Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*

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ABSTRACT

The bottlenose dolphin (*Tursiops truncatus*) is a common species in coastal temperate waters and the ideal candidate for developing a conceptual bioenergetic model given that sufficient information is available to parameterize key input variables. A bioenergetic model was developed to estimate annual energy requirements (MJ/year) and prey biomass consumption (t/year) based on model variations of Field Metabolic Rates (FMR) that included percent of body mass ($FMR_{BodyMass}$), Kleiber's scaling equation ($FMR_{Kleiber}$), and measured FMRs ($FMR_{Measured}$). Bioenergetic requirements were generated by incorporating the intrinsic uncertainty of input model variables based on assumed or data-driven assignments of sampling distributions. Gompertz growth functions were used to generate body lengths (cm) as a function of age, which once converted to body mass (kg), were used in all calculations. Annual bioenergetic estimates differed across model variations ($FMR_{Measured} > FMR_{Kleiber} > FMR_{Body\,Mass}$) and were on average 22%–34% higher in female calves than in male calves, 3%–7% higher in subadult/immature females than in males, and 12%–18% higher in adult males than in non-lactating adult females. Average estimates were ~72% and 31%–34% higher in lactating adult females compared to non-lactating adult females and adult males, respectively. Annual bioenergetic requirements for ≥2 year old dolphins normalized by body mass were $FMR_{Measured}$: 205 ± 29 MJ/kg/year and 34 ± 5 kg/kg/year, $FMR_{Kleiber}$: 151 ± 29 MJ/kg/year and 22 ± 5 kg/kg/year, and $FMR_{BodyMass}$: 138 ± 38 MJ/kg/year and 20 ± 5 kg/kg/year. When applying the bioenergetic model to the US bottlenose dolphin stock with the largest dolphin abundance (n = 950), estimates of annual bioenergetic requirements were 2040–3050 MJ*10^4/year and 2900–5070 t/year. While the existing information provides the foundation to develop a bioenergetic model specific for bottlenose dolphins, improvements of this and related models require additional data on field measurements of metabolic rates, cost of lactation, caloric intake and metabolization efficiency. This bioenergetic model could be used to better understand the complex ecological and trophic interactions of bottlenose dolphins with their prey populations, to evaluate the role of disturbance on bioenergetic requirements, and to inform management and conservation efforts.

1. Introduction

As endotherms, marine mammals have an energetically expensive lifestyle (Costa, 2009; Williams et al., 2001). These high energy requirements, coupled with their role as apex predators, result in marine mammals having a disproportionate effect on the structure of marine communities (Estes et al., 2011; Roman et al., 2014; Williams et al., 2004). As a result, there is increased competition for commercially and recreationally important resources bringing them into conflict with humans (Matthiopoulos et al., 2008; Yodzis, 2001). Bioenergetic models that integrate current knowledge of marine mammal bioenergetics could be vital in informing effective management and conservation strategies for both marine mammals and their prey. These models have proven useful in assessments of the potential impact of disturbance on foraging behavior (NAS, 2005, 2016; New et al., 2014), but a significant issue

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is determining if a disturbance has sufficient biological significance to cause changes in the vital rates and fitness of a population. Bioenergetic models that include costs of reproduction are being used to predict what level and duration of a disturbance is sufficient to cause changes in foraging behavior that result in reduced reproduction and survival (Christiansen et al., 2014; New et al., 2014; New et al., 2013a,b; Villegas-Amtmann et al., 2015; Williams et al., 2006).

The majority of studies of marine mammal bioenergetics have been carried out with pinnipeds and sea otters because they are tractable animals and are conducive for a variety of laboratory and field measurements (Costa, 2008; Dalton et al., 2015; Hurley and Costa, 2001; Maresh et al., 2014; Rosen et al., 2016; Thometz et al., 2016b; Thometz et al., 2014; Williams et al., 2007; Yeates et al., 2007). While a few empirical measurements of energy expenditure have been made with cetaceans (Holt et al., 2015; Williams et al., 1996; Williams et al., 1993), quantification of feeding requirements, energetic needs and prey consumption has predominantly relied on extrapolation from the Kleiber curve for basal metabolic rate (BMR) of terrestrial mammals (Kleiber, 1975; Leaper and Lavigne, 2007; Lockyer, 2007; New et al., 2013b). However, many marine mammals, including cetaceans, have a BMR higher than predicted (Williams et al., 2001). As BMR only accounts for metabolic costs of animals that are resting, in their thermoneutral zone, and postabsorptive state, an adjustment must be made to account for higher metabolic requirements associated with the cost of free-existence (e.g., feeding, locomotion, growth, etc.), which is often referred to as Field Metabolic Rate or FMR (Costa and Williams, 1999; Costa, 2008, 2009). FMR is dynamic and changes as metabolic requirements are influenced by climate-driven factors (e.g., changes in water temperature) and seasonal fluctuations in the abundance and availability of prey (Costa, 2008; Costa et al., 2013). However, it serves as an indicator of the basic bioenergetic requirements of a marine mammal during normal environmental conditions.

While bottlenose dolphins (*Tursiops truncatus*), which are among the most common cetaceans in coastal temperate waters, are arguably the best studied cetaceans in terms of social behavior, echolocation, bioacoustics, learning, ecology and population dynamics, there is surprisingly little information on their bioenergetic requirements. Prior energetics research has focused on their nutritional needs (Cockcroft and Ross, 1990; Geraci, 1981; Kastelein et al., 2003; Kastelein et al., 2002; Reddy et al., 1994; Sergeant, 1969; Shapunov, 1973), diet (Barros, 1993; Barros and Odell, 1990; Barros and Wells, 1998; Berens McCabe et al., 2010; Bowen, 2011; Gannon and Waples, 2004; Wells et al., 2013), and measurements of metabolic rates and physiological capabilities (Meagher et al., 2002; Williams et al., 2001; Yazdi et al., 1999; Yeates and Houser, 2008) along with FMR measurements of animals in the wild (Costa et al., 2013). Taken together, these and related studies provide a solid basis to develop a conceptual bioenergetic model for bottlenose dolphins. This species is the ideal candidate for developing a bioenergetic model because their biology and ecology is relatively well understood when compared to other cetaceans, and could serve as a surrogate for understanding the link between disturbance, and energy expenditures and feeding opportunities in other marine mammal species. These efforts could also highlight the type of information needed to reduce uncertainty of existing models, and guide the prioritization of data collection particularly for marine mammal species for which there is much less information available to develop species-specific bioenergetic models.

The bioenergetic model developed for bottlenose dolphins followed a general framework proposed for marine mammals (Costa, 2009), and it is based on the concept that ingested energy through prey consumption results in energy allocation for maintenance expenditures, after adjustments for energy losses through fecal and urinary energy losses. Energy expenditures or bioenergetic requirements are based on a power function of body mass adjusted to account for the higher metabolic requirements (FMR) of free-living animals, with higher energetic requirements imposed by physiological processes (e.g., lactation). When considering a management or conservation action, decision makers require some sense of the certainty associated with a model prediction. This can be accomplished by developing a model that integrates information on the underlying uncertainties or sampling distribution of each input variable. Consequently, the purpose of this research was to use empirical data from the literature to develop a bioenergetic model specific for bottlenose dolphins, while integrating input variable uncertainty in model outputs. In the current study, three variations for estimating FMR are used and contrasted, with bioenergetic outputs summarized as annual energy requirements and prey biomass consumption.

2. Materials and methods

Three variations of the same model were used to estimate the bioenergetic requirements of bottlenose dolphins. The first variation of FMR (hereafter $FMR_{BodyMass}$) did not use the body mass power function, but used estimates of bioenergetic requirements (kg/d) as the percent of body mass consumed on a daily basis based on data from delphinids under human care (mostly bottlenose dolphins; range 2–12%) (Barros and Odell, 1995; Barros, 1993; Cockcroft and Ross, 1990; Kastelein et al., 2003; Kastelein et al., 2002; Sergeant, 1969). This model variation was included as it provides a lower estimate of bioenergetic requirements, which in animals under human care are expected to be lower than that of wild animals due to lower activity levels (Kastelein et al., 2002).

The second variation of FMR (hereafter $FMR_{Kleiber}$) was based on Kleiber's scaling equation defined by $BMR = 0.293 * BM^{0.75}$ (Kleiber, 1975) where BMR is the basal metabolic rate (mega joules per day; MJ/d) and BM is the body mass (kg). BMR was adjusted upwards using a multiplier ranging between 3 and 6 to account for much higher FMRs of bottlenose dolphins (Costa, 2002; Costa and Williams, 1999; Croll et al., 2006).

The third variation of FMR (hereafter $FMR_{Measured}$) was based on measured daily FMR of bottlenose dolphins during the summer (four non-lactating females and six males) and winter (four males) (Costa, pers. obs.), defined by $FMR_{Summer} = 0.59 \pm 0.10$ MJ/kg and $FMR_{Winter} = 0.42 \pm 0.07$ MJ/kg. Spring and fall FMRs were estimated as the average between FMR_{Summer} and FMR_{Winter}. This assumption is supported by empirical data showing that metabolic requirements of resting bottlenose dolphins are higher at water temperature extremes (Williams et al., 2001), and that spring and fall blubber thickness, at least in large cetaceans, is comparable to the average between summer and winter (Williams et al., 2013).

To incorporate uncertainty of each input variable, data were randomly sampled from an assumed distribution, or from a data-driven sampling distribution closely resembling the distribution of the original observations. An initial examination of the sampling distribution of each input variable was performed graphically (Cullen and Frey, 1999), followed by the selection of the distribution with the best fit (D'Agostino and Stephens, 1986) via goodness-of-fit statistics (e.g., Anderson-Darling) and criteria (i.e., Aikake's Information Criterion and Bayesian Information Criterion). All analyses were performed using R (Delignette-Muller and Dutang, 2015; R Development Core Team, 2015; Venables and Ripley, 2002).

2.1. Bottlenose dolphin growth curves

Bioenergetic requirements vary as a function of body mass, which is a function of body length and age. Data on the relationship between age (year) and standard body length (cm) for female and