to search longer for better foraging hotspots (Lindstedt and Boyce, 1985; Millar and Hickling, 1990; Costa and Favilla, 2023). For diving species, large size increases aerobic dive limit, thereby allowing individuals to exploit deeper and potentially more productive foraging grounds in a three-dimensional environment (Costa et al., 2001; Mori, 2002). In addition to these energetic benefits of large body size, there are reproductive benefits associated with being large. Large individuals typically give birth to larger, healthier offspring that have higher survival probabilities (Bekoff et al., 1981; Mellish et al., 1999). Although it seems as though all species would evolve to larger body size due to the clear energetic and reproductive benefits (Laurin, 2004; Hone and Benton, 2005), most species exhibit small body size to allow for faster reproduction and generational turnover (Roff 1981; Kozłowski et al., 2002; Clauss, 2003). Thus, examining the constraints placed on body size both on the species and individual level will provide insight into how ecology and biology/physiology interact to influence individual fitness, population demography, and population success.

Marine mammals provide a unique system to address questions related to body size as species differ in size by orders of magnitude, with those at the one extreme trending towards gigantism. (Goldbogen, 2018). Currently, extant marine mammals represent 5 lineages that returned to the marine environment, which favors large body size due to density and thermoregulatory properties of water, as well as the patchy distribution of food. Because body weight is supported by water animals are able to reach larger body sizes (Pauly, 1991). Water also has a high thermal conductivity, drawing heat away from the body much more rapidly than in air (Caldwell, 1974). As such, large body size is beneficial as it decreases surface area to volume ratios to reduce heat loss (Worthy and Edwards, 1990; Adamczak et al., 2020). Lastly, the patchy distribution of prey in the marine environment favors large body size which enables the capacity for larger onboard energy reserves to limit starvation (Kawecki, 1993). The spectrum of sizes across marine mammal species present various challenges that have resulted in a range of reproductive (i.e., capital versus income breeding) and life history strategies (i.e., fast versus slow) that influence measures of Darwinian fitness. Therefore, marine mammals allow for a novel examination of the interplay between body size and fitness across a range of reproductive and life history strategies.

To thoroughly examine the impacts of growth and body size on marine mammals, I first aimed to understand how energy is allocated to growth and the total cost of growth across species. Across mammals, energy allocation to growth is thought to be secondary to basic maintenance costs such as basal metabolism and thermoregulation, and competes with other secondary costs such as reproduction (Kozłowski, 1992). As such, life history theory predicts trade-offs between growth and reproduction representing a dilemma whereby animals can either reproduce early and hinder growth, or reproduce later after reaching a larger size at maturity (Kozłowski, 1992; Röpke et al., 2021). Although the primary goal of any individual is to increase fitness by increasing successful reproductive events, evidence shows that slight delays in reproduction to attain larger size may decrease the success of current reproductive efforts while increasing the potential success of future reproductive events (Baron et al., 2013; Fokidis et al., 2007). As such, many mammals exhibit determinate growth patterns marked by rapid early growth mediated by investment in somatic and skeletal tissues followed by a period of no or very minimal growth in adulthood when individuals are investing in reproduction (citation). To understand if marine mammals follow the same growth trajectories and energy allocation priorities as other mammals, I completed a comprehensive review to assess (1) how marine mammals grow, (2) the composition of growth, (3) energetic costs and allocation priorities, (4) empirical estimates of growth costs, and (5) factors influencing total body size.

Chapter 2 explored the physiological and bioenergetic constraints on body size using theoretical modeling for one of the smallest cetaceans, the harbor porpoise (*Phocoena phocoena*). Given its small size relative to other cetaceans, harbor porpoises face unique bioenergetic challenges with high metabolic rates and high foraging rates to support these costs (Wisniewska et al., 2016; Rojano-Doñate et al., 2018; Booth et al., 2020). This makes harbor porpoises an interesting system to examine the importance of body size on individual vital rates and population demographic trajectories. I modeled one real and two theoretical populations of harbor porpoises with varied body size where the real population have the same average body size as wild populations and the two theoretical populations have average body sizes that deviated from average by ± 10 cm, respectively, from the real population. By only varying body size across the modeled populations, I was able to examine the relationship between life history and body size to determine if species with similar life history traits could support themselves with varying constraints in body size.

To better understand body size constraints and fitness trade-offs at a finer scale, I explored how deviations from expected size influence annual and lifetime metrics of fitness, as well as prioritization trade-offs associated with growth using northern elephant seals (*Mirounga angustirostris*) as a model system. The long-term monitoring program of northern elephant seals at Año Nuevo Reserve is one of the few systems that have morphometric, behavioral, and life history data of known females, making it a unique and ideal system to address how variation in body size impacts fitness for a long-lived, large mammal. Elephant seals are the largest phocid species, indicating a large investment in growth, and have a capital breeding strategy highlighting the importance of body size on reproduction (Haley et al., 1994; Crocker et al., 2012). Using the long-term dataset I constructed the first documented growth curves for northern elephant seals and used these curves to determine age-specific deviation in body size. I then examined the annual and lifetime fitness consequences of deviating from the expected body size for a given age, and assessed the trade-offs between growth, reproduction, and survival in this species.

The research topics explored in this dissertation build to a more comprehensive and nuances understanding of how animals allocate resources to growth, the constraints that influence the optimal body size for a species, and how deviations from expected size have measurable fitness consequences. My first chapter presents a comprehensive review of growth across all marine mammal species, providing the foundational knowledge for future research exploring the bioenergetics and fitness impacts of growth and body size. I then focused my research on two vastly different species; the smallest fully aquatic marine mammal with an income breeding strategy (Chapter 2) and the largest partially aquatic marine mammal with a capital breeding strategy (Chapter 3). Given the different challenges of studying these species in the wild (e.g., harbor porpoises are highly cryptic species while elephant seals reliably return to their breeding colony of origin) I used different methodological tools to explore constraints and trade-offs in body size (i.e., theoretical modeling versus analysis of empirical data). This research improves our understanding of the energetics of growth, the influence of body size on fecundity and survival, and the energetic and life history constraints placed on these factors. With this information we can begin to understand how environmental changes will impact the prioritization of growth mediated through changes to bioenergetics and how changes to growth trajectories can have population-level impacts based on changes to individual vital rates and fitness.

References

Adamczak, S. K., Pabst, D. A., McLellan, W. A., & Thorne, L. H. (2020). Do bigger bodies require bigger radiators? Insights into thermal ecology from closely related marine mammal species and implications for ecogeographic rules. *Journal of Biogeography*, *47*(5), 1193–1206. https://doi.org/10.1111/jbi.13796

Adamczak, S. K., Mchuron, E. A., Christiansen, F., Dunkin, R., Mcmahon, C. R., Noren, S., Pirotta, E., Rosen, D., Sumich, J., & Costa, D. P. (2023). Growth in marine mammals: a review of growth patterns, composition and energy investment. *Conservation Physiology*, *11*, 19 pp. https://doi.org/10.1093/conphys/coad035

Baron, J. P., le Galliard, J. F., Ferrière, R., & Tully, T. (2013). Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival. *Functional Ecology*, *27*(1), 173–183. https://doi.org/10.1111/1365-2435.12023

Bekoff, M., Diamond, J., & Mitton, J. B. (1981). Life-history patterns and sociality in Canids: Body Size, reproduction, and behavior. *Oecologia*, *50*, 386–390.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., & Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia*, *37*, 257–272.

Booth, C. G. (2020). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, *36*(1), 195–208. https://doi.org/10.1111/mms.12632

Caldwell, D. R. (1974). Thermal conductivity of sea water. *Deep-Sea Research*, *21*, 131–137.

Costa, D. P., Gales, N. J., & Goebel, M. E. (2001). Aerobic dive limit: How often does it occur in nature? *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *129*(4), 771–783. https://doi.org/10.1016/S1095-6433(01)00346-4

Costa, D. P., and Favilla, A. B. (2023). Field Physiology in the aquatic realm: ecological energetics and behavior provide context for elucidating patterns and deviations. *Journal of Experimental Biology, 226(20):jeb245832.* https://doi.org/100.1242/jeb.245832

Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G. E., & Streich, W. J. (2003). The maximum attainable body size of herbivorous mammals: Morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, *136*(1), 14–27. https://doi.org/10.1007/s00442-003-1254-z

Craig, M. P., & Ragen, T. J. (1999). Body size, survival, and decline of juvenile Hawaiian monk seals, Monachus schauinslandi. *Marine Mammal Science*, *15*(3), 786–809.

Crocker, D. E., Williams, J. D., Costa, D. P., & le Boeuf, B. J. (2001). Maternal traits and reproductive effort in Northern elephant seals. *Ecology*, *82*(12), 3541–3555.

Crocker, D. E., Houser, D. S., & Webb, P. M. (2012). Impact of body reserves on energy expenditure, water flux, and mating success in breeding male northern elephant seals. *Physiological and Biochemical Zoology*, *85*(1), 11–20. https://doi.org/10.1086/663634

Fokidis, H. B., Risch, T. S., & Glenn, T. C. (2007). Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour*, *73*(3), 479–488. https://doi.org/10.1016/j.anbehav.2006.08.010

Goldbogen, J. A. (2018). Physiological constraints on marine mammal body size. *PNAS*, *115*(16), 3995–3997. https://doi.org/10.1073/pnas.1804077115

Gunnlaugsson, T., Víkingsson, G. A., Halldórsson, S. D., Elvarsson, B. Þ., Haug, T., & Lydersen, C. (2020). Body mass, muscle, blubber and visceral fat content and their seasonal, spatial and temporal variability in North Atlantic common minke whales. *Journal of Cetacean Research and Management*, *21*, 59–70. https://iwc.int/permits.

Haley, M. P., Deutsch, C. J., & le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, Mirounga angustirostris. *Animal Behavior*, *48*, 1249–1260.

Kawecki, T. J. (1993). Age and size at maturity in a patchy environment: Fitness maximization versus evolutionary stability. *Oikos*, *66*(2), 309–317. https://www.jstor.org/stable/3544819

Keen, K. A., Beltran, R. S., Pirotta, E., & Costa, D. P. (2021). Emerging themes in Population Consequences of Disturbance models. *Proceedings of the Royal Society B: Biological Sciences*, *288*. https://doi.org/10.1098/rspb.2021.0325

Kleiber, M. (1975). Metabolic turnover rate: A physiological meaning of the metabolic rate per unit body weight. *Journal of Theoretical Biology*, *53*, 199–204.

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology and Evolution*, *7*(1), 15–19.

Kozłowski, J., & Gawelczyk, A. T. (2002). Why are species' body size distributions usually skewed to the right? *Functional Ecology*, *16*(4), 419–432. https://doi.org/10.1046/j.1365-2435.2002.00646.x

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, *125*(6), 873–878. https://about.jstor.org/terms

McNab, B. K. (1980). Food Habits, Energetics, and the Population Biology of Mammals. *The American Naturalist*, *116*(1), 106–124.

Mellish, J.-A. E., Iverson, S. J., & Bowen, W. D. (1999). Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, *72*(6), 677–690.

Millar, J. S., & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. *Ecology*, *4*(1), 5–12.

Molnár, P. K., Klanjscek, T., Derocher, A. E., Obbard, M. E., & Lewis, M. A. (2009). A body composition model to estimate mammalian energy stores and metabolic rates from body mass and body length, with application to polar bears. *Journal of Experimental Biology*, *212*(15), 2313–2323. https://doi.org/10.1242/jeb.026146

Mori, Y. (2002). Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, *15*, 269–276.

Pauly, D. (1991). Geometrical constraints on body size. *Trends in Ecology and Evolution*, *12*(11), 442.

Pianka, E. R. (1970). On r- and K-Selection. *The American Naturalist*, *104*(940), 592–597. https://www.jstor.org/stable/2459020

Roff, D. (1981). On being the right size. *The American Naturalist*, *118*(3), 405–422. https://about.jstor.org/terms

Rojano-Donãte, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., Højer-Kristensen, J., & Madsen, P. T. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*(23), jeb185827. https://doi.org/10.1242/jeb.185827

Röpke, C., Pires, T. H. S., Zuanon, J., Freitas, C. E. C., Hernandes, M. C., Souza, F., & Amadio, S. (2021). Growth–reproduction trade-off and fecundity regulate population stability in Amazon floodplain fishes. *Freshwater Biology*, *66*(6), 1101–1109. https://doi.org/10.1111/fwb.13702

Rytwinski, T., & Fahrig, L. (2011). Reproductive rate and body size predict road impacts on mammal abundance. *Ecological Applications*, *21*(2), 589–600.

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running. *Science*, *177*(4045), 222–228.

Sibly, R. M., & Brown, J. H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *PNAS*, *104*(45), 17707–17712. www.pnas.org/cgi/content/full/

Williams, T. M. (1999). The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society B*, *354*, 193–201. https://royalsocietypublishing.org/

Wisniewska, D. M. M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S., Miller, L. A. A., Siebert, U., & Madsen, P. T. T. (2016). Ultra-High foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, *26*(11), 1441–1446. https://doi.org/10.1016/j.cub.2016.03.069

Worthy, G. A. J., & Edwards, E. F. (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (Phocoena phocoena) and a small tropical cetacean (Stenella attenuata). *Physiological Zoology*, *63*(2), 432–442.

Chapter 1

Growth in marine mammals: a review of growth patterns, composition, and energy investment

Adamczak, S. K., McHuron, E. A., Christiansen, F., Dunkin, R., McMahon, C. R., Noren, S., Pirotta, E., Rosen, D., Sumich, J., and Costa, D. P.

1.1 Abstract

Growth of structural mass and energy reserves influences individual survival, reproductive success, and population and species life history. Metrics of structural growth and energy storage of individuals are often used to assess population health and reproductive potential, which can inform conservation. However, the energetic costs of tissue deposition for structural growth and energy stores and their prioritization within bioenergetic budgets are poorly documented. This is particularly true across marine mammal species as resources are accumulated at sea, limiting the ability to measure energy allocation and prioritization. We reviewed the literature on marine mammal growth to summarize growth patterns, explore their tissue compositions, assess the energetic costs of depositing these tissues, and explore the tradeoffs associated with growth. Generally, marine mammals exhibit logarithmic growth. This means that the energetic costs related to growth and tissue deposition are high for early postnatal animals, but small compared to the total energy budget as animals get older. Growth patterns can also change in response to resource availability, habitat, and other energy demands, such that they can serve as an indicator of individual and population health. Composition of tissues remained

consistent with respect to protein and water content across species; however, there was a high degree of variability in the lipid content of both muscle (0.1-74.3%) and blubber (0.4-97.9%) due to the use of lipids as energy storage. We found that relatively few well-studied species dominate the literature, leaving data gaps for entire taxa, such as beaked whales. The purpose of this review was to identify such gaps, to inform future research priorities, and to improve our understanding of how marine mammals grow and the associated energetic costs.

1.2 Introduction

Body size is an important driver of individual survival and reproductive success, and drives population and species life history (Blueweiss et al., 1978; Lindstedt and Calder, 1981; Lindstedt and Boyce, 1985; Calder, 2001). Being structurally large can provide direct benefits, such as increased performance in intra-specific competition and defense from predation, and energetic benefits, such as decreased mass-specific metabolic costs and increased energy storage (Bartholomew 1970; Kleiber, 1975; McNab et al., 1980; Lindstedt and Boyce, 1985; Millar and Hickling, 1990; Williams, 1999; Molnár et al., 2009; Gunnlaugsson et al., 2020). The capacity of large individuals to deposit and utilize body energy reserves can greatly influence a species' ability to survive periods of low food availability, and to exploit spatially and temporally variable resources (Lindstedt and Boyce, 1985; Costa and Maresh, 2022). Large body size confers a benefit in an aquatic environment by buffering against costs associated with thermal conductivity of water and buffering against extended periods without food due to the ephemeral nature of prey resources.

As such, marine mammals often allocate large amounts of resources to growth of structural size early in life, despite the increased energetic cost of growth, and continue to allocate energy to reserves through adulthood (Christiansen et al., 2022a).

Given the benefits of large body size, neonatal and young animals are at a disadvantage until mature body size is attained. Thus, rapid changes in body size would be expected early in life. Indeed, mammalian growth occurs in two phases: (1) the early life phase when structural lean tissue is primarily deposited, and (2) the physical maturity phase when there is a transition to the deposition of energy stores primarily in the form of lipids (Guenther et al., 1965; Crocker et al., 1998). The initial growth phase determines the asymptotic size of an animal, both in length and mass (McLaren, 1993). In contrast, the second growth phase is characterized by fluctuations in mass and overall body condition, often related to seasonal resource availability of the species' reproductive cycle, with very minimal fluctuations in structural size (McLaren, 1993; Rosen et al., 2021). Energy allocation to both the primary and secondary growth phases varies in response to intrinsic and extrinsic factors, such as energy requirements and prey availability, that influence individual growth rates, size at physical maturity, and body condition. Alterations to growth investment can have lasting effects on an animal's biology and physiology and lead to population-level impacts due to the repercussions of body size on survival and reproduction (Craig and Ragen, 1999; Pomeroy et al., 1999; Crocker et al., 2001; McMahon et al., 2017).

The application of body size and condition metrics to marine mammal and ecosystem conservation and management requires knowledge of how energy is allocated to deposition of structural and reserve tissues, the costs associated with growth, and the factors that influence growth. Improved knowledge of growth processes and energetics can be particularly beneficial for bioenergetic modeling, which explores how energy is metabolized and allocated to various aspects of maintenance, growth, and reproduction. Bioenergetic models have been used to assess how and when anthropogenic disturbances that affect energy budgets result in population-level impacts (Costa, 2012, Pirotta et al., 2018a; Keen et al., 2021; Pirotta 2022). These population-level impacts are a consequence of decreased foraging opportunities, which initially result in reduced investment into non-essential metabolic processes such as growth and reproduction or, ultimately, mortality due to starvation. Accurate quantifications of the costs associated with growth and the factors influencing growth are necessary to improve forecasting via bioenergetic models.

In this review, we synthesize the available literature on marine mammal growth. We aim to address five major themes regarding growth in marine mammals: (1) how marine mammals grow, (2) composition of growth, (3) energetic costs and allocation priorities, (4) empirical estimate of growth costs, and (5) factors influencing total body size and energy reserves. Given how important acquiring, storing, and using resources are in determining vital rates and individual health, we identify data gaps and potential areas for future research.

1.3 Methods

We used Google Scholar with the search terms ‘bioenergetics’, ‘tissue composition’, ‘muscle composition’, ‘blubber composition’, ‘muscle lipid content’, ‘muscle protein content’, ‘blubber lipid content’, ‘blubber protein content’, ‘growth curve’, ‘growth trajectory’, ‘growth cost’, and ‘energy allocation to growth’ with a combination of ‘marine mammal’, species scientific names, and species common names. Additionally, we searched for ‘organohalogen’, ‘organochlorine’, and ‘toxicology’, with a combination of ‘marine mammal’, species scientific names, and species common names as we found this literature to be rich in tissue composition data. While we searched across all marine mammal taxa, our focus was on cetaceans and pinnipeds as these are the most studied and speciose marine mammal taxa.

In addition to the literature review, we used existing data to address two issues that have not been well investigated in the literature: (1) the influence of species and life history stages on muscle protein content in cetaceans and (2) the cost of growth in marine mammals. We used Kruskal-Wallis tests to examine differences in muscle protein content reports between cetacean taxonomic groups ($n = 49$ and 5 for mysticetes and odontocetes, respectively), age classes (for mysticetes only, $n = 7$ and 5 for immature and mature, respectively, excluding reports that clumped data across multiple age classes and reproductive statuses), and sex both across age classes and for mature individuals only (for mysticetes only, $n = 24$ and 6 for males and females of all age classes, respectively, and $n =2$ and $n = 2$ for mature males and females, respectively; McKnight and Najab, 2010).

To estimate the cost of growth, defined as the energy required to synthesize and deposit tissues, in marine mammals, we assessed the relationship between mass deposition rate and resting metabolic rate (measured during regular health examinations) for female juvenile northern fur seals (*Callorhinus ursinus*; n = 6), adult male bottlenose dolphins (*Tursiops truncatus*; n = 2), and a single male gray whale calf (*Eschrichtius robustus*), all managed in human care. Our methods mirrored those used to estimate the cost of growth in domestic cattle and lab rats (Rattray and Joyce 1976). For northern fur seals and bottlenose dolphins, we used respirometry and mass measurements from health assessments conducted at uneven intervals. The gray whale data came from a single juvenile gray whale for which food intake was used as a proxy for metabolic needs. Mass deposition rate was determined as the mass change (g) between examination dates divided by the number of days between examinations. We used Wilcoxon signed rank tests to compare resting metabolic rate in positive growth phases (when mass was gained) and negative growth phases (when mass was lost) for both bottlenose dolphins and northern fur seals to test if resting metabolic rate increased while depositing tissues. To estimate the cost of growth in marine mammals we used the slope derived from a linear model testing the relationship between mass deposition and metabolic rate (Rattray and Joyce, 1976). A combination of response variables, including resting metabolic rate and mass-specific metabolic rate, and explanatory variables, including mass deposition rate and mass deposition rate normalized by body size, were tested in the model. When more than one test subject was available we tested the impact of individuals as random effects with linear mixed effect models (Oberg and Mahoney, 2007). We used Akaike Information Criterion (AIC) to select the most parsimonious model (Portet, 2020). Separate models were constructed for each species to account for differences in age and methods used to estimate metabolic rate. The results of these analyses can be found in the "Empirical estimate of growth costs section". The remaining sections summarize the results of the literature review.

1.4 How do marine mammals grow?

Marine mammals exhibit diminishing structural growth throughout their lifetime, marked by rapid growth prior to physical maturity that slows around adulthood. They are thought to have a finite growing period, causing total body size (or structural size) to reach an asymptote (see below for exceptions). The initial growth phase determines the overall size of an animal, both in length and mass, and includes some fluctuations in mass due to the mobilization and deposition of reserves (Rosen et al., 2021). In contrast, the second growth phase focuses almost entirely on fluctuations in mass due to changes in reserves mediated by season, reproductive status, and prey availability (e.g., Lockyer, 1995; Gallagher et al., 2021; Rosen et al., 2021). These growth stages can be described using growth curves that model the length- and weight-at-age, as well as length-weight relationships (Figure 1).

Growth curves are typically constructed by fitting a Gompertz, von Bertalanffy, or Richards growth model to data on length- or weight-at-age, or a regression of weight-at-length (Zeide, 1993; Tjørve and Tjørve, 2017; Hall et al., 2019; Christiansen et al., 2022). The various stages of growth may not fully be captured by these models, and it may be necessary to construct multiple growth curves for different age classes(e.g., McLaren, 1993; Chabot and Stenson, 2002; Agbayani et al., 2020; Fortune et al., 2021). In particular, growth during the first year of life is often rapid, necessitating a separate model for this life stage (Best and Schell, 1996; Fortune et al., 2021; Rosen et al., 2021). In some cases, males may undergo growth spurts prior to physical maturity that further complicate growth rates for young individuals (e.g., Winship et al., 2001). Additionally, growth models often model asymptotic growth, although research indicates that some species may continue to grow into adulthood, such as mysticetes (Payne, 1979). Such taxonomic groups may not reach an asymptotic size, despite reduced growth rates in adulthood. However, this result may be an artifact of using data from whaled or harvested individuals (see below). Lastly, some species may demonstrate nuanced growth patterns that cannot be represented by a single growth curve. For example, newly weaned bowhead whales (*Balaena mysticetus*) enter a diapause stage where structural growth is halted for three to four years (Schell et al., 1989).

There are limitations in the data sources used to construct growth curves, particularly with respect to cetaceans. Most cetacean growth curves have been derived from stranded, bycaught, or harvested individuals (Figure 2). Such data may be biased, as stranded individuals may be in poor health and whalers targeted larger individuals, resulting in under- and overestimates, respectively, of size at a given age (e.g., Stevick, 1999). Despite these limitations, these observations do provide valuable bioenergetic information (Irvine et al., 2017). Most growth curves collated here were published 20 or more years ago, with the largest proportion of growth curves published between 1990-2010 (Figure 2). Since then, novel technologies have been developed that facilitate data collection using non-lethal methods, warranting a re-analysis of previously constructed curves. For example, the inter-pulse interval of echolocation clicks has been used to determine sperm whale (*Physeter macrocephalus*) length (Dickson, 2020) and aerial- or laser-photogrammetry has been used to estimate length, mass, and volume of free-living animals (e.g., Christiansen et al., 2018; van Aswegen et al., 2019; Fortune et al., 2021). Although using non-lethal methods may reduce sample size due to limitations of accessing wild animals and the small number of individuals that can be held in human care, there are opportunities to collate data from multiple sources to improve sample size (e.g., Clark et al., 2000).

Availability of growth curves and, therefore, our understanding of marine mammal growth patterns, is highly species-dependent. Data are plentiful for pinnipeds; 100% of phocid seals and 79% of extant otariid species have documented length-at-age, weight-at-age, or weight-at-length curves, although, when considering just weight-at-age curves, phocid coverage decreases to just over 50% (Table A1.1). Cetacean growth curves are less common due to their fully aquatic lifestyle. For mysticetes, 73% of known species have documented length-at-age, weight-at-age, or weight-at-length curves, and only 47% of species have weight-at-age curves. Approximately 52% of odontocete species have length-at-age curves, which decreases to 26% when considering just weight-at-age curves (Table A1.1). Although some odontocete families have complete coverage of length-at-age, weight-at-age, and weight-at-length curves, such as the Kogiids and Monodontiids, there is very poor coverage among the most speciose odontocete family, the Delphinids, and little or no data among the beaked whales and river dolphins (Table A1.1).

Growth curves documenting lean mass are much sparser than those discussed above. To obtain these measurements the animal must either be killed or isotopic methods must be used, which requires repeated access to the animal. This limits the species for which lean mass growth curves are available to small and/or partially aquatic species. Although lean mass is an important determinant of resting metabolic rate (Rea and Costa, 1992), the use of mass curves to calculate resting metabolic rate likely provides an adequate estimation of metabolic rate for bioenergetic modeling.

1.5 Composition of growth

1.5.2 Tissue synthesis

The chemical composition of tissues depends on the form of chemical energy ingested, which allows for the synthesis of various types of tissues. In most vertebrates, the synthesis of new tissues relies on the ingestion of three primary organic macromolecules: proteins, carbohydrates, and lipids. Most marine mammals synthesize carbohydrates primarily from protein because they are minimally present in the diet of most species, except for sirenians. Processing ingested lipids into energy reserves is more efficient than processing and depositing protein (Rattray and Joyce, 1976). However, the extent of protein or lipid deposition depends on both the amount and composition of macronutrient intake and growth priorities at that particular life stage.

To synthesize lean muscle tissue, protein intake must exceed protein degradation (Reeds et al., 1982; Fuller and Chen, 1997). Protein intake determines lean mass deposition in marine mammals, although this has predominantly been studied in phocids (Kirsch et al., 2000; Trumble et al., 2003). The deposition of lean muscle tissue has an asymptotic relationship with increasing energy input, as there is a limit to how much lean mass can be deposited within a given timeframe (Fuller and Chen, 1997). In mammals, metabolized protein is excreted as nitrogenous waste in the form of urea (Reeds et al., 1980; Costa et al., 2013), while protein not metabolized can be deposited as structural tissue, and may also be used later as an energy source (Crocker et al., 1998).

When lipids (i.e., triglycerides or wax esters) are ingested, they are broken down into fatty acids and transported through the bloodstream. If energy intake exceeds energy expenditure, these lipids are deposited in adipocytes as energy reserves. Although it was previously thought that wax esters were largely indigestible by mammals, it appears that mysticetes possess the ability to assimilate 99% of dietary wax esters potentially mediated by symbiotic gut microbes (Swaim et al., 2009; Koopman, 2018). In contrast, odontocetes appear to biosynthesize wax esters rather than incorporate dietary wax esters (Koopman, 2018). With respect to triglyceride assimilation, the efficiency of converting ingested lipids to reserve lipids appears to be modulated by diet composition and may be species-specific. In harbor seals (*Phoca vitulina*), lipid and protein digestibility declined on a high lipid diet (Trumble et al., 2003), while in northern fur seals (*Callorhinus ursinus*) lipid digestibility improved with moderate to high lipid ingestion (Diaz Gomez et al., 2020). Lipid-poor diets cause a reduction in lipid reserves when an animal is nutritionally challenged (Rosen and Trites, 2005). Thus, efficient tissue deposition and energy storage rely on an appropriate balance in diet composition.

1.5.3 Tissue composition

Tissues are primarily comprised of protein, lipid, water, and carbohydrates. For most vertebrates, the chemical composition of skeletal muscle is about 70-80% water, 20-30% protein, and 1-2% lipid (Anghihan et al., 1969; Kim, 1974; Listrat et al., 2016). The protein content of marine mammal muscle is on par with those reported for other vertebrates, ranging approximately 18.2-26.9% (fin whale [*Balaenoptera physalus*], sei whale [*Balaenoptera borealis*], and minke whale [*Balaenoptera acutorostrata*]; Lockyer et al., 1985; Víkingsson et al., 2013; bowhead whale [*Balaena mysticetus*]; O'Hara et al., 2004; sperm whale; Watanabe and Suzuki, 1950; harp seal [*Pagophilus groenlandicus*] and hooded seal [*Cystophora cristata*]; Brunborg et al., 2006; Cape fur seal [*Arctocephalus pusillus*]; Koep et al., 2007). We found no significant trends in muscle protein content between taxonomic groups (), age class, or sex amongst age classes or for mature individuals (Kruskall-Wallis test; p = 0.08; p =0.83; p = 0.39; p = 0.32, respectively), although our sample was biased towards female mysticetes.

Skeletal muscle lipids include structural lipids and phospholipids that are necessary to build this tissue, in addition to storage lipids that are deposited and mobilized with energetic needs. Because of the additional storage lipids, it is difficult to determine baseline lipid content (i.e., the lipid content consisting of phospholipids and structural lipids required simply to build this tissue) for marine mammals. Estimates of baseline muscle lipid content may be obtained from fasted animals that have depleted their energy reserves, such as capital breeding marine mammals; however, no such data are currently publicly available. Given the lack of data, the minimum reported value of muscle lipid content, 0.1% in the short-beaked common dolphin (*Delphinus delphis*; Lazar et al., 2002), may represent the best available value for baseline muscle lipid content. Baseline muscle lipid content is important for accurately determining the energetic cost of structural growth (see Energy allocation to growth and energetic costs section). However, it should be noted that the above minimum value for muscle lipid content was derived from the ecotoxicology literature and the age, sex, or nutritional condition of the study animal was not provided.

Additional lipids in skeletal muscle are considered energy reserves, and as such typically take the form of triglycerides (Young, 1976; Trumble et al., 2010). In fin whales and Weddell seals (*Leptonychotes weddellii*), muscle lipid content appears to vary in proportion to the lipid content of blubber (the primary energy reserve tissue), suggesting that muscle lipid content reflects energy storage levels (see Figure 1 in Lockyer, 1986; Figure 1 in Trumble et al., 2010; Víkingsson, 1995). Muscle lipid content is highly variable, ranging between 0.1 and 74.3% in our review, and is dependent on age, species, season, and diet (Figure 3; Beck et al., 1993; Mourot and

Hermier, 2001; Trumble et al., 2010; Shingfield et al., 2013), further indicating the potential importance of skeletal muscle as an energy reserve tissue.

The body compartment most associated with lipid storage is adipose tissue, which takes the form of subcutaneous blubber, the specialized hypodermis in marine mammals. In addition to the lipids found in blubber, this body compartment contains water that varies inversely with lipid content (Dunkin et al., 2005), variable amounts of protein (1.45-35%; Watanabe and Suzuki, 1950; Lockyer et al., 1984; Lockyer, 1991; Gales et al., 1994; Koep et al., 2007; Víkingsson et al., 2013; Anezaki et al., 2016), and minimal amounts of carbohydrate (1-6%; Lockyer, 1991). Blubber also serves for streamlining, locomotion, and thermoregulation, and these uses affect its lipid content (Worthy and Lavigne, 1987; Pabst et al., 1999; Trumble et al., 2010). Deep-diving sperm and beaked whales also incorporate wax esters into their blubber (Koopman, 2007; Bagge et al., 2012). Although the tole of wax esters in marine mammals is not fully known, it is posited that they do not aid in energy storage as they are more difficult to metabolize in vertebrates (Koopman, 2007; Koopman, 2018).

Additional energy reserves may exist in the viscera and bone (Lockyer et al., 1985; Víkingsson et al., 1995). Lipids in the viscera range widely between 0.33 and 96% (from values reported for kidney, liver, and heart), but it is not known what proportion of this lipid content is used for storage as some lipids may be structural (e.g., phospholipids). In the literature, visceral fat stores have been documented in whales that have already amassed large blubber stores (Lockyer et al., 1986).

Anecdotal observations indicate depleted visceral fat stores in other cetaceans and pinnipeds that are nutritionally compromised (pers. comm. R. Dunkin and D. Rosen). The lipid content of bones ranges between 21.1 and 25.9%, however it is unknown what proportion of this is used to store excess lipids (Lockyer et al., 1985; Víkingsson et al., 1995).

1.6 Energy allocation to growth and energetic costs

The cost of depositing structural or reserve tissues, hereby known as the cost of growth, is believed to be small relative to total energy expenditure for most mammals (e.g., Roberts and Young, 1988; Víkingsson, 1995; Dalton et al., 2015; Hin et al., 2019; Christiansen et al., 2022a). To measure the cost of growth, the excess energy above maintenance required to deposit tissues must be uncoupled from other metabolic processes such as locomotion, digestion, and thermoregulation. Due to the difficulties of isolating growth costs, available estimates have been obtained using a variety of methods and assumptions. Some methods use only the energy content of the deposited tissues to estimate the total cost of growth (i.e., 1 kJ of energy is required to deposit 1 kJ of tissue), which does not account for the inefficiencies (secondary costs related to the chemical energy required to synthesize tissues) associated with tissue synthesis and deposition. Studies from other mammals that incorporate these inefficiencies, including from rats, pigs, and cattle, estimate the energetic cost of tissue deposition to range from approximately 1.17 to 1.37 kJ/kJ for fat and 1.92 to 2.38 kJ/kJ for protein (Roberts and Young, 1988). Because of the difference in deposition costs between fat and protein, as well as the higher energy density of lipid, tissues with a higher lipid content (e.g., blubber) require more ingested energy and higher metabolic costs to deposit.

Alternately, the cost of tissue deposition, incorporating energetic inefficiencies, can be estimated by increasing energy intake above maintenance energy intake and measuring concurrent changes in mass (Blaxter, 1968). This technique yields a total cost of growth ranging from 12.2 kJ/g to a maximum of 63 kJ/g in small mammals, humans, and some birds depending on the composition of growth and how growth inefficiencies are calculated (Millward et al., 1976; Rattray and Joyce, 1976; Pullar and Webster, 1977; Roberts and Young, 1988). However, these methods have yet to be applied to marine mammals.

In most cases, the cost of growth in marine mammals has been estimated using the energy density of protein and lipid and the mass of deposited tissues, without accounting for inefficiencies. For example, this method was used to estimate the cost of growth in southern right whales (*Eubalaena australis*) resulting in costs of 27.163 kJ/g for blubber and 9.732 kJ/g for skeletal muscle (Christiansen et al., 2022a). When using this method it is important to remember that skeletal muscle and blubber contain both protein and lipid (i.e., skeletal muscle is not solely protein). Though this can be avoided when using total body protein and lipid content. Additionally, the reported energy density values range from 19.66-26.6 kJ/g for protein and 37.66-39.75 kJ/g for lipid (Brody, 1968; Kleiber, 1947). The energy density of protein differs depending on its use for tissue synthesis or catabolism and at what point in the digestion to deposition chain it is accounted for. The energy density of protein is 26.6 kJ/g, but after oxidation to CO_2, water, and ammonia this is reduced to 23.43 kJ/g (Kleiber, 1975). Once protein is metabolized, creating CO_2, water, and urea, the energy density is reduced to generates 19.66 kJ/g, which pre-accounts for the chemical energy lost in urine as urea (Kleiber, 1961). As such, it is important to understand what the selected energy density value represents (i.e., pre- or post-metabolized protein).

1.7 Empirical estimate of growth costs

In marine mammals, there have been few attempts to empirically estimate the total cost of growth using metabolic rate or energy intake. An approximation of the cost of protein deposition in northern fur seals has been proposed as 7% of daily energy expenditure for postweaning females (Dalton et al., 2015), while Atlantic fin whales must consume 2-3% of body weight in prey to both meet metabolic demands and add additional energy reserves (Víkingsson, 1995). When examining resting metabolic rate in positive and negative growth phases, we found a significant increase in metabolic rate of northern fur seals during positive growth phases (Wilcoxon signed rank test, $p = 2.4 \times 10^{-3}$; Figure 3). There was no significant difference in resting metabolic rate in positive and negative growth phases in bottlenose dolphins likely because these individuals were adults and therefore only depositing small lipid stores in contrast to the greater lipid and protein deposition of juveniles in the primary growth phase. Further, the minimal increase in resting metabolic rate in positive growth phases for bottlenose dolphins may be a result of metabolic compensation to decrease the overall energetic strain of depositing new tissues.

When examining the relationship between mass deposition and metabolic rate, the best model included mass-specific metabolic rate and mass deposition normalized by body size for all species, with a significant random effect of individual only for northern fur seals (AIC = 1559.31, 129.51, and 38.09 for northern fur seals, bottlenose dolphins, and the gray whale, respectively). Mass-specific metabolic rate increased with mass deposition across all species, resulting in an estimated cost of growth of 23.11 kJ/g, 23.76 kJ/g, and 14.35 kJ/g, for northern fur seals, bottlenose dolphins, and the gray whale, respectively (Figure 4). The estimated cost of growth derived in this study is within the range of reported for other mammals (e.g., Millward et al., 1976; Rattray and Joyce, 1976; Pullar and Webster, 1977; Roberts and Young, 1988; Christiansen et al., 2022a). Interestingly, juvenile northern fur seals had a similar cost of growth to adult bottlenose dolphins which may indicate that the composition of tissues deposited are similar, despite the difference in species and age class. The gray whale calf had a much lower estimated cost of growth. This may be an artifact of the sampling method, which used gross energy intake from prey as a proxy for metabolic rate. Alternately, this may indicate that very large animals, such as the gray whale, have proportionally lower costs of growth per their size. However, further investigation into this topic is warranted.

1.8 Factors influencing total body size

1.8.1 Maternal investment

Maternal investment in offspring is vital to growth and development as young animals are fully or partially dependent on milk until they reach weaning age.

Maternal mass is highly correlated with offspring mass at both birth and weaning across mammals (Bowen et al., 2015; Holser et al., 2021; Allen et al., 2022; Christiansen et al., 2022; Costa and Maresh, 2022). Females in better condition yield larger, presumably healthier offspring (e.g., Kovacs and Lavigne, 1986; Taillon et al., 2012; Christiansen et al., 2018; Dias et al., 2018; Holser et al., 2021; Stewart et al., 2022). This pattern holds true for both pinnipeds and cetaceans (e.g., Kovacs and Lavigne, 1986; McDonald et al., 2008; Christiansen et al., 2014; Christiansen et al., 2018) and is likely the result of the relationship between female condition and fetal growth, as well as the relationship between milk quality and quantity and early calf development (e.g., Festa-Bianchet et al., 1998; Georges and Guinet, 2000; West et al., 2007; Costa, 2008; Riet-Sapriza et al., 2012). So important is this relationship between maternal condition and offspring growth that populations may decrease if maternal body condition is chronically poor amongst females. For example, calf growth rates of North Atlantic right whales (*Eubalaena glacialis*) have declined in conjunction with population-wide decreases in maternal body condition (Christiansen et al., 2020; Stewart et al., 2021). Additionally, plasticity in maternal care allows females to allocate resources either to their current reproductive effort or future reproductive success, affecting how young, nutritionally dependent animals grow (Boness et al., 1991; Festa-Bianchet et al., 1998; Costa, 2008; McMahon et al., 2017).

1.8.2 Population dynamics

In vertebrates, density-dependence, increased competition, or predation and mortality risks can affect prenatal stress on the mother which can alter pre- and postnatal growth in offspring (Coslovsky and Richner, 2011; Dantzer et al., 2013; Berghänel et al., 2017; Holser et al., 2021). Some populations experience increases in offspring growth rates as populations near carrying capacity, because larger individuals are superior competitors for resources (Coslovsky and Richner, 2011; Dantzer et al., 2013). However, individual growth rates have also been shown to decline in response to increasing density-dependence (Kato, 1987; Fowler, 1990; Harding et al., 2018), likely due to a decrease in per-capita environmental resources as populations reach carrying capacity.

1.8.3 Environment

Seasonal and annual changes in prey availability and temperature affect the overall energy budget of animals, resulting in unique species-specific changes in energy allocation to growth. For example, during El Niño events, when decreased prey availability in some regions yields reduced energy intake, Galapagos fur seal (*Arctocephalus galapagoensis*) pups were lighter in weight and California sea lion pups were smaller than their predicted size-at-age (Trillmich and Limberger, 1985; Boness et al., 1991). In other species decreased energy intake may not influence growth. For example, Steller sea lions (*Eumetopias jubatus*) maintained structural growth even when fed low energy density diets (Rosen et al., 2006). However, it is important to note that these Steller sea lions experienced short-term reductions in energy intake in human care. Longer-term periods of decreased energy intake could have more severe negative influences on growth because there is limited evidence that pinnipeds can demonstrate compensatory growth to make up for earlier nutritional challenges (du Dot et al., 2008).

The relationship between the environment and growth have been described using ecogeographic rules; Bergmann's rule and McNab's rule. Bergmann's rule and McNab's rule describe a latitudinal increase in overall body size within and amongst species (Bergmann, 1847; Mayr, 1956; McNab, 1971; McNab, 2010). Bergmann's rule posits that larger body size near the poles is driven by greater thermoregulatory needs. Larger organisms have a lower surface area to volume ratio and, therefore, less heat is lost per unit of heat that is produced (McNab, 1971). However, McNab's rule posits that this latitudinal trend may be driven by differences in resource availability. Lower latitudes have lower prey densities, favoring smaller body sizes (McNab, 2010). Latitudinal gradients in marine mammal body size attributed to both Bergmann's and McNab's rules have been identified at broad taxonomic levels and between closely related species (Galatius and Gol'din, 2011; Oosthuizen et al., 2016; Torres-Romero et al., 2016; Best et al., 2017; Ferguson et al., 2018; van Aswegen et al., 2019; Adamczak et al., 2020). For example, closely related pilot whale (*Globicephala* spp.) species differ slightly in body size and surface area to volume ratio, with the larger, more northern species being better equipped for the colder waters within its range, supporting Bergmann's rule (Adamczak et al., 2020). In support of McNab’s rule, harbor porpoise populations along the California coast are larger than other populations, which may be driven by the nutrient-rich upwelling in this region (Galatius and Gol'din, 2011). Additionally, latitudinal gradients in sperm whale body size have been linked to changes in prey size along this gradient (Best et al., 2017). Similar trends are seen when comparing the recently diverged California sea lion and Galápagos sea lion (*Zalophus wollebaeki*). California sea lions are larger in overall size and inhabit more productive northern waters of the Pacific Ocean, which may be driven by latitudinal gradients in food availability rather than genetics (Schramm et al., 2009; Villegas-Amtmann et al., 2011). Although an empirical test of the contribution of genetics or environment to size clines in marine mammals have not been carried out, conclusions from other vertebrates show contrasting results, highlighting the complexity of this question (Teplitsky et al., 2008; Husby et al., 2011; Ballinger and Nachman, 2022).

1.9 Factors influencing energy reserves

1.9.2 Life history events

Reproduction is a period of increased energy expenditure for marine mammals, resulting in changes to body energy reserves (Costa et al., 1989; Arnould and Duck, 1997; Crocker et al., 2012; Bejarano et al., 2017; Christiansen et al., 2022b). However, the nature of investment into deposition and utilization of reserves differs with breeding strategy (Costa and Maresh, 2022). Capital breeding females store proportionally more energy than income breeders of similar size (Irvine et al., 2017) and increase lipid reserves prior to pregnancy (Lockyer, 1986; Miller et al., 2011; Lemos, 2020). These lipid reserves are then quickly depleted during lactation as the female typically fasts during this period (Pettis et al., 2007; Miller et al., 2011; Richard et al., 2014; Lemos, 2020; Aoki et al., 2021). Protein catabolism during lactation also plays an important role in fluctuations of overall body mass in phocids, particularly when lipid reserves are depleted (e.g., Crocker et al., 1998). In contrast, female income breeders typically exhibit a much slower and steadier decrease, or in some cases no decrease, in mass and condition throughout lactation (Costa et al., 1989). This is facilitated by simultaneous feeding over much longer lactation durations (i.e., months to years) when compared to capital breeders (i.e., days to months; Perrin and Reilly, 1984; Read and Hohn, 1995; McDonald and Crocker, 2006; Karniski et al., 2018; Costa and Maresh 2022). Many marine mammals exist on a continuum from capital to income breeders, and others exhibit a mix of these strategies, necessitating different lipid sequestration during reproduction (Noren et al., 2014).

Males also incur reproductive costs that influence body reserves, despite the differing reproductive strategies between the sexes (Arnould and Duck, 1997; Coltman et al., 1998; Crocker et al., 2012). This has predominantly been studied in pinnipeds due to the difficulties associated with studying breeding and reproductive costs in fully aquatic species. In pinnipeds, male reproductive costs are typically incurred via territory defense during which many species fast to maintain a territory or harem (e.g., Anderson and Fedak 1985; Boyd and Duck, 1991; Bartsh et al., 1992; Arnould and Duck 1997). However, some species that reproduce in the water, such as the harbor seal, may opportunistically feed throughout the breeding season, offsetting large declines in body mass (Coltman et al., 1998). Across most pinniped species, larger males lose proportionally more body mass throughout the breeding season in exchange for greater mating success and more breeding opportunities (Anderson and Fedak, 1985; Deutsch et al., 1990; Coltman et al., 1998; Crocker et al., 2012). While defending territories males lose primarily lipid and attempt to conserve protein (Coltman et al., 1998; Crocker et al., 2012).

Molting is an essential life-history event that can also result in a negative energy balance and changes in body mass. Although some cetaceans do molt their skin (St. Aubin et al., 1990; Pitman et al., 2021), the literature on reserve utilization while molting is dominated by pinnipeds that shed fur. Declines in overall body mass are observed in molting pinnipeds attributable to decreases in both lipid and protein reserves (Worthy et al., 1992; Boyd et al., 1993; Field et al., 2005; Noren et al., 2003; Noren and Mangel, 2004; Williams et al., 2007). Although there may be increased metabolic expenditure related to pelage growth and thermoregulation during the molt (Boily 1995; Boily 1996; Pitman et al., 2020; Pearson et al., 2022), the primary cause for decreased reserves in phocids is a reduction in feeding as these animals often haul-out to molt (Thometz et al., 2021).

Similarly, marine mammal migration causes increased metabolic demand from traveling long distances coupled with decreased foraging opportunities and feeding events (Alexander, 1998; Alerstam et al., 2003), likely resulting in declines in overall body size through mobilization of reserves. Migration can cover distances up to 8,000 km, such as humpback whale (*Megaptera novaeangliae*) migration from the cold feeding grounds to warm breeding grounds, during which the animals will not forage or will forage minimally (Corkeron et al., 2019). Amongst migrating cetaceans, typically the larger species with greater energy reserves travel the greatest differences (Boyd, 2004). Even within a species, larger individuals within a species can travel greater distances with fewer consequences on their overall body size and energy reserves (Boyd, 2004).

1.9.3 Prey availability and composition

Prey availability and quality can also influence an animal's energy balance, requiring reliance on energy reserves in resource-poor environments. In mysticetes, lipid reserves typically fluctuate annually in response to prey availability, often decreasing when prey quality and quantity is low (Haug et al., 2002; Konishi et al., 2008; Williams et al., 2013; Braithwaite et al., 2015; Miller et al., 2011; Lemos, 2020). Similarly, phocids typically have larger lipid reserves, often expressed as improved body condition, when inhabiting more productive environments than conspecifics in other habitats (Bailleul et al., 2007; Arce et al., 2022). Although seasonal fluctuations in energy reserves are observed in otariids and odontocetes, there is little documentation of how these seasonal fluctuations relate to prey availability. Seasonal fluctuations in energy reserves with prey availability may be more apparent in capital breeders than income breeders as they have a proclivity to amass proportionally greater energy reserves when prey are abundant (Stewart and Lavigne, 1984; Stephens et al., 2014; Irvine et al., 2017). Relating environmental state, resource availability, and animal performance presents a challenge in ecology, but new tools, software, and in situ communication systems can help inform these transfer functions and are the focus of much attention.

Diet and prey composition also influence lipid reserves in both blubber and muscle; however, the observed trends can be complex. In mysticetes, more lipid-rich prey often yields higher lipid content in blubber and muscle, although the majority of this work has been completed in field experiments and, as such, it is unknown if changes to diets were isocaloric (Næss et al., 1998; Víkingsson et al., 2013). However, in phocids and otariids, the influence of diet on lipid reserves is unclear. High-lipid diets do not consistently increase lipid reserves in phocids, while low-lipid diets – particularly during nutritional challenges - result in a loss of lipid reserves (Kirsch et al., 2000; Rosen and Trites, 2001; Trumble et al., 2003); however, only one of these studies held calorie content of intake constant potentially obscuring results. As such, the role of diet in lipid deposition is somewhat complex and is driven by several intrinsic and extrinsic factors.

1.9.4 Environment

Variation in environmental temperature also affects the accumulation and utilization of lipid reserves. In colder waters, dolphins increase blubber thickness (Noren and Wells, 2009) marine mammals may store more lipids (e.g., Montie et al., 2008); however, this is likely driven by thermoregulatory needs rather than storage needs. Additionally, in regions with large temperature fluctuations, animals appear to store more lipid in preparation for or in response to increased thermoregulatory demands (e.g., Lockyer et al., 2003; Adamczak et al., 2021). Indeed, in controlled studies in human care, body mass and blubber thickness of adult female walruses tracked air temperature, where during warmer periods walruses decreased their food consumption and body mass while blubber thickness decreased (Noren et al., 2015). Furthermore, body mass and blubber thickness of pilot whales tracked water temperature where a dramatic drop in water temperature resulted in increased food consumption and increased body mass and blubber thicknesses (Noren et al., 2021).

1.9.5 Body condition thresholds

Linking energy reserve levels to fitness is a key component of many bioenergetic models. In many models, a minimum body condition threshold is often set to 5% body fat (e.g., Malavear 2002; Beltran et al., 2017; Pirotta et al., 2018b; Gallagher et al., 2021). This value is derived from pigs and is assumed to be the lowest possible fat level that allows for basic metabolic functioning (Whittemore, 1998). Although the use of this 5% body fat minimum may provide a conservative estimate of when individuals may die due to lack of energy stores, it is probable that mortality occurs before this threshold is reached and that declining body condition may progressively increase the probability of mortality or decrease the probability of calving. Anecdotal evidence from stranded and sick animals could be used to define a more realistic minimum body condition threshold for marine mammals. There is sufficient data on stranded marine mammals to compute this threshold; however, these minimum values are often not reported in the literature. A potential body fat minimum derived from a sick northern elephant seal (*Mirounga angustirostris*) that died shortly after morphometric measurements is 18.3%, which is compared to an average of 30.4% in healthy animals (Holser et al., in review). In addition to minimum body storage levels for survival, we can assume that there are minimum body storage levels for successful pregnancy, lactation, and other reproductive events (Laws et al., 1956). However, it is difficult to empirically obtain estimates of those thresholds as it would require monitoring of the storage levels amongst individuals that successfully reproduce and those that do not, which requires long-term monitoring datasets and data collection of behavior, reproductive histories, and morphometrics.

1.10 Data gaps

Measurements of structural mass and energy reserves provide relevant individual and population health proxies and are essential input parameters for bioenergetic models. Despite the importance of these data, there are many species and species groups without adequate growth curves (e.g., river dolphins and beaked whales) and impacts of resource restriction on projected growth curves are difficult to obtain. Evaluating how growth curves from data-rich species can be applied or adjusted to fit the growth of data-poor species can be a valuable tool to fill in gaps for data-poor species. Further, drones and remote three-dimensional imagery provide exciting new opportunities to acquire data on these otherwise hard-to-study species. To address alterations in growth in response to climate and resource-related changes, long-term datasets and long studied populations can begin to elucidate these patterns and may help us target populations that are at risk of decline (e.g., Christiansen et al., 2020). As such, when assessing growth curves in species and populations, it is important to also consider the current population size and population trajectory (i.e., growing, stable, declining) at the time of sampling when possible and if this is representative of current conditions. This will provide baseline information from which we can population health based on growth rates of individuals within a population.

Understanding the preferential storage and mobilization of reserves to different body compartments will allow better estimates of total body lipid and protein reserves. The contribution of protein reserves to critical life-history events, such as molting and lactation, is important to document as the current marker for individual health typically focuses on the size of lipid stores. This is particularly relevant when relying on external morphology (i.e., how wide an animal is) or blubber biopsies to provide a proxy of lipid reserves, as these might not always be representative of the overall energy reserves of the animals (Kershaw et al., 2019, Christiansen et al., 2020). While data on protein catabolism exist for a few pinnipeds, with much of the otariid literature focusing on protein catabolism during post-weaning fasts (Nordøy et al., 1990; Oftedal et al., 1997; Rea et al., 2000), data on cetaceans have only recently been collected with bottlenose dolphins as the primary study species (e.g., Suzuki et al., 2018; Houser et al., 2021; Derous et al., 2022). There are sufficient data to indicate that the interaction between protein and fat content of the diet is complex and deserves further investigation, particularly in the context of bioenergetic models where energy stores are predominantly assumed to be derived from lipids. The advent of metabolic markers and omics technologies provides an opportunity to improve our understanding of how stored energy is mobilized and which stores are preferred during different life-history events (e.g., Derous et al., 2022).

Improving estimates of the cost of growth in marine mammals will improve modeled growth costs in bioenergetic models and provide context for how growth is altered when resources are limited. Until we can empirically measure the cost of growth, we can improve our understanding of these costs with direct energy density measurements for protein and lipid from marine mammals. Surprisingly, little data on this topic have been collected. The methodologies are established and can be used on opportunistic stranded and bycaught animals or biopsy samples. Although the discrepancies between energy density values appear to be relatively small, there can be considerable consequences when estimating growth costs for larger species that must deposit proportionally more protein and lipid.

Figures

Figure 1. 1 Example of length-at-age, weight-at-age (left panel) and weight-at-length (right panel) relationships derived from data on bottlenose dolphins (*Tursiops truncatus*) from the Sarasota Dolphin Research Program. The weight-at-age data demonstrates seasonal fluctuations in mass only in the secondary growth phase, which is not typically captured in weight-at-age curves; meanwhile during the primary growth phase there seems to be no seasonal fluctuations in mass.

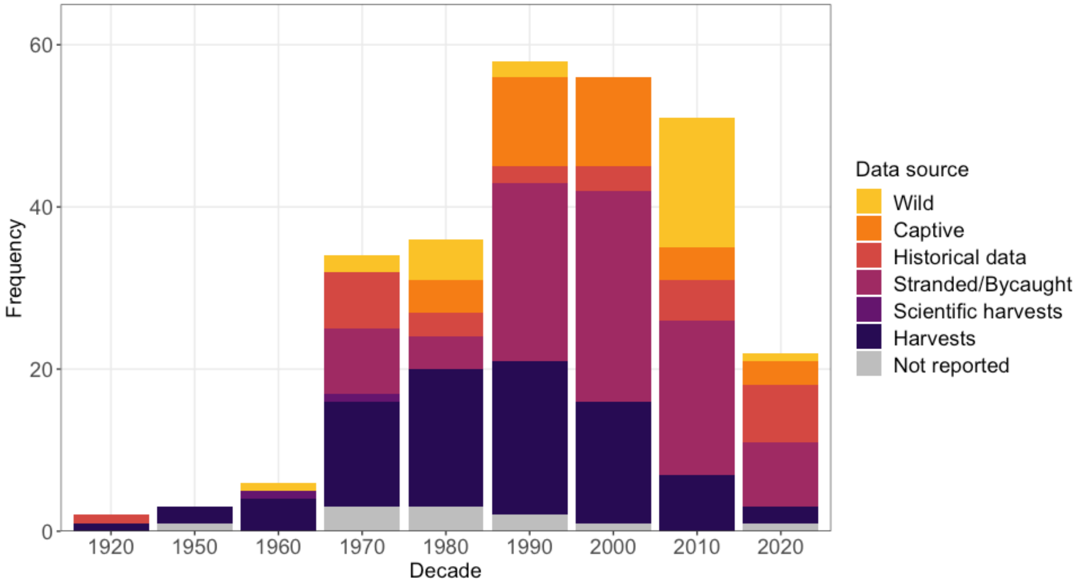

Figure 1. 2 Sources of data used to construct marine mammal growth curves collated in this review with respect to era and data source (n = 277). Some growth curves were constructed using two data sources, but the method with the greatest human impact on the population was presented here. For example, if a paper listed their data sources as harvested and stranded animals, we reported this as a harvest. Historical data includes the use of previously published data and museum specimens, and harvests include commercial and subsistence hunts.

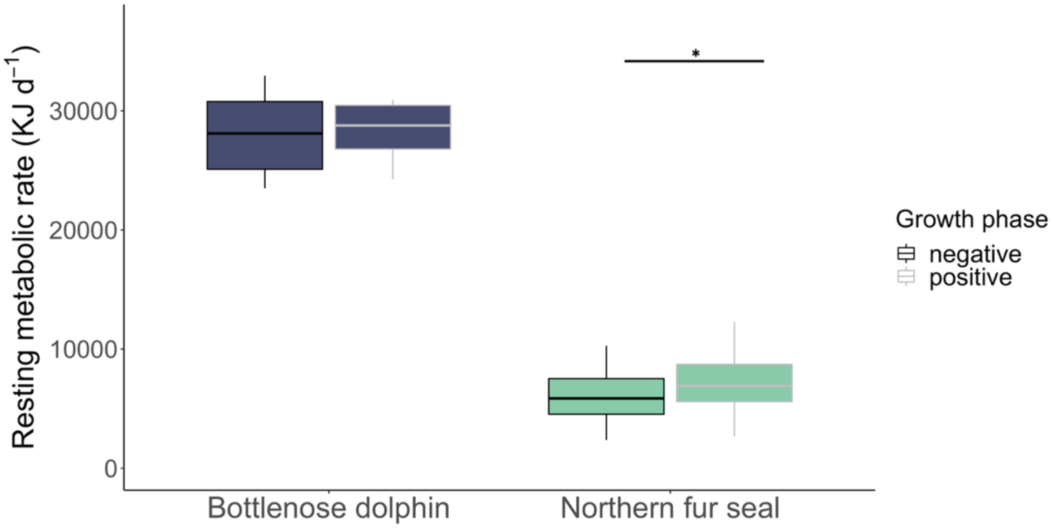

Figure 1. 3 Resting mass-specific metabolic rate (kJ d^{-1}) in negative and positive growth phases for juvenile bottlenose dolphins (n=2) and northern fur seals (n = 6). Vertical line indicates statistically significant difference from Wilcoxon signed rank test results ($p = 2.4 \times 10^{-3}$). Data contributed by the University of California Santa Cruz Long Marine Laboratory and the University of British Columbia Marine Mammal Research Unit.

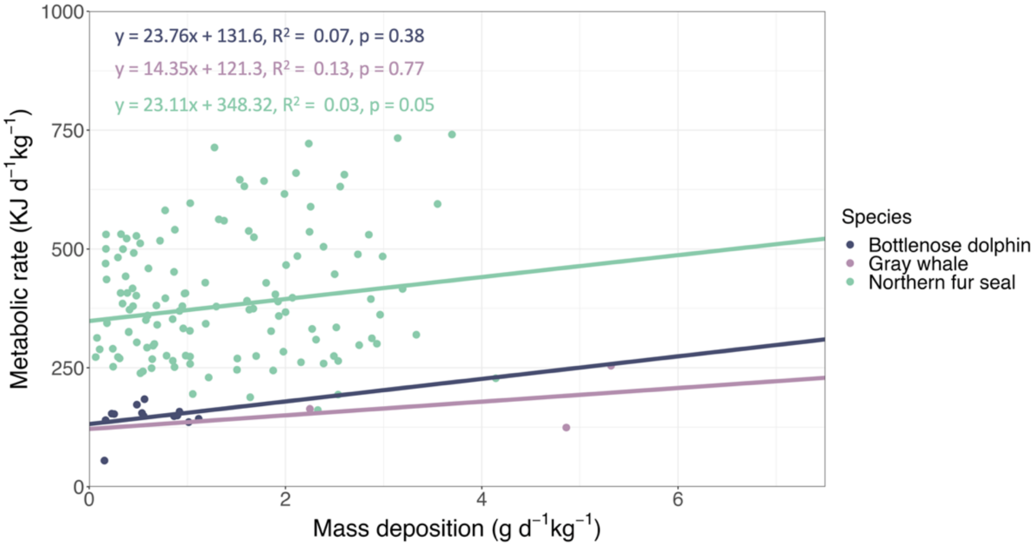

Figure 1. 4 Linear mixed effect model of mass deposition normalized by body size (g d^{-1} kg^{-1}) and resting mass-specific metabolic rate (kJ d^{-1} kg^{-1}) for juvenile bottlenose dolphins (n=2), northern fur seals (n = 6), and a single gray whale with random effects of individuals for northern fur seals. Data contributed by the University of California Santa Cruz Long Marine Laboratory and the University of British Columbia Marine Mammal Research Unit, and SeaWorld.

References

Adachi, T., Maresh, J. L., Robinson, P. W., Peterson, S. H., Costa, D. P., Naito, Y., Watanabe, Y. Y., & Takahashi, A. (2014). The foraging benefits of being fat in a highly migratory marine mammal. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797). https://doi.org/10.1098/rspb.2014.2120

Adamczak, S. K., Pabst, D. A., McLellan, W. A., & Thorne, L. H. (2020). Do bigger bodies require bigger radiators? Insights into thermal ecology from closely related marine mammal species and implications for ecogeographic rules. *Journal of Biogeography*, *47*(5), 1193–1206. https://doi.org/10.1111/jbi.13796

Adamczak, S. K., Holser, R. R., Costa, D. P., Berens McCabe, E. J., & Wells, R. S. (2021). Body Composition of Common Bottlenose Dolphins in Sarasota Bay, Florida. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.615773

Agbayani, S., Fortune, S. M. E., & Trites, A. W. (2020). Growth and development of North Pacific gray whales (Eschrichtius robustus). *Journal of Mammalogy*, *101*(3), 742–754. https://doi.org/10.1093/jmammal/gyaa028

Aguilar, A., & Lockyer, C. H. (1987). Growth, physical maturity, and mortality of fin whales (Balaenoptera physalus) inhabiting the temperate waters of the northeast Atlantic. *Canadian Journal of Zoology*, *65*, 253–264.

Aguilar, A., & Borrell, A. (1990). Patterns of Lipid Content and Stratification in the Blubber of Fin Whales (Balaenoptera physalus). *Journal of Mammalogy*, *71*(4), 544–554.

Alerstam, T., Hedenström, A., Alerstam, kesson, Alerstam, T., & Hedenström, A. (2003). Long-distance migration: evolution and determinants. *OIKOS*, *103*, 247–260.

Alexander, R. McN. (1998). When Is Migration Worthwhile for Animals That Walk, Swim or Fly? *Journal of Avian Biology*, *29*(4), 387–394. https://www.jstor.org/stable/3677157

Allen, S. J. J., Bowen, W. D., & den Heyer, C. E. (2022). Birth-site habitat selection in gray seals (*Halichoerus grypus*): Effects of maternal age and parity and association with offspring weaning mass. *Marine Mammal Science*, *38*(1), 349–363. https://doi.org/10.1111/mms.12867

Anderson, S. S., & Fedak, M. A. (1985). Gray seal males: energetic and behavioural links between size and sexual success. *Animal Behaviour*, *33*, 829–838.

Anezaki, K., Matsuda, A., & Matsuishi, T. (2016). Concentration and congener pattern of polychlorinated biphenyls in blubber and liver of Hubb's beaked whale (*Mesoplodon carlhubbsi*), using a sulfoxide and an AG-ION solid phase extraction cartridge as a simplified cleanup technique for biological samples. *Marine Pollution Bulletin*, *113*(1–2), 282–286.

Anghihan, A., de Jorge, F. B., & Julinho Aisen. (1969). Chemical composition of skeletal muscle. *Arquivos de Neuro-Psiquiatria*, *27*, 324–327.

Aoki, K., Isojunno, S., Bellot, C., Iwata, T., Kershaw, J., Akiyama, Y., Martín López, L. M., Ramp, C., Biuw, M., Swift, R., Wensveen, P. J., Pomeroy, P., Narazaki, T., Hall, A., Sato, K., & Miller, P. J. O. (2021). Aerial photogrammetry and tag-derived tissue density reveal patterns of lipid-store body condition of humpback whales on their feeding grounds. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1943). https://doi.org/10.1098/rspb.2020.2307

Arce, F., Hindell, M. A., McMahon, C. R., Wotherspoon, S. J., Guinet, C., Harcourt, R. G., & Bestley, S. (2022). Elephant seal foraging success is enhanced in Antarctic coastal polynyas. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1967). https://doi.org/10.1098/rspb.2021.2452

Arnould, J. P. Y., & Duck, C. D. (1997). The cost and benefits of territorial tenure, and factors affecting mating success in male Antarctic fur seals. *Journal of Zoology*, *241*(4), 649–664. https://doi.org/10.1111/j.1469-7998.1997.tb05739.x

Bagge, L. E., Koopman, H. N., Rommel, S. A., McLellan, W. A., & Pabst, D. A. (2012). Research article: Lipid class and depth-specific thermal properties in the blubber of the short-finned ilot whale and the pygmy sperm whale. *Journal of Experimental Biology*, *215*(24), 4330–4339. https://doi.org/10.1242/jeb.071530

Ballinger, M. A., & Nachman, M. W. (2022). The Contribution of Genetic and Environmental Effects to Bergmann's Rule and Allen's Rule in House Mice. *The American Naturalist*, 000–000. https://doi.org/10.1086/719028

Bailleul, F., Charrassin, J. B., Monestiez, P., Roquet, F., Biuw, M., & Guinet, C. (2007). Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2169–2181. https://doi.org/10.1098/rstb.2007.2109

Bartholomew, G. A. (1970). A Model for the Evolution of Pinniped Polygyny. *Evolution*, *24*(3), 546–559.

Bartsh, S. S., Paul, S., & Siniff, D. B. (1992). Territorial behavior and breeding frequency of male Weddell seals (Leptonychotes weddellii) in relation to age, size, and concentrations of serum testosterone and cortisol. *Canadian Journal of Zoology*, *70*, 680–692.

Beck, G. G., Smith, T. G., & Hammill, M. O. (1993). Evaluation of body Condition in the Northwest Atlantic harp seal (Phoca groenlandica). *Canadian Journal of Fisheries and Aquatic Science*, *50*, 1372–1381.

Bejarano, A. C., Wells, R. S., & Costa, D. P. (2017). Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin Tursiops truncatus. *Ecological Modelling*, *356*, 162–172. https://doi.org/10.1016/j.ecolmodel.2017.05.001

Beltran, R. S., Testa, J. W., & Burns, J. M. (2017). An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal. *Ecological Modelling*, *351*, 36–50. https://doi.org/10.1016/j.ecolmodel.2017.02.002

Berghänel, A., Heistermann, M., Schülke, O., & Ostner, J. (2017). Prenatal stress accelerates offspring growth to compensate for reduced maternal investment across mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(50), E10658–E10666. https://doi.org/10.1073/pnas.1707152114

Bergmann, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, 1, 595-708.

Best, N. J., Bradshaw, C. J., Hindell, M. A., & Nichols, P. D. (2003). Vertical stratification of fatty acids in the blubber of southern elephant seals (Mirounga leonina): implications for diet analysis. *Comparative Biochemistry and Physiology Part B*, *134*, 253–263.

Best, P. B., Tormosov, D., Brandaõ, A., & Mikhalev, Y. (2017). Geographical variation in the body size of adult female sperm whales (Physeter macrocephalus)-an example of McNab's resource rule? *Mammalia*, *81*(2), 189–196. https://doi.org/10.1515/mammalia-2015-0042

Betty, E. L., Stockin, K. A., Hinton, B., Bollard, B. A., Smith, A. N. H., Orams, M. B., & Murphy, S. (2022). Age, growth, and sexual dimorphism of the Southern Hemisphere long-finned pilot whale (Globicephala melas edwardii). *Journal of Mammalogy*, *XX*(X), 1–16. https://doi.org/10.1093/jmammal/gyab165

Bjørge, A. & Tolley, K. A. (2009). Harbor porpoise: *Phocoena phocoena*. In *Encyclopedia of Marine Mammals (Second Edition*) Academic Press.

Biuw, M., McConnell, B., Bradshaw, C. J. A., Burton, H., & Fedak, M. (2003). Blubber and buoyancy: Monitoring the body condition of free-ranging seals using simple dive characteristics. *Journal of Experimental Biology*, *206*(19), 3405–3423. https://doi.org/10.1242/jeb.00583

Boily, P. (1995). Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *Journal of Theoretical Biology*, *172*, 235–244.

Boily, P. (1996). Metabolic and hormonal changes during the molt of captive gray seals (*Halichoerus grypus*). *American Journal of Physiology*, *270*, R1051–R1058.

Boyd, I. L., & Duck, C. D. (1991). Mass Changes and Metabolism in Territorial Male Antarctic Fur Seals (Arctocephalus gazella). *Physiological Zoology*, *64*(1), 375–392.

Blaxter, K. L. 1968. The effect of the dietary energy supply on growth. In: G. A. Lodge and G. E. Lamming (Ed.) Growth and Development of Mammals. Butterworths, London.

Boness, D. J., Oftedal, O. T., & Ono, K. A. (1991). The effect of EI Niño on pup development in the Califomia sea lion (*Zalophus califronianus*) I. Early Postnatal Growth. In *Pinnipeds and El Niño* (pp. 173–174). Springer.

Booth, C. G. (2020). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, *36*(1), 195–208. https://doi.org/10.1111/mms.12632

Bowen, W. D., den Heyer, C. E., Mcmillan, J. I., & Iverson, S. J. (2015). Offspring size at weaning affects survival to recruitment and reproductive performance of primiparous gray seals. *Ecology and Evolution*, *5*(7), 1412–1424. https://doi.org/10.1002/ece3.1450

Boyd, I., Arnbom, T., & Fedak, M. (1993). Water flux, body composition, and metabolic rate during molt in female southern elephant seals (Mirounga leonina). *Physiological Zoology*, *66*(1), 43–60.

Boyd, I. L. (2000). State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Functional Ecology*, *14*, 623–630.

Boyd, I. (2004). Migration of Marine Mammals. In D. Werner (Ed.), *Biological Resources and Migration* (pp. 203–210). Springer.

Braithwaite, J. E., Meeuwig, J. J., Letessier, T. B., Jenner, K. C. S., & Brierley, A. S. (2015). From sea ice to blubber: linking whale condition to krill abundance using historical whaling records. *Polar Biology*, *38*(8), 1195–1202. https://doi.org/10.1007/s00300-015-1685-0

Brody, S. (1968) Bioenergetics and growth with special reference to the efficiency complex in domestic animals. Hafner Press, New York NY, USA.

Brown, J. H., Hall, C. A. S., & Sibly, R. M. (2018). Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nature Ecology and Evolution*, *2*(2), 262–268. https://doi.org/10.1038/s41559-017-0430-1

Brunborg, L. A., Julshamn, K., Nortvedt, R., & Frøyland, L. (2006). Nutritional composition of blubber and meat of hooded seal (Cystophora cristata) and harp seal (Phagophilus groenlandicus) from Greenland. *Food Chemistry*, *96*(4), 524–531. https://doi.org/10.1016/j.foodchem.2005.03.005

Bryden, M. M. (1964). Insulating capacity of the subcutaneous fat of the southern elephant seal. *Nature*, *203*, 1299–1300.

Bryden, M. M. (1968). Growth and function of the subcutaneous fat of the elephant seal. *Nature*, *220*, 597–599.

Calder, W. A. (2001). Ecological Consequences of Body Size. In *Encyclopedia of Life Sciences*. John Wiley and Sons Ltd. www.els.net

Capdevila, P., Stott, I., Cant, J., Beger, M., Rowlands, G., Grace, M., & Salguero-Gómez, R. (2022). Life history mediates the trade-offs among different components of demographic resilience. *Ecology Letters*, Preprint, https://doi.org/10.1111/ele.14004

Castellini, M., Kooyman, G. L., Castellini, M. A., Davis, R. W., & Maue, R. A. (1983). Aerobic diving limits of immature Weddell seals. In *Journal of Comparative Physiology. B* (Vol. 151). Springer-Verlag.

Chabot, D., & Stenson, G. B. (2002). Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals *Phoca groenlandica*: an analysis using sequential growth curves. *Marine Ecology Progress Seriess*, *227*, 25–42.

Christiansen, F., Víkingsson, G. A., Rasmussen, M. H., & Lusseau, D. (2013). Minke whales maximise energy storage on their feeding grounds. *Journal of Experimental Biology*, *216*(3), 427–436. https://doi.org/10.1242/jeb.074518

Christiansen, F., Víkingsson, G. A., Rasmussen, M. H., & Lusseau, D. (2014). Female body condition affects foetal growth in a capital breeding mysticete. *Functional Ecology*, *28*(3), 579–588. https://doi.org/10.1111/1365-2435.12200

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*(10). https://doi.org/10.1002/ecs2.1468

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–282. https://doi.org/10.3354/meps12522

Christiansen, F., Dawson, S. M., Durban, J. W., Fearnbach, H., Miller, C. A., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., Leunissen, E., Haria, E., Ward, R., Warick, H. A., Kerr, I., Lynn, M. S., Pettis, H. M., & Moore, M. J. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series*, *640*, 1–16. https://doi.org/10.3354/meps13299

Christiansen, F., Bejder, L., Burnell, S., Ward, R., & Charlton, C. (2022a). Estimating the cost of growth in southern right whales from drone photogrammetry data and long-term sighting histories. *Marine Ecology Progress Series*, *687*, 173–194. https://doi.org/10.3354/meps14009

Christiansen, F., Uhart, M. M., Bejder, L., Clapham, P., Ivashchenko, Y., Tormosov, D., Lewin, N., & Sironi, M. (2022b). Fetal growth, birth size and energetic cost of gestation in southern right whales Key points. *The Journal of Physiology*, *600*, 2245–2266. https://doi.org/10.1113/JP282351#support-information-section

Clark, S. T., Odell, D. K., & Lacinak, C. T. (2000). Aspects of growth in captive killer whales (Orcinus orca). *Marine Mammal Science*, *16*(1), 110–123.

Clausius, E., McMahon, C. R., & Hindell, M. A. (2017). Five decades on: Use of historical weaning size data reveals that a decrease in maternal foraging success underpins the long-term decline in population of southern elephant seals (*Mirounga leonina*). *PLoS ONE*, *12*(3). https://doi.org/10.1371/journal.pone.0173427

Cohen, D. (1971). Maximizing final yield when growth is limited by time or by limiting resources. *Journal of Theoretical Biology*, *33*, 299–307.

Coltman, D. W., Don Bowen, W., Iverson, S. J., & Boness, D. J. (1998). The energetics of male reproduction in an aquatically mating pinniped, the harbour seal. *Physiological Zoology*, *71*(4), 387–399. https://doi.org/10.1086/515418

Coslovsky, M., & Richner, H. (2011). Predation risk affects offspring growth via maternal effects. *Functional Ecology*, *25*(4), 878–888. https://doi.org/10.1111/j.1365-2435.2011.01834.x

Costa, D. P. (1993). The relationship between reproductive and foraging energetics and the evolution of *Pinnipedia*. *Symposia of the Zoological Society of London*, *66*, 293–314. https://www.researchgate.net/publication/228328880

Costa, D. P. (2008). A conceptual model of the variation in parental attendance in response to environmental fluctuation: Foraging energetics of lactating sea lions and fur seals. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *17*, S44–S52. https://doi.org/10.1002/aqc.917

Costa, D. P. (2012). A bioenergetics approach to understanding the population consequences of disturbance: Elephant seals as a model system. In A. N. Popper & A. Hawkins (Eds.), *The Effects of Noise on Aquatic Life* (Vol. 730, pp. 423–426). Springer New York LLC. https://doi.org/10.1007/978-1-4939-2981-8_19

Costa, D. P., Croxall, J. P., & Duck, C. D. (1989). Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, *70*(3), 596–606.

Costa, D. P., & Trillmich, F. (1988). Mass changes and metabolism during the perinatal fast: A comparison between Antarctic (Arctocephalus gazella) and Galápagos fur seals (*Arctocephalus galapagoensis*). *Physiological Zoology*, *61*(2), 160–169. https://about.jstor.org/terms

Costa, D. P. (2012). A bioenergetics approach to understanding the population consequences of disturbance: Elephant seals as a model system. In A. N. Popper & A. Hawkins (Eds.), *The Effects of Noise on Aquatic Life* (Vol. 730, pp. 423–426). Springer New York LLC. https://doi.org/10.1007/978-1-4939-2981-8_19

Costa, D. P., & Maresh, J.L. (2017). Energetics. In B. Würsig, J.G.M. Thwewissen, and K. Kovacs (Eds.), *Encyclopedia of marine mammals* (pp. 329-335). Academic Press, San Diego, CA, USA.

Craig, M. P., & Ragen, T. J. (1999). Body size, survival, and decline of juvenile Hawaiian monk seals, *Monachus schauinslandi*. *Marine Mammal Science*, *15*(3), 786–809.

Corkeron, P. J., van Parijs, S. M., & Adamczak, S. K. (2019). Marine mammal migrations and movement patterns. In *Encyclopedia of Ocean Sciences* (pp. 563–571). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.11393-4

Crocker, D. E., Webb, P. M., Costa, D. P., & le Boeuf, B. J. (1998). Protein catabolism and renal function in lactating Northern elephant seals. *Physiological Zoology*, *71*(5), 485–491. https://doi.org/10.1086/515971

Crocker, D. E., Williams, J. D., Costa, D. P., & le Boeuf, B. J. (2001). Maternal traits and reproductive effort in Northern elephant seals. In *Ecology* (Vol. 82, Issue 12).

Crocker, D. E., Houser, D. S., & Webb, P. M. (2012). Impact of body reserves on energy expenditure, water flux, and mating success in breeding male northern elephant seals. *Physiological and Biochemical Zoology*, *85*(1), 11–20. https://doi.org/10.1086/663634

Dalton, A. J. M., Rosen, D. A. S., & Trites, A. W. (2015). Resting metabolic rate and activity: Key components of seasonal variation in daily energy expenditure for the northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Zoology*, *93*(8), 635–644. https://doi.org/10.1139/cjz-2014-0313

Dantzer, B., Newman, A. E. M., Boonstra, R., Palme, R., Boutin, S., Humphries, M. M., & Mcadam, A. G. (2013). Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. *Science*, *340*, 1215–1217. https://doi.org/10.5061/dryad.b3h4q

Derous, D., ten Doeschate, M., Brownlow, A. C., Davison, N. J., & Lusseau, D. (2020). Toward New Ecologically Relevant Markers of Health for Cetaceans. In *Frontiers in Marine Science* (Vol. 7). Frontiers Media S.A. https://doi.org/10.3389/fmars.2020.00367

Derous, D., Kebke, A., Fair, P. A., Styczynski, M., Bossart, G. D., Douglas, A., & Lusseau, D. (2022). Untargeted plasma metabolomic analysis of wild bottlenose dolphins (Tursiops truncatus) indicate protein degradation when in poorer health. *Comparative Biochemistry and Physiology - Part D: Genomics and Proteomics*, *42*. https://doi.org/10.1016/j.cbd.2022.100991

Desprez, M., Gimenez, O., McMahon, C. R., Hindell, M. A., & Harcourt, R. G. (2018). Optimizing lifetime reproductive output: Intermittent breeding as a tactic for females in a long-lived, multiparous mammal. *Journal of Animal Ecology*, *87*(1), 199–211. https://doi.org/10.1111/1365-2656.12775

Deutsch, C. J., Haley, M. P., le Boeuf, B. J., & Boeuf, L. (1990). Reproductive effort of male northern elephant seals: estimates from mass loss. *Canadian Journal of Zoology*, *68*, 2580–2593.

Dias, P. A. D., Cano-Huertes, B., Coyohua-Fuentes, A., Chavira-Ramírez, D. R., Canales-Espinosa, D., & Rangel-Negrín, A. (2018). Maternal condition and maternal investment during lactation in mantled howler monkeys. *American Journal of Physical Anthropology*, *167*(1), 178–184. https://doi.org/10.1002/ajpa.23626

Dickson, T. (2020). Aerial photogrammetry and size structure analysis of sperm whales (*Physeter macrocephalus*) at Kaikōura, New Zealand (Master's thesis, University of Otago, Dunedin, New Zealand). Retrieved from https://ourarchive.otago.ac.nz/bitstream/handle/10523/10260/DicksonTobyWJ2020MSc.pdf?sequence=1&isAllowed=y

Douhard, F., Gaillard, J. M., Pellerin, M., Jacob, L., & Lemaître, J. F. (2017). The cost of growing large: costs of post-weaning growth on body mass senescence in a wild mammal. *Oikos*, *126*(9), 1329–1338. https://doi.org/10.1111/oik.04421

du Dot, J. T., Rosen, D. A. S., & Trites, A. W. (2008). Steller sea lions show diet-dependent changes in body composition during nutritional stress and recover more easily from mass loss in winter than in summer. *Journal of Experimental Marine Biology and Ecology*, *367*(1), 1–10. https://doi.org/10.1016/j.jembe.2008.08.005

du Dot, T. J., Rosen, D. A. S., & Trites, A. W. (2009). Energy reallocation during and after periods of nutritional stress in steller sea lions: Low-quality diet reduces capacity for physiological adjustments. *Physiological and Biochemical Zoology*, *82*(5), 516–530. https://doi.org/10.1086/603637

Dunkin, R. C., McLellan, W. A., Blum, J. E., & Pabst, D. A. (2005). The ontogenetic changes in the thermal properties of blubber from Atlantic bottlenose dolphin Tursiops truncatus. *Journal of Experimental Biology*, *208*(8), 1469–1480. https://doi.org/10.1242/jeb.01559

Ferguson, S. H., Zhu, X., Young, B. G., Yurkowski, D. J., Thiemann, G. W., Fisk, A. T., & Muir, D. C. G. (2018). Geographic variation in ringed seal (Pusa hispida) growth rate and body size. *Canadian Journal of Zoology*, *96*(7), 649–659. https://doi.org/10.1139/cjz-2017-0213

Field, I. C., A Bradshaw, C. J., Burton, H. R., & Hindell, M. A. (2005). Juvenile Southern Elephant Seals Exhibit Seasonal Differences in Energetic Requirements and Use of Lipids and Protein Stores. *Physiological and Biochemical Zoology*, *78*(4), 491–504.

Fokidis, H. B., Risch, T. S., & Glenn, T. C. (2007). Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour*, *73*(3), 479–488. https://doi.org/10.1016/j.anbehav.2006.08.010

Fortune, S. M. E., Moore, M. J., Perryman, W. L., & Trites, A. W. (2021). Body growth of North Atlantic right whales (Eubalaena glacialis) revisited. *Marine Mammal Science*, *37*(2), 433–447. https://doi.org/10.1111/mms.12753

Fowler, C. W. (1990). Density dependence in Northern fur seals (Callorhinus ursinus. *Marine Mammal Science*, *6*(3), 171–195.

Fuller, M. F., & Chen, C. H. (1997). Nutrient intake and protein metabolism: responses to feeding. *Z Ernghrungswiss*, *36*, 332–335.

Galatius, A., & Gol'din, P. E. (2011). Geographic variation of skeletal ontogeny and skull shape in the harbour porpoise (*Phocoena phocoena*). *Canadian Journal of Zoology*, *89*(9), 869–879. https://doi.org/10.1139/z11-059

Gales, R., Renouf, D., & Noseworthy, E. (1994). Body composition of harp seals. *Canadian Journal of Zoology*, *72*, 545–551.

Gallagher, C. A., Stern, S. J., & Hines, E. (2018). The metabolic cost of swimming and reproduction in harbor porpoises (*Phocoena phocoena*) as predicted by a bioenergetic model. *Marine Mammal Science*, *34*(4), 875–900. https://doi.org/10.1111/mms.12487

Gearty, W., McClain, C. R., & Payne, J. L. (2018). Energetic tradeoffs control the size distribution of aquatic mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 4194–4199. https://doi.org/10.1073/pnas.1712629115

Gélin, U., Wilson, M. E., Cripps, J., Coulson, G., & Festa-Bianchet, M. (2016). Individual heterogeneity and offspring sex affect the growth–reproduction trade-off in a mammal with indeterminate growth. *Oecologia*, *180*(4), 1127–1135. https://doi.org/10.1007/s00442-015-3531-z

Georges, J.-Y., & Guinet, C. (2000). Early mortality and perinatal growth in the subantarctic fur seal (Arctocephalus tropicalis) on Amsterdam Island. *Journal of Zoology*, *251*(3), 277–287. https://doi.org/10.1111/j.1469-7998.2000.tb01078.x

Goedegebuure, M., Melbourne-Thomas, J., Corney, S. P., McMahon, C. R., & Hindell, M. A. (2018). Modelling southern elephant seals mirounga leonina using an individual-based model coupled with a dynamic energy budget. *PLoS ONE*, *13*(3). https://doi.org/10.1371/journal.pone.0194950

Goldbogen, J. A. (2018). Physiological constraints on marine mammal body size. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 3995–3997. https://doi.org/10.1073/pnas.1804077115

Green, H. J., Jones, S., Ball-burnett, M. E., Smith, D., Livesey, J., & Farrance, B. W. (1991). Early muscular and metabolic adaptations to prolonged exercise training in humans. *Journal of Applied Physiology*, *70*(5), 2032–2038.

Guenther, J. J., Bushman, D. H., Pope, L. S., & Morrison, R. D. (1965). Growth and development of the major carcass tissues in beef calves from weaning to slaughter weight, with reference to the effect of plane nutrition. *Journal of Animal Science* 24(4): 1184-1191.

Gunnlaugsson, T., Víkingsson, G. A., Halldórsson, S. D., Elvarsson, B. Þ., Haug, T., & Lydersen, C. (2020). Body mass, muscle, blubber and visceral fat content and their seasonal, spatial and temporal variability in North Atlantic common minke whales. *Journal of Cetacean Research and Management*, *21*, 59–70. https://iwc.int/permits.

Gür, H., & Kart Gür, M. (2012). Is spatial variation in food availability an explanation for a Bergmannian size pattern in a North American hibernating, burrowing mammal? An information-theoretic approach. *Journal of Zoology*, *287*(2), 104–114. https://doi.org/10.1111/j.1469-7998.2011.00893.x

Haley, M. P., Deutsch, C. J., & le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, Mirounga angustirostris. *Animal Behavior*, *48*, 1249–1260.

Hall, A. J., Mackey, B., Kershaw, J. L., & Thompson, P. (2019). Age–length relationships in UK harbour seals during a period of population decline. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S1), 61–70. https://doi.org/10.1002/aqc.3104

Harding, K. C., Fujiwara, M., Axberg, Y., & Härkönen, T. (2005). Mass-dependent energetics and survival in Harbour Seal pups. In *Functional Ecology*.

Harding, K. C., Salmon, M., Teilmann, J., Dietz, R., & Härkönen, T. (2018). Population wide decline in somatic growth in harbor seals-early signs of density dependence. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00059

Hart, L. B., Wells, R. S., & Schwacke, L. H. (2013). Reference ranges for body condition in wild bottlenose dolphins *Tursiops truncatus*. *Aquatic Biology*, *18*(1), 63–68. https://doi.org/10.3354/ab00491

Hastings, K. K., & Testa, W. (1998). Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. *Journal of Animal Ecology*, *67*, 722–740.

Haug, T., Lindstrøm, U., & Nilssen, K. T. (2002). Variations in minke whale (Balaenoptera acutorostrata) diet and body condition in response to ecosystem changes in the Barents Sea. *Sarsia: North Atlantic Marine Science*, *87*(6), 409–422. https://doi.org/10.1080/003648202100155715

Hauksson, E. (2006). Growth and reproduction in the Icelandic common seal (Phoca vitulina L., 1758). *Marine Biology Research*, *2*(1), 59–73. https://doi.org/10.1080/17451000600650038

Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, *81*(3), 583–593. https://doi.org/10.1111/j.1365-2656.2011.01942.x

Heino, M., & Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, *12*, 423–429.

Helle, S. (2008). A tradeoff between reproduction and growth in contemporary Finnish women. *Evolution and Human Behavior*, *29*(3), 189–195. https://doi.org/10.1016/j.evolhumbehav.2007.11.009

Hillestad, M., & Johnsen, F. (1994). Aquaculture High-energy/low-protein diets for Atlantic salmon: effects on growth, nutrient retention and slaughter quality. *Aquaculture*, *124*, 109–125.

Holser, R. R., Crocker, D. E., Robinson, P. W., Condit, R., & Costa, D. P. (2021). Density-dependent effects on reproductive output in a capital breeding carnivore, the northern elephant seal (*Mirounga angustirostris*). *Proceedings of the Royal Society B: Biological Sciences*, *288*(1960), 421–425. https://doi.org/10.1098/rspb.2021.1258

Houser, D., & Costa, D. (2001). Protein catabolism in suckling and fasting northern elephant seal pups (*Mirounga angustirostris*). *Journal of Comparative Physiology B*, *171*(8), 635–642. https://doi.org/10.1007/s003600100214

Houser, D. S., Derous, D., Douglas, A., & Lusseau, D. (2021). Metabolic response of dolphins to short-term fasting reveals physiological changes that differ from the traditional fasting model. *Journal of Experimental Biology*, *224*(9). https://doi.org/10.1242/jeb.238915

Houston, A. I. (2011). Assessing models of optimal diving. In *Trends in Ecology and Evolution* (Vol. 26, Issue 6, pp. 292–297). https://doi.org/10.1016/j.tree.2011.03.003

Husby, A., Hille, S. M., & Visser, M. E. (2011). Testing Mechanisms of Bergmann's Rule: Phenotypic Decline but No Genetic Change in Body Size in Three Passerine Bird Populations. *The American Naturalist*, *178*(2). https://doi.org/10.5061/dryad.8989

Irvine, L. G., Hindell, M. A., Hoff, J., & Burton, H. R. (2000). The influence of body size on dive duration of underyearling southern elephant seals (*Mirounga leonina*). *Journal of Zoology*, *251*(4), 463–471. https://doi.org/10.1111/j.1469-7998.2000.tb00802.x

Irvine, L. G., Thums, M., Hanson, C. E., McMahon, C. R., & Hindell, M. A. (2017). Quantifying the energy stores of capital breeding humpback whales and income breeding sperm whales using historical whaling records. *Royal Society Open Science*, *4*(3). https://doi.org/10.1098/rsos.160290

Karniski, C., Krzyszczyk, E., & Mann, J. (2018). Senescence impacts reproduction and maternal investment in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1883). https://doi.org/10.1098/rspb.2018.1123

Keen, K. A., Beltran, R. S., Pirotta, E., & Costa, D. P. (2021). Emerging themes in Population Consequences of Disturbance models. *Proceedings of the Royal Society B: Biological Sciences*, *288*. https://doi.org/10.1098/rspb.2021.0325

Keiver, K. M., Ronald, K., & Beamish, F. W. H. (1984). Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (Phoca groenlandica). *Canadian Journal of Zoology*, *62*, 769–777.

Kershaw, J. L., Brownlow, A., Ramp, C. A., Miller, P. J. O., & Hall, A. J. (2019). Assessing cetacean body condition: Is total lipid content in blubber biopsies a useful monitoring tool? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S1), 271–282. https://doi.org/10.1002/aqc.3105

Kim, Y. S. (1974). Human Tissues: Chemical Composition and Photon Dosimetry Data. *Radiation Research*, *57*(1), 38–45. https://www.jstor.org/stable/3573753

Kirsch, P. E., Iverson, S. J., & Bowen, W. D. (2000). Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (Phoca groenlandica). *Physiologicaland Biochemical Zoology*, *73*(1), 45–59.

Kleiber, M. (1961). The Fire of Life: An Introduction to Animal Energetics. New York: Wiley.

Kleiber, M. (1947). Body size and metabolic rate. *Physiological Reviews*, *27*(4), 511–541.

Kleiber, M. (1975). Metabolic Turnover Rate: A Physiological Meaning of the Metabolic Rate per Unit Body Weight. *Journal of Theoretical Biology*, *53*, 199–204.

Koep, K. S. C., Hoffman, L. C., Dicks, L. M. T., & Slinde, E. (2007). Chemical composition of meat and blubber of the Cape fur seal (Arctocephalus pusillus pusillus). *Food Chemistry*, *100*(4), 1560–1565. https://doi.org/10.1016/j.foodchem.2005.12.035

Konishi, K., Tamura, T., Zenitani, R., Bando, T., Kato, H., & Walløe, L. (2008). Decline in energy storage in the Antarctic minke whale (Balaenoptera bonaerensis) in the Southern Ocean. *Polar Biology*, *31*(12), 1509–1520. https://doi.org/10.1007/s00300-008-0491-3

Koopman, H. N., Iverson, S. J., & Gaskin, D. E. (1996). Stratification and age-related differences in blubber fatty acids of the male harbour porpoise (*Phocoena phocoena*). *Journal of Comparative Physiology B*, *165*, 628–639.

Koopman, H. N. (1998). Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *Journal of Mammalogy*, *79*(1), 260–270. https://academic.oup.com/jmammal/article/79/1/260/842008

Koopman, H. N. (2007). Phylogenetic, ecological, and ontogenetic factors influencing the biochemical structure of the blubber of odontocetes. *Marine Biology*, *151*(1), 277–291. https://doi.org/10.1007/s00227-006-0489-8

Koopman, H. N. (2018). Function and evolution of specialized endogenous lipids in toothed whales. In *Journal of Experimental Biology* (Vol. 121). Company of Biologists Ltd. https://doi.org/10.1242/jeb.161471

Kooyman, G. L., Castellini, M. A., Davis, R. W., & Maue, R. A. (1983). Aerobic diving limits of immature Weddell seals. *Journal of Comparative Physiology B*, *151*(2), 171–174. https://doi.org/10.1007/BF00689915

Kovacs, K. M., & Lavigne, D. M. (1986). Maternal Investment and Neonatal Growth in Phocid Seals. In *Journal of Animal Ecology* (Vol. 55, Issue 3).

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology and Evolution*, *7*(1), 15–19.

Large, V., Peroni, O., Letexier, D., Ray, H., & Beylot, M. (2004). Metabolism of lipids in human white adipocyte Métabolisme lipidique dans le tissu adipeux blanc humain. *Diabetes and Metabolism*, *294*, 294–309. www.e2med.com/dm

Laws, R.M. (1956) Growth and sexual maturity in aquatic mammals. Nature, 178, 193-194, DOI 10.1038/178193a0.Lemos, L. S., Burnett, J. D., Chandler, T. E., Sumich, J. L., & Torres, L. G. (2020). Intra- and inter-annual variation in gray whale body condition on a foraging ground. *Ecosphere*, *11*(4). https://doi.org/10.1002/ecs2.3094

Lidgard, D. C., Boness, D. J., Bowen, W. D., & McMillan, J. I. (2005). State-dependent male mating tactics in the grey seal: The importance of body size. *Behavioral Ecology*, *16*(3), 541–549. https://doi.org/10.1093/beheco/ari023

Lindstedt, S. L., & Calder, W. A. (1981). Body size, physiological time, and longevity of homeothermic animals. *The Quarterly Review of Biology*, *56*(1), 1–16. https://about.jstor.org/terms

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, *125*(6), 873–878. https://about.jstor.org/terms

Listrat, A., Lebret, B., Louveau, I., Astruc, T., Bonnet, M., Lefaucheur, L., Picard, B., & Bugeon, J. (2016). How muscle structure and composition influence meat and flesh quality. In *Scientific World Journal* (Vol. 2016). Hindawi Limited. https://doi.org/10.1155/2016/3182746

Lockyer, C. H., Mcconnell, L. C., & Waters, T. D. (1984). The biochemical composition of fin whale blubber. *Canadian Journal of Zoology*, *62*, 2553–2562.

Lockyer, C. H., McConnell, L. C., & Waters, T. D. (1985). Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. *Canadian Journal of Zoology*, *63*, 2328–2338.

Lockyer, C. (1986). Body fat condition in Northeast Atlantic fin whales, Balaenoptera physalus, and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Science*, *43*, 142–147.

Lockyer, C. (1991). Body composition of the sperm whale, Physeter catodon, with special reference to the possible functions of fat depots. In *Rit Fiskideildar: Vol. 12(2)* (pp. 1–24).

Lockyer, C., Desportes, G., Hansen, K., Labberté, S., & Siebert, U. (2003). Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. *NAMMCO Scientific Publications*, *5*, 107–120.

Malavear, M. Y. G. (2002). *Modeling the Energetics of Steller Sea Lions (Eumetopias jubatus) along the Oregon Coast*. [Thesis] Oregon State University.

Mason, T. H. E., Apollonio, M., Chirichella, R., Willis, S. G., & Stephens, P. A. (2014). Environmental change and long-term body mass declines in an alpine mammal. *Frontiers in Zoology*, *11*(1). https://doi.org/10.1186/s12983-014-0069-6

Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, *10*(1), 105–108.

McClatchie, S., Field, J., Thompson, A. R., Gerrodette, T., Lowry, M., Fiedler, P. C., Watson, W., Nieto, K. M., & Vetter, R. D. (2016). Food limitation of sea lion pups and the decline of forage off central and southern California. *Royal Society Open Science*, *3*(3). https://doi.org/10.1098/rsos.150628

McDonald, B. I., & Crocker, D. E. (2006). Physiology and Behavior Influence Lactation Efficiency in Northern Elephant Seals (*Mirounga angustirostris*). *Physiological and Biochemical Zoology*, *79*(3), 484–496.

McDonald, B. I., Crocker, D. E., Burns, J. M., & Costa, D. P. (2008). Body condition as an index of winter foraging success in crabeater seals (Lobodon carcinophaga). *Deep-Sea Research Part II: Topical Studies in Oceanography*, *55*(3–4), 515–522. https://doi.org/10.1016/j.dsr2.2007.11.002

McHuron, E. A., Aerts, L., Gailey, G., Sychenko, O., Costa, D. P., Mangel, M., & Schwarz, L. K. (2021). Predicting the population consequences of acoustic disturbance, with application to an endangered gray whale population. *Ecological Applications*, *31*(8). https://doi.org/10.1002/eap.2440

McKnight, P. E., & Najab, J. (2009). Kruskal-Wallis Test. In *The Corsini Encyclopedia of Psychology*. Wiley & Sons.

McLaren, I.A. (1993). Growth in Pinnipeds. *Biological Reviews 68***,** 1-79, 10.1111/j.1469-185X.1993.tb00731.x.

McMahon, C. R., Harcourt, R. G., Burton, H. R., Daniel, O., & Hindell, M. A. (2017). Seal mothers expend more on offspring under favourable conditions and less when resources are limited. *Journal of Animal Ecology*, *86*(2), 359–370. https://doi.org/10.1111/1365-2656.12611

McNab, B. K. (1971). On the ecological significance of Bergmann's rule. *Ecology*, *52*(5), 845–854.

McNab, B. K. (1980). Food Habits, Energetics, and the Population Biology of Mammals. *The American Naturalist*, *116*(1), 106–124.

McNab, B. K. (2010). Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia*, *164*, 13–23.

Mellish, J.-A. E., Iverson, S. J., & Bowen, W. D. (1999). Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, *72*(6), 677–690.

Mellish, J.-A. E., Iverson, S. J., & Bowen, W. D. (2000). Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited. *Proceedings of the Royal Society of London B*, *267*, 1245–1251. https://royalsocietypublishing.org/

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *TRENDS in Ecology and Evolution*, *16*(4), 254–260. http://tree.trends.com

Millar, J. S., & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. *Ecology*, *4*(1), 5–12.

Miller, C. A., Reeb, D., Best, P. B., Knowlton, A. R., Brown, M. W., & Moore, M. J. (2011). Blubber thickness in right whales Eubalaena glacialis and Eubalaena australis related with reproduction, life history status and prey abundance. *Marine Ecology Progress Series*, *438*, 267–283. https://doi.org/10.3354/meps09174

Millward, D. J., Garlick, P. J., & Reeds, P. J. (1976). The energy cost of growth. *Proceedings of the Nutrition Society*, *35*(3), 339–349. https://doi.org/10.1079/pns19760054

Molnár, P. K., Klanjscek, T., Derocher, A. E., Obbard, M. E., & Lewis, M. A. (2009). A body composition model to estimate mammalian energy stores and metabolic rates from body mass and body length, with application to polar bears. *Journal of Experimental Biology*, *212*(15), 2313–2323. https://doi.org/10.1242/jeb.026146

Montie, E. W., Garvin, S. R., Fair, P. A., Bossart, G. D., Mitchum, G. B., McFee, W. E., Speakman, T., Starczak, V. R., & Hahn, M. E. (2008). Blubber morphology in wild bottlenose dolphins (Tursiops truncatus) from the Southeastern United States: Influence of geographic location, age class, and reproductive state. *Journal of Morphology*, *269*(4), 496–511. https://doi.org/10.1002/jmor.10602

Mourot, J., Hermier, D., Mourot, J., & Hermier, D. (2001). Lipids in monogastric animal meat. *Reproduction, Nutrition, Development*, *41*, 109–118.

Mueller, B., Pörschmann, U., Wolf, J. B. W., & Trillmich, F. (2011). Growth under uncertainty: The influence of marine variability on early development of Galapagos sea lions. *Marine Mammal Science*, *27*(2), 350–365. https://doi.org/10.1111/j.1748-7692.2010.00404.x

Næss, A., Haug, T., & Nilssen, E. M. (1998). Seasonal variation in body condition and muscular lipid contents in Northeast Atlantic minke whale Balaenoptera acutorostrata. *Sarsia*, *83*(3), 196–218. https://doi.org/10.1080/00364827.1998.10413682

Nerini, M. K., Braham, H. W. , Marquette, W. M., & Rugh, D. J. (1984). Life history of the bowhead whale *Balaena mysticetus* (Mammalia Cetacea). *Journal of Zoology*, *204*, 443–468.

Nordøy, E. S., Ingebretsen, O. C., & Blix, A. S. (1990). Depressed metabolism and low protein catabolism in fasting grey seal pups. *Acta Physiologica*, *139*, 361–369.

Noren, S. R., & Williams, T. M. (2000). Body size and skeletal muscle myoglobin of cetaceans: Adaptations for maximizing dive duration. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *126*(2), 181–191. https://doi.org/10.1016/S1095-6433(00)00182-3

Noren, D. P., Crocker, D. E., Williams, T. M., & Costa, D. P. (2003). Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: Size does matter. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *173*(5), 443–454. https://doi.org/10.1007/s00360-003-0353-9

Noren, D. P., & Mangel, M. (2004). Energy Reserve Allocation in Fasting Northern Elephant Seal Pups: Inter-Relationships between Body Condition and Fasting Duration. *Ecology*, *18*(2), 233–242.

Noren, S. R., & Wells, R. S. (2009). Blubber deposition during ontogeny in free-ranging bottlenose dolphins: balancing disparate roles of insulation and locomotion. *Journal of Mammalogy*, *90*(3), 629–637. www.mammalogy.org

Noren, S. R., Udevitz, M. S., & Jay, C. V. (2014). Energy demands for maintenance, growth, pregnancy, and lactation of female pacific walruses (*Odobenus rosmarus divergens*). *Physiological and Biochemical Zoology*, *87*(6), 837–854. https://doi.org/10.1086/678237

Noren, S. R., & Suydam, R. (2016). Navigating under sea ice promotes rapid maturation of diving physiology and performance in beluga whales. *Journal of Experimental Biology*, *219*(18), 2828–2836. https://doi.org/10.1242/jeb.143644

Noren, S. R., Udevitz, M. S., & Jay, C. V. (2016). Sex-Specific Energetics of pacific walruses (Odobenus rosmarus divergens) during the nursing interval. *Physiological and Biochemical Zoology*, *89*(2), 93–109. https://doi.org/10.1086/685454

Noren, S. R., Schwarz, L., & Robeck, T. R. (2021). Topographic Variations in Mobilization of Blubber in Relation to Changes in Body Mass in Short-Finned Pilot Whales (*Globicephala macrorhynchus*). *Physiological and Biochemical Zoology : PBZ*, *94*(4), 228–240. https://doi.org/10.1086/714637

Oberg, A. L., & Mahoney, D. W. (2007). Linear mixed effect models. *Methods in Molecular Biology*, 404, 213-34.

O'Hara, T. M., Hoekstra, P., Hanns, C., Muir, D., Wetzel, D., & Reynolds, J. (2004). A preliminary assessment of the nutritive value of select tissues from the bowhead whale based on suggested nutrient daily intakes. *International Whaling Commission Scientific Communication Report*, *SC/56/E2*, 1–19.

Oftedal, O. T., Iverson, S. J., & Boness, D. J. (1987). Milk and energy intakes of suckling California sea lion, *Zalophus californianus*, pups in relation to sex, growth, and predicted maintenance requirements. *Physiological Zoology*, *60*(5), 560–575. https://www.jstor.org/stable/30156130

Øigård, T. A., Lindstrøm, U., Haug, T., Nilssen, K. T., & Smout, S. (2013). Functional relationship between harp seal body condition and available prey in the Barents Sea. *Marine Ecology Progress Series*, *484*, 287–301. https://doi.org/10.3354/meps10272

Ono, K. A., & Boness, D. J. (1996). Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behavioral Ecology and Sociobiology*, *38*, 31–41.

Oosthuizen, W. C., de Bruyn, P. J. N., Wege, M., & Bester, M. N. (2016). Geographic variation in subantarctic fur seal pup growth: Linkages with environmental variability and population density. *Journal of Mammalogy*, *97*(2), 347–360. https://doi.org/10.1093/jmammal/gyv181

Pearson, L. E., Weitzner, E. L., Tomanek, L., & Liwanag, H. E. M. (2022). Metabolic cost of thermoregulation decreases after the molt in developing Weddell seal pups. *The Journal of Experimental Biology*, *225*(6). https://doi.org/10.1242/jeb.242773

Perrin, W. F., & Reilly, S. B. (1984). Reproductive Parameters of Dolphins and Small Whales of the Family Deiphinidae. *Reports on the International Whaling Commission*, *6*, 97–133.

Pettis, H. M., Rolland, R. M., Hamilton, P. K., Knowlton, A. R., Burgess, E. A., & Kraus, S. D. (2017). Body condition changes arising from natural factors and fishing gear entanglements in North Atlantic right whales Eubalaena glacialis. *Endangered Species Research*, *32*(1), 237–249. https://doi.org/10.3354/esr00800

Pirotta, E., Booth, C. G., Costa, D. P., Fleishman, E., Kraus, S. D., Lusseau, D., Moretti, D., New, L. F., Schick, R. S., Schwarz, L. K., Simmons, S. E., Thomas, L., Tyack, P. L., Weise, M. J., Wells, R. S., & Harwood, J. (2018a). Understanding the population consequences of disturbance. *Ecology and Evolution*, *8*(19), 9934–9946. https://doi.org/10.1002/ece3.4458

Pirotta, E., Mangel, M., Costa, D. P., Mate, B., Goldbogen, J. A., Palacios, D. M., Hückstädt, L. A., McHuron, E. A., Schwarz, L., & New, L. (2018b). A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. *American Naturalist*, *191*(2), E40–E56. https://doi.org/10.1086/695135

Pirotta, E. (2022). A review of bioenergetic modelling for marine mammal populations. In *Conservation Physiology*, 10(1). https://doi.org/10.1093/conphys/coac036

Pitman, R. L., Durban, J. W., Joyce, T., Fearnbach, H., Panigada, S., & Lauriano, G. (2020). Skin in the game: Epidermal molt as a driver of long-distance migration in whales. *Marine Mammal Science*, *36*(2), 565–594. https://doi.org/10.1111/mms.12661

Pomeroy, P. P., Fedak, M. A., Rothery, P., & Anderson, S. (1999). Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona\ Scotland. *Journal of Animal Ecology*, *68*, 235–253.

Portet, S. (2020). A primer on model selection using the Akaike Information Criterion. *Infectious Disease Modelling*, *5*, 111–128. https://doi.org/10.1016/j.idm.2019.12.010

Pullar, J. D., & Webster, A. J. F. (1977). The energy cost of fat and protein deposition in the rat. *British Journal of Nutrition*, *37*(3), 355–363. https://doi.org/10.1079/bjn19770039

Rattray, P. v., & Joyce, J. P. (1976). Utilisation of metabolisable energy for fat and protein deposition in sheep. *New Zealand Journal of Agricultural Research*, *19*(3), 299–305. https://doi.org/10.1080/00288233.1976.10429069

Rea, L. D., & Costa, D. P. (1992). Changes in Standard Metabolism during Long-Term Fasting in Northern Elephant Seal Pups (*Mirounga angustirostris*). *Physiological Zoology*, *65*(1), 97–111. https://www.jstor.org/stable/30158241

Rea, L. D., Rosen, D. A. S., & Trites, A. W. (2000). Metabolic response to fasting in 6-week-old Steller sea lion pups (*Eumetopias jubatus*). *Canadian Journal of Zoology*, *78*, 890–894.

Read, A. J., Wells, R. S., Hohn, A. A., & Scott, M. D. (1993). Patterns of growth in wild bottlenose dolphins, Tursiops truncatus. *Journal of Zoology*, *231*(1), 107–123. https://doi.org/10.1111/j.1469-7998.1993.tb05356.x

Read, A. J., & Hohn, A. A. (1995). Life in the fast lane: the life history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science*, *11*(4), 423–440.

Reeds, P. J., Wahle, K. W. J., & Haggarty, P. (1982). Energy costs of protein and fatty acid synthesis. *Proceedings of the Nutrition Society*, *41*(2), 155–159. https://doi.org/10.1079/pns19820025

Reilly, J. J., & Fedak, M. A. (1990). Measurement of the body composition of living gray seals by hydrogen isotope diluation. *Journal of Applied Physiology*, *69*(3), 885–891.

Richard, G., Vacquié-Garcia, J., Jouma'a, J., Picard, B., Génin, A., Arnould, J. P. Y., Bailleul, F., & Guinet, C. (2014). Variation in body condition during the post-moult foraging trip of southern elephant seals and its consequences on diving behaviour. *Journal of Experimental Biology*, *217*(14), 2609–2619. https://doi.org/10.1242/jeb.088542

Riet-Sapriza, F. G., Duignan, P. J., Chilvers, B. L., Wilkinson, I. S., Lopez-Villalobos, N., MacKenzie, D. D. S., MacGibbon, A., Costa, D. P., & Gales, N. (2012). Interannual and individual variation in milk composition of New Zealand sea lions (Phocarctos hookeri). *Journal of Mammalogy*, *93*(4), 1006–1016. https://doi.org/10.1644/11-MAMM-A-220.2

Rimbach, R., Amireh, A., Allen, A., Hare, B., Guarino, E., Kaufman, C., Salomons, H., & Pontzer, H. (2021). Total energy expenditure of bottlenose dolphins (Tursiops truncatus) of different ages. *Journal of Experimental Biology*, *224*(15). https://doi.org/10.1242/jeb.242218

Roberts, S. B., & Young, V. R. (1988). Energy costs of fat and protein deposition in the human infantt 3. *American Journal of Clinical Nutrition*, *48*, 951–955. https://academic.oup.com/ajcn/article/48/4/951/4716195

Rojano-Donãte, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., Højer-Kristensen, J., & Madsen, P. T. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*(23), jeb185827. https://doi.org/10.1242/jeb.185827

Ronald, K., Keiver, K. M., Beamish, F. W. H., & Frank, R. (1984). Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). *Canadian Journal of Zoology*, *62*, 1101–1105.

Rosen, D. A., & Renouf, D. (1997). Seasonal changes in blubber distribution in Atlatic harbor seals: indications of thermodynamic considerations. *Marine Mammal Science*, *13*(2), 229–240.

Rosen, D. A. S., & Trites, A. W. (2005). Examining the potential for nutritional stress in young Steller sea lions: Physiological effects of prey composition. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *175*(4), 265–273. https://doi.org/10.1007/s00360-005-0481-5

Rosen, D. A. S., Tollit, D. J., Trites, A. W., & Winship, A. J. (2006). Potential Effects of Short-Term Prey Changes on Sea Lion Physiology. *Sea Lions of the World*, *AK-SG-06-01*, 103–115.

Rosen, D. A. S., Winship, A. J., & Hoopes, L. A. (2007). Thermal and digestive constraints to foraging behaviour in marine mammals. *Philosophical Transactions, Royal Society of London B*, *362*(1487), 2151-2168.

Rosen, D. A. S., Thometz, N. M., & Reichmuth, C. (2021). Seasonal and Developmental Patterns of Energy Intake and Growth in Alaskan Ice Seals. *Aquatic Mammals*, 559–573. https://doi.org/10.1578/am.47.6.2021.559

Rytwinski, T., & Fahrig, L. (2011). Reproductive rate and body size predict road impacts on mammal abundance. *Ecological Applications*, *21*(2), 589–600.

Salogni, E., Galimberti, F., Sanvito, S., & Miller, E. H. (2019). Male and female pups of the highly sexually dimorphic northern elephant seal (*Mirounga angustirostris*) differ slightly in body size. *Canadian Journal of Zoology*, *97*(3), 241–250. https://doi.org/10.1139/cjz-2018-0220

Schell, D. M., Saupe, S. M., & Haubenstock, N. (1989). Bowhead whale (Balaena mysticetus) growth and feeding as estimated by delta13 C techniques. *Marine Biology*, *103*, 443–443.

Schlingermann, M., Berrow, S., Craig, D., McHugh, B., Marrinan, M., O’Brien, J., O’Connor, I., Mudzatsi, E., & White, P. (2020). High concentrations of persistent organic pollutants in adult killer whales (Orcinus orca) and a foetus stranded in Ireland. *Marine Pollution Bulletin*, *151*. https://doi.org/10.1016/j.marpolbul.2019.110699

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running. *Science*, *177*(4045), 222–228.

Schramm, Y., Mesnick, S. L., de La Rosa, J., Palacios, D. M., Lowry, M. S., Aurioles-Gamboa, D., Snell, H. M., & Escorza-Treviño, S. (2009). Phylogeography of California and Galápagos sea lions and population structure within the California sea lion. *Marine Biology*, *156*(7), 1375–1387. https://doi.org/10.1007/s00227-009-1178-1

Schulz, T. M., & Bowen, W. D. (2005). The Evolution of Lactation Strategies in Pinnipeds: A Phylogenetic Analysis. *Ecological Monographs*, *75*(2), 159–177.

Schusterman, R. L., & Gentry, Ronald J. (1971). Development of a fatted male phenomenon in California sea lions. *Developmental Psychobiology*, *4*(4), 333.

Shingfield, K. J., Bonnet, M., & Scollan, N. D. (2013). Recent developments in altering the fatty acid composition of ruminant-derived foods. *Animal*, *7*(SUPPL.1), 132–162. https://doi.org/10.1017/S1751731112001681

Sibly, R. M., & Brown, J. H. (2009). Mammal reproductive strategies driven by offspring mortality-size relationships. *American Naturalist*, *173*(6). https://doi.org/10.1086/598680

Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, *208*(9), 1717–1730. https://doi.org/10.1242/jeb.01556

St. Aubin, D. J., Smith, T. G., & Geraci, J. R. (1990). Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. *Canadian Journal of Zoology*, *68*, 359–367.

Stephens, P. A., Houston, A. I., Harding, K. C., Boyd, I. L., & Mcnamara, J. M. (2014). Capital and income breeding: the role of food supply. *Ecology*, *95*(4), 882–896.

Stevick, P. T. (1999). Age-length relationships in humpback whales: A comparison of strandings in the western North Atlantic with commercial catches. *Marine Mammal Science*, *15*(3), 725–737.

Stewart, R. E. A., & Lavigne, D. M. (1984). Energy transfer and female condition in nursing harp seals *Phoca groenlandica*. *Holarctic Ecology*, *7*, 182–194.

Stewart, J., Durban, J., Europe, H., Fearnbach, H., Hamilton, P., Knowlton, A., Lynn, M., Miller, C., Perryman, W., Tao, B., & Moore, M. (2022). Larger females have more calves: influence of maternal body length on fecundity in North Atlantic right whales. *Marine Ecology Progress Series*, *689*, 179–189. https://doi.org/10.3354/meps14040

Stewart, J.D., Durban, J.W., Knowlton, A.R., Lynn, M.S., Fearnbach, H., Barbaro, J., Perryman, W.L., Miller, C.A., & Moore, M.J. (2021). Decreasing body lengths in North Atlantic right whales. *Current Biology*, *31*(14), 3174-3179.

Struntz, D. J., McLellan, W. A., Dillaman, R. M., Blum, J. E., Kucklick, J. R., & Pabst, D. A. (2004). Blubber Development in Bottlenose Dolphins (Tursiops truncatus). *Journal of Morphology*, *259*(1), 7–20. https://doi.org/10.1002/jmor.10154

Strandberg, U., Käkelä, A., Lydersen, C., Kovacs, K. M., Grahl-Nielsen, O., Hyvärinen, H., & Käkelä, R. (2008). Stratification, composition, and function of marine mammal blubber: The ecology of fatty acids in marine mammals. *Physiological and Biochemical Zoology*, *81*(4), 473–485. https://doi.org/10.1086/589108

Stephens, P. A., Houston, A. I., Harding, K. C., Boyd, I. L., & Mcnamara, J. M. (2014). Capital and income breeding: the role of food supply. In *Ecology* (Vol. 95, Issue 4).

Suzuki, M., Yoshioka, M., Ohno, Y., & Akune, Y. (2018). Plasma metabolomic analysis in mature female common bottlenose dolphins: profiling the characteristics of metabolites after overnight fasting by comparison with data in beagle dogs. *Scientific Reports*, *8*(1). https://doi.org/10.1038/s41598-018-30563-x

Swaim, Z. T., Westgate, A. J., Koopman, H. N., Rolland, R. M., & Kraus, S. D. (2009). Metabolism of ingested lipids by North Atlantic right whales. *Endangered Species Research*, *6*(3), 259–271. https://doi.org/10.3354/esr00163

Taillon, J., Brodeur, V., Festa-Bianchet, M., & Côté, S. D. (2012). Is mother condition related to offspring condition in migratory caribou (rangifer tarandus) at calving and weaning? *Canadian Journal of Zoology*, *90*(3), 393–402. https://doi.org/10.1139/Z2012-001

Tarnawski, B. A., Cassini, G. H., & Flores, D. A. (2014). Skull allometry and sexual dimorphism in the ontogeny of the southern elephant seal (*Mirounga leonina*). *Canadian Journal of Zoology*, *92*(1), 19–31. https://doi.org/10.1139/cjz-2013-0106

Teplitsky, C., Mills, J. A., Alho, J. S., Yarrall, J. W., & Merilä, J. (2008). Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *PNAS*, *105*(36), 13492–13496.

Therrien, J. F., Côté, S. D., Festa-Bianchet, M., & Ouellet, J. P. (2007). Conservative maternal care in an iteroparous mammal: A resource allocation experiment. *Behavioral Ecology and Sociobiology*, *62*(2), 193–199. https://doi.org/10.1007/s00265-007-0453-8

Thometz, N. M., Hermann-Sorensen, H., Russell, B., Rosen, D. A. S., & Reichmuth, C. (2021). Molting strategies of Arctic seals drive annual patterns in metabolism. *Conservation Physiology*, *9*(1). https://doi.org/10.1093/conphys/coaa112

Tjørve, K. M. C., & Tjørve, E. (2017). The use of Gompertz models in growth analyses, and new Gompertz-model approach: An addition to the Unified-Richards family. *PLoS ONE*, *12*(6). https://doi.org/10.1371/journal.pone.0178691

Torres-Romero, E. J., Morales-Castilla, I., & Olalla-Tárraga, M. (2016). Bergmann's rule in the oceans? Temperature strongly correlates with global interspecific patterns of body size in marine mammals. *Global Ecology and Biogeography*, *25*(10), 1206–1215. https://doi.org/10.1111/geb.12476

Trillmich, F., & Limberger, D. (1985). Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia*, *67*, 19–22.

Trillmich, F., & Kooyman, G. L. (2001). Field metabolic rate of lactating female Galápagos fur seals (Arctocephalus galapagoensis): the influence of offspring age and environment. *Comparative Biochemistry and Physiology Part A*, *129*, 741–749.

Trumble, S. J., Barboza, P. S., & Castellini, M. A. (2003). Digestive constraints on an aquatic carnivore: Effects of feeding frequency and prey composition on harbor seals. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *173*(6), 501–509. https://doi.org/10.1007/s00360-003-0358-4

Trumble, S. J., Noren, S. R., Cornick, L. A., Hawke, T. J., & Kanatous, S. B. (2010). Age-related differences in skeletal muscle lipid profiles of Weddell seals: Clues to developmental changes. *Journal of Experimental Biology*, *213*(10), 1676–1684. https://doi.org/10.1242/jeb.040923

van Aswegen, M., Christiansen, F., Symons, J., Mann, J., Nicholson, K., Sprogis, K., & Bejder, L. (2019). Morphological differences between coastal bottlenose dolphin (Tursiops aduncus) populations identified using non-invasive stereo-laser photogrammetry. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-48419-3

van de Ven, T. M. F. N., Fuller, A., & Clutton-Brock, T. H. (2020). Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. *Functional Ecology*, *34*(1), 194–202. https://doi.org/10.1111/1365-2435.13468

Víkingsson, G. (1995). Body condition of fin whales during summer off Iceland. In A. S. Blix, L. Walløe, & Ø. Ultang (Eds.), *Whales, seals, fish and man* (pp. 361–369).

Víkingsson, G. A., Audunsson, G. A., Elvarsson, B. Þ., & Gunnlaugsson, T. (2013). Energy storage in common minke whales (Balaenoptera acutorostrata) in Icelandic waters 2003-2007.-Chemical composition of tissues and organs. *Reports of the International Whaling Commission*, *Document SC/F13/SP10*. https://doi.org/10.13140/RG.2.1.2420.7129

Villegas-Amtmann, S., Simmons, S. E., Kuhn, C. E., Huckstadt, L. A., & Costa, D. P. (2011). Latitudinal range influences the seasonal variation in the foraging behavior of marine top predators. *PLoS ONE*, *6*(8). https://doi.org/10.1371/journal.pone.0023166

Villegas-Amtmann, S., McDonald, B. I., Páez-Rosas, D., Aurioles-Gamboa, D., & Costa, D. P. (2017a). Adapted to change: Low energy requirements in a low and unpredictable productivity environment, the case of the Galapagos sea lion. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *140*, 94–104. https://doi.org/10.1016/j.dsr2.2016.05.015

Villegas-Amtmann, S., Schwarz, L. K., Gailey, G., Sychenko, O., & Costa, D. P. (2017b). East or west: The energetic cost of being a gray whale and the consequence of losing energy to disturbance. *Endangered Species Research*, *34*, 167–183. https://doi.org/10.3354/esr00843

Watanabe, H., & Suzuki, K. (1950). Chemical composition of various parts of sperm whale. *Bulletin of the Japanese Society for the Science Fisheries*, *15*, 735–740.

West, K. L., Oftedal, O. T., Carpenter, J. R., Krames, B. J., Campbell, M., & Sweeney, J. C. (2007). Effect of lactation stage and concurrent pregnancy on milk composition in the bottlenose dolphin. *Journal of Zoology*, *273*, 148–160.

Whittemore, C. T. (1983). The Science and Practice of Pig Production. Blackwell Science, Oxford.

Williams, T. M. (1999). The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society B*, *354*, 193–201. https://royalsocietypublishing.org/

Williams, T. M., Rutishauser, M., Long, B., Fink, T., Gafney, J., Mostman-Liwanag, H., & Casper, D. (2007). Seasonal variability in otariid energetics: Implications for the effects of predators on localized prey resources. *Physiological and Biochemical Zoology*, *80*(4), 433–443. https://doi.org/10.1086/518346

Williams, R., Víkingsson, G. A., Gislason, A., Lockyer, C., New, L., Thomas, L., & Hammond, P. S. (2013). Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four deca. *ICES Journal of Marine Science*, *70*(6), 1273–1280. https://doi.org/10.1093/icesjms/fst059

Winship, A. J., Trites, A. W., & Calkins, D. G. (2001). Growth in body size of the Steller sea lion (Eumetopias jubatus). *Journal of Mammalogy*, *82*(2), 500–519. https://academic.oup.com/jmammal/article/82/2/500/2373087

Woods, C. L., Yust, D., McLeod, C., & Subramanyam, M. (1995). Effects of dietary protein:energy ratio on weight gain, body composition, serum glucose and triglyceride levels, and liver function of striped bass. *Water Science and Technology*, *31*(10), 195–203. https://doi.org/10.1016/0273-1223(95)00439-T

Worthy, G. A. J., & Edwards, E. F. (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (Stenella attenuata). *Physiological Zoology*, *63*(2), 432–442.

Worthy, G. A. J., Morris, P. A., Costa, D. P., & le Boeuf, B. J. (1992). Moult energetics of the northern elephant seal (*Mirounga angustirostris*). *Journal of Zoology*, *227*, 257–265.

Worthy, G. A. J., & Lavigne, D. M. (1987). Mass loss, metabolic rate, and energy utilization by harp and gray seal pups during the postweaning fast. *Zoology*, *60*(3), 352–364. https://www.jstor.org/stable/30162289

Young, R. A. (1976). Fat, Energy and Mammalian Survival. *American Zoology*, *16*, 699–710. https://academic.oup.com/icb/article/16/4/699/2079361

Zeide, B. (1993). Analysis of Growth Equations. *Forest Science*, *39*(3), 594–616.

Chapter 2

Body size is constrained by life history and energetics in the smallest fully aquatic mammal

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2.1 Abstract

Body size confers reproductive success and survival, with larger individuals benefitting from high fasting endurance, lower mass-specific metabolic costs, and larger offspring both intra- and interspecifically. Although these qualities may increase fitness for large individuals, not all species trend towards larger body sizes, indicating constraints placed on body size. To explore the trade-offs associated with body size in marine mammals we used stochastic dynamic programming (SDP) to simulate three populations of female harbor porpoises that differed in body size from small (39 kg and 134 cm), average (48 kg and 145), and large (58 kg and 155 cm). Harbor porpoises provide a unique opportunity to explore body size constraints because they are one of the smallest fully aquatic mammals. While they have very high mass-specific metabolic costs that result in intense foraging rates, their overall metabolic requirements are low. We explored how life history differed between the three size classes, and assessed population resilience by conducting simulations with disturbance that reduced foraging success and increased travel costs to simulate behavioral responses to disturbance. We found that: (1) small females invested heavily in offspring, but had a low net reproductive rate resulting from their

lengthened interbirth interval, low interbirth interval, and high starvation-related mortality when compared to their larger conspecifics; (2) large females experienced marginal benefits in reproductive rates and survivorship when compared to average females, but required approximately 17% more energy intake to support their size; and (3) all size classes experienced decreased survival and population declines in response to disturbance, but large females showed signs of resilience to disturbance as their population growth rate remained unchanged in disturbance scenarios. Despite the benefits of large body size, the relatively high energy requirements of large females make it unlikely that selective pressures will increase the overall body size of harbor porpoises. Additionally, our results indicate that harbor porpoises are already at their optimal body size and live on the edge of their physiologic capabilities as the smallest fully aquatic cetacean.

2.2 Introduction

Body size is a fundamental determinant of fitness (i.e., reproductive output and survival) in mammals. Large animals are thought to have high fitness mediated by lower mass-specific metabolic costs, greater energy stores, and larger, healthier offspring that have increased survival probabilities (Schmidt-Nielsen, 1972; Kleiber, 1975; Bekoff et al., 1981; Mellish et al., 1999; Rollinson and Rowe 2016; Ronget et al., 2017). Yet, mammals range widely in body size from less than 1 kg to greater than 100,000 kg (Figure 2.1). The large range of mammalian body size is likely due to physiologic and environmental constraints on body size, such as optimizing foraging strategies and the need for more overall energy acquisition from the environment, that constrain species from continuously evolving to larger size (Gearty et al., 2018; Goldbogen, 2018; Lindstedt, 2021). The balance between fitness benefits and physiologic constraints is particularly relevant for marine mammals, whose closely related species exhibit vastly different body sizes (Figure 2.1). However, empirical studies on trade-offs between demography and physiology are challenging, especially for free-ranging animals. Mechanistic or process-based models provide greater insight into such biological paradigms while allowing for the manipulation of parameters of interest, such as body size.

Here, we used a process-based modeling approach to quantitatively determine the benefits and limitations of varying body size in marine mammals using the smallest cetacean, harbor porpoises (*Phocoena phocoena*). Harbor porpoises provide a unique opportunity to explore body size constraints because they are one of the smallest fully aquatic marine mammal species, a group that trends towards gigantism (harbor porpoise mean ~50 kg; Read 1990; Read and Tolley, 1997; McLellan et al., 2002; Lockyer and Kinze, 2003; Figure 2.1). Harbor porpoises have a fast life history strategy, producing comparatively large offspring every one to two years and eating near-constantly to keep up with their high metabolic demands (Read, 1990; Read and Hohn, 1995; Wisniewska et al., 2016; Rojano-Doñate et al., 2018). High energy demands are thought to make this species particularly vulnerable to environmental and anthropogenic disturbances that disrupt foraging behavior (Wisniewska et al., 2016; Wisniewska et al., 2018). As such, harbor porpoises face conflicting demands to minimize energetic costs while increasing reproductive output while already living at the edge of their physiologic capabilities. Given the narrow physiological niche within which harbor porpoises exist, it is likely that variations in body size should yield measurable impacts on energetics and reproduction and, ultimately, population viability.

To better understand the constraints on harbor porpoise body size, we simulated three populations: a population of small (39 kg and 134 cm in length), average (48 kg and 145 cm in length), and large (58 kg and 155 cm in length) females (Figure A2.1). These sizes were biologically realistic; the small and large females were within one standard deviation of the mean length of adult female harbor porpoises (Lockyer and Kinze, 2003). The goal of testing these three size classes was to explore the lowest possible threshold of body size for a fully aquatic marine mammal and understand the fitness benefits of becoming larger and potential limitations of attaining large size. To do this, we used stochastic dynamic programming (SDP) to simulate these populations under baseline environmental conditions and a range of anthropogenic disturbance scenarios. Our use of the SDP modeling framework coupled state-dependent life history theory with real-world scenarios to quantify the behavior, physiology, and life history characteristics of individuals and in turn estimate population-level trends in abundance. We used this theoretical modeling approach to address the following questions: (1) how do reproductive rates and population biology differ between size classes and (2) how do responses to disturbance differ between size classes?

2.3 Methods

2.3.1 Model Overview

SDP models consist of two steps, a backward iteration and a forward simulation (Mangel and Clark, 1988; Houston and McNamara 1999; Clark and Mangel 2000). The backward iteration uses optimization theory to identify the state-dependent decisions that maximize a reward (*e.g.*., lifetime fitness). In the backward iteration, the model starts at a terminal time, T, and iterates backwards for each time step (a day in this model) to identify optimal reproductive decisions for all combinations of state variables. In this model, state variables were female body condition (x; represented by the ratio of blubber mass to total body mass), calf body condition when the female was lactating (m), and reproductive state (r; see Appendix for summary of model parameters). An underlying bioenergetic model is used to identify how the state variables change under different reproductive decisions. Optimal decisions are determined by the decision that yields the highest fitness, defined as the female's expected future reproductive potential. In SDP models, the forward simulation involves individual-based simulations where the optimal behavioral decisions determined in the backward iteration can be used to understand the sequence of behaviors, and underlying physiological patterns, that emerge within the population under different environmental conditions. We built the SDP model and conducted all subsequent analyses in R (R Core Team, 2022).

Harbor porpoises are highly seasonal and synchronous breeders; therefore, we used fixed dates for life history events to simplify the model. Births occurred on May 21 (model day 1, 365, etc.), implantation occurred on July 25 (model day 65, 430, etc.), and the maximum wean date was January 16 (model day 240, 605, etc.). These dates accounted for 300 days of gestation and 240 days of nursing (Read, 1990; Read and Gaskin, 1990; Börjesson and Read, 1993; Sørenson and Kinze, 2003; Read and Hohn, 1995). Females could not give birth prior to the fixed date nor continue weaning past the fixed wean date, but they could abort pregnancies and wean calves before these fixed dates.

We set the age at sexual maturity to 3.6 years (Read and Hohn, 1995) and the maximum age to 20 years old due to rare reports of harbor porpoises beyond this age (Read and Hohn, 1995; Murphy et al., 2020). As such, in the forward simulation, starvation-based mortality was an emergent property; however, age-based mortality, β_a, derived from previously documented life history schedules was included in the model as an additional form of stochasticity that could influence population dynamics (Table A2.5; Barlow and Boveng, 1991). For each individual on each day of the forward simulation, a random number from 0 to 1 was drawn from a uniform distribution and if this value was less than β_a the female survived and if it was greater than β_a the female died.

Female harbor porpoises could be in one of four states: 1) non-reproductive (i.e., juvenile and sexually mature but not reproducing), (2) pregnant, (3) lactating, and (4) pregnant and lactating. When harbor porpoises were juveniles (< 3.6 years old) they remained in the same non-reproductive state and no reproductive decisions were made. In the backward iteration, females in the last year of life could only be non-reproductive or lactating and did not have the choice to be pregnant. Transitions between the non-reproductive and pregnant states could only occur at the time of implantation, and transitions between pregnant and lactating states could only occur at the time of birth. However, transitions to lower reproductive states (e.g., pregnant to non-reproductive) could occur via aborting the fetus or weaning the calf at any time.

2.3.2 Model environment

We modeled sea surface temperature (SST) in both the backward iteration and forward simulation, which impacted the cost of thermoregulation in our model. In the backward iteration, we modeled monthly mean sea surface temperature extracted at a single proxy location in the North Sea from the HadISST (*https://climatedataguide.ucar.edu/climate-data/sst-data-hadisst-v11*) dataset from 2010-2020 at 1° spatial resolution using the "rerddapXtracto" package in R (*https://github.com/rmendels/rerddapXtracto*). Then, for each day in the forward simulation we added stochasticity into modeled sea surface temperature by randomly selecting a value from a uniform distribution constructed using the monthly mean and standard deviation derived from the HadISST dataset. On a given day, every female in the forward simulation experienced the same modeled sea surface temperature.

We also assumed stochasticity in the probability of finding food, λ. We set $\lambda = 0.82$ using pattern-oriented modeling whereby we ran a series of simulations and selected the λ which resulted in harbor porpoise body condition that reflected what was observed in the wild (Lockyer, 1993). In the backward iteration, average fitness for each reproductive decision was weighted by the probability of finding food (e.g.,

Appendix 2 eq. 27). In the forward simulation, we assigned a discrete option (food found or food not found) to each individual on each model day based on λ.

2.3.3 Physiology

Body condition, defined here as the ratio of blubber mass to total body mass, was the primary physiological state variable. Female body condition was bounded by the critical value (x_c = 0.05) and the capacity constraint ($C = 0.425$). A critical value of 0.05 is commonly used in the bioenergetic literature, while the capacity constraint was determined from calculations using the maximum blubber mass and maximum total body mass of harbor porpoises (Lockyer, 1995; Beltran et al., 2017; Gallagher et al., 2021). Should the female experience a negative energy balance causing her condition to decline to x_c, she died of starvation. In contrast, when the female reached C, we assumed that excess energy (above that required to remain at C) left the body as waste. Females that were lactating or pregnant and lactating were defined by a secondary physiological state variable, calf body condition, m, which was also bounded by a critical value (m_c = 0.095) and capacity constraint (C_m = 0.62) determined from calculations using the minimum and maximum blubber and total body mass (Lockyer, 1995).

A female's energy balance was mediated by energy intake from the environment and energetic requirements of basal metabolism, locomotion, thermoregulation, growth (if younger than physical maturity; 7.21 years old; Murphy et al., 2020), and pregnancy and lactation when reproductive (Appendix 2 eqs. 13-18). The biomass of prey consumed was scaled as a function of body size to account for the allometry of biomass intake, meaning that small animals consumed proportionally more prey biomass than larger animals to account for their higher mass-specific metabolic costs (Appendix 2 eq. 20). Additionally, juveniles (< 3.6 years old) consumed an additional 10% of their expected biomass intake based on mass to account for the higher mass-specific metabolic costs of juveniles when compared to adults (Figure A2.2). The composition of prey consumed was derived from published accounts of seasonal stomach content analyses and the energy density of prey items were seasonally specific when applicable (Table A2.4; Andreasen et al., 2017; Booth, 2020).

We allowed under- and overweight females to adjust their energy intake proportional to the percent difference between actual female weight and ideal female weight for a given age up to 50% (see Appendix Physiology section). For example, if a female was 25% underweight, she increased her energy gain by 25%. This allowed for more realistic changes in body condition and mass across simulations. Additionally, lactating females increased their predicted energy intake by 20% to account for the increased demands of lactation.

Calves received energy in the form of milk delivered from the mother and independent foraging. Independent foraging began at 3 months old and increased in frequency as the calf aged while milk delivery decreased linearly until the calf was weaned (see Appendix Physiology section).

2.3.4 Size Class Analysis

We ran separate backward iterations and forward simulations for each of three size classes as we assumed that optimal decisions would differ between the three size classes. We varied the Gompertz growth curve of average females by -10 and +10 cm to create the small and large size classes, respectively (Figure A2.1; Appendix 2 eq. 1). We also altered the fetal length function such that fetuses of each size class at birth matched the approximate size at birth of each size class (Appendix 2 eqs. 3-5). Mass curves for adult females and fetuses did not change because our calculations of mass were derived from a weight-at-length curve (Appendix 2 eqs. 2 and 6). Lean mass curves were changed such that the average body condition of females at a certain age was the same across size classes based on the mass curves (Appendix 2 eqs. 7-9). We ran disturbance scenarios for average and large females, only, as small females performed poorly under baseline environmental conditions (see Results). Each bioenergetic equation in our model had a size component and, as such, remained the same throughout model runs but produced different outputs based on the varied growth curves.

2.3.5 Forward simulation

Each size class had a baseline scenario where we assumed there were no environmental or anthropogenic disturbances. In the forward simulation, we included two sources of stochasticity; sea surface temperature (see above) and travel velocity. This added stochasticity attempted to account for slight differences in the environment likely to be experienced by wild porpoises (e.g., daily variation in sea surface temperature, ephemeral and patchy distribution of prey) that affect their bioenergetics. Lastly, travel velocity influenced the cost of locomotion (Appendix 2 eq. 14), and, as such, we aimed to capture the range of velocities at which harbor porpoises are known to travel in the forward simulation. Travel velocity was randomly selected per day and per individual in the simulation from a uniform distribution spanning ± one standard deviation of the mean recorded travel velocity for harbor porpoises (Otani et al., 2001).

For average females, we simulated one disturbance per season (four total). Each disturbance lasted for 50 days and we assumed that 100% of the females in the simulation were impacted by the disturbance. The 50-day disturbance was simulated in the middle of each season unless there was an important reproductive event within that season. As such the winter disturbance occurred from Julian date 1-50 to include the day of weaning on Julian date 16, the spring disturbance occurred from Julian date 115-165 to include the end of pregnancy on Julian date 141, and the summer and fall disturbances occurred on Julian date 186-236 and 288-338, respectively. Once we determined which seasonal disturbance caused the greatest decline in population abundance for average females, we simulated the same disturbance scenario for large females (Fall, see below). Additionally, we ran a repeat disturbance scenario where the 50-day disturbance was repeated each Fall for average and large females. The cost of disturbance was calculated using methods outlined in Czapanskiy et al. (2021). Disturbed females experienced increased travel speed away from the disturbance (velocity = 1.8-2.14 m/s; Kastelein et al., 2018) that lasted for 2 hours (Czapanskiy et al., 2021) and a cessation of foraging that lasted for 8 hours (Czapanskiy et al., 2021).

Disturbances were modeled as novel (i.e., unanticipated disturbances) and as such, we used the optimal decisions derived from the baseline backward iteration.

For each model simulation, we computed daily and whole simulation summary metrics. Daily metrics included population abundance and mean female body condition for all females greater than or equal to 1 year old. Simulation metrics included female body condition for all females greater than or equal to 1 year old, age at death, proportion of deaths per year due to starvation and age-based mortality, calf body condition at recruitment for calves that recruit, average number of yearly recruits, average yearly recruitment rate, average yearly abortion rate, nursing duration, average interbirth interval across females, number of births per females that reach sexual maturity, number of recruits per females that reach sexual maturity, and probability of survival for post-breeding females (determined as the proportion of females that survive at least one year following the time of weaning of her calf). We constructed life history tables for each population that included age-based survival (from both starvation-related mortality and age-based mortality), fecundity, and *lambda* (Gotelli, 2001; see Appendix Life History Table Section).

2.3.6 Sensitivity analysis

We conducted sensitivity analyses on 24 model parameters using the baseline scenario for average females (Table A2.6). For each sensitivity analyses we ran a separate backward iteration and a forward simulation. We varied the parameters by ± 10, 25, and 50%, with the exception of assimilation efficiency, calf body condition at birth, heat increment of feeding, x_c, λ, where we manually selected values to test that remained biologically realistic. We compared sensitivity analysis results using Cohen's D on R_0, population female body condition, calf body condition, proportion of starvation-related deaths, age at death, recruitment rate, nursing duration, and first-year survival on the mean value derived from the 100 Monte Carlo simulations. Cohen's D tests the difference between the mean values of the metric of interest scaled by the pooled standard deviation where a value of 0.2, 0.5, or 0.8 indicates a small, moderate, or large effect size, respectively (Cohen, 1977). Sensitivity analyses were run on an early model iteration where biomass intake was not scaled by body size.

2.4 Results

2.4.1 Size-related differences

Survival of small, average, and large female harbor porpoises was moderate for new recruits and juveniles, but decreased with age (Figure A2.2). Survivorship of young was slightly higher in small females than average and large females. Although this curve was partially impacted by the underlying age-based mortality built into the model, the differences between the three size classes was also driven by age-based differences in starvation-related mortality. Fecundity for small females followed a much stricter two-year pattern of births for the first six years of sexual maturity while, average and large females followed a similar but less consistent two-year fecundity cycle (Figure A2.3).

Mature harbor porpoises experienced annual fluctuations in body condition, irrespective of size class, that varied in accordance with modeled sea surface temperature (Figure 2.2). These fluctuations were likely the result of changing energetic demands of thermoregulation, pregnancy, and lactation throughout the year coupled with fluctuations in energy intake mediated by prey composition and energy density. Body condition was lowest in fall for all size classes following a period of high sea surface temperature in summer combined with energetically intensive reproductive events such as lactation and mid-pregnancy. For all size classes, body condition exhibited a bimodal distribution likely resulting from seasonal fluctuations in body condition (Figure 2; 0.30 and 0.34 for all females). Small females exhibited the largest yearly fluctuation in body size when compared to the other two size classes. Overall, body composition was tightly coupled amongst all three size classes (range = 0.27-0.35 for small female, range = 0.28-0.35 for average females, and range = 0.27-0.35 for large females).

The number of reproductive opportunities varied across the three size classes (Figure 2.3). Small females had a longer interbirth interval (number of years between calving events) when compared to larger conspecifics (Figure 2.3). Interbirth interval decreased with increasing body size, ranging from 1.84 ± 0.02 in small females to 1.74 ± 0.01 in average females, and 1.65 ± 0.01 in large females. Despite the small range in numerical values, Cohen's D analyses revealed a large effect size for all cross-size comparisons (Table A2.7).

The shorter interbirth interval of large females provided a greater number of reproductive opportunities when compared to smaller females (Figure 2.3). Mature females of each size class gave birth to one to two calves in their lifetime, on average, but small females trended towards the lower end of this distribution. All cross-size comparisons yielded in a large effect size; however, the largest difference occurred between small (1.65 ± 0.07) and large females (2.03 ±0.08; Table A2.7). In contrast, small females produced the greatest number of recruits in their lifetime (0.86 ± 0.08) when compared to average and large females (0.70 ± 0.06 and 0.70 ± 0.04). Cohen's D analyses yielded a large effect size for the comparison between small and large and small and average females, and negligible for the comparison between average and large females (Table A2.7).

We also found differences in offspring investment between each size class (Figure 2.4). Small females had the highest annual recruitment rate and the longest nursing duration when compared to average and large females (Figure 2.4). Interestingly, average females produced calves with the lowest body condition, followed by small females. Calves produced by large females had a far greater body condition at recruitment than small and average females (Figure 2.4). Finally, small females had the highest abortion rate, whereas average and large females had similarly low abortion rates (Figure 2.4).

These differences in offspring investment impacted survival probability of recruits and of post-breeding females (Table A2.7; Figure 2.3). The survival probability of calves following recruitment for small females was far higher than that of average and large females, despite the very high body condition of calves produced by large females (Figure 2.3). The effect size for all comparisons was large females was moderate (Table A2.7). The greatest impact of reproduction occurred for small females, which had the lowest post-breeding survival (Figure 2.3). Cohen's D effect size was large for all cross-size comparisons (Table A2.7).

Overall, small females experienced a higher proportion of starvation-related deaths than average and large females (Figure 2.3). More than one-half of all deaths that occurred in small females were due to starvation (0.69 ± 0.01). In contrast, average and large females experienced death primarily due to underlying mortality or age (Figure 2.3). When comparing effect sizes between small and average and small and large females, effect sizes were large (Table A2.7). However, the comparison between average and large females was small as both size classes had the same mean proportion of deaths due to starvation (0.45 ± 0.01 for average females and 0.47 ± 0.01 for large females).

Although there was a high degree of variability in these life history parameters, population trajectories amongst the three size classes remained fairly consistent, as indicated by differences in lambda (Figure 3; Gotelli, 2001). All populations experienced an increasing population trajectory, with lambda values that were slightly greater than 1.

2.4.2 Response to disturbance

Average female harbor porpoises were the most sensitive to disturbance in fall when body condition was the lowest. Because seasonal trends in body condition were the same across size classes, we assumed that small and large harbor porpoises would be similarly impacted by disturbances in the fall. For all simulated populations, disturbance primarily resulted in a substantial increase in the proportion of starvation-related deaths, marked by a large effect size when compared with baseline scenarios for each respective size class (Figure 2.5). For all size classes recruitment rate was negatively impacted by disturbance, but the largest impact on recruit survival occurred for small females (Figure 2.5). Overall, the population was reduced so fewer total females were of mature age and prepared to produce calves that would recruit into the population. For small and large females, these changes to population demography resulted in a decrease in *lambda*; however, large females exhibited resilience to disturbance as *lambda* was not impacted in this population (Figure 2.5).

In the repeat disturbance scenarios, the impacts of disturbance were consistent with observations for the single disturbance scenario for all size classes, however, the impacts of disturbance were amplified, with more large effect sizes and greater percent change in tested metrics (Figure 2.5). Again, large females exhibited resilience and *lambda* indicated that the population could recover following disturbance.

2.4.3 Sensitivity analysis results

The model was most sensitive to parameters that impacted energy intake, calf milk delivery, and energy gained from blubber catabolism (Appendix 2 Figures 5-28). Parameters that impacted energy intake, such as λ, assimilation efficiency, and the heat increment of feeding resulted in substantial changes to female body composition and starvation-related mortality, which had downstream impacts on calf condition and recruitment rates. Parameters relating to blubber catabolism influenced calf body composition, recruitment rates, and female body composition Similarly, changing the intake multiplier for lactating females had a large impact on nursing duration and recruitment rates, whereas changes to mammary gland efficiency had a large effect on calf body composition and recruitment rates. Additionally, the percent lipid in blubber for both mature females and calves had a large influence on all model parameters tested when decreased by 50% and changes made to the deposition efficiency of lipid had a large impact on all model parameters tested in all trials.

2.5 Discussion

Body size played a significant role in harbor porpoise life history. The effects of body size were most notable for interbirth interval, lifetime reproductive success (as represented by the number of births and recruits per mature female), the survival probability of recruits, and the proportion of deaths related to starvation. Despite these differing life history strategies, population trajectories under baseline scenarios remained similar amongst the three size classes, with all populations increasing in abundance (Figure 2.3). Interestingly, life history metrics for large females were only marginally better than those of average females. Small females had greater success recruiting calves into the population, likely facilitated by their longer interbirth interval, which allowed them to skip reproductive events and restore their body reserves to ensure the success of their next calf. Skipped breeding has been surmised to increase offspring survival, which is on par with the theoretical results presented here that indicate high survival of recruits produced by small females (Baron et al., 2013; Shaw and Levin, 2013). Although skipped breeding resulted in high offspring survival for small females, their overall lifetime reproductive success was lower than that of average and large females, as indicated by their lower R_0 value. Further, smaller females had a much higher incidence of starvation-related mortality than larger conspecifics (Figure 2.3). Small females typically have a reduced fasting endurance, facilitated by allometric scaling of energy reserves and metabolic rate, whereby decreasing body size relates to less fat deposition and higher mass-specific metabolic costs (Lindstedt and Boyce, 1985; Millar and Hickling, 1992; Crocker et al., 2012). This reduced fasting endurance likely influenced the survival of females by increasing the incidence of starvation. The increased incidence of mortality in small females had measurable impacts on population success, similar to what has been found in empirical studies that assert that survival of reproductive females are essential determinants of population size (Hatter and Janz, 1994; Gaillard et al., 1998; Gaillard et al., 2000; Pistorius et al., 2004). Therefore, populations with higher and less variable survival rates, such as the populations of average and large females simulated here, are more likely to succeed.

Our findings indicate that large females may more readily prioritize their own survival (and survival of future offspring) over their current reproductive effort due to the high energy investment required to raise a calf (Ono et al., 1987; Hamel et al., 2011; McMahon et al., 2017). We found that large females allocated a greater proportion of their daily energy budget to lactation (mean 31.56%, range 20.35-46.30%) as compared to small and average females (mean 28.64%, range 18.09-43.16% and mean 28.75%, range 18.18%-43.25%, respectively). The high cost of lactation may have resulted in a higher calf-abandonment rate, thereby lowering the number of recruits produced by each large female. Although lactation costs were higher for larger females than the other size classes, it is possible that this results from the lower metabolic overhead of large females, allowing them to spend comparatively more energy on calves (Kleiber, 1975). Additionally, large females had much larger calves that required more energy from their mothers, thereby increasing the cost of lactation for large females. Although the elevated lactation cost for large females may be an artifact of the modeling assumption that large females have proportionally larger calves, this assumption is justified by findings that mammals often give birth to offspring that are proportional in size (e.g., Bekoff et al., 1981; McDonald et al., 2012). Further, we did not account for potential compensatory growth during lactation that would increase the growth rate, and therefore lactation cost, of smaller offspring (e.g., Stewart and Lavigne, 1984). Still, this assumption is justified due to the strong allometry between size at weaning and adult size (Falster et al., 2008).

The high cost of lactation for large females may have led to a higher rate of calf abandonment (Figure 2.4). Large females had more opportunities to give birth due to their shorter interbirth interval; however, the high energetic cost of lactation for large females may have limited their ability to nurse each calf to weaning. Consequently, large females that have more reproductive opportunities than their smaller counterparts may more readily abandon calves to maintain good body condition and reduce the probability of starvation-related mortality. In contrast, small females had fewer overall reproductive opportunities and thus invested heavily in young. This is supported by the increased nursing duration, concurrent with trends found in other mammals (e.g., Kovacs and Lavigne, 1986; Oftedal, 2000), and relatively high body condition of recruited calves in small females (Figure 2.5). Body condition of the recruited offspring of small females was higher than that observed for average females, which is an impressive feat for small reproductive females given their energetic limitations (Figure 2.5). However, the increased investment into offspring of small females likely had negative consequences on body condition as post-breeding survival of small females was lower than that of their larger counterparts (Figure 2.4).

For all size classes, population consequences of disturbance were mediated through impacts on starvation-related mortality and calf production. Decreased survivorship is a typical disturbance response across species that can be caused by decreased food intake or body condition (Sergio et al., 2018). To increase survival probability, breeding effort is often reduced to defray potential energetic costs of disturbance that may further reduce survivorship (Sergio et al., 2018). This can yield decreased reproductive effort and, overall, reduced population growth. Here, starvation-related mortality substantially increased for all three size classes in both the single and repeat disturbance scenarios (Figure 5; Table A2.8). As such, the drive to increase individual survival probability likely resulted in decreased reproductive output, as indicated by the significant effect of disturbance on recruitment rate observed in average and large females (Figure 2.5). Populations subjected to a repeat disturbance experienced larger changes to demographic parameters, irrespective of size class (Figure 5; Table A2.8).

Large females exhibited resilience in the face of disturbance with a largely unchanging *lambda*, indicating that large females may drive population recovery following disturbance. However, it is unclear how this will play out in real-world scenarios as disturbances seem to decrease the overall size trajectory of populations. Across marine mammals, shifts toward smaller body size in the face of anthropogenic disturbance have been more commonly documented than shifts toward larger body size likely due to the energetic challenges presented by decreased foraging opportunities and increased travel away from disturbance sources (Best and Rüther, 1992; Calkins et al., 1998; Christiansen et al., 2016; Christiansen et al., 2018; Harding et al., 2018; Stewart et al., 2021; Bierlich et al., 2023). As such, we may observe shifts to smaller body size in populations faced with disturbance, which may result in fewer large females available to support the post-disturbance recovery of populations.

Our results indicate that populations of harbor porpoises are likely near their optimal body size to maintain population growth in the North Sea. The life history characteristics of average and large females were similar, thus we did not find strong evidence for the benefits of attaining larger-than-average size for harbor porpoises. Further, our results indicated that attaining this large size was energetically expensive and required an increased energy intake of approximately 17%, concurrent with trends found in other marine mammals (Goldbogen et al., 2019). This poses a dilemma for a species thought to forage near-constantly and live at the edge of their physiologic capabilities (Wisniewska et al., 2016) and likely indicates that selective pressures will not push harbor porpoises into larger body sizes, especially given current environmental condition. Although populations of harbor porpoises that are larger in overall body size exist, this larger size is facilitated by increased prey availability. For example, California harbor porpoises are larger than European porpoises in overall size, which is thought to be a result of the productive upwelling off the coast of California (Galatius and Gol'din, 2011). However, as we see global changes to prey availability and anthropogenic disturbances decreasing the ability of animals to effectively forage, we can expect to see shifts to overall size trajectories of populations making it difficult to predict the consequences of these shifts on population demography and population success.

2.6 Conclusion

Our results support the hypothesis that due to physiological and bioenergetic constraints, harbor porpoises are at their optimal body size for a cetacean inhabiting a cold aquatic environment in the North Sea. Average or large body size confer more benefits with respect to survival and lifetime reproductive success than small body size, although smaller females were still able to succeed and exhibited a slightly increasing population growth trajectory under baseline conditions. Under a single disturbance scenario, all size classes experienced decreases in survivorship and recruitment rates, but showed evidence of population recovery. However, repeat disturbances appeared to be detrimental to small, average, and large females, but large females showed evidence of population recovery should the frequency of disturbance decrease or halt altogether. Despite the marginal benefits associated with large body size, energetic costs of attaining large body size may not be feasible given the foraging behavior of harbor porpoises and current environmental conditions. Body size trajectories and population-level effects of harbor porpoises should be further monitored and explored as they face increasing environmental and anthropogenic disturbances that alter access to prey and energy budgets.

Figures

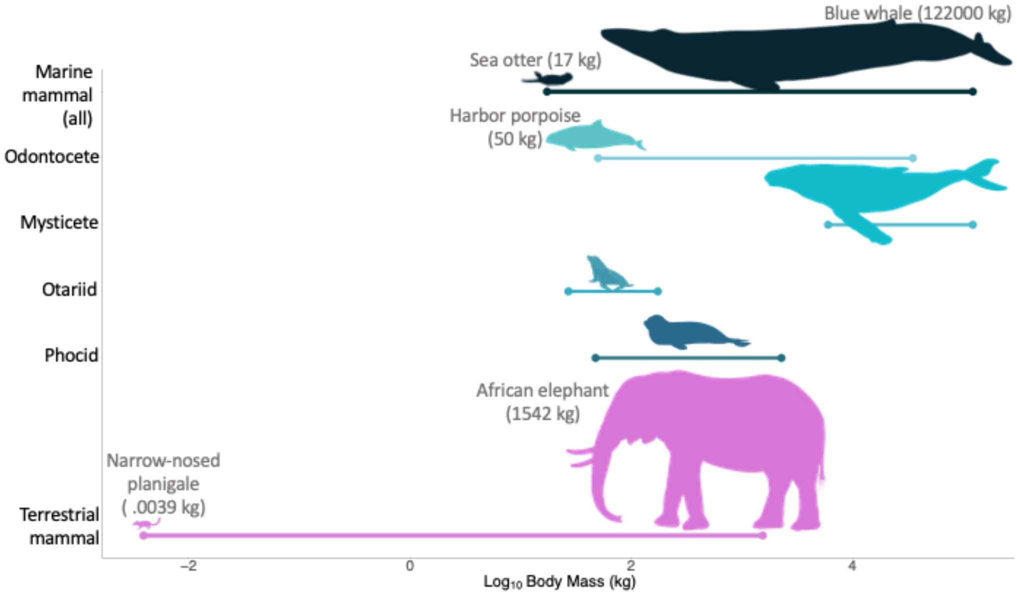


Figure 2. 1 Conceptual diagram demonstrating the range of mammalian body size (represented by mass in kg). Mass estimates derived from Herberstein et al. (2020) and images created with biorender.com.

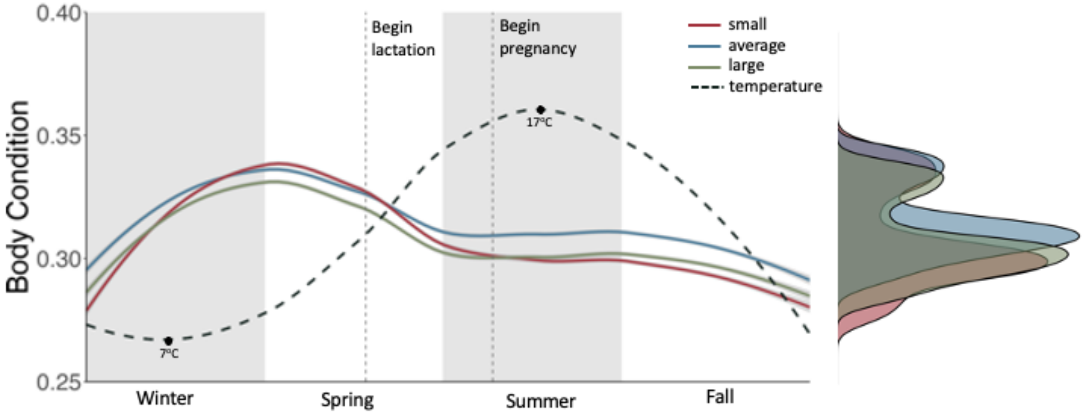
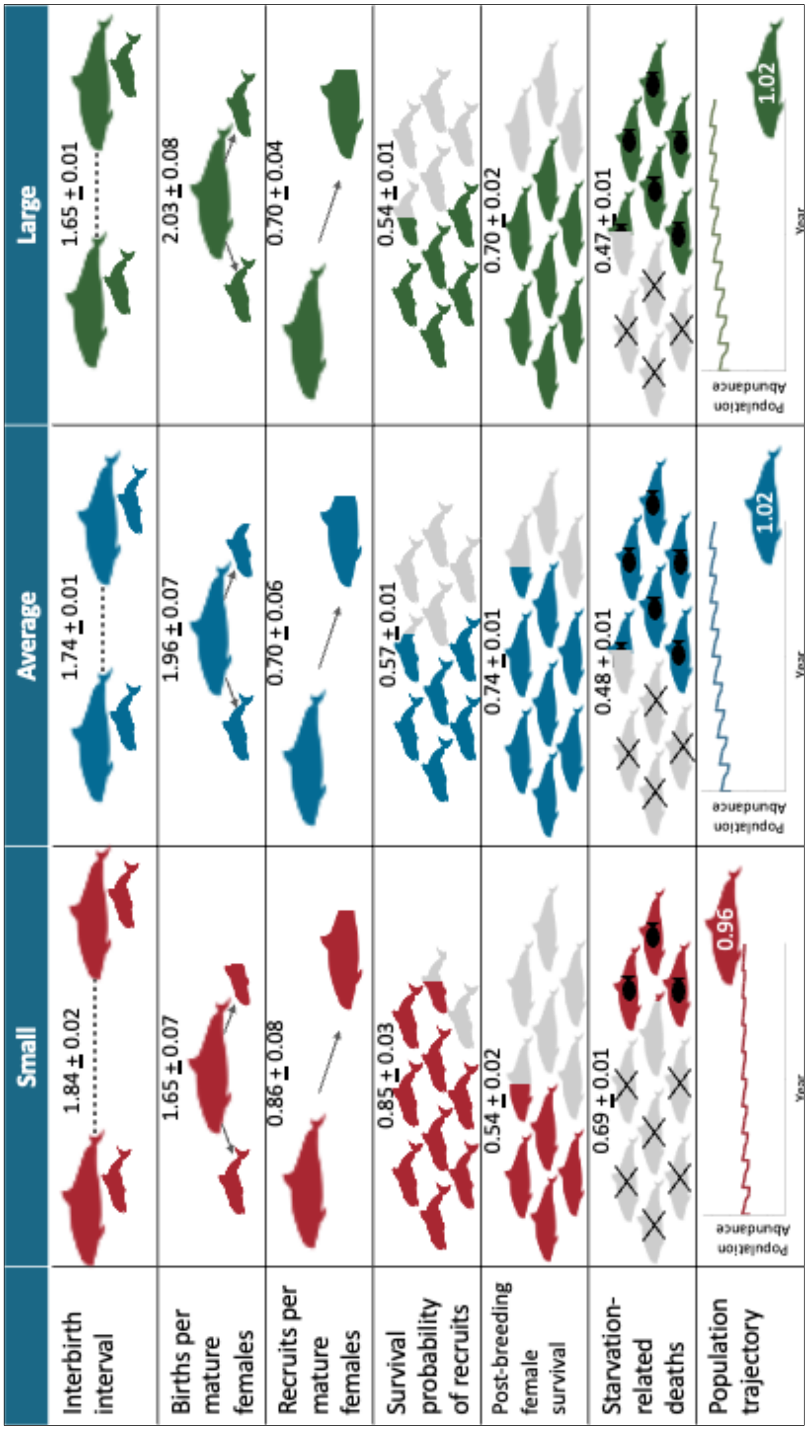


Figure 2. 2 Fluctuations in body condition in a year under baseline conditions averaged for each population (n = 100 for each size class) simulated in forward simulation model runs for small, average, and large females with model sea surface temperature and kernel density averages of body condition.



	Small	Average	Large
Interbirth interval	1.84 ± 0.02	1.74 ± 0.01	1.65 ± 0.01
Births per mature females	1.65 ± 0.07	1.96 ± 0.07	2.03 ± 0.08
Recruits per mature females	0.86 ± 0.08	0.70 ± 0.06	0.70 ± 0.04
Survival probability of recruits	0.85 ± 0.03	0.57 ± 0.01	0.54 ± 0.01
Post-breeding female survival	0.54 ± 0.02	0.74 ± 0.01	0.70 ± 0.02
Starvation-related deaths	0.69 ± 0.01	0.48 ± 0.01	0.47 ± 0.01
Population trajectory	0.96	1.02	1.02

Figure 2. 3 Life history parameters from baseline forward simulation model runs averaged across each simulated population (n = 100 for each size class) for small, average, and large female harbor porpoises.

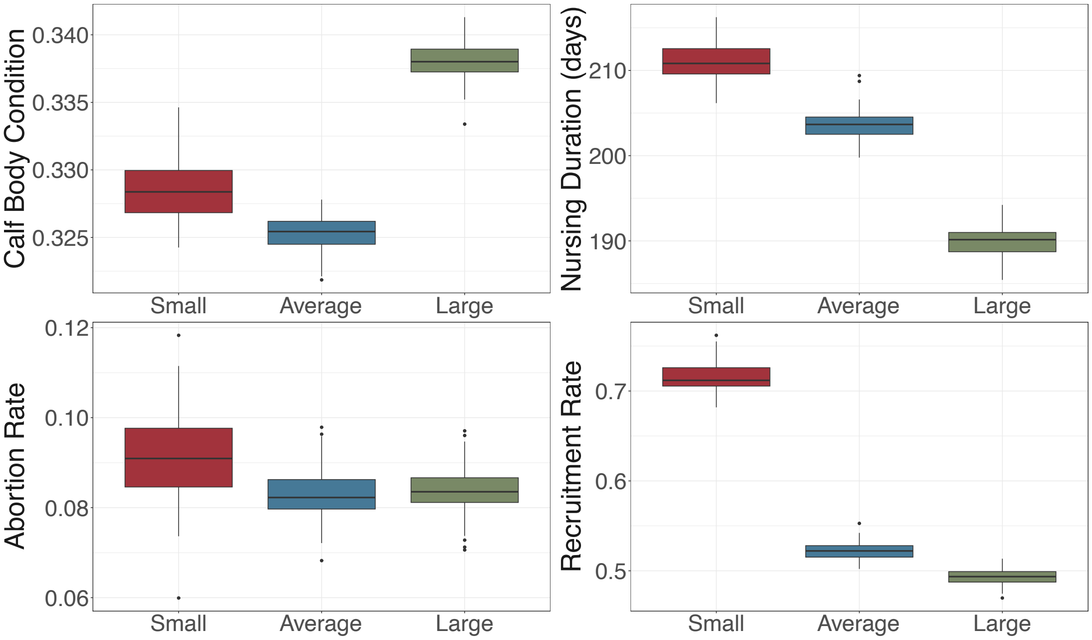


Figure 2. 4 Calf body condition of calves that recruit into the population, nursing duration (days), abortion rate, and recruitment rate for each simulated size class under baseline environmental conditions averaged over each population in forward simulation model runs (n = 100 for each size class).

References

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running. *Science*, *177*(4045), 222–228.

Kleiber, M. (1975). Metabolic turnover rate: A physiological meaning of the metabolic rate per unit body weight. *Journal of Theoretical Biology*, *53*, 199–204.

Barlow, J., & Boveng, P. (1991). Modeling age specific mortality for marine mammal populations. *Marine Mammal Science*, *7*(1), 50–65.

Bekoff, M., Diamond, J., & Mitton, J. B. (1981). Life-history patterns and sociality in Canids: Body Size, reproduction, and behavior. *Oecologia*, *50*, 386–390.

Mellish, J.-A. E., Iverson, S. J., & Bowen, W. D. (1999). Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, *72*(6), 677–690.

Rollinson, N., & Rowe, L. (2016). The positive correlation between maternal size and offspring size: fitting pieces of a life-history puzzle. *Biological Reviews*, *91*(4), 1134–1148. https://doi.org/10.1111/brv.12214

Ronget, V., Gaillard, J. M., Coulson, T., Garratt, M., Gueyffier, F., Lega, J. C., & Lemaître, J. F. (2018). Causes and consequences of variation in offspring body mass: meta-analyses in birds and mammals. *Biological Reviews*, *93*(1), 1–27. https://doi.org/10.1111/brv.12329

Gearty, W., McClain, C. R., & Payne, J. L. (2018). Energetic tradeoffs control the size distribution of aquatic mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 4194–4199. https://doi.org/10.1073/pnas.1712629115

Goldbogen, J. A. (2018). Physiological constraints on marine mammal body size. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 3995–3997. https://doi.org/10.1073/pnas.1804077115

Lindstedt, S. L. (2021). Body size, time and dimensions of oxygen diffusion. *Comparative Biochemistry and Physiology -Part A : Molecular and Integrative Physiology*, *252*. https://doi.org/10.1016/j.cbpa.2020.110847

Read, A. J. (1990). Reproductive seasonality in harbour porpoises, Phocoena phocoena, from the Bay of Fundy. *Canadian Journal of Zoology*, *68*, 284–288.

Read, A. J., & Tolley, K. A. (1997). Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Canadian Journal of Zoology*, *75*, 122–130.

McLellan, W. A., Koopman, H. N., Rommel, S. A., Read, A. J., Potter, C. W., Nicolas, J. R., Westgate, A. J., & Pabst, D. A. (2002). Ontogenetic allometry and body composition of harbour porpoises (Phocoena phocoena, L.) from the western North Atlantic. *Journal of Zoology*, *257*(4), 457–471. https://doi.org/10.1017/S0952836902001061

Lockyer, C., & Kinze, C. (2003). Status, ecology and life history of harbour porpoise (Phocoena phocoena), in Danish waters. *NAMMCO Scientific Publications*, *5*, 143–176.

Read, A. J., & Hohn, A. A. (1995). Life in the fast lane: the life history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science*, *11*(4), 423–440.

Wisniewska, D. M. M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S., Miller, L. A. A., Siebert, U., & Madsen, P. T. T. (2016). Ultra-High foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, *26*(11), 1441–1446. https://doi.org/10.1016/j.cub.2016.03.069

Rojano-Donãte, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., Højer-Kristensen, J., & Madsen, P. T. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*(23), jeb185827. https://doi.org/10.1242/jeb.185827

Wisniewska, D. M., Johnson, M., Teilmann, J., Siebert, U., Galatius, A., Dietz, R., & Madsen, P. T. (2018). High rates of vessel noise disrupt foraging in wild harbour porpoises (Phocoena phocoena). *Proceedings of the Royal Society B: Biological Sciences*, *285*(1872). https://doi.org/10.1098/rspb.2017.2314

Mangel, M. and Clark, C. W. (1988) *Dynamic Modeling in Behavioral Ecology* (Princeton University Press, Princeton, NJ).

Houston, A. I., and McNamara, J. M. (1999). *Models of Adaptive Behavior: An Approach Based on State* (Cambridge University Press, New York, NY).

Clark, C. W., and Mangel, M. (2000). *Dynamic State Variable Models in Ecology: Methods and Applications* (Oxford University Press, New York, NY).

R Core Team (2022). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available online at hrrp:www.R-project.org/.

Read, A. J., & Gaskin, D. E. (1990). Changes in growth and reprodudion of harbour porpoises, Phocoena phocoena, from the Bay of Fundy. *Canadian Journal of Aquatic Fisheries Science*, *47*, 2158–2163.

Börjesson, P., & Read, A. J. (2003). Variation in timing of conception between populations of the harbor porpoise. *Journal of Mammalogy*, *84*(3), 948–955. https://academic.oup.com/jmammal/article/84/3/948/908120

Sørensen, T. B., & Kinze, C. C. (1994). Reproduction and reproductive seasonality in danish harbour porpoises, phocoena phocoena. *Ophelia*, *39*(3), 159–176. https://doi.org/10.1080/00785326.1994.10429541

Murphy, S., Petitguyot, M. A. C., Jepson, P. D., Deaville, R., Lockyer, C., Barnett, J., Perkins, M., Penrose, R., Davison, N. J., & Minto, C. (2020). Spatio-temporal variability of harbor porpoise life history parameters in the North-East Atlantic. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.502352

Barlow, J., & Boveng, P. (1991). Modeling age specific mortality for marine mammal populations. *Marine Mammal Science*, *7*(1), 50–65.

Lockyer, C. (1995). Aspects of the morphology, body fat condition and biology of the harbour porpoise, Phocoena phocoena, in British waters. *Report for the International Whaling Commission*, *16*, 199–209.

Beltran, R. S., Testa, J. W., & Burns, J. M. (2017). An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal. *Ecological Modelling*, *351*, 36–50. https://doi.org/10.1016/j.ecolmodel.2017.02.002

Gallagher, C. A., Grimm, V., Kyhn, L. A., Kinze, C. C., & Nabe-Nielsen, J. (2021). Movement and seasonal energetics mediate vulnerability to disturbance in marine mammal populations. *The American Naturalist*, *197*, 000–000. https://doi.org/10.5061/dryad.80gb5mkpn

Andreasen, H., Ross, S. D., Siebert, U., Andersen, N. G., Ronnenberg, K., and Gilles, A. (2017). Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. . *Marine Mammal Science*, *33*(4), 1053–1079.

Booth, C. G. (2020). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, *36*(1), 195–208. https://doi.org/10.1111/mms.12632

Otani, S., Naito, Y., Kato, A., & Kawamura, A. (2001). Oxygen consumption and swim speed of the harbor porpoise Phocoena phocoena. *Fisheries Science*, *67*, 894–898.

Czapanskiy, M. F., Savoca, M. S., Gough, W. T., Segre, P. S., Wisniewska, D. M., Cade, D. E., & Goldbogen, J. A. (2021). Modelling short-term energetic costs of sonar disturbance to cetaceans using high-resolution foraging data. *Journal of Applied Ecology*, *58*(8), 1643–1657. https://doi.org/10.1111/1365-2664.13903

Kastelein, R. A., van de Voorde, S., & Jennings, N. (2018). Swimming speed of a harbor porpoise (Phocoena phocoena) during playbacks of offshore pile driving sounds. *Aquatic Mammals*, *44*(1), 92–99. https://doi.org/10.1578/AM.44.1.2018.92

Gotelli, N. J. (2001). *A Primer of Ecology, Third Edition*. (Sinauer Associates, Sutherland, MA).

Cohen, J. (1977). *Statistical power analysis for the behavioral sciences*. Academic Press, New York, NY.

Baron, J. P., le Galliard, J. F., Ferrière, R., & Tully, T. (2013). Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival. *Functional Ecology*, *27*(1), 173–183. https://doi.org/10.1111/1365-2435.12023

Shaw, A. K., & Levin, S. A. (2013). The evolution of intermittent breeding. *Journal of Mathematical Biology*, *66*(4–5), 685–703. https://doi.org/10.1007/s00285-012-0603-0

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, *125*(6), 873–878. https://about.jstor.org/terms

Millar, J. S., & Hickling, G. J. (1992). The fasting endurance hypothesis revisited. *Ecology*, *6*(4), 496–498.

Crocker, D. E., Houser, D. S., & Webb, P. M. (2012). Impact of body reserves on energy expenditure, water flux, and mating success in breeding male northern elephant seals. *Physiological and Biochemical Zoology*, *85*(1), 11–20. https://doi.org/10.1086/663634

Hatter, I. W., & Janz, D. W. (1994). Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. *Canadian Journal of Zoology*, *72*, 878–884.

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*(2), 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toïgo, C. (2000). Temporal variation in fitness component and population dynamics of large herbivores. *Annual Review of Ecology, Evolution, and Systematics*, *31*, 367–393. www.annualreviews.org

Pistorius, P. A., Bester, M. N., Lewis, M. N., Taylor, F. E., Campagna, C., & Kirkman, S. P. (2004). Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (Mirounga leonina). *Journal of Zoology*, *263*(2), 107–119. https://doi.org/10.1017/S0952836904004984

Ono, K. A., Boness, D. J., & Oftedal, O. T. (1987). The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Sociobiology*, *21*(2), 109–118. https://www.jstor.org/stable/4600064

Hamel, S., Côté, S. D., & Festa-Bianchet, M. (2011). Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal. *Oikos*, *120*(5), 690–695. https://doi.org/10.1111/j.1600-0706.2011.19382.

McMahon, C. R., Burton, H. R., & Bester, M. N. (2000). Weaning mass and the future survival of juvenile southern elephant seals, Mirounga leonina, at Macquarie Island. *Antarctic Science*, *12*(2), 149–153. https://doi.org/10.1017/s0954102000000195

Baker, J. D. (2008). Variation in the relationship between offspring size and survival provides insight into causes of mortality in Hawaiian monk seals. *Endangered Species Research*, *5*(1), 55–64. https://doi.org/10.3354/esr00122

Bowen, W. D., den Heyer, C. E., Mcmillan, J. I., & Iverson, S. J. (2015). Offspring size at weaning affects survival to recruitment and reproductive performance of primiparous gray seals. *Ecology and Evolution*, *5*(7), 1412–1424. https://doi.org/10.1002/ece3.1450

Mcmahon, C. R., New, L. F., Fairley, E. J., Hindell, M. A., & Burton, H. R. (2015). The effects of body size and climate on post-weaning survival of elephant seals at Heard Island. *Journal of Zoology*, *297*(4), 301–308. https://doi.org/10.1111/jzo.12279

Ono, K. A., Boness, D. J., & Oftedal, O. T. (1987). The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Sociobiology*, *21*(2), 109–118. https://www.jstor.org/stable/4600064

Hamel, S., Côté, S. D., & Festa-Bianchet, M. (2011). Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal. *Oikos*, *120*(5), 690–695. https://doi.org/10.1111/j.1600-0706.2011.19382.x

McMahon, C. R., Harcourt, R. G., Burton, H. R., Daniel, O., & Hindell, M. A. (2017). Seal mothers expend more on offspring under favourable conditions and less when resources are limited. *Journal of Animal Ecology*, *86*(2), 359–370. https://doi.org/10.1111/1365-2656.12611

McDonald, B. I., Goebel, M. E., Crocker, D. E., & Costa, D. P. (2012). Dynamic influence of maternal and pup traits on maternal care during lactation in an income breeder, the antarctic fur seal. *Physiological and Biochemical Zoology*, *85*(3), 243–254. https://doi.org/10.1086/665407

Falster, D. S., Moles, A. T., & Westoby, M. (2008). A general model for the scaling of offspring size and adult size. *American Naturalist*, *172*(3), 299–317. https://doi.org/10.1086/589889

Kovacs, K. M., & Lavigne, D. M. (1986). Maternal investment and neonatal growth in Phocid seals. *Journal of Animal Ecology*, *55*(3), 1035–1051.

Oftedal, O. T. (2000). Use of maternal reserves as a lactation strategy in large mammals. *Proceedings of the Nutrition Society*, *59*(1), 99–106. https://doi.org/10.1017/S0029665100000124

Sergio, F., Blas, J., & Hiraldo, F. (2018). Animal responses to natural disturbance and climate extremes: a review. In *Global and Planetary Change* (Vol. 161, pp. 28–40). Elsevier B.V. https://doi.org/10.1016/j.gloplacha.2017.10.009

Best, P. B., & Rüther, H. (1992). Aerial photogrammetry of southern right whales, Eubalaena australis. *Journal of Zoology*, *228*(4), 595–614. https://doi.org/10.1111/j.1469-7998.1992.tb04458.x

Stewart, R. E. A., & Lavigne, D. M. (1984). Energy transfer and female condition in nursing harp seals Phoca groenlandica. *Holarctic Ecology*, *7*, 182–194.

Calkins, D. G., Becker, E. F., & Pitcher, K. W. (1998). Reduced body size of female steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science*, *14*(2), 232–244. https://doi.org/10.1111/j.1748-7692.1998.tb00713.x

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*(10). https://doi.org/10.1002/ecs2.1468

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–282. https://doi.org/10.3354/meps12522

Harding, K. C., Salmon, M., Teilmann, J., Dietz, R., & Härkönen, T. (2018). Population wide decline in somatic growth in harbor seals-early signs of density dependence. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00059

Stewart, J. D., Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Casler, P. K., Ward, E. J., & Dapp, D. R. (2021). Survival of the fattest: linking body condition to prey availability and survivorship of killer whales. *Ecosphere*, *12*(8). https://doi.org/10.1002/ecs2.3660

Bierlich, K. C., Kane, A., Hildebrand, L., Bird, C. N., Fernandez Ajo, A., Stewart, J. D., Hewitt, J., Hildebrand, I., Sumich, J., & Torres, L. G. (2023). Downsized: gray whales using an alternative foraging ground have smaller morphology. *Biology Letters*, *19*(8). https://doi.org/10.1098/rsbl.2023.0043

Goldbogen, J. A., Cade, D. E., Wisniewska, D. M., Potvin, J., Segre, P. S., Savoca, M. S., Hazen, E. L., Czapanskiy, M. F., Kahane-Rapport, S. R., DeRuiter, S. L., Gero, S., Tønnesen, H., Gough, W. T., Hanson, M. B., Holt, M. M., Jensen, F. H., Simon, M., Stimpert, A. K., Arranz, P., … Pyenson, N. D. (2019). Why whales are big but not bigger: physiological drivers and ecological limits in the age of ocean giants. *Science*, *366*, 1367–1372.

Galatius, A., & Gol'din, P. E. (2011). Geographic variation of skeletal ontogeny and skull shape in the harbour porpoise (Phocoena phocoena). *Canadian Journal of Zoology*, *89*(9), 869–879. https://doi.org/10.1139/z11-059

Chapter 3

Fitness consequences of deviation from body size in a long-lived mammal

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3.1 Abstract

Life history theory predicts that there are trade-offs associated with growth investment to attain large size. Although the benefits of large body size are well documented, the costs to survival and reproductive effort are not well documented. High growth investment is thought to force reduced investment in current reproductive efforts through skipped breeding or decreased lifespan. Here we explore the trade-offs between growth investment, as measured by deviation from expected body size, reproduction, and survival in a long-lived, iteroparous marine mammal, the northern elephant seal (*Mirounga angustirostris*). We used 19 years of morphometric and life history data for individually marked females. We found that increasing length by 5 cm resulted in a 2-3% increase in survival, and the probability of survival for the same increase in length increased with age. Additionally, we found that increasing mass by 50 kg increased the probability of pupping success by 34-36% depending on age. Contrary to the expectation that there may be a fitness cost to growth, we discovered that larger animals had a lower incidence of skipped breeding events. Interestingly, we found that growth investment primarily occurred before primiparity (prior to age 4), and that individuals with higher growth rates between weaning and primiparity became larger-than-average adults. However, rapid growth resulted in

decreased longevity, indicating a trade-off between growth and long-term survival. Our results indicate that the optimal balance between growth and longevity occurs for average females who have maximized annual survival and reproductive success while minimizing the impacts of rapid early growth and longevity.

3.2 Introduction

Life history theory predicts a trade-off between energy allocation to growth to attain large body size and fitness mediated through reproduction and survival (Charnov, 2004; Bartke et al., 2013; Morano et al., 2013; Sibly and Brown, 2007). Early investment in growth to attain large body size may result in a decrease in reproductive events or delay in age at primiparity, but an increase in future reproductive opportunities through increased offspring recruitment rates and individual survival (Laws, 1956; Wootton, 1987; Kozłowski, 1992; Fokidis et al., 2007; Baron et al., 2013; Rollinson and Rowe, 2016; le Boeuf et al., 2019). However, selection does not always favor large body size as there are often energetic and physiological constraints associated with being large, resulting in a continuum of sizes within a population or species (Pauly, 1991; Clauss et al., 2003; Goldbogen, 2018; Costa and Favilla, 2023). Due to the difficulty of longitudinally measuring body size in individually identifiable wild animals, it is currently unclear how individuals prioritize growth and fitness to optimize lifetime reproductive success (LRS). To better understand trade-offs between growth, reproduction, and survival we assessed the fitness consequences of deviating from expected body size in a long-lived, iteroparous capital breeder.

Iteroparous species tend to trade immediate fitness benefits for a higher probability of survival and longevity (Warner, 1998; Hamel et al., 2011; Shaw and Levin, 2013). In other words, species that have many reproductive opportunities in a lifetime invest more in strategies that increase their lifespan as the benefits of current reproduction only marginally increase LRS (Warner, 1998). This is demonstrated by the intermittent breeding strategy that often coincides with iteroparity (Bull and Shine, 1979; Therrien et al, 2007; Hamel et al., 2011; Griffen, 2018; Monteith et al., 2013). Skipping a reproductive event is thought to increase survival the following year or increase the probability of reproductive success in the future when the female is in poor condition (Therrien et al., 2007; Desprez et al., 2018; Griffen, 2018). However, intermittent breeding prior to reaching physical maturity may alternatively facilitate somatic growth (e.g., Baron et al., 2013).

Elephant seals (*Mirounga* spp.) provide a unique model system to explore the trade-offs between growth and fitness. They are long-lived, iteroparous marine mammals with an extreme capital breeding strategy, highlighting the importance of body size on reproductive success and survival, and they are the largest phocid species, indicating a large investment in growth (Haley et al., 1994; Crocker et al., 2012). Older females typically produce larger, healthier pups (Crocker et al., 2001; le Boeuf et al., 2019; Holser et al., 2021) and most females reproduce every year, although skipped breeding has been observed or modeled in both northern (*M. angustirostris*) and southern elephant seals (*M. leonina*; Reiter and le Boeuf, 1991; Desprez et al., 2018; Griffen, 2018). While age seems to positively impact reproduction and survival, it is unclear whether this is a benefit of body size or experience, particularly because elephant seals have a high degree of variability in body size relative to length and mass (Figure 3.1). Additionally, elephant seal females reach sexual maturity (between ages 2 and 6) much earlier than physical maturity (between ages 7 and 9), requiring simultaneous allocation of resources to growth and reproduction (Deutsch et al., 1994). Due to a long-term mark-recapture program on individual seals that quantified annual reproductive success and survival for known-age seals (Beltran et al., 2023), coupled with a long-term handling program in which animals are sedated and measured (Robinson et al., 2012), we are able to finally combine these two data streams and ask how elephant seals prioritize growth reproduction, and survival, and how deviations from expected body size impact fitness.

We explored how elephant seals prioritize growth, reproduction, and survival and how deviations from expected body size impact fitness using data from a long-term research program (Beltran et al., 2023, Robinson et al., 2012). We evaluated the influence of body size, with somatic growth represented by length and growth of energy reserves represented by mass, on annual pupping success and survival. Additionally, we explored the trade-offs between somatic growth and reproduction by examining how these metrics influenced intermittent breeding and age at primiparity. Lastly, we assessed potential mechanisms through which individuals attained large body size. We hypothesized that above-average body size would increase annual pupping success and survival, but that increased investment in somatic growth would delay or hinder reproduction for young females. We did not make a priori predictions regarding the mechanisms through which females attained large body size.

3.3 Methods

3.3.1 Data collection

We used data from weanling, juvenile, and adult female elephant seals included in the long-term research program at Año Nuevo Reserve (Robinson et al., 2012; le Boeuf et al., 2019). Elephant seals at this colony are tagged with unique alpha-numeric codes that allow individuals to be resighted and handled throughout their lifetime. Resights are conducted between October and June, with increasing frequency throughout the research season. During the breeding season (between December and March), the presence or absence of a pup is recorded for all adult females. Select females were chosen for instrumentation prior to the post-breeding (PB) and post-molt (PM) foraging trips each year from 2004-2023. When instrumented females depart on their foraging trip and arrive back to the beach we measured standard length measurements to the nearest cm from the tip of the nose to the end of the tail using a flexible measuring tape and measured mass to the nearest kg using a Dynalink digital scale. We used the same morphometric measurement techniques on recently weaned individuals, identified as young individuals that remain on the beach in the absence of a mother or other adult. A detailed account of the animal handling process can be found in Robinson et al. (2012). Females are typically measured approximately five days after arriving to the beach, because females arrive typically 5.5 days prior to birth (range 1-11; Condit et al., 2022). To correct for the mass lost while fasting on the beach for approximately five days, as well as further mass lost before departure from the beach, we used a correction to estimate mass at departure and arrival based on equations derived from previous analyses (mass change (kg d^{-1}) = 0.51 x 7.6 x 10^{-3} x mass; n = 27, $r^2 = 0.79$, $p < 0.01$; D. Crocker and D. Costa unpublished data; Simmons et al., 2010). For lactating females, the correction is slightly different to account for increased mass loss during lactation (Deutsch et al., 1994).

From the resight history, we defined annual pupping success for all females in all observation years as the presence on the breeding colony with a minimum of one confirmed pup sighting. This assumption is supported by the high pregnancy rate of females and follows the definition from previous papers (e.g., Reiter and Le Boeuf 1991; Beltran et al., 2023). LRS was defined as the total number of successful pupping events (using the above condition) in a female's lifetime. A female's lifespan was determined as the difference between the final year of observation and birth year; however, we excluded females that were both younger than 15 years old and observed within the last five years (since 2018) as such females may be still alive. All following statistical analyses were conducted in R v. 4.2.2 (R Core Team, 2022).

3.3.2 Growth models

We fit Gompertz growth models for length-at-age for all females (n = 507) and weight-at-age curves for PM arrival (n = 456), PB departure (n = 471), PB arrival (n = 469), and PM departure females (n = 461) using a non-linear least squares regression (NLS; Tjørve and Tjørve, 2017; Figure 3.2B). For the length-at-age curve we averaged the departure and arrival standard length measurements for each foraging trip to minimize potential measurement error (i.e., the PM arrival standard length for a female was calculated as the average of the PM departure and PM arrival measurement). To account for individuals that had an arrival length without a departure length (n = 1) or a departure length without an arrival length (n = 93) we compared the growth models with and without these individuals and found no statistically significant difference in model parameters (F(420, 341) = 0.89, p = 0.73). Therefore, we included all females in the length-at-age growth curve. When constructing both length and mass growth curves, when an individual had repeat morphometric measurements at the same time (i.e., two PM arrival mass measurements from different years) we randomly selected a single measurement point to reduce the impact of individuals with multiple measurements on the growth model. For PM arrival females we assigned whole ages and for PB arrival female we assigned half ages (i.e., a seven-year-old female would be assigned an age of seven if morphometric measurements were collected for the PM foraging trip, and 7.5 if morphometric measurements were collected for the PB foraging trip). We constructed individual mass-at-age curves for each of the four measurement points (Figure 3.3B) to account for the large seasonal fluctuations in mass that result from the fasting strategy of elephant seals. We recognize that the majority of females included in our PM arrival mass-at-age growth curve were females that produced a pup due to the high pregnancy rate of elephant seal females (Le Boeuf et al., 2019), producing a potential bias. However, the use of age-based deviation in size allows us to account for the range of possible female masses in relation to females that pupped. To calculate age-based deviation from expected length and mass for a given age we used the residual between the measured morphometric value and the predicted morphometric value for that age (Figure 3.2C).

3.3.3 Analysis of annual fitness metrics

To determine the influence of deviation in length (n = 270) and mass (n = 211) on annual pupping success of PM arrival females we fit a generalized linear mixed effect model (GLMM) using the lme4 package with a binomial distribution where pupping success was the response variable and length and mass, were the predictor variables in each respective model (Bates et al., 2014). We included age as a fixed effect and individual seal as a random effect to account for repeat measures; however, this resulted in a singular fit when testing the impact of deviation in mass on pupping success, indicating that the model was overfit and. Thus, we ran a generalized linear model testing the impact of deviation in mass on pupping success with a fixed effect of age and removed the random effect of individual. Then, we ran a GLMM with a binomial distribution testing if deviation in PM departure mass influenced pupping success (n = 269) to determine if pupping success could be predicted from body size prior to the PM foraging trip.

Additionally, we examined the effect of deviation in length (n = 455) and mass (n = 875) on annual survival with a GLMM with a binomial distribution including age as a fixed effect and individual seal as a random effect for all females for which morphometric measurements were available. Survival was defined as a confirmed sighting of the female at least one year or more following the time of measurement (Figure 3.2B). For example, if a female was measured during the breeding season in 2012 and was observed in the breeding season of 2013 or later, she survived. However, if she was only seen again during the 2012 molt, she was considered dead. Females that were observed beyond 2018 and were younger than 15 years old, they were considered to be alive and were excluded from these analyses.

3.3.4 Analysis of lifetime fitness metrics

To link our point estimates of deviation in body size to lifetime fitness metrics, we first tested the repeatability of deviation in length, deviation in arrival mass, and deviation in departure mass irrespective of season using the intra-class correlation coefficient in the R package 'ICC' (Wolak et al., 2012). We found that deviation in length and deviation in departure mass had moderate repeatability (see Results) and thus used these metrics for our lifetime fitness analyses. We averaged the deviation in length and deviation in departure mass metrics for individuals with multiple measurements so each individual had only one point metric for deviation in body size for the lifetime analyses.

To examine if large body size conferred lifetime fitness benefits we fit linear regression exploring the relationship between the deviation in both length (n = 201) and departure mass (n = 201) and the proportion of missed reproductive events during a lifetime for all females with available morphometric measurements. The proportion of missed reproductive events was calculated as one minus the total number of successful reproductive events divided by the reproductive lifespan, calculated as lifespan minus two to account for the time to reach sexual maturity (Reiter and le Boeuf, 1991). Additionally, we fit linear regressions exploring the effect of deviation in length and departure mass on LRS and lifespan. For all analyses of skipped reproductive events, LRS, and lifespan, we excluded females that may still be alive according to the above conditions.

3.3.5 Analysis of trade-offs between growth, reproduction, and survival

We sought to assess if the timing of somatic growth investment influenced reproduction. To accomplish this we first fit a linear regression of deviation in length by age at primiparity. Then, we visually assessed the proportion of individuals of a given age class that skipped a reproductive event separated by size class. Size classes included "small" females that had a negative deviation in length and "large" females had a positive deviation in length.

Finally, we fit linear regressions to adult deviation in length by weanling length (n = 138) and mass (n = 143) to determine if larger weanlings become larger females and to assess to role of maternal investment in deviations from body size (Holser et al., 2021). We compared growth trajectories from weaning to age at primiparity (estimated to be age 4 based on our analyses, see Results below) by performing a Wilcoxon signed rank test on growth rate estimates (calculated as centimeters gained between weaning and age 4 divided by the number of days) between females classified as small (n = 87) or large (n = 82) as adults (Woolson, 2007). To assess fitness consequences of growth trajectories we fit a generalized linear model with a lognormal distribution to the relationship between lifespan and growth rate for females that had a length measurement at weaning and again at four years of age.

3.4 Results

3.4.1 Deviation in body size

We observed a high degree of variability in female elephant seal body size for a given age both in terms of length (minimum = -22.1 cm, maximum = 35.5 cm, mean = 1.5 ± 9.4 cm) and mass (minimum = -247.3 kg, maximum = 272.4 kg, mean = -12.62 ± 65.20 kg), even when accounting for seasonal differences in mass (Figure A3.1). The highest variability in mass occurred in PM arrival females, following their long foraging trip. Deviation in length and deviation in mass scaled linearly (Figure A3.2).

3.4.2 Annual fitness metrics

There was a significant relationship between deviation in mass for PM arrival females and the probability of pupping ($p = 2.47 \times 10^{-8}$; Figure 3.3) with no significant effect of age ($p = 0.34$). Our model predicted that females of average size (deviation in mass = 0 kg) had 54.7% and 89.4% (for a 17-year-old and four-year-old, respectively) probability of pupping success depending on their age. Increasing body mass from 50 kg underweight to the expected mass for a four-year-old increased the probability of pupping success by 34%, and this same change for a 17-year-old increased the probability of pupping success by 36%. We found no significant relationship between deviation in mass and annual pupping success for PM departure females ($p = 0.18$) or between deviation in mass and annual pupping success for PM females ($p = 0.51$).

When exploring the effect of deviation from expected body size on annual survival we found no significant impact of deviation in mass ($p = 0.50$), but a borderline significant impact of deviation in length ($p = 0.06$) with a significant additive effect of age ($p = 0.03$; Figure 3.3) where larger size and younger age yielded higher survival probability. A female of average body size (deviation in length = 0 cm) had a 57.2% to 84.0% (for a four-year-old and 17-year-old, respectively) survival probability depending on age, with older females having a lower survival probability per the same deviation in length (Figure 3.3). Increasing length by 5 cm resulted in a 2-3% increase in survival and the survival benefits increased with age. The relationship between deviation in length and survival appeared to asymptote for more positive deviations in mass, indicating that being smaller than expected resulted in a greater detriment to annual survival probability than the benefit accrued from being larger than expected (Figure 3.3).

3.4.3 Lifetime fitness metrics

We found moderate repeatability in deviation in length measurements (ICC value = 0.66) and deviation in mass at departure measurements (ICC value = 0.60). Deviation in mass at arrival had poor repeatability, likely because these measurements were an indicator of how successful a foraging trip was, rather than actual body size. As such, the following analyses use average deviation in length and deviation in departure mass for each individual.

Being larger than expected in length significantly decreased the proportion of skipped reproductive events that occurred over a lifetime ($p = 0.03$), whereas being heavier than expected yielded no significant results ($p = 0.54$; Figure 3.4). Based on these analyses, a 10-year-old female that is of average size for her age will have had approximately 5 successful reproductive events, whereas a female of the same age that is larger in expected size by 10 cm will have only had approximately 3 successful events (Figure 3.4). However, the explanatory power of both relationships was low ($R^2 = 0.02$ and $R^2 = 1.84 \times 10^{-3}$, respectively). We did not find significant results between deviation in body size and LRS or lifespan (Table A3.1).

Concerning trade-offs between growth and reproduction, we did not find a significant relationship between deviation in length and age at primiparity ($p = 0.74$; $R^2 = -2.93 \times 10^{-3}$; Figure A3.3). Age at primiparity began at three years old, but most females reached primiparity at age 4 irrespective of deviation in body size (Figure A3.3). Both small and large females (as determined by adult deviation in length) had a similarly low incidence of skipped breeding events before physical maturity, although young females that became large adults had a slightly higher proportion of skipped breeding events than young females that became small adults (Figure 3.5). However, at age 11 this relationship reversed and small females experienced an increase in the incidence of skipped breeding events (Figure 3.5).

Length and mass at weaning were significant predictors of adult deviation in length ($p = 0.01$ and $p = 2.57 \times 10^{-3}$, respectively; Figure 3.6). Interestingly, we found that weanlings that grow to larger than average adult sizes had a significantly higher growth rate prior to sexual maturity than smaller conspecifics that was independent of length at weaning (W = 23.50 df = 23, p = 0.01; Figure 3.7). However, more rapid growth early in life had fitness consequences mediated through reduced lifespan ($p = 1.27 \times 10^{-8}$; $R^2 = 0.22$; Figure 3.8).

3.5 Discussion

Here, we demonstrate that increased investment in growth, as indicated by larger-than-average body size, confers annual fitness benefits in a long-lived, iteroparous capital breeder. Previous literature exploring the physiological and fitness benefits of body size have focused primarily on mass; however, our research highlights the importance of length when assessing trade-offs between growth and fitness. Although obtaining accurate standard length measurements may prove difficult in field settings (Committee on Marine Mammals, 1967; Waite and Mellish, 2009), it is an important metric to consider as mass may not provide the most accurate proxy for growth or body size. Mass can show strong fluctuations that are influenced by environmental conditions, season, or reproductive status, particularly for capital breeders (e.g., Costa et al., 1986; Adamczak et al., 2023 Gunnlaugsson et al., 2020). The poor repeatability in deviation in mass measurements for elephant seal females arriving from their foraging trip demonstrates that seasonal fluctuations in mass may reduce our ability to make inferences about body size depending on when mass was measured. However, there is often a relationship between body mass and body length such that larger individuals in length are also larger in mass (e.g., Figure 3.3.1). As such, due to the paucity of data detailing the physiological and fitness impacts of body size mediated through length measurements, we include literature that uses mass as a metric of body size in the following discussion but urge researchers to consider length in analyses of body size.

Intermittent breeding was not frequently documented in physically immature females; however, young females that attained large adult body size had a slightly higher incidence of skipped breeding when compared to smaller conspecifics until approximately 11 years old, when skipped breeding greatly increased for mature females with small adult body size (Figure 3.5). This translated to a lower proportion of skipped breeding events throughout the lifetime of larger-than-average females. Thus, we did not document a direct trade-off between growth and reproduction because intermittent breeding in younger animals did not facilitate increased somatic growth. However, we found that rapid growth following weaning facilitated larger adult body size, but decreased longevity, indicating a trade-off between faster early growth and long-term survival.

Being larger than average yielded clear annual fitness benefits for female elephant seals, irrespective of age (Figure 3.3). Females that were heavier than average when they arrived at the beach before giving birth had the highest probability of successful pupping; however, being heavier during other times of year had no impact on the probability of pupping success. After females arrive on the beach, they fast while they give birth to a pup and nurse for approximately 26 days (Costa et al., 1986). This fasting lactation period is energetically expensive and results in decreases in both lipid and protein stores (Crocker et al., 1998; Crocker et al., 2001). As such, arriving on the beach with large energy reserves accrued during the foraging trip can provide a buffer against the energy demands of lactation and potentially allow mothers to provide more resources to her offspring (Crocker et al., 2001; McDonald and Crocker, 2006). These results confirmed that a key component of the life history of a capital breeder includes increasing mass prior to parturition (Costa and Maresh, 2022; Beltran et al., 2023); however, what is more notable is the deviation in mass threshold observed whereby females more than 90 kg underweight never pupped, regardless of age. Although it is unclear if being underweight precludes these individuals from mating, or from successfully carrying the pregnancy to parturition, females that do not increase their mass during the PM foraging trip will likely not produce a pup upon returning to the beach. This highlights the importance of the PM foraging trip on supporting pregnancy and potentially predicting pupping probability upon returning, which has been observed previously in elephant seals and in Weddell seals (Salas et al., 2017; Beltran et al., 2023).

Females that were larger than average relative to their length had an increased annual survival probability. Thus, large body size may confer benefits related to foraging success and fasting endurance, driven by the relationship between large body size and the ability to store more energy reserves, which yields increased survival probability (Millar and Hickling, 1990). For diving marine mammals, larger individuals have a higher aerobic dive limit allowing them to dive deeper and longer (Irvine et al., 2000; Costa et al., 2001; Hassrick et al., 2010; Hassrick et al., 2013). Improved diving capability allows larger animals to exploit dense prey patches for a longer period of time, which is critical in the marine environment where prey are ephemeral and patchily distributed (Adachi et al., 2021; Costa and Valenzuela-Toro, 2021). Further, increasing body size, measured via body mass, is correlated with improved fasting endurance, which allows individuals to survive long periods without food (Lindstedt and Boyce, 1985; Millar and Hickling, 1990; Costa and Maresh, 2021). This reduces starvation risk in the marine environment while animals search for prey patches. Although the bulk of this literature has focused on mass and not length, we surmise that these benefits are a result of the overall size of an individual (which is dependent on length) rather than fluctuations in reserves. For example, aerobic dive limit is a determined by available oxygen stores and metabolic rate, which are functions of the absolute size of an animal rather than changes in mass that can be altered by increased energy reserves (Kooyman et al., 1983). Further, large overall body size, potentially facilitated by larger length, permits the accrual of excess energy reserves, thereby facilitating improved fasting endurance (Millar and Hickling, 1990).

Overall, our results indicated that being smaller than expected with respect to length was much more detrimental to annual survival than it was beneficial to be large. This is likely because all females are subject to stochastically-driven mortality, such as predation and disease, that is independent of body size (Henderson et al., 2020). Further, potential drawbacks of large body size may decrease survival probability for exceptionally large females. For example, large individuals require more absolute energy when compared to small conspecifics. Although they are efficient foragers, have lower metabolic rates, and can withstand long periods without food, large females still must acquire more food to maintain good body condition (Costa and Favilla, 2023).

Additionally, body size and body condition can impact risk tolerance while foraging, which may impact survivorship. For example, large females may have more risk-averse foraging strategies due to their high foraging success rate as the fitness losses of death outweigh the potential fitness benefit of attaining additional food (Real and Caraeo, 1986; Lima and Dill, 1990; Houston et al., 1993). As such, smaller females who are at higher risk of starvation may accept more risk when foraging, thereby increasing mortality through predation. However, elephant seal foraging strategies are highly dependent on individuals, and inter-sex analyses of this highly sexually dimorphic species reveal that large males typically employ a high-risk high-reward foraging strategy when compared to females that are smaller in size (Kienle et al., 2022), warranting further analysis on foraging success and risk acceptance in female elephant seals of diverging sizes. Additionally, much of this work has focused primarily on body mass as the metric of size, which accounts for an individual's available energy stores and overall health. As such, further exploration into how length influences risk in behavioral strategies is recommended.

Overall, our results indicate that large individuals, with respect to length and mass, have a physiological advantage when compared to small individuals which may contribute to the fitness benefits that we observed in this study. Large individuals have lower mass-specific metabolic rates, increased fasting endurance, and larger oxygen stores (Kleiber, 1975; Lindstedt and Boyce, 1985; Millar and Hickling, 1990; Hassrick et al., 2010). These benefits provide a link to both starvation avoidance and predator avoidance mediated through foraging strategy and diving physiology (Beltran et al., 2021). Large females can travel further distances to exploit more lucrative foraging grounds, thereby increasing the probability of pupping success due to the link between heavier body size and pupping success found here and the previously documented link between mass gain and pupping success (Beltran et al., 2023). Additionally, large females have a greater capacity to dive longer and deeper than smaller conspecifics, allowing them to avoid predation more effectively in a three-dimensional environment (Beltran et al., 2021).

Contrary to our initial hypothesis, large body size as indicated by larger than expected length reduced the incidence of intermittent breeding in mature females when compared to small conspecifics (Figure 3.5). Intermittent breeding optimizes lifetime reproductive output while minimizing survival costs of the current reproductive effort when the female is in poorer condition (Baron et al., 2013; Griffen, 2018; Desprez et al., 2018). For capital breeders, investment in somatic growth often relates to increased LRS, whereas investment in body reserves relates to increased success for the current reproductive effort (Bonnet et al., 2002; Stephens et al., 2009; Ejsmond et al., 2015). Our results indicated that small, young female elephant seals prioritize current reproductive efforts over somatic growth, thereby reducing investment in somatic growth and future LRS. In contrast, large, young elephant seals may have enough body reserves to allocate resources to reproduction and somatic growth simultaneously.

To attain large size in adulthood, represented by length, weaned elephant seals benefitted from large size at weaning (Figure 3.6; Figure 3.7), indicating that maternal investment is likely a key determinant of adult body size of their offspring. Elephant seal mothers invest heavily in offspring, losing nearly 50% of their total body mass, including a combination of both lipid and protein stores, during lactation (Costa et al., 1986; Crocker et al., 1998). This high maternal cost appears to have long-lasting fitness impacts as larger weanlings, measured through body mass, have a higher probability of survival and are better equipped to survive their post-weaning fast (Noren et al., 2003; McMahon et al., 2015; Oosthuizen et al., 2018).

Although large weanlings had a higher probability of becoming large adults, rapid growth before primiparity, independent of weanling body size, was a strong predictor of large adult body size. Rapid growth was seen in the majority of females that attained large body size, and we found evidence of compensatory growth in females that were weaned at smaller body size but still attained larger-than-average adult body size (Figure 3.7). However, higher growth rates in young elephant seals were associated with a decrease in overall lifespan, signaling a trade-off between growth and longevity (Figure 3.8). This phenomenon has been documented across taxa but the mechanisms for fitness consequences of accelerated growth are not well understood (MetCalfe and Monaghan, 2001; Metcalfe and Monaghan, 2003; Charnov, 2004; Lee et al., 2013). Fitness consequences of rapid growth may occur on a physiological level, facilitated by increased oxidative stress causing cellular damage (Merry, 1995; Rollo, 2002) and a reduction in cellular repair (Cichoń, 1997). Ultimately, the accumulation of cellular damage can increase the probability of senescence and reduce longevity. However, more research is necessary to better understand the mechanism through which rapid growth reduces lifespan.

Interestingly, the females in our study that reached more mature ages trended towards average expected body size with minimal deviation in length (close to 0; Figure A3.3). These surviving females may represent the optimal prioritization of growth, reproduction, and survival, where annual size benefits and longevity are balanced to maximize LRS. Elephant seal females that survive to old age are typically classified as "super moms" that recruit heavily into the population (le Boeuf et al., 2019). Our results indicate that this "super mom" status may represent the ideal growth trajectory that increases annual reproductive success and survival, while minimizing negative impacts on lifespan from rapid early growth. However, it is unclear if the physiology and growth dynamics of these females are predetermined by genetics, state-dependent decision-making, silver spoon effects, or random chance (e.g., Beckerman et al., 2002; Solberg et al., 2007; Steiger, 2013; Snyder and Ellner, 2018). As such, further investigation into the conditions that create these large, successful females is warranted.

Although we did not find strong evidence for trade-offs between somatic growth and reproduction, the growth and reproduction strategies observed here may be the result of specific selective pressures influenced by trends in population demography. For example, the documented age at primiparity in our study was delayed compared to studies completed 25 or more years ago, where the age at primiparity was typically around 2-5 years old for northern elephant seals (le Boeuf et al., 1989). Here, we found that females became sexually mature from 3 to 6 years old, with most females maturing at 4 years old (Figure A3.3). The shift in age of primiparity can be indicative of density-dependence as the population was experiencing rapid expansion when earlier sexual maturity was documented (Stopher et al., 2008; Lowry et al., 2014). As the population continues to increase, selective pressures on early reproduction and high LRS may be de-prioritized, shifting the need for trade-offs between somatic growth and reproduction (Cole, 1954). As such, life history trade-offs should continue to be examined under shifting selection pressures to better understand how individuals respond and predict the optimal life history strategy.

It is also possible that there was limited evidence of trade-offs between somatic growth and reproduction due to individual quality of females driven by genetics or other mechanisms not tested in this study. Some females may have a predisposition for more efficient foraging with higher resource attainment, allowing them to expend energy on both reproduction and survival without sacrificing somatic growth. In elephant seals, large individuals are more efficient foragers and gain more energy while foraging and individual differences in maternal foraging strategy has been linked to differences in pup mass, indicating individual differences in reproductive success based on foraging strategy (Authier et al., 2012; Hassrick et al., 2013), potentially allowing these already large individuals to attain more resources while at sea, thereby limiting the need for a trade-off between growth and reproduction. Further, in southern elephant seals there is evidence of mother-daughter similarities in reproductive phenology, which may influence individual differences in reproductive success (Oosthuizen et al., 2023). As such, it is possible that some females are genetically predisposed to higher reproductive success, reducing the utility of trade-offs between growth and reproduction.

Here, we assumed that annual metrics of body size (i.e., length and departure mass) could be representative of lifetime trends in body size, and related this to lifetime fitness metrics. Although we acknowledge the mismatch in timing between annual and lifetime measurements, elephant seals demonstrate high repeatability in behavior and individual life history (Abrahms et al., 2018; Beltran et al., 2023). Our data suggest some consistency in these annual body size metrics with an emphasis on the repeatability of length (Figure A3.4). However, we acknowledge the limitations of length measurements as there is some evidence to suggest that length undergoes some seasonal fluctuations (e.g., Trites and Bigg, 1996) although the drivers of these fluctuations are not well documented. Thus, we recommend a more in-depth analysis of length as a function of age and season. Animals in human care provide an ideal opportunity to examine growth trajectories on finer scale and assess the repeatability of deviation in body size for future studies.

Understanding the trade-offs between growth, reproduction, and survival plays a critical role in determining the individual fitness consequences of different prioritization strategies, and the population consequences of large-scale adoption of specific strategies. We have shown that under current demographic conditions, female elephant seals accrue annual benefits from increased growth investment but experience decreased overall longevity from this investment. These results point to an optimal average body size that maximizes annual benefits while minimizing impacts on longevity. However, the current optimum may change as population trends or increasing climatic and anthropogenic stressors alter selective pressures faced by this population (Baron et al., 2013; Oosthuizen et al., 2019; Holser et al., 2021). There is evidence of shifting body size trajectories due to increasing incidence of human-induced stressors (e.g., Best and Rüther, 1992; Harding et al., 2018; Christiansen et al., 2020; Stewart et al., 2021; Bierlich et al., 2023; Geeson et al., 2023), which may decrease survival and reproductive success, or create a new prioritization hierarchy to account for changes in body size and concurrent changes to lifetime reproductive success and longevity. Thus, further documentation of the optimal prioritization of growth, reproduction, and survival, and the fitness consequences of deviating from this ideal scenario, can improve management and conservation of wildlife populations in a world with ever-changing stressors and environmental conditions.

Figures

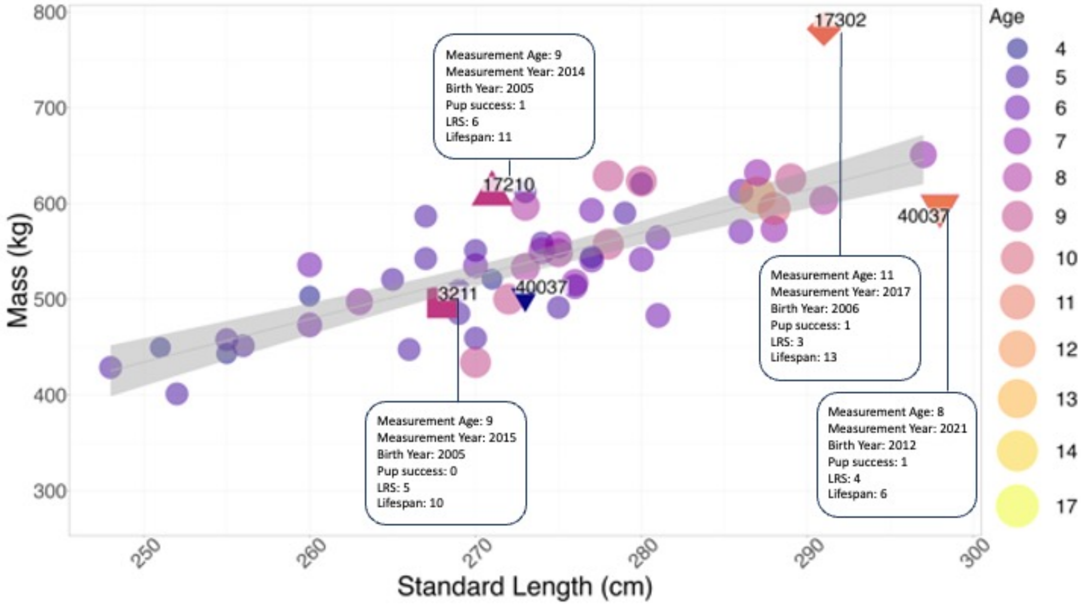

Figure 3. 1 The relationship between standard length (cm) and mass (kg) fit with linear regression for post-molt arrival females, only (Intercept = -637.81 + 77.19, t = -8.26, p = 7.20 x 10^-5; standard length = 4.39 + 0.29, t = 15.20, p = 2.2 x 10^-16). Individual seals are highlighted to represent how body size varies across ages and differences in pupping success at the time of measurement, lifetime reproductive success (LRS), and lifespan.

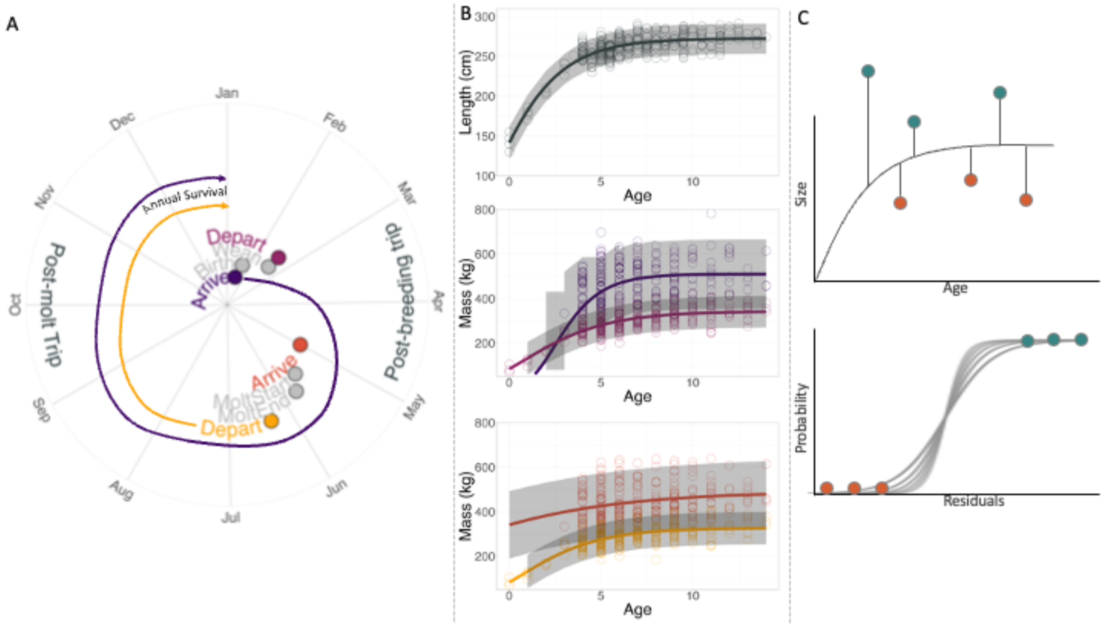

Figure 3. 2. Annual cycle of elephant seals starting January with post-molt arrival females (A), including when our measurements of pupping success (indicated by the birth data point) and annual survival occurred based on time of morphometric measurement, length-at-age for all females and weight-at-age curves for females before and after breeding and before and after molting (B), and a conceptual diagram of how deviation from expected size was calculated (C). The line in the size-at-age curve is the expected body size based on the constructed Gompertz growth model and the dots are the raw data points. Individuals that are larger than expected fall on the right side of the residuals plot and individuals that are smaller than expected fall on the left side of the residuals plot. Individual growth curves can be viewed in Figure A3.1.

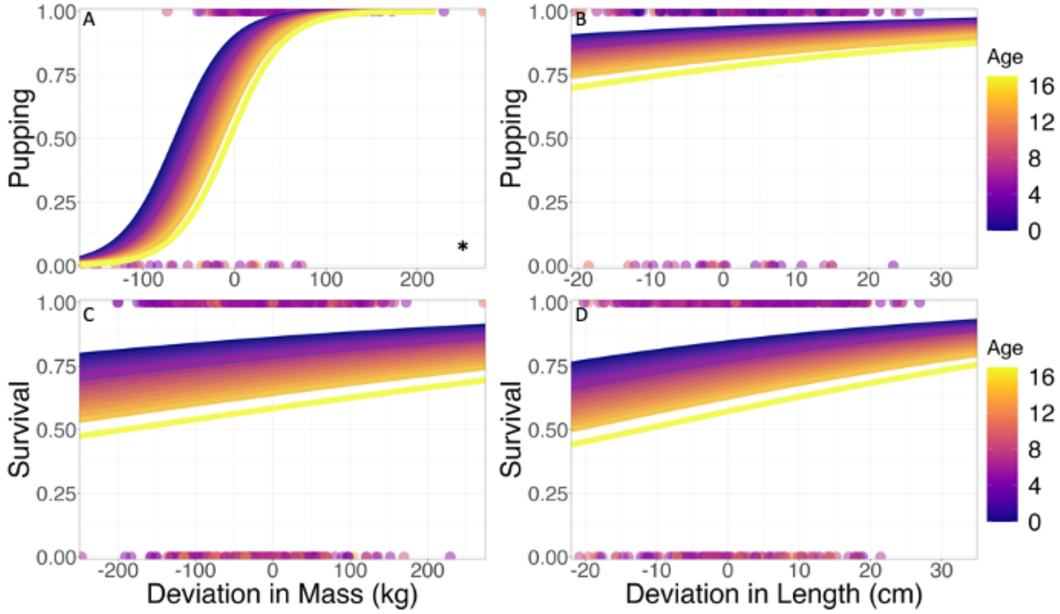

Figure 3. 3. The relationships between deviation in mass (kg) (panels A and C) and deviation in length (cm) (panels B and D) and annual probability of pupping success (panels A and B) and annual probability of survival (panels B and D). Relationships are from a generalized linear mixed effect model fit using a binomial distribution with a logit link, a fixed effect of age, and a random effect of individual seal. Pupping success analyses were conducted on post-molt arrival females only and survival analyses were conducted on all females. An asterisk indicates a significant effect of deviation in mass on annual probability of pupping success (Intercept = 2.13 ± 0.85, z = 2.52, p = 0.01; deviation in mass = 0.03 + 6.0 x 10^-3, z = 5.64, p = 1.72 x 10^-8; age = -0.11 + 0.12, z = -0.98, p = 0.33, n = 211) and a plus indicated borderline significance (Intercept = 2.21 ± 0.53, z = 4.15, p = 3.3 x 10^-5; deviation in length = 0.03 + 0.02, z = 1.91, p=0.06; age = -0.13 + 0.06, z = -2.13, p = 0.03, n = 455).

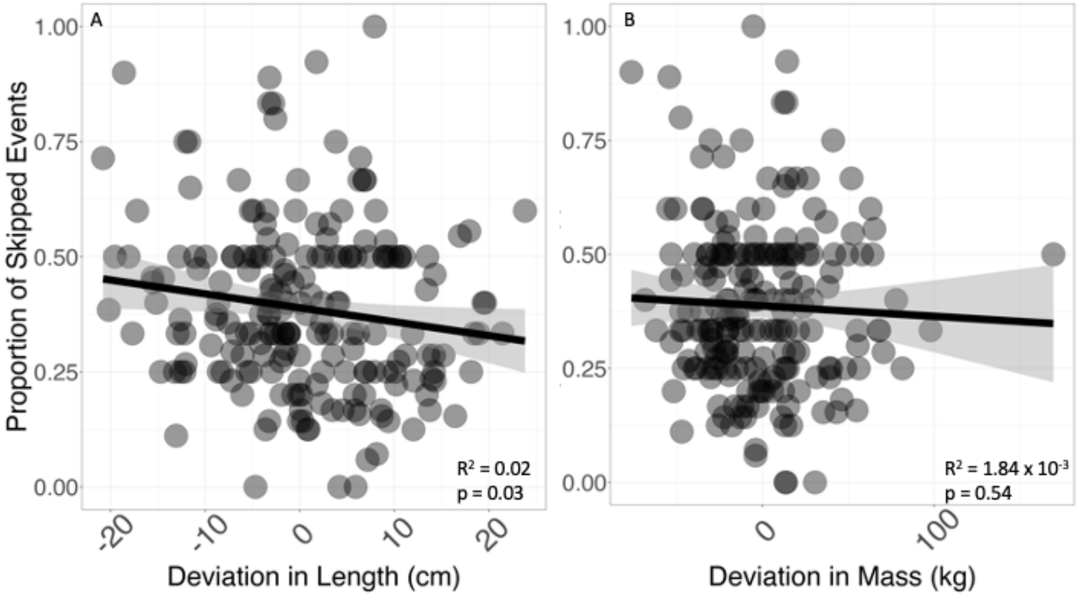

Figure 3. 4 The relationship between deviation in length (cm; Panel A) and deviation in mass (kg; Panel B) against proportion of skipped reproductive events fit with a linear regression with a random effect of individual seal for all females with a known age at death (Deviation in length: Intercept = 0.39 + 0.01, t = 30.45, p = 2.2 x 10^-16; slope = -3.02 x 10^-3 + 1.41 x 10^-3, t = -2.15, p = 2.2 x 10^-16; n = 201; Deviation in mass: Intercept = 0.39 + 0.01, t = 30.03, p = 2.2 x 10^-16; slope = -2.29 x 10^-4 + 3.77 x 10^-4, t = -0.61, p = 0.54; n = 201).

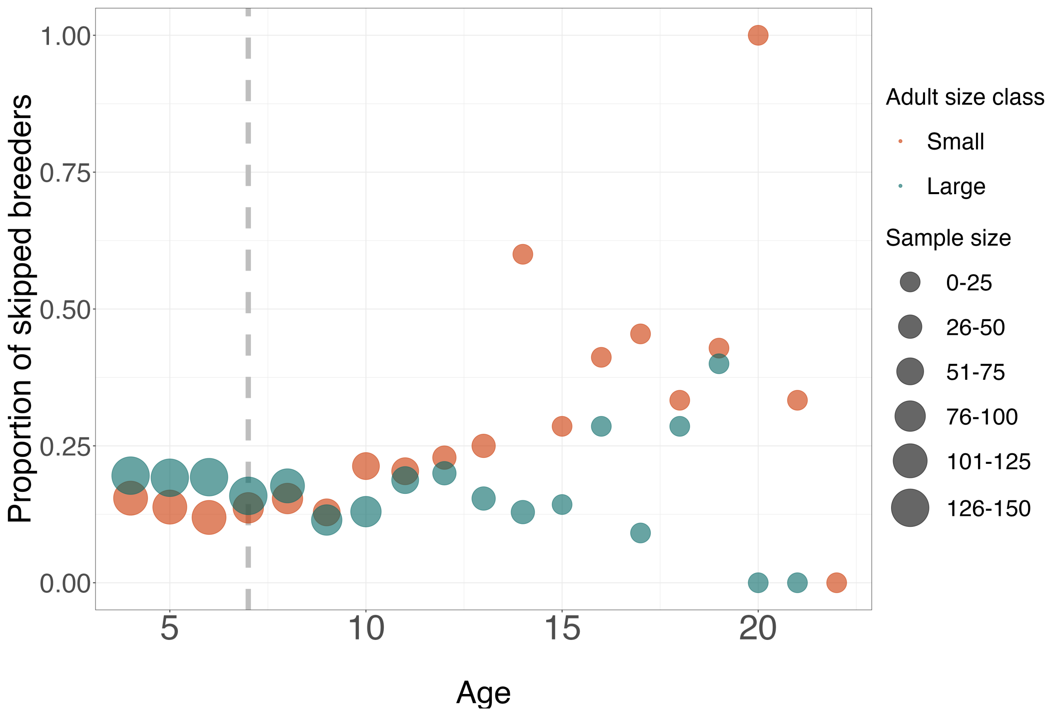

Figure 3. 5. Proportion of individuals per age class that missed a reproductive event, separated by adult size class where small size is determined by a negative deviation in length and large size is determined by positive deviation in length. The sample size for each age class is indicated by point size.

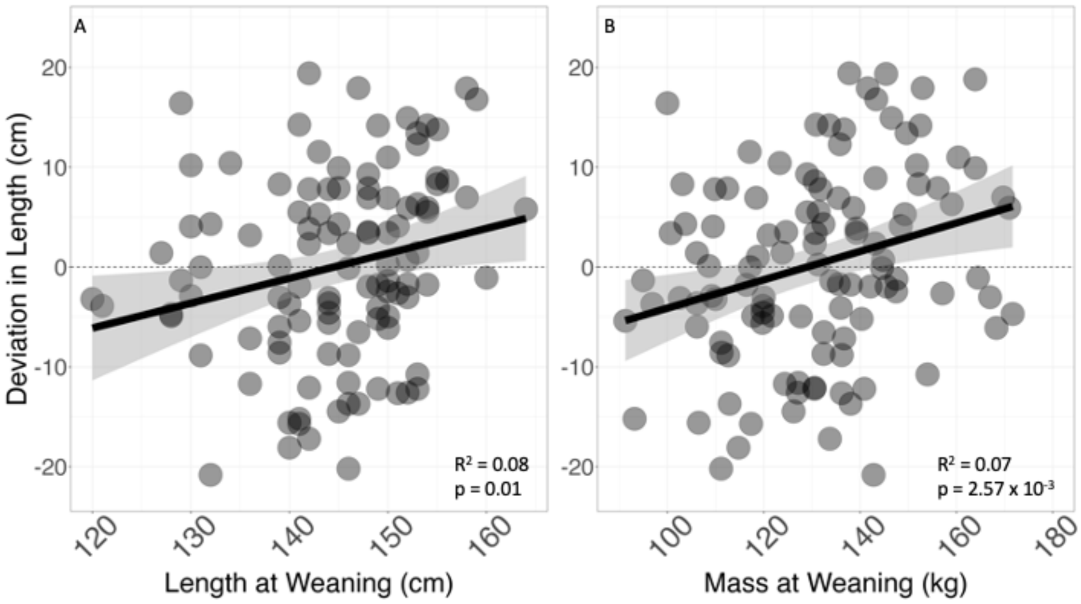

Figure 3. 6 The relationship between length at weaning (cm; Panel A) and mass at weaning (kg; Panel B) against adult deviation in length fit with a linear regression with a random effect of individual seal for all females for which measurements were available (Deviation in length: Intercept = -45.15 + 16.16, t = -2.79, p = 6.30 x 10^-3; slope = 0.31 + 0.11, t = 2.80, p =6.27 x 10^-3; n = 134; Deviation in mass: Intercept = -14.18 + 5.55, t = -2.56, p = 0.01; slope= 0.13 + 0.04, t = 3.09, p = 2.57 x 10^-3; n = 113).

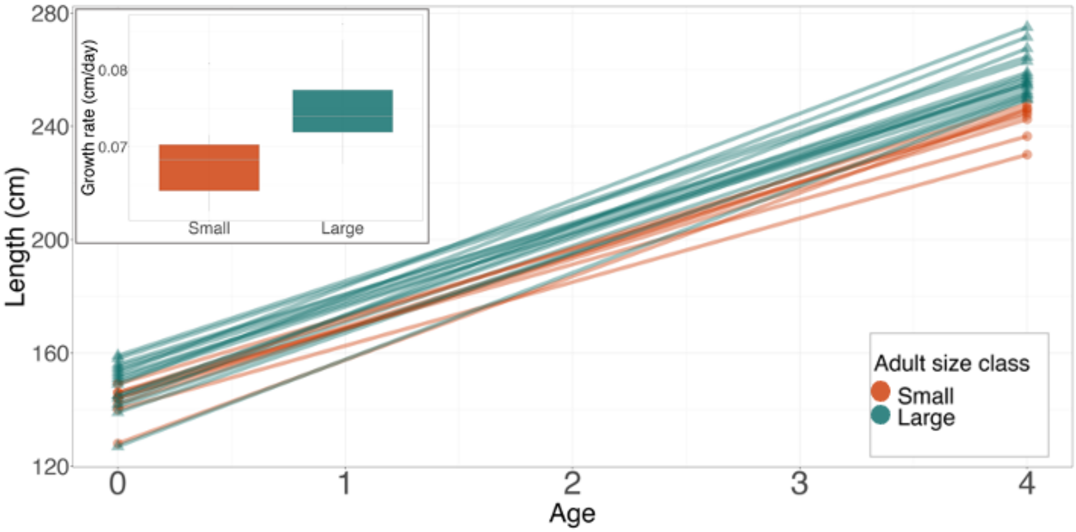

Figure 3. 7 Growth trajectories between size at weaning and size at age 4 for females that reach small (negative deviation in length) and large (positive deviation in length) body size in adulthood. The inset boxplot shows differences in growth rate, calculated as the change in length over the number of days between weaning and age 4) for small and large females (W = 23.50; p = 0.01, n = 25).

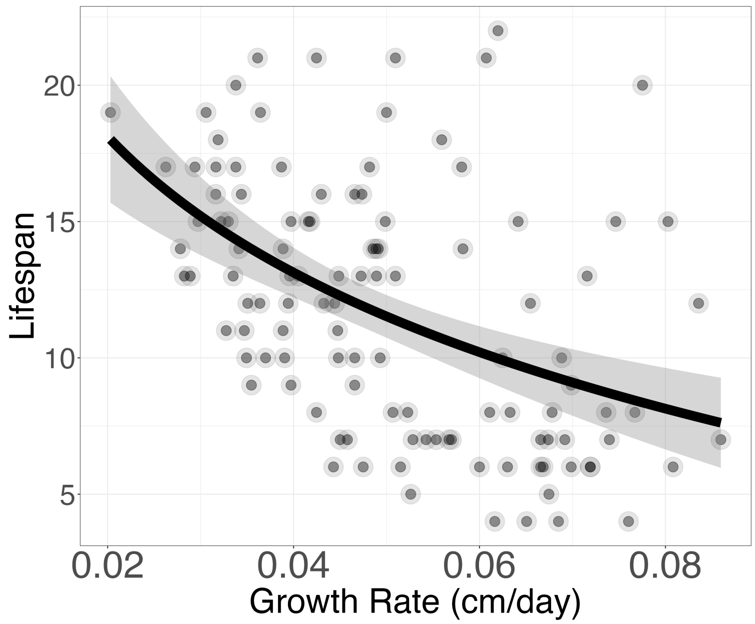

Figure 3. 8 The relationship between growth rate before sexual maturity (estimated at age 4) and lifespan fit with a generalized linear model fit using a lognormal distribution for female elephant seals with a known age at death (Intercept = -10.05 ± 3.88, t = -2.59, p = 0.01; growth rate = -7.20 + 1.27, t = -5.65, p = 1.27 x 10^-7; n = 211).

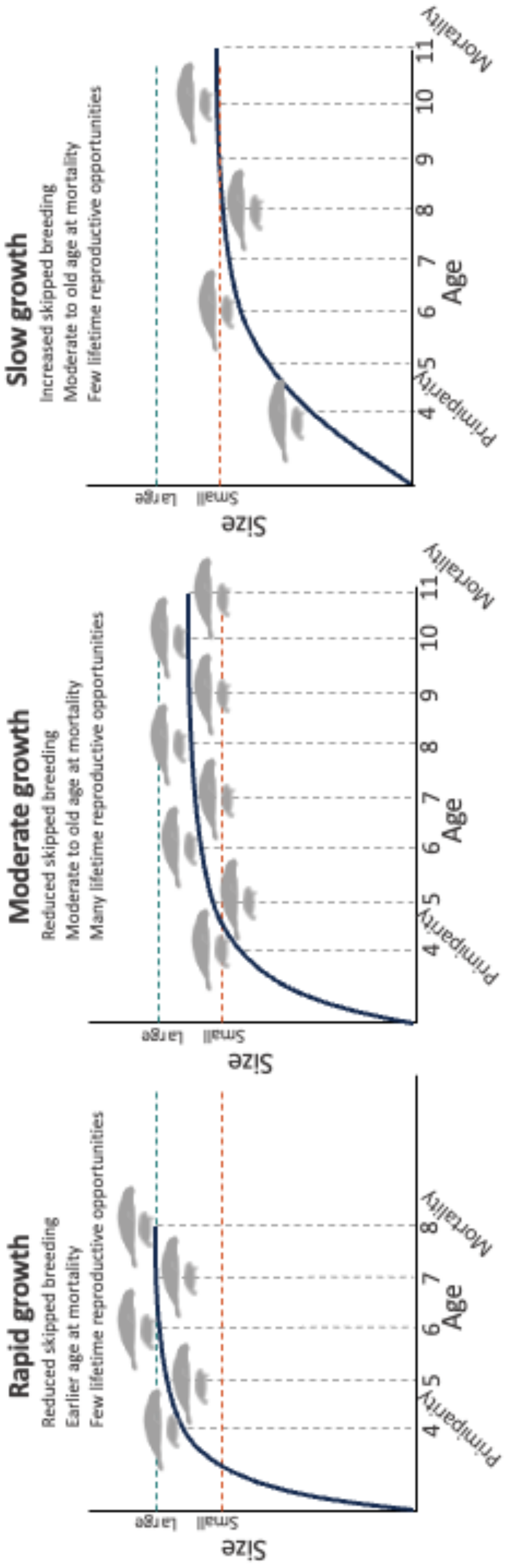
Rapid growth
Reduced skipped breeding
Earlier age at mortality
Few lifetime reproductive opportunities
Size
Large
Small
Age
4
5
6
7
8
Primiparity
Mortality
Moderate growth
Reduced skipped breeding
Moderate to old age at mortality
Many lifetime reproductive opportunities
Size
Large
Small
Age
4
5
6
7
8
9
10
11
Primiparity
Mortality
Slow growth
Increased skipped breeding
Moderate to old age at mortality
Few lifetime reproductive opportunities
Size
Large
Small
Age
4
5
6
7
8
9
10
11
Primiparity
Mortality

Figure 3. 9 Conceptual figure demonstrating the different growth patterns exhibited by elephant seals and the resulting fitness consequences.

References

Abrahms, B., Hazen, E. L., Bograd, S. J., Brashares, J. S., Robinson, P. W., Scales, K. L., Crocker, D. E., & Costa, D. P. (2018). Climate mediates the success of migration strategies in a marine predator. In *Ecology Letters* (Vol. 21, Issue 1, pp. 63–71). Blackwell Publishing Ltd. https://doi.org/10.1111/ele.12871

Adachi, T., Takahashi, A., Costa, D. P., Robinson, P. W., Hückstädt, L. A., Peterson, S. H., Holser, R. R., Beltran, R. S., Keates, T. R., & Naito, Y. (2021). Forced into an ecological corner: Round-the-clock deep foraging on small prey by elephant seals. *Science Advances*, *7*, 3628–3640. https://www.science.org

Adamczak, S. K., Mchuron, E. A., Christiansen, F., Dunkin, R., Mcmahon, C. R., Noren, S., Pirotta, E., Rosen, D., Sumich, J., & Costa, D. P. (2023). Growth in marine mammals: a review of growth patterns, composition and energy investment. *Conservation Physiology*, *11*, 19 pp. https://doi.org/10.1093/conphys/coad035

Authier, M., Dragon, A. C., Richard, O., Cherel, Y., and Guinet, C. (2012). O' mother where wert thou? Maternal strategies in the southern elephant seal: a stable isotope investigation. *Proceedings of the Royal Society B*, 279(1738): 2681-2690. https://doi.org/10.1098/rspb.2012.0199

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bartke, A., Sun, L. Y., & Longo, V. (2013). Somatotropic signaling: Trade-Offs between growth, reproductive development, and longevity. *Physiological Reviews*, *93*, 571–598. https://doi.org/10.1152/physrev.00006.2012.-Growth

Baron, J. P., le Galliard, J. F., Ferrière, R., & Tully, T. (2013). Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival. *Functional Ecology*, *27*(1), 173–183. https://doi.org/10.1111/1365-2435.12023

Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V., & Lundberg, P. (2002). Population dynamic consequences of delayed life-history effects. *TRENDS in Ecology & Evolution*, *17*(6). http://tree.trends.com0169-5347/02/$-seefrontmatter

Beltran, R. S., Kendall-Bar, J. M., Pirotta, E., Adachi, T., Naito, Y., Takahashi, A., Cremers, J., Robinson, P. W., Crocker, D. E., & Costa, D. P. (2021). Lightscapes of fear: How mesopredators balance starvation and predation in the open ocean. *Scientific Advances*, *7*, 9818–9835. https://www.science.org

Beltran, R. S., Hernandez, K. M., Condit, R., Robinson, P. W., Crocker, D. E., Goetsch, C., Kilpatrick, A. M., & Costa, D. P. (2023). Physiological tipping points in the relationship between foraging success and lifetime fitness of a long-lived mammal. *Ecology Letters*. https://doi.org/10.1111/ele.14193

Best, P. B., & Rüther, H. (1992). Aerial photogrammetry of southern right whales, Eubalaena australis. *Journal of Zoology*, *228*(4), 595–614. https://doi.org/10.1111/j.1469-7998.1992.tb04458.x

Bierlich, K. C., Kane, A., Hildebrand, L., Bird, C. N., Fernandez Ajo, A., Stewart, J. D., Hewitt, J., Hildebrand, I., Sumich, J., & Torres, L. G. (2023). Downsized: gray whales using an alternative foraging ground have smaller morphology. *Biology Letters*, *19*(8). https://doi.org/10.1098/rsbl.2023.0043

Bonnet, X., Lourdais, O., Shine, R., & Naulleau, G. (2002). Reproduction in a typical capital breeder: Costs, currencies, and complications in the aspic viper. *Ecology*, *83*(8), 2124–2135. https://doi.org/10.1890/0012-9658(2002)083[2124:RIATCB]2.0.CO;2

Bull, J. J., & Shine, R. (1979). Iteroparous animals that skip opportunities for reproduction. *The American Naturalist*, *114*(2), 296–303. https://about.jstor.org/terms

Charnov, E. (2004). The optimal balance between growth rate and survival in mammals. *Evolutionary Ecology Research*, *6*, 307–313. https://digitalrepository.unm.edu/biol_fsp

Christiansen, F., Dawson, S. M., Durban, J. W., Fearnbach, H., Miller, C. A., Bejder, L., Uhart, M., Sironi, M., Corkeron, P., Rayment, W., Leunissen, E., Haria, E., Ward, R., Warick, H. A., Kerr, I., Lynn, M. S., Pettis, H. M., & Moore, M. J. (2020). Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series*, *640*, 1–16. https://doi.org/10.3354/meps13299

Cichoń, M. (1997). Evolution of longevity through optimal resource allocation. *Proceedings of the Royal Society: B*, *264*, 1838–1388.

Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G. E., & Streich, W. J. (2003). The maximum attainable body size of herbivorous mammals: Morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, *136*(1), 14–27. https://doi.org/10.1007/s00442-003-1254-z

Condit, R., Beltran, R. S., Robinson, P. W., Crocker, D. E., & Costa, D. P. (2022). Birth timing after the long feeding migration in northern elephant seals. *Marine Mammal Science* 38(3): 10 pp. https://doi.org/10.1111/mms.12896

Committee on Marine Mammals. (1967). Standard measurements of seals. *Journal of Mammalogy*, *48*(3), 459–462.

Cole, L. C. (1954). The population consequences of life history phenomena. *The Quarterly Review of Biology*, *29*(2), 103–137. https://www.jstor.org/stable/2817654?seq=1&cid=pdf-

Costa, D. P., Boeuf, B. J. L., Huntley, A. C., & Ortiz, C. L. (1986). The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology*, *209*(1), 21–33. https://doi.org/10.1111/j.1469-7998.1986.tb03563.x

Costa, D. P., Gales, N. J., & Goebel, M. E. (2001). Aerobic dive limit: How often does it occur in nature? *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *129*(4), 771–783. https://doi.org/10.1016/S1095-6433(01)00346-4

Costa, D. P., and Maresh, J. L. (2021). When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids. Pages 21-50 *in* C. Campagna and R. Harcourt (eds.). Ethology and Behavioral Ecology of Otariids and the Odobenid. Springer International Publishing, Cham.

Costa, D. P., and Valenzuela-Toro, A. (2021). When Physiology and Ecology Meet: The Interdependency Between Foraging Ecology and Reproduction in Otariids. Pages 21-50 *in* C. Campagna and R. Harcourt (eds.). Ethology and Behavioral Ecology of Otariids and the Odobenid. Springer International Publishing, Cham.

Costa, D. P., and Maresh, J. L. (2022). Reproductive Energetics of Phocids. Pages 281-309 *in* D. P. Costa and E. A. McHuron (eds.). Ethology and Behavioral Ecology of Phocids. Springer International Publishing, Cham.

Costa, D. P., and Favilla, A. B. (2023). Field Physiology in the aquatic realm: ecological energetics and behavior provide context for elucidating patterns and deviations. *Journal of Experimental Biology, 226(20):jeb245832.* https://doi.org/100.1242/jeb.245832

Crocker, D. E., Webb, P. M., Costa, D. P., & le Boeuf, B. J. (1998). Protein catabolism and renal function in lactating Northern elephant seals. *Physiological Zoology*, *71*(5), 485–491. https://doi.org/10.1086/515971

Crocker, D. E., Williams, J. D., Costa, D. P., & le Boeuf, B. J. (2001). Maternal traits and reproductive effort in Northern elephant seals. *Ecology*, *82*(12), 3541–3555.

Crocker, D. E., Houser, D. S., & Webb, P. M. (2012). Impact of body reserves on energy expenditure, water flux, and mating success in breeding male northern elephant seals. *Physiological and Biochemical Zoology*, *85*(1), 11–20. https://doi.org/10.1086/663634

Desprez, M., Gimenez, O., McMahon, C. R., Hindell, M. A., & Harcourt, R. G. (2018). Optimizing lifetime reproductive output: Intermittent breeding as a tactic for females in a long-lived, multiparous mammal. *Journal of Animal Ecology*, *87*(1), 199–211. https://doi.org/10.1111/1365-2656.12775

Deutsch, C., Crocker, D. E., Costa, D. P., & Boeuf, B. J. I. E. (1994). Sex-and age-related variation in reproductive effort of northern elephant seals. In *Elephant Seals*.

Ejsmond, M. J., Varpe, Ø., Czarnoleski, M., & Kozłowski, J. (2015). Seasonality in offspring value and trade-offs with growth explain capital breeding. *American Naturalist*, *186*(5), E111–E125. https://doi.org/10.1086/683119

Fokidis, H. B., Risch, T. S., & Glenn, T. C. (2007). Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour*, *73*(3), 479–488. https://doi.org/10.1016/j.anbehav.2006.08.010

Geeson, J. J., Hindell, M. A., Hobday, A. J., Speakman, C. N., and Arnould, J. P. (2023). Long-term decline in body condition of female Australian fur seals: potential causes and implications. *Frontiers in Marine Science*, 10. https://doi.org/10.3389//fmars/2023.1231337

Griffen, B. D. (2018). Reproductive skipping as an optimal life history strategy in the southern elephant seal, *Mirounga leonina*. *Ecology and Evolution*, *8*(18), 9158–9170. https://doi.org/10.1002/ece3.4408

Goldbogen, J. A. (2018). Physiological constraints on marine mammal body size. *PNAS*, *115*(16), 3995–3997. https://doi.org/10.1073/pnas.1804077115

Gunnlaugsson, T., Víkingsson, G. A., Halldórsson, S. D., Elvarsson, B. Þ., Haug, T., & Lydersen, C. (2020). Body mass, muscle, blubber and visceral fat content and their seasonal, spatial and temporal variability in North Atlantic common minke whales. *Journal of Cetacean Research and Management*, *21*, 59–70. https://iwc.int/permits.

Haley, M. P., Deutsch, C. J., & le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behavior*, *48*, 1249–1260.

Hamel, S., Côté, S. D., & Festa-Bianchet, M. (2011). Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal. *Oikos*, *120*(5), 690–695. https://doi.org/10.1111/j.1600-0706.2011.19382.x

Harding, K. C., Salmon, M., Teilmann, J., Dietz, R., & Härkönen, T. (2018). Population wide decline in somatic growth in harbor seals-early signs of density dependence. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00059

Hassrick, J. L., Crocker, D. E., Teutschel, N. M., McDonald, B. I., Robinson, R. W., Simmons, S. E., & Costa, D. R. (2010). Condition and mass impact oxygen stores and dive duration in adult female northern elephant seals. *Journal of Experimental Biology*, *213*(4), 585–592. https://doi.org/10.1242/jeb.037168

Hassrick, J. L., Crocker, D. E., & Costa, D. P. (2013). Effects of maternal age and mass on foraging behaviour and foraging success in the northern elephant seal. *Functional Ecology*, *27*(4), 1055–1063. https://doi.org/10.1111/1365-2435.12108

Henderson, A. F., McMahon, C. R., Harcourt, R., Guinet, C., Picard, B., Wotherspoon, S., & Hindell, M. A. (2020). Inferring variation in southern elephant seal at-sea mortality by modelling tag failure. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.517901

Holser, R. R., Crocker, D. E., Robinson, P. W., Condit, R., & Costa, D. P. (2021). Density-dependent effects on reproductive output in a capital breeding carnivore, the northern elephant seal (*Mirounga angustirostris*). *Proceedings of the Royal Society B: Biological Sciences*, *288*(1960), 421–425. https://doi.org/10.1098/rspb.2021.1258

Houston, A. I., Mcnamara, J. M., & Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London B*, *341*, 375–397. https://royalsocietypublishing.org/

Irvine, L. G., Hindell, M. A., Hoff, J., & Burton, H. R. (2000). The influence of body size on dive duration of underyearling southern elephant seals (*Mirounga leonina*). *Journal of Zoology*, *251*(4), 463–471. https://doi.org/10.1111/j.1469-7998.2000.tb00802.x

Kienle, S. S., Friedlaender, A. S., Crocker, D. E., Mehta, R. S., & Costa, D. P. (2022). Trade-offs between foraging reward and mortality risk drive sex-specific foraging strategies in sexually dimorphic northern elephant seals. *Royal Society Open Science*, *9*(1). https://doi.org/10.1098/rsos.210522

Kleiber, M. (1975). Metabolic turnover rate: A physiological meaning of the metabolic rate per unit body weight. *Journal of Theoretical Biology*, *53*, 199–204.

Kooyman, G. L., Castellini, M. A., Davis, R. W., & Maue, R. A. (1983). Aerobic diving limits of immature Weddell seals. *Journal of Comparative Physiology B*, *151*(2), 171–174. https://doi.org/10.1007/BF00689915

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology and Evolution*, *7*(1), 15–19.

Laws, R. M. (1956). Growth and sexual maturity in aquatic mammals. *Nature*, *178*, 193–194.

le Boeuf, B. J., Condit, R., & Reiter, J. (1989). Parental investment and the secondary sex ratio in northern elephant seals. *Behavioral Ecology and Sociobioly*, *25*, 109–117.

le Boeuf, B., Condit, R., & Reiter, J. (2019). Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). *Canadian Journal of Zoology*, *97*, 1203–1217. https://doi.org/10.7291/D18084

Lee, W. S., Monaghan, P., & Metcalfe, N. B. (2013). Experimental demonstration of the growth rate-lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1752). https://doi.org/10.1098/rspb.2012.2370

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, *125*(6), 873–878. https://about.jstor.org/terms

Lowry, M. S., Condit, R., Hatfield, B., Allen, S. G., Berger, R., Morris, P. A., le Boeuf, B. J., & Reiter, J. (2014). Abundance, distribution, and population growth of the northern elephant seal (*Mirounga angustirostris*) in the united states from 1991 to 2010. *Aquatic Mammals*, *40*(1), 20–31. https://doi.org/10.1578/AM.40.1.2014.20

McDonald, B. I., & Crocker, D. E. (2006). Physiology and behavior influence lactation efficiency in Northern elephant seals (*Mirounga angustirostris*). *Physiological and Biochemical Zoology*, *79*(3), 484–496.

Mcmahon, C. R., New, L. F., Fairley, E. J., Hindell, M. A., & Burton, H. R. (2015). The effects of body size and climate on post-weaning survival of elephant seals at Heard Island. *Journal of Zoology*, *297*(4), 301–308. https://doi.org/10.1111/jzo.12279

Merry, B. J. (1995). Effect of dietary restriction on aging - an update. *Reviews in Clinical Gerontology*, *5*(3), 247–258. https://doi.org/10.1017/S0959259800004305

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *TRENDS in Ecology and Evolution*, *16*(4), 254–260. http://tree.trends.com

Metcalfe, N. B., & Monaghan, P. (2003). Growth versus lifespan: Perspectives from evolutionary ecology. In *Experimental Gerontology* (Vol. 38, Issue 9, pp. 935–940). Elsevier Inc. https://doi.org/10.1016/S0531-5565(03)00159-1

Millar, J. S., & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. *Ecology*, *4*(1), 5–12.

Mishra, A., Tiwary, D., & Singh, S. K. (1960). A class of quasi-binomial distributions. *The Indian Journal of Statistics, Series B*, *54*(1), 67–76. https://about.jstor.org/terms

Monteith, K. L., Stephenson, T. R., Bleich, V. C., Conner, M. M., Pierce, B. M., & Bowyer, R. T. (2013). Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology*, *82*(2), 377–388. https://doi.org/10.1111/1365-2656.12016

Morano, S., Stewart, K. M., Sedinger, J. S., Nicolai, C. A., & Vavra, M. (2013). Life-history strategies of North American elk: Trade-offs associated with reproduction and survival. *Journal of Mammalogy*, *94*(1), 162–172. https://doi.org/10.1644/12-MAMM-A-074.1

Noren, D. P., Crocker, D. E., Williams, T. M., & Costa, D. P. (2003). Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: Size does matter. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *173*(5), 443–454. https://doi.org/10.1007/s00360-003-0353-9

Oosthuizen, W. C., Altwegg, R., Nevoux, M., Bester, M. N., and de Bruyn, P. J. N. (2018). Phenotypic selection and covariation in the life-history trats of elephant seals: heavier offspring grain a double selective advantage. *Oikos* 126(6), 875-889. https://doi.org/10.1111.oik.04998

Oosthuizen, W. C., Postma, M., Altwegg, R., Nevoux, M., Pradel, R., Bester, M. N., & de Bruyn, P. J. N. (2019). Individual heterogeneity in life-history trade-offs with age at first reproduction in capital breeding elephant seals. *Population Ecology*, *61*(4), 421–435. https://doi.org/10.1002/1438-390X.12015

Oosthuizen, W. C., Pistorius, P. A., Bester, M. N., Altwegg, R., & de Bruyn, P. J. N. (2023). Reproductive phenology is a repeatable, heritable trait linked to the timing of other life-history events in a migratory marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2003). https://doi.org/10.1098/rspb.2023.1170

Pauly, D. (1991). Geometrical constraints on body size. *Trends in Ecology and Evolution*, *12*(11), 442.

R Core Team (2022). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available online at hrrp:www.R-project.org/.

Real, L., & Caraeo, T. (1986). Risk and foraging in a stochastic environment. *Annual Review of Ecological Systems*, *17*, 371–390. www.annualreviews.org

Reiter, J., & le Boeuf, B. J. (1991). Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioral Ecology and Sociobiology*, *28*, 153–160.

Robinson, P. W., Costa, D. P., Crocker, D. E., Gallo-Reynoso, J. P., Champagne, C. D., Fowler, M. A., Goetsch, C., Goetz, K. T., Hassrick, J. L., Hückstädt, L. A., Kuhn, C. E., Maresh, J. L., Maxwell, S. M., McDonald, B. I., Peterson, S. H., Simmons, S. E., Teutschel, N. M., Villegas-Amtmann, S., & Yoda, K. (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). https://doi.org/10.1371/journal.pone.0036728

Rollinson, N., & Rowe, L. (2016). The positive correlation between maternal size and offspring size: fitting pieces of a life-history puzzle. *Biological Reviews*, *91*(4), 1134–1148. https://doi.org/10.1111/brv.12214

Rollo, C. D. (2002). Growth negatively impacts the life span of mammals. *Evolution and Development*, *4*(1), 55–61. https://doi.org/10.1046/j.1525-142x.2002.01053.x

Salas, L., Nur, N., Ainley, D., Burns, J., Rotella, J., & Ballard, G. (2017). Coping with the loss of large, energy-dense prey: A potential bottleneck for Weddell Seals in the Ross Sea: A. *Ecological Applications*, *27*(1), 10–25. https://doi.org/10.1002/eap.1435

Shaw, A. K., & Levin, S. A. (2013). The evolution of intermittent breeding. *Journal of Mathematical Biology*, *66*(4–5), 685–703. https://doi.org/10.1007/s00285-012-0603-0

Sibly, R. M., & Brown, J. H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *PNAS*, *104*(45), 17707–17712. www.pnas.org/cgi/content/full/

Snyder, R. E., & Ellner, S. P. (2018). Pluck or luck: Does trait variation or chance drive variation in lifetime reproductive success? *The American Naturalist*, *191*(4), E90–E107. https://doi.org/10.5061/dryad.pd959

Solberg, E. J., Heim, M., Grøtan, V., Sæther, B. E., & Garel, M. (2007). Annual variation in maternal age and calving date generate cohort effects in moose (*Alces alces*) body mass. *Oecologia*, *154*(2), 259–271. https://doi.org/10.1007/s00442-007-0833-9

Steiger, S. (2013). Bigger mothers are better mothers: Disentangling size-related prenatal and postnatal maternal effects. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1766). https://doi.org/10.1098/rspb.2013.1225

Stephens, P. A., Boyd, I. L., Mcnamara, J. M., & Houston, A. I. (2009). Capital breeding and income breeding: Their meaning, measurement, and worth. *Ecology*, *90*(8), 2057–2067. https://doi.org/10.1890/08-1369.1

Stewart, J. D., Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Casler, P. K., Ward, E. J., & Dapp, D. R. (2021). Survival of the fattest: linking body condition to prey availability and survivorship of killer whales. *Ecosphere*, *12*(8). https://doi.org/10.1002/ecs2.3660

Stopher, K. v., Pemberton, J. M., Clutton-Brock, T. H., & Coulson, T. (2008). Individual differences, density dependence and offspring birth traits in a population of red deer. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1647), 2137–2145. https://doi.org/10.1098/rspb.2008.0502

Therrien, J. F., Côté, S. D., Festa-Bianchet, M., & Ouellet, J. P. (2007). Conservative maternal care in an iteroparous mammal: A resource allocation experiment. *Behavioral Ecology and Sociobiology*, *62*(2), 193–199. https://doi.org/10.1007/s00265-007-0453-8

Tjørve, K. M. C., & Tjørve, E. (2017). The use of Gompertz models in growth analyses, and new Gompertz-model approach: An addition to the Unified-Richards family. *PLoS ONE*, *12*(6). https://doi.org/10.1371/journal.pone.0178691

Trites, A. W., & Bigg, M. A. (1996). Physical growth of northern fur seals (Callorhinus ursinus): seasonal fluctuations and migratory influences. *Journal of Zoology*, *238*, 459–482.

Waite, J. N., & Mellish, J. A. E. (2009). Inter- and intra-researcher variation in measurement of morphometrics on Steller sea lions (Eumetopias jubatus). *Polar Biology*, *32*(8), 1221–1225. https://doi.org/10.1007/s00300-009-0649-7

Warner, R. R. (1998). The role of extreme iteroparity and risk avoidance in the evolution of mating systems. *Journal of Fish Biology*, *53*(SUPPL. A), 82–93. https://doi.org/10.1111/j.1095-8649.1998.tb01019.x

Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, *3*(1), 129–137. https://doi.org/10.1111/j.2041-210X.2011.00125.x

Woolson, R. F. (2007). Wilcoxon Signed Rank Test. *Wiley Encyclopedia of Clinical Trials*. New York, pp. 1-3.

Wootton, J. T. (1987). The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. *Evolution*, *41*(4), 732–749. https://doi.org/10.1111/j.1558-5646.1987.tb05849.x

Conclusion

Growth and body size are key factors influencing life history. Understanding how growth costs and body size at maturity influence bioenergetics, physiology, and fitness is important when assessing broader topics ranging from individual health to population demography. This dissertation aimed to improve our understanding of how animals grow and how energy is allocated to growth (Chapter 1) while leveraging theoretical modeling and empirical data from a long-term monitoring program to address the bioenergetic and life history impacts of variation in body size on a species (Chapter 2) and individual level (Chapter 3). I applied theoretical modeling to the smallest fully aquatic marine mammal species, the harbor porpoise (*Phocoena phocoena*; Chapter 2) to determine how size influenced life history traits and population success. Additionally, I used empirical data from a long-term monitoring program for norther elephant seals (*Mirounga angustirostris*; Chapter 3) to examine individual and lifetime fitness consequences of deviation from expected body size. Further, I tested for trade-offs between reproduction, longevity, and growth in northern elephant seals to examine theories of energy allocation prioritization (Chapter 3).

Growth costs for marine mammals were relatively small when compared to other metabolic costs (Chapter 1). Information on growth and the energy required to deposit tissues is fundamental to our understanding of marine mammal bioenergetics and the use of body size as a proxy for individual and population health. Knowledge gaps regarding estimates of growth costs, partitioning of energy between skeletal muscle and blubber, and growth trajectories of numerous data-poor species still remain. Advances in technology, including unmanned aerial vehicles, blubber biopsies, and tag-based buoyancy estimates, provide an exciting new landscape to better measure body size and energy reserves (e.g., Biuw et al., 2003; Christiansen et al., 2016; Kershaw et al., 2019). Use of these resources is crucial to obtain better estimates of growth in marine mammals as the challenges of global climate change, anthropogenic disturbance, and reduced prey availability threaten the allocation and investment of energy to growth in marine mammals and alter the associated physiological and fitness benefits of large body size.

Further, I identified numerous gaps in our documentation of growth curves. Existing curves are biased towards more well-studied species [e.g., bottlenose dolphins (*Tursiops truncatus*), harbor porpoise (*Phocoena phocoena*), and monodontids (family *Monodontidae*)], leaving many species groups with very limited data [e.g., beaked whales (family *Ziphiidae*) and river dolphins (families *Iniidae, Pontoporiidae*); Chapter 1]. These data gaps limit our ability to use body size as a marker for population health for numerous marine mammal species. Although length-at-age curves are more prevalent in the literature than mass-at-age curves, published studies on the physiological and fitness benefits of body size typically use mass as a proxy for size. This indicates a mismatch between our understanding of variation in and the benefits of body size. Thus, I recommend that future studies exploring impacts of body size on physiology, behavior, or fitness consider both length and mass.

Although the cost of growth is relatively small for marine mammals, the repercussions of variation in growth investment are substantial. Overall, large females had higher annual reproductive success and survival probabilities (Chapter 2; Chapter 3), and in some instances higher lifetime reproductive success (Chapter 2). Higher reproductive success of large females influenced population demography by increasing population growth rates and improving population success (Chapter 2). Despite the fitness benefits of large body size, it may be challenging to meet the overall higher energetic requirements of large body size (Chapter 2). For example, I estimated that large harbor porpoises that increased body size by only 10 cm in standard length required nearly 20% more energy, which likely prevents most females from attaining this larger body size.

Contrary to the prevailing literature, I did not find evidence for trade-offs between somatic growth and reproduction (Chapter 3). Although increased investment in growth for younger individuals is thought to delay or hinder reproductive efforts for young individuals, I found that trade-offs with increased growth investment were not mediated through reproduction but rather through longevity (Chapter 3). Individuals that attained large body size by growing rapidly may experience increased mortality risks later in life due to accumulated cell damage during early growth and reductions in cellular repair (Merry, 1995; Cichoń, 1997; Rollo, 2002).

Energetic constraints combined with impacts of early growth investment on longevity are likely to result in selection of an optimal body size for individual species (Chapter 2; Chapter 3). Access to resources, habitat availability, and metabolic constraints are well documented drivers of optimal body size in mammals. Individuals within a species aim to maximize the conversion of energy intake to reproductive output through modulations to body size specific to their environment (Rosenzweig, 1968; Sibly and Brown, 2007; Lomolino et al., 2011; Goldbogen 2018). Attaining ever-increasing growth trajectories is unlikely for most species because of constraints placed on large body size, particularly due to the finite resources available to support these individuals.

Although there are clear energetic constraints placed on evolving continuously larger sizes, there are individuals that attain larger than average body size with high reproductive success and survival (e.g., le Boeuf et al., 2019). High reproductive rates of these individuals prove to be important to the resilience and success of a population. As such, an improved understanding of the traits enabling these individuals to attain large body size is required. It is possible that maternal effects and higher maternal investment influence an individual's ability to attain large size (e.g., Steiger, 2013), particularly because of the link between larger size at weaning and large adult body size (Chapter 3). Alternately, cohort effects may influence the ability of an individual to grow larger and a have higher reproductive rate (Toïgo et al., 1999; Solberg et al., 2007). However, disentangling the individual contribution of specific factors driving individual quality is challenging as it requires a combination of genetic, environmental, and individual life history data which exists for only a few research systems focused on large, long-lived species.

The research in this dissertation will aid in our understanding of how deviations from body size can influence individual fitness. This is critically important as we continue to observe shifting body size trajectories for marine mammals in the face of climate- and anthropogenically-mediated disturbances (Best and Rüther, 1992; Calkins et al., 1998; Christiansen et al., 2016; Christiansen et al., 2018; Harding et al., 2018; Stewart et al., 2021; Bierlich et al., 2023). Disturbance appears to drive shifts to smaller body size which could have lasting impacts on the success of the population due to the importance of large individuals with high reproductive rates. Although there does not yet appear to be empirical data outlining the population consequences of these shifts, modeling efforts like those presented in Chapter 2, paired with empirical analyses of body size deviations and fitness consequences (Chapter 3), can help us begin to understand how these changes will impact population success and therefore identify populations of high conservation concern.

References

Best, P. B., & Rüther, H. (1992). Aerial photogrammetry of southern right whales, Eubalaena australis. *Journal of Zoology*, *228*(4), 595–614. https://doi.org/10.1111/j.1469-7998.1992.tb04458.x

Bierlich, K. C., Kane, A., Hildebrand, L., Bird, C. N., Fernandez Ajo, A., Stewart, J. D., Hewitt, J., Hildebrand, I., Sumich, J., & Torres, L. G. (2023). Downsized: gray whales using an alternative foraging ground have smaller morphology. *Biology Letters*, *19*(8). https://doi.org/10.1098/rsbl.2023.0043

Biuw, M., McConnell, B., Bradshaw, C. J. A., Burton, H., & Fedak, M. (2003). Blubber and buoyancy: Monitoring the body condition of free-ranging seals using simple dive characteristics. *Journal of Experimental Biology*, *206*(19), 3405–3423. https://doi.org/10.1242/jeb.00583

Calkins, D. G., Becker, E. F., & Pitcher, K. W. (1998). Reduced body size of female steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science*, *14*(2), 232–244. https://doi.org/10.1111/j.1748-7692.1998.tb00713.x

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*(10). https://doi.org/10.1002/ecs2.1468

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267–282. https://doi.org/10.3354/meps12522

Cichoń, M. (1997). Evolution of longevity through optimal resource allocation. *Proceedings of the Royal Society: B*, *264*, 1838–1388.

Goldbogen, J. A. (2018). Physiological constraints on marine mammal body size. *PNAS*, *115*(16), 3995–3997. https://doi.org/10.1073/pnas.1804077115

Harding, K. C., Salmon, M., Teilmann, J., Dietz, R., & Härkönen, T. (2018). Population wide decline in somatic growth in harbor seals-early signs of density dependence. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00059

Kershaw, J. L., Brownlow, A., Ramp, C. A., Miller, P. J. O., & Hall, A. J. (2019). Assessing cetacean body condition: Is total lipid content in blubber biopsies a useful monitoring tool? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S1), 271–282. https://doi.org/10.1002/aqc.3105 le Boeuf, B., Condit, R., & Reiter, J. (2019). Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). *Canadian Journal of Zoology*, *97*, 1203–1217. https://doi.org/10.7291/D18084

Lomolino, M. v., Sax, D. F., Palombo, M. R., & van der Geer, A. A. (2012). Of mice and mammoths: Evaluations of causal explanations for body size evolution in insular mammals. *Journal of Biogeography*, *39*(5), 842–854. https://doi.org/10.1111/j.1365-2699.2011.02656.x

Merry, B. J. (1995). Effect of dietary restriction on aging - an update. *Reviews in Clinical Gerontology*, *5*(3), 247–258. https://doi.org/10.1017/S0959259800004305

Rollo, C. D. (2002). Growth negatively impacts the life span of mammals. *Evolution and Development*, *4*(1), 55–61. https://doi.org/10.1046/j.1525-142x.2002.01053.x

Rosenzweig, M. L. (1968). The strategy of body size in mammalian carnivores. *The American Midland Naturalist*, *80*(2), 299–315.

Sibly, R. M., & Brown, J. H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *PNAS*, *104*(45), 17707–17712. www.pnas.org/cgi/content/full/

Solberg, E. J., Heim, M., Grøtan, V., Sæther, B. E., & Garel, M. (2007). Annual variation in maternal age and calving date generate cohort effects in moose (*Alces alces*) body mass. *Oecologia*, *154*(2), 259–271. https://doi.org/10.1007/s00442-007-0833-9

Steiger, S. (2013). Bigger mothers are better mothers: Disentangling size-related prenatal and postnatal maternal effects. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1766). https://doi.org/10.1098/rspb.2013.1225

Stewart, J. D., Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Casler, P. K., Ward, E. J., & Dapp, D. R. (2021). Survival of the fattest: linking body condition to prey availability and survivorship of killer whales. *Ecosphere*, *12*(8). https://doi.org/10.1002/ecs2.3660

Toïgo, C., Gaillard, J.-M., & Michallet, J. (1999). Cohort affects growth of males but not females in alpine ibex (*Capra ibex ibex*). *Journal of Mammalogy*, *80*(3), 1021–1027. https://academic.oup.com/jmammal/article/80/3/1021/993619

Appendices

Appendix A1

Table A1. 1 List of documented marine mammal growth curves.

Suborder	**Family**	**Species**	**reference**
Mysticete	Balaenidae	Bowhead whale	(Lubetkin *et al.*, 2012)
Mysticete	Balaenidae	Bowhead whale	(Lubetkin *et al.*, 2008)
Mysticete	Balaenidae	Bowhead whale	(Schell et al., 1989)
Mysticete	Balaenidae	Bowhead whale	(George, 2009)
Mysticete	Balaenidae	Bowhead whale	(Nerini et al., 1984)
Mysticete	Balaenidae	Bowhead whale	(Reese et al., 2001)
Mysticete	Balaenidae	Bowhead whale	(George et al., 1999)
Mysticete	Balaenidae	Bowhead whale	(George et al., 2021)
Mysticete	Balaenidae	North Atlantic right whale	(Fortune *et al.*, 2012)
Mysticete	Balaenidae	North Atlantic right whale	(Fortune *et al.*, 2020)
Mysticete	Balaenidae	North Pacific right whale	(Omura *et al.*, 1969)
Mysticete	Balaenidae	North Pacific right whale	(Fortune *et al.*, 2020)
Mysticete	Balaenidae	Southern right whale	(Christiansen *et al.*, 2019)
Mysticete	Balaenidae	Southern right whale	(Best and Schell, 1996)

Mysticete	Balaenopteridae	Blue whale	(Lockyer, 1976, 1981a)
Mysticete	Balaenopteridae	Blue whale	(Lanzetti *et al.*, 2020)
Mysticete	Balaenopteridae	Blue whale	(Mackintosh and Wheeler, 1929)
Mysticete	Balaenopteridae	Blue whale	(Frazer and Huggett, 1973)
Mysticete	Balaenopteridae	Bryde's whale	(Lockyer, 1976)
Mysticete	Balaenopteridae	Fin whale	(Lockyer, 1976, 1981a)
Mysticete	Balaenopteridae	Fin whale	(Lanzetti *et al.*, 2020)
Mysticete	Balaenopteridae	Fin whale	(Mackintosh and Wheeler, 1929)
Mysticete	Balaenopteridae	Fin whale	(Ohsumi *et al.*, 1958)
Mysticete	Balaenopteridae	Fin whale	(Frazer and Huggett, 1973)
Mysticete	Balaenopteridae	Fin whale	(Aguilar and Lockyer, 1987)
Mysticete	Balaenopteridae	Fin whale	(Lockyer and Waters, 1986)
Mysticete	Balaenopteridae	Humpback whale	(Lanzetti *et al.*, 2020)
Mysticete	Balaenopteridae	Humpback whale	(Stevick, 1999)

Mysticete	Balaenopteridae	Humpback whale	(Boye *et al.*, 2020)
Mysticete	Balaenopteridae	Humpback whale	(Lockyer, 1976)
Mysticete	Balaenopteridae	Humpback whale	(Frazer and Huggett, 1973)
Mysticete	Balaenopteridae	Humpback whale	(Chittleborough, 1965)
Mysticete	Balaenopteridae	Minke whale	(Lockyer, 1981b)
Mysticete	Balaenopteridae	Minke whale	(Markussen *et al.*, 1992)
Mysticete	Balaenopteridae	Minke whale	(Lanzetti *et al.*, 2020)
Mysticete	Balaenopteridae	Minke whale	(Frazer and Huggett, 1973)
Mysticete	Balaenopteridae	Minke whale	(Kato, 1987; Honda et al. 1987)
Mysticete	Balaenopteridae	Sei whale	(Lockyer, 1976, 1981a)
Mysticete	Balaenopteridae	Sei whale	(Lanzetti *et al.*, 2020)
Mysticete	Balaenopteridae	Sei whale	(Frazer and Huggett, 1973)
Mysticete	Balaenopteridae	Sei whale	(Best and Lockyer, 2002)
Odontocete	Delphinidae	Atlantic spotted dolphin	Siciliano et al., 2007)

Odontocete	Delphinidae	Atlantic white-sided dolphin	Rogan et al. 1997)
Odontocete	Delphinidae	Bottlenose dolphin	(Cockcroft, 1989)
Odontocete	Delphinidae	Bottlenose dolphin	(Kasuya *et al.*, 1986)
Odontocete	Delphinidae	Bottlenose dolphin	(Bejarano *et al.*, 2017)
Odontocete	Delphinidae	Bottlenose dolphin	(Gol'din and Gladilina, 2015)
Odontocete	Delphinidae	Bottlenose dolphin	(Mattson *et al.*, 2006)
Odontocete	Delphinidae	Bottlenose dolphin	(Neuenhoff *et al.*, 2011)
Odontocete	Delphinidae	Bottlenose dolphin	(McFee *et al.*, 2010)
Odontocete	Delphinidae	Bottlenose dolphin	(McFee *et al.*, 2012)
Odontocete	Delphinidae	Bottlenose dolphin	(Venuto *et al.*, 2020)
Odontocete	Delphinidae	Bottlenose dolphin	(Mallette et al., 2016)
Odontocete	Delphinidae	Bottlenose dolphin	(Gol'din and Gladilina, 2015)
Odontocete	Delphinidae	Bottlenose dolphin	(Stolen et al., 2002)
Odontocete	Delphinidae	Bottlenose dolphin	(Hohn, 1980)
Odontocete	Delphinidae	Bottlenose dolphin	(Kastelein et al., 2002)
Odontocete	Delphinidae	Bottlenose dolphin	(Read et al., 1993; Adamczak et al. 2021)

Odontocete	Delphinidae	Bottlenose dolphin	(Neuenhoff, 2009)
Odontocete	Delphinidae	Bottlenose dolphin	(Fernandez and Hohn, 1998)
Odontocete	Delphinidae	Bottlenose dolphin	(Kastelein and Wiepkema, 1997)
Odontocete	Delphinidae	Bottlenose dolphin	(Bishop, 2014b)
Odontocete	Delphinidae	Bottlenose dolphin	(Turner et al., 2006)
Odontocete	Delphinidae	Bottlenose dolphin	(Pribanič et al., 2000)
Odontocete	Delphinidae	Bottlenose dolphin	(Hart et al., 2013)
Odontocete	Delphinidae	Bottlenose dolphin	(Peddemors et al., 1992)
Odontocete	Delphinidae	Bottlenose dolphin	(Ridgway, 1995)
Odontocete	Delphinidae	Bottlenose dolphin	(Lockyer and Morris, 1987)
Odontocete	Delphinidae	Bottlenose dolphin	(Kastelein et al., 2003)
Odontocete	Delphinidae	Bottlenose dolphin	(Kastelein et al., 1998)
Odontocete	Delphinidae	Bottlenose dolphin	(Cheney et al., 2017)
Odontocete	Delphinidae	Commerson's dolphin	(Kastelein et al., 1993)
Odontocete	Delphinidae	Common dolphin	(Ferrero and Walker, 1995)
Odontocete	Delphinidae	Common dolphin	(Murphy *et al.*, 2009)
Odontocete	Delphinidae	Common dolphin	(Danil and Chivers, 2007)
Odontocete	Delphinidae	Common dolphin	(Lanzetti *et al.*, 2020)
Odontocete	Delphinidae	Common dolphin	(Kastelein, Staal and Wiepkema, 1998)

Odontocete	Delphinidae	Dusky dolphin	(Kastelein *et al.*, 2000)
Odontocete	Delphinidae	Dusky dolphin	(van Waerebeek and Read, 1994)
Odontocete	Delphinidae	Dusky dolphin	(CIPRIANO, 1992)
Odontocete	Delphinidae	Dusky dolphin	(Kastelein et al., 2000)
Odontocete	Delphinidae	False killer whale	(Ferreira *et al.*, 2014)
Odontocete	Delphinidae	False killer whale	(Purves and Pilleri, 1978)
Odontocete	Delphinidae	False killer whale	(Kastelein et al., 2000)
Odontocete	Delphinidae	Fraser's dolphin	(Amano *et al.*, 1996)
Odontocete	Delphinidae	Guiana dolphin	(Ramos *et al.*, 2010)
Odontocete	Delphinidae	Hector's dolphin	(Slooten, 1991)
Odontocete	Delphinidae	Hector's dolphin	(Webster *et al.*, 2010)
Odontocete	Delphinidae	Indo-Pacific humpback dolphin	(Jefferson *et al.*, 2012)
Odontocete	Delphinidae	Indo-Pacific humpback dolphin	(Nolte, 2013)
Odontocete	Delphinidae	Killer whale	(Clark *et al.*, 2000)
Odontocete	Delphinidae	Killer whale	(Bigg, 1982)

Odontocete	Delphinidae	Killer whale	(Best *et al.*, 2010)
Odontocete	Delphinidae	Killer whale	(Kastelein *et al.*, 2003)
Odontocete	Delphinidae	Killer whale	(Kriete, 1995)
Odontocete	Delphinidae	Killer whale	(Asper *et al.*, 1988)
Odontocete	Delphinidae	Killer whale	(Kastelein and Vaughan, 1989)
Odontocete	Delphinidae	Killer whale	(Kastelein et al., 1998)
Odontocete	Delphinidae	Long-finned pilot whale	(Kasuya *et al.*, 1988)
Odontocete	Delphinidae	Long-finned pilot whale	(Bloch *et al.*, 1993)
Odontocete	Delphinidae	Long-finned pilot whale	(Lockyer, 1993)
Odontocete	Delphinidae	Long-finned pilot whale	(Betty, 2019)
Odontocete	Delphinidae	Long-finned pilot whale	(Frazer and Huggett, 1973)
Odontocete	Delphinidae	Long-finned pilot whale	(Anabella *et al.*, 2017)
Odontocete	Delphinidae	Long-finned pilot whale	(Cowan, 1966)
Odontocete	Delphinidae	Long-finned pilot whale	(Sergeant, 1962)
Odontocete	Delphinidae	Long-finned pilot whale	(Martin and Rothery, 1993)
Odontocete	Delphinidae	Long-finned pilot whale	(Betty et al., 2022)

Odontocete	Delphinidae	Melon-headed whale	(Amano *et al.*, 2014)
Odontocete	Delphinidae	Melon-headed whale	(Bryden *et al.*, 1977)
Odontocete	Delphinidae	Melon-headed whale	(Miyazaki *et al.*, 1998)
Odontocete	Delphinidae	Northern right whale dolphin	(Ferrero and Walker, 1993)
Odontocete	Delphinidae	Pacific white-sided dolphin	(Ferrero and Walker, 1993)
Odontocete	Delphinidae	Pacific white-sided dolphin	(Heise, 1996)
Odontocete	Delphinidae	Pacific white-sided dolphin	(Walker et al., 1984)
Odontocete	Delphinidae	Pantropical spotted dolphin	(Lanzetti *et al.*, 2020)
Odontocete	Delphinidae	Pantropical spotted dolphin	(Kasuya *et al.*, 1974)
Odontocete	Delphinidae	Peale’s dolphin	(Boy *et al.*, 2011)
Odontocete	Delphinidae	Risso’s dolphin	(Amano and Miyazaki, 2004)

Odontocete	Delphinidae	Risso's dolphin	(Bloch *et al.*, 2012)
Odontocete	Delphinidae	Risso's dolphin	(Chen *et al.*, 2011)
Odontocete	Delphinidae	Risso's dolphin	(Plön et al., 2020)
Odontocete	Delphinidae	Rough-toothed dolphin	(Siciliano *et al.*, 2007)
Odontocete	Delphinidae	Rough-toothed dolphin	(West, 2002)
Odontocete	Delphinidae	Short-beaked common dolphin	(Murphy and Rogan, 2006)
Odontocete	Delphinidae	Short-beaked common dolphin	(Kastelein et al., 2000b)
Odontocete	Delphinidae	Short-finned pilot whale	(Kasuya and Matsui, 1984)
Odontocete	Delphinidae	Short-finned pilot whale	(Kasuya and Tai, 1993)
Odontocete	Delphinidae	Spinner dolphin	(Perrin *et al.*, 1977)
Odontocete	Delphinidae	Spinner dolphin	(Larese and Chivers, 2009)
Odontocete	Delphinidae	Spinner dolphin	(Chivers *et al.*, 2019)
Odontocete	Delphinidae	Spinner dolphin	(Perrin and Henderson, 1979)
Odontocete	Delphinidae	Spinner dolphin	(Perrin et al., 2005)
Odontocete	Delphinidae	Spotted dolphin	(Kasuya, 1976)
Odontocete	Delphinidae	Spotted dolphin	(Hohn and Hammond, 1985)

Odontocete	Delphinidae	Striped dolphin	(Kasuya, 1972)
Odontocete	Delphinidae	Striped dolphin	(Kasuya, 1976)
Odontocete	Delphinidae	Striped dolphin	(Miyazaki, 1977)
Odontocete	Delphinidae	Striped dolphin	(Calzada *et al.*, 1997)
Odontocete	Delphinidae	Striped dolphin	(Bishop, 2014)
Odontocete	Delphinidae	Striped dolphin	(Kasuya, 1972b)
Odontocete	Delphinidae	Striped dolphin	(Di-Meglio et al., 1996)
Odontocete	Delphinidae	Striped dolphin	(Marsili et al., 1997)
Odontocete	Delphinidae	Striped dolphin	(Andre et al., 1991)
Odontocete	Delphinidae	Striped dolphin	(Guarino et al., 2021)
Odontocete	Delphinidae	Striped dolphin	(Honda et al., 1983)
Odontocete	Delphinidae	Striped dolphin	(Marsili et al., 2004)
Odontocete	Delphinidae	Tucuxi	(Di Beneditto and Ramos, 2004)
Odontocete	Delphinidae	Tucuxi	(Ramos *et al.*, 2000)
Odontocete	Delphinidae	Tucuxi	(Rosas et al., 2003)
Odontocete	Delphinidae	White-beaked dolphin	(Galatius *et al.*, 2013)
Mysticete	Eschrichtiidae	Gray whale	(Sumich *et al.*, 2013)
Mysticete	Eschrichtiidae	Gray whale	(Agbayani *et al.*, 2020)
Mysticete	Eschrichtiidae	Gray whale	(Lockyer, 1976)

Odontocete	Kogiidae	Dwarf sperm whale	(Plön, 2004)
Odontocete	Kogiidae	Pygmy sperm whale	(Plön, 2004)
Odontocete	Monodontidae	Beluga	Perrin et al., 1976)
Odontocete	Monodontidae	Beluga	(Heide-Jørgensen and Teilmann, 1994)
Odontocete	Monodontidae	Beluga	(Burns and Seaman, 1986)
Odontocete	Monodontidae	Beluga	(Brodie, 1971)
Odontocete	Monodontidae	Beluga	(Robeck *et al.*, 2005)
Odontocete	Monodontidae	Beluga	(Robeck *et al.*, 2015)
Odontocete	Monodontidae	Beluga	(Vos *et al.*, 2020)
Odontocete	Monodontidae	Beluga	(Luque and Ferguson, 2010)
Odontocete	Monodontidae	Beluga	(Doidge, 1990b)
Odontocete	Monodontidae	Beluga	(Suydam, 2009)
Odontocete	Monodontidae	Beluga	(Luque and Ferguson, 2006)
Odontocete	Monodontidae	Beluga	(Doidge, 1991)
Odontocete	Monodontidae	Beluga	(Sudyam, 2009)
Odontocete	Monodontidae	Beluga	(Braham, 1984)

Odontocete	Monodontidae	Beluga	(Noren et al., 2018)
Odontocete	Monodontidae	Beluga	(Kastelein et al., 1994)
Odontocete	Monodontidae	Narwhal	(Heide-Jørgensen and Garde, 2011)
Odontocete	Monodontidae	Narwhal	(Garde *et al.*, 2007)
Odontocete	Monodontidae	Narwhal	(Hay, 1984)
Odontocete	Monodontidae	Narwhal	(Garde et al. 2015)
Carnivora	Mustelidae	Sea otter	(Laidre et al., 2006)
Pinnipedia	Odobenidae	Walrus	(Knutsen and Born, 1994)
Pinnipedia	Odobenidae	Walrus	Garlich-Miller and Stewart 1998
Pinnipedia	Odobenidae	Walrus	Garlich-Miller and Stewart 1999
Pinnipedia	Otariidae	Antarctic fur seal	Payne, 1979)
Pinnipedia	Otariidae	Antarctic fur seal	Doidge, Croxall, and Ricketts, 1984)
Pinnipedia	Otariidae	Antarctic fur seal	Payne 1979
Pinnipedia	Otariidae	Antarctic fur seal	McLaren 1993
Pinnipedia	Otariidae	California sea lion	(Greig, Gulland, and Kreuder, 2005)
Pinnipedia	Otariidae	California sea lion	(Laake et al., 2016)
Pinnipedia	Otariidae	Cape fur seal	Arnould and Hindell, 2001)
Pinnipedia	Otariidae	Cape fur seal	Gibbens and Arnould, 2009)
Pinnipedia	Otariidae	Cape fur seal	(Stewardson et al., 2009)
Pinnipedia	Otariidae	Cape fur seal	(Guinet et al., 1998)
Pinnipedia	Otariidae	Galapagos fur seal	(Trillmich, 1986)
Pinnipedia	Otariidae	Galapagos sea lion	(Mueller et al., 2011)
Pinnipedia	Otariidae	Galapagos sea lion	Mueller et al 2011
Pinnipedia	Otariidae	Juan Fernández fur seal	(Gallo-Reynoso and Figueroa-Carranza, 2010)

Pinnipedia	Otariidae	Juan Fernández fur seal	(Osman et al., 2010)
Pinnipedia	Otariidae	New Zealand fur seal	(Crawley, 1975)
Pinnipedia	Otariidae	New Zealand fur seal	(Mattlin, 1981)
Pinnipedia	Otariidae	New Zealand fur seal	(Goldsworthy, 1981)
Pinnipedia	Otariidae	New Zealand fur seal	Dickie and Dawson 2003
Pinnipedia	Otariidae	New Zealand fur seal	McKenzie et al 2007
Pinnipedia	Otariidae	New Zealand sea lion	(Childerhouse et al., 2010)
Pinnipedia	Otariidae	Northern fur seal	(Boltnev, York, and Antonelis, 1997)
Pinnipedia	Otariidae	Northern fur seal	(Trites and Bigg, 1996)
Pinnipedia	Otariidae	Northern fur seal	(Trites and Bigg, 1992)
Pinnipedia	Otariidae	South American fur seal	(Lima and Paez, 1995)
Pinnipedia	Otariidae	South American sea lion	(Grandi et al., 2010)
Pinnipedia	Otariidae	Steller sea lion	(Winship, Trites, and Calkins, 2001)
Pinnipedia	Otariidae	Steller sea lion	Winship et al 2002
Pinnipedia	Otariidae	Subantarctic fur seal	(Georges and Guinet, 2000)
Pinnipedia	Otariidae	Subantarctic fur seal	(Guinet and Georges, 2000)
Pinnipedia	Otariidae	Subantarctic fur seal	(Oosthuizen et al., 2016)
Pinnipedia	Otariidae	Subantarctic fur seal	(Beauplet et al., 2005)
Pinnipedia	Otariidae	Subantarctic fur seal	(Kirkman et al., 2002)
Pinnipedia	Otariidae	Subantarctic fur seal	(Bester and Van Jaarzveld, 1994)
Pinnipedia	Otariidae	Subantarctic fur seal	Authier et al 2011
Pinnipedia	Otariidae	Subantarctic fur seal	Dabin et al 2004
Pinnipedia	Otariidae	Subantarctic fur seal	Bester and Jaarsveld 1994
Pinnipedia	Phocidae	Baikal seal	Amano et al 2000

Pinnipedia	Phocidae	Bearded seal	McLaren, 1958)
Pinnipedia	Phocidae	Bearded seal	Kovacs, Krafft, and Lydersen, 2019)
Pinnipedia	Phocidae	Bearded seal	Rosen, Thometz, and Reichmuch, 2021)
Pinnipedia	Phocidae	Bearded seal	Burns and Frost, 1979
Pinnipedia	Phocidae	Bearded seal	Benjaminsen 1973
Pinnipedia	Phocidae	Bearded seal	Andersen et al 1999
Pinnipedia	Phocidae	Caspian seal	McLaren 1993
Pinnipedia	Phocidae	Crabeater seal	Laws et al. 2003a
Pinnipedia	Phocidae	Crabeater seal	Laws et al 2003b
Pinnipedia	Phocidae	Crabeater seal	(Bryden and Erickson, 1976)
Pinnipedia	Phocidae	Gray seal	Yunker et al 2005
Pinnipedia	Phocidae	Gray seal	Hauksson 2007
Pinnipedia	Phocidae	Harbor seal	(Cottrell et al., 2002)
Pinnipedia	Phocidae	Harbor seal	(Bishop, 1967)
Pinnipedia	Phocidae	Harbor seal	Burns and Gol'tsev 1984
Pinnipedia	Phocidae	Harbor seal	Naito and Nishiwaki 1972
Pinnipedia	Phocidae	Harbor seal	Harding et al 2018
Pinnipedia	Phocidae	Harbor seal	Hutchinson et al 2016
Pinnipedia	Phocidae	Harp seal	(Innes, Stewart, and Lavigne, 1981)
Pinnipedia	Phocidae	Harp seal	Chabot and Stenson 2002
Pinnipedia	Phocidae	Harp seal	Hammill et al 1995
Pinnipedia	Phocidae	Harp seal	Stewart et al 1989
Pinnipedia	Phocidae	Hawaiian monk seal	(Baker et al., 2014)
Pinnipedia	Phocidae	Hooded seal	(Wiig, 1985)
Pinnipedia	Phocidae	Leopard seal	McLaren 1993
Pinnipedia	Phocidae	Mediterranean monk seal	Murphy et al 2012
Pinnipedia	Phocidae	Northern elephant seal	Holser et al 2021, Clinton 1994

Pinnipedia	Phocidae	Ribbon seal	(Quakenbush and Citta, 2008)
Pinnipedia	Phocidae	Ringed seal	(Ryg, Smith and Øritsland, 1990)
Pinnipedia	Phocidae	Ringed seal	(Auttila et al., 2015)
Pinnipedia	Phocidae	Ringed seal	(Ferguson et al., 2018)
Pinnipedia	Phocidae	Ringed seal	(Rosen, Thometz, and Reichmuch, 2021)
Pinnipedia	Phocidae	Ross seal	(Skinner and Klages, 1994)
Pinnipedia	Phocidae	Ross seal	Skinner and Klages 1994
Pinnipedia	Phocidae	Southern elephant seal	(Bell, 1997)
Pinnipedia	Phocidae	Southern elephant seal	(Field et al., 2005)
Pinnipedia	Phocidae	Southern elephant seal	(Kastelein, Kershaw, and Wiepkema, 1991)
Pinnipedia	Phocidae	Southern elephant seal	Bell et al 2005
Pinnipedia	Phocidae	Spotted seal	(Rosen, Thometz, and Reichmuch, 2021)
Pinnipedia	Phocidae	Spotted seal	(Quakenbush, Citta and Crawford, 2009)
Pinnipedia	Phocidae	Spotted seal	McLaren 1993
Pinnipedia	Phocidae	Weddell seal	(Stirling, 1971)
Pinnipedia	Phocidae	Weddell seal	McLaren 1993
Odontocete	Phocoenidae	Dall's porpoise	(Gaskin et al., 1984)
Odontocete	Phocoenidae	Dall's porpoise	(Kasuya and Shiraga, 1985)
Odontocete	Phocoenidae	Dall’s porpoise	(Kasuya, 1978)
Odontocete	Phocoenidae	Dall’s porpoise	(Ferrero and Walker, 1999)

Odontocete	Phocoenidae	Finless porpoise	(Shirakihara *et al.*, 1993)
Odontocete	Phocoenidae	Finless porpoise	(Jefferson *et al.*, 2002)
Odontocete	Phocoenidae	Finless porpoise	(Kasuya *et al.*, 1986)
Odontocete	Phocoenidae	Finless porpoise	(Daoquan et al., 2006)
Odontocete	Phocoenidae	Harbor porpoise	(Read, 1990)
Odontocete	Phocoenidae	Harbor porpoise	(Sørensen and Kinze, 1994)
Odontocete	Phocoenidae	Harbor porpoise	(Ólafsdóttir *et al.*, 2003)
Odontocete	Phocoenidae	Harbor porpoise	(Learmonth *et al.*, 2014)
Odontocete	Phocoenidae	Harbor porpoise	(Read and Hohn, 1995)
Odontocete	Phocoenidae	Harbor porpoise	(Richardson *et al.*, 2003)
Odontocete	Phocoenidae	Harbor porpoise	(Lockyer *et al.*, 2003)
Odontocete	Phocoenidae	Harbor porpoise	(Read and Tolley, 1997)
Odontocete	Phocoenidae	Harbor porpoise	(Gol'din, 2004)
Odontocete	Phocoenidae	Harbor porpoise	(Gaskin et al., 1984)
Odontocete	Phocoenidae	Harbor porpoise	(van Utrecht, 1978)
Odontocete	Phocoenidae	Harbor porpoise	(Gaskin and Blair, 1977)

Odontocete	Phocoenidae	Harbor porpoise	(Olafsdottir et al., 2003)
Odontocete	Phocoenidae	Harbor porpoise	(Lockyer et al., 2001)
Odontocete	Phocoenidae	Harbor porpoise	(Lockyer and Kinze, 2003)
Odontocete	Phocoenidae	Harbor porpoise	(Gallagher et al., 2021)
Odontocete	Phocoenidae	Harbor porpoise	(Lockyer, 2003)
Odontocete	Phocoenidae	Harbor porpoise	(Arai et al., 2017)
Odontocete	Phocoenidae	Harbor porpoise	(Read and Gaskin, 1990)
Odontocete	Phocoenidae	Harbor porpoise	(Watts and Gaskin, 1989)
Odontocete	Phocoenidae	Harbor porpoise	(Kastelein Hardeman, and Boer, 1998)
Odontocete	Phocoenidae	Vaquita	(Hohn et al., 1996)
Odontocete	Physeteridae	Sperm whale	(Ohsumi, 1965)
Odontocete	Physeteridae	Sperm whale	(Lockyer, 1991)
Odontocete	Physeteridae	Sperm whale	(Clarke *et al.*, 2011)
Odontocete	Physeteridae	Sperm whale	(Evans and Hindell, 2004)
Odontocete	Physeteridae	Sperm whale	(Dickson, 2020)
Odontocete	Platanistidae	Franciscana	(Negri et al., 2014)
Odontocete	Platanistidae	Indian river dolphin	(Kasuya, 1972)
Odontocete	Pontoporiidae	Franciscana	(Harrison *et al.*, 1981)
Odontocete	Pontoporiidae	Franciscana	(Ramos *et al.*, 2000)

Odontocete	Pontoporiidae	Franciscana	(Kasuya and Brownell-Jr., 1979)
Odontocete	Pontoporiidae	Franciscana	(Botta *et al.*, 2010)
Odontocete	Pontoporiidae	Franciscana	(Barreto and Rosas, 2006)
Odontocete	Pontoporiidae	Franciscana	(Denuncio *et al.*, 2018)
Sirenia	Trichechidae	Amazonian manatee	(Amaral, Da Silva, and Rosas, 2010)
Sirenia	Trichechidae	Amazonian manatee	Mendoza et al 2019
Sirenia	Trichechidae	Amazonian manatee	Vergara-Parente et al 2010
Sirenia	Trichechidae	Dugong	(Cherdsukjai et al., 2020)
Sirenia	Trichechidae	Dugong	Marsh 1980
Sirenia	Trichechidae	West Indian manatee	(Schwarz and Runge, 2009)
	Ursidae	Polar bear	Derocher and Wiig 2002
Odontocete	Ziphiidae	Baird's beaked whale	Kasuya, 1977)
Odontocete	Ziphiidae	Baird's beaked whale	Kasuya, 1977)
Odontocete	Ziphiidae	Baird's beaked whale	Omura, et al. 1955)
Odontocete	Ziphiidae	Northern bottlenose whale	(Benjaminsen and Christensen, 1979)
Odontocete	Ziphiidae	Northern bottlenose whale	(Bloch *et al.*, 1996)

Table A1. 2 List of lipid content in blubber and muscle for marine mammals. For sex, F represents females, M represents males, U represents unknown, and B represents both. For age class, I represents immature, M represents mature, C represents calf, F represents Fetus, and Mu represents Multiple.

Species	**Sex**	**Age Class**	**Blubber**	**sd**	**Muscle**	**sd**	**Reference**
Bowhead whale	U	U	70.50				Tittlemier et al. 2002
Bowhead whale	M	U	76.00	1.60	2.39	1.85	Bolton et al. 2020
Bowhead whale	M	U	70.00	2.60	0.86	0.27	Bolton et al. 2020
Bowhead whale	M	U	79.00	2.00	0.78	0.29	Bolton et al. 2020
Bowhead whale	M	U	81.00	0.79	0.90	0.21	Bolton et al. 2020
Bowhead whale	M	U	83.00	1.60	0.58	0.07	Bolton et al. 2020
Bowhead whale	M	U	84.00	0.82	0.84	0.11	Bolton et al. 2020
Bowhead whale	M	U	85.00	1.10	0.64	0.13	Bolton et al. 2020
Bowhead whale	M	U	82.00	1.20	0.73	0.55	Bolton et al. 2020
Bowhead whale	M	U	85.00	0.59	1.10	0.42	Bolton et al. 2020
Bowhead whale	M	U	79.00	0.76			Bolton et al. 2020
Bowhead whale	M	U	70.00	0.86	0.39		Bolton et al. 2020
Bowhead whale	M	U	80.00	1.70	0.58	0.16	Bolton et al. 2020
Bowhead whale	U	U	75.80	1.60			Hoekstra et al. 2002
Bowhead whale	U	U	75.30	8.00			O'Hara et al. 1999
Bowhead whale	U	U	70.40	2.82			Hoekstra et al. 2002b

North Atlantic right whale	M	M	12.90				Woodley et al. 1991
North Atlantic right whale	F	M	16.10				Woodley et al. 1991
North Atlantic right whale	M	I	21.70				Woodley et al. 1991
North Atlantic right whale	B	C	16.90				Woodley et al. 1991
North Atlantic right whale	U	U	21.10				Woodley et al. 1991
North Atlantic right whale	B	Mu	18.40	25.20			Weisbrod et al. 2000
North Atlantic right whale	B	Mu	10.00	9.10			Weisbrod et al. 2000
North Atlantic right whale	B	Mu	16.00	12.40			Weisbrod et al. 2000
North Atlantic right whale	B	Mu	3.60	3.50			Weisbrod et al. 2000
North Atlantic right whale	M	M	12.90				Woodley et al. 1991
North Atlantic right whale	F	M	16.10				Woodley et al. 1991
North Atlantic right whale	M	I	21.70				Woodley et al. 1991
North Atlantic right whale	B	C	16.90				Woodley et al. 1991
North Atlantic right whale	U	U	21.10				Woodley et al. 1991

Southern right whale	U	U	42.90	1.36			Reeb 2001
Antarctic minke whale	M	Mu	61.66	2.50			Tanabe et al. 1986
Antarctic minke whale	F	Mu	64.98	3.11			Tanabe et al. 1986
Antarctic minke whale	M	M	61.20				Yasunaga and Fujise 2016
Balaenopterids	U	U	47.00				Miller and Hall 2018
Balaenopterids	U	U	58.00				Kershaw et al. 2019
Balaenopterids	U	U	13.00				Kershaw et al. 2019
Blue whale	M	U	50.33	4.98			Gauthier et al. 1997
Blue whale	M	U	55.43	3.47			Gauthier et al. 1997
Blue whale	M	U	42.00	3.19			Gauthier et al. 1997
Blue whale	F	M	70.00				Ackman et al. 1975
Blue whale	F	M	54.20				Ackman et al. 1975
Blue whale	F	M	87.40				Ackman et al. 1975
Bryde's whale	M	M	51.90				Yasunaga and Fujise 2016
Bryde's whale	M	M	61.50	6.93			Yasunaga and Fujise 2009
Bryde's whale	M	M	60.10	0.62			Yasunaga and Fujise 2009
Bryde's whale	M	M	62.80	11.88			Yasunaga and Fujise 2009
Fin whale	U	U	12.00				Das et al. 2015
Fin whale	U	U	84.00				Das et al. 2015
Fin whale	B	M	35.16	3.09			Tanaiguchi et al. 2019
Fin whale	M	U	77.50	7.80			Borrell 1993
Fin whale	F	U	69.00	3.80			Borrell 1993
Fin whale	M	U	31.90	9.60			Pinzone et al. 2015

Fin whale	F	U	28.20	11.80			Pinzone et al. 2015
Fin whale	B	Mu	52.50	4.40	3.60	0.60	Lockyer et al. 1985
Fin whale	B	Mu	44.30	1.30	3.40	0.60	Lockyer et al. 1985
Fin whale	B	Mu	29.10	2.70	3.90	1.30	Lockyer et al. 1985
Fin whale	B	Mu	56.20	1.10	5.10	0.70	Lockyer et al. 1985
Fin whale	B	Mu	44.50	3.40	3.80	0.60	Lockyer et al. 1985
Fin whale	B	Mu	29.50	4.40	4.40	0.90	Lockyer et al. 1985
Fin whale	B	Mu	53.20	3.40	16.20	1.90	Lockyer et al. 1985
Fin whale	B	Mu	48.40	3.90	6.10	1.70	Lockyer et al. 1985
Fin whale	B	Mu	46.30	2.90	9.40	1.70	Lockyer et al. 1985
Fin whale	U	F	1.20		2.40		Lockyer et al. 1985
Fin whale	M	Mu	75.30				Aguilar and Borrell 1990
Fin whale	F	I	77.50				Aguilar and Borrell 1990
Fin whale	F	M	81.40				Aguilar and Borrell 1990
Fin whale	F	M	57.50				Aguilar and Borrell 1990
Fin whale	F	M	60.80				Aguilar and Borrell 1990
Fin whale	M	I	53.20	7.90	7.80	4.30	Lockyer 1986
Fin whale	M	M	52.70	11.60	15.60	6.40	Lockyer 1986
Fin whale	F	I	58.50	9.10	15.80	2.80	Lockyer 1986
Fin whale	F	M	65.50	0.30	21.60	10.10	Lockyer 1986
Fin whale	F	M	45.00	6.40	18.80	4.00	Lockyer 1986
Fin whale	F	M	39.40		17.60		Lockyer 1986
Fin whale	M	I	70.60	1.50	12.40	1.60	Lockyer 1986
Fin whale	M	M	72.50	2.40	11.50	1.30	Lockyer 1986
Fin whale	F	I	71.00	1.20	21.20	0.70	Lockyer 1986

Fin whale	F	M	76.80		29.30		Lockyer 1986
Fin whale	F	M	75.10	3.30	26.00	1.90	Lockyer 1986
Fin whale	F	M	59.00		18.50		Lockyer 1986
Fin whale	U	U	70.27	3.00	6.48	1.40	Aguilar and Borrell 1994
Fin whale	M	I	71.60	14.90			Aguilar and Borrell 1988
Fin whale	M	M	76.76	6.60			Aguilar and Borrell 1988
Fin whale	M	M	67.27	11.70			Aguilar and Borrell 1988
Fin whale	F	I	75.85	8.20			Aguilar and Borrell 1988
Fin whale	F	M	72.45	11.90			Aguilar and Borrell 1988
Fin whale	F	M	62.86	17.10			Aguilar and Borrell 1988
Fin whale	M	M	67.50				Ackman et al. 1965
Fin whale	M	M	37.70				Ackman et al. 1965
Fin whale	M	M	18.60				Ackman et al. 1965
Fin whale	F	M	43.62	8.38			Lockyer et al. 1984
Fin whale	M	M	48.00	9.98			Lockyer et al. 1984
Fin whale	F	M	43.83	19.79			Lockyer et al. 1984
Fin whale	M	I	50.77	18.74			Lockyer et al. 1984
Fin whale	F	F	1.20				Lockyer et al. 1984
Fin whale	F	I	40.95	8.24			Lockyer et al. 1984
Fin whale	M	M	81.00	1.20			Ryan et al. 2013
Fin whale	B	U	70.27	3.00	6.48	1.40	Aguilar and Borrell 1994
Fin whale	F	M	55.75	3.87			Niño-Torres et al. 2009
Fin whale	M	M	60.11	5.95			Niño-Torres et al. 2009

Fin whale	F	U	31.08	5.95			Taniguchi et al. 2019
Fin whale	M	U	35.86	3.95			Taniguchi et al. 2019
Fin whale	B	U	34.66	3.10			Taniguchi et al. 2019
Fin whale	M	M	45.20				Ackman et al. 1975b
Fin whale	M	M	66.00				Ackman et al. 1975b
Fin whale	M	M	55.30				Ackman et al. 1975b
Fin whale	M	M	70.20				Ackman et al. 1975b
Fin whale	F	M	60.10				Ackman et al. 1975b
Fin whale	F	M	71.30				Ackman et al. 1975b
Fin whale	M	M	57.10				Ackman et al. 1975b
Fin whale	M	M	62.50				Ackman et al. 1975b
Fin whale	F	M	12.10				Ackman et al. 1975b
Fin whale	F	M	57.20				Ackman et al. 1975b
Fin whale	F	M	28.00				Ackman et al. 1975b
Fin whale	F	M	61.50				Ackman et al. 1975b
Fin whale	M	M	34.40				Ackman et al. 1975b
Fin whale	M	M	55.00				Ackman et al. 1975b
Fin whale	M	M	57.50				Ackman et al. 1975b
Fin whale	M	M	71.20				Ackman et al. 1975b
Fin whale	F	M	59.40				Ackman et al. 1975b
Fin whale	F	M	69.70				Ackman et al. 1975b

Fin whale	M	M	61.00				Ackman et al. 1975b
Fin whale	M	M	76.00				Ackman et al. 1975b
Fin whale	F	M	14.10				Ackman et al. 1975b
Fin whale	F	M	63.00				Ackman et al. 1975b
Fin whale	F	M	18.00				Ackman et al. 1975b
Fin whale	F	M	56.00				Ackman et al. 1975b
Fin whale	M	M	20.50				Ackman et al. 1975b
Fin whale	M	M	41.00				Ackman et al. 1975b
Fin whale	M	M	26.80				Ackman et al. 1975b
Fin whale	M	M	49.20				Ackman et al. 1975b
Fin whale	F	M	42.10				Ackman et al. 1975b
Fin whale	F	M	47.30				Ackman et al. 1975b
Fin whale	M	M	58.00				Ackman et al. 1975b
Fin whale	M	M	74.00				Ackman et al. 1975b
Fin whale	F	M	14.70				Ackman et al. 1975b
Fin whale	F	M	52.00				Ackman et al. 1975b
Fin whale	F	M	35.20				Ackman et al. 1975b
Fin whale	F	M	56.00				Ackman et al. 1975b
Fin whale	M	M	47.10				Ackman et al. 1975b
Fin whale	M	M	27.00				Ackman et al. 1975b
Fin whale	M	M	25.50				Ackman et al. 1975b

Fin whale	M	M	51.90				Ackman et al. 1975b
Fin whale	F	M	11.00				Ackman et al. 1975b
Fin whale	F	M	23.50				Ackman et al. 1975b
Fin whale	M	M	31.00				Ackman et al. 1975b
Fin whale	M	M	10.00				Ackman et al. 1975b
Fin whale	F	M	15.00				Ackman et al. 1975b
Fin whale	F	M	13.10				Ackman et al. 1975b
Fin whale	F	M	10.10				Ackman et al. 1975b
Fin whale	F	M	41.00				Ackman et al. 1975b
Fin whale	M	M	33.00				Ruchonnet et al. 2006
Fin whale	M	M	69.00				Ruchonnet et al. 2006
Humpback whale	M	M	78.67	13.35			Tanabe et al. 1993
Humpback whale	U	U	45.80	22.60			Bachman et al. 2014
Humpback whale	M	M	43.30	2.50			Waugh et al. 2012
Humpback whale	M	M	32.00	5.00			Waugh et al. 2012
Humpback whale	F	M	46.70	2.70			Waugh et al. 2012
Humpback whale	F	M	46.10	4.80			Waugh et al. 2012
Humpback whale	B	U	31.60	2.20			Elfes et al. 2010
Humpback whale	B	U	28.50	2.90			Elfes et al. 2010
Humpback whale	B	U	14.30	2.80			Elfes et al. 2010
Humpback whale	B	U	27.20	4.20			Elfes et al. 2010

Humpback whale	B	U	25.20	3.60			Elfes et al. 2010
Humpback whale	B	U	31.10	6.30			Elfes et al. 2010
Humpback whale	B	U	20.50	3.90			Elfes et al. 2010
Humpback whale	B	U	27.20	3.80			Elfes et al. 2010
Humpback whale	B	U	16.10	3.00			Elfes et al. 2010
Humpback whale	B	U	19.10	3.30			Elfes et al. 2010
Humpback whale	B	Mu	48.20	12.80			Christiansen et al. 2020
Humpback whale	M	M	51.24	3.10			Waugh et al. 2014
Humpback whale	F	M	59.50	6.40			Waugh et al. 2014
Humpback whale	M	M	44.46	7.09			Waugh et al. 2014
Humpback whale	M	M	44.46	5.14			Waugh et al. 2014
Humpback whale	F	M	33.15	9.45			Waugh et al. 2014
Humpback whale	M	M	44.46	5.79			Waugh et al. 2014
Humpback whale	M	M	50.00	13.00			Nash et al. 2013
Humpback whale	M	M	39.00	18.20			Nash et al. 2013
Humpback whale	M	M	35.50	14.30			Grob et al. 2020
Humpback whale	M	M	35.50	16.60			Grob et al. 2020
Humpback whale	M	M	56.70	14.80			Grob et al. 2020
Humpback whale	F	M	18.00				Ackman et al. 1975b
Humpback whale	F	M	47.30				Ackman et al. 1975b
Humpback whale	F	M	10.00				Ackman et al. 1975b

Humpback whale	F	M	18.00				Ackman et al. 1975b
Humpback whale	F	M	21.00				Ackman et al. 1975b
Humpback whale	F	M	15.00				Ackman et al. 1975b
Humpback whale	F	M	23.00				Ackman et al. 1975b
Humpback whale	U	I	66.84				Holyoake et al. 2012
Humpback whale	U	I	87.67				Holyoake et al. 2012
Humpback whale	U	I	79.12				Holyoake et al. 2012
Humpback whale	F	I	12.44				Holyoake et al. 2012
Humpback whale	F	I	2.57				Holyoake et al. 2012
Humpback whale	F	I	2.56				Holyoake et al. 2012
Humpback whale	U	I	2.45				Holyoake et al. 2012
Humpback whale	U	I	0.71				Holyoake et al. 2012
Humpback whale	U	I	1.29				Holyoake et al. 2012
Humpback whale	M	I	4.11				Holyoake et al. 2012
Humpback whale	M	I	3.65				Holyoake et al. 2012
Humpback whale	M	I	1.40				Holyoake et al. 2012
Humpback whale	M	I	4.10				Holyoake et al. 2012
Humpback whale	M	I	1.06				Holyoake et al. 2012
Humpback whale	M	I	0.44				Holyoake et al. 2012
Humpback whale	F	I	45.42				Holyoake et al. 2012
Humpback whale	F	I	49.38				Holyoake et al. 2012

Humpback whale	F	I	50.00				Holyoake et al. 2012
Humpback whale	F	I	3.26				Holyoake et al. 2012
Humpback whale	F	I	0.75				Holyoake et al. 2012
Humpback whale	F	I	0.43				Holyoake et al. 2012
Humpback whale	M	I	10.30				Holyoake et al. 2012
Humpback whale	M	I	5.58				Holyoake et al. 2012
Humpback whale	M	I	2.06				Holyoake et al. 2012
Humpback whale	M	U			50.00	13.00	Bengtson Nash, Waugh and Schlabach 2013
Humpback whale	M	U			39.00	18.20	Bengtson Nash, Waugh and Schlabach 2013
Minke whale	F	M			2.35	2.47	Víkingsson et al. 2013
Minke whale	F	M			11.04	10.72	Víkingsson et al. 2013
Minke whale	F	M			12.10	8.29	Víkingsson et al. 2013
Minke whale	F	M			1.88	2.09	Víkingsson et al. 2013
Minke whale	F	M			3.73	3.29	Víkingsson et al. 2013
Minke whale	F	M			3.05	2.55	Víkingsson et al. 2013
Minke whale	F	M			1.85	1.59	Víkingsson et al. 2013
Minke whale	F	M			7.85	8.59	Víkingsson et al. 2013
Minke whale	F	M	19.18	11.41			Víkingsson et al. 2013
Minke whale	F	M	53.81	12.89			Víkingsson et al. 2013
Minke whale	F	M	59.68	13.63			Víkingsson et al. 2013

Minke whale	F	M	76.02	16.30			Víkingsson et al. 2013
Minke whale	F	M	61.05	15.77			Víkingsson et al. 2013
Minke whale	F	M	66.87	12.79			Víkingsson et al. 2013
Minke whale	F	M	65.06	10.48			Víkingsson et al. 2013
Minke whale	F	M	54.31	15.13			Víkingsson et al. 2013
Minke whale	F	M	64.77	8.32			Víkingsson et al. 2013
Minke whale	M	I	81.02	5.63			Víkingsson et al. 2013
Minke whale	M	M	64.86	24.75			Víkingsson et al. 2013
Minke whale	M	I	73.56	28.01			Víkingsson et al. 2013
Minke whale	F	M	68.47	16.71			Víkingsson et al. 2013
Minke whale	F	I	77.91	9.60			Víkingsson et al. 2013
Minke whale	F	M	76.02	16.30			Víkingsson et al. 2013
Minke whale	M	I			4.20	3.84	Víkingsson et al. 2013
Minke whale	M	M			8.29	8.11	Víkingsson et al. 2013
Minke whale	M	I			14.39	11.11	Víkingsson et al. 2013
Minke whale	F	M			4.00	1.90	Víkingsson et al. 2013
Minke whale	F	I			5.82	4.69	Víkingsson et al. 2013
Minke whale	F	M			12.10	8.29	Víkingsson et al. 2013
Minke whale	U	U			9.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			9.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			8.00		Niæss, Haug, and Nilssen 1998

Minke whale	U	U			9.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			8.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			20.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			12.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			13.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			6.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			16.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			6.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			17.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			20.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			30.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			12.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			35.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			12.00		Niæss, Haug, and Nilssen 1998
Minke whale	U	U			44.00		Niæss, Haug, and Nilssen 1998
Fin/minke whale	B	I	61.00	24.00			Yamato et al. 2014
Sei whale	M	U	57.20	1.50			Borrell 1993
Sei whale	F	U	67.80	1.30			Borrell 1993
Sei whale	B	Mu	53.60	2.80	6.90	1.80	Lockyer et al. 1985
Sei whale	B	Mu	45.40	2.50	11.40	2.20	Lockyer et al. 1985
Sei whale	B	Mu	39.20	4.10	6.10	0.90	Lockyer et al. 1985
Sei whale	B	Mu	57.90	2.20	7.50	2.00	Lockyer et al. 1985

Sei whale	B	Mu	58.80	3.60	5.00	1.10	Lockyer et al. 1985
Sei whale	B	Mu	42.80	2.50	3.80	0.70	Lockyer et al. 1985
Sei whale	B	Mu	70.50	1.20	15.30	2.60	Lockyer et al. 1985
Sei whale	B	Mu	67.70	2.10	8.30	2.00	Lockyer et al. 1985
Sei whale	B	Mu	53.90	5.10	8.50	1.00	Lockyer et al. 1985
Sei whale	M	M	75.20		3.20		Bottino 1978
Sei whale	F	M	76.30				Ackman et al. 1975
Sei whale	F	M	66.66				Ackman et al. 1975
Sei whale	F	M	88.89				Ackman et al. 1975
Sei whale	M	M	73.00				Yasunaga and Fujise 2016
Sei whale	M	M	49.00				Ackman et al. 1975b
Sei whale	M	M	61.00				Ackman et al. 1975b
Sei whale	F	M	40.00				Ackman et al. 1975b
Sei whale	F	M	68.50				Ackman et al. 1975b
Sei whale	F	M	39.00				Ackman et al. 1975b
Sei whale	F	M	62.80				Ackman et al. 1975b
Sei whale	M	M	29.80				Ackman et al. 1975b
Sei whale	M	M	59.60				Ackman et al. 1975b
Sei whale	M	M	38.40				Ackman et al. 1975b
Sei whale	M	M	63.40				Ackman et al. 1975b
Sei whale	F	M	52.50				Ackman et al. 1975b
Sei whale	F	M	79.00				Ackman et al. 1975b

Sei whale	M	M	49.40				Ackman et al. 1975b
Sei whale	M	M	55.60				Ackman et al. 1975b
Sei whale	M	M	35.00				Ackman et al. 1975b
Sei whale	M	M	54.00				Ackman et al. 1975b
Sei whale	F	M	36.30				Ackman et al. 1975b
Sei whale	F	M	68.70				Ackman et al. 1975b
Sei whale	F	M	28.80				Ackman et al. 1975b
Sei whale	F	M	50.50				Ackman et al. 1975b
Sei whale	M	M	22.90				Ackman et al. 1975b
Sei whale	M	M	60.80				Ackman et al. 1975b
Sei whale	M	M	32.10				Ackman et al. 1975b
Sei whale	M	M	33.00				Ackman et al. 1975b
Sei whale	M	M	57.90	4.92			Yasunaga and Fujise 2009
Sei whale	M	M	59.30	8.57			Yasunaga and Fujise 2009
Sei whale	M	M	64.60	6.97			Yasunaga and Fujise 2009
Humpback whale	U	U	12.00				Das et al. 2015
Humpback whale	U	U	84.00				Das et al. 2015
Minke whale	M	I	38.00	8.60			Moon et al. 2010
Minke whale	M	M	44.00	12.00			Moon et al. 2010
Minke whale	F	I	32.00	10.00			Moon et al. 2010
Minke whale	M	M	74.00				Aono et al. 1997

Minke whale	M	M	74.00				Aono et al. 1997
Minke whale	M	M	80.00				Aono et al. 1997
Minke whale	M	M	79.00				Aono et al. 1997
Minke whale	M	M	78.00				Aono et al. 1997
Minke whale	M	M	85.00				Aono et al. 1997
Minke whale	F	U	56.92	6.30			Gauthier et al. 1997
Minke whale	F	U	63.50	7.01			Gauthier et al. 1997
Minke whale	F	U	58.70	7.65			Gauthier et al. 1997
Minke whale	M	M	29.30				Yasunaga and Fujise 2016
Minke whale	M	M	75.70	3.99			Yasunaga and Fujise 2009
Minke whale	M	M	65.70	7.12			Yasunaga and Fujise 2009
Minke whale	M	M	66.40	6.32			Yasunaga and Fujise 2009
Minke whale	F	M	20.35		2.35	2.47	Víkingsson et al. 2013
Minke whale	F	M			11.04	10.72	Víkingsson et al. 2013
Minke whale	F	M			12.10	8.29	Víkingsson et al. 2013
Minke whale	F	M			1.88	2.09	Víkingsson et al. 2013
Minke whale	F	M			3.73	3.29	Víkingsson et al. 2013
Minke whale	F	M			3.05	2.55	Víkingsson et al. 2013
Minke whale	F	M			1.85	1.59	Víkingsson et al. 2013
Minke whale	F	M			7.85	8.59	Víkingsson et al. 2013
Minke whale	F	M	20.35	1.70			Víkingsson et al. 2013

Minke whale	F	M	16.31	5.74			Víkingsson et al. 2013
Minke whale	F	M	14.09	4.48			Víkingsson et al. 2013
Minke whale	F	M	5.89	3.19			Víkingsson et al. 2013
Minke whale	F	M	12.86	3.29			Víkingsson et al. 2013
Minke whale	F	M	11.36	3.49			Víkingsson et al. 2013
Minke whale	F	M	11.08	4.54			Víkingsson et al. 2013
Minke whale	F	M	12.98	5.32			Víkingsson et al. 2013
Minke whale	F	M	10.75	4.69			Víkingsson et al. 2013
Minke whale	M	I	81.02	5.63			Víkingsson et al. 2013
Minke whale	M	M	64.86	24.75			Víkingsson et al. 2013
Minke whale	M	I	73.56	28.01			Víkingsson et al. 2013
Minke whale	F	M	68.47	16.71			Víkingsson et al. 2013
Minke whale	F	I	77.91	9.60			Víkingsson et al. 2013
Minke whale	F	M	76.02	16.30			Víkingsson et al. 2013
Minke whale	M	I			4.20	3.84	Víkingsson et al. 2013
Minke whale	M	M			8.29	8.11	Víkingsson et al. 2013
Minke whale	M	I			14.39	11.11	Víkingsson et al. 2013
Minke whale	F	M			4.00	1.90	Víkingsson et al. 2013
Minke whale	F	I			5.82	4.69	Víkingsson et al. 2013
Minke whale	F	M			12.10	8.29	Víkingsson et al. 2013
Minke whale	U	U	46.00				Kvadsheim et al. 1996

Minke whale	U	U	83.00				Kvadsheim et al. 1996
Minke whale	U	U	72.00				Kvadsheim et al. 1996
Minke whale	U	U	96.00				Kvadsheim et al. 1996
Minke whale	U	U	68.00				Kvadsheim et al. 1996
Minke whale	U	U	88.00				Kvadsheim et al. 1996
Minke whale	U	U	42.00				Kvadsheim et al. 1996
Minke whale	U	U	66.00				Kvadsheim et al. 1996
Atlantic spotted dolphin	M	I	19				Kajiwara et al. 2004
Atlantic spotted dolphin	M	M	18				Kajiwara et al. 2004
Atlantic spotted dolphin	U	U	48.4	11.7			Koopman 2007
Atlantic spotted dolphin	U	U	54.3	9.9			Koopman 2007
Atlantic spotted dolphin	M	M	54.80	9.97			Yogui et al. 2011
Atlantic spotted dolphin	B	Mu	62.00	5.25			Leonel et al. 2012
Atlantic spotted dolphin	B	M	56.02	2.93			Isobe et al. 2009
Atlantic spotted dolphin	M	U	11.40	7.03			Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	F	U	15.10	13.90			Mendez-Fernandez et al. 2018

Atlantic spotted dolphin	M	U	47.50	15.20			Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	F	U	64.00	14.30			Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	U	U	26.40				Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	F	U	13.40				Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	M	U	20.40	13.40			Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	F	U	25.70	23.70			Mendez-Fernandez et al. 2018
Atlantic spotted dolphin	U	U	21.00	8.90			Mendez-Fernandez et al. 2018
Atlantic white-sided dolphin	U	U	43.80	17.20			Weisbrod et al 2001
Atlantic white-sided dolphin	U	U	71.60	1.48			Peck et al. 2008
Atlantic white-sided dolphin	M	U	80.30	5.00			Borrell 1993
Atlantic white-sided dolphin	F	U	83.70	3.70			Borrell 1993
Atlantic white-sided dolphin	B	Mu	67.80	2.51			McKenzie et al. 1997
Atlantic white-sided dolphin	U	U	85.19				Troisi et al. 2018
Bottlenose dolphin	F	M	96.10		2.00		Duinker et al 1989
Bottlenose dolphin	B	I	57.00				Struntz et al 2004

Bottlenose dolphin	B	I	74.00				Struntz et al 2004
Bottlenose dolphin	B	I	57.00				Struntz et al 2004
Bottlenose dolphin	B	M	68.00				Struntz et al 2004
Bottlenose dolphin	M	U	33	3			Lailson-Brito et al. 2012
Bottlenose dolphin	M	C	45.00				Karuppiah et al. 2005
Bottlenose dolphin	F	I	50.00				Karuppiah et al. 2005
Bottlenose dolphin	M	M	42.00				Karuppiah et al. 2005
Bottlenose dolphin	F	M	43.00				Karuppiah et al. 2005
Bottlenose dolphin	B	I	28.30				Hansen et al. 2004
Bottlenose dolphin	M	M	29.50				Hansen et al. 2004
Bottlenose dolphin	F	M	30.00				Hansen et al. 2004
Bottlenose dolphin	B	I	31.00				Hansen et al. 2004
Bottlenose dolphin	M	M	19.90				Hansen et al. 2004
Bottlenose dolphin	F	M	29.70				Hansen et al. 2004
Bottlenose dolphin	M	M	39.40				Hansen et al. 2004
Bottlenose dolphin	F	M	46.80				Hansen et al. 2004
Bottlenose dolphin	B	Mu					Watanabe et al. 2000
Bottlenose dolphin	B	U	61.19	22.88			Borrell et al. 2006
Bottlenose dolphin	B	U	67.34	15.21			Borrell et al. 2006
Bottlenose dolphin	B	U	36.90	18.52			Borrell et al. 2006
Bottlenose dolphin	B	U	51.65	11.14			Borrell et al. 2006

Bottlenose dolphin	B	U	41.12	13.5			Borrell et al. 2006
Bottlenose dolphin	U	U	69.8	3.3			Koopman 2007
Bottlenose dolphin	U	U	59.6	3.5			Koopman 2007
Bottlenose dolphin	B	F	35.06	6.09			Dunkin et al. 2005
Bottlenose dolphin	B	I	55.82	2.86			Dunkin et al. 2005
Bottlenose dolphin	B	I	69.72	4.08			Dunkin et al. 2005
Bottlenose dolphin	B	I	62.59	2.31			Dunkin et al. 2005
Bottlenose dolphin	B	M	54.31	4.88			Dunkin et al. 2005
Bottlenose dolphin	F	M	69.20	5.73			Dunkin et al. 2005
Bottlenose dolphin	B	M	28.22	9.14			Dunkin et al. 2005
Bottlenose dolphin	B	Mu	42.05	12.44726	0.69	0.17	Yordy et al. 2010
Bottlenose dolphin	U	U	22				Balmer et al. 2015
Bottlenose dolphin	U	U	25				Balmer et al. 2015
Bottlenose dolphin	U	U	27				Balmer et al. 2015
Bottlenose dolphin	U	U	27				Balmer et al. 2015
Bottlenose dolphin	U	U	25				Balmer et al. 2015
Bottlenose dolphin	U	U	15				Balmer et al. 2015
Bottlenose dolphin	B	Mu	36.00	10.00			Fair et al. 2007
Bottlenose dolphin	B	I	49.30	1.90			Montie et al. 2008
Bottlenose dolphin	B	I	34.20	1.70			Montie et al. 2008
Bottlenose dolphin	B	F	36.50	4.35			Dunkin et al. 2010

Bottlenose dolphin	B	I	55.80	4.70			Dunkin et al. 2010
Bottlenose dolphin	B	I	69.70	5.14			Dunkin et al. 2010
Bottlenose dolphin	B	I	62.03	4.35			Dunkin et al. 2010
Bottlenose dolphin	B	M	54.30	4.70			Dunkin et al. 2010
Bottlenose dolphin	F	M	69.20	5.76			Dunkin et al. 2010
Bottlenose dolphin	B	M	28.20	5.76			Dunkin et al. 2010
Bottlenose dolphin	U	U	39.40				McLelland et al. 2012
Bottlenose dolphin	U	U	59.90				McLelland et al. 2012
Bottlenose dolphin	U	U	42.00				McLelland et al. 2012
Bottlenose dolphin	U	U	2.00				Das et al. 2015
Bottlenose dolphin	U	U	46.00				Das et al. 2015
Bottlenose dolphin	B	M	57.25	6.76			Tanabe et al. 1993
Bottlenose dolphin	B	I	38.00				Fair et al. 2010
Bottlenose dolphin	F	M	37.90				Fair et al. 2010
Bottlenose dolphin	M	M	32.40				Fair et al. 2010
Bottlenose dolphin	B	I	45.50				Fair et al. 2010
Bottlenose dolphin	F	M	38.60				Fair et al. 2010
Bottlenose dolphin	M	M	32.60				Fair et al. 2010
Bottlenose dolphin	U	U	47.00				Tittlemier et al. 2002
Bottlenose dolphin	M	M	25.12				Balmer et al. 2011
Bottlenose dolphin	M	M	27.90				Balmer et al. 2011

Bottlenose dolphin	M	M	23.57				Balmer et al. 2011
Bottlenose dolphin	F	M	32.80				Balmer et al. 2011
Bottlenose dolphin	F	M	28.61				Balmer et al. 2011
Bottlenose dolphin	F	M	36.44				Balmer et al. 2011
Bottlenose dolphin	M	U	50.00				Kucklick et al. 2011
Bottlenose dolphin	M	U	51.50				Kucklick et al. 2011
Bottlenose dolphin	M	U	60.60				Kucklick et al. 2011
Bottlenose dolphin	M	U	56.20				Kucklick et al. 2011
Bottlenose dolphin	M	U	32.10				Kucklick et al. 2011
Bottlenose dolphin	M	U	22.00				Kucklick et al. 2011
Bottlenose dolphin	M	U	23.90				Kucklick et al. 2011
Bottlenose dolphin	M	U	26.40				Kucklick et al. 2011
Bottlenose dolphin	M	U	26.40				Kucklick et al. 2011
Bottlenose dolphin	M	U	36.70				Kucklick et al. 2011
Bottlenose dolphin	M	U	15.70				Kucklick et al. 2011
Bottlenose dolphin	M	U	30.40				Kucklick et al. 2011
Bottlenose dolphin	M	U	32.30				Kucklick et al. 2011
Bottlenose dolphin	M	U	29.20				Kucklick et al. 2011
Bottlenose dolphin	U	U	36.50				Johnson-Restrepo et al. 2005
Bottlenose dolphin	U	U	34.60				Johnson-Restrepo et al. 2005
Bottlenose dolphin	U	U	39.00				Johnson-Restrepo et al. 2005

Bottlenose dolphin	M	M	18.10	12.00			Damseaux et al. 2017
Bottlenose dolphin	F	M	27.60	11.40			Damseaux et al. 2017
Bottlenose dolphin	M	M	7.40	5.20			Damseaux et al. 2017
Bottlenose dolphin	F	M	6.80	2.80			Damseaux et al. 2017
Bottlenose dolphin	M	M	73.60				Yogui et al. 2011
Bottlenose dolphin	M	U	11.00	6.00			Zanuttini et al. 2019
Bottlenose dolphin	F	U	11.00	4.00			Zanuttini et al. 2019
Bottlenose dolphin	B	Mu	45.90	7.00			StorellMuarcotrigiano 2003
Bottlenose dolphin	U	U	37.90	22.40			Bachman et al. 2014
Bottlenose dolphin	U	U			7.47		Lavandier et al. 2019
Bottlenose dolphin	B	M	33.00	20.00			Romanic et al. 2014
Bottlenose dolphin	M	Mu	29.00				Balmer et al. 2018
Bottlenose dolphin	M	Mu	26.00				Balmer et al. 2018
Bottlenose dolphin	M	Mu	26.00				Balmer et al. 2018
Bottlenose dolphin	M	I	44.20	12.70			Yordy et al. 2010b
Bottlenose dolphin	F	I	43.20	11.70			Yordy et al. 2010b
Bottlenose dolphin	M	M	20.00	10.50			Yordy et al. 2010b
Bottlenose dolphin	F	M	37.10	11.70			Yordy et al. 2010b
Bottlenose dolphin	B	I	47.30				Yordy et al. 2010c
Bottlenose dolphin	M	M	25.90				Yordy et al. 2010c
Bottlenose dolphin	F	M	39.70				Yordy et al. 2010c

Clymene's dolphin	U	U	61.6	.6			Koopman 2007
Clymene's dolphin	U	U	77	7.3			Koopman 2007
Common dolphin	F	U	93.90		1.20		Duinker et al 1989
Common dolphin	F	M	57.00				Borell and Aguilar 2005
Common dolphin	B	C	73.00				Borell and Aguilar 2005
Common dolphin	U	U	67.00				Minh et al. 2000
Common dolphin	F	M	52.00000	5.12			Stockin et al. 2007
Common dolphin	M	M	58.36364	3.33			Stockin et al. 2007
Common dolphin	M	U	57.50000	0.50			Stockin et al. 2007
Common dolphin	F	U	83.37	0.89			Law et al. 2013
Common dolphin	U	U	56.2	4.5			Koopman 2007
Common dolphin	U	U	52.1	3.4			Koopman 2007
Common dolphin	B	I	64.08	11.78			Tornero et al. 2006
Common dolphin	M	M	59.11	8.28			Tornero et al. 2006
Common dolphin	F	M	58.21	11.55			Tornero et al. 2006
Common dolphin	M	M	65.64	4.85			Durante et al. 2016
Common dolphin	U	U	80.85				Troisi et al. 2018
Dusky dolphin	U	U	57	4.9			Koopman 2007
False killer whale	F	U	18				Lailson-Brito et al. 2012
False killer whale	M	M	89				Jarman et al. 1996
False killer whale	B	U	93				Jarman et al. 1996

False killer whale	U	U	46.50				Bachman et al. 2014
Franciscana	F	I	87				Kajiwara et al. 2004
Franciscana	F	M	79				Kajiwara et al. 2004
Franciscana	M	I	87				Kajiwara et al. 2004
Franciscana	M	M	80				Kajiwara et al. 2004
Franciscana	M	Mu	83.70	2.79			Yogui et al. 2011
Franciscana	F	Mu	85.20	6.82			Yogui et al. 2011
Fraser's/spinner dolphin	U	U	54.20				Tittlemier et al. 2002
Fraser's dolphin	U	U	70.00				Minh et al. 2000
Fraser's dolphin	U	U	66.00				Minh et al. 2000
Fraser's dolphin	B	U	16	6			Lailson-Brito et al. 2012
Fraser's dolphin	U	U	35.8				Koopman 2007
Fraser's dolphin	U	U	59.1				Koopman 2007
Fraser's dolphin	M	M	44.50	6.79			Durante et al. 2016
Guiana dolphin	F	I	81				Kajiwara et al. 2004
Guiana dolphin	F	M	55				Kajiwara et al. 2004
Guiana dolphin	M	I	76				Kajiwara et al. 2004
Guiana dolphin	M	M	72				Kajiwara et al. 2004
Guiana dolphin	F	I	59.60000	12.882546			Santos-Neto et al. 2014
Guiana dolphin	M	I	54.40000	9.760123			Santos-Neto et al. 2014
Guiana dolphin	U	I	26.00000				Santos-Neto et al. 2014
Guiana dolphin	F	M	52.42857	7.714727			Santos-Neto et al. 2014

Guiana dolphin	M	M	52.85714	4.973399			Santos-Neto et al. 2014
Guiana dolphin	M	M	67.80	6.31			Yogui et al. 2011
Guiana dolphin	F	M	70.10	9.19			Yogui et al. 2011
Guiana dolphin	B	Mu	20.00				Alonso et al. 2010
Guiana dolphin	B	Mu	50.00				Alonso et al. 2010
Guiana dolphin	M	Mu	20.00				Alonso et al. 2010
Guiana dolphin	M	Mu	33.00				Alonso et al. 2010
Hector's dolphin	F	U	85.17	3.27			Stockin et al. 2010
Hector's dolphin	M	U	87.50	1.87			Stockin et al. 2010
Hector's dolphin	U	U	83.5	3.2			Koopman 2007
Hector's dolphin	U	U	85.1	2.3			Koopman 2007
Hector's dolphin	U	U	50.60				Tittlemier et al. 2002
Indo-Pacific bottlenose dolphin	M	F	29.7				Mwevura et al. 2010
Indo-Pacific bottlenose dolphin	F	I	36.35	1.666583			Mwevura et al. 2010
Indo-Pacific bottlenose dolphin	M	I	34.32	1.547062			Mwevura et al. 2010
Indo-Pacific bottlenose dolphin	F	M	39.85	2.439091			Mwevura et al. 2010
Indo-Pacific bottlenose dolphin	M	M	43.525	1.961876			Mwevura et al. 2010
Indo-Pacific humpback dolphin	U	U	46.00				Minh et al. 2000

Indo-Pacific humpback dolphin	M	M	55.00				Karuppiah et al. 2005
Indo-Pacific humpback dolphin	F	U	46.500	28.50			Ramu et al. 2005
Indo-Pacific humpback dolphin	M	U	29.63	4.765716			Ramu et al. 2005
Indo-Pacific humpback dolphin	U	U	31.84	9.385393			Ramu et al. 2005
Indo-Pacific humpback dolphin	B	Mu	46.70	19.70			Gui et al. 2014
Indo-Pacific humpback dolphin	U	U	39.30				Tittlemier et al. 2002
Indo-Pacific humpback dolphin	B	M	17.40	2.22			Wu et al. 2013
Indo-Pacific humpback dolphin	U	U	36.00				Sun et al. 2020
Indo-Pacific humpback dolphin	U	U	86.90				Sun et al. 2020
Indo-Pacific humpback dolphin	B	Mu	51.86	8.93			Parsons and Chan 1998
Irrawaddy dolphin	M	I	53.00		12.00		Kannan et al. 2005
Irrawaddy dolphin	F	M	13.00		16.00		Kannan et al. 2005
Irrawaddy dolphin	M	M	17.00				Kannan et al. 2005
Irrawaddy dolphin	F	M	22.00				Kannan et al. 2005
Killer whale	F	U	44				Lailson-Brito et al. 2012
Killer whale	Mu	U	28.00	9.80			Ylitalo et al. 2001

Killer whale	Mu	U	24.00	9.50			Ylitalo et al. 2001
Killer whale	B	M	91				Jarman et al. 1996
Killer whale	F	U	31	16			Krahn et al. 2004
Killer whale	F	U	25	12			Krahn et al. 2004
Killer whale	F	U	40	5			Krahn et al. 2004
Killer whale	F	U	37	18			Krahn et al. 2004
Killer whale	F	U	35	5			Krahn et al. 2004
Killer whale	F	U	10				Krahn et al. 2004
Killer whale	F	U	9				Krahn et al. 2004
Killer whale	F	U	8.3				Krahn et al. 2004
Killer whale	F	U	51	11			Krahn et al. 2004
Killer whale	F	U	50	13			Krahn et al. 2004
Killer whale	M	U	29	4			Krahn et al. 2004
Killer whale	M	M	10.2	10.6			Herman et al. 2005
Killer whale	M	M	16.9	17.3			Herman et al. 2005
Killer whale	M	M	17.3	18.4			Herman et al. 2005
Killer whale	U	U	57.80				Koopman 2007
Killer whale	U	U	2.70				Koopman 2007
Killer whale	U	U	87.90				Tittlemier et al. 2002
Killer whale	U	U	38.80				Bachman et al. 2014
Killer whale	F	M	66.33	3.16			Schlingermann et al. 2020
Killer whale	U	F	22.81	6.55			Schlingermann et al. 2020
Killer whale	F	M	67.56	12.32			Schlingermann et al. 2020
Killer whale	M	M	56.50	6.22			Schlingermann et al. 2020
Killer whale	B	Mu	57.10				Pedro et al. 2017
Killer whale	M	M	67.70				Pedro et al. 2017
Killer whale	F	M	57.20				Pedro et al. 2017
Killer whale	B	I	54.70				Pedro et al. 2017
Killer whale	B	F	45.20				Pedro et al. 2017

Killer whale	F	Mu	61.30				Pedro et al. 2017
Killer whale	M	I	83.70				Pedro et al. 2017
Killer whale	F	M	68.70				Ikonomou, Rayne, and Crewe 2007
Killer whale	M	M	6.30	1.10			Lawson et al. 2020
Killer whale	M	M	19.00	2.20			Lawson et al. 2020
Killer whale	M	M	19.00	2.20			Lawson et al. 2020
Killer whale	M	M	9.50	1.20			Lawson et al. 2020
Killer whale	B	Mu	23.87				Krahn et al. 2009
Long-beaked common dolphin	B	U	41	34			Lailson-Brito et al. 2012
Long-beaked common dolphin	M	M	57				Kajiwara et al. 2004
Long-beaked common dolphin	M	M	15.10				Gallo-Reynoso et al. 2015
Long-beaked common dolphin	F	M	18.50				Gallo-Reynoso et al. 2015
Long-beaked common dolphin	M	I	16.00				Gallo-Reynoso et al. 2015
Long-beaked common dolphin	F	I	22.50				Gallo-Reynoso et al. 2015
Long-beaked common dolphin	M	M	41.00	8.10			Moon et al. 2010

Long-beaked common dolphin	F	M	41.00	12.00			Moon et al. 2010
Long-finned pilot whale	B	Mu	40.20	22.50	1.80	1.10	Weisbrod et al. 2001
Long-finned pilot whale	M	I	79.4	7.2			Borrell et al. 1995
Long-finned pilot whale	M	M	79.9	2.4			Borrell et al. 1995
Long-finned pilot whale	F	I	78.6	7.6			Borrell et al. 1995
Long-finned pilot whale	F	M	79.2	6			Borrell et al. 1995
Long-finned pilot whale	F	M	24	6			Borrell et al. 1995
Long-finned pilot whale	U	U	71.4	6.8			Koopman 2007
Long-finned pilot whale	U	U	53.2	5.5			Koopman 2007
Long-finned pilot whale	M	U	73	2			Muir et al. 1988
Long-finned pilot whale	F	U	70	19			Muir et al. 1988
Long-finned pilot whale	B	Mu	51.30	14.20			Garcia-Cegarra et al. 2021
Long-finned pilot whale	U	U	4.00				Das et al. 2015
Long-finned pilot whale	U	U	80.00				Das et al. 2015
Long-finned pilot whale	M	U	77.20	6.50			Borrell 1993
Long-finned pilot whale	F	U	77.00	10.10			Borrell 1993
Long-finned pilot whale	M	U	23.00	16.00			Pinzone et al. 2015
Long-finned pilot whale	F	U	22.00	10.00			Pinzone et al. 2015
Long-finned pilot whale	U	U	60.39				Troisi et al. 2018
Long-finned pilot whale	F	M	79.00				Lindström et al. 1999

Long-finned pilot whale	M	M	66.00				Lindström et al. 1999
Long-finned pilot whale	M	I	76.00				Lindström et al. 1999
Long-finned pilot whale	F	I	72.00				Lindström et al. 1999
Long-finned pilot whale	F	M	82.00				Lindström et al. 1999
Long-finned pilot whale	B	I	86.00	6.60			Dam and Bloch 2000
Long-finned pilot whale	F	M	86.40	6.70			Dam and Bloch 2000
Long-finned pilot whale	M	M	89.10	6.30			Dam and Bloch 2000
Long-finned pilot whale	F	M	76.00	7.10			Tilbury et al. 1999
Long-finned pilot whale	B	F	4.70	2.50			Tilbury et al. 1999
Long-finned pilot whale	F	M	75.00	3.20			Tilbury et al. 1999
Long-finned pilot whale	M	M	69.00	3.40			Tilbury et al. 1999
Longman's beaked whale	U	U	57.10				Bachman et al. 2014
Maui's dolphin	F	U	86.80	8.70			Stockin et al. 2010
Maui's dolphin	M	U	66.10				Stockin et al. 2010
Melon-headed whale	B	F	42.00				Kajiwara et al. 2008
Melon-headed whale	M	I	66.00				Kajiwara et al. 2008
Melon-headed whale	M	M	61.00				Kajiwara et al. 2008
Melon-headed whale	F	M	55.00				Kajiwara et al. 2008

Melon-headed whale	M	M	66.00				Kunisue et al. 2021
Melon-headed whale	M	M	53.00				Kunisue et al. 2021
Melon-headed whale	M	M	52.00				Kunisue et al. 2021
Melon-headed whale	M	I	51.00				Kunisue et al. 2021 (from Bachman et al. 2014)
Melon-headed whale	M	C	56.00				Kunisue et al. 2021 (from Bachman et al. 2014)
Melon-headed whale	M	M	8.90				Kunisue et al. 2021 (from Bachman et al. 2014)
Melon-headed whale	U	U	29.60	27.50			Bachman et al. 2014
Northern right whale dolphin	U	U	82.00				Minh et al. 2000
Northern right whale dolphin	U	U	80.2	2.3			Koopman 2007
Northern right whale dolphin	U	U	77.7	.8			Koopman 2007
Pacific white-sided dolphin	B	U	81.50	7.80			Graham unpulished as cited in Rechsteiner et al 2013
Pacific white-sided dolphin	U	U	76.00				Minh et al. 2000

Pantropical spotted dolphin	U	U	67.70				Koopman 2007
Pantropical spotted dolphin	U	U	94.40				Koopman 2007
Pygmy killer whale	U	U	38.8	11.4			Koopman 2007
Pygmy killer whale	U	U	36.3	8.2			Koopman 2007
Pygmy killer whale	U	U	34.35				Bachman et al. 2014
Risso's dolphin	M	M	30				Jarman et al. 1996
Risso's dolphin	U	U	64.3	3.6			Koopman 2007
Risso's dolphin	U	U	50.6	2.9			Koopman 2007
Risso's dolphin	U	U	76.10				Tittlemier et al. 2002
Risso's dolphin	U	U	18.90				Troisi et al. 2018
Rough-toothed dolphin	B	U	18	21			Lailson-Brito et al. 2012
Rough-toothed dolphin	U	U	15.7	7.7			Koopman 2007
Rough-toothed dolphin	U	U	12.2	4.1			Koopman 2007
Rough-toothed dolphin	M	M	70.20				Yogui et al. 2011
Rough-toothed dolphin	U	U	36.00				Bachman et al. 2014
Short-beaked common dolphin	M	M	60.58	1.12			Tornero et al. 2004
Short-beaked	M	M	55.79	8.57			Tornero et al. 2004

common dolphin							
Short-beaked common dolphin	M	M	58.02	8.24			Tornero et al. 2004
Short-beaked common dolphin	F	M	56.26	7.57			Tornero et al. 2004
Short-beaked common dolphin	F	M	59.50	8.89			Tornero et al. 2004
Short-beaked common dolphin	F	M	62.36	8.77			Tornero et al. 2004
Short-beaked common dolphin	M	M	52.85	7.15			Tornero et al. 2004
Short-beaked common dolphin	M	M	64.12	6.78			Tornero et al. 2004
Short-beaked common dolphin	M	M	59.63	6.33			Tornero et al. 2004
Short-beaked common dolphin	M	M	53.25	10.30			Tornero et al. 2004
Short-beaked common dolphin	M	M	58.60	8.27			Tornero et al. 2004
Short-beaked common dolphin	M	M	63.07	4.34			Tornero et al. 2004

Short-beaked common dolphin	M	M	49.84	9.68			Tornero et al. 2004
Short-beaked common dolphin	F	M	67.00	10.61			Tornero et al. 2004
Short-beaked common dolphin	F	M	63.42	5.41			Tornero et al. 2004
Short-beaked common dolphin	F	M	67.55	4.64			Tornero et al. 2004
Short-beaked common dolphin	F	M	68.32	7.53			Tornero et al. 2004
Short-beaked common dolphin	F	M	55.38	5.96			Tornero et al. 2004
Short-beaked common dolphin	M	M	67.47	5.98			Tornero et al. 2004
Short-beaked common dolphin	M	M	65.29	4.21			Tornero et al. 2004
Short-beaked common dolphin	M	M	68.94	7.29			Tornero et al. 2004
Short-beaked common dolphin	M	M	58.64	5.47			Tornero et al. 2004
Short-beaked	M	M	67.60	11.77			Tornero et al. 2004

common dolphin							
Short-beaked common dolphin	F	M	62.25	5.37			Tornero et al. 2004
Short-beaked common dolphin	F	M	62.53	6.30			Tornero et al. 2004
Short-beaked common dolphin	B	U	25.84	18.32			Borrell et al. 2001
Short-beaked common dolphin	B	U	51.49	13.18			Borrell et al. 2001
Short-beaked common dolphin	B	U	46.96	16.09			Borrell et al. 2001
Short-beaked common dolphin	B	U	52.97	10.90			Borrell et al. 2001
Short-beaked common dolphin	M	U	90.00	5.00			Smyth et al. 2000
Short-beaked common dolphin	F	U	76.00	25.00			Smyth et al. 2000
Short-beaked common dolphin	B	U	14.00		0.10		Lazar et al. 2012
Short-finned pilot whale	U	U	79.9	2.7			Koopman 2007
Short-finned pilot whale	U	U	55.7	2.7			Koopman 2007

Short-finned pilot whale	F	M	62.17	2.02			Bagge et al. 2012
Spinner dolphin	U	U	66.00				Minh et al. 2000
Spinner dolphin	U	U	66.00				Minh et al. 2000
Spinner dolphin	M	C	36.00				Karuppiah et al. 2005
Spinner dolphin	M	M	25.00				Karuppiah et al. 2005
Spinner dolphin	F	M	48.00				Karuppiah et al. 2005
Spinner dolphin	F	I	46.00				Karuppiah et al. 2005
Spinner dolphin	F	I	34.53333	3.499683			Mwevura et al. 2010
Spinner dolphin	M	I	29.6				Mwevura et al. 2010
Spinner dolphin	F	M	35.025	1.381047			Mwevura et al. 2010
Spinner dolphin	M	M	36.27	1.388208			Mwevura et al. 2010
Spinner dolphin	B	M	46.00	7.49			Tanabe et al. 1993
Spinner dolphin	U	U	21.90				Bachman et al. 2014
Spotted dolphin	U	U	54.9	2.8			Worthy and Edwards 1990
Spotted dolphin	U	U	81.55				Bachman et al. 2014
Spotted dolphin	U	U			6.08		Lavandier et al. 2019
Striped dolphin	U	U	50.00				Minh et al. 2000
Striped dolphin	U	U	63.9	12.1			Koopman 2007
Striped dolphin	U	U	73	6.9			Koopman 2007
Striped dolphin	M	M	73.60		1.70		Kawai et al. 1988
Striped dolphin	F	M	94.00		1.60		Kawai et al. 1988

Striped dolphin	B	Mu	50.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	70.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	58.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	57.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	61.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	48.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	52.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	60.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	50.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	55.00				Gomez-Campos et al. 2015
Striped dolphin	B	Mu	54.00				Gomez-Campos et al. 2015
Striped dolphin	U	U	38.40				Tittlemier et al. 2002
Striped dolphin	U	U	18.60				Johnson-Restrepo et al. 2005
Striped dolphin	B	C	63.38	16.08			Gomez-Campos et al. 2011
Striped dolphin	B	I	59.13	16.60			Gomez-Campos et al. 2011
Striped dolphin	F	M	67.67	13.87			Gomez-Campos et al. 2011
Striped dolphin	F	M	48.36	13.86			Gomez-Campos et al. 2011
Striped dolphin	F	M	36.43	12.25			Gomez-Campos et al. 2011
Striped dolphin	M	M	46.40	18.57			Gomez-Campos et al. 2011
Striped dolphin	U	U	97.52				Troisi et al. 2018
Striped dolphin	U	U	90.52				Troisi et al. 2018

Striped dolphin	U	U	92.88				Troisi et al. 2018
Striped dolphin	U	U	84.47				Troisi et al. 2018
Striped dolphin	U	U	33.70	10.90			Bachman et al. 2014
Striped dolphin	U	U	55.88	8.82			Aguilar and Borrell 2005
Striped dolphin	U	U	60.80	7.89			Aguilar and Borrell 2005
Striped dolphin	U	U	58.74	11.34			Aguilar and Borrell 2005
Striped dolphin	U	U	59.74	10.37			Aguilar and Borrell 2005
Striped dolphin	U	U	38.48	12.62			Aguilar and Borrell 2005
Striped dolphin	U	U	58.37	7.71			Aguilar and Borrell 2005
Striped dolphin	U	U	27.63	15.11			Aguilar and Borrell 2005
Striped dolphin	U	U	58.45	17.80			Aguilar and Borrell 2005
Striped dolphin	U	U	57.04	8.72			Aguilar and Borrell 2005
Striped dolphin	B	M	43.30		1.00		Storelli et al. 2012
Bottlenose/striped dolphin	U	U	87.18		36.13		Wafo et al. 2005
Tucuxi	F	M	76.20		1.50		Duinker et al 1989
Tucuxi	M	M	90.80		4.10		Duinker et al 1989
Tucuxi	B	U	79.33	3.58			Lailson-Brito et al. 2004
White-beaked dolphin	F	U	91.70		1.20		Duinker et al 1989
White-beaked dolphin	M	U	79.80		1.10		Duinker et al 1989

White-beaked dolphin	F	U	97.90		0.80		Duinker et al 1989
White-beaked dolphin	M	U	66	18			Muir et al. 1988
White-beaked dolphin	F	U	71	9			Muir et al. 1988
White-beaked dolphin	U	U	63.00				Miller and Hall 2018
Gray whale	B	I	48.00	5.20	0.40	0.10	Tilbury et al. 2002
Gray whale	F	M	48.00	6.10			Tilbury et al. 2002
Gray whale	M	M	48.00	11.00			Tilbury et al. 2002
Gray whale	F	M	9.70	4.80			Tilbury et al. 2002
Gray whale	M	M	9.10	5.10			Tilbury et al. 2002
Gray whale	U	U	2.00	1.00			Tilbury et al. 2002
Gray whale	B	I	13.00	6.00			Tilbury et al. 2002
Gray whale	M	U	8.00	5.10			Varanasi et al. 1994
Gray whale	B	U	17.00	9.80			Varanasi et al. 1994
Gray whale	B	U	5.00	3.70			Varanasi et al. 1994
Gray whale	U	U	2.10	1.20			Varanasi et al. 1994
Gray whale	B	U	1.70	0.20			Varanasi et al. 1994
Gray whale	B	U	8.50	3.40			Varanasi et al. 1994
Gray whale	U	U			0.50		Tsygankov et al. 2018
Gray whale	U	U			4.10		Tsygankov et al. 2018

Dwarf sperm whale	U	U	65.5	3.9			Koopman 2007
Dwarf sperm whale	U	U	79.3	4.5			Koopman 2007
Dwarf sperm whale	U	U	75.60				Bachman et al. 2014
Pygmy sperm whale	M	M					Watanabe et al. 2000
Pygmy sperm whale	U	U	67.3	3.5			Koopman 2007
Pygmy sperm whale	U	U	31.3	8.2			Koopman 2007
Pygmy sperm whale	B	M	56.64	1.73			Bagge et al. 2012
Pygmy sperm whale	U	U	33.70				McLelland et al. 2012
Pygmy sperm whale	U	U	75.10				McLelland et al. 2012
Pygmy sperm whale	U	U	69.20				McLelland et al. 2012
Pygmy sperm whale	U	U	47.70	24.00			Bachman et al. 2014
Beluga	M	M	89.00	7.00			LeBeuf et al 2004
Beluga	F	M	92.00	5.00			LeBeuf et al 2004
Beluga	B	U	80.00		1.00		Kicuenik et al 1997
Beluga	M	M			0.98		Metcalfe et al 1999
Beluga	M	M			1.44		Metcalfe et al 1999
Beluga	U	U	85.60				Yang et al 1998
Beluga	F	C	86.00				Yang et al 1998
Beluga	F	I	86.00				Yang et al 1998
Beluga	M	I	87.00				Yang et al 1998
Beluga	F	M	86.94	2.52			Yang et al 1998
Beluga	M	M	82.00	7.84			Yang et al 1998
Beluga	F	U	86.20	0.56			Bennie et al 2000
Beluga	M	U	83.50	2.20			Bennie et al 2000
Beluga	M	M	91.30				LeBeuf et al 2007

Beluga	F	M	94.10				LeBeuf et al 2007
Beluga	M	M	91.30				Yang et al 1998
Beluga	F	M	93.30				Yang et al 1998
Beluga	B	M	96.00				Masse et al 1986
Beluga	M	M	91.30				LeBeuf et al. 2014
Beluga	F	M	93.30				LeBeuf et al. 2014
Beluga	M	I	73	10			Krahn et al. 2004
Beluga	F	M	72	1.2			Krahn et al. 2004
Beluga	M	M	75	7.2			Krahn et al. 2004
Beluga	F	M	24	19			Krahn et al. 2004
Beluga	F	M	9.4	5.1			Krahn et al. 2004
Beluga	F	M	24.55	7.27			Hobbs et al. 2003
Beluga	M	M	56.96	3.24			Hobbs et al. 2003
Beluga	M	Mu	86.8	2.7			Beland et al. 1993
Beluga	F	Mu	86.6	3.9			Beland et al. 1993
Beluga	F	M	88.99130	2.282135			Muir et al. 1996a
Beluga	M	I	74.60000				Muir et al. 1996a
Beluga	M	M	82.68571	3.035990			Muir et al. 1996a
Beluga	F	M	94.3				Muir et al. 1996b
Beluga	M	I	92.6				Muir et al. 1996b
Beluga	F	U	96.77143	2.629749			Martineau et al. 1987
Beluga	M	U	87.89286	4.173944			Martineau et al. 1987
Beluga	M	U	90.4	1.1			Noel et al. 2018
Beluga	M	U	94.3	.9			Noel et al. 2018
Beluga	M	U	81.2	.9			Noel et al. 2018
Beluga	M	U	92.3	1.4			Noel et al. 2018
Beluga	M	U	82.1	.9			Noel et al. 2018
Beluga	M	U	90.9	.8			Noel et al. 2018
Beluga	M	U	91.2	1.3			Noel et al. 2018

Beluga	M	U	84.9	2.2			Noel et al. 2018
Beluga	M	U	92.3	1.1			Noel et al. 2018
Beluga	M	U	90.5	1.7			Noel et al. 2018
Beluga	M	U	85.7	2.2			Noel et al. 2018
Beluga	M	U	79.9	1.9			Noel et al. 2018
Beluga	M	U	93.9	1.3			Noel et al. 2018
Beluga	M	U	92.1	1.1			Noel et al. 2018
Beluga	M	U	92.3	1.2			Noel et al. 2018
Beluga	M	U	93.5	.6			Noel et al. 2018
Beluga	M	U	94.7	2.9			Noel et al. 2018
Beluga	M	U	96.7	1.6			Noel et al. 2018
Beluga	M	U	91.5	2.1			Noel et al. 2018
Beluga	U	U	86.2	2.74			Simond et al. 2017
Beluga	U	U	26.3	5.2			Simond et al. 2017
Beluga	U	U	93.30	3.07			Simond et al. 2017
Beluga	U	U	96.30	3.67			Simond et al. 2017
Beluga	F	U	91.65	0.99			Gouteux et al. 2003
Beluga	M	U	88.77	1.53			Gouteux et al. 2003
Beluga	U	U	94.00				Tittlemier et al. 2002
Beluga	U	U	86.90				Tittlemier et al. 2002
Beluga	U	U	66.60				Tittlemier et al. 2002
Beluga	U	U	83.30				Tittlemier et al. 2002
Beluga	U	U	88.50				Tittlemier et al. 2002
Beluga	M	M	20.17				Andersen et al. 2001
Beluga	M	U	86.30				Hoguet et al. 2013
Beluga	F	U	86.30				Hoguet et al. 2013

Beluga	M	U	86.60				Hoguet et al. 2013
Beluga	F	U	84.40				Hoguet et al. 2013
Beluga	B	M	90.00		10.00		Hickie et al. 2000
Narwhal	M	U	83.9	3.9			Muir et al. 1992
Narwhal	F	U	86.4	1.8			Muir et al. 1992
Narwhal	U	U	89.2	1.5			Koopman 2007
Narwhal	U	U	88	1.7			Koopman 2007
Walrus	M	M	84.50	4.70			Muir et al. 1995
Walrus	F	M	82.30	4.20			Muir et al. 1995
Walrus	M	M	83.20	5.50			Muir et al. 1995
Walrus	F	M	87.40	2.30			Muir et al. 1995
Walrus	M	M	82.40	6.00			Muir et al. 1995
Walrus	M	M	82.80	2.40			Muir et al. 1995
Walrus	M	M	77.70	6.40			Muir et al. 1995
Walrus	F	M	81.00	5.20			Muir et al. 1995
Walrus	M	Mu	78.60	11.80			Seagard and Garlich-Miller 2001
Walrus	F	Mu	82.70	3.70			Seagard and Garlich-Miller 2001
Walrus	U	Mu	77.80				Born, Kraul, and Kristensen 1981
Antarctic fur seal	F	M	79.40	4.94			Arnould, Boyd, and Speakman 1995
Antarctic fur seal	B	I	59.73	11.37			Arnould, Boyd, and Speakman 1995
Antarctic fur seal	B	I	49.00	32.00			Schiavone et al. 2009
California sea lion	M	M	45.00	29.00			Ylitalo et al. 2005
California sea lion	F	M	34.00	23.00			Ylitalo et al. 2005
California sea lion	B	M	55.00	32.00			Blasius and Goodmanlow 2008

California sea lion	B	M	50.00	24.00			Le Boeuf et al. 2002
California sea lion	B	Mu	45.58	20.59			Stapleton et al. 2006
California sea lion	B	Mu	61.78	19.08			Kannan et al. 2004
California sea lion	M	M	50.00	24.00			Kannan et al. 2004
California sea lion	F	M	51.00	23.00			Kannan et al. 2004
California sea lion	M	I	54.00	25.00			Kannan et al. 2004
California sea lion	M	I	44.00	17.00			Kannan et al. 2004
Cape fur seal	B	I	77.20	1.90	73.00	1.60	Koep et al. 2007
Cape fur seal	B	I	67.10	4.80	74.30	1.60	Koep et al. 2007
Northern fur seal	M	I	54.00	14.00			Krahn et al. 1997
Northern fur seal	F	M	64.00	21.00			Kajiwara et al. 2004
Northern fur seal	M	M	71.00	10.00			Loughlin, Castellini, and Ylitalo 2002
Northern fur seal	M	M	60.00	12.00			Loughlin, Castellini, and Ylitalo 2002
Northern fur seal	M	M	73.10	21.90			Wang et al. 2010
Steller sea lion	M	M	74.00	12.00			Lee et al. 1996
Steller sea lion	F	M	82.00	5.00			Lee et al. 1996
Steller sea lion	B	M	68.00		0.64		Kim et al. 1996
Steller sea lion	B	I	36.60	12.30			Keogh et al. 2020
Bearded seal	F	Mu	78.00	NA			Krahn et al. 1997
Bearded seal	M	Mu	80.00	5.00			Krahn et al. 1997

Crabeater seal	U	U	85.60	7.60			Schneifer, Steinhagen-Schneider, and Drescher 1985
Crabeater seal	U	U	69.80	12.30			Schneifer, Steinhagen-Schneider, and Drescher 1985
Gray seal	U	I	79.63				Sørmo et al. 2009
Gray seal	U	I	76.46				Sørmo et al. 2009
Gray seal	U	I	74.21				Sørmo et al. 2009
Gray seal	U	I	55.32				Sørmo et al. 2009
Gray seal	U	I	78.50				Robinson et al. 2018
Gray seal	U	I	82.90				Robinson et al. 2018
Gray seal	F	M	48.90				Sørmo et al. 2003
Gray seal	F	M	46.30				Sørmo et al. 2003
Harbor seal	B	M	72.10	25.80			She et al. 2002
Harbor seal	U	F	66.90				She et al. 2002
Harbor seal	F	M	85.10	14.10			She et al. 2002
Harbor seal	M	M	63.40	29.30			She et al. 2002
Harbor seal	B	I	39.00	14.00			Greig et al. 2011
Harbor seal	B	I	44.00	13.00			Greig et al. 2011
Harbor seal	B	I	53.00	12.00			Greig et al. 2011
Harbor seal	B	I	46.00	18.00			Greig et al. 2011
Harbor seal	B	I	50.00	11.00			Greig et al. 2011
Harbor seal	B	I	34.00	23.00			Greig et al. 2011
Harbor seal	B	I	43.00	11.00			Greig et al. 2011
Harbor seal	B	F	24.00	9.90			Greig et al. 2011
Harbor seal	B	I	65.00	9.00			Greig et al. 2011
Harbor seal	B	I	49.00	14.00			Greig et al. 2011
Harbor seal	B	I	57.50	3.54			Greig et al. 2011
Harbor seal	B	Mu	61.00	13.00			Greig et al. 2011
Harbor seal	F	Mu	89.00	0.00			Krahn et al. 1997
Harbor seal	M	Mu	66.00	23.00			Krahn et al. 1997
Harbor seal	F	Mu	86.00	2.00			Krahn et al. 1997
Harbor seal	M	Mu	73.00	21.00			Krahn et al. 1997

Harbor seal	B	Mu	93.00				Wang et al. 2007
Harbor seal	B	M	48.64	30.15			Blasius and Goodmanlow 2008
Harp seal	F	M			1.80	0.40	Brunborg et al. 2006
Harp seal	B	Mu	97.20	1.30	9.10	2.40	Beck, Smith, and Hammill 1993
Harp seal	M	I	93.00				Kleivane et al. 1997
Harp seal	F	I	94.00				Kleivane et al. 1997
Harp seal	M	M	94.00				Kleivane et al. 1997
Harp seal	M	M	94.00				Kleivane et al. 1997
Harp seal	F	M	92.00				Kleivane et al. 1997
Harp seal	U	F			5.20		Worthy and Lavigne 1983
Harp seal	U	I			3.60	1.41	Worthy and Lavigne 1983
Harp seal	U	I			3.73	1.11	Worthy and Lavigne 1983
Harp seal	U	I			4.15	0.07	Worthy and Lavigne 1983
Harp seal	U	I			7.40		Worthy and Lavigne 1983
Harp seal	U	I			8.20		Worthy and Lavigne 1983
Harp seal	U	I			8.70		Worthy and Lavigne 1983
Harp seal	U	I			2.07	0.40	Worthy and Lavigne 1983
Harp seal	U	I			4.60		Worthy and Lavigne 1983
Harp seal	F	M	92.80				Espeland et al. 1997
Harp seal	U	I	68.00				Espeland et al. 1997
Harp seal	B	Mu	87.70	4.10	3.60	1.20	Gales, Renouf and Noseworthy 1994

Hawaiian monk seal	B	I	65.00	4.30			Lopez et al. 2012
Hawaiian monk seal	F	M	44.00	13.00			Lopez et al. 2012
Hawaiian monk seal	M	M	39.00	4.00			Lopez et al. 2012
Hawaiian monk seal	M	M	27.00	11.00			Willcox et al. 2004
Hawaiian monk seal	B	I	23.00	10.00			Willcox et al. 2004
Hawaiian monk seal	F	M	28.00	10.00			Willcox et al. 2004
Hooded seal	F	M			1.60	0.20	Brunborg et al. 2006
Hooded seal	F	M	88.20				Espeland et al. 1997
Hooded seal	U	I	75.50				Espeland et al. 1997
Meditteranean monk seal	M	M	88.30		18.40		Henderson, Kalogeropoulos, and Alexis 1994
Northern elephant seal	B	I	85.00				Louis et al. 2014
Northern elephant seal	B	I	80.00				Louis et al. 2014
Northern elephant seal	B	I	85.00				Louis et al. 2014
Northern elephant seal	B	I	83.00				Louis et al. 2014
Northern elephant seal	B	I	82.00				Louis et al. 2014
Northern elephant seal	B	I	82.00				Louis et al. 2014
Northern elephant seal	B	M	74.00	37.00			Kajiwara et al. 2001

Northern elephant seal	B	M	32.21	33.29			Blasius and Goodmanlow 2008
Ringed seal	F	Mu	87.00	1.00			Krahn et al. 1997
Ringed seal	M	Mu	89.00	4.00			Krahn et al. 1997
Ringed seal	B	M	85.50				Kucklick et al. 2002
Ringed seal	M	M	87.60	2.30			Severinsen, Skaare, and Lydersen 2000
Ringed seal	M	M	87.60	4.10			Severinsen, Skaare, and Lydersen 2000
Ringed seal	M	M	86.90	3.10			Severinsen, Skaare, and Lydersen 2000
Ringed seal	F	M	89.50	4.50			Severinsen, Skaare, and Lydersen 2000
Ringed seal	F	M	89.70	1.10			Severinsen, Skaare, and Lydersen 2000
Ringed seal	F	M	86.80	1.30			Severinsen, Skaare, and Lydersen 2000
Ringed seal	B	I	86.80	10.30			Severinsen, Skaare, and Lydersen 2000
Ringed seal	B	I	86.50	11.30			Severinsen, Skaare, and Lydersen 2000
Ringed seal	B	I	84.00	12.80			Severinsen, Skaare, and Lydersen 2000
Ringed seal	M	M	87.50	0.80			Severinsen, Skaare, and Lydersen 2000
Ringed seal	M	M	88.40	2.70			Severinsen, Skaare, and Lydersen 2000
Ringed seal	M	M	86.70	2.60			Severinsen, Skaare, and Lydersen 2000

Ringed seal	F	M	89.50	4.50			Severinsen, Skaare, and Lydersen 2000
Ringed seal	F	M	89.70	1.10			Severinsen, Skaare, and Lydersen 2000
Ringed seal	F	M	86.60	1.30			Severinsen, Skaare, and Lydersen 2000
Ringed seal	B	I	86.80	3.40			Severinsen, Skaare, and Lydersen 2000
Ringed seal	B	I	84.00	10.80			Severinsen, Skaare, and Lydersen 2000
Ringed seal	B	I	89.50	1.80			Severinsen, Skaare, and Lydersen 2000
Ringed seal	M	M	94.70	1.00			Muir et al. 1995
Ringed seal	F	M	92.90	5.30			Muir et al. 1995
Ringed seal	M	Mu	44.69	4.69			Strandberg et al. 2008
Ringed seal	F	Mu	40.43	6.84			Strandberg et al. 2008
Southern elephant seal	M	I	62.93	8.03			Tsuyuki and Itoh
Spotted seal	U	M	74.00				Watanabe t al. 1999
Spotted seal	U	I	75.50				Watanabe t al. 1999
Spotted seal	M	M	83.00	7.20			Nakata et al. 1998
Spotted seal	F	M	84.00	6.20			Nakata et al. 1998
Spotted seal	M	M	85.00	4.60			Chiba et al. 2002
Spotted seal	F	M	88.00	8.80			Chiba et al. 2002
Spotted seal	B	Mu	71.40	5.70			Trukhin and Boyarova 2020
Weddell seal	U	U	71.60	6.50			Schneifer, Steinhagen-

							Schneider, and Drescher 1985
Weddell seal	U	U	71.40	17.80			Schneifer, Steinhagen-Schneider, and Drescher 1985
Weddell seal	F	M	83.00	6.00			Kawano et al. 1984
Weddell seal	M	M	87.33	4.62			Kawano et al. 1984
Weddell seal	M	I	30.00	5.29			Kawano et al. 1984
Burmeister's porpoise	U	U	72.9	2.8			Koopman 2007
Burmeister's porpoise	U	U	75.9	3.6			Koopman 2007
Burmeister's porpoise	F	M	78.55	6.39			Corcuera et al. 1995
Burmeister's porpoise	M	M	71.96	4.92			Corcuera et al. 1995
Dall's porpoise	F	M	87.00				Minh et al. 2000
Dall's porpoise	U	U	86.00				Minh et al. 2000
Dall's porpoise	U	U	87.00				Minh et al. 2000
Dall's porpoise	B	Mu	98				Jarman et al. 1996
Dall's porpoise	M	M	92				Kajiwara et al. 2002
Dall's porpoise	M	I	81				Kajiwara et al. 2002
Dall's porpoise	M	M	79				Kajiwara et al. 2002
Dall's porpoise	F	I	83				Kajiwara et al. 2002
Dall's porpoise	F	M	82				Kajiwara et al. 2002
Dall's porpoise	M	M	88				Kajiwara et al. 2002
Dall's porpoise	M	M	88				Kajiwara et al. 2002

Dall's porpoise	M	M	87				Kajiwara et al. 2002
Dall's porpoise	M	M	78				Kajiwara et al. 2002
Dall's porpoise	F	I	86				Kajiwara et al. 2002
Dall's porpoise	F	M	94				Kajiwara et al. 2002
Dall's porpoise	U	U	71.4	1.6			Koopman 2007
Dall's porpoise	U	U	71.1	.9			Koopman 2007
Dall's porpoise	U	U	72.40				Tittlemier et al. 2002
Dall's porpoise	B	U	76.00	13.00			Fujii et al. 2018
Finless porpoise	U	U	64.00				Minh et al. 2000
Finless porpoise	F	U	28.000				Ramu et al. 2005
Finless porpoise	M	U	46.800	7.15			Ramu et al. 2005
Finless porpoise	U	U	27				Ramu et al. 2005
Finless porpoise	U	U	81.9	1.4			Koopman 2007
Finless porpoise	U	U	78.1	2.7			Koopman 2007
Finless porpoise	M	I	82.00	4.00			Park et al. 2010 and Moon et al. 2011
Finless porpoise	F	I	78.00	7.00			Park et al. 2010 and Moon et al. 2011
Finless porpoise	M	M	81.00	8.00			Park et al. 2010 and Moon et al. 2011
Finless porpoise	F	M	76.00	9.00			Park et al. 2010 and Moon et al. 2011
Finless porpoise	B	Mu	82.88	1.25			Isobe et al. 2011

Finless porpoise	B	Mu	71.84	7.99			Parsons and Chan 1998
Finless porpoise	B	M	80.20	5.57			Nakata et al. 2010
Finless porpoise	B	Mu	78.60	9.58			Jeong et al. 2020
Finless porpoise	B	Mu	70.90	10.90			Jeong et al. 2020
Harbor porpoise	M	U	72.40		1.00		Duinker et al 1989
Harbor porpoise	M	I	67.30	8.60			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	I	69.30	11.60			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	B	I	67.90	9.20			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	M	I	87.10	5.70			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	I	82.80	7.20			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	B	I	85.40	6.50			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	M	M	87.20	5.20			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	Mu	86.60	6.80			Lockyer 1995 (Aspects of Biology in British Waters)

Harbor porpoise	B	Mu	86.90	6.00			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	I	85.30	6.40			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	M	85.50	8.10			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	M	86.80	6.30			Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	F	M	83.00				Lockyer 1995 (Aspects of Biology in British Waters)
Harbor porpoise	U	U	77.00				Minh et al. 2000
Harbor porpoise	F	I	90.30	1.72			Scheppingen et al. 1996
Harbor porpoise	M	I	92.50	1.24			Scheppingen et al. 1996
Harbor porpoise	F	M	91.79	0.90			Scheppingen et al. 1996
Harbor porpoise	M	M	92.87	1.26			Scheppingen et al. 1996
Harbor porpoise	F	U	85.60				Scheppingen et al. 1996
Harbor porpoise	F	I	81.00	2.80			Tilbury et al. 1997
Harbor porpoise	M	I	83.00	1.90			Tilbury et al. 1997
Harbor porpoise	M	M	82.00	2.30			Tilbury et al. 1997
Harbor porpoise	F	U	73.55	3.15			Calambokidis 1986
Harbor porpoise	M	U	71.75	2.99			Calambokidis 1986

Harbor porpoise	U	U	17.00	2.00			Calambokidis 1986
Harbor porpoise	F	C	85.37	3.17			Borrell et al. 2004
Harbor porpoise	F	I	83.11	5.40			Borrell et al. 2004
Harbor porpoise	F	M	82				Borrell et al. 2004
Harbor porpoise	M	C	85.07				Borrell et al. 2004
Harbor porpoise	M	I	82.67	5.20			Borrell et al. 2004
Harbor porpoise	M	M	84.03	2.26			Borrell et al. 2004
Harbor porpoise	F	C	86.46	3.22			Borrell et al. 2004
Harbor porpoise	F	I	79.80	9.33			Borrell et al. 2004
Harbor porpoise	F	M	85.204	4.45			Borrell et al. 2004
Harbor porpoise	M	C	86.83	1.89			Borrell et al. 2004
Harbor porpoise	M	I	82.42	1.64			Borrell et al. 2004
Harbor porpoise	M	M	81.53	2.48			Borrell et al. 2004
Harbor porpoise	F	C	83.44	3.02			Borrell et al. 2004
Harbor porpoise	F	I	86.54	1.87			Borrell et al. 2004
Harbor porpoise	M	C	86.55	4.31			Borrell et al. 2004
Harbor porpoise	M	I	84.76	.9			Borrell et al. 2004
Harbor porpoise	M	M	85.25				Borrell et al. 2004
Harbor porpoise	B	Mu	92				Jarman et al. 1996
Harbor porpoise	B	Mu	73				Jarman et al. 1996
Harbor porpoise	F	U	85.0	2.7			Borrell et al. 1999

Harbor porpoise	M	U	85.8	3.2			Borrell et al. 1999
Harbor porpoise	F	U	83.1	7.8			Borrell et al. 1999
Harbor porpoise	M	U	83.8	3.2			Borrell et al. 1999
Harbor porpoise	F	U	84.2	4.2			Borrell et al. 1999
Harbor porpoise	M	U	83.7	3.1			Borrell et al. 1999
Harbor porpoise	F	U	75.57692	2.847494			Calambokidis and Barlow 1991
Harbor porpoise	M	U	70.35294	3.010937			Calambokidis and Barlow 1991
Harbor porpoise	U	U	17.00000	2.000000			Calambokidis and Barlow 1991
Harbor porpoise	U	U	81.6	3.6			Worthy and Edwards 1990
Harbor porpoise	U	U	84.7	1.1			Koopman 2007
Harbor porpoise	U	U	83.1	.9			Koopman 2007
Harbor porpoise	U	U	56				Law et al. 2008
Harbor porpoise	U	U	97				Law et al. 2008
Harbor porpoise	B	Mu	92.00				Lockyer et al. 2003a
Harbor porpoise	B	Mu	96.00				Lockyer et al. 2003a
Harbor porpoise	B	I	84.50	0.80			Koopman, Iverson and Read 2003
Harbor porpoise	B	I	75.00	2.70			Koopman, Iverson and Read 2003
Harbor porpoise	U	U	93.40				Tittlemier et al. 2002
Harbor porpoise	M	U	86.50	1.10			Borrell 1993
Harbor porpoise	F	U	94.00	3.10			Borrell 1993

Harbor porpoise	U	U	70.55				Troisi et al. 2018
Harbor porpoise	B	U	78.00	11.00			Fujii et al. 2018
Harbor porpoise	F	I	84.86	2.55			Tanabe et al. 1997
Harbor porpoise	F	M	81.50	4.50			Tanabe et al. 1997
Harbor porpoise	M	I	86.71	0.80			Tanabe et al. 1997
Harbor porpoise	M	M	86.22	1.37			Tanabe et al. 1997
Harbor porpoise	M	I	86.00	3.49			Tanabe et al. 1997
Harbor porpoise	M	M	89.00	2.00			Tanabe et al. 1997
Harbor porpoise	M	M	93.00	0.97			Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M	94.00	0.78			Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M	95.00	0.66			Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M	94.00	0.99			Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M	84.00	4.60			Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M	95.00	0.27			Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M			1.70	0.19	Ishaq, Karlson, and Näf 2000
Harbor porpoise	M	M	77.00				Strandberg et al. 1998
Harbor porpoise	M	M	88.00				Strandberg et al. 1998
Harbor porpoise	F	M	92.00				Strandberg et al. 1998
Harbor porpoise	F	M	89.00				Strandberg et al. 1998
Harbor porpoise	B	Mu	87.85				Law et al. 2006a
Harbor porpoise	B	Mu	88.29	1.12			Law et al. 2013b

Harbor porpoise	M	U	22.00	11.00			Smyth et al. 2000
Harbor porpoise	F	U	22.00	6.00			Smyth et al. 2000
Mixed porpoise/dolphin	B	Mu	84.50		1.80		Duinker et al 1989
Spectacled porpoise	U	U	11.1				Koopman 2007
Spectacled porpoise	U	U	29.7				Koopman 2007
Vaquita	F	I	80.00	5.00			Calambokidis 1988
Vaquita	M	I	82.50	0.50			Calambokidis 1988
Vaquita	F	M	83.67	9.53			Calambokidis 1988
Vaquita	M	M	70.00				Calambokidis 1988
Vaquita	U	U	79.1	5.3			Koopman 2007
Vaquita	U	U	84.8	1.9			Koopman 2007
Sperm whale	M	M	92.10		18.50		Duinker et al 1989
Sperm whale	B	Mu	3.00				Lockyer 1991
Sperm whale	B	Mu	48.00				Lockyer 1991
Sperm whale	U	U	35.1	5.9			Koopman 2007
Sperm whale	U	U	42.5	16.5			Koopman 2007
Sperm whale	M	M	58.74	5.08	3.86	0.75	Watanabe and Suzuki 1950
Sperm whale	U	U	2.00				Das et al. 2015
Sperm whale	U	U	30.00				Das et al. 2015
Sperm whale	B	Mu	49.20	17.90			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004

Sperm whale	F	Mu	50.40	18.10			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	F	I	56.80	27.80			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	F	M	54.80	19.40			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	F	M	48.80	18.30			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	F	M	44.40	14.10			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	F	M	41.80	0.10			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	M	Mu	41.30	15.60			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	M	I	44.60	26.90			Evans, Hindell, and Thiele 2003 and Evans, Hindell, and Hince 2004
Sperm whale	M	M	42.30	12.10			Evans, Hindell, and Thiele 2003 and Evans,

							Hindell, and Hince 2004
Sperm whale	M	M	66.38		1.35		Aguilar 1983
Sperm whale	F	M	68.88		1.01		Aguilar 1983
Sperm whale	U	M	64.00				Vetter et al. 2018
Sperm whale	M	U	40.30	6.70			Borrell 1993
Sperm whale	M	U	10.00	8.00			Pinzone et al. 2015
Sperm whale	F	U	18.00	8.00			Pinzone et al. 2015
Sperm whale	U	U	39.90				Bachman et al. 2014
Ganges river dolphin	B	M	39.00	8.53	9.48	2.80	Kannan et al. 1994
Ganges river dolphin	B	M	64.00	10.00			Senthilkumar et al. 1999
Ganges river dolphin	B	M	4.45	0.95			Senthilkumar et al. 1999
Ganges river dolphin	B	Mu	45.00	9.89	11.60	3.88	Kannan et al. 1993 and Kannan et al. 1997
Ganges river dolphin	M	C	42.00		10.00		Subramanian et al. 1999
Ganges river dolphin	F	M	37.00		9.60		Subramanian et al. 1999
Dugong	M	M	82.80		2.10		Vijayasarathy et al. 2019
Dugong	M	I			1.70		Vijayasarathy et al. 2019
Dugong	M	M			0.40		Vijayasarathy et al. 2019
Dugong	M	I	8.40		0.20		Vijayasarathy et al. 2019

Dugong	F	M	3.00		0.20		Vijayasarathy et al. 2019
Dugong	F	M	42.20				Vijayasarathy et al. 2019
Dugong	F	M	89.70				Vijayasarathy et al. 2019
Dugong	F	M	80.30				Vijayasarathy et al. 2019
Dugong	M	Mu	53.50	3.40			Horgan et al. 2014
Dugong	F	Mu	54.90	2.70			Horgan et al. 2014
Blainville's beaked whale	M	I	83				Kajiwara et al. 2004
Blainville's beaked whale	M	M	81				Kajiwara et al. 2004
Blainville's beaked whale	U	U	76.80				Bachman et al. 2014
Cuvier's beaked whale	U	U	78.5				Koopman 2007
Cuvier's beaked whale	U	U	50.80				Bachman et al. 2014
Gervais' beaked whale	U	U	74.7	5.2			Koopman 2007
Gervais' beaked whale	U	U	61.4	9.5			Koopman 2007
Hubb's beaked whale	M	M	89.80				Anezaki, Matsuda, and Matsuishi 2016
Sowerby's beaked whale	U	U	79.8	4			Koopman 2007
Sowerby's beaked whale	U	U	81.2	3.1			Koopman 2007

Ziphiids	U	U	68.00				Miller and Hall 2018
Ziphiids	U	U	64.00				Kershaw et al. 2019
Ziphiids	U	U	73.00				Kershaw et al. 2019
Southern bottlenose whale	U	U	69.00				Zemskii and Budylenko 1970 (via O 1994)
Southern bottlenose whale	U	U	71.00		1.20		Zemskii and Budylenko 1970
Bowhead whale	F	I	80.00		1.40		O'Hara et al. 2004

Table A1. 3 List of protein content in blubber and muscle for marine mammals. For sex, F represents females, M represents males, U represents unknown, and B represents both. For age class, I represents immature, M represents mature, C represents calf, F represents Fetus, and Mu represents Multiple.

Species	**Sex**	**Age Class**	**Blubber**	**sd**	**Muscle**	**sd**	**Reference**
Beluga	M	M					Raach et al 2011
Beluga	F	M					Raach et al 2011
Sperm whale	B	Mu	10-35				Lockyer 1991
Harbor porpoise	F	M	1.45				Sergeant 1962
Fin whale	B	M	13.1	1	20.2	0.6	Lockyer et al. 1985
Fin whale	B	Mu	12.3	1.4	22.3	1.6	Lockyer et al. 1985
Fin whale	B	Mu	17.6	1.6	21.8	1.4	Lockyer et al. 1985
Fin whale	B	Mu	11.9	2.1	20.4	1.4	Lockyer et al. 1985

Fin whale	B	Mu	12.7	2.1	21.6	1.1	Lockyer et al. 1985
Fin whale	B	Mu	16.8	1.6	23.2	1.4	Lockyer et al. 1985
Fin whale	B	Mu	6.7	1.3	18.4	0.9	Lockyer et al. 1985
Fin whale	B	Mu	10.8	2	21.4	2	Lockyer et al. 1985
Fin whale	B	Mu	9	1.5	20.3	1.3	Lockyer et al. 1985
Sei whale	B	Mu	14	1.6	25.9	0.6	Lockyer et al. 1985
Sei whale	B	Mu	10.3	1.9	22.5	1.4	Lockyer et al. 1985
Sei whale	B	Mu	13.9	1.8	18.9	1.6	Lockyer et al. 1985
Sei whale	B	Mu	10.4	1.3	24.2	0.9	Lockyer et al. 1985
Sei whale	B	Mu	11.8	1.7	25.6	0.8	Lockyer et al. 1985
Sei whale	B	Mu	16.7	1.4	23.5	2.1	Lockyer et al. 1985
Sei whale	B	Mu	4.6	0.7	23.9	1.3	Lockyer et al. 1985
Sei whale	B	Mu	8.9	3.1	23.7	1.4	Lockyer et al. 1985
Sei whale	B	Mu	7	0.6	26.1	0.9	Lockyer et al. 1985
Fin whale	U	F	10.6		6.6		Lockyer et al. 1985
Minke whale	F	M			25.55	0.97	Víkingsson et al. 2013
Minke whale	F	M			22.32	2.85	Víkingsson et al. 2013
Minke whale	F	M			22.69	1.95	Víkingsson et al. 2013
Minke whale	F	M			23.4	1.61	Víkingsson et al. 2013
Minke whale	F	M			24.47	1.4	Víkingsson et al. 2013
Minke whale	F	M			24.6	1.07	Víkingsson et al. 2013

Minke whale	F	M			25.87	1.02	Víkingsson et al. 2013
Minke whale	F	M			22.59	2.73	Víkingsson et al. 2013
Minke whale	F	M	20.34	1.7			Víkingsson et al. 2013
Minke whale	F	M	16.31	5.74			Víkingsson et al. 2013
Minke whale	F	M	14.09	4.48			Víkingsson et al. 2013
Minke whale	F	M	5.89	3.19			Víkingsson et al. 2013
Minke whale	F	M	12.86	3.29			Víkingsson et al. 2013
Minke whale	F	M	11.36	3.49			Víkingsson et al. 2013
Minke whale	F	M	11.08	4.54			Víkingsson et al. 2013
Minke whale	F	M	12.98	5.32			Víkingsson et al. 2013
Minke whale	F	M	10.75	4.69			Víkingsson et al. 2013
Minke whale	M	I	3.54	2.92			Víkingsson et al. 2013
Minke whale	M	M	7.18	3.81			Víkingsson et al. 2013
Minke whale	M	I	5.97	2.17			Víkingsson et al. 2013
Minke whale	F	M	6.72	2.89			Víkingsson et al. 2013
Minke whale	F	I	4.88	1.38			Víkingsson et al. 2013
Minke whale	F	M	5.89	3.19			Víkingsson et al. 2013
Minke whale	M	I			23.76	0.45	Víkingsson et al. 2013
Minke whale	M	M			23.01	1.54	Víkingsson et al. 2013
Minke whale	M	I			21.95	2.21	Víkingsson et al. 2013
Minke whale	F	M			24.59	0.77	Víkingsson et al. 2013

Minke whale	F	I			23.42	1.19	Víkingsson et al. 2013
Minke whale	F	M			22.69	1.95	Víkingsson et al. 2013
Bowhead whale	F	I	5.17		22.4		O'Hara et al. 2004

Appendix A2

Growth curves and morphology

Each size class had a unique Gompertz growth curve for length, von Bertalanffy curve for lean mass, and Huggett-Widdas for fetal length. We first adjusted the Gompertz growth curve for average females from Murphy et al. (2020) to ensure that length for calves and juveniles matched what was reported in the literature (Lockyer, 2003), where *SL* is standard length in cm and *a* is age in years. For small and large females we adjusted the average female growth curve by subtracting and adding 10 cm, respectively.

$$SL_{avg} = 155.37e^{-0.7e^{-0.6a}} \quad \text{eq. 1}$$

We adjusted a weight-at-length curve (Lockyer and Kinze, 2003) such that weight-at-age derived from our calculations of standard length matched the mass values reported in Lockyer and Kinze (2003). This modulated weight-at-length curve was also used to derive mass for small and large females.

$$mass = 8.1\ x\ 10^{-5}SL^{2.678} - 2 \quad \text{eq. 2}$$

We used the Huggett-Widdas equation with a lag time of 38 days to calculate fetus length (Huggett and Widdas, 1951; Börjesson and Read, 2003). We modified the equation such that fetal length at the time of birth was equal to the standard length of a female at 1 day old using the Gompertz growth curve.

$$SL_{fetus_{avg}} = 0.2908397a_{fetus} - 11.05191 \quad \text{eq. 3}$$

$$SL_{fetus_{small}} = 0.2988363a_{fetus} - 11.05191 \quad \text{eq. 4}$$

$$SL_{fetus_{large}} = 0.3240212a_{fetus} - 11.05191 \quad \text{eq. 5}$$

We applied the fetal mass equation from Lockyer and Kinze (2003) for all size classes. The input was fetal length in cm and the output was fetal mass in kg.

$$mass_{fetus} = 0.05\, SL_{fetus}{}^{2.72}/1000 \quad \text{eq. 6}$$

Additionally, we calculated lean mass of porpoises using a von Bertalanffy growth curve (Gallagher et al., 2021). We modified the original equation to ensure that the calculated lean mass at a given age resulted in a body condition value that matched what is reported in the literature to the nearest 100th decimal place (Lockyer, 2003). For the small and large size class, we manually manipulated the von Bertalanffy growth curve so it matched the same body condition-at-age relationship that we constructed for average females.

$$mass_{stmass_{avg}} = 46.7 * (1 - \left(1 - \frac{4.5^{\frac{1}{3}}}{46.7}\right) * \, e^{\frac{-1.16a}{3}})^3 \quad \text{eq. 7}$$

$$mass_{stmass_{small}} = 38.65 * \left(1 - \left(1 - \frac{2.74^{\frac{1}{3}}}{36.65}\right) * \, e^{\frac{-1.22a}{3}}\right)^3 \quad \text{eq. 8}$$

$$mass_{stmass_{large}} = 55.5 * (1 - \left(1 - \frac{6.71^{\frac{1}{3}}}{55.5}\right) * \, e^{\frac{-1.129a}{3}})^3 \quad \text{eq. 9}$$

The functions for thermoregulation and locomotion require additional morphological inputs, such as surface area, *SA,* and blubber depth, *BD* (Hind and Gurney, 1997; Gallagher et al., 2021). The input for the surface area function is mass in kg and the output is surface area in m^2. Calves and females (juveniles and adults) have their own unique equation for blubber depth. The input for calves is body condition, m, and for females is blubber mass ($mass_{blubber}$), blubber density ($densBlubb$), and surface area, *SA*.

$$SA = 0.093 * \ mass^{0.57} \quad \text{eq. 10}$$

$$BD_{calf} = (6.2154 * m + 0.2512)/100 \quad \text{eq. 11}$$

$$BD_{female} = \frac{{mass_{blubber}}/{d_b}}{SA*100} \quad \text{eq. 12}$$

Physiology

Basal metabolic rate was determined by body mass to the ¾ power, following Kleiber (1975). We used a normalization constant of 11.13 from Gallagher et al. (2021), as opposed to the typical 3.4 in Kleiber (1975), to account for the elevated metabolic rate documented in harbor porpoises (Rojano-Doñate et al., 2018) which resulted in biologically accurate emergent properties of the model with respect to body condition and energy expenditure.

$$C_{BMR} = 11.13 * mass^{3/4} \quad \text{eq. 13}$$

The cost of locomotion is determined by the metabolic cost of producing a propulsive force, which depends on the aerobic efficiency and the propeller efficiency. Aerobic efficiency is the efficiency of converting chemical energy to muscular work, while propeller efficiency is the efficiency of converting muscular work to forward movement. It is assumed that the propulsive forces must balance the drag forces, which are influenced by individual surface area, velocity, drag coefficient, and water density. In the backward iteration, we assumed that harbor porpoises were in constant motion at a velocity of 0.84 m/s; however, in the forward simulation we selected individual velocity on a given day from a uniform distribution ranging from 0.66 m/s to 1.02 m/s (Otani et al., 2001; Gallagher et al., 2021). Thermoregulatory costs were defined as the difference between heat lost to the environment (Q_{CR}) and internal heat generation (Q_{CM}) and only occur when the heat transfer coefficient (h_{ce}) is greater than the calculated lower limit of the heat transfer coefficient (h_{cl}; Hind and Gurney, 1997). It is assumed that forced convection is the primary method of heat transfer from the body to the surrounding environment via the skin-water boundary. We assumed that internal heat generation was predominantly driven by basal metabolism and the heat produced during swimming.

$$C_{loc} = (l * p * SA * drag_{coeff} * v^3)/(2ea * ep) \quad \text{eq. 14}$$

$$C_{therm} = \begin{matrix} h_{ce} > h_{cl} & 0 \\ h_{ce} \leq h_{cl} & Q_{CR} - Q_{CM} \end{matrix} \quad \text{eq. 15}$$

Reproductive females incurred additional costs of either pregnancy or lactation (or both). The cost of pregnancy includes the heat of gestation, in addition to the cost of tissue synthesis associated with fetal growth (Brody, 1968). The heat of gestation is defined as the metabolic work required to maintain pregnancy and provide nutrients to the developing fetus, while the cost of tissue synthesis is determined by the energy density of deposited fetal tissues on a given day (Gallagher et al. 2021). The cost of lactation was directly determined from the energetic needs of the calf, as there are currently no empirical estimates of the cost of lactation in harbor porpoise. When the calf is less than three months old and the female is in ideal body condition, all calf costs were covered. These calf costs include basal metabolism, thermoregulation, and growth. We included a multiplier that increased the calf costs by 5% to account for inefficiencies in the transfer of milk. Without this multiplier calf survival was very low and the emergent properties of the model did not align with values reported in the literature. We assumed that locomotive costs would be negligible due to echelon swimming (e.g., Gallagher et al., 2021). As the calf grows beyond three months old, milk dependency will decrease linearly until the calf weans at 8 months old (Gallagher et al., 2021). We assumed that the calf forages for the additional energy needed (Learmonth et al., 2014). In the backward iteration, a lactating female's fitness is weighted by the probability of finding food, where finding food means the calf will receive milk in addition to energy from independently foraging and not finding food means the calf will only receive milk. In the forward simulation, the calf only accrues additional energy from independent foraging if food is found on that given model day. Female milk delivery decreased with decreasing body condition such that she delivered 75% of the calf’s needs when between ideal condition and the lactation critical value, and 0% of the calf’s needs when below the lactation critical value (McLellan et al., 2002). We assumed that the calf cannot supplement for decreased milk delivery resulting from poor female body condition.

$$C_{preg} = HIG + C_{ts} \quad \text{eq. 16}$$

$$C_{lac} =$$

$$\begin{array}{cc}
x \geq 0.275 & (C_{BMRcalf} + C_{thermcalf} + C_{growcalf}) * 1.05/lacEff) * \%_{calfDep} \\
0.1 \geq x < 0.275 & (C_{BMRcalf} + C_{thermcalf} + C_{growcalf}) * 1.05/lacEff) * \%_{calfDep} \\
x < 0.1 & 0
\end{array}$$

eq. 17

For calves and females that have not reached physical maturity, we calculated a cost of growth which related to the metabolic cost of depositing lean mass, as changes in blubber mass are accounted for later in the model with changes to bioenergetics and female state. The cost of growth was calculated using the energy density of the deposited lean mass, determined by the lipid and protein content, and the deposition efficiency of lean mass (Boult et al., 2018). Deposition of blubber mass was calculated similarly, but changes in blubber mass were facilitated by bioenergetic changes.

$$C_{grow} = \Delta_{stmass} * (ED_{stmass} + (ED_{stmass} * (1 - DE_{stmass}))) \quad \text{eq. 18}$$

$$x = (mass_{blubb} + (\Delta_{energy} * \ DE_{lip} * \ \%Lipid_{blubb}/ED_{lip}))/mass_{body} \quad \text{eq. 19}$$

The biomass of prey consumed was calculated using the following equation to account for allometric changes in biomass based on body size.

$$intake = \frac{(mass_{ref} * \%_{mass})}{{mass_{ref}}^{3/4} * {mass_{ind}}^{3/4}} \quad \text{eq. 20}$$

Where $mass_{ref}$ is a reference mass for which biomass intake is known (set to 38 kg), $\%_{mass}$ is the known proportion of body mass consumed for the reference animal (set to 0.11), and $mass_{ind}$ is the ideal mass of the modeled individual. The input parameters for the above equation were derived from harbor porpoise biomass intake reported in the literature (Kastelein et al., 1997) with a slight adjustment to the known proportion of body mass consumed to account for the increased energy intake of wild porpoises. We used the ideal mass of the modeled individual for their given age as the primary driver of mass-related changes to energy intake are based on proportional changes to basal metabolic rate which are determined by lean mass and not blubber mass. For juvenile individuals who had not yet reached sexual maturity, we included a 10% increase in their biomass intake to account for the increased mass-specific energy expenditure of juveniles when compared to adults (Appendix Figure 2). Prey composition was derived from seasonal accounts of stomach content analyses and energy density of prey items changed seasonally when data were available (Table A2.4; Andreasen et al., 2017; Booth, 2020).

We accounted for the ability of females to modulate their food intake based on their current condition such that underweight females would increase energy intake and overweight females would decrease energy intake. We used the percent difference between actual female weight and ideal female weight for a given age, bounded by a percent difference of 50%, as the percent increase in overall energy intake for under- and over-weight females. We allotted 20% more energy to lactating females to cover the additional costs of lactation.

Energy intake for calves was a combination of milk delivered from the mother and independent foraging. Independent foraging was calculated as the difference between the calf's energetic requirements and the energy that would be delivered by the mother if she were in ideal condition (i.e., we assumed calves were able to acquire all of their energy needs to maintain energy balance through independent foraging).

Oceanographic parameters

The thermoregulation and locomotion equations required oceanographic parameters to be calculated (Hind and Gurney, 1997). We calculated the dynamic and kinematic viscosity (u_s and v_s), the thermal conductivity (k_w), specific heat capacity (C_p), and Prandtl number (Pr) of seawater (Jamieson et al., 1969; Caldwell, 1974; Coulson et al., 1999; El-Dessouky and Ettouney, 2002; Sharqaway et al., 2010). The input for these functions included the salinity (S_w) and density (p) of seawater and temperature (t).

$$u_s = (4.2844 \ast\ 10^{-5} + (0.157(temp + 64.993)^2 - 91.296)^{-1}) \ast (1 +$$

$$(1.541 + (1.998 \ast 10^{-2}) \ast temp - (9.52 \ast\ 10^{-5}) \ast temp^2) \ast \frac{S_w}{1000} + (7.974 +$$

$$(7.561 \ast\ 10^{-2}) \ast temp - (4.724 \ast 10^{-4}) \ast temp^2 \ast \frac{S_w}{1000}^2)) \quad \text{eq. 21}$$

$$v_s = {}^{u_s}\!/_{p} \quad \text{eq. 22}$$

$$k_w = 0.5715 \ast (1 + (0.003 \ast temp) - (1.025 \ast 10^{-5} \ast temp^2) + \Big(6.53 \ast 10^{-4} \ast$$

$$\frac{p}{1000}\Big) - \Big(0.00029 \ast \frac{S_w}{1000}\Big)) \quad \text{eq. 23}$$

$$C_p = \Big(5.328 - (9.76 \ast\ 10^{-2}) \ast \frac{S_w}{1000} + (4.04 \ast 10^{-4}) \ast \frac{S_w}{1000}^2\Big) + \Bigg(\Bigg((-6.913 \ast$$

$$10^{-3}) + (7.351 \ast 10^{-4}) \ast \frac{S_w}{1000} - \Bigg((3.15 \ast 10^{-6}) \ast \frac{S_w}{1000}^2\Bigg)\Bigg) \ast temp + 273.15\Bigg) +$$

$$\Bigg(\Bigg((9.6 \ast\ 10^{-6}) - (1.927 \ast 10^{-6}) + (8.23 \ast 10^{-9}) \ast \frac{S_w}{1000}^2\Bigg) \ast (temp +$$

$$273.15)^2\Bigg) + \Bigg(\Bigg((2.5 \ast 10^{-9}) + (1.666 \ast 10^{-9}) \ast \frac{S_w}{1000} - \Bigg((7.125 \ast 10^{-12}) \ast 10^{-12} \ast$$

$$\frac{S_w}{1000}\Bigg)\Bigg) \ast (t + 273.15)^3\Bigg) \ast 1000 \quad \text{eq. 24}$$

$$\mathrm{Pr} = \frac{u_s + C_p}{k_w} \quad \text{eq. 25}$$

SDP equations

In the backward iteration, after determining the resulting female's state at the end of each model day by incorporating energy gained from food and energy lost from metabolic costs, her potential fitness (define as future reproductive potential) was calculated. The backward iteration began on model day T, which was the final day of a female harbor porpoise's life, and the model then moved backwards in time from this point. Fitness on the final model day was 0 for reproductive states 1 (non-reproductive) and 2 (pregnant) and as defined by the sigmoidal function outlined in eq. 26 for reproductive states 3 (lactating) and 4 (pregnant and lactating; Pirotta et al., 2018). The inflection point of the curve was defined by m_{50}^{γ}, indicating the body condition at which 50% of calves survived, and the steepness of the curve was defined by γ. $m_{50}^{\gamma}$was age-specific to account for the changes in body condition that occur throughout lactation. As such, m_{50}^{γ} was set to 0.36 for calves on day 1 and 0.24 for calves on day 240, and decreased linearly throughout lactation. These values were one standard deviation below the mean body composition for neonates and calves, respectively, reported in the literature (Lockyer, 1995; McLellan et al., 2002).

$$\phi(m) = m^{\gamma}/(m^{\gamma} + m_{50}^{\gamma}) \qquad \text{eq. 26}$$

On all other model days, the fitness of females in reproductive state 1 was defined by eq. 27 where x' was the body condition of an individual at age $t + 1$ if food was found (determined by λ), x'' is the body condition of an individual at age $t + 1$ if food was not found, and Υ is the energy gained from food if food was found. The function is multiplied by the probability of surviving this time step, calculated as the inverse of the probability of age-based mortality, β_a, based on the female's age in years (a).

$$V_r(x,t) = (1 - \beta_a)[\,\lambda * F_r(x', t + 1, \Upsilon) + \,(1 - \,\lambda) * F_r(x'', t + 1) \qquad \text{eq. 27}$$

When there are no possible decisions for a female in reproductive state 1, her fitness, F_1, is fixed (eq. 28). However, at the time of implantation, t_i, a female in reproductive state 1 could choose to implant and transition to reproductive state 2 (pregnant) or remain in reproductive state 1 depending on which decision yielded the highest fitness (eq. 28).

$$F_1(x,t) = \begin{matrix} t \neq t_i & F_1(x,t) = V_1(x,t) \\ t = t_i & F_1(x,t) = \max\{V_1(x,t), V_2(x,t)\} \end{matrix} \qquad \text{eq. 28}$$

A female in reproductive state 2 (pregnant), had the decision to maintain the pregnancy or abort the fetus and return to reproductive state 1 at any time during pregnancy. At the time of birth, t_b, a female had to give birth and transition to reproductive state 3 or abandon the fetus and transition to reproductive state 1.

$$F_2(x,t) = \begin{matrix} t \neq t_b & F_2(x,t) = \max\{V_1(x,t), V_2(x,t)\} \\ t = t_b & F_2(x,t) = V_3(x,m,t) \end{matrix} \qquad \text{eq. 29}$$

In reproductive state 3, a female was lactating and could choose to wean the calf early and transition to reproductive state 1 or remain lactating; however, all females had to wean their calves on the forced weaning date. The female gained additional fitness when a calf was weaned based on the future survival probability of her calf. The future survival probability of a calf was calculated using eq. 26 and her expected body condition at the time of weaning (calculated by accounting for the energy lost in the absence of milk delivery from the mother).

At the time of implantation, a female in reproductive state 3 could wean the calf early and transition to reproductive state 1, wean the calf early while implanting and transition to reproductive state 2, or continue nursing and become pregnant to transition to reproductive state 4 (pregnant and lactating; eq. 30). At the time of weaning, t_w, a female had to wean the calf and transition to reproductive state 1 (eq. 30).

$$F_3(x,m,t) = \begin{array}{lc} t \neq t_i \,\&\, t \neq t_w & \max\{V_1(x,t) + \phi(m), V_3(x,m,t)\} \\ t = t_i & \max\{(V_1(x,a) + \phi(m), V_2(x,t) + \phi(m), V_3(x,m,t), V_4(x,m,t)\} \\ t = t_w & V_1(x,t) + \phi(m) \end{array}$$

eq. 30

Finally, in reproductive state 4 a female could choose to remain pregnant and lactating, abort the fetus while nursing the calf and transition to reproductive state 3, wean the calf early and maintain the pregnancy, therefore transitioning to reproductive state 2, or both abort the fetus and wean the calf early to transition to reproductive state 1 (eq. 31). As with a lactating female, additional fitness was gained depending on the survival probability of the calf at the time of weaning (eq. 31).

$$F_4(x,m,t) = \begin{array}{lc} t \neq t_w & \max\{V_1(x,t) + \phi(x,m), V_2(x,t) + \phi(x,m), V_3(x,m,t), V_4(x,m,t)\} \\ t = t_w & \max\{V_1(x,t) + \phi(x,m), V_2(x,t) + \phi(x,m)\} \end{array}$$

eq. 31

In the instance that two decisions yielded the same fitness value, both decisions were recorded in the backward iteration. Then, in the forward simulation, the decision was randomly selected with equal probability assigned to each decision.

Forward simulation

Forward simulation initialization

Body condition of starting individuals was pulled from a beta distribution that was constructed using pattern-oriented modeling from early model iterations (shape 1 = 17.06, shape 2 = 30.64). If body condition was less than the critical value, x_c, or greater than the capacity constraint, C, these values were assigned to $x_c$or C, respectively. If individuals were less than the age of sexual maturity they were automatically in reproductive state 1, and if they were older they were assigned to either reproductive state 1 or 3 using the probability of being pregnant calculated in early model iterations (95%). Females that started the simulation in reproductive state 3 were assigned a calf whose body condition was randomly selected from a beta distribution that was similarly bounded by the calf-specific critical value, m_c and capacity constraint (mC, shape 1 = 8.45, shape 2 = 13.98).

Age at the offset of growth was extracted from a uniform distribution ranging from 7 to 12 as this was the range of values for asymptotic age in growth curves constructed in Murphy et al. (2020). Additionally, Gompertz growth parameters A, b, and k and the mass exponent parameter were all derived from uniform distributions that spanned ± one standard deviation of mean values for each parameter reported in the literature (Lockyer and Kinze, 2003). This was also done for all calves that entered the simulation.

Running the forward simulation

We assessed the life history, population demography, and response to disturbance of harbor porpoises in the forward simulation. For each forward simulation a population was simulated, and this process was repeated 100 times in a Monte Carlo simulation to ensure that mean population responses were obtained. For each individual population simulation, we calculated daily and population metrics. Each simulation began with an initial population size of 3000 female individuals. The model began at the time of birth, and ran for 15 years, 5 of which served as a normalization time to ensure that model output was not impacted by initial parameterization. Data from this normalization time was not used in model analyses. The age distribution of starting individuals was selected between the ages of 1 and 20 from a life history schedule (Barlow and Boveng, 1991). For each starting individual, body condition, calf body condition (if lactating), reproductive state (if older than sexual maturity), age at physical maturity, Gompertz growth curve parameters, and the mass curve parameter were randomly selected from unique distributions determined using pattern-oriented modeling (Appendix: Forward simulation initialization).

For each female that gave birth, the bioenergetics of the calf were tracked until weaning. At the time of weaning, her body condition at the time of recruitment was calculated by simulating her metabolic costs from the time of weaning to recruitment and her energy intake from independent foraging alone. Then, the calf's survival probability at the time of recruitment was calculated using eq. 26 where m_{50}^{γ} was set to 0.24 as this was one standard deviation below the mean body composition of an immature female (McLellan et al., 2002). We then generated a random number between 0 and 1 using a uniform distribution and if the value was less than the calculated survival probability of the calf we assumed that the calf recruited into the population and was added to the simulation at age 1 on the first day of the following model year if the calf was a female. We assumed a 50/50 sex ratio of male and female calves. Male calves were included in population abundance estimates and in mean calf body condition calculations but were otherwise not accounted for in the model beyond the time of recruitment.

In the forward simulation, a female could die of starvation or an underlying age-based mortality derived from the literature (see above; Murphy et al., 2020). On a given model day if a female's body condition reached the critical value, x_c, she exited the simulation and her cause of death was listed as starvation. Additionally, once the female reached the maximum age of 20 she exited the simulation and her cause of death was listed as age. On each model day, there was a probability of dying from underlying, age-based mortality which was determined by assigning a discrete option based on the probability of age-based mortality (Murphy et al., 2020; Table A2.5).

Energy intake on each model day was calculated using the same equation described in the backward iteration; however, a discrete option based on the probability of finding food, λ, was assigned for each individual on each model day to determine if she did or did not find food.

Life history table

Using the final simulation year, we calculated the number of individuals that survive to the next age class, *S(a)*, and the average number of births per age class, *b(a)* using methods outlined in Gotelli (2001). From this the proportion of individuals that survive to a given age, *l(a)* or survivorship, was calculated. Finally, we calculated the net reproductive rate, R_0, as an indicator of lifetime reproductive success of females in the population and we calculated the finite population growth rate, *lambda* (Gotelli, 2001). If *lambda* is greater than 1 the population is expected to increase and if *lambda* is less than 1 the population is expected to decline. Cohen's D was used to compare all three size classes to assess which combinations had the greatest difference (Cohen, 1977).

$$l(a) = S(a)/S(0) \quad \text{eq. 32}$$

$$R_0 = \Sigma_0^{20} l(a)b(a) \quad \text{eq. 33}$$

$$lambda = \frac{N_{t+1}}{N_t} \quad \text{eq. 34}$$

Emergent model properties

We found that the emergent properties of the model matched values reported in the literature for the average female baseline scenario. Body condition for average females in our model had a mean of 0.29, which is on par with reports from the literature for mature females (0.24-0.37; Lockyer, 1995; McLellan et al., 2002; Rojano-Doñate et al., 2018). Energy intake in the model experienced average seasonal fluctuations that ranged from 21 MJ in Spring to 29 MJ in Winter. Although this is on the higher end of reported values for harbor porpoises (e.g. 15-31 MJ; Rojano-Doñate et al., 2018) our model values were averaged across all individuals, including reproductive females and females in poor condition that increased energy intake.

It has been reported that most females give birth every other year, with some females reproducing every year, which is similar to the fecundity schedule documented here (Figure 3); however, this data has only been reported for California harbor porpoises (Hohn and Brownwell, 1990). The average pregnancy rate of harbor porpoises in this simulation was 0.57, which was in-between values reported in the literature; however, there is a high degree of variability in this metric throughout the literature (0.34-0.86; Read, 1990; Learmonth et al., 2014). Due to the cryptic nature of this species, not much is known about their general biology, particularly with respect to abortion rates, calf abandonment rates, and population trajectories. However, we feel that the congruencies between our data and the literature with respect to body composition, birthing interval, and energy intake indicates that our model has successfully captured some aspects of the biology of North Sea harbor porpoises.

Appendix A2 Tables and Figures

Table A2. 1 List of all parameters used in equations.

Parameter	Symbol
Female body condition	x
Female blubber mass	$mass_{blubb}$
Calf body condition	m
Calf body condition at which the survival probability is .5	m_{50}
Time	t
Final model time	T
Time of implantation	t_i
Time of birth	t_b
Time of weaning	t_w
Probability of underlying mortality (age-based)	β_a
Probability of finding food	λ
Energetic gain from food	Υ
Shape parameter for calf survival function $\boldsymbol{\varphi}$	γ
Reproductive state	r
Reproductive state: juvenile and non-reproductive	1
Reproductive state: pregnant	2
Reproductive state: lactating	3
Reproductive state: pregnant and lactating	4
Deposition efficiency of lipid	DE_{lip}
Deposition efficiency of protein	DE_{pro}
Energy density of lipid	ED_{lip}
Energy density of protein	ED_{pro}
Percent lipid in blubber (unique for age class)	$\%Lipid_{blubb}$
Percent protein in blubber (unique for age class)	$\%Protein_{blubb}$
Percent lipid in structural mass (unique for age class)	$\%Lipid_{stmass}$
Percent protein in structural mass (unique for age class)	$\%Protein_{stmass}$
Percent lipid in fetus	$\%Lipid_{fetus}$
Percent protein in fetus	$\%Protein_{fetus}$
Deposition efficiency of structural mass	DE_{stmass}
Delta fetal mass	$\Delta_{fetalmass}$
Ratio of active to passive drag	l
Density of seawater	p
Surface area	SA
Reynold's number	Re
Drag coefficient	$drag_{coeff}$
Velocity	v
Aerobic efficiency	ea
Propeller efficiency	ep

Heat transfer coefficient	h_{ce}
Lower limit of heat transfer coefficient	h_{cl}
Heat generation required to remain thermoneutral	Q_{CR}
Internal heat generation from metabolism	Q_{CM}
Temperature of the muscle-blubber interface	T_{MB}
Forced convection scaling coefficient	h_k
Realized skin temperature	T_{SR}
Conductivity of blubber	k_b
Aerobic efficiency	ea
Propeller efficiency	ep
Core body temperature	T_C
Gravitational acceleration	g
Density of blubber	p_b
Change in structural mass	Δ_{stmass}
Energy density of structural mass	ED_{stmass}
Deposition efficiency of structural mass	DE_{stmass}
Heat increment of gestation	HIG
Cost of fetal tissue synthesis	C_{ts}
Total calf costs	$Costs_{calf}$
Lactation efficiency	$lacEff$
Percent of calf dependency on female	$\%_{calfDep}$
Lactation duration	lac_{dur}
Standard length	SL
Age	a
Blubber depth	d_b
Salinity of seawater	S_w
Kinematic viscosity of seawater	v_s
Dynamic viscosity of seawater	u_s
Specific heat capacity of seawater	C_p
Thermal conductivity of seawater	k_w
Prandtl number	Pr
Reynold’s number	Re
Sea surface temperature	$temp$
Cost of basal metabolism	C_{BMR}
Cost of thermoregulation	C_{therm}
Cost of locomotion	C_{loc}
Cost of growth	C_{grow}
Cost of pregnancy	C_{preg}
Cost of lactation	C_{lact}
Calf cost of basal metabolism	$C_{BMRCalf}$
Calf cost of thermoregulation	$C_{thermCalf}$
Calf cost of growth	$C_{growCalf}$

Table A2. 2 SDP model functions.

State dynamics		
Non-reproductive	$\Delta_{energy}' = C_{BMR} - C_{therm} - C_{loc} - C_{grow} + \Upsilon$ $\Delta_{energy}'' = C_{BMR} - C_{therm} - C_{loc} - C_{grow}$	(34)
Pregnant	$\Delta_{energy}' = C_{BMR} - C_{therm} - C_{loc} - C_{preg} - C_{grow} + \Upsilon$ $\Delta_{energy}'' = C_{BMR} - C_{therm} - C_{loc} - C_{preg} - C_{grow}$	(35)
Lactating	$\Delta_{energy}' = C_{BMR} - C_{therm} - C_{loc} - C_{lact} - C_{grow} + \Upsilon$ $\Delta_{energy}'' = C_{BMR} - C_{therm} - C_{loc} - C_{lact} - C_{grow}$	(36)
Pregnant and lactating	$\Delta_{energy}' = C_{BMR} - C_{therm} - C_{loc} - C_{preg} - C_{lact} - C_{grow} + \Upsilon$ $\Delta_{energy}'' = C_{BMR} - C_{therm} - C_{loc} - C_{preg} - C_{lact} - C_{grow}$	(37)
Convert Δ_{energy} to body condition	$x = (mass_{blubb} + (\Delta_{energy} * DE_{lip} * \%Lipid_{blubb}/ED_{lip}))/mass_{body}$	(38)
Terminal Fitness Function	$\phi = 0$ (no calf) $\phi(m) = m^{\gamma}/(m^{\gamma} + m_{50}^{\gamma})$	(39)
SDP equations		
Fitness function (not lactating)	$V_r(x,t) = (1-\beta_a)[\lambda * F_r(x', t+1, \Upsilon) + (1-\lambda) * F_r(x'', t+1)$	(40)
Fitness function (lactating)	$V_r(x,m,t) = (1-\beta_a)[\lambda * F_r(x', t+1, m', \Upsilon) + (1-\lambda) * F_r(x'', t+1, m'')$	(41)

Table A2. 3 Additional equations used in physiological equations.

Parameter	Equation		Citation
Re	$Re = (v * \frac{SL}{100})/v_s$	(42)	Fish, 1998

$\boldsymbol{drag_{coeff}}$	$drag_{coeff} = 10^{-0.1132*log_{10}(Re)-1.5358}$	(43)	Tanaka et al., 2019; Gallagher et al., 2021
$\boldsymbol{ea}$	$ea = 0.1378 + \left(0.441 * (\frac{v}{4.2})^{3}\right) - \left(0.422 * (\frac{v}{4.2})^{6}\right)$	(44)	Fish, 1993
$\boldsymbol{Pr}$	$\mathrm{Pr} = (u_s * C_p)/k_w$	(45)	Coulson et al., 1999
$\boldsymbol{Q_{CM}}$	$Q_{CM} = C_{BMR} + (1 - ea) * C_{loc}$	(46)	Hind and Gurney, 1997
$\boldsymbol{h_{cl}}$	$h_{cl} = k_b/d_b$	(47)	Hind and Gurney, 1997
$\boldsymbol{h_k}$	$h_k = .036 * \left(\left(\frac{k_w}{SL/100}\right)^{\frac{1}{5}}\right) * v_s^{\frac{4}{5}} * Pr^{\frac{1}{3}} * v^{\frac{4}{5}}$	(48)	Hind and Gurney, 1997
$\boldsymbol{T_{mb}}$	$T_{mb} = T_C - (T_C - temp) * 0.25$	(49)	Hind and Gurney, 1997
$\boldsymbol{T_{SR}}$	$T_{SR} = \left(11.4 * k_b * \frac{SL}{100} * T_{MB}\right) + \left(\frac{SA * temp * h_k * \ln\left(\frac{mass}{mass_{stmass}}\right)}{11.4 * k_b * \frac{SL}{100}}\right) + (SA * h_k * \ln\left(\frac{mass}{mass_{stmass}}\right))$	(50)	Hind and Gurney, 1997
$\boldsymbol{h_{ce}}$	$h_{ce} = Q_{CM}/(SA * (T_C - T_{SR}))$	(51)	Hind and Gurney, 1997
$\boldsymbol{h_{cl}}$	$h_{cl} = k_b/d_b$	(52)	Hind and Gurney, 1997
$\boldsymbol{ED_{stmass}}$	$ED_{stmass} = \left(\%Protein_{stmass} * ED_{pro}\right) + \left(\%Lipid_{stmass} * ED_{lip}\right) +$	(53)	Boult et al., 2018
$\boldsymbol{DE_{stmass}}$	$DE_{stmass} = (\left(\%Protein_{stmass} * DE_{pro}\right) + (\%Lipid_{stmass} * DE_{lip}))/(\%Protein_{stmass} + \%Lipid_{stmass})$	(54)	Boult et al., 2018
$\boldsymbol{HIG}$	$HIG = 4400 * \Delta_{fetalmass}{}^{1.2} * 4184$	(55)	Brody, 1968
$\boldsymbol{C_{ts}}$	$C_{ts} = \Delta_{fetalmass} * \left(\frac{\%Lipid_{fetus} * ED_{lip}}{DE_{lip}}\right) + \left(\frac{\%Protein_{fetus} * ED_{pro}}{DE_{pro}}\right)$	(56)	Brody, 1968
$\%_{\boldsymbol{calfDep}}$		(57)	Gallagher et al., 2021

$$\%_{calfDep} = \begin{array}{ll} a_{calf} \leq 91 & 100\% \\ a_{calf} > 91 & \dfrac{a_{calf}}{lac_{dur} - 91} * 100 \end{array}$$

Table A2. 4 Proportion of each prey item in adult and juvenile diet by season and associated energy density (MJ) derived from Booth et al. (2020).

	Herring	**Cod**	**Eelpout**	**Gobie**	**Whiting**
Adult proportions					
Winter	0.635	0.365	0	0	0
Spring	0.560	0.440	0	0	0
Summer	0.223	0.463	0.313	0	0
Fall	0.370	0.630	0	0	0
Juvenile proportions					
Winter	0.540	0	0	0.460	0
Spring	0.360	0.270	0	0.360	0
Summer	0	0.690	0	0	0.310
Fall	0	0.455	0	0.545	0
Energy density (MJ)					
Winter	8500000	4200000	5100000	4400000	4200000
Spring	4900000	4200000	5100000	4400000	4200000
Summer	11900000	4200000	5100000	4400000	4200000
Fall	8800000	4200000	5100000	4400000	4200000

Table A2. 5 Age-based survival probability from Barlow and Boveng (1991).

Age	Survival probability
1	0.702
2	0.814
3	0.885
4	0.928
5	0.951
6	0.964
7	0.969
8	0.969
9	0.964
10	0.956

11	0.943
12	0.923
13	0.894
14	0.854
15	0.799
16	0.726
17	0.631
18	0.515
19	0.384

Table A2. 6 List of parameters tested in sensitivity analysis and values tested.

Parameter	**Tested values**
Assimilation efficiency	0.80, 0.85, 0.95
Calf body condition at recruitment	0.20, 0.30, 0.35, 0.40
Deposition efficiency of lipid	± 10%, 25%, 50%
Deposition efficiency of protein	± 10%, 25%, 50%
Energy density of lipid	± 10%, 25%, 50%
Energy density of protein	± 10%, 25%, 50%
Female critical value	0.10, 0.15, 0.20, 0.25
Heat increment of feeding	0.025, 0.075, 0.125, 0.10, 0.15
Intake multiplier for lactating females	1.0, 1.4, 1.6, 1.8, 2.0
Mammary gland efficiency	± 10%, 25%, 50%
Percent lipid in blubber for females	± 10%, 25%, 50%
Percent lipid in blubber for calves	± 10%, 25%, 50%
Percent lipid in structural mass for mature females	± 10%, 25%, 50%
Percent lipid in structural mass for juveniles	± 10%, 25%, 50%
Percent lipid in structural mass for calves	± 10%, 25%, 50%
Percent lipid in fetus	± 10%, 25%, 50%
Percent protein in structural mass for mature females	± 10%, 25%, 50%
Percent protein in structural mass for juveniles	± 10%, 25%, 50%
Percent protein in structural mass for calves	± 10%, 25%, 50%
Percent protein in blubber for calves	± 10%, 25%, 50%
Percent protein in fetus	± 10%, 25%, 50%
Scale parameter fitness function	± 10%, 25%, 50%
Shape parameter fitness function	± 10%, 25%, 50%
Urinary energy loss	0.06, 0.07, 0.09, 0.10
λ	0.5, 0.75, 0.9

Table A2. 7 Cohen's D value for comparisons between small and average females, average and large females, and small and large females. Effect size was negligible when less than 0.2, small when between 0.2 and 0.5, moderate when between 0.5 and 0.8, and large when greater than 0.8.

Parameter	Cohen's D
Interbirth interval	Small-Average: -6.93 (large) Average-Large: 6.20 (large) Small-Large: -12.27 (large)
Births per mature females	Small-Average: 4.36 (large) Average-Large: -0.88 (large) Small-Large: 5.15 (large)
Recruits per mature females	Small-Average: -2.18 (large) Average-Large: 0.08 (negligible) Small-Large: -2.48 (large)
Survival probability of recruits	Small-Average: -13.37 (large) Average-Large: 2.35 (large) Small-Large: -15.37 (large)
Post-breeding female survival	Small-Average: 10.89 (large) Average-Large: 2.10 (large) Small-Large: 8.23 (large)
Proportion of deaths related to starvation	Small-Average: -14.70 (large) Average-Large: 0.86 (large) Small-Large: -15.59 (large)
λ	Small-Average: 3.80 (large) Average-Large: 0.84 (large) Small-Large: 3.27 (large)
Calf body condition	Small-Average: 1.75 (large) Average-Large: -9.07 (large) Small-Large: -5.23 (large)
Nursing duration	Small-Average: -8.45 (large) Average-Large: 7.37 (large) Small-Large: -2.73 (large)
Abortion rate	Small-Average: 1.11 (small) Average-Large: -0.08 (negligible) Small-Large: 1.06 (large)
Recruitment rate	Small-Average: 14.61 (large) Average-Large: 2.74 (large) Small-Large: 17.57 (large)

Table A2. 8 Raw values of female body condition, age at death, starvation-related death, post-breeding survival, interbirth interval, births per mature females, abortion rate, recruits per mature females, recruitment rate, nursing duration, calf body condition, calf recruitment body condition, recruit survival, R_0 for average and large females under baseline scenarios, a single disturbance in Fall, and a repeat disturbance in Fall.

		Baseline	*Single Fall*	*Repeat Fall*
Small	Female body condition	0.31 ± 1.20 x 10^{-3}	0.30 ± 2.05 x 10^{-3}	0.28 ± 1.55 x 10^{-3}
	Age at death	8.67 ± 0.08	8.37 ± 0.08	8.16 ± 0.07
	Starvation-related death	0.69 ± 0.01	0.80 ± 0.01	0.94 ± 8.80 x 10^{-3}
	Post-breeding survival	0.54 ± 0.02	0.47 ± 0.03	0.09 ± 0.03
	Interbirth interval	1.84 ± 0.02	1.86 ± 0.03	1.59 ± 0.12
	Births per mature female	1.64 ± 0.07	1.53 ± 0.18	0.86 ± 0.10
	Abortion rate	0.91 ± 9.20 x 10^{-3}	0.88 ± 0.02	0.70 ± 0.11
	Recruits per mature female	0.86 ± 0.08	0.88 ± 0.13	0.22 ± 0.07
	Recruitment rate	0.72 ± 0.02	0.68 ± 0.03	0.27 ± 0.10
	Nursing duration	211.79 ± 2.28	201.46 ± 2.86	168.02 ± 2.50
	Calf body condition	0.33 ± 2.22 x 10^{-3}	0.33 ± 3.32 x 10^{-3}	0.33 ± 3.76 x 10^{-3}
	Calf recruitment body condition	0.31 ± 1.89 x 10^{-3}	0.32 ± 3.37 x 10^{-3}	0.35 ± 6.95 x 10^{-3}
	Recruit survival	0.85 ± 0.03	0.82 ± 0.04	0.68 ± 0.06
	λ	0.96 ± 6.55 x 10^{-3}	0.98 ± 6.32 x 10^{-3}	0.96 ± 2.23 x 10^{-3}
Average	Female body condition	0.31 ± 1.08 x 10^{-3}	0.31 ± 1.47 x 10^{-3}	0.28 ± 1.53 x 10^{-3}
	Age at death	9.27 ± 0.08	8.77 ± 0.08	8.34 ± 0.06
	Starvation-related death	0.48 ± 0.01	0.66 ± 0.01	0.91 ± 8.44 x 10^{-3}
	Post-breeding survival	0.74 ± 0.01	0.69 ± 0.03	0.41 ± 0.03
	Interbirth interval	1.74 ± 0.01	1.75 ± 0.02	1.67 ± 0.04

	Births per mature female	1.96 ± 0.07	1.93 ± 0.11	1.50 ± 0.10
	Abortion rate	0.92 ± 5.18 x 10^{-3}	0.90 ± 7.09 x 10^{-3}	0.87 ± 0.04
	Recruits per mature female	0.70 ± 0.06	0.74 ± 0.07	0.42 ± 0.06
	Recruitment rate	0.53 ± 0.01	0.52 ± 0.01	0.30 ± 0.07
	Nursing duration	237.97 ± 0.16	201.32 ± 1.90	219.97 ± 1.61
	Calf body condition	0.32 ± 1.47 x 10^{-3}	0.32 ± 1.82 x 10^{-3}	0.33 ± 2.41 x 10^{-3}
	Calf recruitment body condition	0.31 ± 1.55 x 10^{-3}	0.32 ± 1.70 x 10^{-3}	0.33 ± 4.37 x 10^{-3}
	Recruit survival	0.57 ± 0.01	0.56 ± 0.02 x 10^{-3}	0.47 ± 0.03
	λ	1.02 ± 2.76 x 10^{-3}	0.95 ± 5.93 x 10^{-3}	0.93 ± 2.39 x 10^{-3}
Large	Female body condition	0.31 ± 1.00 x 10^{-3}	0.31 ± 1.00 x 10^{-3}	0.28 ± 1.75 x 10^{-3}
	Age at death	9.18 ± 0.07	9.18 ± 0.07	8.32 ± 0.05
	Starvation-related death	0.47 ± 0.01	0.47 ± 0.01	0.90 ± 8.07 x 10^{-3}
	Post-breeding survival	0.70 ± 0.02	0.70 ± 0.02	0.37 ± 0.03
	Interbirth interval	1.65 ± 0.01	1.65 ± 0.01	1.48 ± 0.04
	Births per mature female	2.03 ± 0.08	2.03 ± 0.08	1.59 ± 0.10
	Abortion rate	0.92 ± 5.14 x 10^{-3}	0.92 ± 5.14 x 10^{-3}	0.88 ± 0.04
	Recruits per mature female	0.70 ± 0.04	0.70 ± 0.04	0.41 ± 0.06
	Recruitment rate	0.50 ± 9.34 x 10^{-3}	0.48 ± 0.01	0.27 ± 0.06
	Nursing duration	236.53 ± 0.23	191.09 ± 1.67	213.32 ± 1.58
	Calf body condition	0.34 ± 1.40 x 10^{-3}	0.34 ± 1.40 x 10^{-3}	0.35 ± 2.59 x 10^{-3}
	Calf recruitment	0.33 ± 1.34 x 10^{-3}	0.33 ± 1.34 x 10^{-3}	0.35 ± 3.41 x 10^{-3}

body condition			
Recruit survival	0.54 ± 0.01	0.54 ± 0.01	0.41 ± 0.03
λ	1.02 ± 2.31 x 10^{-3}	0.94 ± 5.11 x 10^{-3}	0.93 ± 2.32 x 10^{-3}

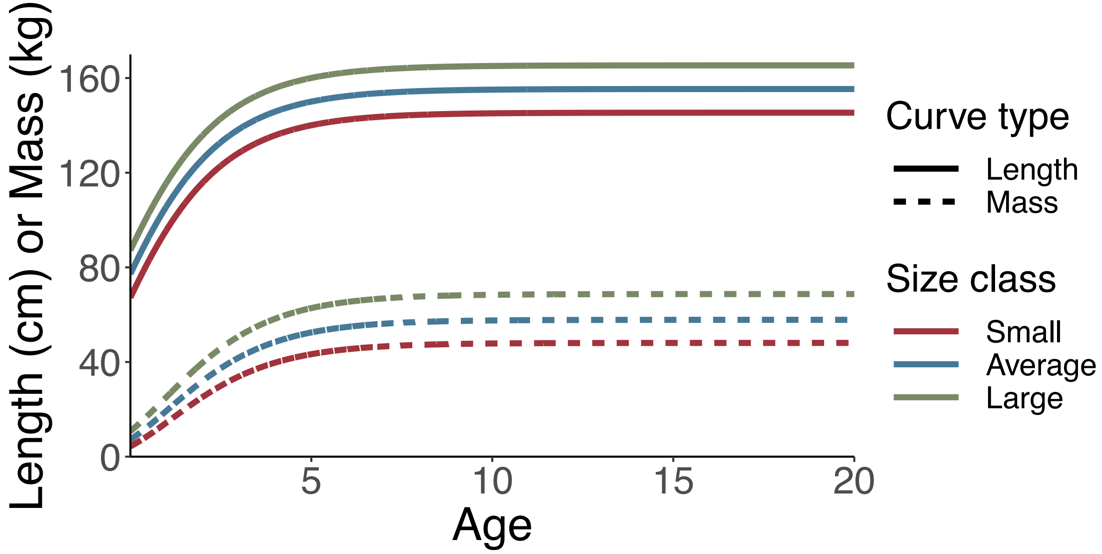

Figure A2. 1 Gompertz growth curve for length (cm) and mass (kg) of three size classes of harbor porpoises simulated in the SDP model.

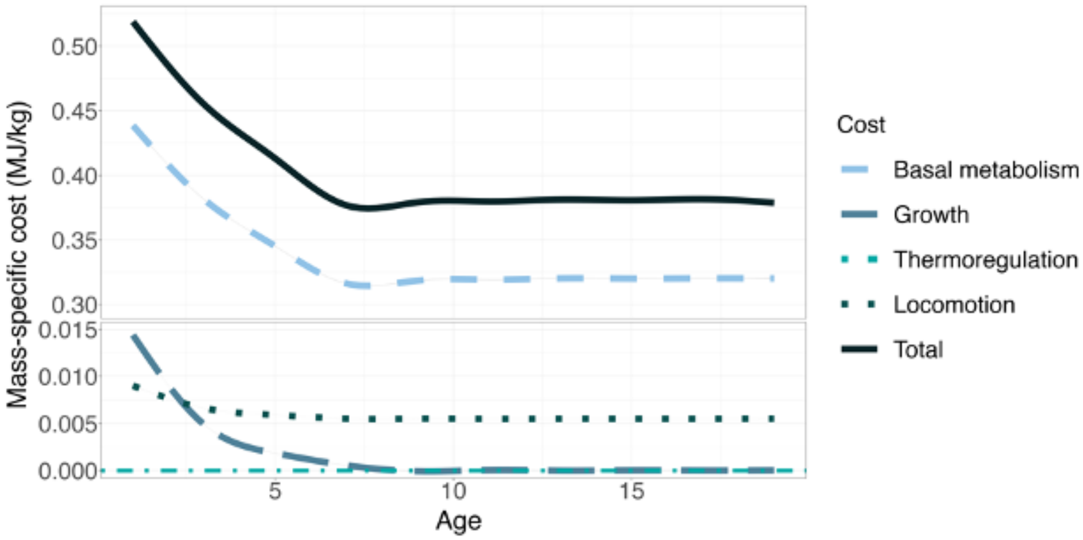

Figure A2. 2 Mass specific metabolic costs of an average-sized female harbor porpoise as a function of age. Note the break in the y-axis. Break was added using ggbreak package in R (Xu et al., 2021).

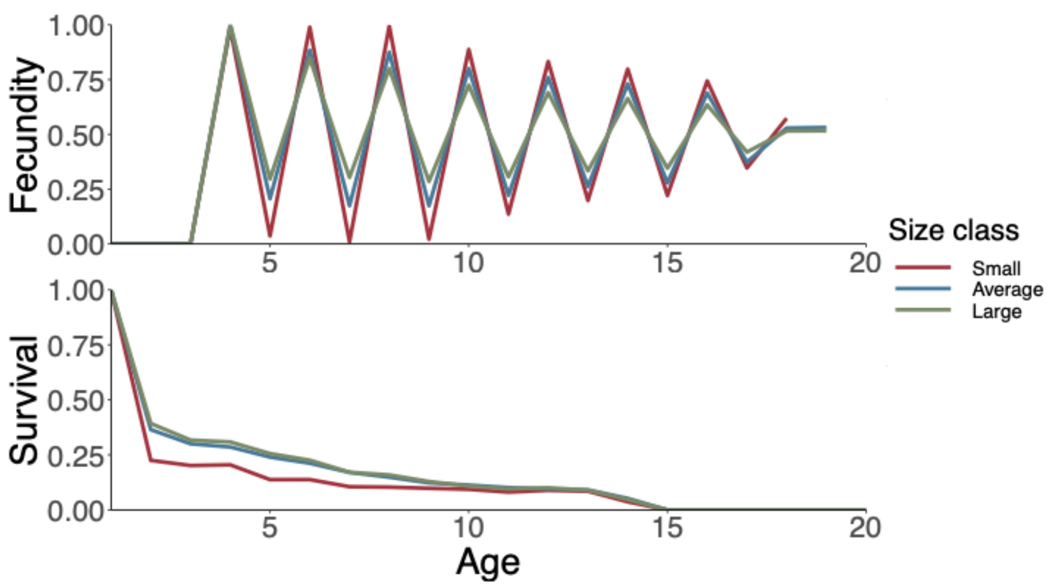

Figure A2. 3 Fecundity and survivorship curves derived from baseline forward simulation runs for all three simulated size classes.

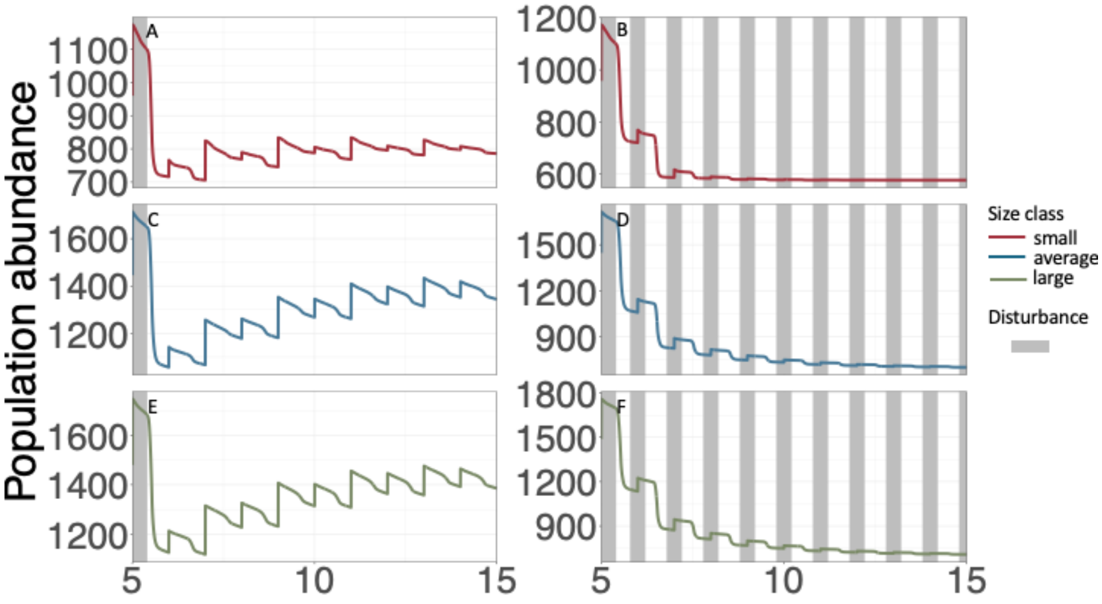

Figure A2. 4 Population abundance trajectories for small (panels A and B), average (panels C and D), and large (panels E and F) females under a single disturbance scenario simulated in Fall for 50 days in model year 1 (panels A, B, C) and a repeat disturbance scenario simulated in Fall for 50 days each year (panels B, D, E).

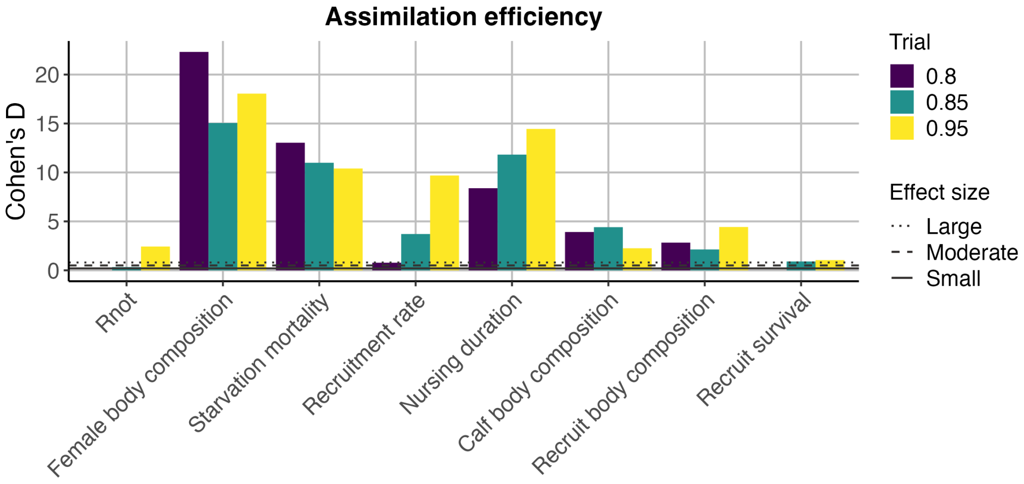

Figure A2. 5 Sensitivity analysis results testing the effect of assimilation efficiency on model results.

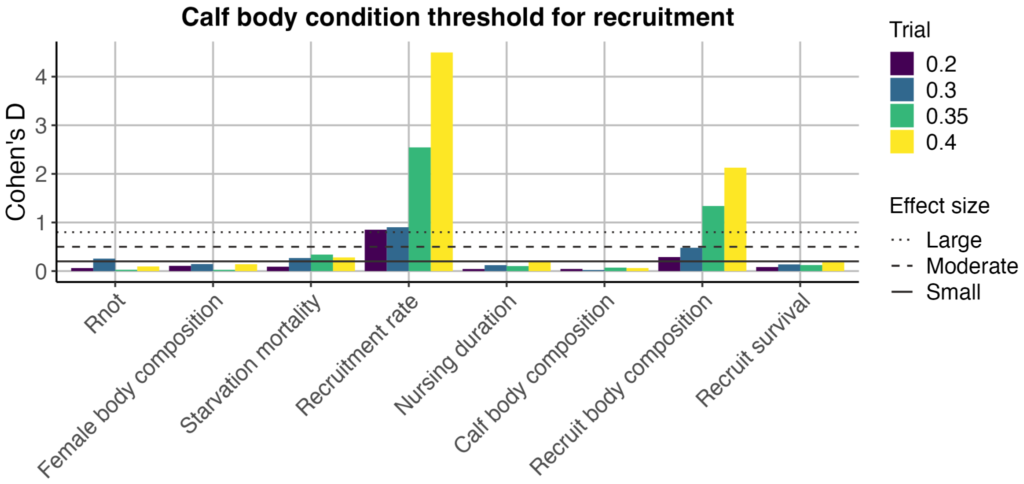

Figure A2. 6 Sensitivity analysis results testing the effect of calf body condition threshold for recruitment on model results.

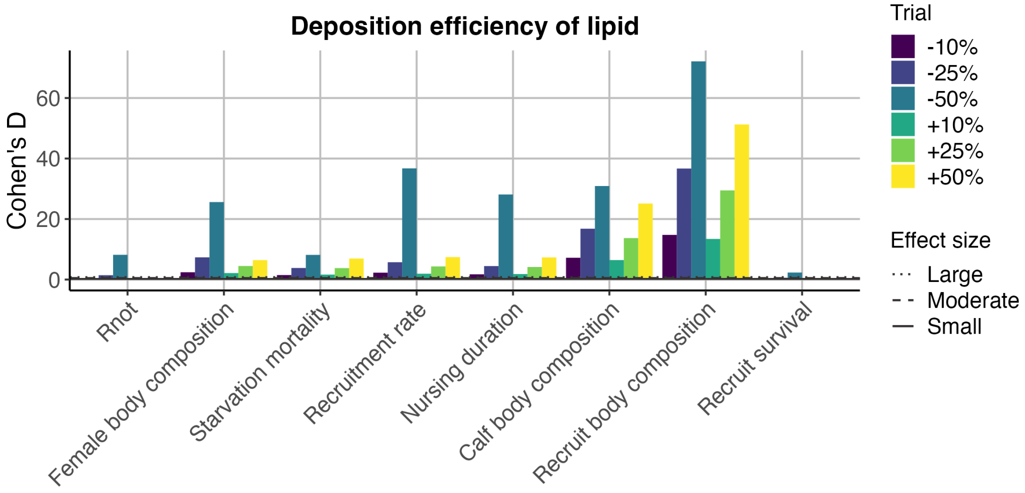

Figure A2. 7 Sensitivity analysis results testing the effect of the deposition efficiency of lipid on model results.

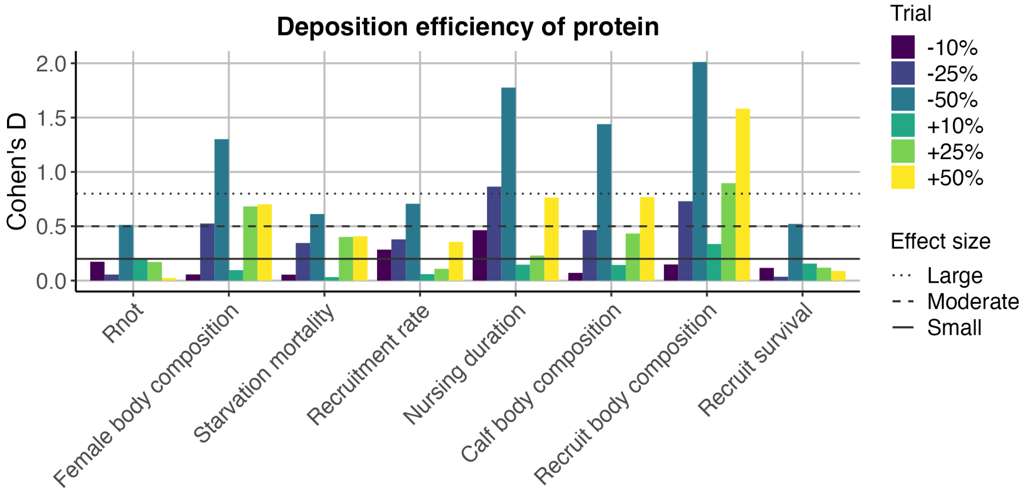

Figure A2. 8 Sensitivity analysis results testing the effect of the deposition efficiency of protein on model results.

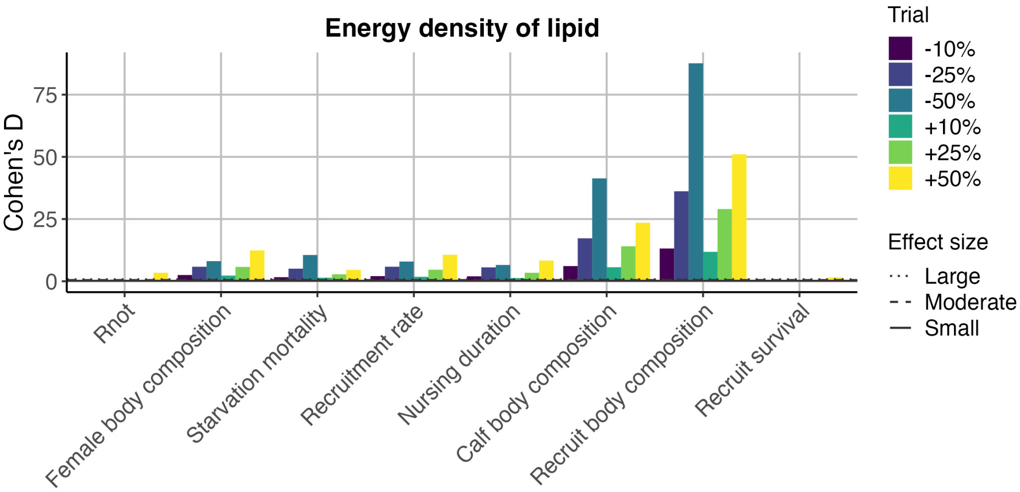

Figure A2. 9 Sensitivity analysis results testing the effect of the energy density of lipid on model results.

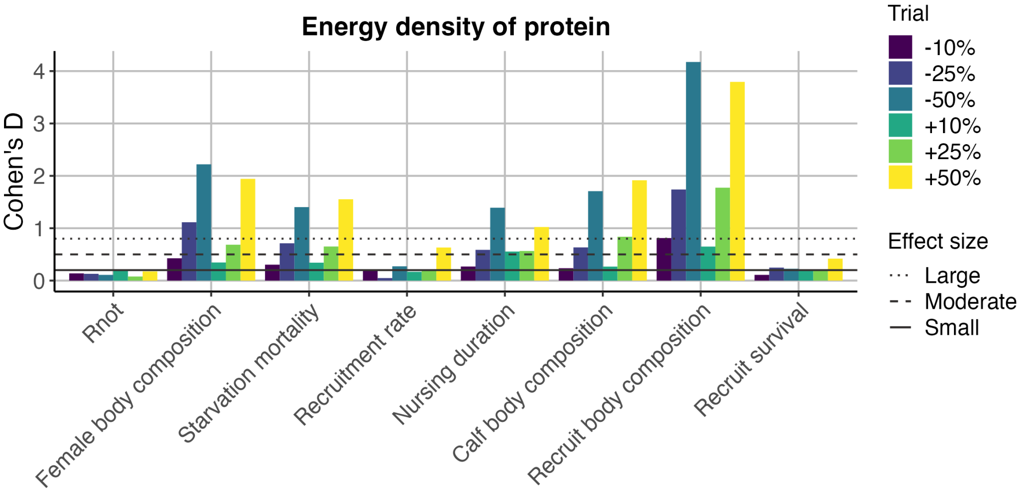

Figure A2. 10 Sensitivity analysis results testing the effect of the energy density of protein on model results.

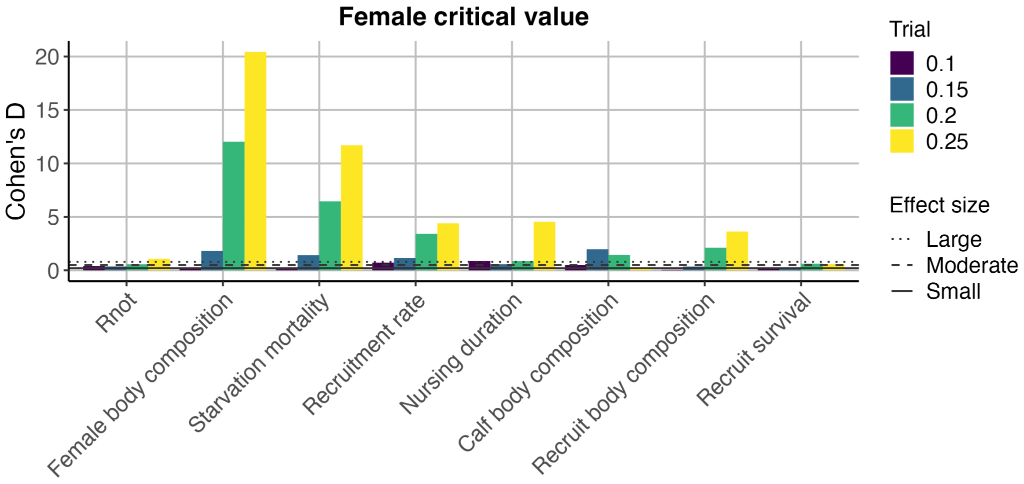

Figure A2. 11 Sensitivity analysis results testing the effect of female critical value on model results. This parameter did not have a large impact on Rnot or recruit survival, but impacted female body condition, starvation-related mortality, recruitment rate, and nursing duration at higher values (0.2 and 0.25).

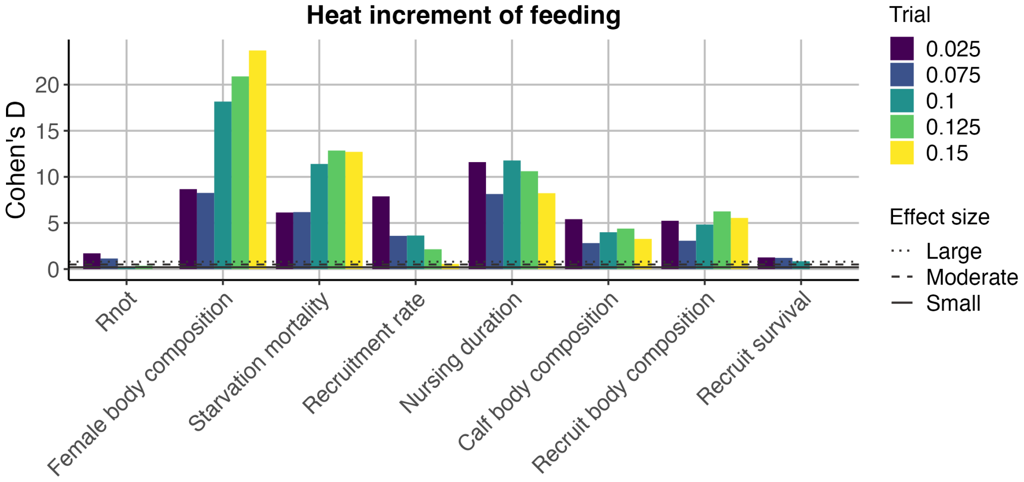

Figure A2. 12 Sensitivity analysis results testing the effect of the heat increment of feeding on model results.

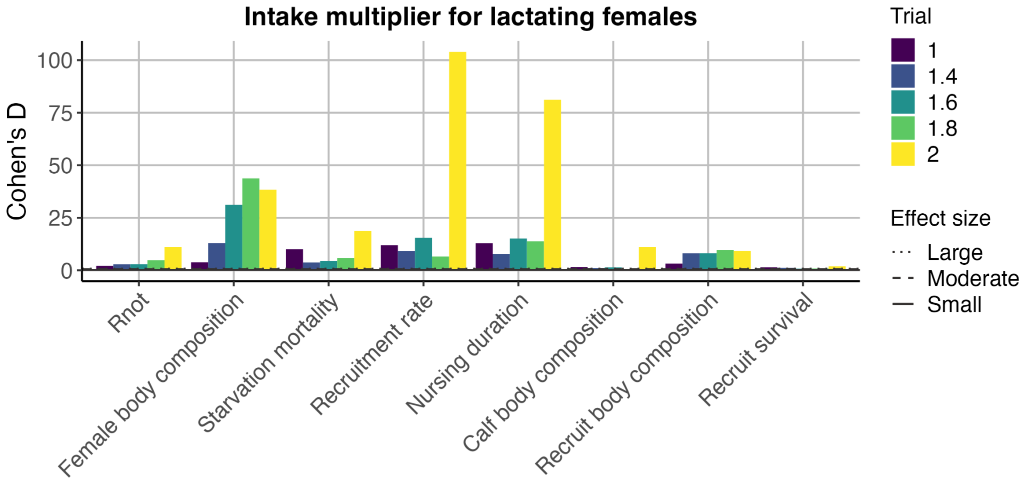

Figure A2. 13 Sensitivity analysis results testing the effect of the intake multiplier for lactating females on model results.

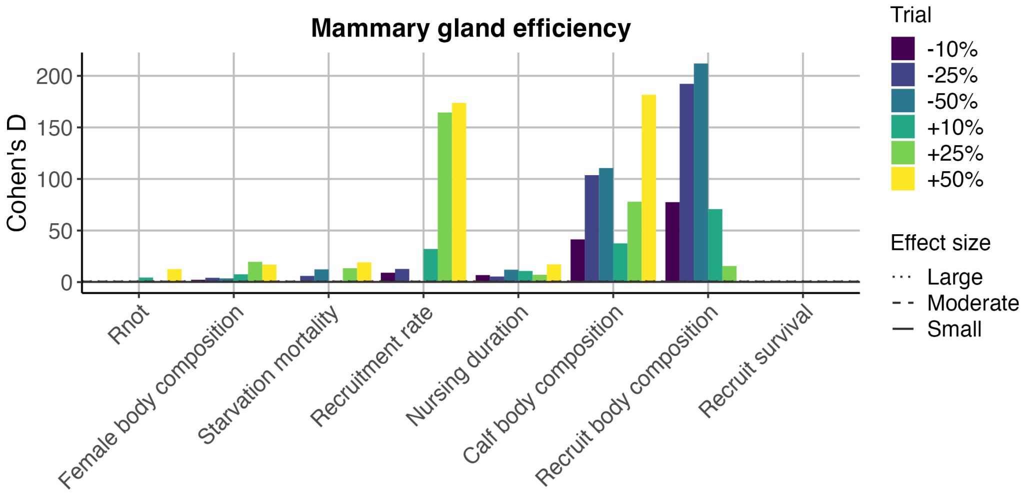

Figure A2. 14 Sensitivity analysis results testing the effect of mammary gland efficiency on model results.

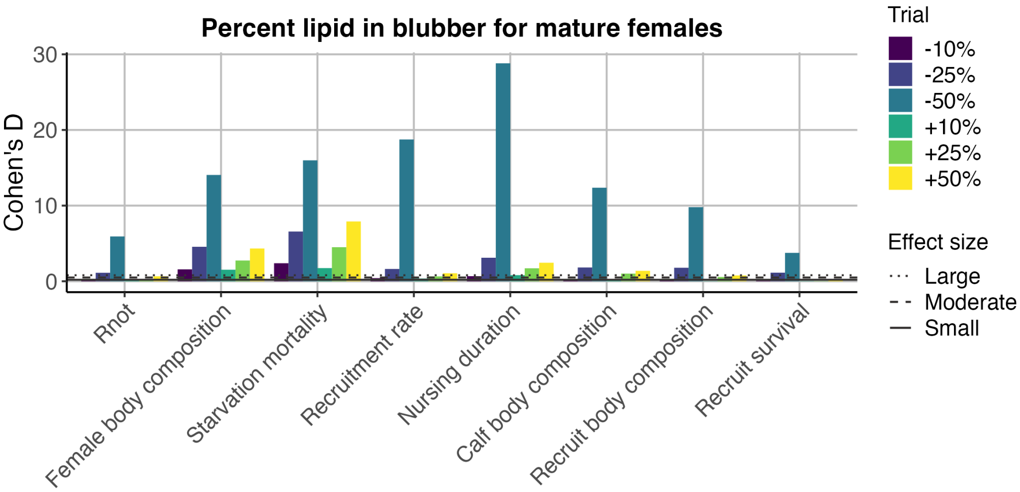

Figure A2. 15 Sensitivity analysis results testing the effect of percent lipid in blubber for mature females on model results.

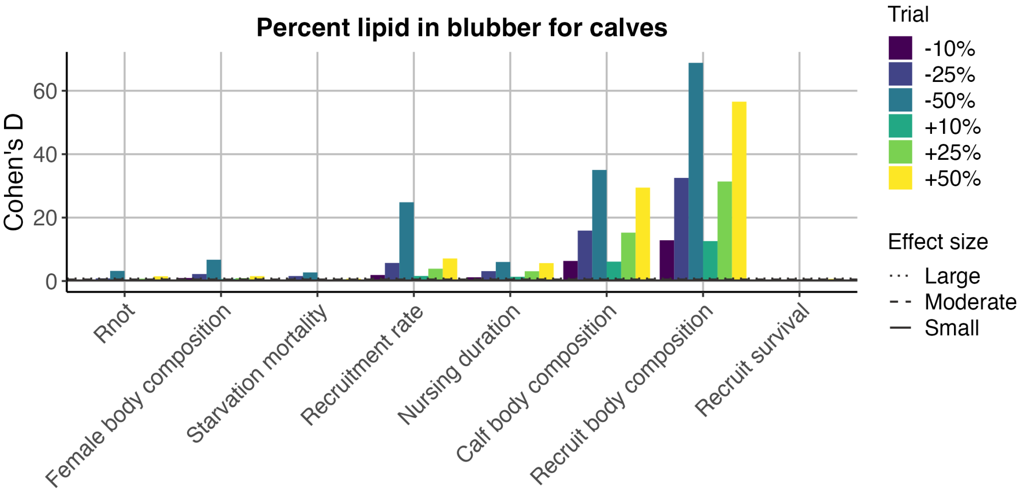

Figure A2. 16 Sensitivity analysis results testing the effect of percent lipid in blubber for calves on model results.

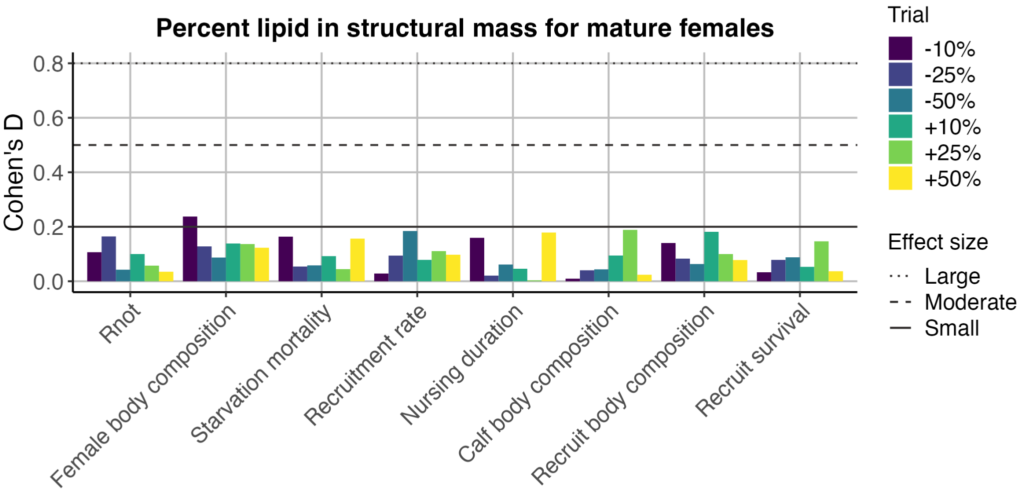

Figure A2. 17 Sensitivity analysis results testing the effect of percent lipid in structural mass for mature females on model results.

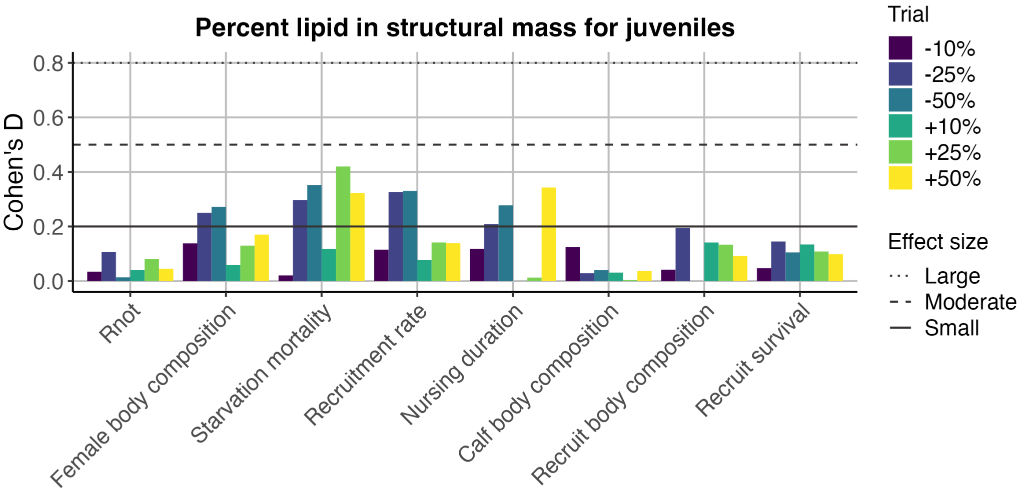

Figure A2. 18 Sensitivity analysis results testing the effect of percent lipid in structural mass for juveniles on model results.

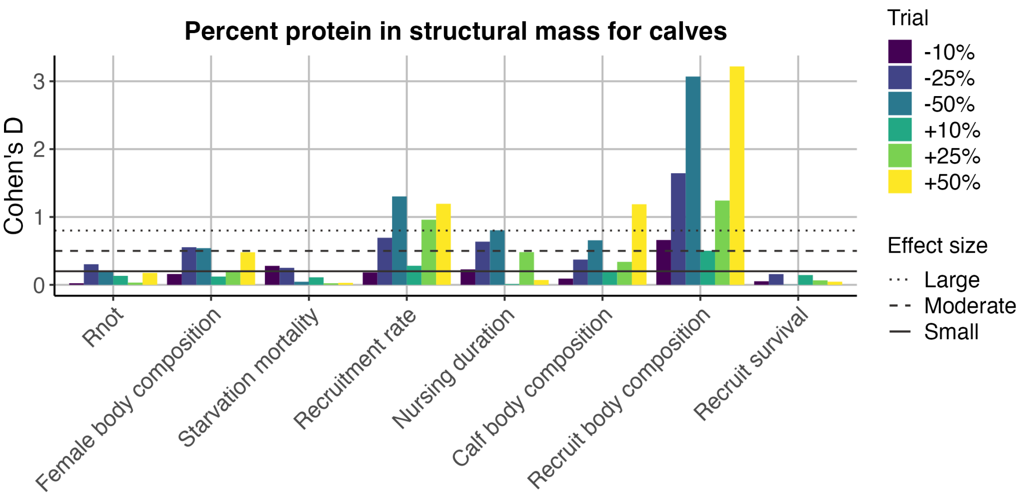

Figure A2. 19 Sensitivity analysis results testing the effect of percent lipid in structural mass for calves on model results.

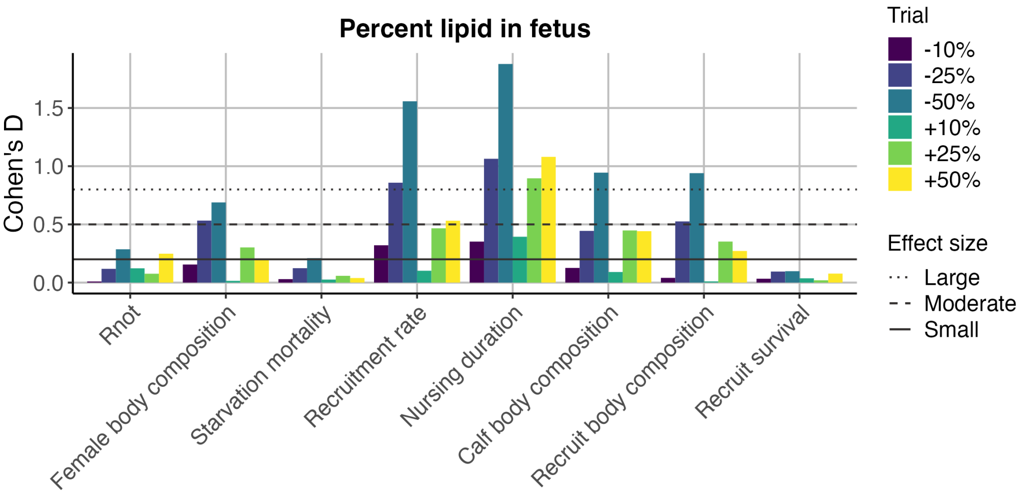

Figure A2. 20 Sensitivity analysis results testing the effect of percent lipid in the fetus on model results.

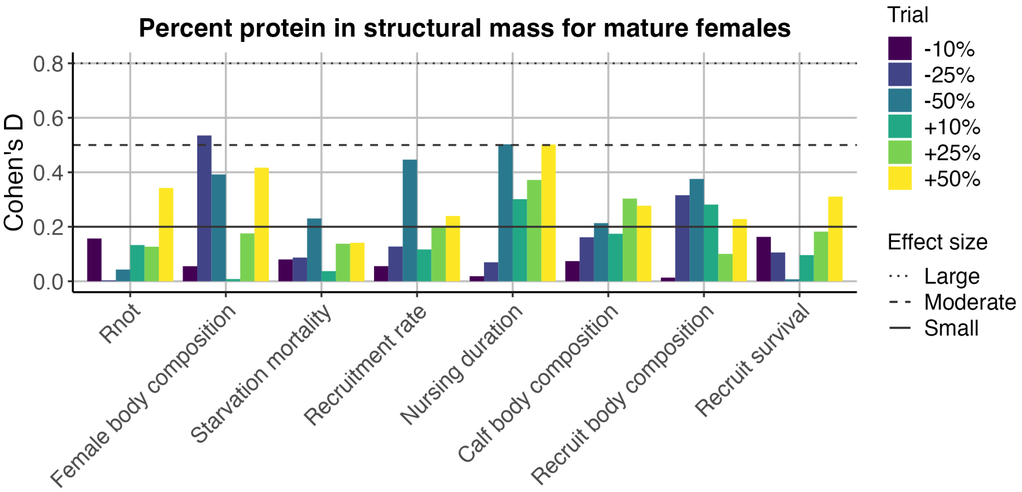

Figure A2. 21 Sensitivity analysis results testing the effect of percent protein in structural mass for mature females on model results.

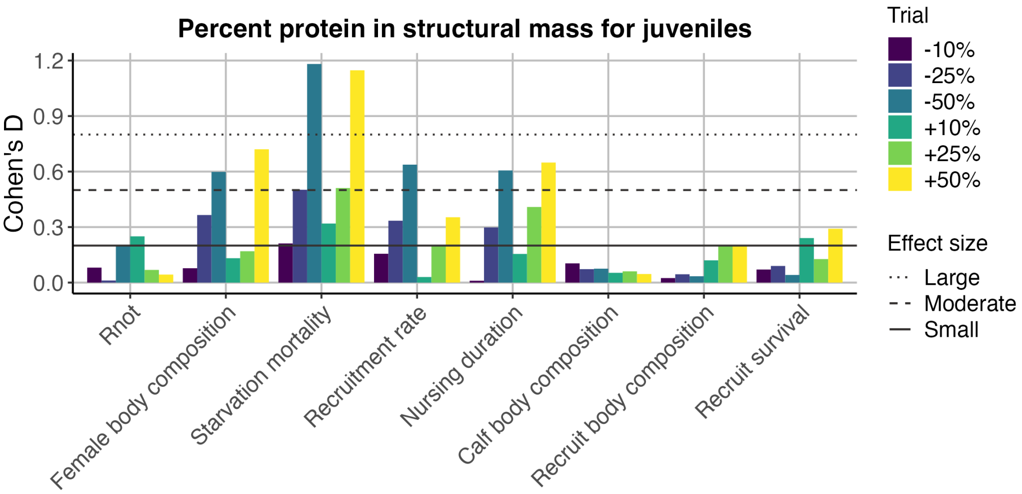

Figure A2. 22 Sensitivity analysis results testing the effect of percent protein in structural mass for juveniles on model results.

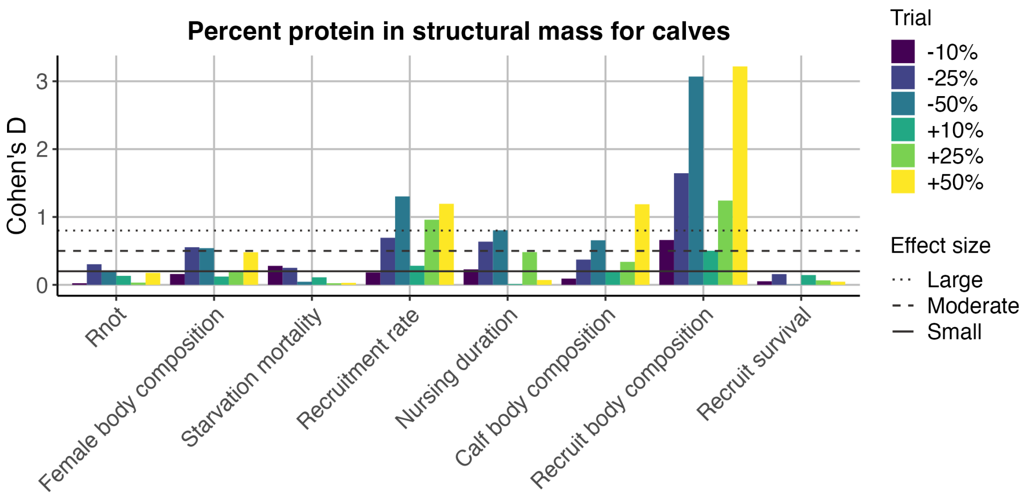

Figure A2. 23 Sensitivity analysis results testing the effect of percent protein in structural mass for calves on model results.

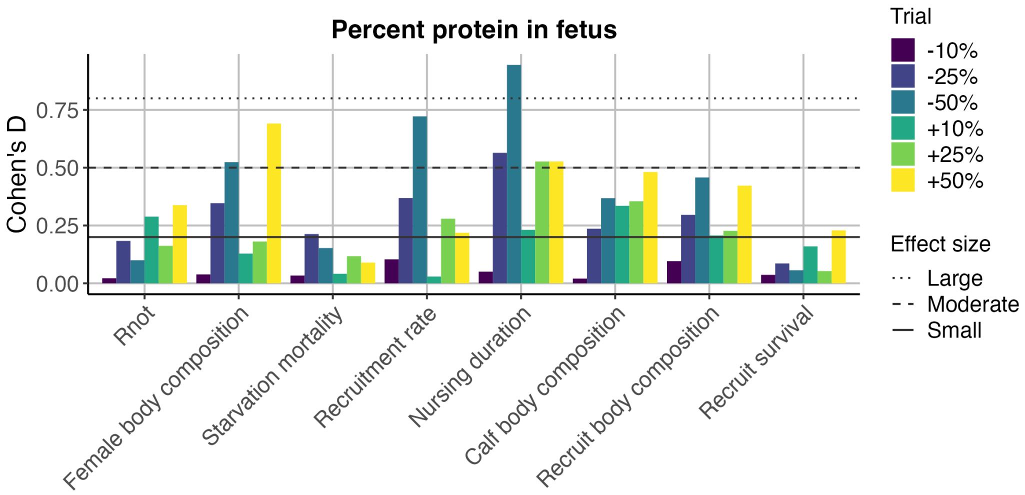

Figure A2. 24 Sensitivity analysis results testing the effect of percent protein in the fetus model results.

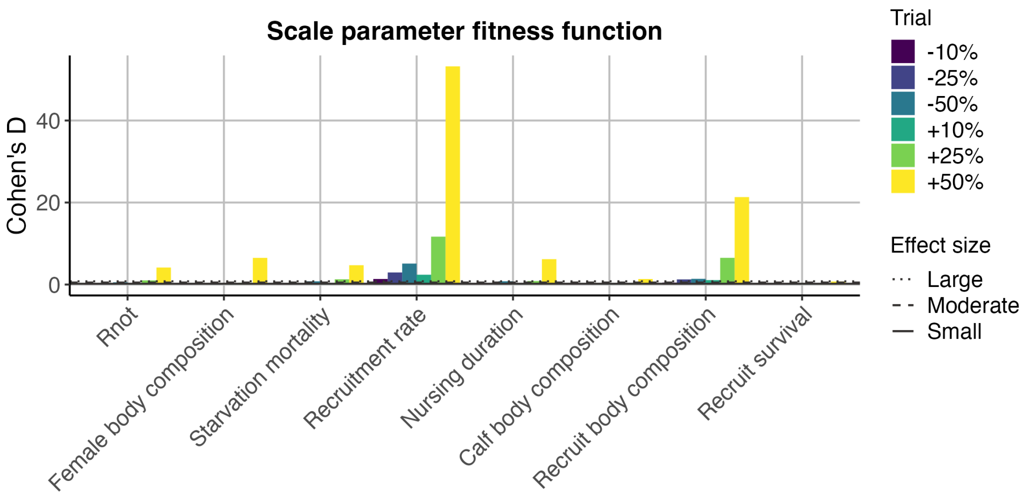

Figure A2. 25 Sensitivity analysis results testing the effect the scale parameter fitness function on model results.

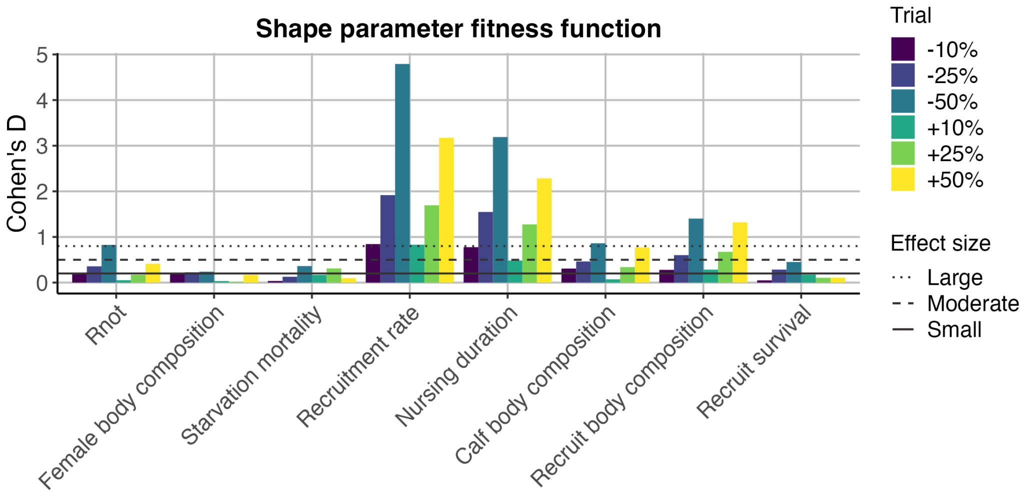

Figure A2. 26 Sensitivity analysis results testing the effect the shape parameter fitness function on model results.

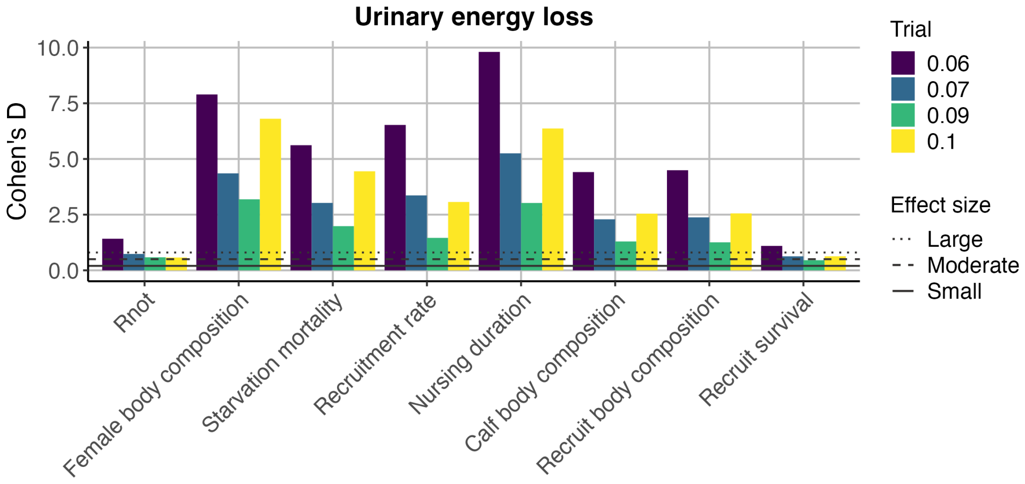

Figure A2. 27 Sensitivity analysis results testing the effect urinary energy loss on model results.

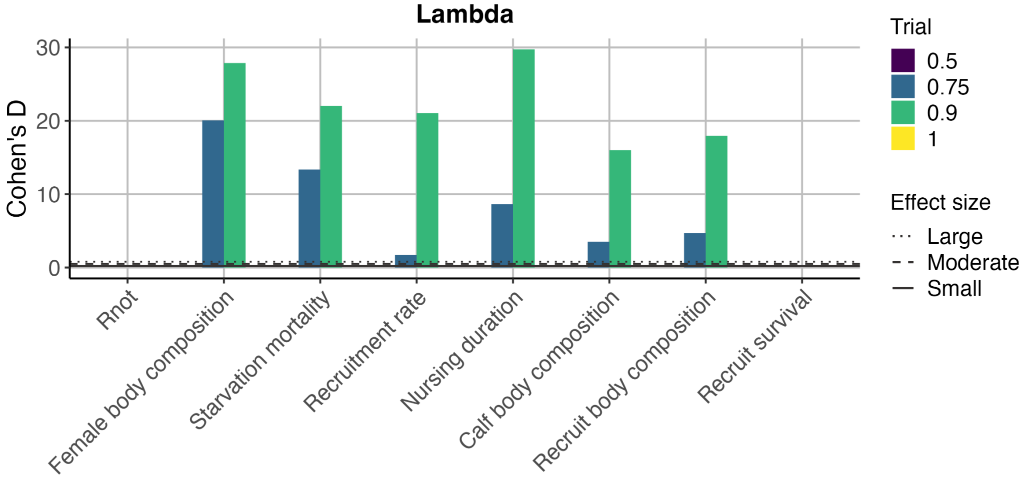

Figure A2. 28 Sensitivity analysis results testing the effect λ on model results. Note that results for the "0.5" and "1" trials are not shown. The 0.5 trial resulted in too many females dying before the five year model normalization time and, therefore, results could not be obtained. The "1" trial resulted in too many females surviving which caused memory allocation errors in the model.

References

Fish, F. E. (1998). Comparative kinematics and hydrodynamics of odontocete cetaceans: morphological and ecological correlates with swimming performance. *The Journal of Experimental Biology*, *201*, 2867–2877.

Tanaka, H., Li, G., Uchida, Y., Nakamura, M., Ikeda, T., & Liu, H. (2019). Measurement of time-varying kinematics of a dolphin in burst accelerating swimming. *PLoS ONE*, *14*(1). https://doi.org/10.1371/journal.pone.0210860

Gallagher, C. A., Grimm, V., Kyhn, L. A., Kinze, C. C., & Nabe-Nielsen, J. (2021). Movement and seasonal energetics mediate vulnerability to disturbance in marine mammal populations. *The American Naturalist*, *197*, 000–000. https://doi.org/10.5061/dryad.80gb5mkpn

Fish, F. E. (1993). Power output and propulsize efficiency of swimming bottlenosed dolphins (Tursiops truncatus). *Journal of Experimental Biology*, *185*, 179–193. http://works.bepress.com/frank_fish/7/

Coulson, J. M., Richardson, J. F., Backhurst, J. R., and Harker, J. H. (1999). *Chemical Engineering Vol. 1: Fluid Flow, Heat Transfer, and Mass Tranfer*. Coulson and Richardson's Chemical Engineering Series. Oxford, U.K.: Butterworth-Heinemann

Hind, A. T., & Gurney, W. S. C. (1997). The metabolic cost of swimming in marine homeotherms. *The Journal of Experimental Biology*, *200*, 531–542.

Boult, V. L., Quaife, T., Fishlock, V., Moss, C. J., Lee, P. C., & Sibly, R. M. (2018). Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. *Ecological Modelling*, *387*, 187–195. https://doi.org/10.1016/j.ecolmodel.2018.09.010

Brody, S. (1968). Bioenergetics and Growth. Hafner Publishing Co., Inc. New York, NY.

Booth, C. G. (2020). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, *36*(1), 195–208. https://doi.org/10.1111/mms.12632

Murphy, S., Petitguyot, M. A. C., Jepson, P. D., Deaville, R., Lockyer, C., Barnett, J., Perkins, M., Penrose, R., Davison, N. J., & Minto, C. (2020). Spatio-temporal variability of harbor porpoise life history parameters in the North-East Atlantic. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.502352

Lockyer, C. (2003). Harbour porpoises (Phocoena phocoena) in the North Atlantic: Biological parameters. *NAMMCO Scientific Publications*, *5*, 71–90.

Lockyer, C., & Kinze, C. (2003). Status, ecology and life history of harbour porpoise (Phocoena phocoena), in Danish waters. *NAMMCO Scientific Publications*, *5*, 143–176.

Barlow, J., & Boveng, P. (1991). Modeling age specific mortality for marine mammal populations. *Marine Mammal Science*, *7*(1), 50–65.

Huggett, A. St. G., & Widdas, W. F. (1951). The relationship between mammalian foetal weight and conception age. *Journal of Physiology*, *114*, 306–317.

Börjesson, P., & Read, A. J. (2003). Variation in timing of conception between populations of the harbor porpoise. *Journal of Mammalogy*, *84*(3), 948–955. https://academic.oup.com/jmammal/article/84/3/948/908120

Kleiber, M. (1975). Metabolic turnover rate: A physiological meaning of the metabolic rate per unit body weight. *Journal of Theoretical Biology*, *53*, 199–204.

Rojano-Donãte, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., Højer-Kristensen, J., & Madsen, P. T. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*(23), jeb185827. https://doi.org/10.1242/jeb.185827

Otani, S., Naito, Y., Kato, A., & Kawamura, A. (2001). Oxygen consumption and swim speed of the harbor porpoise Phocoena phocoena. *Fisheries Science*, *67*, 894–898.

Learmonth, J. A., Murphy, S., Luque, P. L., Reid, R. J., Patterson, I. A. P., Brownlow, A., Ross, H. M., Barley, J. P., Santos, M. B., & Pierce, G. J. (2014). Life history of harbor porpoises (Phocoena phocoena) in Scottish (UK) waters. *Marine Mammal Science*, *30*(4), 1427–1455. https://doi.org/10.1111/mms.12130

McLellan, W. A., Koopman, H. N., Rommel, S. A., Read, A. J., Potter, C. W., Nicolas, J. R., Westgate, A. J., & Pabst, D. A. (2002). Ontogenetic allometry and body composition of harbour porpoises (Phocoena phocoena, L.) from the western North Atlantic. *Journal of Zoology*, *257*(4), 457–471. https://doi.org/10.1017/S0952836902001061

Andreasen, H., Ross, S. D., Siebert, U., Andersen, N. G., Ronnenberg, K., and Gilles, A. (2017). Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. . *Marine Mammal Science*, *33*(4), 1053–1079.

Kastelein, R. A., Hardeman, J., & Boer, H. (1997). Food consumption and body weight of harbour porpoises. In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The Biology of the Harbor Porpoise* (pp. 217–233). DeSpil Publishers.

Jamieson, D. T., Tudhope, J. S., Morris, R., and Cartwright, G. (1969). Physical properties of sea water solutions: heat capacity. *Desalination*, 7(1), 23-30.

Caldwell, D. (1974). Thermal conductivity of sea water, *Deep Sea Research and Oceanographic Abstracts*, 21(2), 131-137.

El-Dessouky, H., and Ettouney, H. *Fundamentals of Salt Water Desalination* (Elsevier, New York, NY).

Sharqawy, M. H., Lienhard V, J. H., & Zubair, S. M. (2010). Thermophysical properties of seawater: A review of existing correlations and data. *Desalination and Water Treatment*, *16*(1–3), 354–380. https://doi.org/10.5004/dwt.2010.1079

Pirotta, E., Mangel, M., Costa, D. P., Mate, B., Goldbogen, J. A., Palacios, D. M., Hückstädt, L. A., McHuron, E. A., Schwarz, L., & New, L. (2018). A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. *American Naturalist*, *191*(2), E40–E56. https://doi.org/10.1086/695135

Gotelli, N. J. (2001). *A Primer of Ecology, Third Edition*. (Sinauer Associates, Sutherland, MA).

Xu, S., Chen, M., Feng, T., Zhan, L., Zhou, L., and Yu, G. (2021). Use ggbreak to effectively utilize plotting space to deal with large datasets and outliers. *Frontiers in Genetics* 12:77486, 7 pp. https://doi.org/10.3389/fgene.2021.774846

Lockyer, C. (1995). Aspects of the morphology, body fat condition and biology of the harbour porpoise, Phocoena phocoena, in British waters. *Report for the International Whaling Commission*, *16*, 199–209.

Hohn, A. A., and Brownell, R. L. (1990). Harbor porpoise in central Californian waters: life history and incidental catches. IWC Report SC/42/SM47. Cambridge, UK: International Wahling Commission

Read, A. J. (1990). Age at sexual maturity and pregnancy rates of harbour porpoises *Phocoena phocoena* from the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(3): 561-555.

Appendix A3

Table A3. 1 Linear regression model results exploring the impact of deviation in length (cm) and mass (kg) on lifetime reproductive success (LRS) and lifespan with a random effect of individual to account for repeated measures.

Model	*F-statistic*	*P-value*	R^2
LRS ~ deviationLength + (1|AnimalID)	3.35	0.07	9.4 x 10^{-3}
Lifespan ~ deviationLength + (1|AnimalID)	0.02	0.894	-3.98 x 10^{-3}
LRS ~ deviationMass + (1|AnimalID)	3.45	0.47	-1.74 x 10^{-3}
Lifespan ~ deviationMass + (1|AnimalID)	3.38	0.07	-8.63 x 10^{-3}

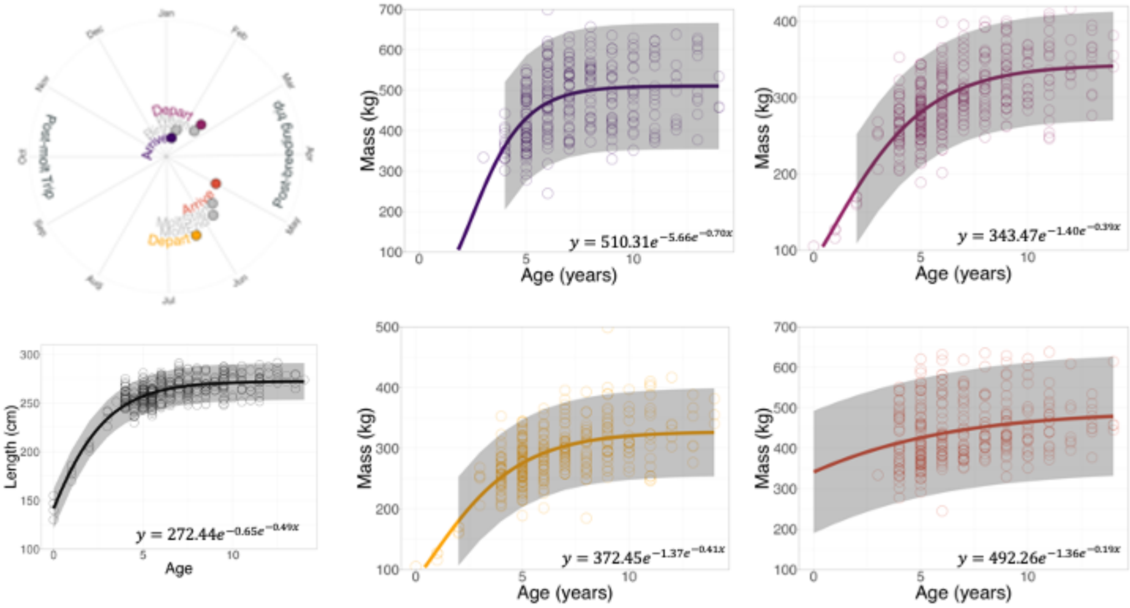

Figure A3. 1 Length-at-age curve for all females (A), mass-at-age curve for post-molt arrival females (B), mass-at-age curve for post-breeding departure (C), mass-at-age-curve for post-molt departure, and (D) mass-at-age curve for post-breeding arrival females.

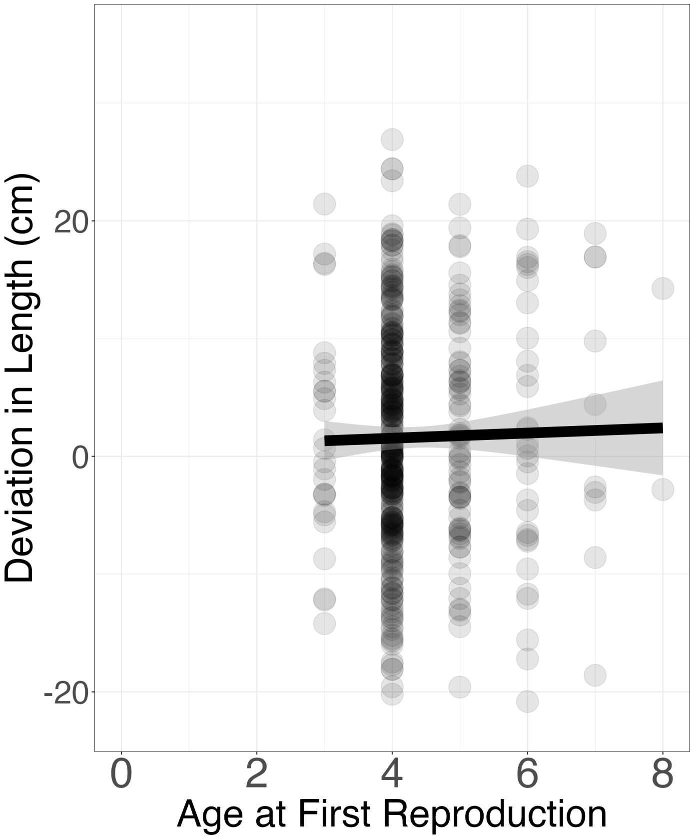

Figure A3. 2 Relationship between age at first reproduction and deviation in length (cm) for all female northern elephant seals for which measurements were available (n = 439). Linear regression model results were not significant.

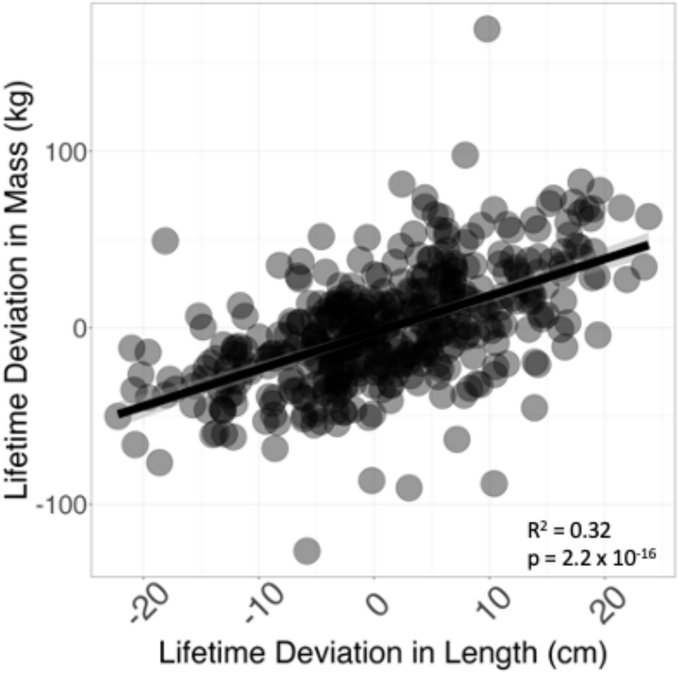

Figure A3. 3 Relationship between deviation in length (cm) and deviation in mass (kg) for all female northern elephant seals for which measurements were available (n = 571).

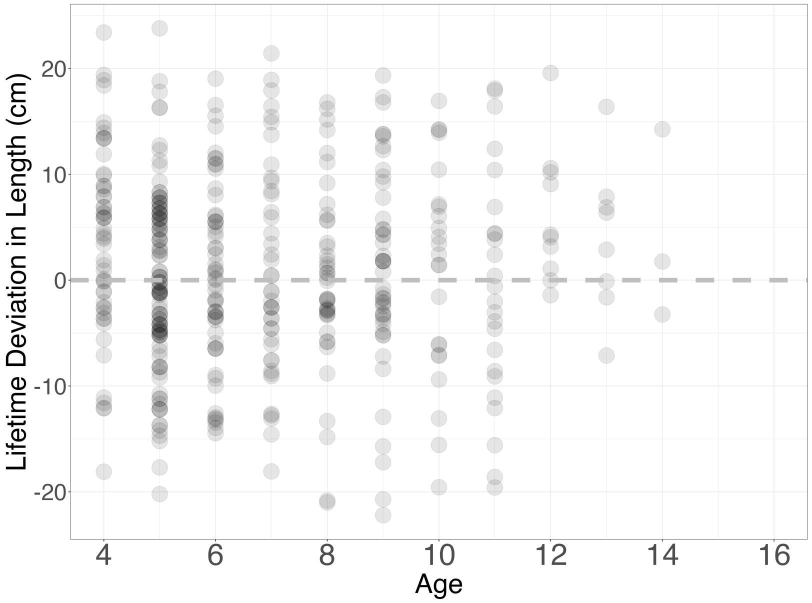

Figure A3. 4 Relationship between deviation in length (cm) and age at time of measurement for all female northern elephant seals for which measurements were available (n = 571). Linear regression model results were not significant.

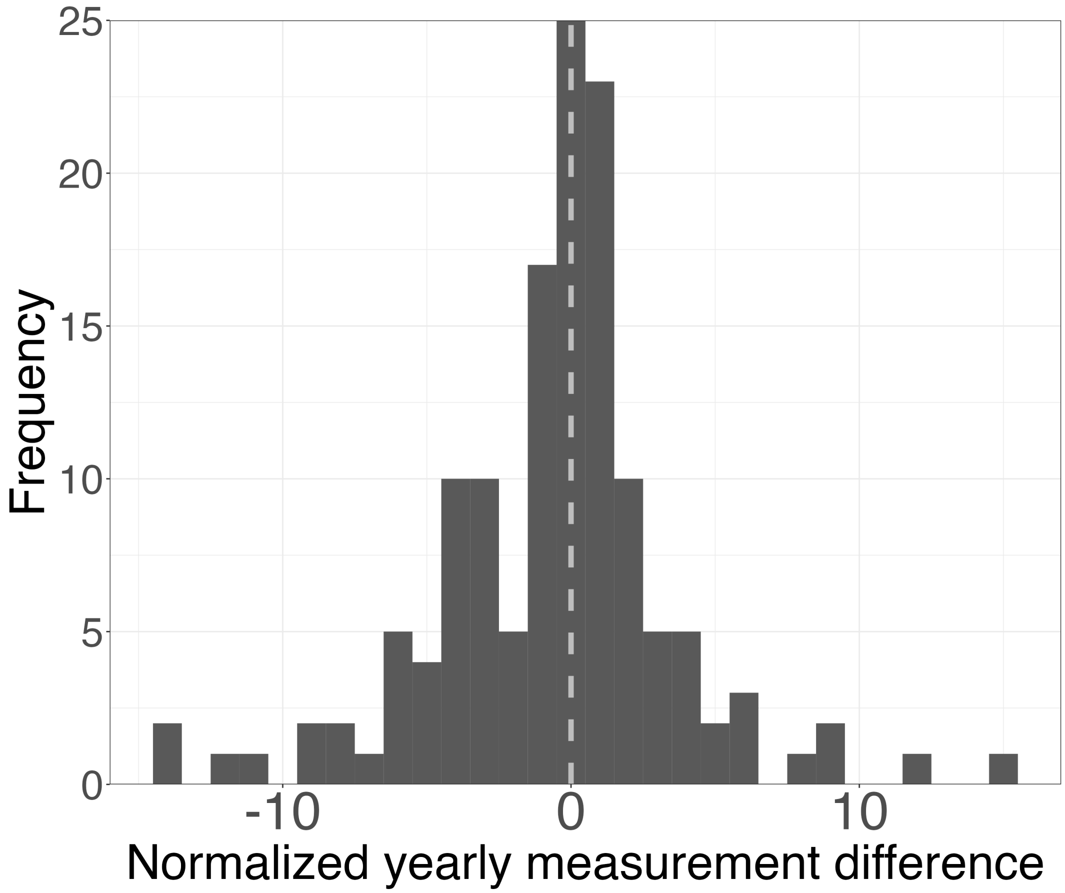

Figure A3. 5 Yearly difference between length measurements to demonstrate that most individuals did not strongly deviate in length between measurements.