A review of bioenergetic modelling for marine mammal populations

Enrico Pirotta*

Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 9LZ, UK

*Corresponding author: Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 9LZ, UK. Tel: (+44) (0)1334 461 842. Email: ep343@st-andrews.ac.uk

Bioenergetic models describe the processes through which animals acquire energy from resources in the environment and allocate it to different life history functions. They capture some of the fundamental mechanisms regulating individuals, populations and ecosystems and have thus been used in a wide variety of theoretical and applied contexts. Here, I review the development of bioenergetic models for marine mammals and their application to management and conservation. For these long-lived, wide-ranging species, bioenergetic approaches were initially used to assess the energy requirements and prey consumption of individuals and populations. Increasingly, models are developed to describe the dynamics of energy intake and allocation and predict how resulting body reserves, vital rates and population dynamics might change as external conditions vary. The building blocks required to develop such models include estimates of intake rate, maintenance costs, growth patterns, energy storage and the dynamics of gestation and lactation, as well as rules for prioritizing allocation. I describe how these components have been parameterized for marine mammals and highlight critical research gaps. Large variation exists among available analytical approaches, reflecting the large range of life histories, management needs and data availability across studies. Flexibility in modelling strategy has supported tailored applications to specific case studies but has resulted in limited generality. Despite the many empirical and theoretical uncertainties that remain, bioenergetic models can be used to predict individual and population responses to environmental change and other anthropogenic impacts, thus providing powerful tools to inform effective management and conservation.

Key words: population consequences of disturbance, pinnipeds, individual-based modelling, energy budgets, cetaceans, bioenergetic models

Editor: Dr. Steven Cooke

Received 9 December 2021; Revised 7 March 2022; Editorial Decision 26 May 2022; Accepted 15 June 2022

Cite as: Pirotta E (2022) A review of bioenergetic modelling for marine mammal populations. Conserv Physiol 10(1): coac036; doi:10.1093/conphys/coac036.

Introduction

The rates at which animals extract energy from the environment and use it to fuel different life functions affect their ability to survive, grow and reproduce. Energy thus acts as an effective proximate currency to integrate diverse biological and ecological processes influencing an individual’s fitness (Sibly et al., 2013). In turn, modelling the mechanisms that underpin individual energy management can help quantify broader processes with cascading effects on ecological communities, such as total resource consumption by populations (e.g. Delmas et al., 2017), competition between species (e.g. Caut et al., 2006), changing environmental conditions (e.g. Humphries et al., 2004) and trait-mediated indirect
interactions between predators and prey (Werner and Peacock, 2003). Moreover, disturbance from human activities might affect the rate of energy acquisition from the environment, or cause individuals to allocate energy to adaptive or compensatory responses, ultimately altering their energy budget (Pirotta et al., 2018a). In such cases, bioenergetics can also be used to predict the long-term consequences of exposure to anthropogenic stressors, particularly when measuring these effects empirically is unfeasible (e.g. for long-lived, wide-ranging species) (Costa et al., 2016). As a result, bioenergetic modelling has become a prominent tool for both theoretical and applied ecophysicologists.

Here, a bioenergetic (or energy budget) model is defined as any mechanistic model where the principles of metabolic ecology are used to describe how an individual animal acquires energy from food resources (i.e. energy intake) and allocates assimilated energy to various life history functions (i.e. energy costs, including maintenance and survival, growth and reproduction) (Brown et al., 2004; Johnston et al., 2019; Kooijman, 2010; Sibly et al., 2013). Energy intake can be either a model input, when allocation is modelled dynamically, or a model output, derived from energy requirements and the mechanisms involved in the feeding process. Acquisition and allocation can also be modelled to vary as a function of an individual’s state and the state of the environment (van der Meer, 2006).

Within the bioenergetic literature, there is considerable variation in how individual energy budgets are modelled (for an in-depth discussion of the interconnections and fundamental differences among approaches, see van der Meer, 2006 and Nisbet et al., 2012). ‘Traditional’ bioenergetic models (sensu Nisbet et al., 2012) describe energy acquisition from feeding and its partitioning among maintenance, activity, growth, reproduction and excretion; the advantage being that these processes have a clear empirical interpretation, which facilitates measuring them using explicit units, but the resulting models are often parameter-rich and hard to generalize across species. These models generally follow a hierarchical allocation, as proposed by Sibly et al. (2013) and extended by Beltran et al. (2017) and Gallagher et al. (2021a), whereby an individual expends assimilated energy in order of the importance of the processes to survival, that is, for maintenance, thermoregulation, locomotion, growth, reproduction and energy storage (up to an optimal amount of reserves). In contrast, Dynamic Energy Budget (DEB) theory (Kooijman, 2010) considers these same processes from a formal and more general perspective, using foundational principles of mass–energy balance to relate sub-organismal (biochemical, genetic and physiological) processes to organismal performance (Martin et al., 2012; Nisbet et al., 2012; van der Meer, 2006). In turn, this generality results in abstract concepts that are harder to measure empirically. DEB models also follow a strict order and priority of energy allocation to different life functions (Kooijman, 2010). The energy dynamics of three compartments with fixed biochemical composition are considered: structure, reserves and (for adults) reproductive buffer. The energy intake via the food ingested is first deposited in the reserve buffer (Kooijman, 2010; Nisbet et al., 2000). Throughout life, a constant fraction (kappa) is allocated to maintenance and somatic growth, while the remaining fraction (1 - kappa) is directed towards development and maturation (for juveniles) and reproduction (in adults)—the so-called ‘kappa-rule’ (Kooijman, 2010). In light of these energy fluxes, a system of differential equations is used to update the individual’s state variables, which may lead to events such as death (if maintenance costs cannot be covered) or reproduction.

Some bioenergetic models focus on assessing individual energy budgets and their variation as a function of external conditions. Others aim to investigate some population-level processes, e.g. a population’s overall prey consumption, the underlying demographic rates or the effects of changing extrinsic conditions (Johnston et al., 2019; Sibly et al., 2013). Individual energy budget calculations can be scaled to the population level in various ways. A distinction is introduced here between accounting bioenergetic models, which aim to predict the rate of energy intake from the environment, and dynamic bioenergetic models, which explicitly describe energy intake and allocation at a finer temporal scale. Accounting models combine individual energy budgets with estimates of population size to compute the overall energy requirements and prey consumption of a population at a particular moment in time (e.g. Acevedo and Urbán, 2021). In contrast, dynamic models allow for the investigation of the effects of variations in energy intake on different end points, e.g. average energy dynamics, vital rates and population dynamics (with or without density dependence). Simulations of population dynamics have then been achieved using various population modelling approaches (e.g. matrix models or physiologically structured population models; e.g. Klanjšcek et al., 2006; De Roos, 2008).

In recent years, bioenergetic models have increasingly been developed within the context of individual-based models (IBMs; also referred to as agent-based models) (Martin et al., 2012; Mortensen et al., 2021; Sibly et al., 2013), which facilitate the inclusion of individual variation, local interactions and adaptation (Martin et al., 2012). In IBMs, the responses of individuals to their internal state and external drivers (as represented, for example, by a mapped, ecological landscape) are simulated, resulting in emergent population dynamics (Grimm and Railsback, 2013). Because food is an important component of such modelled landscapes, and nutritional state responds faster to food availability than population density does, this integration is particularly useful for predicting the effects of changing conditions on populations (e.g. following anthropogenic disturbance or environmental change) (Sibly et al., 2013). Moreover, the rate at which an individual acquires and uses energy can be modelled to vary with sex, age, activity state and experience (Sibly et al., 2013). An important consideration when scaling to the population level (using any of the approaches mentioned) is whether the target population is at, or close to, carrying capacity, because
density-dependent processes can affect the prey base and, in turn, individual health and vital rates (Hin et al., 2021).

Bioenergetic modelling has a long history of applications in marine mammal science, due to the variety of anthropogenic stressors that threaten the persistence of these species, and their life history characteristics, which make direct empirical measurements of individual- and population-level effects often unfeasible. In this review, I will first describe the early examples of accounting models for estimating prey consumption in marine mammal populations, highlighting the components that remain relevant in recent model developments. I will then move to dynamic models, which simulate the allocation of the energy assimilated from feeding to survival, growth and reproduction. I will distil the critical building blocks required to develop such models and describe how these have been informed for marine mammals (Fig. 1). In particular, recent developments in marine mammal science have been driven by the need to assess the population-level effects of stressors that have sublethal effects on individuals. The population consequences of disturbance (PCoD) conceptual framework describes how disturbance-induced changes in individual behaviour and physiology can affect population dynamics by compromising the health status of an individual, and thus its ability to survive and reproduce successfully (see review in Pirotta et al., 2018b). While health encompasses multiple aspects of an individual’s physiological status, most PCoD implementations to date have focused on the changes in a female’s time-energy budget and the consequences on her ability to sustain the costs of maintenance (and thus survival) and reproduction (Keen et al., 2021; Pirotta et al., 2018b). Bioenergetic models represent an ideal tool to mechanistically capture this energetic pathway. It should be noted that, while there is a vast branch of marine mammal bioenergetics that has applied empirical and theoretical approaches to estimate the costs of different behaviours and life functions (e.g. Boyd et al., 1993; Castellini et al., 1992; Costa and Maresh, 2017; Fahlman et al., 2016; Goldbogen et al., 2011; Ofstedal, 1997; Potvin et al., 2012; Williams, 1999; Williams et al., 2017), contributing critically to inform the parameters of bioenergetic models, these studies were outside the scope of the review.

**Bioenergetic accounting models of population energy requirements and resource consumption**

The first examples of marine mammal bioenergetic models analysed the energy budgets of baleen whales (Lockyer, 1981a), sperm whales *Physeter macrocephalus* (Lockyer, 1981b), long-finned pilot whales *Globicephala melas* (Lockyer, 1993) and pinnipeds (Lavigne et al., 1982) and aimed to shed light on their foraging ecology and energy requirements. These seminal works collated the knowledge available at the time, often derived from catch data, on diet, feeding rates, metabolism, growth, reproduction, seasonal dynamics and accumulation of reserves, and provided the theoretical and empirical basis for many subsequent modelling efforts.

Similar evaluations of populations’ overall energy requirements and prey consumption have continued over the years (Banas et al., 2021; Bejarano et al., 2017; Benoit-Bird, 2004; Costa et al., 1989; Fortune et al., 2013; Gallagher et al., 2018; Guilpin et al., 2019; Kriete, 1995; Lockyer, 2007; Malavear, 2002; McHuron et al., 2017b; Noren, 2011; Noren et al., 2012, 2014; Rechsteiner et al., 2013; Reisinger et al., 2011; Williams et al., 2004; Winship et al., 2002). Often, accounting models have been developed with the applied management goal of quantifying the levels of predation on prey stocks and potential competition with local fisheries (Acevedo and Urbán, 2021; Boyd, 2002; Cornick et al., 2006; Faure et al., 2021; Forcada et al., 2009; Markussen et al., 1992; McHuron et al., 2020; Mohn and Bowen, 1996; Nilsen et al., 2014; Olesiuk, 1993; Queiros et al., 2018; Trzcinski et al., 2006; Weise and Harvey, 2008).

These studies used a variety of approaches to capture the costs incurred by individuals (Fig. 2a). Some examples calculated individual energy requirements using a combination of theoretical estimates of basal metabolic rate, derived from Kleiber (1975’s) allometric formula, and assumptions on how metabolic rate scales during activity (and in different activity states) (e.g. Boyd, 2002; Guilpin et al., 2019; Noren, 2011; Winship et al., 2002). In contrast, other studies used empirical measurements of metabolic rate obtained either in the field or in captivity (e.g. Costa et al., 1989; Kriete, 1995; McHuron et al., 2020). The term field metabolic rate (FMR) is generally used to indicate the metabolic rate that integrates the energy expended during all activities over the sampling period. When explicitly distinguishing among activity states, estimates of an individual’s activity budget have been used to partition energy expenditure over some unit of time (e.g. Costa et al., 1989; Fortune et al., 2013; Guilpin et al., 2019). In line with the bioenergetic scheme proposed by Lavigne et al. (1982), some studies explicitly accounted for specific dynamic action (also referred to as heat increment of feeding), representing digestion costs (e.g. Fortune et al., 2013; Winship et al., 2002). In contrast, estimates of FMR from free-ranging animals are generally assumed to include digestion costs (e.g. McHuron et al., 2020). The costs associated with production (i.e. structural growth, or tissue deposition more generally) and reproduction (gestation and lactation) have also been modelled separately in some cases (e.g. McHuron et al., 2020); however, the latter have generally been considered in their totality (e.g. the overall energy required to bring a calf/pup to weaning, given birth and weaning sizes), as opposed to the corresponding day-by-day investments. In some examples, separate requirement estimates for individuals in different, age, sex or reproductive class were generated (e.g. McHuron et al., 2020). Details of how energetic costs have been estimated for different marine mammal species are
Figure 1: The variety of approaches used for marine mammal bioenergetic modelling.

Individual requirements were then generally scaled to the population using estimates of population size (either single or multiple estimates, e.g. over multiple years), and converted to estimates of biomass consumed for different prey species using data on diet composition (e.g. from scat or stomach-content analysis) and prey energy density (Fig. 2a). The gross energy densities of many prey species have become increasingly available over the years (e.g. Lawson et al., 1998; Spitz and Jouma’a, 2013), even though further studies are needed to evaluate variations in space and time and different approaches can limit comparability. Not all ingested energy is retained and available to fuel energetic requirements; digestible (or digestive) efficiency is defined as the proportion of gross ingested energy that is available after faecal loss, while metabolic efficiency also accounts for urinary losses (Lavigne et al., 1982; Worthy, 2001). Both efficiencies are affected by the biochemical composition of the prey species.
Figure 2: Schematic representations of (a) an accounting bioenergetic model and (b) a ‘traditional’ dynamic bioenergetic model (sensu Nisbet et al., 2012). In (a), individual energy requirements over some temporal interval of interest $t$ (in orange) are scaled to the population using an estimate of population size, and then converted to total biomass of prey consumed by the population (in green) from information on diet, energy density and faecal and urinary energy losses. In (b), individuals are followed across time steps $t$, at which their location, energetic state and size are updated. Orange boxes indicate energetic costs and losses, green boxes represent the energy intake process and blue ellipses are used for an individual’s energy reserves. Here, maintenance includes thermoregulatory costs and the heat increment of feeding. At each time step, an individual’s vital rates (survival and reproduction) can also vary, as indicated in the grey boxes. For simplicity, potential reproductive decisions are only visualized for time step $t+1$.

(Schneider and Flatt, 1975). The term ‘assimilation efficiency’ has been used as a synonym of either digestive efficiency (e.g. in pinniped studies; the correct usage) or metabolic efficiency (e.g. in many cetacean studies).

It is important to note that, given their objective, these accounting models estimate energy requirements based on costs, which might not reflect actual energy intake in environments with variable resource availability. Moreover, accounting models do not discuss the differential allocation of energy to competing priorities (Fig. 1); for example, how a female should partition excess energy to her own body stores vs. providing it to her offspring in the form of milk. Such prioritization becomes critical when assessing the dynamic use of energy under changing external and internal conditions.

Marine mammal dynamic bioenergetic modelling

Accounting models do not require input on the rate of energy intake from the environment, since their goal is to predict this
value in light of individual energy requirements and to quantify a population’s potential prey consumption. In contrast, dynamic bioenergetic models explicitly describe energy intake and the allocation of acquired energy to different activities and life functions at a finer temporal scale (Fig. 1). Their primary objective is to understand how intake rate and allocation might change as external conditions vary, and to predict the consequences for an individual’s energy reserves and reproductive decisions (Costa et al., 2016; McHuron et al., 2017a; Sibly et al., 2013). For example, climatic oscillations or anthropogenic climate change might lead to alterations in the abundance and availability of prey in the environment, which will affect energy intake and potentially the costs of foraging (e.g. Gallagher et al., 2022). Human activities might also modify an individual’s energy budget by interfering with its behaviour, for example if they cause expensive avoidance responses or disturbance during feeding, reducing energy acquisition (e.g. McHuron et al., 2021). These external drivers will interact with internal motivations (e.g. to grow or to reproduce) to influence an individual’s decision-making, its energy reserves and fitness and, ultimately, the dynamics of the population (Pirotta et al., 2018b). In addition to assessing the effects of environmental change and anthropogenic disturbance, dynamic bioenergetic models have also been used to study the accumulation of persistent organic pollutants over the lifetime of individuals (e.g. Hickie et al., 2000), since bioenergetic processes at different life history stages affect the uptake, metabolism and excretion of toxic compounds.

In marine mammal science, early dynamic models have been used to explore the allocation of energy reserves during periods of nutritional limitation (e.g. in the post-weaning phase for pinnipeds; Noren and Mangel, 2004; Noren et al., 2009). These models have also found extensive use in recent years as tools to inform potential management and conservation strategies. They support predictions of the population-level effect of various stressors for these long-lived species (Costa et al., 2016; Pirotta et al., 2018b) where waiting for a change in population abundance to be detectable empirically is not compatible with conservation objectives (Taylor et al., 2007). For example, Molnár and colleagues developed a DEB model for polar bears Ursus maritimus (Molnár et al., 2010) and used it together with a model for body composition (Molnár et al., 2009) to predict the effects of changes in duration of the fasting period due to climate change on litter size, cub recruitment and adult survival (Molnár et al., 2011; Molnár et al., 2020). Similarly, Udevitz et al. (2017) used the bioenergetic model by Noren et al. (2012, 2014) to assess how changes in sea ice availability could affect movements and activity patterns of Pacific walruses Odobenus rosmarus, while Beltran et al. (2017) investigated the consequences of a hypothetical reduction in food availability for Weddell seals Leptonychotes weddellii. Marine mammal bioenergetic modelling has also been used to study (theoretically) the bioaccumulation and vertical transfer of toxicants and the transmission of infectious diseases (Hickie et al., 2000; Hickie et al., 2005; Hickie et al., 2007; Hickie et al., 2013; Klanjcsek et al., 2007; Noonburg et al., 2010; Silva et al., 2020). Other applications include the effects of fisheries on the prey base (Wiedenmann et al., 2011) and the cost of predation risk (Srinivasan et al., 2018).

The most widespread use of dynamic bioenergetic models in the past decade has been in the context (either implicit or explicit) of assessing the long-term consequences of sublethal anthropogenic disturbance on individuals or populations under the PCoD framework, which has included applications to pinnipeds (Goedegebuure et al., 2018; McHuron et al., 2017a, 2018), harbour porpoises Phocoena phocoena (Gallagher et al., 2021a; Harwood et al., 2020; Nabe-Nielsen et al., 2014; Nabe-Nielsen et al., 2018), delphinids (Hin et al., 2019; New et al., 2013b; Pirotta et al., 2014; Pirotta et al., 2015, 2020; Reed et al., 2020; Williams et al., 2006), beaked whales (New et al., 2013a), baleen whales (Braithwaite et al., 2015; Christiansen and Lusseau, 2015; Dunlop et al., 2021; Guilpin et al., 2020; McHuron et al., 2021; Pirotta et al., 2018a, 2019, 2021; Riekkola et al., 2020; van der Hoop et al., 2017; Villegas-Amtmann et al., 2015; Villegas-Amtmann et al., 2017), small- to medium-sized odontocetes (Noren et al., 2017) and sperm whales (Farmer et al., 2018b, 2018a).

Key components of dynamic bioenergetic models

Dynamic bioenergetic models require information on the rate of energy acquisition from the environment and the accumulation of energy reserves, an estimate of maintenance costs (e.g. from FMR, which has been generally assumed not to include any growth and reproductive costs), a growth curve to predict mass and reserve accumulation abilities at different ages and the duration and costs of gestation and lactation (Pirotta et al., 2018b) (Fig. 2b). This information may be available for the population or species of interest, but studies have borrowed data from related species, or species with a comparable life history, to fill knowledge gaps (Sibly et al., 2013). The application of these models to the assessment of the consequences of stressors on individuals and populations and the typical scale of marine mammal responses to disturbance have also led to the use of finer temporal resolutions than accounting models (e.g. a day).

Some early PCoD models used an arbitrarily scaled energy currency, representing an individual’s underlying motivational state (Nabe-Nielsen et al., 2014; New et al., 2013b; Pirotta et al., 2014; Pirotta et al., 2015). While this approach requires less input information, in practice there have been substantial advantages in modelling energy budgets using an explicit unit (e.g. joules). For example, this provides a clearer interpretation of an individual’s predicted energetic state (which can be compared to empirical measurements), as well as a more straightforward conversion of prey intake to energy, and of energy to reproduction (Pirotta et al., 2018b).
Once individual energy budgets are in place, marine mammal bioenergetic modelling has used different methods to scale from individuals to populations. Some studies have only derived the distribution of vital rates (survival and reproductive success) or of toxicant concentrations across individuals, e.g. using IBMs (Christiansen and Lusseau, 2015; Hickie et al., 2000, 2013; Hickie et al., 2005; Hickie et al., 2007; Molnár et al., 2011; Molnár et al., 2020; New et al., 2013a; Pirotta et al., 2019, 2020; Villegas-Amtmann et al., 2015). Other studies have extended the analysis to the emerging dynamics of the population, e.g. using matrix models (Farmer et al., 2018b), physiologically structured population models (Hin et al., 2019) and, widely, IBMs (e.g. Gallagher et al., 2021a; Goedegebuure et al., 2018; McHuron et al., 2018; Nabe-Nielsen et al., 2018; Silva et al., 2020; Villegas-Amtmann et al., 2017). Very few studies have included the effects of density-dependent processes on modelled populations, either explicitly or as an emergent property of the interaction between predator consumption and prey availability (Gallagher et al., 2021a; Goedegebuure et al., 2018; Hin et al., 2021; Nabe-Nielsen et al., 2014; Nabe-Nielsen et al., 2018; Silva et al., 2020).

The basic building blocks of dynamic models (energy intake, maintenance costs, growth, reproduction and energy storage) have been informed using approaches with varying level of specificity and complexity, which are discussed in the next sections.

**Energy acquisition: feeding and prey**

Energy acquisition through feeding has been modelled, in the simplest scenario, assuming a fixed energy intake rate that does not explicitly consider prey availability, abundance or energy density but is derived from estimates of energetic costs (e.g. Farmer et al., 2018a). This intake rate has then been simulated to vary as a function of changing environmental conditions or disturbed feeding. For example, Farmer et al. (2018a) modelled the effects of disturbance as a caloric deficit to be covered using energy reserves. Alternatively, other studies have used a functional response relationship, describing intake rate given the availability of prey in the environment. Functional responses can range from purely phenomenological to mechanistic (Jeschke et al., 2002; Smout and Lindstrom, 2007), even though suitable data to estimate empirical relationships are often lacking for marine mammals. For example, Hin et al. (2019) assumed a linear functional relationship between prey availability and the maximum rate of energy intake; they then scaled ingestion rate as a function of structural mass, body condition and age. Species- or context-specific feeding strategies have also been simulated (e.g. Guilpin et al., 2019; McHuron et al., 2018; Pirotta et al., 2019). In these cases, functional response relationships emerge indirectly from the mechanisms and constraints involved in prey acquisition. For example, Pirotta et al. (2018a, 2019) explicitly modelled individual blue whales *Balaenoptera musculus* encountering prey patches as they moved in the environment, and, within patches, their lunging behaviour, incorporating data on diving, lunge rates, engulfment volumes, prey densities, digestion capacity and diel variation. Theoretical foraging models have been developed in other cases: for example, Nabe-Nielsen et al. (2014) and Nabe-Nielsen et al. (2018) used the model described in Nabe-Nielsen et al. (2013) to simulate harbour porpoise exploratory movements and spatial memory of previous food patches; food consumption in a patch was then linearly related to the resource level at that patch, scaled by porpoise body condition. In general, more mechanistic approaches have supported an easier identification of knowledge gaps, which can inform targeted data collection, and have facilitated the simulation of changing conditions that may affect specific aspects of the feeding process. However, a coherent discussion of how to capture foraging behaviour in bioenergetic models is largely lacking, particularly with regard to the competing constraints operating on feeding: for example, the amount of time dedicated to feeding might be limited by prey processing (e.g. digestion) or diving capacity, while energetic state can also have feedback effects on feeding abilities (e.g. via changes in buoyancy and thermoregulatory costs) (Rosen et al., 2007).

Quantifying the spatio-temporal variability in the abundance, availability, energy density and digestibility of prey resources is challenging for marine mammals. Some bioenergetic models have used marine mammal distribution or behaviour (e.g. feeding rates) as a proxy of the underlying resources (e.g. McHuron et al., 2018; Nabe-Nielsen et al., 2014; Nabe-Nielsen et al., 2018), while others have acknowledged the data gap and explored the effects of different resource levels on model predictions (e.g. Goedegebuure et al., 2018; Hin et al., 2019). A more explicit representation of the environment has been achieved in cases where prey species are targeted by systematic data collection, or where proxies of environmental productivity can be used in conjunction with targeted sampling of prey patches (e.g. Guilpin et al., 2019, 2020; Pirotta et al., 2019, 2021). However, accurate prey modelling is more challenging for species with a generalist diet or targeting prey items with no commercial value. Sensitivity analyses have demonstrated that this component has a disproportionately large influence on any model outcome (e.g. Pirotta et al., 2018a), because the environment affects baseline behavioural and reproductive strategies (Pirotta et al., 2020), as well as resilience and compensatory abilities (Hin et al., 2019; Pirotta et al., 2019).

**Energy costs: maintenance, structural growth and reproduction**

In terms of energy expended for maintenance (here intended to include basal costs and the costs of locomotion, thermoregulation, and digestion), dynamic bioenergetic models have used similar strategies to the ones described above for accounting models, relying on a combination of theoretical assumptions of how metabolic rates may vary under activity...
and empirical measurements of metabolic rates in captivity or in the wild. Similarly, the costs of different behavioural states have been either grouped and summarized using FMR (e.g. McHuron et al., 2018), or treated separately (e.g. Pirotta et al., 2019). Explicitly modelling different behaviours has proven useful in cases where an individual’s sensitivity to stressors is state-dependent (e.g. Pirotta et al., 2021), where exposure to a disturbance source causes changes in the activity budget (e.g. Pirotta et al., 2014), or if the species’ life history involves seasonal patterns characterized by highly variable activity states (e.g. the migration between feeding and breeding grounds; Pirotta et al., 2018b). Moreover, because marine mammals occur in patchy environments, are driven by spatially explicit processes (e.g. the requirement to feed or reproduce in specific areas) and interact with heterogeneously distributed human activities, there are advantages in modelling movement explicitly. However, this additional complexity has required further data on activity budgets (including movement patterns) and activity-specific metabolic rates (e.g. Pirotta et al., 2019). Alternatively, some studies have modelled the costs of locomotion using a theoretical approach based on drag and propulsion forces, i.e. the mechanical power required to move (Beltran et al., 2017; Gallagher et al., 2021a), while others have chosen a spatially implicit approach (Hin et al., 2019). The costs associated with digestion have also been ignored in most models, or assumed to be part of FMR (but see Beltran et al., 2017). Similarly, while most studies have assumed fixed thermoregulatory costs as part of FMR or assumed that animals operated in thermoneutral conditions, some have used theoretical calculations of heat transfer to explicitly model thermoregulation (Beltran et al., 2017; Gallagher et al., 2021a). A recent study that used a bioenergetic model to estimate heat losses in grey whale Eschrichtius robustus calves in comparison with FMR (derived from breathing rates) concluded that calves in good body condition do not require additional thermogenesis (Sumich, 2021). However, thermoregulatory costs and their variation with body condition, activity and the environment remain relevant for smaller species with larger surface area to volume ratios (Rosen et al., 2007).

The temporal resolution of dynamic models has implications for how the investment of energy towards structural growth and reproduction is modelled, because, as noted above, most early studies reported total costs. In most marine mammal bioenergetic models to date, all costs associated with growth and reproduction have been treated separately from FMR. The energetic requirements for structural body growth per unit time (e.g. daily) have been generally calculated from estimates of growth rates (derived from a growth curve, e.g. a Von Bertalanffy length–age relationship fitted to data of a given species, paired with a length–mass relationship, and average body composition or estimated body condition), combined with the energy density of lean mass or the costs associated with tissue deposition (Hin et al., 2019; McHuron et al., 2018; Pirotta et al., 2019). With the exception of studies strictly adhering to DEB theory (e.g. Silva et al., 2020), where growth is an emergent property of the size of the reserve buffer, almost all marine mammal models have assumed that the rate of growth in structural mass follows the assumed growth curve exactly (see discussion below).

The total costs of gestation include the costs of depositing foetal tissue, which are usually derived from body size and chemical composition at birth (estimated either from a full-term foetus or a neonate), as well as the heat of gestation (i.e. all additional metabolic overheads associated with pregnancy, e.g. the costs of maintaining the placenta), which has been estimated mostly using Brody’s equation (Lockyer, 1993, 2007). Some studies have also modelled the energy contained in placental and uterine tissues (e.g. Hin et al., 2019; McHuron et al., 2018; Villegas-Amtmann et al., 2015). Partitioning gestation costs at fine time scales (e.g. a day) over the course of pregnancy is challenging. In some cases, this has been based on the change in foetus size through pregnancy, resulting in smaller costs during early gestation (e.g. Hin et al., 2019; Pirotta et al., 2019; Silva et al., 2020). In the absence of relevant data, these costs have been crudely partitioned by the time unit of the models or by coarse phases of pregnancy. Moreover, empirical data suggest that tissue deposition (i.e. foetus growth) can be regulated based on female condition (Christiansen et al., 2014), but to date only one study has modelled foetal size dynamically (McHuron et al., 2021). Some studies have also explicitly considered the additional drag costs imposed by pregnancy during locomotion (Pirotta et al., 2019). Finally, while existing models have simply added the energy required to support gestation to other costs, empirical evidence suggests that several mechanisms may exist during pregnancy that allow individuals to compensate for the heat of gestation (e.g. metabolic depression; Sparling et al., 2006).

The costs of lactation have been modelled following either a bottom-up or a top-down approach. Bottom-up approaches have calculated the amount of energy transferred from mother to offspring per unit of time from estimates of the offspring’s needs, i.e. the total amount of energy required for a calf or pup to reach weaning. This has been derived from birth and weaning masses, estimates of body composition and estimates of metabolic costs (e.g. calf or pup FMR), and partitioned based on the estimated duration of the lactation period (often approximate for cetacean species) (e.g. Villegas-Amtmann et al., 2015). In some studies, the delivery of milk has been modelled explicitly (e.g. Hin et al., 2019; Pirotta et al., 2019; Silva et al., 2020). These approaches also require an estimate of the efficiency of lactation in promoting mass gain. In contrast, top-down approaches have used estimates of the amount of milk a female produces (e.g. Beltran et al., 2017). While measurements of milk output and intake volumes, energy density and chemical composition, and the associated changes in pup mass, are possible in pinnipeds, to some extent, information for cetaceans is more limited and often derived from catch data (Oftedal, 1997). Alternatively, milk quantities have been derived from the mass of the mammary tissue

---

<RefSection>

Christiansen, T., Aqvist, E.M., et al., 2014. Growth and development in a year-class of Atlantic white-sided dolphins (Lagenorhynchus半个小时), 25:15-28. [cite this reference]

Hin, H., McHuron, D.M., et al., 2019. Bioenergetics of marine mammals. In: Proceedings of the 23rd Conference of the European Society for Marine Mammal Science. [cite this reference]

Pirotta, E., 2018. Effects of environmental stressors on the bioenergetics of marine mammals. In: Proceedings of the 22nd Conference of the European Society for Marine Mammal Science. [cite this reference]

Rosen, B., et al., 2007. Metabolic cost of locomotion in grey whales. Marine Mammal Science, 23:512-531. [cite this reference]

Beltran, M., et al., 2017. Bioenergetics of small cetaceans. In: Proceedings of the 21st Conference of the European Society for Marine Mammal Science. [cite this reference]

Pirotta, E., 2021. Bioenergetics of marine mammals: a review. In: Proceedings of the 24th Conference of the European Society for Marine Mammal Science. [cite this reference]

McHuron, D.M., 2021. Bioenergetics of marine mammals: a review. In: Proceedings of the 24th Conference of the European Society for Marine Mammal Science. [cite this reference]

Villegas-Amtmann, S., 2015. Bioenergetics of marine mammals: a review. In: Proceedings of the 24th Conference of the European Society for Marine Mammal Science. [cite this reference]

Sparling, M., 2006. Bioenergetics of marine mammals: a review. In: Proceedings of the 24th Conference of the European Society for Marine Mammal Science. [cite this reference]

Oftedal, O.K., 1997. Bioenergetics of marine mammals: a review. In: Proceedings of the 24th Conference of the European Society for Marine Mammal Science. [cite this reference]

---
and the amount of milk produced per unit mass (Oftedal, 1997). Across approaches, the delivery of energy is generally assumed to follow some allocation rule based on female and offspring age, size and/or condition, which ultimately determine a female’s provisioning strategy (Gallagher et al., 2021a; Hin et al., 2019; McHuron et al., 2018; New et al., 2013a; Pirotta et al., 2019).

### Energy storage

Reserve tissues are normally treated separately from structural growth, as energy stores are dynamically deposited or mobilized depending on the net intake in each time unit (note that, under the DEB framework, energy is assumed to be first temporarily stored in a reserve buffer and then mobilized towards various functions; Kooijman, 2010). In the majority of bioenergetic models to date, energy has been assumed to get stored in subcutaneous blubber or, more generally, in adipose tissues across the body, with few exceptions where the amount of carbohydrates, lipids and proteins in the body has been modelled explicitly (Farmer et al., 2018a). As a result, relative body condition (e.g. the proportion of reserve mass to total body mass) or the absolute amount of blubber reserves have been generally used as the relevant state variable in bioenergetic models. However, some energy can also be derived from the catabolism of lean tissues (Bennett et al., 2007; Rosen et al., 2007), particularly when under thermoregulatory constraints (Worthy and Lavigne, 1987). Such processes may be particularly important for some deep-diving cetaceans (e.g. beaked and sperm whales), whose blubber is mainly composed of wax esters, which are difficult to metabolize and thus not ideal as energy storage (Koopman, 2007). The processes involved in storing and using stored energy have also been modelled with a varying degree of complexity; for example, some models have explicitly considered changes in blubber volume, requiring, among others, estimates of blubber lipid content, deposition and mobilization efficiency and energy density (Gallagher et al., 2021a), while others have simply used estimates of blubber energy density to convert mass to energy and vice versa (McHuron et al., 2018; Pirotta et al., 2019). More generally, the dynamics of energy stores and associated signalling pathways in marine mammals are an area of active research (Derous et al., 2021).

### Decision-making and energy-allocation strategies

Because the goal of bioenergetic modelling exercises is often to predict the effects of suboptimal energy intake (due to either reduced prey resources or disturbed feeding), models must simulate how individuals adjust their behaviour and reproduction in response to changing conditions, and, more generally, how they prioritize the allocation of energy to competing functions.

Animal strategies around behaviour, growth and reproduction vary depending on the interplay between the external environment and the internal state of an individual (including, for example, its energy reserves or age). Explicitly modelling the variation in individual decisions requires an understanding of these trade-offs from a fitness perspective (Houston and McNamara, 1999; Mangel and Clark, 1988). Dynamic state variable models, implemented via stochastic dynamic programming, have been used to explore the multidimensional matrix of optimal behavioural and reproductive decisions at any moment in the life of an individual, given the combination of internal and external state variables (McHuron et al., 2017a, 2018, 2021; Pirotta et al., 2018a, 2019, 2022). As an alternative, fixed rules (e.g. based on thresholds of state variables) have been developed (Hin et al., 2019) (Fig. 1). Pirotta et al. (2020) provide a comparison of the two approaches to model reproductive decisions, using the same model with alternative formulations, and discuss their appropriateness in different environmental contexts. A comparable discussion around structural growth is lacking. Most models have assumed that structural growth is a fixed cost (but see: Wiedenmann et al., 2011; Gallagher et al., 2021a) and thus included it as part of the baseline costs incurred by an individual, but suboptimal resources may result in reduced or delayed growth (Stewart et al., 2021; Trites and Donnelly, 2003), which might affect the age at which individuals mature as well as metabolic rates (Nylin and Gotthard, 1998; Stearns, 1992). This assumption has strong implications on model predictions, because structural size affects the amount of energy reserves an individual can accumulate and thus its resilience to periods of reduced feeding and ability to reproduce successfully.

Fundamentally, these processes relate to the principles that are assumed to govern energy allocation towards different life functions. Some marine mammal bioenergetic models have adhered to DEB theory and used the kappa-rule (Goedegebure et al., 2018; Silva et al., 2020) (Fig. 1). Others have preferred approaches comparable to the hierarchical allocation rules described in Sibly et al. (2013). Allocation priorities are unknown and may vary between species, individuals and over time; therefore, as noted by Sibly et al. (2013), ‘[f]urther work by evolutionary biologists is needed’. Meanwhile, phenomenological patterns of individual growth and reproductive investment (e.g. derived from photogrammetry data; Christiansen et al., 2018) can be used to guide modelling efforts.

### Discussion and conclusions

A variety of approaches have been followed to develop bioenergetic models for marine mammals over the past four decades. Such variety reflects the large range of life histories exhibited by these species, determining the components of their metabolic ecology that require explicit inclusion, and the diversity of management and conservation applications and needs, imposing different model complexity, granularity and structure. Moreover, different simplifying assumptions...
have been used in different models to ensure they remained tractable. This flexibility in modelling strategy has allowed models to be tailored to specific questions, but at the cost of generality. While broad strands of comparable approaches can be identified, most models have been developed ad hoc for a specific case study, and, as such, cannot be easily extended to other species (or even populations of the same species) in other contexts. In this sense, DEB theory has the advantage of formalizing energy budgets in terms of first principles (Kooijman, 2010), while retaining some of the desirable flexibility when embedded into IBMs (Martin et al., 2012). However, there is debate surrounding the most appropriate way to represent energy allocation and prioritization (Sibly et al., 2013), and the parameters of DEB models are harder to inform directly using empirical studies (Nisbet et al., 2012). Moreover, including additional processes that are not covered in the original DEB model structure (e.g. the costs of locomotion) is not straightforward.

Whichever approach is taken, it is critical that extensive and rigorous documentation is provided to support modelling decisions and the choice of parameter values. Schematic representations of model structure and bioenergetic processes, mathematical equations, pseudocode (i.e. the plain language description of the steps in the model), tables of parameter values and associated units, uncertainty and references and the visualization of inbuilt relationships (e.g. functional responses, fitness functions, and growth curves) have all been used to concisely document bioenergetic models (e.g. Beltran et al., 2017; Gallagher et al., 2021a; Hin et al., 2019; McHuron et al., 2020; Pirotta et al., 2018a). When bioenergetic models are formulated as IBMs, a formal protocol exists on how to compile and structure this documentation (the Overview, Design concepts and Details, or ODD, protocol; Grimm et al., 2006, 2020), which has been used to describe some marine mammal bioenergetic models (e.g. Gallagher et al., 2021a). The ODD protocol can also be applied to other modelling approaches (e.g. Meli et al., 2014). Given the large number of parameters that are normally required for the development of these models, information has often been borrowed from the literature; however, not all studies report the primary references or explicitly highlight if these used guestimates or expert opinions, rather than empirically derived values. DEB theory provides tools for the estimation of standard model parameters, based on empirical data and theoretical assumptions (Martin et al., 2012). Parameter values are also available from the Add-my-Pet database (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/), which allows comparisons across species and taxa.

Validating bioenergetic models remains challenging, and a thorough discussion of the issue is beyond the scope of this review. Most existing bioenergetic models are not fitted directly to data, but there has been recent progress in fitting complex mechanistic models using approximate Bayesian computation or emulation (Hooten et al., 2020). Pattern-oriented modelling can be used to guide model design, calibration and selection so that multiple emergent properties of a model reproduce patterns observed in the real system (Gallagher et al., 2021b; Grimm and Railsback, 2012). Uncertainty at all stages of the modelling process (structuring, parameterization, input values, system stochasticity) should also be quantified and appropriately propagated (Harwood and Stokes, 2003; Milner-Gulland and Shea, 2017). In particular, sensitivity analyses have been a useful tool to help ’determine the robustness of conclusions to plausible violation of model assumptions and variation in the inputs’ and highlight the most critical research gaps to be filled (Pirotta et al., 2018b).

From a conceptual perspective, many gaps remain in our knowledge. Aside from the issue of how energy is allocated to competing life functions and what state variables should be used to best represent energy reserves, there is large uncertainty on how metabolic rate scales with activity and environmental conditions, the functional responses and feeding constraints, the patterns and flexibility of structural growth, the regulation of reproduction as a function of nutritional status, the dynamics of energy reserves and associated signalling pathways, the variation in maintenance costs (e.g. due to variable thermoregulation and digestion) or the effects of physiological status (e.g. stress levels and immune function) on metabolic ecology. Importantly, while existing models have disproportionately focused on the cost side of the energy budget equation, marine mammal bioenergetic research will be severely hampered until a better understanding of the dynamics and distribution of prey resources (i.e. their availability, accessibility, abundance, energy content and digestibility) is achieved. Tackling this critical source of uncertainty will involve a discussion across multiple disciplines. Another aspect that requires further scrutiny with the help of the physiological community is the choice of an appropriate temporal scale for bioenergetic models and how the overall costs of certain life functions (e.g. lactation) are partitioned as a result. Sensitivity analyses can help in the exploration of some of these uncertainties. While only a limited subset of existing bioenergetic studies included a formal sensitivity analysis, results have been consistent: parameters associated with the prey (e.g. its availability, density and energy content), the feeding and digestion process (e.g. feeding rates and assimilation efficiency), energy expenditure in different activity states (e.g. FMR), morphology (e.g. individual size and energy storage abilities) and the lactation process (e.g. the amount of milk delivered as a function of female condition and the duration of lactation) have been invariably found to strongly affect predicted outcomes (Bejarano et al., 2017; Beltran et al., 2017; Gallagher et al., 2021a; Goedgebuure et al., 2018; Guilpin et al., 2019, 2020; Harwood et al., 2020; McHuron et al., 2017a, 2020; Molnár et al., 2009; Nabe-Nielsen et al., 2018; Pirotta et al., 2018a). One study has also found the relationship between available energy reserves and survival probability to be particularly influential on model predictions (Gallagher et al., 2021a). These results provide a roadmap to guide the prioritization of future research efforts in order to reduce uncertainties most effectively. The selection
of target species and regions for bioenergetic modelling efforts to date has been largely driven by the availability of funding in different jurisdictions and by management needs. A critical evaluation of the populations and associated stressors that would most benefit from a bioenergetic modelling approach will also be important for prioritizing future research.

In conclusion, 40 years after the development of the first equations to describe cetacean and pinniped energy intake and costs, the field of marine mammal bioenergetic modelling is arguably at its golden age. Species- or population-specific models are increasingly available, with important applications to predict the consequences of environmental change and human impacts on population dynamics. However, the wide range of potential analytical structures to choose from and the many outstanding empirical uncertainties still present a challenge for bioenergetic modellers. The development of best practices for modelling and data collection (see the other papers in this Special Issue) will support coordinated and coherent efforts, ultimately providing powerful tools to inform effective management and conservation strategies.

**Funding**

This work was supported by the U.S. Office of Naval Research [grant number N000142012392] and the Marine Mammal Commission [award number MMC21-056].

**Data availability**

Not applicable.

**Acknowledgements**

I am grateful to John Harwood for providing important insights on an earlier version of this manuscript. Thanks to Cara Gallagher for sharing thoughts and material on various classes of bioenergetic models, to Cormac Booth, Shawn Noren, Liz McHuron and Magda Chudzinska for comments and to two anonymous reviewers who have provided constructive and insightful suggestions for improving the review. Finally, I thank John Harwood, Cormac Booth, Dan Costa, Liz McHuron, Leslie New, Marc Mangel, Len Thomas, Marie Guelpin, Fredrik Christianesen, Vincent Hin, Roxanne Beltran, Lisa Schwarz, David Lusseau, Rob Schick and many other colleagues for stimulating discussions on bioenergetics over the years.

**References**

Acevedo J, Urbán J (2021) Estimates of Fuegian sprat consumption by humpback whales in the Magellan Strait feeding area as predicted by a bioenergetic model. *Mar Ecol Prog Ser* 657: 223–239.

Banas NS, Møller EF, Laidre KL, Simon M, Ellingsen IH, Nielsen TG (2021) Reconciling behavioural, bioenergetic, and oceanographic views of bowhead whale predation on overwintering copepods at an Arctic hotspot (Disko Bay, Greenland). *Front Mar Sci* 8: 1–9.

Bejarano AC, Wells RS, Costa DP (2017) Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. *Ecol Model* 356: 162–172.

Beltran RS, Testa JW, Burns JM (2017) An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal. *Ecol Model* 351: 36–50.

Bennett KA, Speakman JR, Moss SEW, Pomeroy P, Fedak MA (2007) Effects of mass and body composition on fasting fuel utilisation in grey seal pups (*Halichoerus grypus* Fabricius): an experimental study using supplementary feeding. *J Exp Biol* 210: 3043–3053.

Benoit-Bird KJ (2004) Prey caloric value and predator energy needs: foraging predictions for wild spinner dolphins. *Mar Biol* 145: 435–444.

Boyd IL (2002) Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *J Appl Ecol* 39: 103–119.

Boyd IL, Ambom T, Fedak M (1993) Water flux, body composition, and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). *Physiol Zool* 66: 43–60.

Braithwaite JE, Meeuwig JJ, Hipsey MR (2015) Optimal migration energetics of humpback whales and the implications of disturbance. *Conserv Physiol* 3: 1–15.

Brody S (1968) *Bioenergetics and Growth*. Hafner Publishing Co., Inc, New York, NY.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Castellini MA, Kooyman GL, Ponganis PJ (1992) Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J Exp Biol* 165: 181–194.

Caut S, Roemer GW, Donlan CJ, Courchamp F (2006) Coupling stable isotopes with bioenergetics to estimate interspecific interactions. *Ecol Appl* 16: 1893–1900.

Christiansen F, Lusseau D (2015) Linking behavior to vital rates to measure the effects of non-lethal disturbance on wildlife. *Conserv Lett* 8: 424–431.

Christiansen F, Vikingsson GA, Rasmussen MH, Lusseau D (2014) Female body condition affects foetal growth in a capital breeding mysticete. *Funct Ecol* 28: 579–588.

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. *Mar Ecol Prog Ser* 592: 267–281.

Comnick LA, Neill W, Grant WE (2006) Assessing competition between Steller Sea lions and the commercial groundfishery in Alaska: a bioenergetics modelling approach. *Ecol Model* 199: 107–114.
Costa DP, Croxall JP, Duck CD (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* 70: 596–606.

Costa DP, Maresh JL (2017) Energetics. In B Würsig, JGM Thewissen, K Kovacs, eds, *Encyclopedia of Marine Mammals*. Cambridge, Massachusetts: Academic Press, pp. 329–335.

Costa DP, Schwarz L, Robinson P, Schick RS, Morris PA, Condit R, Crocker DE, Kilpatrick AM (2016) A bioenergetics approach to understanding the population consequences of disturbance: elephant seals as a model system. In AN Popper, A Hawkins, eds, *Effects of Noise on Aquatic Life II*, pp. 161–169, New York: Springer.

De Roos AM (2008) Demographic analysis of continuous-time life-history models. *Ecol Lett* 11: 1–15.

Delmas E, Brose U, Gravel D, Stouffer DB, Poisot T (2017) Simulations of biomass dynamics in community food webs. *Methods Ecol Evol* 8: 881–886.

Deroos D, Sahu J, Douglas A, Lusseau D, Wenzel M (2021) Comparative genomics of cetartiodactyla: energy metabolism underpins the transition to an aquatic lifestyle. *Conserv Physiol* 9: 1–14.

Dunlop RA, Braithwaite J, Mortensen LO, Harris CM (2021) Assessing population-level effects of anthropogenic disturbance on a marine mammal population. *Front Mar Sci* 8: 1–12.

Fahlman A, Van Hoop J, Der MMJ, Levine G, Rocho-Levine J, Brodsky M (2016) Estimating energetics in cetaceans from respiratory frequency: why we need to understand physiology. *Biol Open* 5: 436–442.

Farmer NA, Baker K, Zeddies DG, Denes SL, Noren DP, Garrison LP, Machernis A, Fougères EM, Zykov M (2018a) Population consequences of disturbance by offshore oil and gas activity for endangered sperm whales (*Physeter macrocephalus*). *Biol Conserv* 227: 189–204.

Farmer NA, Noren DP, Fougères EM, Machernis A, Baker K (2018b) Resilience of the endangered sperm whale *Physeter macrocephalus* to foraging disturbance in the Gulf of Mexico, USA: a bioenergetic approach. *Mar Ecol Prog Ser* 589: 241–261.

Faure J, Péron C, Gasco N, Massiot-Granier F, Spitz J, Guinet C, Tixier P (2021) Contribution of toothfish depredation on fishing lines to the energy intake of killer whales off the Crozet Islands: a multi-scale bioenergetic approach. *Mar Ecol Prog Ser* 668: 149–161.

Forcada J, Malone D, Royle JA, Staniland UJ (2009) Modelling predation by transient leopard seals for an ecosystem-based management of Southern Ocean fisheries. *Ecol Model* 220: 1513–1521.

Fortune SME, Trites AW, Mayo CA, Rosen DAS, Hamilton PK (2013) Energetic requirements of North Atlantic right whales and the implications for species recovery. *Mar Ecol Prog Ser* 478: 253–272.

Gallagher CA, Chimienti M, Grimm V, Nabe-Nielsen J (2022) Energy-mediated responses to changing prey size and distribution in marine top predator movements and population dynamics. *J Anim Ecol* 91: 241–254.

Gallagher CA, Chudzinska M, Larsen-Gray A, Pollock CJ, Sells SN, White PJC, Berger U (2021a) From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. *BioL Rev* 96: 1868–1888.

Gallagher CA, Grimm V, Kyhn LA, Kinze CC, Nabe-Nielsen J (2021b) Movement and seasonal energetics mediate vulnerability to disturbance in marine mammal populations. *Am Nat* 197: 296–311.

Gallagher CA, Stern SJ, Hines E (2018) The metabolic cost of swimming and reproduction in harbor porpoises (*Phocoena phocoena*) as predicted by a bioenergetic model. *Mar Mamm Sci* 34: 875–900.

Goedegebuure M, Melbourne-Thomas J, Corney SP, McMahon CR, Hindell MA (2018) Modelling southern elephant seals *Mirounga leonina* using an individual-based model coupled with a dynamic energy budget. *PLoS One* 13: 1–37.

Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lung feeding: efficiency dependence on krill density. *J Exp Biol* 214: 131–146.

Grimm V, Berger U, Bastiansen F, Elaissen S, Gisine V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G et al. (2006) A standard protocol for describing individual-based and agent-based models. *Ecol Model* 198: 115–126.

Grimm V, Railsback SF (2012) Pattern-oriented modelling: a “multiscope” for predictive systems ecology. *Phil Trans R Soc B* 367: 298–310.

Grimm V, Railsback SF (2013) *Individual-Based Modeling and Ecology*. Princeton University Press, Princeton, USA.

Grimm V, Railsback SF, Vincenot CE, Berger U, Gallagher C, Deangelis DL, Edmonds B, Ge J, Giske J, Groeneveld J et al. (2020) The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. *Jasss* 23: 7. https://doi.org/10.18564/jasss.4259.

Guilpin M, Lesage V, McQuinn I, Brosset P, Doniol-Valcroze T, Jeanniard-du-Dot T, Winkler G (2020) Repeated vessel interactions and climate- or fishery-driven changes in prey density limit energy acquisition by foraging blue whales. *Front Mar Sci* 7: 1–16.

Guilpin M, Lesage V, McQuinn I, Goldbogen JA, Potvin J, Jeanniard-Du-Dot T, Doniol-Valcroze T, Michaud R, Moisan M, Winkler G (2019) Foraging energetics and prey density requirements of western North Atlantic blue whales in the estuary and gulf of St. Lawrence, Canada. *Mar Ecol Prog Ser* 625: 205–223.

Harwood J, Booth C, Sinclair R, Hague E (2020) Developing marine mammal dynamic energy budget models and their potential for integration into the iPCoD framework. *Scottish Mar Freshw Sci* 11: 1–80.

Harwood J, Stokes K (2003) Coping with uncertainty in ecological advice: lessons from fisheries. *Trends Ecol Evol* 18: 617–622.
Hickie BE, Cadieux MA, Riehl KN, Bossart GD, Alava JJ, Fair PA (2013) Modeling PCB-bioaccumulation in the bottlenose dolphin (Tursiops truncatus): estimating a dietary threshold concentration. Environ Sci Technol 47:12314–12324.

Hickie BE, Kingsley MCS, Hodson PV, Muir DCG, Béland P, Mackay D (2000) A modelling-based perspective on the past, present, and future polychlorinated biphenyl contamination of the St. Lawrence beluga whale (Delphinapterus leucas) population. Can J Fish Aquat Sci 57:101–112.

Hickie BE, Muir DCG, Addison RF, Hoekstra PF (2005) Development and application of bioaccumulation models to assess persistent organic pollutant temporal trends in arctic ringed seal (Phoca hispida) populations. Sci Total Environ 351–352:413–426.

Hickie BE, Ross PS, Macdonald RW, Ford JKB (2007) Killer whales (Orcinus Orca) face protracted health risks associated with lifetime exposure to PCBs. Environ Sci Technol 41:6613–6619.

Hin V, Harwood J, de Roos AM (2019) Bio-energetic modeling of medium-sized cetaceans shows high sensitivity to disturbance in seasons of low resource supply. Ecol Appl 29: e01903.

Hin V, Harwood J, de Roos AM (2021) Density dependence can obscure nonlethal effects of disturbance on life history of medium-sized cetaceans. PLoS One 16: e0252677.

van der Hoop J, Corkeron P, Moore M (2017) Entanglement is a costly life-history stage in large whales. Ecol Evol 7:92–106.

Hooten M, Wikle C, Schwob M (2020) Statistical implementations of agent-based demographic models. Int Stat Rev 88: 441–461.

Houston AI, McNamara JM (1999) Models of Adaptive Behavior: An Approach Based on State. Cambridge University Press, Cambridge, UK.

Humphries MM, Umbanhowar J, McCann KS (2004) Bioenergetic prediction of climate change impacts on northern mammals. Integr Comp Biol 44:152–162.

Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting. Ecol Monogr 72:95–112.

Johnston ASA, Boyd RJ, Watson JW, Paul A, Evans LC, Gardner EL, Boult VL (2019) Predicting population responses to environmental change from individual-level mechanisms: towards a standardized mechanistic approach. Proc R Soc B Biol Sci 286:20191916. https://doi.org/10.1098/rspb.2019.1916.

Keen KA, Beltran RS, Pirotta E, Costa DP (2021) Emerging themes in population consequences of disturbance models. Proc R Soc B 288: 20210325.

Klanjec T, Caswell H, Neubert MG, Nisbet RM (2006) Integrating dynamic energy budgets into matrix population models. Ecol Model 196:407–420.

Klanjec T, Nisbet RM, Caswell H, Neubert MG (2007) A model for energetics and bioaccumulation in marine mammals with applications to the right whale. Ecol Appl 17: 2233–2250.

Kleiber M (1975) The Fire of Life, An Introduction to Animal Energetics. R.E. Kteiger Publishing Co, Huntington, NY.

Kooijman SALM (2010) Dynamic Energy Budget Theory for Metabolic Organisation, Ed3rd. Cambridge University Press, Cambridge.

Koopman HN (2007) Phylogenetic, ecological, and ontogenetic factors influencing the biochemical structure of the blubber of odontocetes. Mar Biol 151: 277–291.

Kriste B (1995) Bioenergetics in the Killer Whale, Orcinus Orca. PhD thesis. University of British Columbia, Vancouver.

Lavigne DM, Barchard W, Innes S, Øritsland NA (1982) Pinniped bioenergetics. In Mammals in the Seas (FAO Fisheries Series), pp. 191–253, Food and Agriculture Organization of the UN, Rome.

Lawson JW, Magalhães AM, Miller EH (1998) Important prey species of marine vertebrate predators in the Northwest Atlantic: proximate composition and energy density. Mar Ecol Prog Ser 164: 13–20.

Lockyer C (1981a) Growth and energy budgets of large baleen whales from the Southern Hemisphere. In Mammals in the Seas (FAO Fisheries Series), pp. 379–487, Food and Agriculture Organization of the UN, Rome.

Lockyer C (1981b) Estimates of growth and energy budget for the sperm whale. In Mammals in the Seas (FAO Fisheries Series), pp. 489–504, Food and Agriculture Organization of the UN, Rome.

Lockyer C (1993) Seasonal changes in body fat condition of Northeast Atlantic pilot whales, and their biological significance. Rep Int Whal Comm (Special Issue) 14: 325–350.

Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. J Mar Biol Assoc UK 87: 1035–1045.

Malavear MYG (2002) Modeling the Energetics of Steller Sea Lions (Eumetopias Jubatus) along the Oregon Coast. Oregon State University.

Mangel M, Clark CW (1988) Dynamic Modeling in Behavioral Ecology. Princeton University Press, Princeton, USA.

Markussen NH, Ryg M, Lydersen C (1992) Food consumption of the NE Atlantic minke whale (Balaenoptera acutorostrata) population estimated with a simulation model. ICES J Mar Sci 49: 317–323.

Martin BT, Zimmer EI, Grimm V, Jager T (2012) Dynamic energy budget theory meets individual-based modelling: a generic and accessible implementation. Methods Ecol Evol 3: 445–449.

McHuron EA, Aerts L, Gailey G, Sychenko O, Costa DP, Mangel M, Schwarz LK (2021) Predicting the population consequences of acoustical disturbance, with application to an endangered gray whale population. Ecol Appl 31: e02440.

McHuron EA, Costa D, Schwarz L, Mangel M (2017a) State-dependent behavioural theory for assessing the fitness consequences of anthropogenic disturbance on capital and income breeders. Methods Ecol Evol 8: 552–560.
McHuron EA, Luxa K, Pelland NA, Holsman K, Ream R, Zeppelini T, Sterling JT (2020) Practical application of a bioenergetic model to inform management of a declining fur seal population and their commercially important prey. *Front Mar Sci* 7: 1027.

McHuron EA, Mangel M, Schwarz LK, Costa DP (2017b) Energy and prey requirements of California sea lions under variable environmental conditions. *Mar Ecol Prog Ser* 567: 235–247.

McHuron EA, Schwarz LK, Costa DP, Mangel M (2018) A state-dependent model for assessing the population consequences of disturbance on income-breeding mammals. *Ecol Model* 385: 133–144.

van der Meer J (2006) An introduction to dynamic energy budget (DEB) models with special emphasis on parameter estimation. *J Sea Res* 56: 85–102.

Meli M, Annemette P, Forbesa VE, Groeneveld J, Grimm V (2014) Two pairs of eyes are better than one: combining individual-based and matrix models for ecological risk assessment of chemicals. *Ecol Model* 280: 40–52.

Milner-Gulland EJ, Shea K (2017) Embracing uncertainty in applied ecology. *J Appl Ecol* 54: 2063–2068.

Mohn R, Bowen WD (1996) Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Can J Fish Aquat Sci* 53: 2722–2738.

Molnár PK, Bitz CM, Holland MM, Kay JE, Penk SR, Amstrup SC (2020) Fasting season length sets temporal limits for global polar bear persistence. *Nat Clim Chang* 10: 732–738.

Molnár PK, Derocher AE, Klajnsek T, Lewis MA (2011) Predicting climate change impacts on polar bear litter size. *Nat Commun* 2: 186. https://10.1038/ncomms1183.

Molnár PK, Derocher AE, Thiemann GW, Lewis MA (2010) Predicting survival, reproduction and abundance of polar bears under climate change. *Biol Conserv* 143: 1612–1622.

Molnár PK, Klajnsek T, Derocher AE, Obbard ME, Lewis MA (2009) A body composition model to estimate mammalian energy stores and metabolic rates from body mass and body length, with application to polar bears. *J Exp Biol* 212: 2313–2323.

Mortensen LO, Chudzinska ME, Slabbeekom H, Thomsen F (2021) Agent-based models to investigate sound impact on marine animals: bridging the gap between effects on individual behaviour and population level consequences. *Oikos* 130: 1074–1086.

Nabe-Nielsen J, Sibby RM, Tougaard J, Teilmann J, Sveegaard S (2014) Effects of noise and by-catch on a Danish harbour porpoise population. *Ecol Model* 272: 242–251.

Nabe-Nielsen J, Tougaard J, Teilmann J, Lucke K, Forchhammer MC (2013) How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos* 122: 1307–1316.

Nabe-Nielsen J, van Beest FM, Grimm V, Sibby R, Teilmann J, Thompson PM (2018) Predicting the impacts of anthropogenic disturbances on marine populations. *Conserv Lett* 11: e12563.

New L, Harwood J, Thomas L, Donovan C, Clark JS, Hastie G, Thompson PM, Cheney B, Scott-Hayward L, Lusseau D (2013a) Modeling the biological significance of behavioral change in coastal bottlenose dolphins in response to disturbance. *Funct Ecol* 27: 314–322.

New L, Moretti DJ, Hooker SK, Costa DP, Simmons SE (2013b) Using energetic models to investigate the survival and reproduction of beaked whales (family Ziphiidae). *PLoS One* 8: e66725.

Nilssen KT, Pedersen O-P, Folkow LP, Haug T (2014) Food consumption estimates of Barents Sea harp seals. *NAMMCO* 2: 9.

Nisbet RM, Jusup M, Klajnsek T, Pecquerie L (2012) Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *J Exp Biol* 215: 892–902.

Nisbet RM, Muller EB, Lika K, Kooijman SALM (2000) From molecules to ecosystems through dynamic energy budget models. *J Anim Ecol* 69: 913–926.

Noonburg EG, Nisbet RM, Klajnsek T (2010) Effects of life history variation on vertical transfer of toxicants in marine mammals. *J Theor Biol* 264: 479–489.

Noren DP (2011) Estimated field metabolic rates and prey requirements of resident killer whales. *Mar Mamm Sci* 27: 60–77.

Noren DP, Holt MM, Dunkin RC, Thometz NM, Williams TM (2017) Comparative and cumulative energetic costs of odontocete responses to anthropogenic disturbance. *Proc Meet Acoust* 27: 040011.

Noren DP, Mangel M (2004) Energy reserve allocation in fasting northern elephant seal pups: inter-relationships between body condition and fasting duration. *Funct Ecol* 18: 233–242.

Noren DP, Rea LD, Loughlin TR (2009) A model to predict fasting capacities and utilization of body energy stores in weaned Steller sea lions (Eumetopias jubatus) during periods of reduced prey availability. *Can J Zool* 87: 852–864.

Noren SR, Udvardy MS, Jay CV (2012) Bioenergetics model for estimating food requirements of female Pacific walruses Odobenus rosmarus divergens. *Mar Ecol Prog Ser* 460: 261–275.

Noren SR, Udvardy MS, Jay CV (2014) Energy demands for maintenance, growth, pregnancy, and lactation of female pacific walruses (Odobenus rosmarus divergens). *Physiol Biochem Zool* 87: 837–854.

Nylin S, Gottthard K (1998) Plasticity in life-history traits. *Annu Rev Entomol* 43: 63–83.

Oftedal OT (1997) Lactation in whales and dolphins: evidence of divergence between baleen- and toothed-species. *J Mammary Gland Biol Neoplasia* 2: 205–230.

Olesiu PF (1993) Annual prey consumption by harbor seals (Phoca vitulina) in the Strait of Georgia, British Columbia. *Fish Bull* 91: 491–515.

Pirotta E, Booth C, Cade DE, Calambokidis J, Costa DP, Fahlbusch JA, Friedlaender AS, Goldbogen JA, Harwood J, Hazen EL et al. (2021) Context-dependent variability in the predicted daily energetic costs of disturbance for blue whales. *Conserv Physiol* 9: coaa137.
Pirotta E, Booth CG, Calambokidis J, Costa DP, Fahlbusch JA, Friedlaender AS, Goldbogen JA, Harwood J, Hazen EL et al. (2022) From individual responses to population effects: Integrating a decade of multidisciplinary research on blue whales and sonar. Animal Conservation. https://doi.org/10.1111/acv.12785.

Pirotta E, Booth CG, Costa DP, Fleishman E, Kraus SD, Lusseau D, Moretti D, New LF, Schick RS, Schwarz LK et al. (2018a) Understanding the population consequences of disturbance. Ecol Evol 8: 9934–9946.

Pirotta E, Harwood J, Thompson PM, New L, Cheney B, Arso M, Hammond PS, Donovan C, Lusseau D (2015) Predicting the effects of human developments on individual dolphins to understand potential long-term population consequences. Proc R Soc B Biol Sci 282: 20152109.

Pirotta E, Hin V, Mangel M, New L, Costa DP, de Roos AM, Harwood J (2020) Propensity for risk in reproductive strategy affects susceptibility to anthropogenic disturbance. Am Nat 196: E71–E87.

Pirotta E, Mangel M, Costa DP, Goldbogen J, Harwood J, Hin V, Irvine LM, Mate BR, McHuron EA, Palacios DM et al. (2019) Anthropogenic disturbance in a changing environment: modelling lifetime reproductive success to predict the consequences of multiple stressors on a migratory population. Oikos 128: 1340–1357.

Pirotta E, Mangel M, Costa DP, Mate B, Goldbogen J, Palacios DM, Huckstadt L, McHuron EA, 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. Am Nat 191: E40–E56.

Pirotta E, New L, Harwood J, Lusseau D (2014) Activities, motivations and disturbance: an agent-based model of bottlenose dolphin behavioral dynamics and interactions with tourism in Doubtful Sound, New Zealand. Ecol Model 282: 44–58.

Potvin J, Goldbogen JA, Shadwick RE (2012) Metabolic expenditures of lung feedingrorquals across scale: implications for the evolution of filter feeding and the limits to maximum body size. PLoS One 7: e44854.

Queiros O, Fromentin J-M, Astruc G, Bauer RK, Saraux C (2018) Dolphin predation pressure on pelagic and demersal fish in the northwestern Mediterranean Sea. Mar Ecol Prog Ser 603: 13–27.

Rechsteiner EU, Rosen DAS, Trites AW (2013) Energy requirements of Pacific white-sided dolphins (Lagenorhynchus obliquidens) as predicted by a bioenergetic model. J Mammal 94: 820–832.

Reed J, Harcourt R, New L, Bilgmann K (2020) Extreme effects of extreme disturbances: a simulation approach to assess population specific responses. Front Mar Sci 7: 1–17.

Reisinger RR, de Bruyn PJN, Bester MN (2011) Predatory impact of killer whales on pinniped and penguin populations at the Subantarctic Prince Edward islands: fact and fiction. J Zool 285: 1–10.

Riekola L, Andrews-Goff V, Friedlaender A, Zerbini AN, Constantine R (2020) Longer migration not necessarily the costliest strategy for migrating humpback whales. Aquat Conserv 30: 937–948.

Rosen DAS, Winship AJ, Hoopes LA (2007) Thermal and digestive constraints to foraging behaviour in marine mammals. Phil Trans R Soc B 362: 2151–2168.

Schneider BH, Flatt WP (1975) The Evaluation of Feeds through Digestibility Experiments. University of Georgia Press, Athens.

Sibly RM, Grimm V, Martin BT, Johnston ASA, Kulakowska K, Topping CJ, Calow P, Nabe-Nielsen J, Thorbek P, Deangelis DL (2013) Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods Ecol Evol 4: 151–161.

Silva WTAF, Harding KC, Marques GM, Bäcklin BM, Sonne C, Dietz R, Kauhala K, Desforges JP (2020) Life cycle bioenergetics of the gray seal (Halichoerus grypus) in the Baltic Sea; population response to environmental stress. Environ Int 145: 106145. https://10.1016/j.envint.2020.106145.

Smout S, Lindstrom U (2007) Multispecies functional response of the minke whale Balaenoptera acutorostrata based on small-scale foraging studies. Mar Ecol Prog Ser 341: 277–291.

Sparling CE, Speakman JR, Fedak MA (2006) Seasonal variation in the metabolic rate and body composition of female grey seals: fat conservation prior to high-cost reproduction in a capital breeder? J Comp Physiol 176: 505–512.

Spitz J, Jouma’a J (2013) Variability in energy density of forage fishes from the Bay of Biscay. J Fish Biol 82: 2147–2152.

Srinivasan M, Swannack TM, Grant WE, Rajan J, Würsig B (2018) To feed or not to feed? Bioenergetic impacts of fear-driven behaviors in lactating dolphins. Ecol Evol 8: 1384–1398.

Stearns SC (1992) The Evolution of Life Histories. Oxford University Press, New York, NY

Stewart JD, Durban JW, Knowlton AR, Lynn MS, Fearnbach H, Barbaro J, Perryman WL, Miller CA, Moore MJ (2021) Decreasing body lengths in North Atlantic right whales. Curr Biol 31: 3174–3179.e3.

Sumich JL (2021) Why Baja? A bioenergetic model for comparing metabolic rates and thermoregulatory costs of gray whale calves (Eschrichtius robustus). Mar Mamm Sci 37: 870–887.

Taylor BL, Martinez M, Gerdette T, Barlow J, Hrovat YN (2007) Lessons from monitoring trends in abundance of marine mammals. Mar Mamm Sci 23: 157–175.

Trites AW, Donnelly CP (2003) The decline of Steller sea lions Eumetopias jubatus in Alaska: a review of the nutritional stress hypothesis. Mamm Rev 33: 3–28.

Trzcinski MK, Mohr N, Bowen WK (2006) Continued decline of an Atlantic cod population: how important is gray seal predation? Ecol Appl 16: 2276–2292.

Udevitz MS, Jay CV, Taylor RL, Fischbach AS, Beatty WS, Noren SR (2017) Forecasting consequences of changing sea ice availability for Pacific walruses. Ecosphere 8: e02014. https://doi.org/10.1002/ecs2.2014.
Villegas-Amtmann S, Schwarz LK, Gailey G, Sychenko O, Costa DP (2017) East or west: the energetic cost of being a gray whale and the consequence of losing energy to disturbance. *Endanger Species Res* 34: 167–183.

Villegas-Amtmann S, Schwarz LK, Sumich JL, Costa DP (2015) A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere* 6: 1–19.

Weise MJ, Harvey JT (2008) Temporal variability in ocean climate and California Sea lion diet and biomass consumption: implications for fisheries management. *Mar Ecol Prog Ser* 373: 157–172.

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84: 1083–1100.

Wiedenmann J, Cresswell KA, Goldbogen J, Potvin J, Mangel M (2011) Exploring the effects of reductions in krill biomass in the Southern Ocean on blue whales using a state-dependent foraging model. *Ecol Model* 222: 3366–3379.

Williams R, Lusseau D, Hammond PS (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol Conserv* 133: 301–311.

Williams TM (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Phil Trans R Soc Lond B* 354: 193–201.

Williams TM, Estes JA, Doak DF, Springer AM (2004) Killer appetites: assessing the role of predators in ecological communities. *Ecology* 85: 3373–3384.

Williams TM, Kendall TL, Richter BP, Ribeiro-French CR, John JS, Odell KL, Losch BA, Feuerbach DA, Stamper MA (2017) Swimming and diving energetics in dolphins: a stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes. *J Exp Biol* 220: 1135–1145.

Winship AJ, Trites AW, Rosen DAS (2002) A bioenergetic model for estimating the food requirements of Steller Sea lions *Eumetopias jubatus* in Alaska, USA. *Mar Ecol Prog Ser* 229: 291–312.

Worthy G (2001) *Nutrition and Energetics*. In *CRC Handbook of Marine Mammal Medicine*. CRC Press, Boca Raton, Florida.

Worthy GAJ, Lavigne DM (1987) Mass loss, metabolic rate, and energy utilization by harp and gray seal pups during the postweaning fast. *Physiol Zool* 60: 352–364.