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Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model

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Apex predators such as Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) have the potential to impact prey populations and to be affected by changes in prey abundance. As abundant predators that range widely across the North Pacific Ocean, their interactions with prey populations may have conservation implications. The energy required by individual Pacific white-sided dolphins was estimated using a bioenergetic model that accounted for different age classes and reproductive stages (calf, juvenile, adult, pregnant, and lactating). Monte Carlo simulations incorporating variability in model parameters (i.e., body mass, growth rate, costs of gestation and lactation, metabolic rate, cost of activity, and assimilation efficiencies) were used to predict ranges in energetic requirements of this species. Mean (± *SD*) total energy requirements in MJ/day were 40.3 ± 6.2 for calves, 70.8 ± 8.2 for juveniles, 69.0 ± 3.6 for adults, 70.3 ± 3.6 for pregnant females, and 98.4 ± 20.0 for lactating females. Estimates of energy requirements were most sensitive to uncertainty in values used for resting metabolic rates and energetic costs of activity. Estimated mass-specific energy requirements in MJ kg^{-1} day^{-1} were elevated in calves (1.55 ± 0.23), juveniles (0.97 ± 0.11), and lactating females (1.01 ± 0.21) when compared with nonreproductive adults and pregnant females (∼0.71 ± 0.04). Based on a high-energy diet, an average-sized dolphin (78 kg) would consume approximately 12.5–15.8 kg of fish or 16–20% of its body mass per day. These high energetic requirements may indicate a reliance of dolphins on energy-rich prey, which has implications for fisheries management and conservation of marine mammals.

Key words: apex predator, bioenergetic model, dolphin energetics, food consumption, *Lagenorhynchus obliquidens*, marine mammal physiology, Pacific white-sided dolphin, prey biomass

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The Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) is an abundant cetacean that inhabits the temperate North Pacific Ocean from California to the Bering Sea, and south to Taiwan (Stacey and Baird 1991). These dolphins number ∼1 million animals (95% confidence interval [95% *CI*] ∼200,000–4,000,000 [Buckland et al. 1993] and 95% *CI* ∼150,000–7,000,000 [Miyashita 1993]) and exploit a large habitat including both oceanic and nearshore waters. Pacific white-sided dolphins are gregarious and forage in coordinated groups (Heise 1997a; Van Waerebeek and Würsig 2002), and are considered to be an acrobatic and high-energy species (Van Waerebeek and Würsig 2002). As such, they may have elevated energy needs and may exert significant ecosystem-level effects on prey.

Pacific white-sided dolphins primarily consume high-energy fish, including anchovy, sardine, herring, and salmon, and other prey such as squid, which are commercially or culturally valuable (Stroud et al. 1981; Walker et al. 1986; Miyazaki et al. 1991; Walker and Jones 1993; Black 1994; Heise 1997a; Morton 2000; Kitamura et al. 2008). Marine mammals have often been cited as having heightened energy needs when compared to terrestrial mammals of similar size (Worthy 2001; Benoit-Bird 2004; Barlow et al. 2008; Spitz et al. 2010) that can result in conflict with fisheries (Trites et al. 1997). However, the extent to which Pacific white-sided dolphins may interact with fisheries, or how much energy they require to meet their nutritional needs, is unknown.

Concerns about whether the energetic needs of Pacific white-sided dolphins are adequately met by available prey, as well as the potential for this species to deplete fish stocks or compete with commercial fisheries, can be addressed in part by knowing the prey requirements of the dolphins. However, it is difficult to directly measure the prey requirements of cetaceans because most foraging and prey consumption occurs beneath the sea surface. One method used to study the energy requirements of fish, birds, and mammals is bioenergetic modeling (Laurence 1977; Edwards 1992; Bunce 2001; Winship et al. 2002). Although bioenergetic modeling has been used to estimate the energy needs of several cetacean species (Kenney et al. 1986; Benoit-Bird 2004; Lockyer 2007; Barlow et al. 2008; Noren 2010), a model has never been built for Pacific white-sided dolphins.

Herein, we construct a bioenergetic model to predict the energy requirements of individual Pacific white-sided dolphins during various reproductive stages, and incorporated with the energetic content of their prey to predict the food biomass required by wild populations of dolphins globally. This model provides the 1st estimates of the energy and prey biomass requirements of Pacific white-sided dolphins, and provides direction for future research by identifying which bioenergetic parameters have the greatest influence on total energy needs. Estimates of prey biomass requirements based on model predictions may assist local fisheries management and provide a global perspective on the nutritional and conservation needs of Pacific white-sided dolphins in the North Pacific.

Materials and Methods

The energy requirements of wild Pacific white-sided dolphins were estimated using a bioenergetic model that incorporated estimates of body mass, production, metabolic rate, activity, heat increment of feeding, and digestive efficiency. Requirements were determined for calf, juvenile, adult, pregnant, and lactating dolphins, and model parameters were tested for sensitivity to provide direction for future research.

Individual energy requirements.—Energy requirements were calculated separately for different age and reproductive groups. Age was categorized into calves, juveniles, and adults. Newborn to 1-year-old dolphins were considered to be calves (Ferrero and Walker 1996; Heise 1997b). Dolphins from 1 to 7 years of age were classified as juveniles (Heise 1997b). Dolphins $\geq$ 8 years old were considered sexually mature adults (males, nonpregnant females, pregnant females, and lactating females).

Energy requirements for adult males and nonreproductive adult females were not predicted separately because length-at-age estimates for male and female Pacific white-sided dolphins do not differ significantly (Heise 1997b). Energy requirements for pregnant or lactating females were predicted by adding the daily energetic costs of either pregnancy or lactation to the requirements of nonreproductive adult females.

Gross energy requirements (GERs) were estimated for each age class of dolphin. Traditionally, GER is expressed using the equation:

$$\mathrm{GER} = \frac{\mathrm{P} + \mathrm{A} \times \mathrm{E_m}}{(1 - \mathrm{HIF})(\mathrm{F} + \mathrm{U})},$$

where P is production energy (body growth), A is the cost of activity, $\mathrm{E_m}$ is maintenance costs, HIF is the heat increment of feeding as a proportion of metabolizable energy, and F + U is the fecal and urinary digestive efficiency as a proportion of GER (Lavigne 1982; Winship et al. 2002; Iverson et al. 2010). However, because HIF is usually empirically measured and reported as a proportion of GER, the equation must be modified as:

$$\mathrm{GER} = \frac{\mathrm{P} + \mathrm{A} \times \mathrm{E_m}}{1 - \mathrm{HIF} - (\mathrm{F} + \mathrm{U})}, \tag{1}$$

where HIF and F + U are both energy losses expressed as a proportion of GER.

Production (P).—Total body lengths of Pacific white-sided dolphins of various age classes were estimated from a von Bertalanffy growth model fit to body length data by Heise (1997b). The 95% confidence intervals (95% *CI*s) on this model were calculated by bootstrapping these data 1,000 times, and then selecting the 25th and 975th replicates of the bootstrap-generated curves (ordered by y-intercept) to approximate the confidence limit (i.e., 2 complete curves were chose to represent the percentiles [Whitlock and Schluter 2009; R Development Core Team 2011]). The same method was applied to the mass-at-length model and associated data contained in Heise (1997b; Fig. 1). During Monte Carlo analyses (see "*Data analyses*" section) entire growth curves were resampled in each model iteration.

The mass-at-length and von Bertalanffy length-at-age models were combined using a random bootstrapped von Bertalanffy length-at-age curve to inform a randomly selected curve from the bootstrapped mass-at-length curves, and resampled with replacement for each iteration of the model. Combining these 2 curves produced a mass-at-age curve that incorporated variability from both length and mass estimates. The process was repeated 1,000 times to estimate a range of mass-at-age curves and the 95% *CI*. Yearly changes in mass were determined from each mass-at-age curve, and divided by 365 days to determine average daily changes in mass in kg (ΔM).

The daily energetic cost of change in mass was estimated by multiplying ΔM by the total body proportions of blubber and lean body mass, the energetic densities of lipid and protein, and the efficiency of production of lipid and protein. The body was divided into 2 categories: lean body mass and fat mass (Iverson et al. 2010). These proportions were taken from another small temperate cetacean, the harbor porpoise (*Phocoena phocoena*), due to the lack of data on Pacific white-sided dolphins. Mean ($\pm$ *SD*) proportions of blubber ($\mathrm{P_{blu}}$) in the bodies of harbor porpoises were 37.45% ($\pm$ 6.13%) for calves, 29.62% ($\pm$ 2.04%) for sexually immature males, 26.49% ($\pm$ 2.46%) for mature males, 25.81% ($\pm$ 2.75%) for pregnant nonlactating females, and 23.54% ($\pm$ 3.97%) for lactating females (McLellan et al. 2002). We assumed that these proportions of blubber were consistent between Pacific white-sided dolphins and harbor porpoises, and between males and resting females, and used these normally distributed values in the model.

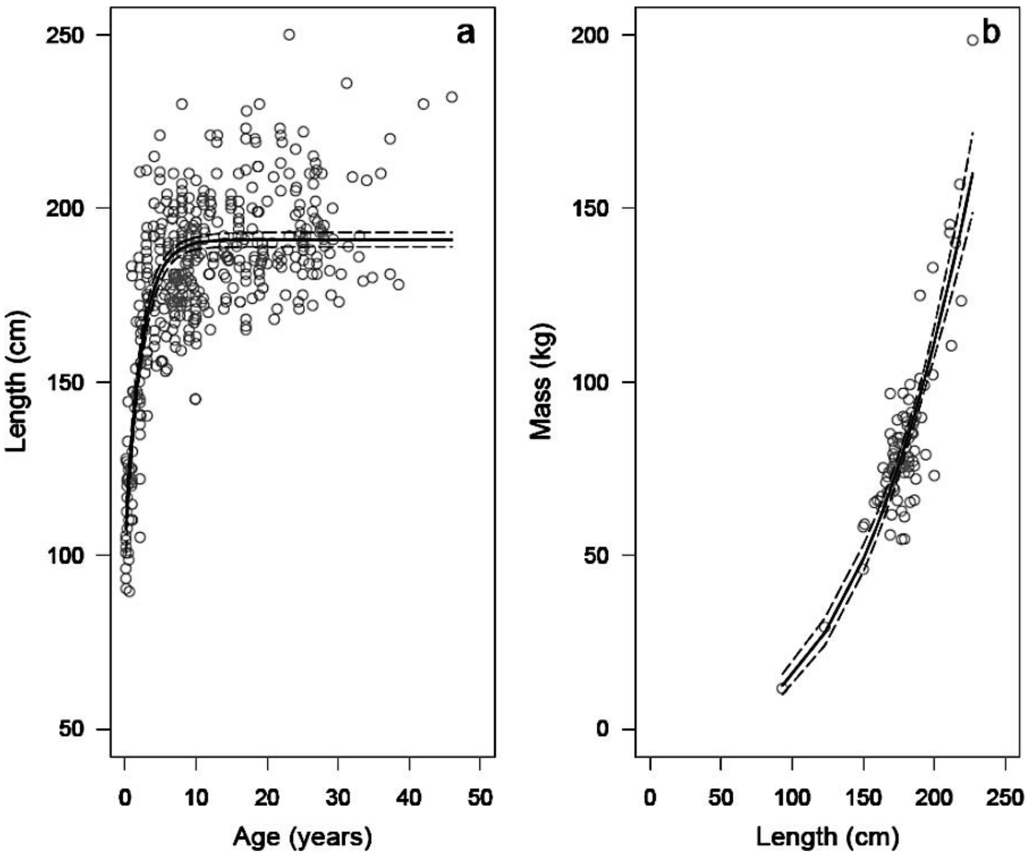

FIG. 1.—The relationships between a) length and age and b) mass and length of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*); data are from Heise (1997b). Solid lines represent mean growth curves and dashed lines represent the 95% confidence interval of the growth models.

Normally distributed proportions of lipid (P_{lip}) in the blubber of Pacific white-sided dolphins were used in the model; mean (± *SD*) of 81.5% ± 7.8% (based on data collected from 5 Pacific white-sided dolphins [G. A. J. Worthy, Physiological Ecology and Bioenergetics Lab, University of Central Florida, pers. comm.]). Lean body mass was assumed to be 73% water (Pace and Rathburn 1945). Standardized energy densities of 39.5 MJ/kg for lipid (ED_{lip}) and 23.5 MJ/kg for protein (ED_{pro}—Schmidt-Nielson 1990), and growth efficiencies of 0.75 for lipid growth ($GE_{lip} = 1.33$) and 0.45 for protein growth ($GE_{pro} = 2.22$—Webster 1985) were used to estimate energetic costs of depositing new tissues during production.

Thus, energetic costs of production (P) were predicted in MJ, using:

$$P = \Delta M\left[P_{blu}P_{lip}ED_{lip}GE_{lip} + (1 - P_{blu})(1 - P_w)ED_{pro}GE_{pro}\right], \tag{2}$$

where ΔM is the daily change in mass in kg, P_{blu} is the proportion of the body that is blubber, P_{lip} is the proportion of blubber that is lipid, ED_{lip} is the energetic density of lipid in MJ/kg, GE_{lip} is the growth efficiency of lipid, P_w is the proportion of the lean body mass that is water, ED_{pro} is the energetic density of protein in MJ/kg, and GE_{pro} is the growth efficiency of protein.

Energetic costs of resting metabolism and thermoregulation (E_m).— The combined energy cost of resting metabolism and thermoregulation was estimated using:

$$E_m = X \times RMR + E_{therm}, \tag{3}$$

where E_m is the metabolic rate in MJ/day, X is a multiplier of resting metabolic rate that varies with age class, RMR is the resting metabolic rate, and E_{therm} is the cost of thermoregulation in MJ.

Resting metabolic rate was measured for 3 adult (late teens and early 20s) dolphins housed at the Vancouver Aquarium (Rechsteiner 2012). Open-circuit gas respirometry was used to measure oxygen consumption while adult dolphins were postabsorbtive and resting calmly at the pool surface under a metabolic chamber to which they had been desensitized over a 10-month period (Rechsteiner 2012). Measurements were taken biweekly for 1 year, and were seasonally constant at approximately 3 times Kleiber's (1975) predictions of basal metabolic rates for terrestrial mammals (Rechsteiner 2012). Resting metabolic rates for adult dolphins were normally distributed around a mean of 3.19 ± 0.34 *SD* times Kleiber's prediction (Rechsteiner 2012).

The resting metabolic rate of immature Pacific white-sided dolphins was assumed to be elevated 1.5 times the adult resting metabolic rate, and we assumed that the elevated metabolic rates of growing animals decreased linearly from 1.5 to 1.0 times adult resting metabolic rate between the ages of 0–1 and 8 years old. This assumption was supported by data on killer whales (*Orcinus orca*) showing that juveniles had elevated rates of 1.2–1.3 times the basal rates of adults (Kasting et al. 1989) and was consistent with basal metabolic rates of northern fur seals (*Callorhinus ursinus*) and harp seals (*Pagophilus groenlandicus*), which were elevated by 1.4 times the rates of adults (Innes et al. 1987). These methodologies also were consistent with those employed by Winship et al. (2002) to estimate elevated resting metabolism of subadult Steller sea lions (*Eumetopias jubatus*).

Toothed whales are thought to typically inhabit waters within their thermoneutral zone (Costa and Williams 1999). Small temperate odontocetes may have a modified proportion of lipid in their blubber as an adaptation to cold temperatures. Thus, harbor porpoises, and likely Pacific white-sided dolphins, common dolphins (*Delphinus delphis*), and bottlenose dolphins (*Tursiops truncatus*), do not expend extra energy for thermoregulation in waters above 10°C (Worthy 1991, not seen, cited in Worthy 2001). We therefore assumed there were no additional costs of thermoregulation beyond normal metabolic requirements (i.e., $E_{\mathrm{therm}} = 0$ MJ).

Activity (A).—As used by Iverson et al. (2010), Noren (2010), Williams et al. (2004), and Williams et al. (1993), resting metabolism was scaled with a constant to estimate the energetic costs of activity. This method was employed in the absence of data on the specific activities and associated swimming speeds, respiration rates, heart rates, or other means of determining energetic costs for specific activities of Pacific white-sided dolphins. Dolphins swimming at mean cruising speeds have activity costs near to, or slightly elevated above, their resting metabolic rates (Williams et al. 1993). However, heart rates measured for dolphins swimming at various speeds indicated that the energetic costs of swimming are elevated at nonaverage speeds (Williams et al. 1993). The field metabolic rate of marine mammals is thought to be no more than 6 times Kleiber, or 3 times resting metabolic rate of marine mammals (Williams et al. 2004 and references therein). To reflect parameter uncertainty, and the possible range of costs of activity, a metabolic scaler with uniformly distributed values between 1 and 3, was used in the model, so that the costs of activity would range from 1 to 3 times the measured resting metabolic rates of Pacific white-sided dolphins.

Heat increment of feeding (HIF).—The proportion of energy discharged as heat due to the heat increment of feeding was estimated from a plot showing the change in oxygen consumption of a bottlenose dolphin during and after eating 1.4 kg of capelin (Yeates and Houser 2008). The bottlenose dolphin consumed about 3.8 ml O_2 min^{-1} kg^{-1} while at rest and about 5.6 ml O_2 min^{-1} kg^{-1} at peak digestion (Yeates and Houser 2008). By integrating the area under the oxygen consumption curve above baseline levels from the time the meal was consumed until 250 min after the meal (when oxygen consumption rates returned to baseline levels), the total oxygen consumption after feeding was calculated (~235 ml O_2/kg). Using a conversion factor of 1 liter $O_2 = 20.1$ kJ (Blaxter 1989), an assumed energetic density for capelin of 5.0 kJ/g (Anthony et al. 2000), and the dolphin's mass of 219.7 kg, it was determined that the bottlenose dolphin lost 1,037 kJ of the 7,000 kJ consumed in the meal. This equated to an energy loss of 15% gross energy requirement due to heat increment of feeding.

Heat increment of feeding has been measured as 4.7–9.0% of gross energy intake in harbor seals (*Phoca vitulina*) consuming herring (Markussen et al. 1994). Harp seals expressed a heat increment of feeding of 11–13% of total energy intake when eating herring (Gallivan and Ronald 1981), and in Steller sea lions the heat increment of feeding varied from 9.9% to 12.4% of the total intake, depending on the meal size (Rosen and Trites 1997). Uniformly distributed values between 0.05 and 0.15 were used to reflect parameter uncertainty and represent the proportion of gross energy allocated to the heat increment of feeding.

Fecal and urinary digestive efficiency (F + U).—Fecal and urinary digestive efficiency varies with diet. In general, diets that are low in lipids have a lower efficiency, whereas diets high in lipids have a higher efficiency (Lawson et al. 1997a, 1997b; Williams et al. 2001). No data were available to predict the fecal and urinary digestive efficiencies separately for Pacific white-sided dolphins; however, data did exist to predict the combined fecal and urinary digestive efficiency as a proportion of total energy intake in other species of marine mammals.

The digestive efficiency for odontocetes eating marine animal– or fish-based diets is 0.90–0.95 (Lockyer 2007). Pinnipeds consuming a diet of herring or squid have measured digestive efficiencies of ~0.90–0.97 (Keiver et al. 1984; Fadely et al. 1990; Fisher et al. 1991; Lawson et al. 1997a). We therefore assumed the digestive efficiency of Pacific white-sided dolphins was uniformly distributed between 0.90 and 0.97 (i.e., energy loss was uniformly distributed from 3% to 10% of total energy intake).

Energy costs associated with gestation.—The energetic cost of gestation ($E_{\mathrm{gestation}}$) was predicted by:

$$E_{\mathrm{gestation}} = 18.42\mathrm{bm}^{1.2}, \quad (4)$$

where $E_{\mathrm{gestation}}$ is in MJ/day, and bm is mass at birth in kg (Brodie 1975; Lockyer 2007). The gestation period of Pacific white-sided dolphins is approximately 12 months (Robeck et al. 2009). The estimated length of Pacific white-sided dolphins at birth is 90–105 cm (Iwasaki and Kasuya 1997). The postnatal equation ($\mathrm{mass} = 0.000035 \times \mathrm{length}^{2.82}$, where mass is in kg and length is in cm [Heise 1997b]) was used to estimate birth mass from estimated lengths. We assumed uniformly distributed birth mass across a range of 11–18 kg, and used these values in the model.

Energy costs associated with lactation.—Two independent methods were used to account for the energetic costs of lactation. The 1st method assumed the mother needed to provide all of the energy needed by the calf to meet its daily energetic requirements for 365 days. This assumed that model

Table 1.—Parameter values used in the bioenergetic model of Pacific white-sided dolphins (*Lagenorhynchus obliquidens* references are given in the text).

Parameter	Symbol	Equation	Value	Details
Fecal and urinary digestive efficiency	F + U	1	0.90–0.97	All animals
Heat increment of feeding	HIF	1	0.05–0.15	All animals
Activity	A	1	1–3	All animals
Proportion of body growth that is blubber	P_{blu}	2	37.45 ± 6.13	Calf
			29.62 ± 2.04	Juvenile
			26.49 ± 2.46	Adult
			25.81 ± 2.75	Pregnant
			23.54 ± 3.97	Lactating
Proportion of lipid in the blubber	P_{lip}	2	0.81 ± 0.078	All animals
Energetic density of lipid	ED_{lip}	2	39.5 MJ/kg^{-1}	All animals
Energetic density of protein	ED_{pro}	2	23.5 MJ/kg^{-1}	All animals
Growth efficiency of lipid	GE_{lip}	2	1.33	All animals
Growth efficiency of protein	GE_{pro}	2	2.22	All animals
Proportion of lean body mass that is water	P_w	2	0.73	All animals
Scaler to multiply times Kleiber predictions to estimate resting metabolic rate	X	3	4.79 ± 0.34	0 < 1 years
			4.59 ± 0.34	1 < 2 years
			4.39 ± 0.34	2 < 3 years
			4.19 ± 0.34	3 < 4 years
			3.99 ± 0.34	4 < 5 years
			3.79 ± 0.34	5 < 6 years
			3.59 ± 0.34	6 < 7 years
			3.39 ± 0.34	7 < 8 years
			3.19 ± 0.34	8+ years
Mass at birth	bm	4	11–18 kg	Pregnant

predictions of calf requirements were reasonable. The overall conversion of total energy intake to milk in lactating humans is 83% of energy consumed (Prentice and Prentice 1988) and in gray seals (*Halichoerus grypus*) is 85% (Anderson and Fedak 1987). Assuming an 84% conversion in Pacific white-sided dolphins, a lactating dolphin would need to consume an additional 119% of the calf's total energy requirements to meet its requirements through milk energy. Lactation thus increased the total energy requirements of lactating adult female Pacific white-sided dolphins to 170% of nonlactating females. The energetic requirements of lactating female marine mammals are generally estimated to be 130–190% of the energetic requirements of resting females, based on studies of northern fur seals, long-finned pilot whales (*Globicephala melas*), bottlenose dolphins, and minke whales (*Balaenoptera acutorostrata*—see Kastelein et al. [2002], Lockyer [1993, 2007], and Perez and Mooney [1986]).

In addition to deriving lactation costs by accounting for direct growth and maintenance of the calves as predicted by the model, a 2nd method that combined the lactation period with the energetic density of milk, the efficiency of conversion from total energy intake to milk, and an estimate of the biomass of milk produced each day of the lactation period was used to estimate lactation costs. We assumed the energetic content of Pacific white-sided dolphin milk was uniformly distributed between 12 and 14.3 MJ/kg based on the energetic density of spinner dolphin (*Stenella longirostris*) milk, ∼12 MJ/kg (Pilson and Waller 1970), and short-beaked common dolphin (*Delphinus delphis*) milk, 14.3 MJ/kg (Oftedal 1997). Based on an 84% conversion efficiency from total energy intake to milk, an adult dolphin would need to consume ∼120% more energy than usual for a given production of milk. Therefore, lactating females would need to consume 14.4–17.2 MJ of energy for each kilogram of milk produced. Small odontocetes typically produce 0.30–0.90 kg of milk per day (Oftedal 1997). Assuming a uniform distribution of energetic requirements per kilogram of milk produced (14.4–17.2 MJ/kg of milk) and a uniform distribution of the mass of milk produced (0.30–0.90 kg/day), these values were multiplied together to estimate the energetic costs of lactation. This method increased lactating female requirements by ∼115% above nonreproductive adult requirements.

Monte Carlo simulations were run (see next section) to alternate between estimates from the 1st and 2nd method of assessing costs of lactation so that model outputs would reflect uncertainty in both attempts of determining the cost of lactation.

Data analyses.—Energetic needs were predicted for each day of life from birth to 45 years of age. Daily energetic requirements also were grouped by life stage. To incorporate parameter uncertainty, 10,000 Monte Carlo simulations were run to estimate a distribution and range for average daily energetic requirements for each age class. Values used in Monte Carlo analyses are provided in Table 1.

Sensitivity analyses determined which model parameters were most sensitive to change. Each major model parameter (production—P, metabolism—E_m and A, assimilation—E_{HIF} and E_{F+U}, and gestation and lactation estimates) was run through the Monte Carlo analysis 10,000 times while keeping all other parameters at their mean values (e.g., Winship et al. 2002). Parameters that resulted in the greatest variation in model outputs when allowed to run through the Monte Carlo

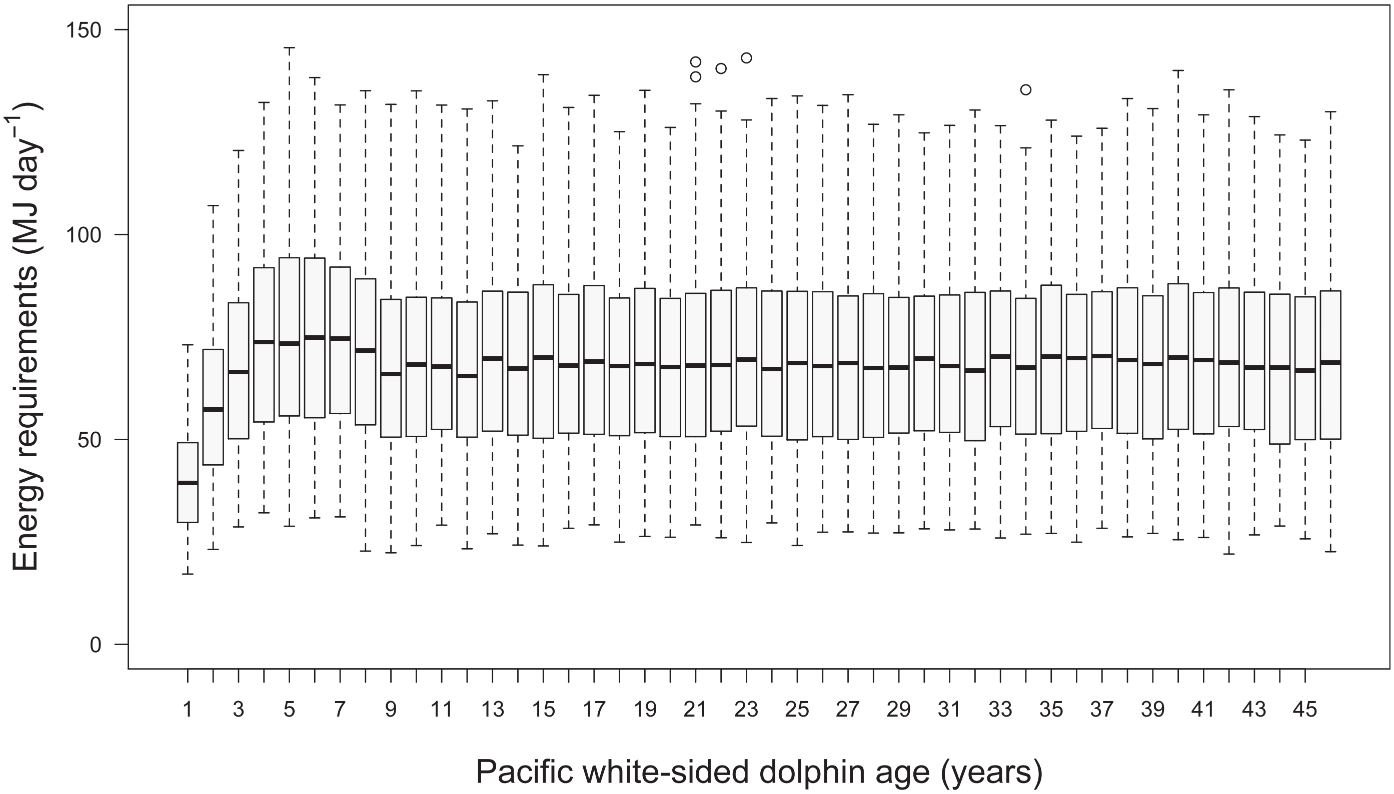

FIG. 2.—Daily gross energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) aged 1–45 years. Numbers on the x-axis represent age up to that year, for example, at x = 1, the dolphins are ≤ 1 year. Bold lines in center of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution, and whiskers represent the range. Open circles represent model outliers.

analyses were considered the most senstivie. Box plots were used to illustrate the effects of allowing for variation in each set of parameters.

RESULTS

Model predictions indicated that the total daily energy requirements of Pacific white-sided dolphins increase rapidly from birth to sexual maturity (Fig. 2). However, mass-specific energy requirements decrease rapidly from calves to adults (Fig. 3).

Predicted average daily energy requirements (mean ± *SD*) were 40.3 ± 6.2 MJ/day for calves and 70.8 ± 8.2 MJ/day for juveniles. Juveniles required more energy than calves, and nonreproductive adults (males and females) required slightly less energy than juveniles (69.0 ± 3.6 MJ/day) due to decreased growth costs. Energetic costs of gestation were only marginally (2%) greater than the energetic requirements of nonreproductive adults (70.3 ± 3.6 MJ/day; Fig. 4). However, the estimated energetic costs of lactation were 40% higher than the energetic costs of nonreproductive females (98.4 ± 20.0 MJ/day; Fig. 4). Mass-specific energetic needs of calves, juveniles, and lactating females were much higher than those of other life stages—calves required 1.55 ± 0.23 MJ kg^{-1} day^{-1}, juveniles 0.97 ± 0.11 MJ kg^{-1} day^{-1}, and lactating females 1.01 ± 0.21 MJ kg^{-1} day^{-1}, whereas the nonreproductive adults and pregnant females only required ~0.71 ± 0.04 MJ kg^{-1} day^{-1} (Fig. 5).

Sensitivity analyses revealed that the predicted energy requirements were most sensitive to uncertainty in the estimates of metabolism, which includes estimates of resting metabolic rate and activity costs (Fig. 6). Changes in metabolism resulted in the greatest changes to total energy requirements. Growth was the 2nd most sensitive parameter, and assimilation of energy was the least sensitive to changes. These trends were consistent for Pacific white-sided dolphins in all life stages, except for lactating females, where the parameter range associated with incorporating the 2 disparate methodologies of lactation overshadowed variability in other parameters.

DISCUSSION

This model predicted the energetic requirements of Pacific white-sided dolphins at different ages and reproductive states. Combining model predictions with population demographics and diet parameters allows energy requirements to be calculated for Pacific white-sided dolphins in any region of the North Pacific. These estimates of energetic requirements can be used to assist with the conservation of dolphins and the management of fisheries at local and global scales.

Energetic requirements.—Total energy requirements of Pacific white-sided dolphins were generally high when

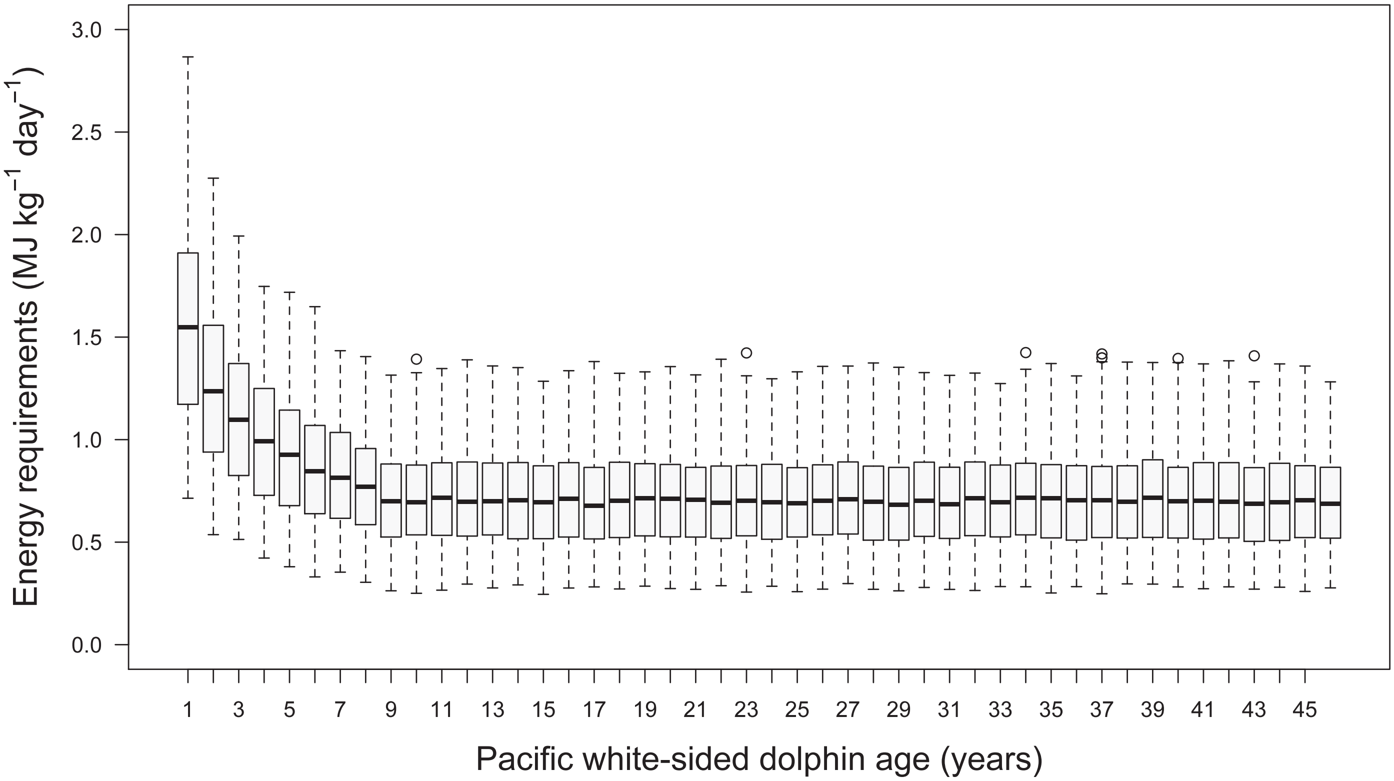

FIG. 3.—Daily mass-specific (per kilogram) energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) aged 1–45 years. Numbers on the x-axis represent age up to that year, for example, at x = 1, the dolphins are ≤ 1 year. Bold lines in center of boxes show median value, and whiskers represent the range. Circles indicate model outliers.

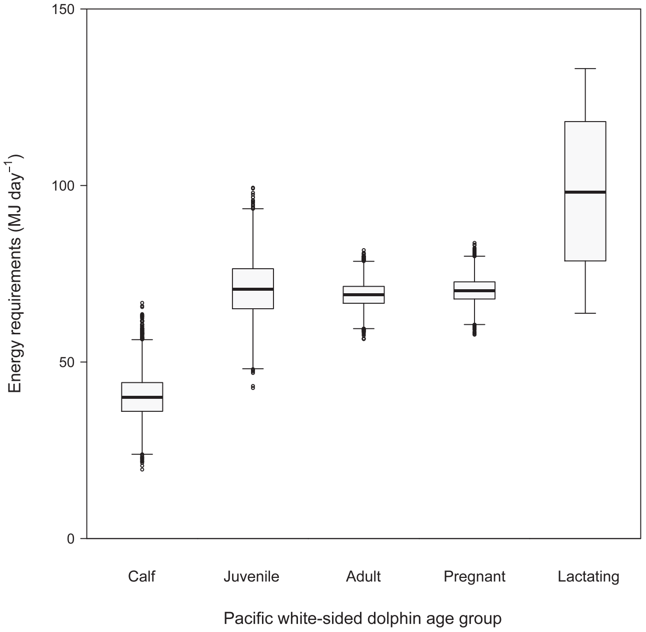

FIG. 4.—Total daily energy requirements for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in each reproductive stage. Bold lines in center of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution, and whiskers represent the range. Open circles represent model outliers.

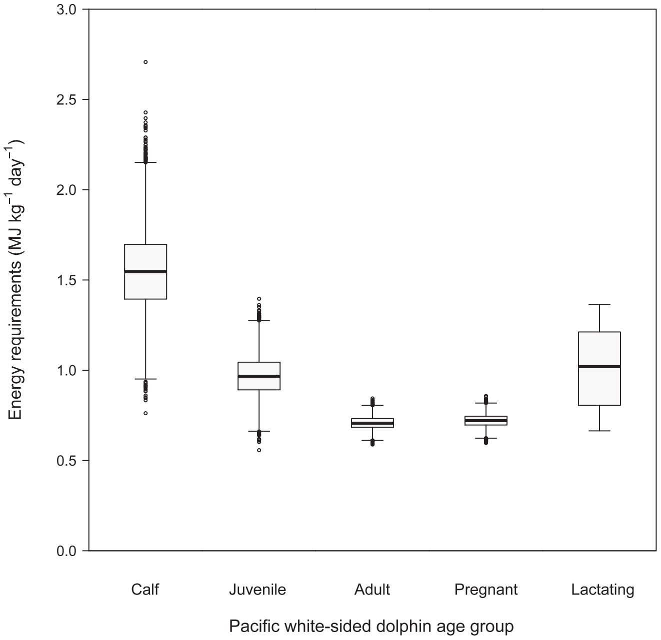

FIG. 5.—Per kilogram requirements for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in each reproductive stage. Bold lines in center of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution, and whiskers represent the range. Open circles represent model outliers.

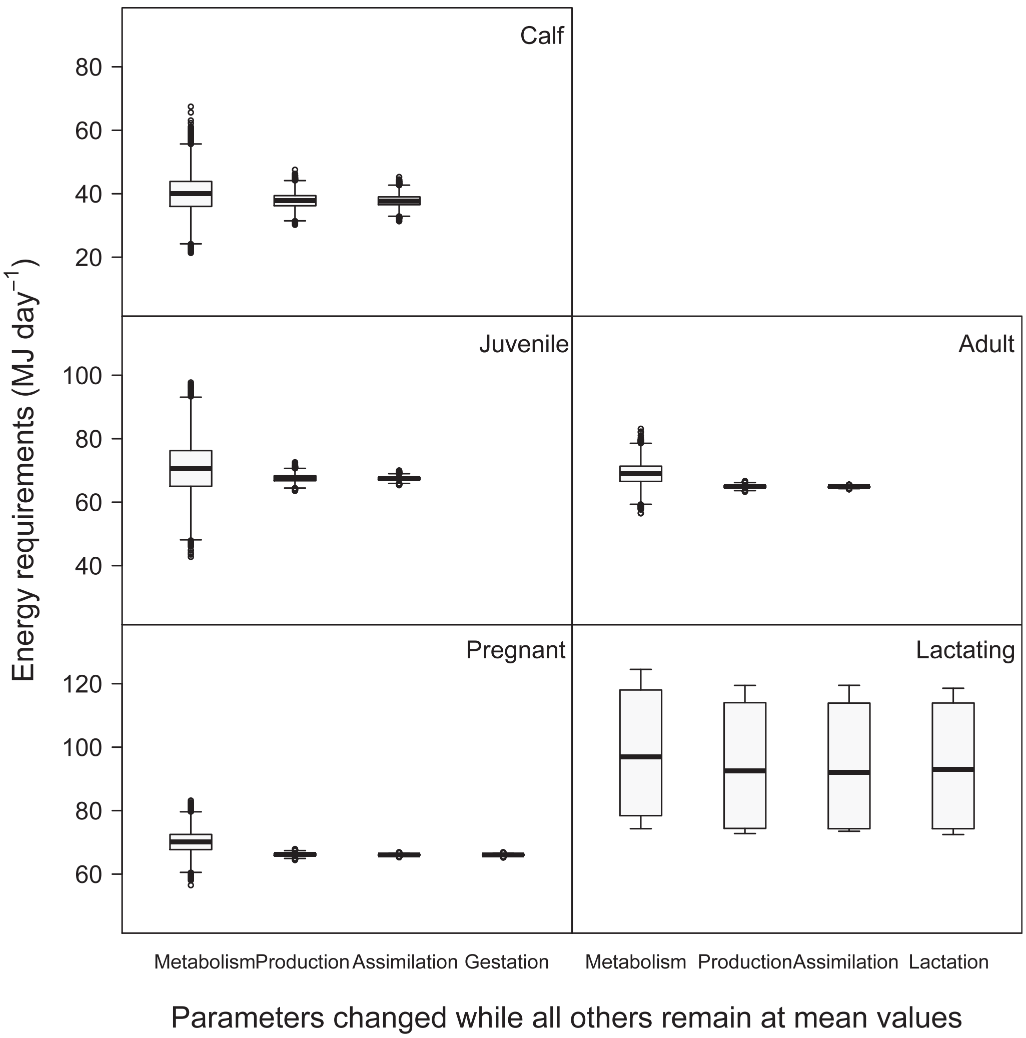

Fig. 6.—The effect of changes in model parameters on estimates of total energetic requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in different demographic groups. Bold lines in center of boxes represent the median value, box edges represent the 25th and 75th percentiles of the data distribution, and whiskers represent the range. Open circles represent model outliers. Note that y-axis scales vary, but range is consistent (60 MJ), and distribution of energetic costs of lactation is bimodal at ~80 and ~110 MJ/day.

compared to similar-sized cetaceans, and varied for dolphins in different life stages. As expected, calves had the lowest total energetic requirements but the highest mass-specific requirements, a pattern consistent with most mammals that have been investigated to date. Juveniles, adults, and pregnant females required similar total energy intake. However, mass-specific requirements of juveniles were greater than mass-specific requirements of non-reproductive adults. These results also were consistent with studies of beluga whales (*Delphinapterus leucas*—Kastelein et al. 1994), bottlenose dolphins (Kastelein et al. 2003), and dusky dolphins (*Lagenorhynchus obscurus*—Kastelein et al. 2000) fed in aquaria, that show per kilogram requirements decrease as odontocetes age, and level out when they mature.

Lactating females required the highest total energy intake. The tremendous cost of lactation may make this demographic exceedingly vulnerable to nutritional stress. Additionally, if lactating females balance time spent on prey acquisition with a need to protect calves from predators (i.e., by remaining in sheltered habitats and not searching for prey), the potential for energetic vulnerability would be compounded. These observations suggest that females supporting calves may specifically require high-energy prey to meet their needs.

The predicted energetic requirements for nonreproductive adult Pacific white-sided dolphins were higher than modeled energetic requirement estimates for other small to medium-sized odontocetes inhabiting temperate waters. For example, the energetic requirements of Dall's porpoises (*Phocoenoides dalli*) were ~0.25 MJ kg^{-1} day^{-1} (0.8 MJ kg$^{-0.75}$ day^{-1}), or just over one-third of the mass-specific estimates for Pacific white-sided dolphins (Ohizumi and Miyazaki 1998). Killer whale energetic requirements were estimated at ~0.17 MJ kg^{-1}day^{-1} (1.2 MJ kg$^{-0.75}$ day^{-1}) or just over one-quarter the mass-specific requirements of white-sided dolphins (Sigurjónsson and Vikingsson 1997) and at ~0.21 MJ kg^{-1} day^{-1} (males; 1.6 MJ kg$^{-0.75}$ day^{-1}) and 0.25 MJ kg^{-1} day^{-1} (females; 1.7

TABLE 2.—Estimates of gross energetic requirements for nonreproductive adult small temperate delphinids in the wild.

Species	Mass (kg)	MJ/day	MJ kg^{-1} day^{-1}	MJ $kg^{-0.75}$ day^{-1}	Reference
Harbor porpoise	39	21	0.54	1.3	Sigurjónsson and Vikingsson 1997
Pacific white-sided dolphin	95	69	0.71	2.7	This study
Pacific white-sided dolphin	95	65	0.68	2.1	Sigurjónsson and Vikingsson 1997; mass adjusted[a]
Dall's porpoise	108	27	0.25	0.8	Ohizumi and Miyazaki 1998
Pacific white-sided dolphin	190	65	0.34	1.3	Sigurjónsson and Vikingsson 1997
Killer whale	2,350	400	0.17	1.2	Sigurjónsson and Vikingsson 1997
Female killer whale	3,338	763	0.25	1.7	Noren 2010
Male killer whale	4,434	876	0.21	1.6	Noren 2010

[a] Mass adjusted from 190 kg to 95 kg as commonly accepted (Ferrero and Walker 1996; Heise 1997b; Trites and Pauly 1998).

MJ $kg^{-0.75}$ day^{-1}Noren 2010). The only small cetacean that approximates the mass-specific energy requirements of a Pacific white-sided dolphin is the harbor porpoise at 0.54 MJ $kg^{-1}day^{-1}$ (1.2 MJ $kg^{-0.75}$ day^{-1}—Sigurjónsson and Vikingsson 1997; Table 2).

The total energy requirements of Pacific white-sided dolphins estimated by Sigurjónsson and Vikingsson (1997; ~65 MJ/day) were similar to our bioenergetic model predictions. However, their (Sigurjónsson and Vikingsson 1997) mass-specific estimates for Pacific white-sided dolphins were ~0.34 MJ kg^{-1} day^{-1} based on a mean mass of 190 kg, which seems heavy for an adult Pacific white-sided dolphin (see Ferrero and Walker [1996], Heise [1997b], and Trites and Pauly [1998]). Using the more typical mass estimate of 95 kg for adult Pacific white-sided dolphins (Heise 1997b), the mass-adjusted energy requirement estimates of Sigurjónsson and Vikingsson (1997) would be ~0.68 MJ kg^{-1} day^{-1} (2.1 MJ $kg^{-0.75}$ day^{-1}) and similar to our model predictions (Table 2).

A question that naturally arises from our model is whether the elevated energetic requirement estimates for Pacific white-sided dolphins genuinely reflected higher food needs, or whether the model overestimated energetic needs. The food intake of Pacific white-sided dolphins in aquaria is greater than that of other small captive cetaceans (Table 3). For example, nonreproductive adult Pacific white-sided dolphins consumed ~7% of their body mass daily while in aquaria, on a diet of herring, salmon, capelin, and squid (Rechsteiner 2012). This was more than twice the relative biomass consumed by Amazon river dolphins (*Inia geoffrensis*; 3% of body mass) on a diet of primarily trout and carp (Kastelein et al. 1999). Similarly, an adult bottlenose dolphin consumed only 2% of its body mass in herring, mackerel, and squid (Kastelein et al. 2002). Although an adult dusky dolphin consumed slightly more (about 10% body mass) than the Pacific white-sided dolphins, this was while eating a lower-energy diet of hake, cephalopods, and teleost fishes (Kastelein et al. 2000). Collectively, examination of these data indicates that Pacific white-sided dolphins do indeed have elevated energetic needs, even in aquaria, when compared with other small odontocetes.

Recorded energy consumption of adult nonreproducing Pacific white-sided dolphins in aquaria was about two-thirds our estimates of energy consumption of wild Pacific white-sided dolphins (Rechsteiner 2012). This difference is likely due to the energetic cost associated with activity, which is higher for wild dolphins than for those housed in aquaria. Activity budgets constructed for captive Pacific white-sided dolphins in aquaria indicate they spend 60–80% of their time resting (Javdan 2010), whereas activity budgets constructed for wild Pacific white-sided dolphins indicate that resting accounts for only ~3% of their activity budget (Black 1994).

Study limitations.—As with any model, this bioenergetics model is a simplified description of a complex system. The model is limited by the availability of data to parameterize each of the variables, and incorporated many values that were not estimated specifically from Pacific white-sided dolphins. However, the data used were the best currently available, and yielded values that are consistent with those for related species of odontocetes.

Pacific white-sided dolphins likely inhabit areas within their thermoneutral zone (Costa and Williams 1999; Worthy 2001), although Stacey and Baird (1991) reported an extensive range for this species, which occurs in both the cold waters of the Bering Sea and the warmer waters off southern California. Given the range of water temperatures inhabited by Pacific white-sided dolphins, the assumption that they remain within their thermoneutral zone may not be valid across all habitats. They may thus expend some energy for thermoregulation in the temperature extremes of their habitat, which would increase their gross energy requirements.

TABLE 3.—Biomass measurements of food intake for nonreproductive adult odontocetes in aquaria.

Species	Mass (kg)	Daily food intake (kg)	% body mass	Diet	Reference
Dusky dolphin	70	7.0	10	Hake, cephalopods, teleost fishes	Kastelein et al. 2000
Pacific white-sided dolphin	116	8.5	7	40% herring, 40% capelin, 10% salmon, 10% squid	Rechsteiner et al. 2012
Amazon river dolphin	145	3.6	2	Trout, carp	Kastelein et al. 1999
Bottlenose dolphin	225	4.7	2	Herring, mackerel, squid	Kastelein et al. 2002

Another assumption needing further scrutiny is the way in which the energetic costs of lactation were estimated. We 1st assumed the modeled energy requirements for calves were reasonable, and based the costs of lactation incurred by the mother on these model results. This method inferred that lactation costs increased energy requirements by 170% over the energy required by resting females, and agreed with the bulk of studies regarding lactation costs in marine mammals—including the lactation costs of pinnipeds, mysticetes, and bottlenose dolphins (Perez and Mooney 1986; Lockyer 1993, 2007; Kastelein et al. 2002). However, these model-based estimates of lactation may be an overestimate for Pacific white-sided dolphins given that the costs of activity included in the estimated daily energy needs of calves might be lower than estimated, if calves regularly draft behind their mothers.

As a 2nd means to avoid using the bioenergetic model results for calves, we used energetic densities of delphinid milks, and generalized estimates of quantities of milk produced daily by lactating dolphins, to determine the cost of lactation (Oftedal 1997). This method inferred that the cost of lactation increased energy requirements by ~115% of the energy requirements of resting females. The possibility that lactation costs could be this low may have some merit given the slow rate of growth of young dolphins. Pacific white-sided dolphin fetuses have often been measured in excess of 80 cm, and calves are born between 90 and 100 cm long (Ferrero and Walker 1996; Heise 1997b). As such, the length at birth is ~50% of the asymptotic length of adults (~190 cm). The length at weaning is thought to be between 125 and 130 cm—when animals are ~65% of their asymptotic adult length at about 1 year old (8–16 months—Ferrero and Walker 1996; Heise 1997b). Thus, the growth rate of calves is relatively slow compared with that of mysticetes or pinnipeds, but is typical of small delphinids (Perrin et al. 1977; Marsili et al. 1997). Furthermore, the cost of lactation in odontocetes is thought to be lower than in mysticetes and pinnipeds because the fat content of odontocete milk is lower (10–15% as opposed to ~50% in mysticetes and up to 80% in pinnipeds—Oftedal 1997), which would further support a lower cost of lactation.

Despite potential shortcomings in model assumptions regarding the costs of lactation and thermoregulation, this model used the best available information to estimate the energy requirements of Pacific white-sided dolphins. The model estimates are considered reasonable when compared with food intake of related species, and conspecifics housed in aquaria, and are associated with large error bounds that reflect uncertainty in the model parameters. Further refinement of the mean estimates will require additional study, particularly to refine lactation and thermoregulation parameters.

Ecological implications.—In the coastal waters of British Columbia, Canada, sightings of Pacific white-sided dolphins have increased markedly since the 1980s (Heise 1997a). Pacific white-sided dolphins are now regularly found in areas containing several culturally and commercially important fish species. Recent stomach contents obtained from 15 stranded or bycaught animals on the British Columbian coast indicate that salmon and sardine are the most important prey (of all prey that composed more than 10% of the diet by biomass—Rechsteiner 2012). Herring also are important prey and were the most common prey observed in diets of Pacific white-sided dolphins during the 1990s (Heise 1997a). These prey species are consistent with the observation that Pacific white-sided dolphins primarily consume high-energy prey throughout their range (Stroud et al. 1981; Walker et al. 1986; Miyazaki et al. 1991; Walker and Jones 1993; Black 1994; Heise 1997a; Morton 2000; Kitamura et al. 2008).

One useful application of this bioenergetic model is to estimate the prey base required by populations of Pacific white-sided dolphins in different areas throughout their extensive range. Based on limited dietary information, we assumed the diet of dolphins in the North Pacific was composed primarily of high-energy fish. For dolphins consuming prey in British Columbian waters, this model based prey biomass estimates on a diet of salmon and sardine, although herring may well be underrepresented in the small data set of stomachs ($n = 15$). Because salmonids (63% of diet by biomass) and sardine (17% of diet by biomass) together only comprised 80% of the biomass consumed by the dolphins, generic high-energy fish also was included in the diet of British Columbian dolphins.

According to the bioenergetic model, an average subadult Pacific white-sided dolphin with a mean mass of 78 kg (Trites and Pauly 1998) would require 70.8 ± 8.2 MJ/day. This single dolphin would therefore consume 12.5–15.8 kg of a generic high-energy fish if consuming only that prey and assuming an energetic density of 5 kJ/g wet weight (Anthony et al. 2000). If consuming a more realistic mixed-species diet, the dolphin would consume ~8.9 kg of salmon, 2.4 kg of sardine, and 2.8 kg of generic high-energy fish to meet its mean of 14.2 kg in prey biomass requirements (assuming that 63% of the biomass consumed was from salmon, 17% from sardine, and 20% generic high-energy fish, as indicated by the 15 stomachs analyzed), although seasonal variability in prey species availability would influence these numbers.

The entire North Pacific population of about 1 million Pacific white-sided dolphins (95% *CI* ~200,000–4,000,000 [Buckland et al. 1993] and 95% *CI* ~150,000–7,000,000 [Miyashita 1993]) would consume 1,900–111,000 metric tons ($\bar{X} = \sim$14,200 metric tons) of high-energy, mixed-species fish daily if uncertainty in population size and energetic requirements are included in estimates. Of this total, the ~25,000 Pacific white-sided dolphins thought to reside in British Columbia in spring and summer (95% *CI* ~12,000–52,000—Williams and Thomas 2007), would consume 150–820 metric tons ($\bar{X} = \sim$355 metric tons) of high-energy fish daily if uncertainty in population size and energetic requirements are included in estimates. In comparison, the total catch of all bony fishes in the North Pacific in 2009 was 15,162,676 metric tons (FISHSTAT database; Food and Agriculture Organization of the United Nations [FAO], Rome, Italy), and in British Columbian waters, the total catch of groundfish, halibut, herring, and salmon in 2011 was 132,818 metric tons (Pacific

Fisheries Catch Statistics; Fisheries and Oceans Canada, Ottawa, Canada).

Future research.—It would be ideal to test the model predictions against other modeling methods that predict energy needs for this species, and to ground-truth predictions from this model against a field study recording energy consumption of wild Pacific white-sided dolphins. A range of bioenergetic modeling methods have been used to estimate the food requirements of cetaceans and some of them could be applied to Pacific white-sided dolphins. For example, respiration rates, activity states, and swimming speeds of wild animals can be used to predict field metabolic rate (e.g., Williams and Noren 2009; Noren 2010) and this methodology could be used to determine daily energy requirements of Pacific white-sided dolphins and support or refute this model's predictions. Tagging Pacific white-sided dolphins with accelerometers and camera loggers may allow researchers to identify prey capture events and estimate energy consumed in the wild.

The model predictions were most sensitive to uncertainty in resting metabolic rates and activity, which indicates that data for these parameters are the most informative for predicting energetic requirements, at least within the parameter ranges used in this model. Prior to this study, resting metabolic rates were measured using captive Pacific white-sided dolphins in an aquarium biweekly for 1 year (Rechsteiner 2012). To ensure calmness in these study animals, they were desensitized to the study procedures for 10 months prior to data collection (Rechsteiner 2012). We are therefore confident that we have attained robust resting metabolic rate data as an input to our model; however, it would be useful to measure active metabolic rates and compare them to the activity scaler used in this bioenergetic model. To determine the costs of activity more precisely, measurements of oxygen consumption of captive animals in various activity states that approximate activities performed by wild dolphins could be determined (e.g., Williams et al. 1993; Kriete 1995; Fahlman et al. 2008). Future research should thus focus on determining the energetic costs of various activities, the activity budget of this species in the wild, and on ground-truthing model predictions using other modeling methods and field study.

At the population level, the ability to apply total prey requirements is limited due to the wide-ranging distribution of this species and difficulties associated with surveying habitat during all seasons and in offshore waters, which limit accuracy of population counts from the field; a lack of certainty in the population demographics of Pacific white-sided dolphins; and a lack of information regarding the seasonal diets or prey preferences of Pacific white-sided dolphins. Further knowledge in these areas would increase the applicability of this model to ecological processes both globally and locally. Daily prey requirements of populations of Pacific white-sided dolphins should therefore be treated as 1st estimates until further data are gathered. Aerial surveys may be a cost-effective alternative to efficiently survey more habitat, and incorporating data from stranding networks may alleviate some of the biases associated with determining population demographics from bycaught animals (i.e., affinity of juveniles to fishing boats—Ferrero and Walker 1996; Heise 1997b). Finally, a continuous long-term study of the diet of Pacific white-sided dolphins should be undertaken to better predict ecosystem-level impacts caused by, or experienced by, Pacific white-sided dolphins (e.g., Ford and Ellis 2006). Given the paucity of information regarding the population demographics and diets of Pacific white-sided dolphins, this research provides a 1st estimate of prey requirements that can be refined and used for conservation and fisheries management.

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