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Seasonal Resting Metabolic Rate and Food Intake of Captive Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)

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Abstract

Like many marine mammals, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) consume prey that change seasonally in numbers, distribution, and energy density. However, it is not known whether these ecological factors are associated with underlying seasonal changes in energy requirements. We investigated these potential seasonal shifts in physiology by measuring resting metabolic rate (a conserved physiological trait) and recording associated daily food energy intake of three captive adult Pacific white-sided dolphins over 12 consecutive months. Two dolphins that met the criteria for measuring resting metabolism had a mean (± SE) mass-specific rate of 0.31 ± 0.0047 MJ kg^{-1} day^{-1} (~34 MJ day^{-1}), which was higher than that of other species of small cetaceans. Resting metabolic rates of Pacific white-sided dolphins did not vary seasonally and, hence, were not related to observed seasonal changes in water or air temperature, total energy intake, or body mass. Overall, resting metabolism accounted for ~70% of total energy intake. However, total food energy intake changed seasonally and was highest during the fall (October to December). While levels of food intake were not predicted by resting metabolic rate, body mass, or water and air temperatures, the increased intake in the fall resulted in the seasonal increase in body mass exhibited by all three dolphins. Our estimates of resting metabolic rates and relative changes in total energy intake can be used to parameterize bioenergetic models needed to estimate the ecological impacts and energetic requirements of Pacific white-sided dolphins in the wild, which will have conservation implications.

Key Words: energetics, oxygen consumption, Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, season, food intake, metabolic rate

Introduction

Concerns about dolphin conservation and the effect dolphins have on marine ecosystems typically revolve around the amounts and types of food that dolphins need to consume to support healthy populations (e.g., Ford et al., 2010) or the extent to which they compete with fisheries for commercially important species (e.g., Trites et al., 1997; Lockyer, 2007). Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are one of the most abundant and gregarious cetaceans in the North Pacific Ocean (Stacey & Baird, 1991; Buckland et al., 1993), and potentially play a large ecological role as an apex predator. They inhabit both open ocean and near-shore environments, and they may experience acute changes in prey availability that could drive seasonal changes in their energy budgets.

Bioenergetic models that predict energetic requirements of cetaceans have been used to estimate prey biomass requirements and to inform management decisions (Kriete, 1995; Benoit-Bird, 2004; Williams et al., 2004; Barlow et al., 2008; Noren, 2010). Bioenergetic models are parameterized with estimates of various energetic costs incurred by the study species. However, resting metabolic rate (RMR) is typically the most important model parameter in determining total energy requirements of animals because daily metabolic rate is often scaled to it (e.g., Winship et al., 2002; Iverson et al., 2010; Noren, 2010). Bioenergetic models typically assume that seasonal changes in gross energy intake are also reflected in parallel changes in RMRs (e.g., Winship et al., 2002; Iverson et al., 2010). Certainly, RMRs have been known to change seasonally among some species of mammals (Rosen & Renouf, 1998; Fuglei & Øritsland, 1999; Donohue et al., 2000; Rosen & Trites, 2002) and might drive simultaneous changes in food intake. However, empirical evidence suggests that this is not always the case (e.g., Rosen & Renouf, 1998, and references therein).

While seasonal changes in gross energy intake of mammals may be a response to seasonal changes in resting metabolism, it is also possible that they instead reflect parallel changes in prey availability (e.g., Fuglei & Øritsland, 1999), physiological shifts associated with different life history events, or changes in the physical environment (e.g., water temperatures;

Piercey et al., 2013). Seasonal changes in feeding rates have been documented in small cetaceans housed in aquaria and have been linked to changes in pool temperature (Cheal & Gales, 1992; Kastelein et al., 2000), mating season (Kastelein et al., 1999), and changes in behavior or activity levels (Kastelein et al., 2003). Whether or not these patterns are also expressed in wild conspecifics is unknown.

Seasonal changes in resting metabolism represent a basic physiological function that seems more likely to be conserved between wild and captive animals than total food energy intake measurements. Monitoring seasonal changes in resting metabolism and food intake of cetaceans in captivity should therefore contribute to understanding whether seasonality in energy needs should be considered when assessing the food requirements of wild cetaceans, and whether seasonal changes in gross energy intake are reflected in seasonal changes in resting metabolic rate, or vice versa.

The goal of our study was to test whether food ingestion and resting metabolic rates varied seasonally over a 1-y period in a small cetacean, the Pacific white-sided dolphin. We also considered whether changes in food consumption and resting metabolism were related, and we assessed whether Pacific white-sided dolphins have elevated RMRs relative to other species of delphinids and terrestrial mammals.

Methods

Study Animals

We measured resting metabolism and recorded the food intake of three nonreproductive adult Pacific white-sided dolphins that were housed at the Vancouver Aquarium (British Columbia, Canada) since 2001 (a male, M001–*Spinnaker*) and 2005 (two females, F002–*Hana* and F003–*Helen*). These three dolphins were bycaught in fishing nets near Japan in three separate incidents in the 1990s and early 2000s, and were believed to be in their late teens (F002) and early 20s (M001 and F003) during our study period (January to December 2011).

The Pacific white-sided dolphins were housed in three interconnected outdoor pools (2,460 m^3, 1,136 m^3, and 190 m^3, respectively) with filtered sea water pumped from Burrard Inlet and were exposed to ambient environmental conditions. Pool temperatures ranged from ~10 to 15° C over the 12-mo study period.

Data Collection

Food intake data were obtained from detailed electronic records maintained by the Vancouver Aquarium. All three Pacific white-sided dolphins were normally fed *ad libitum* within training requirements. Training regimes/dolphin activity levels were relatively constant throughout the year with more shows occurring in summer than in winter, but more training sessions taking place in winter than in summer (B. Sheehan, Curator, Vancouver Aquarium, pers. comm.). The dolphins typically consumed ~8 to 9 kg of food daily (~42 MJ day^{-1}), consisting of about 40% herring, 40% capelin, 10% salmon, and 10% squid, and supplemented with vitamins (Mazuri VitaZoo) to counteract potential nutrient losses in food due to freezing (Worthy, 2001). The dolphins were usually fed three times/d, and their food intake during each session was carefully weighed to 100 g. Daily energy intakes were averaged over a 1-wk period; and energy density of the prey was calculated from proximate composition analysis of representative samples performed by a commercial laboratory (SGS Laboratories, Vancouver, BC).

Open-circuit gas respirometry was used to measure the rate of oxygen consumption and carbon dioxide production of each Pacific white-sided dolphin while it rested under a clear plastic floating respirometry chamber (detailed below). Data were collected twice per month for each dolphin between 0800 and 0900 h, after the dolphins had fasted ≥ 15 h overnight and were presumably post-absorptive. The dolphins were weighed on a slide-out scale (± 0.10 kg) within 24 h of each trial. During trials, the dolphins were fed small pieces of herring, capelin, and squid to maintain their position under the dome (maximum total = 1 kg). Energetic costs associated with digestion were considered to be negligible over the short duration of the trials given that the trials were considerably shorter than the reported time elapsed before the onset of increased metabolic rates due to feeding in other small cetaceans (e.g., Williams et al., 1993; Yeates & Houser, 2008). The ranges of temperatures experienced by the dolphins at the Vancouver Aquarium (~10 to 15° C) were presumed to be within their thermal neutral zone (TNZ). Although the TNZ of Pacific white-sided dolphins is not specifically known, bottlenose dolphins (*Tursiops truncatus*) have a lower critical temperature between 5.7 and 10.6° C (Yeates & Houser, 2008). Regardless, the effect of water temperature on RMR was explicitly tested.

The Pacific white-sided dolphins were trained to rest calmly in the chamber for a minimum of 10 min while respiratory gases were collected. The dolphins maintained a vertical position while in the dome (Figure 1) based on pre-trial tests that revealed them using minimal fluke strokes and pectoral fin movements to maintain this position. Given the potential for anxiety or stress to inflate metabolic rates, the dolphins were acclimatized to the equipment and experimental procedures over a 10-mo period prior to data collection to ensure they were calm. All training used standard operant conditioning procedures, and experimental protocols were approved by the Animal Care Committees of the Vancouver Aquarium and University of British Columbia (Permit A10-0015).

The metabolic chamber measured 1.4 m × 1.1 m × 0.7 m (volume = 1,078 L) and had a small feeding tube designed to preclude air loss mounted on the top (Figure 1). Air was drawn through the chamber via a hose running from the respirometry dome to a mass flow pump on the dock. Ambient air was drawn through the respiratory dome at a rate of 350 L min^{-1}, and it was sufficient to prevent build-up of carbon dioxide and stagnant air from accumulating in the corners of the dome. A dispersed air inflow system was designed to maximize air mixing within the chamber. We performed a nitrogen dilution test at the start of the study to test the integrity of the system and ensure there were no leaks. The respirometry chamber was sealed against the water surface, and negative pressure prevented air-loss or leakage.

The excurrent airstream was continuously subsampled, and oxygen and carbon dioxide concentrations were determined in a desiccated (Drierite, W. A. Hammond Drierite Company, Xenia, OH, USA) subsample of exhaust air using either a Sable System FC-1B oxygen analyzer and a CA-1B carbon dioxide analyzer coupled to a 500H mass flow generator and controller or a FoxBox P-Series Field Metabolic System (Sable Systems, Las Vegas, NV, USA). Flow rates were corrected to STPD (standard temperature and pressure, dry). Gas analyzers were periodically calibrated against gases of known concentrations as per manufacturer recommendations. Electronic drift during trials was accounted for using ambient air to baseline gas concentrations at the start and end of each trial. A Sable Data Acquisition System was used to record the average gas concentrations over each 1-s interval to a PC. Respiration rate (monitored visually), pool temperature, and air temperature were also recorded during trials.

Data Analyses

Raw gas concentrations were converted to rates of oxygen consumption using LabAnalyst (M. Chappell, University of California at Riverside) and incorporating the appropriate equation (3b) from Withers (1977). Rates of oxygen consumption were calculated as the average of the most-level 5-min period within each 10-min trial, which was when gas concentrations (O_2 and CO_2) in the respiratory dome were level and animals were considered to have met resting conditions (Figure 2). Air flow through the chamber was not turned on until 2.5 min into the trial to allow a build-up of gases in the respiratory dome to the estimated equilibrium point. This permitted oxygen and carbon dioxide gas concentrations to typically stabilize within 3.0 to 4.5 min after the start of the trial. Although the exact conversion between rates of oxygen consumption and energy used depends on the specific energy source the animal uses, the variation is small in mammals (Blaxter, 1989). Therefore, oxygen consumption (L day^{-1}) was converted to energy requirements (MJ day^{-1}), using the equation 1 L O_2 = 20.1 kJ (Schmidt-Nielson, 1997).

We used linear mixed-effects models to determine whether absolute or mass-specific RMR varied with an individual's mass, total energy intake, air temperature, or pool temperature. The same models were used to test whether RMR varied seasonally, where seasons were defined as *winter* (January-March), *spring* (April-June), *summer* (July-September), and *fall* (October-December). Seasons were defined on a calendar basis, which facilitated groupings of potentially

Figure 1. Experimental set-up shows Pacific white-sided dolphin F002 stationed under the floating respirometry dome. A vacuum hose runs from the dome to the mass flow pump (far right to far left of the photo), and the excurrent air flow is subsampled for gas concentrations (far left of the photo).

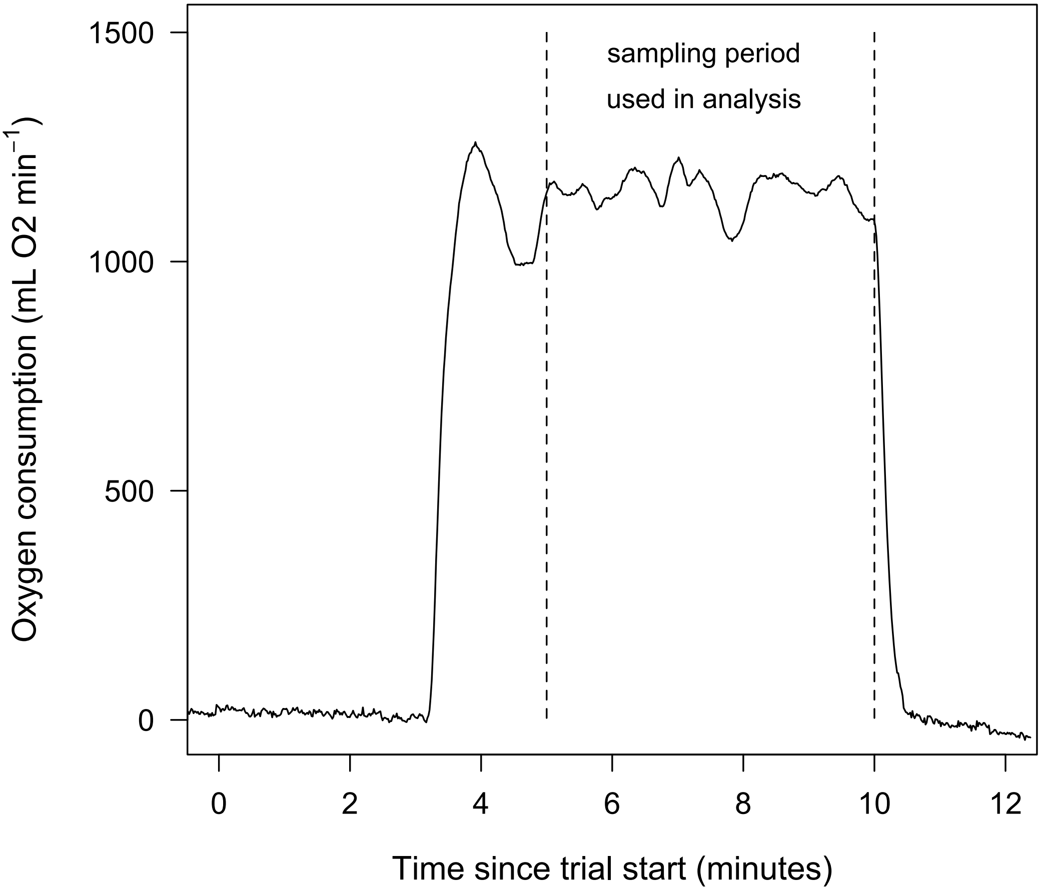

Figure 2. Oxygen consumption of a 110 kg Pacific white-sided dolphin (M001) during a resting metabolic rate (RMR) trial selected randomly from the dataset. The solid line shows oxygen consumed from the metabolic chamber. At 0 min, the dolphin is at rest and stationed in the metabolic chamber. From 0 to 2.5 min, the pump is not running to allow sufficient depletion of oxygen and accumulation of carbon dioxide for measurements. The pump is turned on at 2.5 min (the results of this take ~0.5 min to show up in the data), and the gas concentrations (both oxygen and carbon dioxide) are measured until 10 min into the trial when the air pump is turned off and the dolphin exits the chamber.

similar environmental conditions (i.e., January and December of 2011 are 11 mo apart and not likely to boast the same environmental variable, hence January-March were grouped, and October-December were grouped). Linear mixed-effects models were built in *R*, Version 2.14.1 (R Development Core Team, 2011) with the package *nlme* (Pinheiro et al., 2009) using the maximum likelihood method. Season was input as a fixed effect, and mass, total food intake, air temperature, and pool temperature were input as random effects and as continuous data. Animal ID was incorporated into all the models as a repeated measures effect. A nested model design was used, whereby air temperature and pool temperature were nested in season, and where food intake and mass were nested in animal ID. The number of fixed and random effects was varied within each model to determine which were important in predicting RMR. Akaike Information Criterion (AIC) model selection was used to determine the model that best fit the data (lowest AIC score). This process was repeated for gross and mass-specific energy intake, except that metabolic rate was input as a random effect instead of food energy intake acting as a random effect. A *post-hoc* general linear hypotheses and multiple comparison test (glht) using the Tukey method was implemented to test for significant differences in food intake or RMR in different seasons (*multcomp package* in *R*; Hothorn et al., 2012).

Results

Despite an extensive 10-mo pre-experimental conditioning period, a probable training effect was seen while measuring RMR in one of the Pacific white-sided dolphins (F002). Although the effect was subtle, F002 appeared somewhat nervous during her trials. Most notably, she exhibited stiffened body posture with eyes opened wider than usual, and she appeared slightly less focused on trainers than usual during some of her metabolic trials. The metabolic rate of F002 was 50.90 ± 2.91 MJ day^{-1} (0.40 ± 0.02 MJ kg^{-1} day^{-1}) at the start of the study in winter, which was equivalent to about 135% of her total daily food intake. Her measured metabolism steadily decreased over the following 12 mo to the equivalent of about 94% of total food intake at the end of the study in the fall (42.07 ± 1.82 MJ day^{-1}; 0.34 ± 0.01 MJ kg^{-1} day^{-1}), which we suspect was due to her becoming more comfortable with the metabolic trial methods over time. Due to both the presumed training effect and the overall high metabolic rate relative to food intake, we do not believe that results from F002 approached a metabolic rate that could be classified as "resting." Thus, we did not test whether F002's metabolic rate changed with season and omitted F002 from further results regarding the metabolic rate measurements.

Over the 12-mo study, the mean RMRs of the two remaining Pacific white-sided dolphins averaged 34.19 ± 0.51 MJ day^{-1} (0.31 ± 0.0047 MJ kg^{-1} day^{-1}; Figures 3a & 3b). The mean RMR of the female

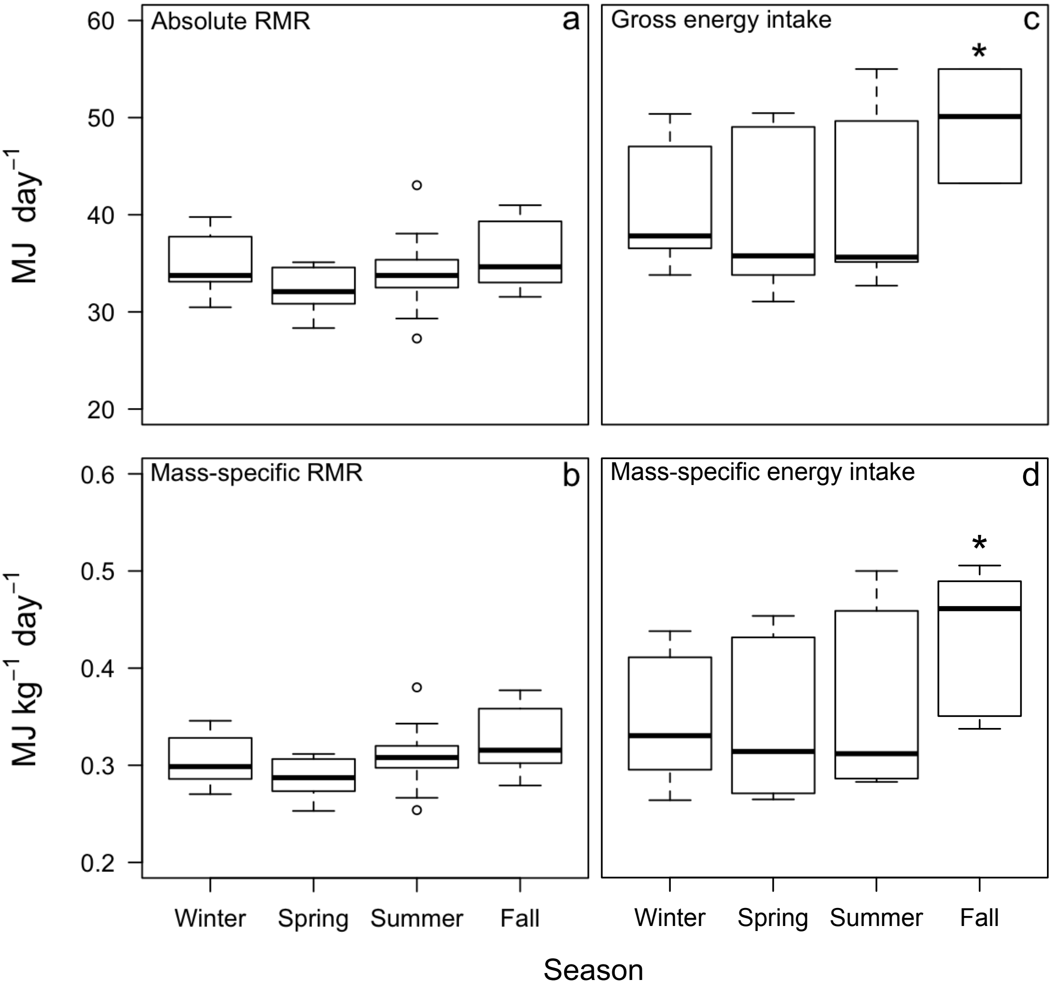

Figure 3. The effect of season on (a) absolute RMR, (b) mass-specific RMR, (c) gross energy intake, and (d) mass-specific energy intake of Pacific white-sided dolphins; energy intake measurements are presented for all three dolphins that participated in the study, while RMR measurements are only presented for the two individuals that were judged to meet resting criteria. Energy intake was significantly greater in fall (October to December) than in other seasons. Bold lines in the center of the 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 outliers.

(F003) was 33.33 ± 2.20 MJ day^{-1} or 0.29 ± 0.02 MJ kg^{-1} day^{-1}, which was equivalent to 64% of her total daily food intake (~51 MJ); and the mean RMR of the male (M001) was 35.17 ± 2.48 MJ day^{-1} or 0.32 ± 0.03 MJ kg^{-1} day^{-1} and accounted for 84% of his total daily food intake (~42 MJ). Based on the AIC values, the linear mixed effects model that best described the absolute RMRs of the two dolphins was the null model that accounted for repeated measures only and did not include the effects of season, pool or air temperatures, total food intake, or body mass (AIC = 242.33, log likelihood = -118.16). The same was true for the model that best described the mass-specific metabolic rates of the two dolphins (AIC = -180.48, log likelihood = 93.24).

Average metabolic rates were about three times those predicted for adult terrestrial mammals (Kleiber, 1975), and they were higher than most other values reported for cetaceans (Figure 4). However, the values obtained in our study are similar to those reported by Ohizumi et al. (2009) for Pacific white-sided dolphins.

Mean (± SE) average daily gross energy intake of the three Pacific white-sided dolphins was 42.84 ± 4.54 MJ day^{-1} (0.37 ± 0.05 MJ kg^{-1} day^{-1}; Figures 3c & 3d). The model that best fit the gross energy intake data included only the fixed effect of season and only the random effect of animal ID (AIC = 338.16, log likelihood = -162.08). Models that included nested effects of pool temperature, air temperature, individual mass, and resting metabolism did not improve the model fit. Similarly, the model that best fit the mass-specific energy intake data also accounted for the random effect of animal ID and the fixed effect of season, and was not influenced by any other parameters, including air temperature, water temperature,

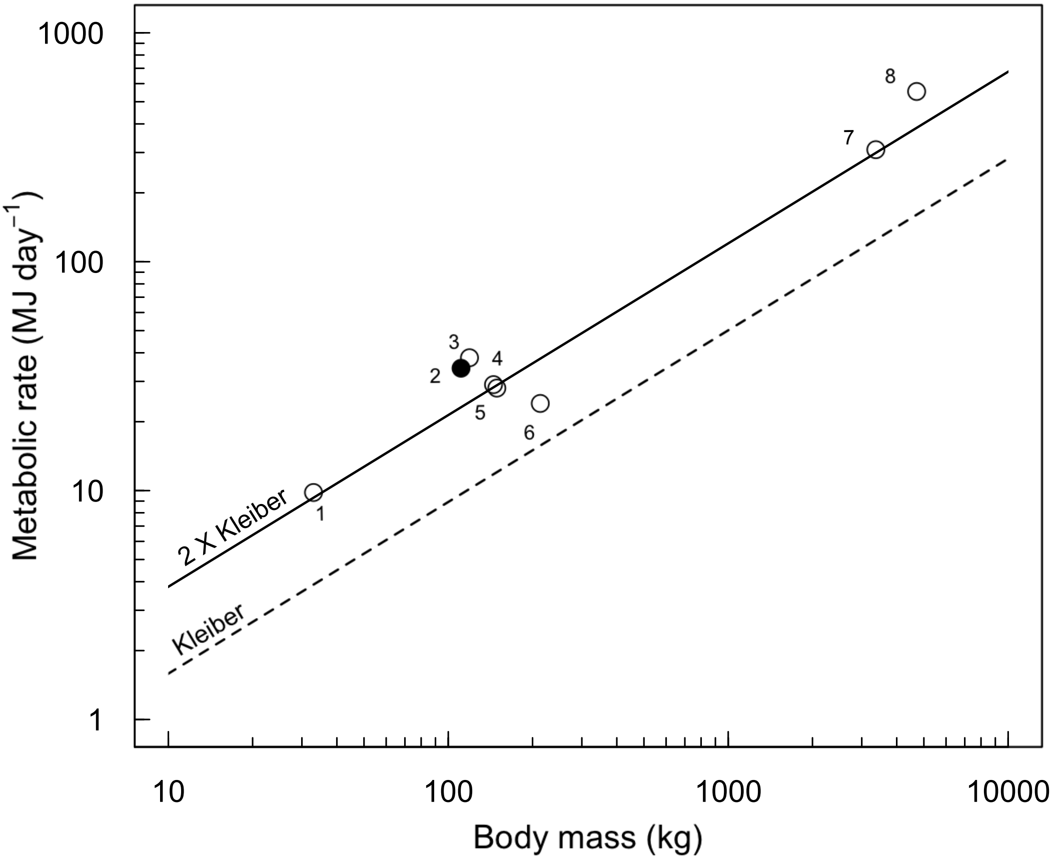

Figure 4. RMRs of dolphins and porpoises as predicted by body mass; the filled circle (2) are data from M001 and F003 (Pacific white-sided dolphins – our study), and open circles indicate data from previously published research: (1) harbor porpoise (Karandeeva et al., 1973), (3) Pacific white-sided dolphin (Ohizumi et al., 2009), (4) bottlenose dolphin (Williams et al., 1993), (5) bottlenose dolphin (Williams, 2001), (6) bottlenose dolphin (Karandeeva et al., 1973), and (7 & 8) female and male killer whales (Kriete, 1995). Some of these data were previously summarized in Costa & Williams (1999) and Hunter (2005). The dashed line represents Kleiber's (1975) mouse to elephant curve, and the solid line represents two times Kleiber's predictions (predicted regression for marine mammals; Costa & Williams, 1999).

or changes in body mass (AIC = -303.04, log likelihood = 158.52). *Post-hoc* glht results revealed that both total and mass-specific food intake were significantly highest in fall (October-December; mean 49.56 ± 3.61 MJ day^{-1}, 0.43 ± 0.04 MJ kg^{-1}day^{-1}; $p < 0.001$) and relatively constant during the other seasons (Figures 3c & 3d). The increase in food intake during the fall was matched by an increase in body mass in each individual, but the relationship between food intake and body mass was inconsistent at other times of the year and between individuals (Figure 5).

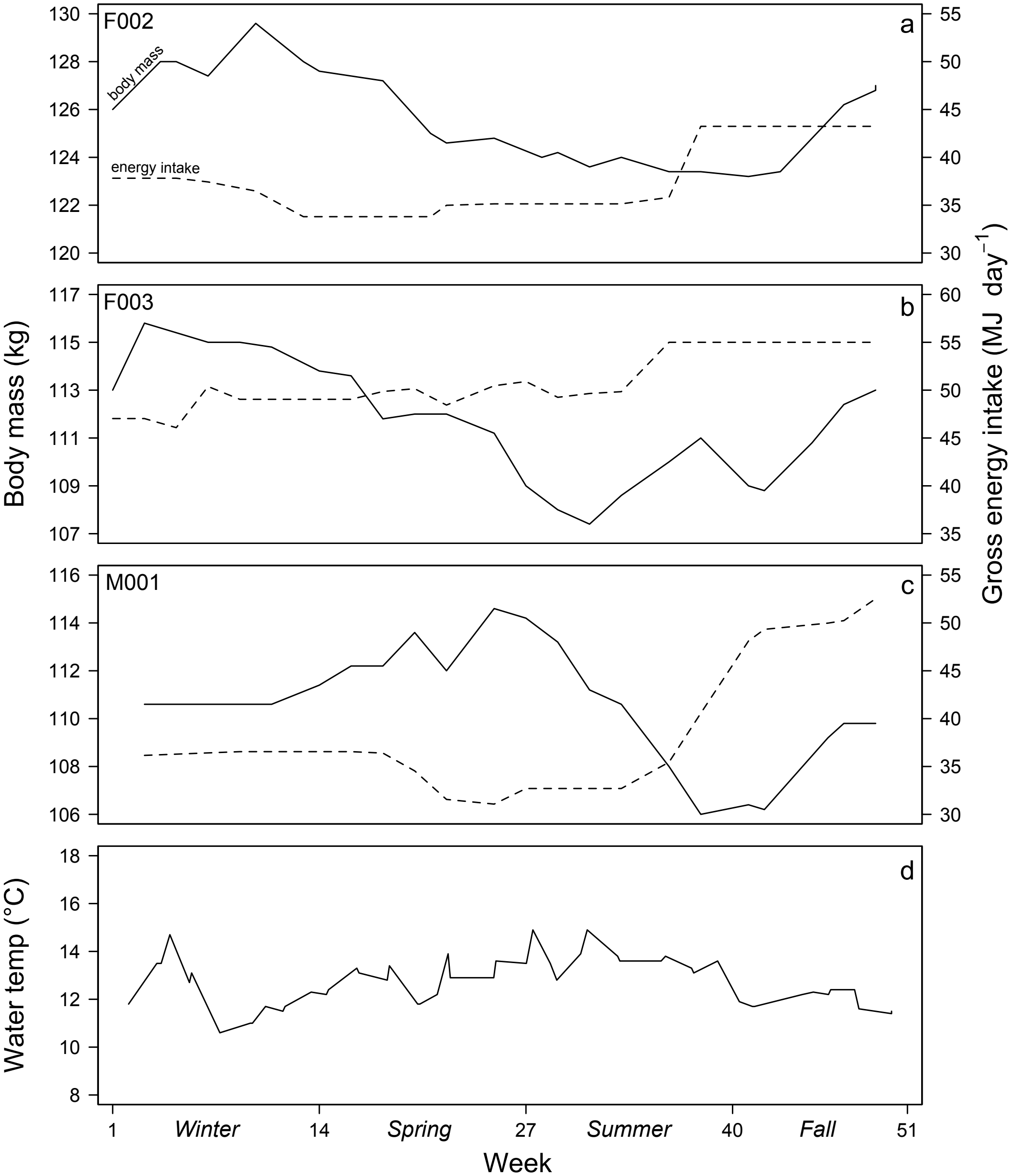

Figure 5. Weekly mass measurements of three Pacific white-sided dolphins—F002 (a), F003 (b), and M001 (c)—from the 1st to the 52nd week of 2011 (solid line) and weekly average gross energy intake of these three dolphins in 2011 (dashed line). Note the y-axes scales for each animal have different intercepts but have a 10 kg range (mass; panels a-c) and a 25 MJ range (energy intake; panels a-c). Water temperatures (d) were measured concurrently with RMR trials.

Discussion

The RMRs (resting metabolic rates) of the two Pacific white-sided dolphins were constant throughout the year despite their increased food intake in the fall. We suspect that this finding can be applied to wild dolphins given that resting metabolism represents a basic physiological function that should be conserved between wild and captive animals. The same cannot be said for food intake, however, which is likely lower in captivity due to reduced levels of activity and possibly warmer water temperatures. Instead, seasonal changes in food intake in captivity and the wild are more likely due to physiological processes associated with key life history events (i.e., seasonality in estrous, calving, and lactation) and changes in the abiotic environment (e.g., Cheal & Gales, 1992; Kastelein et al., 2000; Piercey et al., 2013).

We regret having to discard the metabolic data from one Pacific white-sided dolphin due to the presumed training effect, leaving us with data from only two individuals. Interestingly, the subtle behaviors we noted (stiffened body posture and eyes opened wider than usual) indicating that she was slightly nervous or excited had a marked effect on her metabolic rate which was almost 50% higher than the other conspecifics. This demonstrates the importance of ensuring a calm behavioral state when taking measurements of resting metabolism. Despite this shortcoming, the data collected from these three individuals represent the most comprehensive energetics study conducted to date with Pacific white-sided dolphins and the only cetacean energetics study that has spanned multiple seasons and examined both RMRs and total calories ingested. As such, it provides a starting point upon which further energetic studies of small cetaceans can build.

Resting Metabolic Rates

There has been disagreement regarding how many calories marine mammals require to meet maintenance requirements. Some research suggests that the RMRs of marine mammals are elevated when compared to terrestrial species (Brodie, 1975; Snyder, 1983; Costa & Williams, 1999; Hunter, 2005). Other researchers suggest marine mammals have similar maintenance metabolic rates as their terrestrial counterparts (Gaskin, 1982; Lavigne, 1982; Worthy, 1987; Kasting et al., 1989) and that many of the differences reported are due to experimental errors, including animal stress levels.

Metabolic rates of our two Pacific white-sided dolphins that met the criteria for "resting" were generally high, but within the upper expected range of values predicted for marine mammals by Costa & Williams (1999). Proximally, this high metabolic rate may be associated with Pacific white-sided dolphins having unusually large thyroid glands relative to their body size when compared to other odontocetes and to terrestrial mammals of similar masses (Ridgway & Patton, 1971; Kot, 2010). Ultimately, the high metabolism observed in Pacific white-sided dolphins might be used to support physiological readiness for high energetic output of fast muscles such as the sudden bursts of high activity (e.g., in predator avoidance and in acrobatic displays) that this species typically exhibits (Van Waerebeek & Würsig, 2002). Physiologically, elevated resting metabolic rates may be driven by high mitochondrial density in muscle tissue—an adaption to fuel the pursuit of high-energy prey (Spitz et al., 2012).

The RMRs of our two study animals accounted for ~75% of their total energy intake, which is similar to previous estimates (~60 to 80% of energy intake) of two other Pacific white-sided dolphins at an aquarium in Japan (Ohizumi et al., 2009). Our observation that food intake was only about 25% higher than resting metabolic requirements concurs with behavioral observations of these same individuals that indicated generally low levels of activity within their aquarium pools. Activity budgets constructed for these same three dolphins at the Vancouver Aquarium in June and July of 2010 (Javdan, 2010) and in January of 2012 (Rechsteiner, 2012) indicated that they spent ~70% of their time resting, or in low-energy, stereotypical behaviors. By comparison, wild conspecifics are thought to spend only about 3% of their time at rest (Black, 1994).

The RMRs for our Pacific white-sided dolphins were seasonally constant. Cetaceans generally appear to have elevated thyroid sizes in comparison with terrestrial mammals of similar masses, which may indicate an elevated and seasonally constant metabolic rate (Ridgway & Patton, 1971; Kot, 2010). However, it is unclear whether our results are typical in the absence of other seasonal measurements of resting metabolic rate in other cetaceans. Research with pinnipeds has sometimes shown seasonal changes in RMR. For example, RMRs may be depressed in times of low food availability (Fuglei & Øritsland, 1999; Rosen & Trites, 2002), or they may change seasonally with physiological or morphological changes such as molting (Donohue et al., 2000). Research with cetaceans has shown fluctuations in metabolic rates that correspond with environmental temperature changes within shorter timeframes (Williams, 2001; Yeates & Houser, 2008), although there was no relationship between water or air temperature and metabolism in our study.

Seasonal Changes in Total Food Intake

Total food intake increased in the fall for all three Pacific white-sided dolphins (October-December), with the greatest increase occurring for the male. This increased food intake during fall was not driven by an increase in RMR.

Food intake among mammals is known to be influenced by a variety of factors such as changes in resting metabolism (Rosen & Trites, 2002), ambient temperature (Cheal & Gales, 1992; Kastelein et al., 2000), diet (Knott, 1998), body condition (Lager et al., 1994), food availability (Aleksiuk, 1970; Moen, 1978; Knott, 1998), and behavior and activity (Rosen & Renouf, 1998; Kastelein et al., 1999). Of these factors, we could determine that changes in diet or prey composition (prey composition of the diet remained constant), resting metabolism, and pool temperature did not predict the food consumption of the study animals. Neither were changes in food intake directly related to changes in body mass.

We constructed the linear mixed-effects models to infer population trends from limited data in a small sample using a repeated measures framework. As such, the models identified overall trends in the data. Changes in body mass occurred with different timing and to different extents in each study animal. However, the increased energy intake in fall resulted in increases in body mass in all three animals. The changes in body mass observed at other times of the year were clearly not related to changes in either RMR or food energy intake. Given that the dolphins were mature, it is likely that body mass changes were due to differences in blubber mass, although the degree to which this would reflect cycles in the wild is unknown. However, given the potential role of body composition to explain variation in metabolic rate, future work should measure seasonal changes in blubber mass.

Pacific white-sided dolphins are known to have seasonally distinct reproductive cycles, with the majority of successful mating occurring in late summer and early fall (Robeck et al., 2009). It is thus possible that mating behavior in summer increased the energy used by the male. Hormonal changes associated with the mating season may not trigger an increase in appetite to match increased energy output due to sexual behavior. This is consistent with husbandry staff at the Vancouver Aquarium having noted decreased interest in food during times of the year when mating behaviors are prevalent (B. Sheehan, Curator, Vancouver Aquarium, pers. comm.). The females may also be triggered to increase mass in fall as an adaption to fuel a potential pregnancy; Pacific white-sided dolphin conceptions peak from August to October (Robeck et al., 2009).

Alternatively, the observed changes in body mass and food intake may have been a byproduct of innate adaptations to seasonal aggregations of high-energy prey in the wild. Captive animals do not experience the same changes in prey availability or prey quality as their wild counterparts; therefore, the relationship between the two variables in captive studies might be a byproduct of artificially constant prey availability or quality. For example, Pacific white-sided dolphins in waters near Japan (where these dolphins were captured) primarily consume sardines (Miyazaki et al., 1991) and anchovy (Kitamura et al., 2008), which typically have their highest energetic densities during spring and summer (Ikeda, 1987; Shirai et al., 2002) when our dolphins were losing weight at the aquarium.

Our difficulty in ascertaining the extent and cause of the changes in food intake is partly due to our small sample size. Further data collection spanning years and sexes of dolphins, and involving other aquaria, could determine whether seasonal trends in food consumption are sex-specific and if such changes occur in Pacific white-sided dolphins at the population level.

Ecological Implications and Conclusions

Our estimates of resting metabolic rates can be used to parameterize bioenergetics models needed to estimate annual and seasonal energy and food biomass requirements of Pacific white-sided dolphins in the wild. Resting metabolism is a key parameter that predicts the daily total metabolic requirements of mammals and impacts other bioenergetic parameters (such as activity rates), which are typically scaled to RMR (e.g., Winship et al., 2002; Iverson et al., 2010; Noren, 2010). Although it is difficult to extrapolate results of captive animal studies to wild populations, it is generally assumed that RMR is a physiological trait that is consistent between wild and captive animals (e.g., Winship et al., 2002; Noren, 2010). Therefore, the results of our study can be used as a basis for certain predictions regarding the energetics of wild Pacific white-sided dolphins.

The high resting metabolic rates displayed by our study animals suggest that Pacific white-sided dolphins have high energy requirements. In the wild, Pacific white-sided dolphins spend approximately 3% of their time at rest (Black, 1994) compared with our study animals which spent ~70% of time resting (Javdan, 2010; Rechsteiner, 2012). This implies that wild dolphins would consume more food than the dolphins used in our study due to their increased activity levels. Wild dolphins are believed to consume ~65 to 70 MJ day^{-1} (Sigurjónsson & Vikingsson, 1997; Rechsteiner et al., 2013), which is about 35% higher than the

~43 MJ day^{-1} our study animals consumed. This has important conservation implications as the apparent relatively high energetic requirement of Pacific white-sided dolphins may make them more susceptible to changes in fish availability or quality.

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