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Seasonal Changes in the Food Intake of Captive Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)

Rebecca S. Piercey, Erin U. Rechsteiner, Brian C. Battaile, and Andrew W. Trites

Marine Mammal Research Unit (MMRU), Fisheries Centre, University of British Columbia,
2202 Main Mall, Vancouver, BC, Canada V6T 1Z4
E-mail: a.trites@fisheries.ubc.ca

Abstract

The Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) is one of the most abundant apex predators in the North Pacific Ocean, but little is known about how much food they consume and whether their food requirements vary seasonally. We attempted to address these two issues using the feeding records of five Pacific white-sided dolphins housed at the Vancouver Aquarium. These individuals consumed an average of 7.9 kg ± 0.35 (± SE) of fish and squid per day (~11,000 kcal day^{-1}), which equated to ~7% of their body mass and an annual mean intake of 2,880 kg ± 131.8 (± SE) per dolphin (N = 5). Patterns of food consumption and seasonal changes were assessed using long-term feeding records (1977 to 2001) from a single adult female, and were found to be highest in terms of biomass and calories in late December, and about 15% less in late May and early June. Seasonal pool temperatures (range 6.5 to 21.5° C) were inversely related to food intake and accounted for part of the variation, suggesting that seasonal cues other than temperature triggered the changes in food consumption. Amounts of prey consumed by Pacific white-sided dolphins are undoubtedly higher in the wild than in captivity due to relative differences in their respective behaviors in the two environments. However, relative seasonal changes in energy requirements are likely to be independent of living conditions and have implications for estimating the energy requirements of Pacific white-sided dolphins in the wild.

Key Words: season, Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, cetacean, captive, food intake

Introduction

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are distributed throughout the temperate waters of the North Pacific Ocean and are one of the most abundant top predators (numbering ~1 million individuals, 95% CI ~200,000 to 4,000,000, CV = 0.900; Buckland et al., 1993). They are believed to eat up to 60 species of fish and 20 species of cephalopods (Black, 2009), but how much they eat and how it might change seasonally is unknown.

A variety of different methods can be used to estimate the food intake and energy requirements of cetaceans (Trites, 2003). One approach is to directly estimate food intake by measuring the frequency of capture, the capture efficiency, and the handling times of cetaceans observed in the wild (e.g., Ford et al., 2005, 2010, 2011; Hanson et al., 2010). Stomach content analysis can also be used to determine biomass and species type consumed (Benoit-Bird, 2004). Another method to infer food intake is to mathematically model the biomass of prey required to support the energetic cost of growth, reproduction, maintenance, and activity (e.g., Rosen & Trites, 1999; Winship et al., 2002; Noren, 2011). A fourth way to determine food requirements of cetaceans is to record the amounts of prey consumed in captivity (e.g., Kastelein & Vaughan, 1989; Kastelein et al., 1993, 2002).

Determining food intake using captive feeding records has a number of advantages over other methods (Trites, 2003). Principally, there is no ambiguity in the amounts of food consumed by captive animals compared with drawing inferences about consumption from stomach contents without any prior knowledge about feeding frequency, digestibility of prey, and whether the prey was consumed by the marine mammal or by one of its prey species. Cetaceans housed in captivity are easily accessed, unlike their wild counterparts that must be sighted and followed to collect data. Data can also be collected 365/y from captive cetaceans as can information about age, body weight, and size; health; social setting; diet composition; ambient environmental conditions; and breeding status (e.g., Kastelein & Vaughan, 1989; Kastelein et al., 2000a, 2003a).

Captive feeding records have been used to determine the food requirements for many delphinids, including killer whales (*Orcinus orca*; Kastelein et al., 2000c, 2003b), dusky dolphins (*Lagenorhynchus obscurus*; Kastelein et al., 2000b), false killer whales (*Pseudorca crassidens;* Kastelein et al., 2000a), Atlantic bottlenose dolphins (*Tursiops truncatus*; Kastelein et al., 2002, 2003a), Commerson's dolphins (*Cephalorhynchus commersonii*; Kastelein et al., 1993), and Amazon River dolphins (*Inia geoffrensis*; Kastelein et al., 1999), but have not been assessed for Pacific white-sided dolphins due in part to their relative rarity in captivity. The Vancouver Aquarium has housed Pacific white-sided dolphins since the 1970s and has maintained daily feeding records, pool temperatures, and other information related to age, size, and sex of individuals. These data can be used to estimate the amounts that Pacific white-sided dolphins eat in captivity, whether consumption changes seasonally, and whether it is influenced by water temperature.

We analyzed the feeding records of five captive Pacific white-sided dolphins to determine how much they ate, and we used historical feeding records from one individual to assess seasonal influences in food requirements. Our results are useful for assessing the food requirements of Pacific white-sided dolphins in aquaria, and our research may improve the understanding of seasonal nutritional needs of animals in both captive and wild environments. Determining the seasonal and average food requirements may also help to identify times of the year during which changes in food requirements may have a heightened effect on individual survival in Pacific white-sided dolphins (e.g., during lactation or gestation when caloric requirements are presumably elevated), and it may call attention to times of potential competition between humans and dolphins for food resources (Trites et al., 1997).

Methods

Study Animals and Habitats

We obtained food intake records from five adult Pacific white-sided dolphins housed at the Vancouver Aquarium (Vancouver, British Columbia) between 1971 and 2010, as well as daily recordings of pool water temperature. The five study animals (1 male—M001-*Spinnaker*; and 4 females—F001-*Whitewings*, F002-*Hana,* F003-*Helen*, and F004-*Lavern*; Table 1) participated in daily shows at the Vancouver Aquarium and were fed Pacific herring (*Clupea pallasii*), Chinook salmon (*Oncorhynchus tshawytscha*), California squid (*Loligo opalescens*), capelin (*Mallotus villosus*), and Atka mackerel (*Pleurogrammus monopterygius*). Mackerel was only fed to a few animals for a few days upon their arrival at the Vancouver Aquarium and then substituted by other food species. The diets and amounts consumed by each Pacific white-sided dolphin varied daily depending on the appetite and behavioural motivations of the dolphins and the availability of the food species.

Food intake was recorded either as the biomass of each food species consumed (food intake records pre-March 2007) or as both biomass and caloric content of each food species consumed (post-March 2007). Caloric values provided in the feeding records were measured using proximate composition analysis of representative food samples. For feeding records pre-March 2007, caloric values of individual food intake were estimated using prey caloric values in the available literature (Table 2). From 1977 to 2001, the average diet of F001 consisted of 91.4% herring, 6.8% squid, 1.6% capelin, and 0.2% salmon. After 2001, M001, F002, F003, and F004 were fed an average diet of 67% herring, 26% capelin, 5% squid, 2% salmon and 0.4% mackerel (percentages determined by mass).

Of the five Pacific white-sided dolphins, F001 was wild-caught as a subadult off the coast of British Columbia in the late 1960s and believed to have been in her mid-30s upon her death (early 2002). M001, F002, and F003 were rescued after being injured in Japanese fisheries in the 1990s (M001) and early 2000s (F002 and F003); they arrived at the Vancouver Aquarium in 2001 (M001) from the Kaiyukan Aquarium and in 2005 (F002 and F003) from the Enoshima Aquarium in Japan. They were thought to be in their mid-20s

Table 1. Mean morphometrics and mean daily food intake of the five Pacific white-sided dolphins used in this study

							Mean daily food intake			
Code	Name	Sex	Study period	Age at study end (y)	Mean length (cm)	Mean mass (kg)	Range (kg)	Mean (kg)	SE	*n*
F001	Whitewings	F	1971-2001	mid-30s	198	118	2.4-10.6	6.7	0.03	1,302
M001	Spinnaker	M	2001-2010	mid-20s	195	110	3.7-11.4	8.0	0.05	490
F002	Hana	F	2005-2010	late-teens	226	123	3.4- 9.0	7.9	0.07	270
F003	Helen	F	2005-2010	mid-20s	206	107	5.1-13.8	8.8	0.09	271
F004	Lavern	F	2005-2008	mid-30s	212	123	1.7-12.4	8.0	0.12	178

Table 2. Estimates of energetic density of food (1977-2010)

Food species	Time of capture	Year	Energy density (kcal kg^{-1})	Source
Clupea pallasii (Pacific herring)	November-December	1977-1999, 2003, 2007, 2008	1,879	Bomb-calorimeter at Vancouver Aquarium
		2000	2,301	
		2001	1,965	
		2002	1,941	
		2004	1,678	
		2005	1,757	
		2006	1,875	
		2007-2010		
Oncorhynchus tshawytscha (Chinook salmon)	June	1977-2010	1,745	Logerwell et al., 2005
Loligo opalescens (California squid)	Summer	1977-2005	674	Bomb-calorimeter at Vancouver Aquarium
		2006	621	
		2007-2010		
Mallotus villosus (Capelin)	July-August	1977-1992, 1995-2000, 2002-2007	943	Van Pelt et al., 1997; Logerwell et al., 2005; bomb-calorimeter at Vancouver Aquarium
		1993-1994	981	Van Pelt et al., 1997
		2001	1,207	Logerwell et al., 2005
		2007-2010		Bomb-calorimeter at Vancouver Aquarium

(M001), late-teens (F002), and mid-20s (F003) at the study-end. F004 was wild-caught as a calf in the 1970s in California, was brought from the San Antonio SeaWorld in 2005, and was thought to have been in her mid-30s upon her death.

The study animals inhabited three interconnected outdoor pools consisting of a main pool (2,461 m^3), a smaller adjacent pool (1,136 m^3), and a medical pool (190 m^3). Ambient sea water was filtered and pumped into the dolphin pools from nearby Burrard Inlet. The Pacific white-sided dolphins were exposed to ambient temperature and environmental conditions consistent with those of a temperate environment (49º 18' N, 123º 08' W). Pool temperatures were measured daily from 1977 to 2010. Although the dolphin habitat was occasionally heated, no distinction was made between heated and nonheated temperature readings. We averaged pool temperatures by week, and linked these measurements with food intake data so that average pool temperatures and food intake were calculated on the same days.

F001 resided with up to three killer whales (*Orcinus orca*) at one time from 1971 to 2001. F001 later lived with one other Pacific white-sided dolphin. M001, F002, F003, and F004 resided alone, or with conspecifics, depending on the year.

Data Analyses

We averaged daily total food intake (biomass and calories) by week. Daily total food intake (kg day^{-1}) as well as intake as a percentage of the individuals' average body mass was plotted for each of the five animals, as well as mean intake and mean intake as a proportion of mass for all animals. We used a linear model to compare the average consumption of each individual with its body weight. Separate linear models were fit to food consumption data recorded in either kg or calories.

We restricted the seasonal analysis to the food intake of F001 (1977 to 2001). This individual was selected for exploration of seasonal trends in food intake because her training and husbandry requirements differed from the four other Pacific white-sided dolphins housed at the Vancouver Aquarium in more recent years. Most notably, F001 was not the focus of shows (unlike the killer whales with which she resided), and less emphasis appears to have been paid to having her maintain a specific body condition (i.e., her mass was allowed to fluctuate within healthy limits). Amounts of food offered to F001 were based on trainers scoring her attentiveness and energy level each day on scales of 1 to 5, and this resulted in food baselines being increased on following days if trends in scores were high, or lowered if scores were low (B. Sheehan, pers. comm.). Thus, seasonal variations in the food intake of F001 from 1977 to 2001 were not dampened by training (i.e., shows) and husbandry requirements (i.e., maintaining body weights and girths within set ranges, or keeping pool temperatures within narrower limits by heating and cooling the water). Exploratory analysis of the feeding records for M001, F002, F003, and F004 from the more recent years (2001 to 2010) showed little if any seasonality in their consumption and suggests that these factors (training and husbandry initiatives) likely influenced the seasonal food intake of these four individuals.

We explored seasonal trends in food intake in the 24 y in which F001 was sexually mature, based on an assumed age of sexual maturity of 8 y for Pacific white-sided dolphins (Heise, 1997). Removing feeding records prior to 1977 (when F001 would have been sexually immature) avoided the confounding influences of growth and development on food intake—such as the elevated metabolic rates of juvenile animals (Kasting et al., 1989; Kastelein et al., 1993, 2003b; Allen, 2009) that are associated with increased growth costs and other physiological factors (i.e., activity, thermoregulation), which may in turn mask seasonal changes in food intake.

We applied LOESS smoothing functions to determine the presence of seasonal changes in food intake (*R*, Version 2.14.1; R Development Core Team, 2011). We also used the same smoother to identify seasonal changes in water temperatures, and fit a linear model to the weekly temperature and consumption data to assess whether pool temperature alone could predict changes in food intake.

Results

On average, the five Pacific white-sided dolphins consumed 7.9 kg day^{-1} ± 0.35 (± SE) or ~11,000 kcal day^{-1} (Figure 1a). This equated to a food consumption of about 7% (± 0.44) of their body weight per day (Figure 1b). There were no significant correlations between the mean body

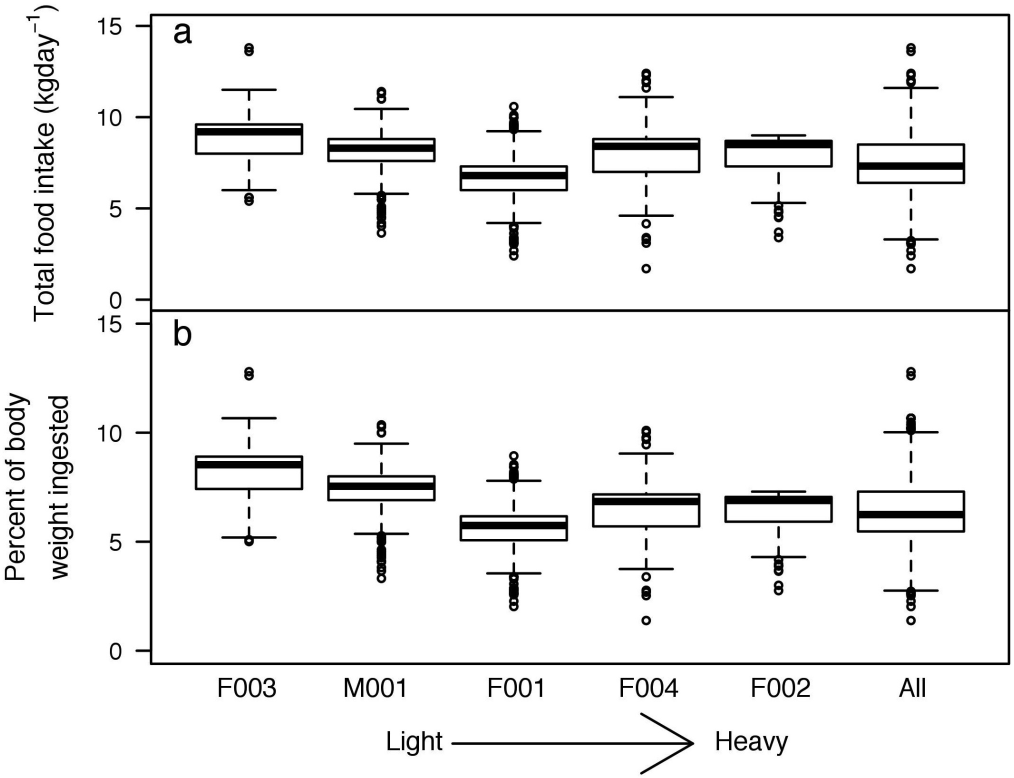

Figure 1. Daily food intake of five Pacific white-sided dolphins (F001-F004, M001) expressed as (a) total mass consumed by an individual and (b) a percentage of total body mass consumed. Bold lines representing the median, top, and bottom box edges indicate the 25th and 75th percentiles, the whiskers show the length of the interquartile range, and open circles are outliers. The box plots are ordered from the lightest (left) to heaviest dolphins (right).

masses of the Pacific white-sided dolphins and their mean total food intake in kg ($R^2 = 0.24$, $p = 0.40$; Figure 2a), or calories ($R^2 = 0.13$, $p = 0.55$; Figure 2b).

The annual average food intake of F001 compared well with data from the other four study animals. F001 consumed an average of 2,430 kg of food annually, while the other three females (F002, F003, and F004) consumed an average of 2,875 kg, 3,250 kg, and 2,880 kg, respectively. The male, M001, consumed an annual average intake of 2,965 kg.

F001 consumed an average of 6.7 ± 0.03 kg day^{-1} (11,187 ± 71 kcal day^{-1}) or about 6% (± 0.03) of her body mass throughout the study period (1977 to 2001). Her food intake ranged from 2.4 to 10.6 kg day^{-1} from 1977 to 2001 (4,700 to 18,400 kcal day^{-1}) and showed seasonal fluctuations (Figure 3a). On average, food intake was highest in winter at the end of the year (December) and lowest at the start of summer (June). The minimum mean (± 95% CI) food intake was ~6.3 ± ~0.15 kg day^{-1} (~11,100 kcal day^{-1}) in summer and rose to a high of ~7.2 ± ~0.15 kg day^{-1} (~13,200 kcal day^{-1}) in winter. F001 consumed 15% less in summer (average of 4 mo) than in winter (average of 4 mo) (Figure 3a).

Seasonal fluctuation in pool temperature followed seasonal changes in food intake (Figure 3), but it was inversely related to food intake (Figure 4) and could account for only a small portion of the variation of food consumed ($R^2 = 0.07$, $p < 0.001$; Figure 4). Water temperature (1977 to 2001) ranged from 6.5 to 21.5º C, and had an average seasonal low of ~10.2º C ± ~0.15 (95% CI) during Week 5 (early February), and an average seasonal high of ~15.7º C ± ~0.2 (95% CI) during Week 32 (mid-August). Mean pool temperature was 12.9 ± 0.07º C throughout the study period.

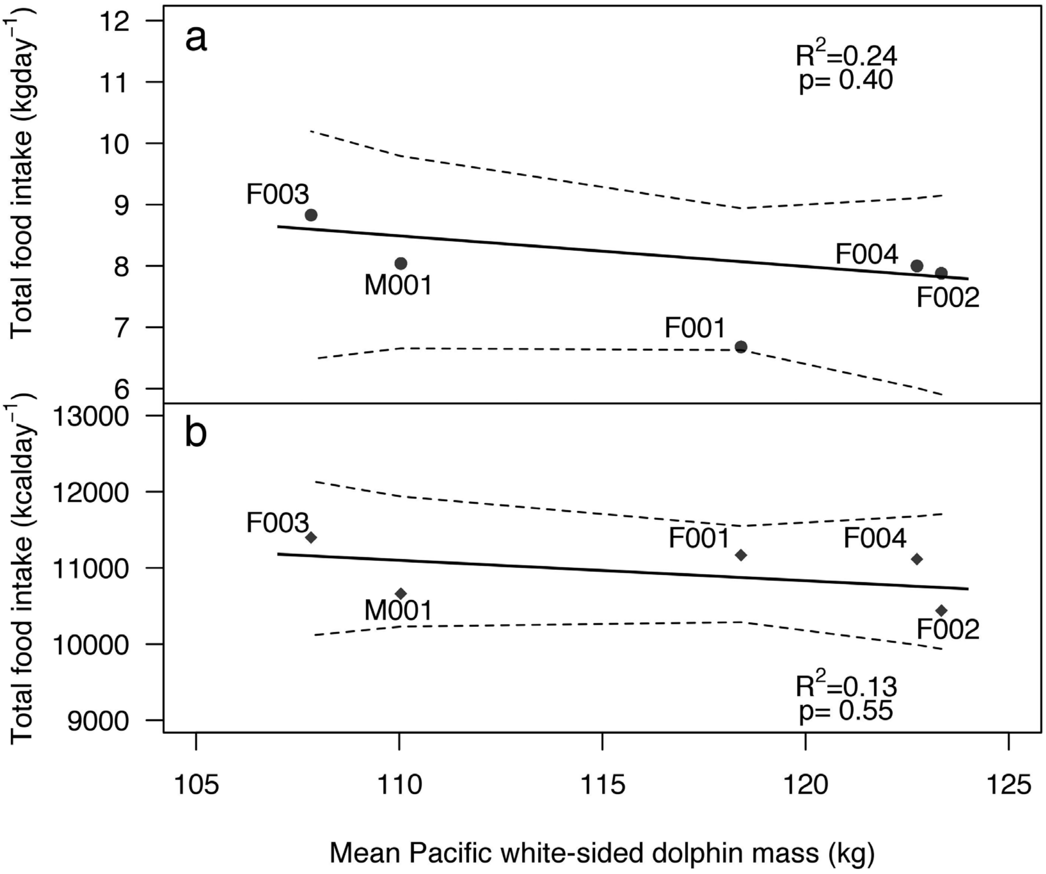

Figure 2. Average food intake of five captive Pacific white-sided dolphins (F001-F004, M001) as a function of mean body mass showing (a) food intake in kg and (b) intake in kcal as predicted by linear models. The dashed lines are 95% confidence intervals (CI). Note that neither regression was statistically significant.

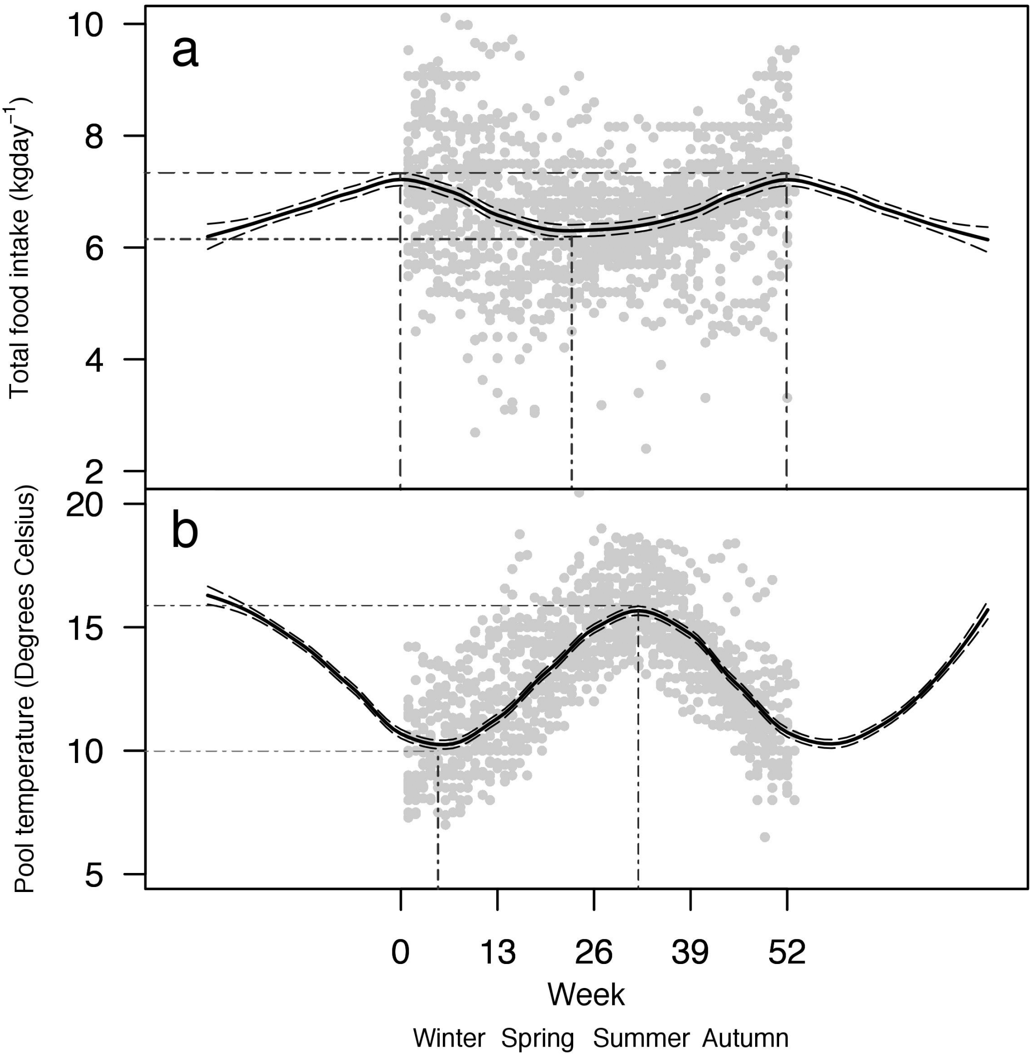

Figure 3. (a) Average daily food intake (kg day^{-1}) for a captive female Pacific white-sided dolphin (F001) weekly from 1977 to 2001 as described by a LOESS smoothing function and 95% CI; (b) weekly average water temperature from 1977 to 2001 as shown by LOESS smoothing function and 95% CI (black dashed lines).

Discussion

On average, the five Pacific white-sided dolphins at the Vancouver Aquarium consumed ~8 kg/d (~11,000 kcal day^{-1}), which equates to ~7% of body mass. The only animal with sufficient data to assess seasonal consumption patterns (F001) consumed 15% less (biomass and calories) during the summer than in winter. However, only a small part of the seasonal fluctuation in food consumption could be explained by seasonal changes in water temperature. On average, food intake was lowest from late May to early June (2 mo earlier than the warmest water temperatures in August); while food intake peaked in late December, and water temperatures were coldest 2 mo later in February.

Our finding that the five Pacific white-sided dolphins (107 to 123 kg) in our study consumed ~7% of their body mass a day is lower than the consumption of a 70-kg captive dusky dolphin (*L. obscurus* at ~10% body weight; Kastelein et al., 2000b) and captive adult (~30 to 55 kg) Commerson's dolphins (~9 to 13% body weight; Kastelein et al., 1993). In contrast, Atlantic bottlenose dolphins (160 to 230 kg; Kastelein et al., 2002) consumed a daily average of 2 to 4% of their body weight each day, and beluga whales (*Delphinapterus leucas*;

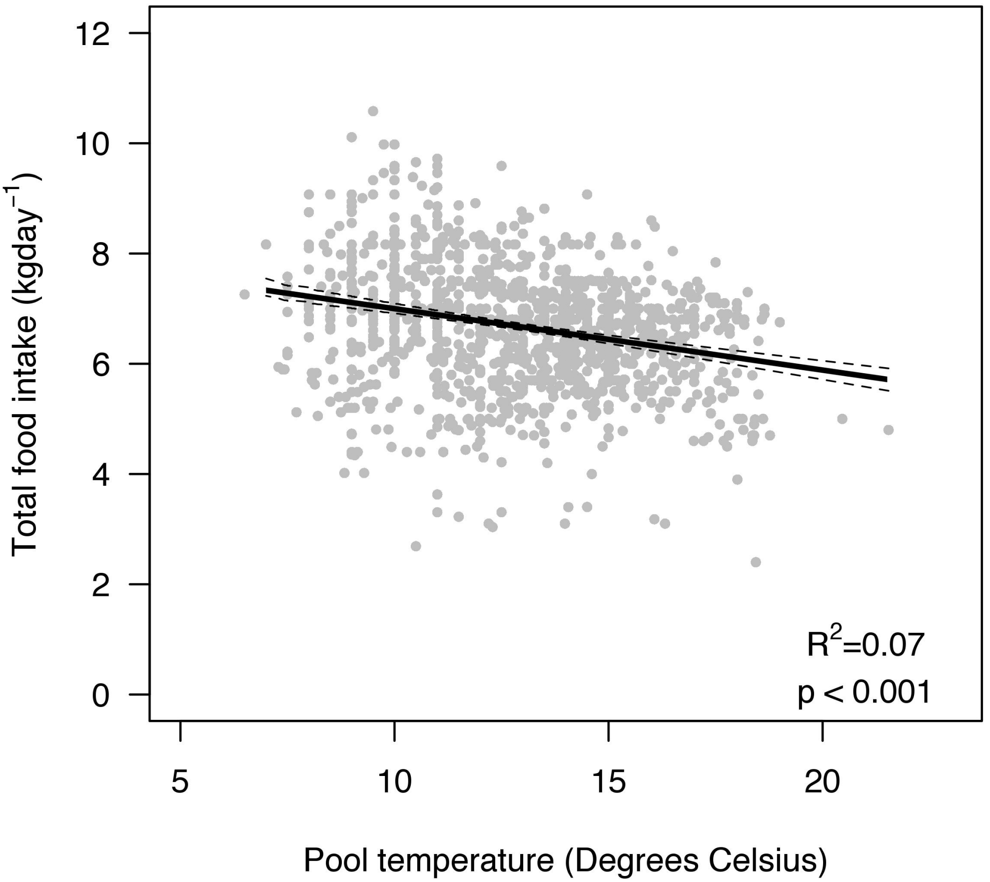

Figure 4. Pool water temperature vs daily food intake (kg/d) for a captive female Pacific white-sided dolphin (F001) from 1977 to 2001 as described by a linear model and 95% CI (black dashed lines).

400 to 1,400 kg; Kastelein et al., 1994) consumed a mere 1% of their body weight. Reasons for these differences in intake between species likely reflect differences in body sizes, life histories, metabolic demands (Worthy, 2001), activity levels, difference in energy density of food species consumed, and ambient environmental conditions.

The seasonal pattern we found in the food consumption of our Pacific white-sided dolphin (F001) has been reported for other species of cetaceans, but the proposed drivers of seasonal food intake have varied. For example, seasonal fluctuations in the food intake of beluga whales (Kastelein et al., 1994) and Amazon River dolphins (Kastelein et al., 1999) corresponded with a change in sexual behaviour (Kastelein et al., 1994) and were thought to reflect a change in hormone levels associated with reproduction (Kastelein et al., 1999). In contrast, seasonal patterns in food intake of a dusky dolphin were inversely related to pool temperature, but with a delay (Kastelein et al., 2000b). However, water temperature in our study only had a weak influence on the seasonal increases and decreases in food intake of Pacific white-sided dolphins, and changes in food consumption occurred prior to, rather than after, changes in water temperature.

It was once widely accepted that marine mammals had significantly higher metabolic rates compared to terrestrial mammals of similar sizes due to the thermal challenges of living in an aquatic environment (Irving et al., 1935; Scholander et al., 1942). However, more recent research has shown that marine mammals do not require more energy to stay warm until ambient temperatures have fallen below their lower thermal neutral limits (Worthy et al., 1987; Kasting et al., 1989; Worthy, 2001). It appears instead that physiological and behavioral explanations unassociated with the assumed cost of thermoregulation may explain the elevated metabolic rates of marine mammals.

Animals exposed to prolonged conditions below their lower thermal neutral limits may produce more insulation to shift their thermal neutral zones and decrease their metabolisms (i.e., increase blubber depth or lipid concentration within the blubber). This has been shown for harbour porpoises (*Phocoena phocoena*; Kastelein et al., 1997) and Atlantic bottlenose dolphins that seasonally change their blubber depth relative to changes in water temperature (unpub. data from Worthy et al., 1994, cited in Worthy, 2001). Harbour porpoise, Pacific white-sided dolphins, and other species are also thought to have elevated lipid content in their blubber (Worthy & Edwards, 1990; Worthy, 1991). Together, these factors may account for the small proportion of variation in food consumption of our Pacific white-sided dolphin (F001) that could be explained by ambient water temperature.

Alternative explanations to thermoregulation being the primary driver of the seasonal changes in food requirements of F001 include hormones, photoperiod and behavioral changes related to animal training, and interactions with other animals. Variation in photoperiod could indicate an impending change in season and could alter hormone levels and influence food intake levels as proposed by Kastelein et al. (1999) to explain the seasonal shift in the food intake of Amazon River dolphins. Another possibility is that the killer whales that resided with F001 for the majority of the study years could have altered her behaviour and influenced her food intake. Trainer discretion used to maintain animal motivation or maintain body condition may also have influenced food intake, especially in more recent years. Food intake can be regulated to positively reinforce the cooperation of animals participating in shows or research. Food intake may also be altered by husbandry staff to regulate body mass and shape.

Of the possible explanations for seasonal consumption in our Pacific white-sided dolphin, behavioral explanations seem unlikely because the seasonality in food intake was maintained after the number of killer whales decreased and eventually no longer resided with F001. Hormonal changes were prevalent, however, in her behavioral interactions with the killer whales and her indifference at times towards food (B. Sheehan, pers. comm.). Thus, hormonal changes related to maintaining body and reproduction condition may best account for the seasonal changes noted in the amounts of food consumed. Pacific white-sided dolphins have seasonally distinct reproductive cycles, and the majority of mating events occur in late-summer (Robeck et al., 2009). Thus, it is possible that hormonal changes associated with the mating season or increased sexual behaviour may have limited food intake in summer.

The applicability of our results to wild Pacific white-sided dolphins is limited in part by differences in the activity budgets of wild animals compared with those housed in aquaria. For example, wild Pacific white-sided dolphins have been noted to spend 3% of their time resting (Black, 1994), whereas our study animals spent 60 to 80% of their time resting or engaged in low-energy activities in both summer (Javdan, 2010) and winter (Rechsteiner, 2012). Because wild animals have to expend energy searching for prey and avoiding predators, they may be more active than their captive counterparts and would therefore likely require more food than the animals in our study. Recent estimates suggest the energetic intake of Pacific white-sided dolphins is likely to be ~35% higher in the wild than our food intake records indicate (Rechsteiner et al., 2013). Differences associated with habitat can account for differences in total consumption but are unlikely to have any bearing on seasonal changes in energy requirements. Thus, we propose that the relative seasonality in the food intake we observed in captivity also exists among Pacific white-sided dolphins in the wild. Such a possibility has implications for understanding and estimating the seasonal food requirements of free-living white-sided dolphins.

Our study provides insight into the nutritional needs of Pacific white-sided dolphins in captivity and provides hypotheses of relative changes in food intake that may be experienced by wild conspecifics. Knowledge of seasonal and absolute food requirements may help guide the husbandry of captive Pacific white-sided dolphins and may also be useful in aiding in the assessments of the biomass of fish required for wild Pacific white-sided dolphins globally. Understanding the prey biomass needs of such apex predators and how these needs vary by the time of year may further help to identify times of the year when humans and commercial fisheries could have greater effects on dolphins or when predation by Pacific white-sided dolphins could impact commercially or culturally important fish populations.

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