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

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 predominately 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 require-

ments 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

male bottlenose dolphins were extracted from different sources (Fernandez and Hohn, 1998; Hohn et al., 1989; Mattson et al., 2006; McFee et al., 2010; Read et al., 1993; Stolen et al., 2002) and used to develop growth curves, following the standard Gompertz equation of the form TL = A*exp (-b*k^y), where TL represents the estimated total body length (cm), A is the asymptotic value, b is the constant of integration, k is the intrinsic growth rate constant, and y is age (years).

The age (years) of 2000 females and males, each, were randomly generated within the age range of reported values for each sex. Non-parametric bootstrapping was used to resample each fitting parameter from the Gompertz equation for females and males, which were used to calculate body lengths (cm). All body lengths were converted to body mass (kg) using the equations $BM_{Females} = 10^{-4.29}*TL^{2.73}$ and $BM_{Males} = 10^{-5.40}*TL^{3.20}$ (Hart et al., 2013) where BM is the body mass (kg) and TL the total body length (cm). These equations yielded comparable results (values within ±10% of each other) to other commonly used length-mass relationships for bottlenose dolphins (Barros, 1993). Body mass was then used to estimate the energy requirement and prey biomass consumption of females and males dolphins.

2.2. Adjustments to the bioenergetic model

Calculations of energy requirements based on FMR variations were made taking into account the body mass (kg) of each modeled dolphin. However, for bottlenose dolphins between 1 and 2 years of age, only the fraction of body mass that depends on the caloric intake from fish, and not milk, was used in these calculations. This fraction was estimated from a linear function between body mass and age, under the assumptions that 1 year old dolphins are entirely dependent on milk (100% milk dependency), whereas 2 year olds are completely independent and capable of surviving on their own (0% milk dependency) (Wells, per. obs.).

Lactating females typically have the highest energy demands of any demographic group within their species, and often have nutrient requirements that differ from non-lactating females and males. While direct measures of the increased energy intake required to support lactation are not available, studies have reported greater food requirements of lactating versus non-lactating dolphins (Cheal and Gales, 1991; Cockcroft and Ross, 1990; Kastelein et al., 2003; Kastelein et al., 2002), which were used to create a multiplier for the increased cost of lactation (range 0.48–0.86) for adult females ≥9 years of age. These values are consistent with the lactating demands of female odontocetes, which are approximately 50% higher during lactation than during pregnancy (Whitehead and Mann, 2000). In the current study, pregnant females were not included as it is anticipated that their bioenergetic requirements are slightly higher, but somewhat comparable to those of adult females (Costa, 2002; Costa, 2009; Kastelein et al., 2002). This assumption is further supported by documented increases in food intake of pregnant bottlenose dolphin females just prior to parturition (Reddy et al., 1994).

Bioenergetic requirements also included an adjustment for the fraction of food energy that remains after energy losses through faces and urine, or metabolic efficiency. Data for cetaceans on digested or assimilated food energy remaining after fecal losses include studies with minke whales feeding on krill (93%) (Mårtensson et al., 1994) and bottlenose dolphins feeding mostly on fish (89%–96%) (Reddy et al., 1994), which are comparable to the ranges measured on pinnipeds (73–98%) for a fish diet (Costa, 2002; Costa and Williams, 1999; Lawson et al., 1997; Leaper and Lavigne, 2007; Mårtensson et al., 1994; Rosen and Trites, 2000; Worthy, 2001). Urinary energy loss of nitrogen as urea for pinnipeds ranges from 7% to 10% (Fisher et al., 1992; Keiver et al., 1984; Ronald et al., 1984), which were used to adjust the assimilated food energy to obtain the metabolic efficiency (range 0.78–0.92).

2.3. Diet composition and caloric content of prey

Bioenergetic model outputs were used to estimate the total daily caloric content (MJ/kg) and daily biomass consumption (kg) after accounting for the relative contribution of key prey species and their caloric content to the diet of bottlenose dolphins. Given the plasticity in the diet of bottlenose dolphins, a generic diet was reconstructed from studies primarily with coastal dolphins from the Indian River Lagoon, FL (Barros, 1993; Barros and Odell, 1990; Worthy et al., 2008), Sarasota Bay, FL (Barros and Wells, 1998; Berens McCabe et al., 2010; Wells et al., 2013), the Florida panhandle (Bowen, 2011), and North Carolina (Gannon and Waples, 2004). Based on the reported numerical abundance, the mean and standard deviation proportions of each prey item in the diet of bottlenose dolphins were calculated for the most commonly reported species across studies. This generic diet was comprised of Atlantic croaker (*Micropogonias undulates*), grunts (*Haemulon plumieri, H. sciurus, Haemulon* sp.), pigfish (*Orthopristis chrysoptera*), pinfish (*Lagodon rhomboides*), seatrout (*Cynoscion arenarius, C. nebulosus, C. regalis, Cynoscion* spp.), silver perch (*Bairdiella chrysoura*), spot (*Leiostomus xanthurus*), squid (Loliginidae, *Lolliguncula brevis*), toadfish (*Opsanus beta, O. tau*), and other prey items (invertebrates and other less common fish prey species). While studies have documented spatial, seasonal and ontogenetic changes in the diet composition of coastal dolphins (Barros, 1993; Barros and Odell, 1990; Gannon and Waples, 2004; Worthy et al., 2008), it is assumed that diet was spatially and seasonally constant, and identical regardless of age or sex. Assignments of the relative contribution of each key prey species to the overall diet of individual modeled bottlenose dolphins were made with the sum of all prey accounting for 100% of the total daily diet.

The caloric content (MJ/kg wet weight) of key prey species was compiled across multiple studies (Barros, 1993; de Mutsert, 2010; Korzhova, 1969; Lindberg et al., 2002; McKinnon, 1994; Mollet et al., 2002; Pettitt-Wade et al., 2011; Worthy et al., 2008), and where appropriate, conversions were made from protein and lipid to caloric content (Brett and Groves, 1979), and from dry to wet weights assuming a 75% moisture content. The caloric content of key prey species was verified against calorimetric measurements of representative prey samples (n = 158; Wells, unpublished data) from Sarasota Bay, FL.

For ease of comparisons, all estimates of total daily caloric content and prey biomass consumption were converted to annual estimates and reported as MJ and metric tons (t), respectively. The above described approach is summarized in Fig. 1.

2.4. Uncertainty and sensitivity analysis

An uncertainty analysis was performed to determine the contribution of each input variable to the overall model uncertainty (variance). Input variables with assigned sampling distributions (assumed or data-driven) were set to a nominal value (i.e., mean), while randomly resampling all remaining variables from their respective sampling distributions. Comparisons of model output variance from uncertainty analyses were made relative to the original model (i.e., uncertainty in all variables). A sensitivity analysis was also performed to assess the sensitivity of model outputs to changes in each input variable. Input variables with assigned sampling distributions (assumed or data-driven) were set to a nominal value (i.e., mean), and allowed to increase or decrease by 10% of this nominal value, one variable at a time. Comparisons of model outputs from sensitivity analyses were made relative to the original
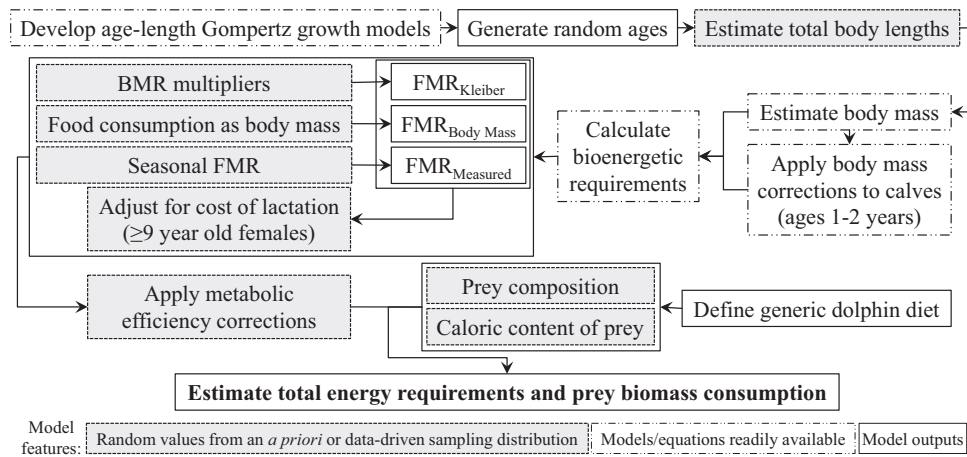
Fig. 1. Diagram summarizing the information and model input variables used to develop a bioenergetic model for estimating energy requirements and prey biomass consumption of bottlenose dolphins.
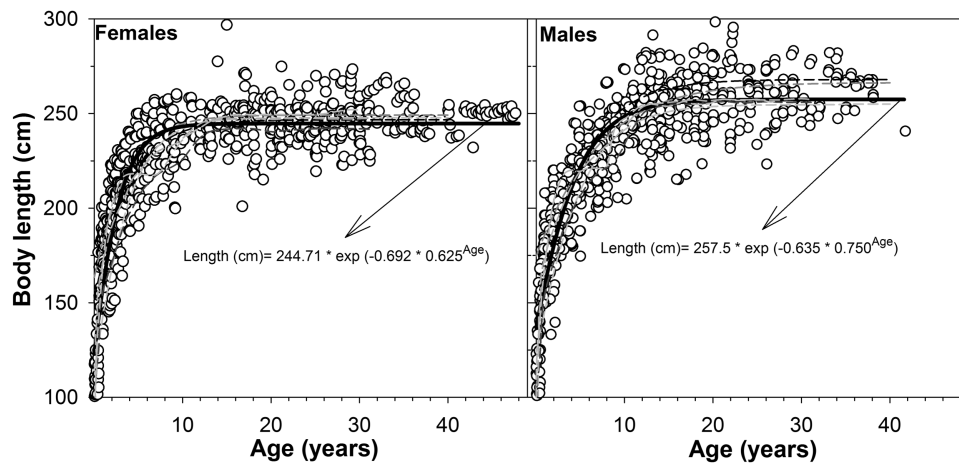

Fig. 2. Gompertz growth models for female (left) and male (right) bottlenose dolphins based on data (females n = 689, males n = 723) from several sources (Fernandez and Hohn, 1998; Hohn et al., 1989; Mattson et al., 2006; McFee et al., 2010; Read et al., 1993; Stolen et al., 2002). The solid line represents the fitted model of the current study, while dashed lines represent previously reported models (Fernandez and Hohn, 1998; Mattson et al., 2006; McFee et al., 2010; Read et al., 1993; Stolen et al., 2002).

model (i.e., all variables set to a nominal value). Both uncertainty and sensitivity analyses were only performed for lactating females.

2.5. Practical application

To demonstrate the practical application of the bioenergetic model, annual energy requirements and prey biomass consumption were estimated for selected US bottlenose dolphin stocks, using best estimates of dolphin abundance by stock (N_{best}) from stock assessments (bay, sound and estuaries only) (NMFS, 2016). Age and sex assignments to N_{best} were needed to estimate representative bioenergetic requirements of each stock. Although the age and sex distribution likely change in space and time, for the purpose of these calculations, it was assumed that the age class and sex distribution within each stock followed that of the relatively well-studied Sarasota Bay stock. The proportion of known age and sex of resident dolphins (averaged over 1993–2012) in Sarasota Bay are as follows: calf females and males (≤3 years old): 0.136 and 0.079, respectively; subadult/immature females and males (4–8 years old): 0.078 and 0.08, respectively; non-lactating adult female and adult male (≥9 years old): 0.198 and 0.285, respectively; and lactating females (≥9 years old): 0.14 (equivalent to 2/3 of all calves) (Wells, pers. obs.).

3. Results

3.1. Bottlenose dolphin growth models

Despite the fact that data sources used to develop growth models encompassed several geographical locations (i.e., Indian River Lagoon and Sarasota Bay- Florida, Mississippi, South Carolina and Texas) with known variability in population morphometrics, there appear to be remarkable similarities in growth patterns across locations. Gompertz growth models for females and males developed in the current study fit the data well (based on non-linear regression diagnostic analyses via residuals), and were in general agreement with previously published models (Fernandez and Hohn, 1998; Mattson et al., 2006; McFee et al., 2010; Read et al., 1993; Stolen et al., 2002) (Fig. 2). These models showed a clear dimorphism in growth rates (0.625 and 0.750 intrinsic growth rate constant for females and males, respectively), with asymptotic body lengths of females and males occurring at 11.8 and 17.8 years old, corresponding to a body length of 244 cm and 256 cm, respectively. Once both sexes reach this asymptote, males are generally 12.6 cm longer and 36 kg heavier than females.

Based on these revised Gompertz growth models, as well as on length conversions to body mass (Hart et al., 2013), the range of ages, total body length and body mass of females and

Table 1

Sampling distributions of input variables based on assumed or data-driven assignments, including a qualitative assessment of their uncertainty. Symbols: Normal distribution: mean = μ, standard deviation = σ; Log-normal distribution: log-mean = log-μ, log- standard deviation = log-σ; Logistic distribution: location = μ, scale = s; Beta distribution: daphe1 = s1, shape2 = s2.

Variable [Sources]	Sampling distribution Assumptions (parameters) Transformations	Uncertainty
Feeding as% of body mass [1]	Logistic (μ= 0.72, s = 0.017) [t1]	High
BMR multipliers [2]	Uniform (min = 3, max = 6)	Moderate
Field metabolic rate (MJ/kg) [3]		
Summer	Normal (μ= 0.59, σ= 0.10)	Moderate
Winter	Normal (μ= 0.41, σ= 0.07)	
Cost of lactation, adult female [4]	Normal[a] (μ= 0.71, σ= 0.15)	High
Diet composition [5]		
Atlantic croaker	Normal[a] (μ= 0.11, σ= 0.08)	Moderate
Grunt	Normal[a] (μ= 0.11, σ= 0.08)	
Pigfish	Normal[a] (μ= 0.06, σ= 0.09)	
Pinfish	Normal[a] (μ= 0.07, σ= 0.09)	
Seatrout	Normal[a] (μ= 0.08, σ= 0.11)	
Silver perch	Normal[a] (μ= 0.12, σ= 0.10)	
Spot	Normal[a] (μ= 0.10, σ= 0.07)	
Squid	Normal[a] (μ= 0.07, σ= 0.02)	
Toadfish	Normal[a] (μ= 0.13, σ= 0.10)	
Caloric content (MJ/kg wet weight) of prey or related species [6]		
Atlantic croaker	Logistic (μ= 5.9E + 08, s = 1.1E + 08) [t1]	Moderate
Grunt	Logistic (μ= 4.33, s = 0.21)	
Pigfish	Logistic (μ= 6.1E + 08, s = 2.5E + 08) [t1]	
Pinfish	Logistic (μ= 4.4E + 08, s = 1.2E + 08) [t1]	
Seatrout	Logistic (μ= 3.6E + 13, s = 4.7E + 12) [t2]	
Silver perch	Normal (μ= 2.2E + 13, σ= 5.6E + 12) [t2]	
Spot	Log-normal (log-μ= 1.96, log-σ= 0.11)	
Squid	Normal (μ= 3.93, σ= 0.61)	
Toadfish	Logistic (μ= 8.07, s = 0.05)	
Other [d]	Logistic (μ= 6.0E + 08, s = 1.5E + 08) [t1]	
Metabolic efficiency [7]	Beta (s1 = 43.60, s2 = 5.71)	Moderate

Data sources: [1] Based on data from animals under human care – (Barros, 1993; Barros and Odell, 1990; Kastelein et al., 2003; Kastelein et al., 2002; Sergeant, 1969; Shapunov, 1973; Spotte and Babus, 1980); [2] (Costa, 2002; Costa and Williams, 1999; Croll et al., 2006); [3] (Costa et al., 2013); [4] Based on data from animals under human care – (Cheal and Gales, 1991; Cockcroft and Ross, 1990; Kastelein et al., 2003; Kastelein et al., 2002); [5] (Barros, 1993; Barros and Odell, 1990; Berens McCabe et al., 2010; Bowen, 2011; Gannon and Waples, 2004; Wells et al., 2013; Worthy et al., 2008); [6] Primarily from Worthy et al. (2008), using lipid and protein conversions [8.7 and 5.7, respectively] from Brett and Groves (1979), and augment from additional data sources (Barros, 1993; de Mutsert, 2010; Korzhova, 1969; Lindberg et al., 2002; McKinnon, 1994; Mollet et al., 2002; Pettitt-Wade et al., 2011); [7] Based on data for cetaceans and pinnipeds- (Costa, 2002; Costa and Williams, 1999; Fisher et al., 1992; Keiver et al., 1984; Lawson et al., 1997; Leaper and Lavigne, 2007; Lockyer, 1981; Mårtensson et al., 1994; Reddy et al., 1994; Ronald et al., 1984; Rosen and Trites, 2000; Worthy, 2001). Sampling distribution information: [a] Assumed distribution given data limitations; Outputs requiring back-transformation: [t1] 1̂/10 back transformation; [t2] 1̂/15 back transformation. Diet information: [d] Includes crustaceans (shrimp, crabs), mullets, kingfish, drums, etc.

males used in bioenergetic estimates were as follows: females-1.2–48 years, 163–247 cm, 11–175 kg; and males- 1.2–42 years, 163–261 cm, 10–214 kg. The average total body length and body mass of non-lactating adult female and adult male (≥9 years old), which comprised 81% of all modeled dolphins, were: females-28 ± 11 years, 245 ± 1 cm, 170 ± 2 kg; and males- 25 ± 10 years, 256 ± 3 cm, 203 ± 7 kg.

3.2. Sampling distributions of input variables

Sampling distributions were defined based on either assumptions about the distributions of input variables, or driven by the distributions of the original observations. The general characteristics of the sampling distributions (assumed or data-driven) for key input variables (Table 1; see Supplementary Information A, Figure SA.1 for details) were as follows: 1) normal distributions were assumed for variables for which there were insufficient data for assignments of a specific sampling distribution (i.e., prey composition in diet), or used for variables that are symmetrical around the mean (i.e., FMR, cost of lactation); 2) log-normal distributions were used for right-skewed variables with a lower limit of zero and no upper bound (i.e., caloric content of spot); 3) logistic distributions were used for variables that are symmetric around the mean,

but with longer tail-end distributions than the normal distribution (i.e., caloric content of most prey species); 4) uniform distributions were used for variables with an upper and lower limit, where sampling probabilities are constant between the limits (i.e., BMR adjustment); and 5) beta distributions were used for left-skewed variables with upper and lower bound (i.e., metabolic efficiency).

Average values of input variables (hereafter, modifiers) were as follows: food consumption as a percent of body mass $(FMR_{BodyMass})$ = 4.05 ± 1.85%, FMR adjustments $(FMR_{Kleiber})$ = 4.5 ± 0.86, and seasonal metabolic rates $FMR_{Measured}$: Summer = 0.59 ± 0.10 (MJ/d/kg), Winter = 0.41 ± 0.07 (MJ/d/kg), Spring and Fall = 0.50 ± 0.12 (MJ/d/kg). Average values for cost of lactation were 0.69 ± 0.10 (proportion of added energetic requirement), while for metabolic efficiency were 0.87 ± 0.03 (proportion of metabolized food). The relative contribution of each prey species (or groups of closely related species) to the overall generic diet was as follows: other prey (0.14 ± 0.11), toadfish (0.12 ± 0.07), silver perch (0.11 ± 0.07), grunts (0.10 ± 0.06), Atlantic croaker (0.10 ± 0.06), spot (0.09 ± 0.06), seatrout (0.09 ± 0.06), pigfish (0.09 ± 0.06), pinfish (0.08 ± 0.06) and squid (0.07 ± 0.02). Although there are differences in the caloric content (wet weight) across prey species, there is relatively little variation within species. The species with higher average caloric contents were toadfish

Table 2
Bioenergetic requirements across model variations by age class: female and male calves (≤3 years old), subadult/immature females and males (4–8 years old), non-lactating adult females, adult males (≥9 years old), and lactating females (≥9 years old). Estimates for non-lactating females and males of all ages are included as a comparison. Values represent the mean and standard deviation of model outputs CR: caloric requirements (MJ*10^3/year), and PB: prey biomass consumption (t/year).

Age class	$FMR_{BodyMass}$		$FMR_{Kleiber}$		$FMR_{Measured}$	
	CR	PB	CR	PB	CR	PB
Female calf	9.9 ± 4.99	1.41 ± 0.72	12.73 ± 5.47	1.93 ± 0.86	14.95 ± 7.07	2.49 ± 1.22
Male calf	6.79 ± 4.53	0.97 ± 0.65	9.94 ± 5.72	1.5 ± 0.87	10.03 ± 6.19	1.65 ± 1.03
Subadult/immature females	21 ± 5.77	2.98 ± 0.8	23.03 ± 4.45	3.46 ± 0.69	31.19 ± 4.81	5.12 ± 0.89
Subadult/immature males	19.94 ± 5.9	2.83 ± 0.85	22.29 ± 4.46	3.34 ± 0.68	28.94 ± 5.21	4.76 ± 0.95
Non-lactating adult females	23.49 ± 6.2	3.35 ± 0.87	25.55 ± 4.95	3.86 ± 0.77	34.92 ± 4.92	5.77 ± 0.88
Lactating females	40.07 ± 10.9	5.71 ± 1.53	43.57 ± 9.04	6.58 ± 1.42	59.62 ± 9.2	9.84 ± 1.65
Adult males	27.68 ± 7.85	3.95 ± 1.11	28.72 ± 6.08	4.34 ± 0.96	41.13 ± 6.96	6.76 ± 1.23
Non-lactating females (all ages)	22.76 ± 6.68	3.24 ± 0.94	24.84 ± 5.53	3.75 ± 0.86	33.83 ± 6.34	5.59 ± 1.1
Males (all ages)	40.07 ± 10.9	5.71 ± 1.54	43.57 ± 9.04	6.58 ± 1.42	59.62 ± 9.2	9.84 ± 1.65

Table 3
Sex-specific (F = non-lactating females, M = males) Gompertz parameters of annual energy requirements and prey biomass consumption of bottlenose dolphins as a function of age (ln(years)) described by standard Gompertz growth models. Parameters include: A = asymptotic value, b = constant of integration, and k = intrinsic rate of change constant.

Gompertz parameters	Energy requirements (MJ/year)			Prey biomass consumption (kg/year)		
	$FMR_{BodyMass}$	$FMR_{Kleiber}$	$FMR_{Measured}$	$FMR_{BodyMass}$	$FMR_{Kleiber}$	$FMR_{Measured}$
A_F	23,823	25,970	35,460	3381	3925	5867
b_F	3.379	2.715	3.470	3.403	2.702	3.518
k_F	0.158	0.158	0.152	0.156	0.159	0.146
A_M	29,915	30,760	45,092	4263	4656	7360
b_M	3.973	2.674	3.81	3.966	2.667	3.845
k_M	0.253	0.277	0.270	0.254	0.279	0.264

(8.07 ± 0.1 MJ/kg) and seatrout (8 ± 0.14 MJ/kg), followed by silver perch (7.73 ± 0.15 MJ/kg), Atlantic croaker (7.49 ± 0.31 MJ/kg), pigfish (7.49 ± 0.57 MJ/kg), other prey (7.48 ± 0.4 MJ/kg), pinfish (7.26 ± 0.4 MJ/kg) and spot (7.18 ± 0.79 MJ/kg), while those with lower caloric contents were grunts (4.33 ± 0.37 MJ/kg) and squid (3.94 ± 0.53 MJ/kg).

3.3. Estimates of energy content and prey biomass consumption

Estimates of bioenergetic requirements were higher for $FMR_{Measured}$ followed by $FMR_{Kleiber}$, and in all cases higher than those based on Kleiber's scaling equation (Supplementary Information A, Figure SA.2). Regardless of model variation, there is great variability in estimates of bioenergetic requirements for individuals of the same age, resulting from the introduction of input variable uncertainty (Fig. 3). Mean annual bioenergetic requirement estimates were consistently higher for lactating females than for males and females (all ages combined; 1.75 times higher than females, and 1.54–1.60 times higher than males), with males having slightly higher estimates (1.11–1.14 times higher) than females. Given that bioenergetics are driven by body mass, estimates of annual energy requirements and prey biomass consumption varied across age classes (Table 2). Average estimates were 22%–34% higher in female calves compared to male calves, but only 3%-7% higher in subadult/immature females compared to males. Higher estimates for female calves were the result of their slightly higher growth rates when compared to male calves of the same age. In contrast, average estimates were 12%–18% higher in adult males compared to non-lactating adult females. Similarly, average estimates were ~70% and 31%–34% higher in lactating adult females compared to non-lactating adult females and adult males, respectively.

Bioenergetic estimates for non-lactating females and males followed a standard Gompertz equation of the form $BR_{Annual} = A^*exp(-b^*k^y)$, where BR represents the estimated annual bioenergetic requirements (MJ/year or kg/year), A is the asymptotic value, b is the constant of integration, k is the intrinsic rate of change constant, and y is age (ln(years)) (Table 3). Intrinsic rates of change

were higher for males than for non-lactating females, reflecting higher bioenergetic requirements of adult males. Consistent with previous discussions, asymptotic annual energy requirements and prey biomass consumption were higher for $FMR_{Measured}$, followed by $FMR_{Kleiber}$ and $FMR_{BodyMass}$, and higher for males than for non-lactating females. Once both sexes reach this asymptote, males have on average 16–21% higher bioenergetic requirements than non-lactating females of the same age.

Annual energy requirements and prey biomass consumption normalized by body mass for dolphins that do not depend on milk (≥2 years) and excluding lactating females were as follows: $FMR_{Measured}$: 205 ± 29 MJ/kg body mass/year and 34 ± 5 kg/kg body mass/year, $FMR_{Kleiber}$: 151 ± 29 MJ/kg body mass/year and 22 ± 5 kg/kg body mass/year, and $FMR_{BodyMass}$ (138 ± 38 MJ/kg body mass/year and 20 ± 5 kg/kg body mass/year. When compared to other bioenergetic studies primarily with bottlenose dolphins (Barlow et al., 2008; Barros, 1993; Benoit-Bird, 2004; Costa, 2002; Kastelein et al., 2003; Reddy et al., 1994; Williams et al., 2004; Williams et al., 2001; Yazdi et al., 1999), with only one exception (Costa, 2002), most previously published estimates fell within the range of values produced with $FMR_{Kleiber}$ and $FMR_{BodyMass}$, and below the estimates produced with $FMR_{Measured}$ (Fig. 4).

3.4. Sensitivity and uncertainty analysis

Estimates of bioenergetic requirements for lactating females with uncertainty in all variables (base model) were $FMR_{BodyMass}$: 33,950 ± 15,570 MJ/year and 4.83 ± 2.20 t/year, $FMR_{Kleiber}$ 43,080 ± 8790 MJ/year and 6.51 ± 1.39 t/year, and $FMR_{Measured}$ 59,370 ± 8880 MJ/year and 8.97 ± 1.42 t/year. Uncertainty analysis of input variables with assigned sampling distributions indicated that most variables had a relatively small influence over model variance (≤14%), with the exception of modifiers (i.e., $FMR_{BodyMass}$: food consumption as a percent of body mass; $FMR_{Kleiber}$: FMR adjustments; and $FMR_{Measured}$: seasonal metabolic rates), which contributed the most to the overall model variability (Supplementary Information A, Figure SA.3). Cost of lactation had a moderate
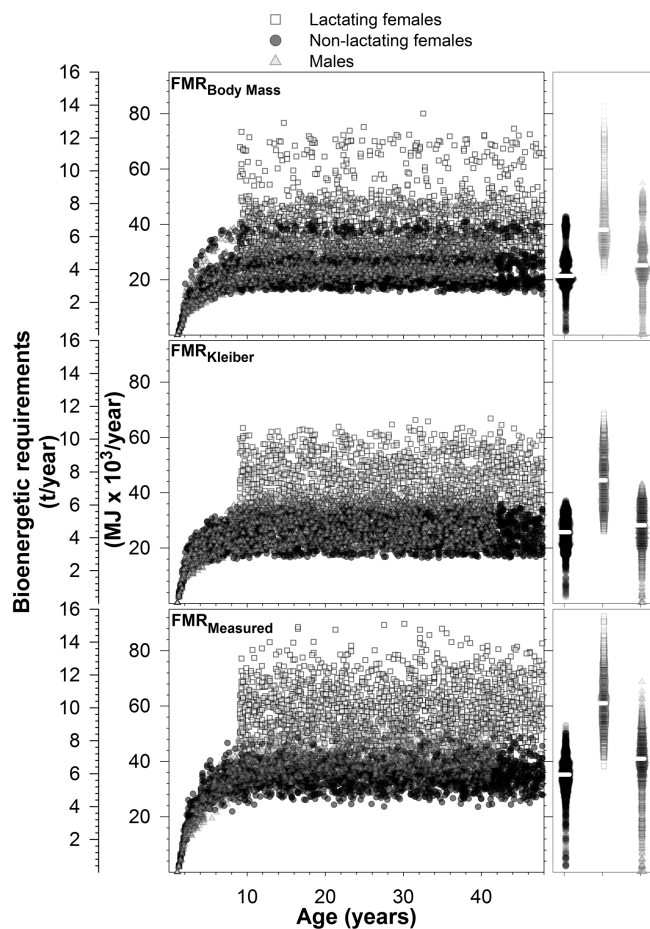
Fig. 3. Left: Annual prey biomass consumption and energy requirements for females, lactating adult females (ages ≥ 9 years) and males as a function of age (years) across model variations. Right: density distribution of annual bioenergetic requirements for the three demographics- length: range of values, width: frequency distribution, horizontal white line: median value. See Table 2 and Supplementary Information B for details.
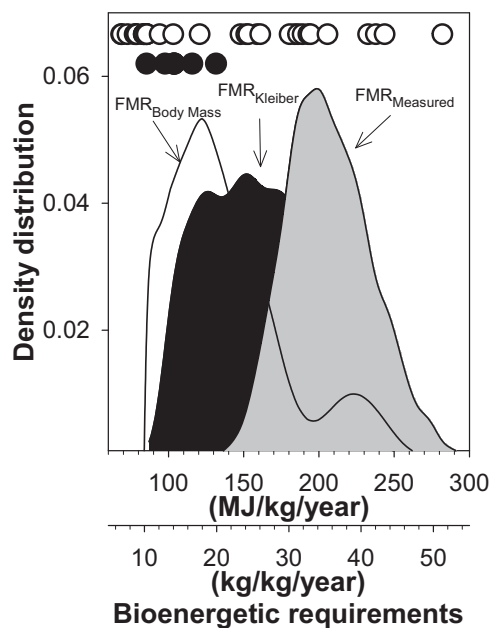

Fig. 4. Comparison of bioenergetic requirements across model variations with those from previous studies. White circles represent estimates based on MJ/kg body mass/year (Barros, 1993; Benoit-Bird, 2004; Costa, 2002; Kastelein et al., 2003; Reddy et al., 1994; Williams et al., 2004; Williams et al., 2001; Yazdi et al., 1999); black circles represent estimates based on kg/kg body mass/year (Barlow et al., 2008; Barros, 1993; Kastelein et al., 2003).

contribution to the overall variance of $FMR_{Kleiber}$ followed by $FMR_{BodyMass}$. Across model variations, $FMR_{Measured}$ appears to be less influenced by input variable uncertainty, with the exception of modifiers.

Estimates of bioenergetic requirements for lactating females with all variables set to a nominal value (base model) were $FMR_{BodyMass}$: $34,500 \pm 170$ MJ/year and 4.93 ± 0.02 t/year, $FMR_{Kleiber}$ $43,790 \pm 130$ MJ/year and 6.62 ± 0.02 t/year, and $FMR_{Measured}$ $60,080 \pm 250$ MJ/year and 9.08 ± 0.04 t/year. Sensitivity analyses showed that when comparisons of estimated bioenergetic requirements were made based on $\pm 10\%$ changes of individual input variables, slightly larger changes in estimates were associated with the caloric content of prey, metabolization efficiency and modifiers. Changes in all other variables resulted in $\leq 4\%$ change of base values (Figure A.3).

3.5. Practical application

Under an assumed age class distribution, annual energy requirements and prey biomass consumption for selected US bottlenose dolphin stocks ranged widely as a function of N_{best}. For example, for the stock with the smallest dolphin abundance (n = 29), energy requirements ranged from 60 to 80 MJ*10^4/year, while prey biomass consumption ranged from 90 to 140 t/year, depending on the model variation. By contrast, for the stock with the largest

dolphin abundance (n = 950), energy requirements ranged from 2040 to 3050 MJ*10^4/year, while annual prey biomass consumption ranged from 2900 to 5070 t/year, depending on model variation (see Supplementary Information A, Table SA.1).

Interpretations of model outputs could also be extended to estimates by individual prey species within the average generic diet (see Supplementary Information A, Figure SA.4). The prey species with greater contributions to the generic diet were the toad-fish, silver perch, grunts and Atlantic croaker. Using $FMR_{Measured}$, estimates of prey biomass consumption for the stock with the largest dolphin abundance were 604 t/year, 562 t/year, 524 t/year and 519 t/year for toadfish, silver perch, grunts and Atlantic croaker, respectively, equivalent to 363 MJ*10^4/year, 338 MJ*10^4/year, 315 MJ*10^4/year and 312 MJ*10^4/year, respectively. By contrast, outputs using $FMR_{Kleiber}$ and $FMR_{BodyMass}$ were substantially smaller (1.5 and 1.7 times smaller, respectively).

Despite differences in estimates of annual bioenergetic requirements across model variations, the wide variability of N_{best} values allowed the development of linear relationships (Fig. 5), which could be used to estimate bioenergetic requirements of stocks not included in these analyses, or of stocks with revised N_{best} values. Further refinements of bioenergetic requirement estimates could be achieved by incorporating stock-specific age class and sex information into the allocation of individuals within N_{best}. Because $FMR_{BodyMass}$ produced estimates primarily derived from information on animals under human care, estimates bounded by $FMR_{Measured}$ and $FMR_{Kleiber}$ are recommended.

4. Discussion

The primary goal of the current study was to develop a bioenergetic model specific for bottlenose dolphins, using information on input variables compiled across published studies. This effort focused on this species because it is a relatively well-studied cetacean that has a worldwide distribution, and is often used as an indicator of environmental health. Thus, this conceptual model
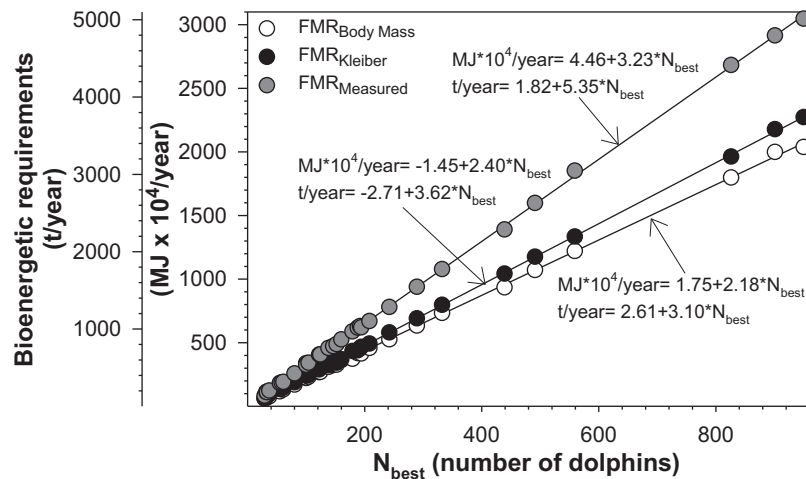
Fig. 5. Estimated annual bioenergetic requirements for selected bottlenose dolphin stocks under an assumed age class distribution. N_{best} = best estimate of dolphin abundance by stock.

could serve as a surrogate for understanding the link between disturbance, and energy expenditures and feeding opportunities in other marine mammal species.

There are several contributions of the current study. The first contribution relates to the revised Gompertz growth models for bottlenose dolphins developed using a large dataset (n = 689 females, n = 723 males) combined across several sources. While previous studies used slightly different approximations of the Gompertz growth model used here (Fernandez and Hohn, 1998; Mattson et al., 2006; McFee et al., 2010; Read et al., 1993; Stolen et al., 2002), model parameters were comparable leading to similar predicted growth curves. For example, asymptotic body lengths obtained with the revised Gompertz growth models were within ±4% of values previously reported. Moreover, the sexual dimorphism of mature female and male dolphins at their asymptotic body lengths reported here confirms similar conclusions with Sarasota Bay dolphins (Read et al., 1993).

While a large body of literature has provided valuable insights and basic knowledge on the bioenergetic requirements of marine mammals, there are substantial gaps in important metrics, but obtaining direct measurements are either challenging or unfeasible. As a result, the second contribution of this work deals with the development of a bioenergetic model that allows for quantitative contrasts across model variations and age classes. It is worth noting that the bioenergetic model showed slightly higher bioenergetic requirements for female calves compared to male calves, while somewhat comparable estimates between subadult/immature females and males. These observations are consistent with previous assessments in Sarasota Bay indicating that female calves grow faster and are slightly larger than male calves of the same age (Read et al., 1993). These findings are also supported by long-term studies noting that females mature socially, physically and sexually earlier than males possibly in response to the evolutionary need of investing in reproduction at an earlier age (Wells, 2003; Wells and Scott, 1999). In addition, higher bioenergetic requirements of adult males (15–21% higher) compared to non-lactating adult females of the same age are also consistent with the size dimorphism of adult dolphins.

Previous studies have indicated that the metabolic requirements of free-living cetaceans are several times higher than those predicted by BMR (Costa, 2002; Costa and Williams, 1999; Costa et al., 2013; Croll et al., 2006). Even while resting, BMRs of bottlenose dolphins were 2.3 times those predicted by scaling equations (Williams et al., 2001), while measured FMR were up

to 7 times the resting metabolic rate (Costa et al., 2013). In the current study, bioenergetic requirements of bottlenose dolphins from $FMR_{BodyMass}$, $FMR_{Kleiber}$ and $FMR_{Measured}$ were 6 ± 3, 6 ± 2, 8 ± 3 higher, respectively, than those predicted by BMR scaling equations. Similarly, bioenergetic estimates based on modifications of BMR that do not account for seasonality or added costs due to physiological processes (e.g., growth, lactation) likely result in the underestimation of bioenergetic requirements of free-ranging dolphins. As a result, when bioenergetic requirements were normalized by body mass, most previously published values (Barlow et al., 2008; Barros, 1993; Benoit-Bird, 2004; Costa, 2002; Kastelein et al., 2003; Reddy et al., 1994; Williams et al., 2004; Williams et al., 2001; Yazdi et al., 1999) were below the estimates produced with $FMR_{Measured}$. Thus, estimates from modifications of BMR or $FMR_{Kleiber}$ that are contextualized to account for seasonal and physiological changes would converge with estimates from $FMR_{Measured}$, but improved model parametrization requires additional field measurements (see below).

The third contribution of this work relates to its practical application, where bioenergetic estimates were obtained for entire bottlenose dolphin stocks. Although estimates could be refined by incorporating stock-specific information, these preliminary assessments provide quantitative bounds on the potential interaction of stocks with fishery resources, and could help inform conservation and management strategies aimed at addressing concerns specific to each stock. These may include efforts that improve the quantity and quality of prey thereby potentially enhancing female fecundity of dolphin populations impacted by catastrophes. For example, studies have documented changes in foraging activity and subsequent increases in bottlenose dolphin density and fecundity with increased food availability and improved quality of shallow vegetated habitats (Eide, 1998; Miller et al., 2010). Similarly, the bioenergetic requirements of specific bottlenose dolphin stocks could be integrated into estimates of the total annual production associated with seagrass beds or saltmarshes, which could be used to quantify the benefit of habitat restoration to these marine mammals.

Model outputs presented here provide initial approximations of the bioenergetic requirements of bottlenose dolphins, with analyses pointing the way for future research that specifically addresses key underlying assumptions. Uncertainty and sensitivity analyses highlighted input variables that have strong effects on model predictions, which require further research. Of all modifiers, seasonal FMR values used in $FMR_{Measured}$ would be of greatest research

priority. Improved knowledge on FMR and additional field measurements as those performed in Sarasota Bay dolphins (Costa et al., 2013) could lead to more accurate bioenergetic model estimates from FMR$_{Measured}$, and inform better parameterization and adjustments of BMR (FMR$_{Kleiber}$). Moreover, these data would be useful to reduce estimate uncertainty, hence avoiding over or underestimation of predation on specific prey species. The uncertainty analysis showed a moderate influence of cost of lactation on model input variance. Given the higher cost associated with lactation (Cheal and Gales, 1991; Cockcroft and Ross, 1990; Kastelein et al., 2003; Kastelein et al., 2002; Whitehead and Mann, 2000) females may target prey with higher caloric content (Beck et al., 2007), switch to a preferred diet (Young and Cockcroft, 1994), or favor habitats with a reliable prey source ensuring higher foraging success while maximizing energy intake (Whitehead and Mann, 2000). In sea otters, for example, lactation imposes high bioenergetic demands on females (i.e., 85–110% higher 3–6 months postpartum than non-reproductive demands), which contributes to their disproportionately high mortality at the end of the lactation period and makes them vulnerable to reduced prey availability (Thometz et al., 2016a,b; Thometz et al., 2014). Thus, a greater understanding of the bioenergetic requirements of lactating female bottlenose dolphins is of great conservation importance as the breeding season, and therefore reproductive fitness and population dynamics, may be influenced by environmental factors including prey availability and quality, and water temperature (Lusseau and Wing, 2006; Urian et al., 2009; Yeates and Houser, 2008). Additional research needed to reduce model estimate uncertainty includes measurements of the energy consumption of dolphins that include the range of energy intake that a dolphin can sustain. These controlled studies could also generate data on the metabolizable energy of prey, which are currently limited for this species.

The bioenergetic model developed in the current study built on previous knowledge, but much like previous bioenergetic models, these are simplified representations of the likely bioenergetic requirements of bottlenose dolphins in the wild, and therefore a number of assumptions need further investigation. For example, this model does not address uncertainties associated with variations in space and time, including but not limited to prey availability, caloric content of prey, dolphin density and their influence on food availability, increased bioenergetic demands associated with mating, and other factors that influence metabolic rates and food consumption. Several studies have documented shifts in the abundance of bottlenose dolphins with changes in sea surface temperature, which may be associated with temporal and spatial changes in prey composition, size and abundance (Barco et al., 1999; Barros and Wells, 1998; Friedlaender et al., 2001; Torres et al., 2005; Zolman, 2002). There are also sex- and seasonal-specific behavioral differences (Wells et al., 2013), as well as changes in prey abundance, requiring adjustments of daily bioenergetic requirements that may not be adequately and entirely captured by the bioenergetic model. Despite any potential shortcomings, the model variations presented here used bounded data based on available information almost entirely specific to bottlenose dolphins that estimate sex and age-specific bioenergetic requirements. A recommendation emerging from the current study is the use of model estimates bounded by FMR$_{Kleiber}$ and FMR$_{Measured}$, or based solely on FMR$_{Measured}$.

The larger contribution of the current and similar efforts is that these provide useful information towards understanding top-down ecological and trophic interactions of marine mammals with marine resources, and their impact on ecosystem productivity and on species of commercial and recreational value (Barlow et al., 2008; Barros, 1993; Estes et al., 2011; Roman et al., 2014; Williams et al., 2004). Improving upon these types of models would also allow for better risk assessments associated with trophic transfer,

uptake rates and exposure to biotoxins or persistent contaminants via consumption of prey (Bejarano et al., 2007; Hickie et al., 2013; Law et al., 1995), including assessments of pathogen exposure resulting from fluctuations in prey availability. As noted previously, bioenergetic models could be used to evaluate the impact of disturbance (i.e., noise, boat traffic, habitat alteration, coexisting stressors) on the loss of foraging opportunities and alterations of bioenergetic requirements, and to evaluate adaptive management strategies aimed at mitigating their impact on vital rates. Understanding bioenergetic requirements of marine mammals is important for their conservation and management, and to enable conservation strategies aimed at sustaining predator-prey interactions.

Appendix A. Supplementary Information

Supplementary information associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.05.001.

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