

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

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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 \pm 0.35 (\pm SE) of fish and squid per day (\sim 11,000 kcal day⁻¹), which equated to \sim 7% of their body mass and an annual mean intake of 2,880 kg \pm 131.8 (\pm 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

\sim 1 million individuals, 95% CI \sim 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

Code	Name	Sex	Study period	Age at study end (y)	Mean length (cm)	Mean mass (kg)	Mean daily food intake			
							Range (kg)	Mean (kg)	SE	<i>n</i>
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
<i>Clupea pallasii</i> (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		
<i>Oncorhynchus tshawytscha</i> (Chinook salmon)	June	1977-2010	1,745	Logerwell et al., 2005
<i>Loligo opalescens</i> (California squid)	Summer	1977-2005	674	Bomb-calorimeter at Vancouver Aquarium
		2006	621	
		2007-2010		
<i>Mallotus villosus</i> (Capelin)	July-August	1977-1992, 1995- 2000, 2002-2007	943	Van Pelt et al., 1997; Logerwell et al., 2005; bomb-calorimeter at Vancouver Aquarium Van Pelt et al., 1997 Logerwell et al., 2005 Bomb-calorimeter at Vancouver Aquarium
		1993-1994	981	
		2001	1,207	
		2007-2010		

(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 m³), a smaller adjacent pool (1,136 m³), and a medical pool (190 m³). 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 (49° 18' N, 123° 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 $7.9 \text{ kg day}^{-1} \pm 0.35$ ($\pm \text{SE}$) or $\sim 11,000 \text{ kcal day}^{-1}$ (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

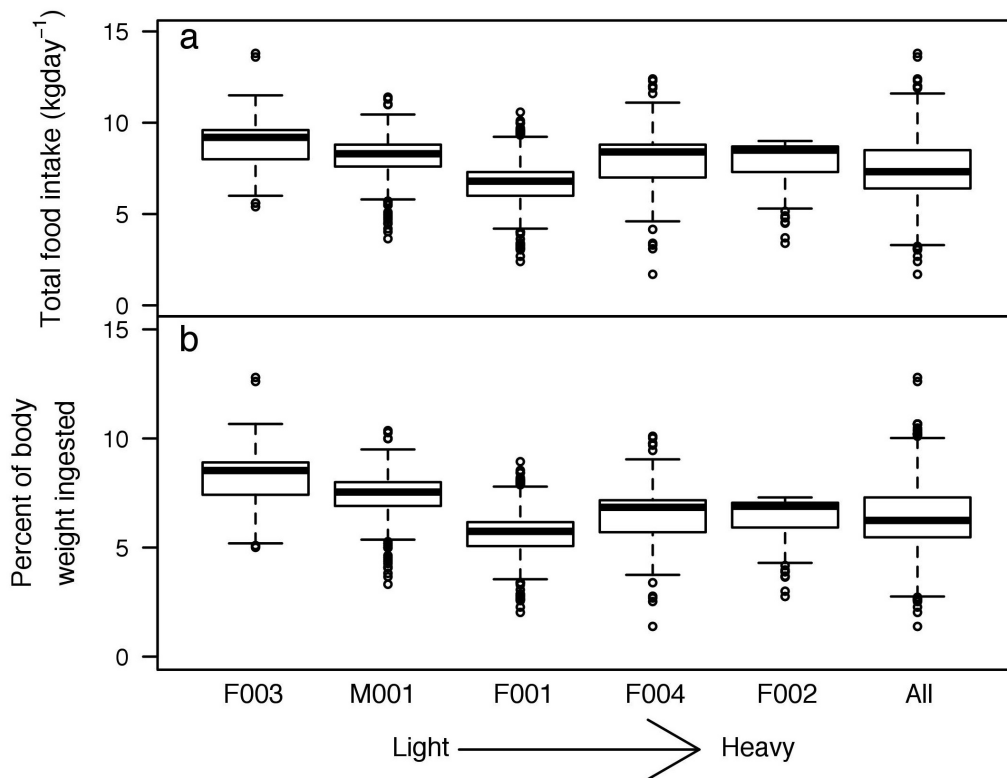


Figure 1. Daily food intake of five Pacific white-sided dolphins (F001-F004, M001) expressed as (a) total mass consumed by an individual and (b) a percentage of total body mass consumed. Bold lines representing the median, top, and bottom box edges indicate the 25th and 75th percentiles, the whiskers 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} ($11,187 \pm 71$ 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 ($\pm 95\%$ CI) food intake was $\sim 6.3 \pm \sim 0.15$ kg day^{-1} ($\sim 11,100$ kcal day^{-1}) in summer and rose to a high of $\sim 7.2 \pm \sim 0.15$ kg day^{-1} ($\sim 13,200$ 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 21.5°C, and had an average seasonal low of $\sim 10.2^\circ\text{C} \pm \sim 0.15$ (95% CI) during Week 5 (early February), and an average seasonal high of $\sim 15.7^\circ\text{C} \pm \sim 0.2$ (95% CI) during Week 32 (mid-August). Mean pool temperature was $12.9 \pm 0.07^\circ\text{C}$ throughout the study period.

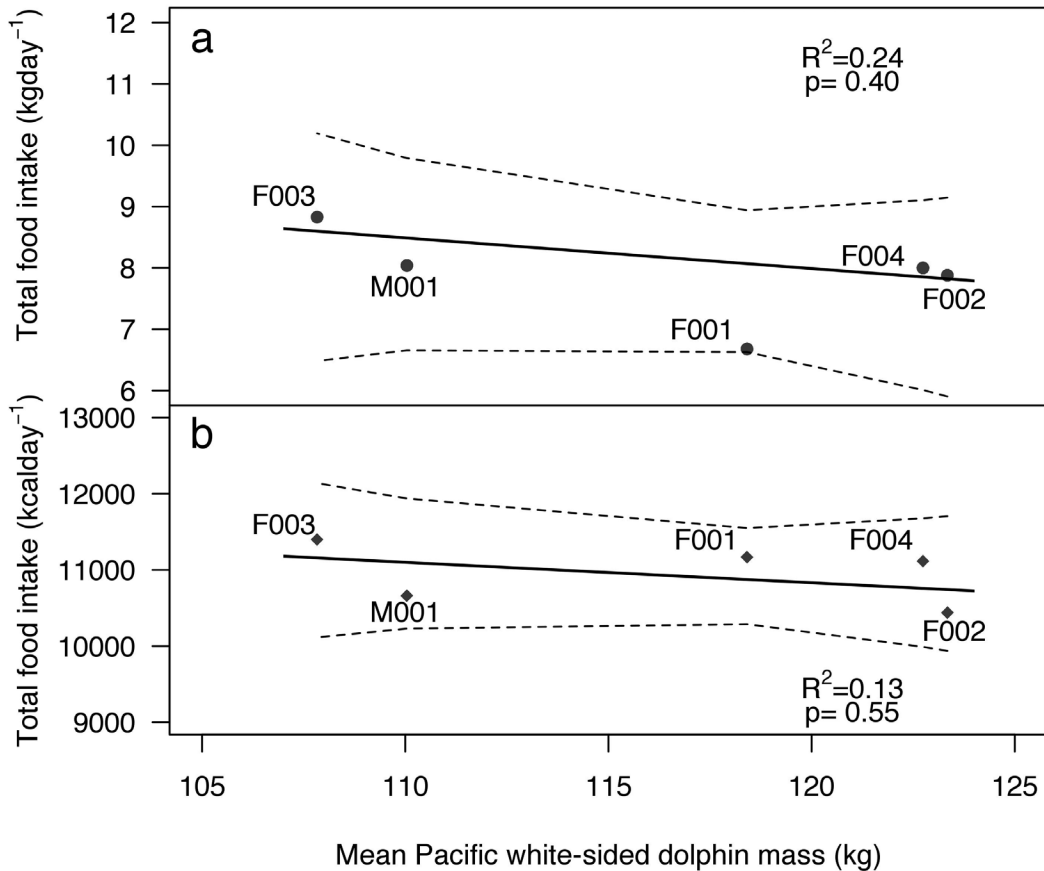


Figure 2. Average food intake of five captive Pacific white-sided dolphins (F001-F004, M001) as a function of mean body mass showing (a) food intake in kg and (b) intake in kcal as predicted by linear models. The dashed lines are 95% confidence intervals (CI). Note that neither regression was statistically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

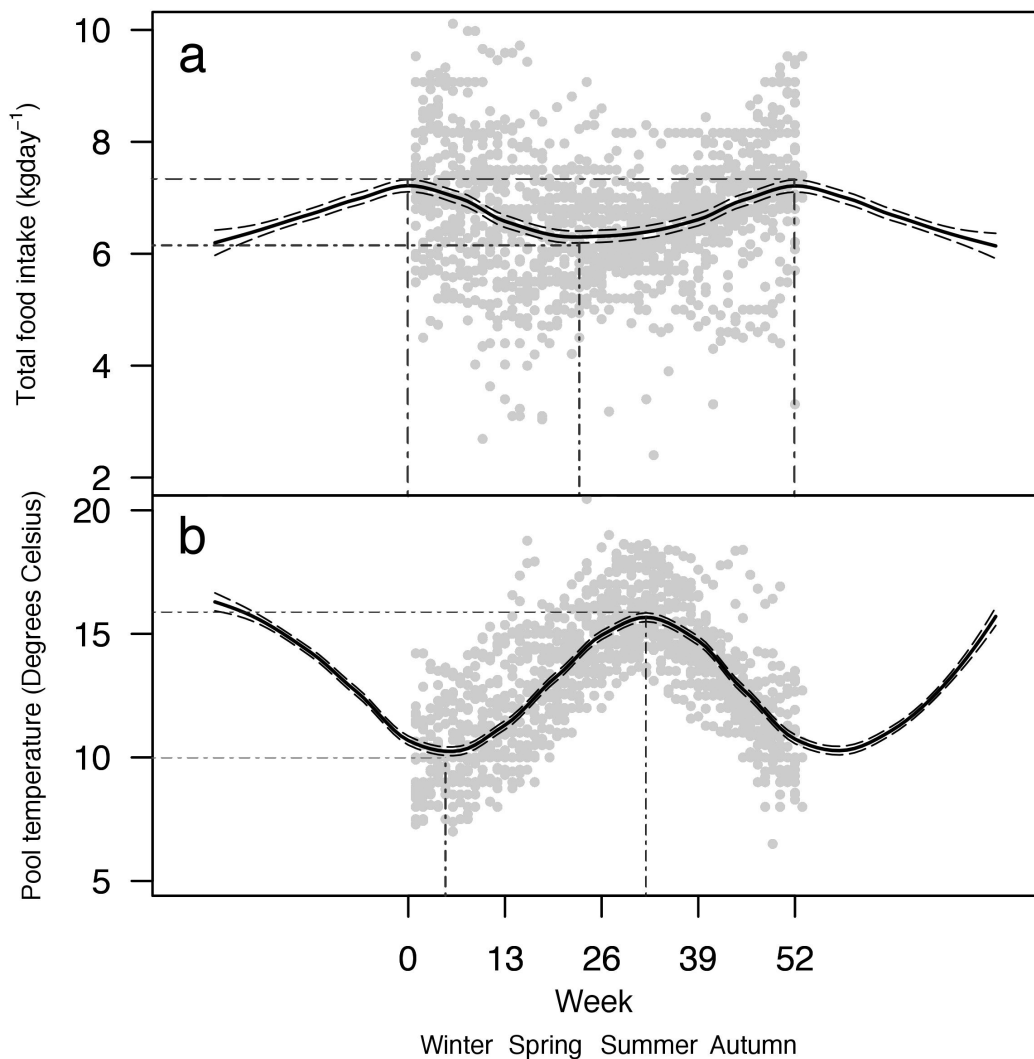


Figure 3. (a) Average daily food intake (kg day⁻¹) for a captive female Pacific white-sided dolphin (F001) weekly from 1977 to 2001 as described by a LOESS smoothing function and 95% CI; (b) weekly average water temperature from 1977 to 2001 as shown by LOESS smoothing function and 95% CI (black dashed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

Discussion

On average, the five Pacific white-sided dolphins at the Vancouver Aquarium consumed ~ 8 kg/d ($\sim 11,000$ kcal day⁻¹), which equates to $\sim 7\%$ 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 $\sim 7\%$ of their body mass a day is lower than the consumption of a 70-kg captive dusky dolphin (*L. obscurus*) at $\sim 10\%$ 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*;

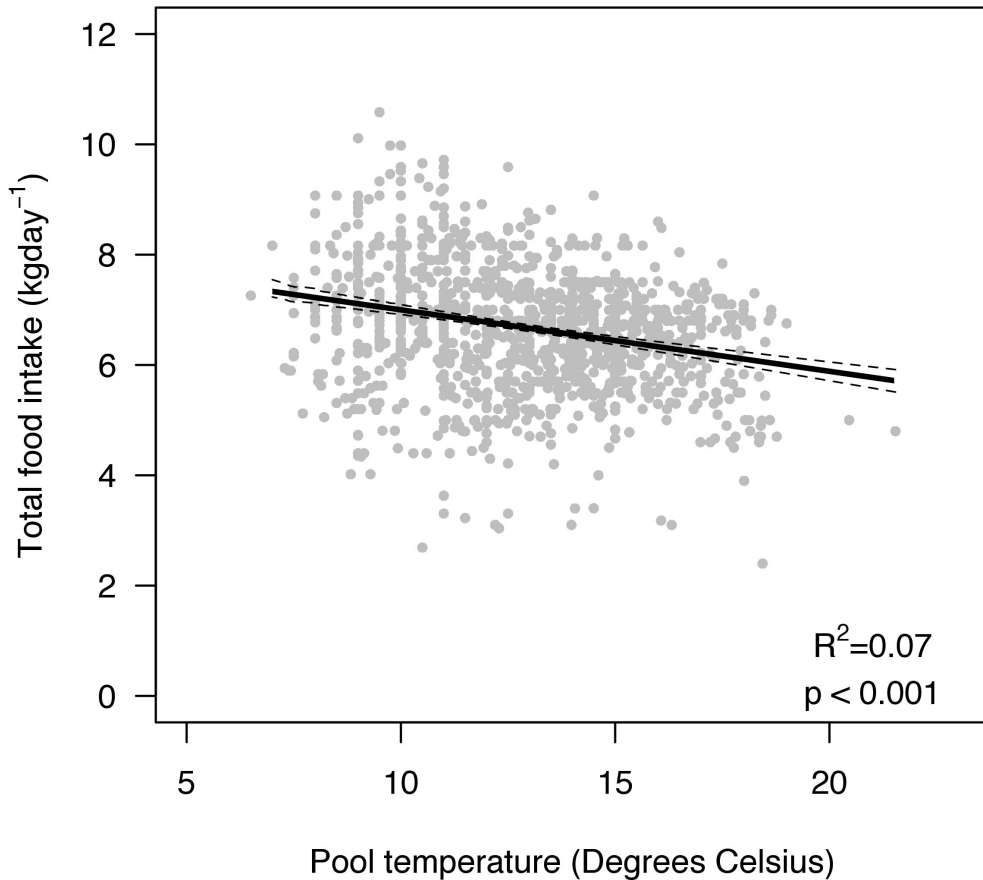


Figure 4. Pool water temperature vs daily food intake (kg/d) for a captive female Pacific white-sided dolphin (F001) from 1977 to 2001 as described by a linear model and 95% CI (black dashed lines).

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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Literature Cited

- Allen, P. C. (2009). *Seasonal oscillations in the mass and food intake of Steller sea lions* (Master's thesis). University of British Columbia, Vancouver.
- Benoit-Bird, K. J. (2004). Prey caloric value and predator energy needs: Foraging predictions for wild spinner dolphins. *Marine Biology*, 145(3), 435-444. <http://dx.doi.org/10.1007/s00227-004-1339-1>.
- Black, N. A. (1994). Behaviour and ecology of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in Monterey Bay, California (Master's thesis). San Francisco State University, San Francisco, CA.
- Black, N. A. (2009). Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 817-818). San Diego: Academic Press. <http://dx.doi.org/10.1016/B978-0-12-373553-9.00191-7>
- Buckland, S. T., Cattanach, K. L., & Hobbs, R. C. (1993). *Abundance estimates of Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise and northern fur seal in the North Pacific, 1987/90*. INPFC Symposium: Biology, Distribution and Stock Assessment of Species Caught in the High Seas Driftnet Fisheries in The North Pacific Ocean. Tokyo, Japan.
- Ford, J. K. B., Ellis, G. M., Olesiuk, P. F., & Balcomb III, K. C. (2010). Linking killer whale survival and prey abundance: Food limitation in the oceans' apex predator? *Biology Letters*, 6, 139-142. <http://dx.doi.org/10.1098/rsbl.2009.0468>
- Ford, J. K. B., Ellis, G. M., Matkin, D. R., Balcomb III, K. C., Briggs, D., & Morton, A. B. (2005). Killer whale attacks on minke whales: Prey capture and antipredator tactics. *Marine Mammal Science*, 21, 603-618. <http://dx.doi.org/10.3354/ab00307>
- Ford, J. K. B., Ellis, G. M., Matkin, C. O., Wetklo, M. H., Barrett-Lennard, L. G., & Withler, R. E. (2011). Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology*, 11, 213-224. <http://dx.doi.org/10.3354/ab00307>
- Hanson, M. B., Baird, R. W., Ford, J. K. B., Hempelmann-Halos, J., Van Doornik, D. M., Candy, J. R., . . . Ford, M. J. (2010). Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. *Endangered Species Research*, 11, 69-82. <http://dx.doi.org/10.3354/esr00263>
- Heise, K. A. (1997). Life history and population parameters of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). *Report of the International Whaling Commission*, 47, 817-825.
- Irving, L., Fisher, K. C., & McIntosh, F. C. (1935). The water balance of a marine mammal, the seal. *Journal of Cellular and Comparative Physiology*, 6, 387-391. <http://dx.doi.org/10.1002/jcp.1030060305>
- Javdan, S. (2010). A preliminary study on the effect of visitor density and intensity of the space use, behaviour, and vocalization patterns of captive Pacific white-sided dolphins, *Lagenorhynchus obliquidens* (Master's thesis). University of St. Andrews, St. Andrews, UK.
- Kastelein, R. A., & Vaughan, N. (1989). Food consumption, body measurements and weight changes of a female killer whale (*Orcinus orca*). *Aquatic Mammals*, 15(1), 18-21.
- Kastelein, R. A., Staal, C., & Wiepkema, P. R. (2003a). Food consumption, food passage time, and body measurements of captive bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, 29(1), 53-66. <http://dx.doi.org/10.1578/016754203101024077>
- Kastelein, R. A., Kershaw, J., Berghout, E., & Wiepkema, P. R. (2003b). Food consumption and suckling in killer whales (*Orcinus orca*) at Marineland Antibes. *International Zoo Yearbook*, 38, 204-218. <http://dx.doi.org/10.1111/j.1748-1090.2003.tb02081.x>
- Kastelein, R. A., Mosterd, J., Schooneman, N. M., & Wiepkema, P. R. (2000a). Food consumption, growth, body dimensions, and respiration rates of captive false killer whales (*Pseudorca crassidens*). *Aquatic Mammals*, 26(1), 33-44.
- Kastelein, R. A., Neurohr, B., Nieuwstraten, S. H., & Wiepkema, P. R. (1999). Food consumption and body measurements of Amazon River dolphins (*Inia geoffrensis*). *Aquatic Mammals*, 25(3), 173-182.
- Kastelein, R. A., Sijs, S. J., van der Staal, C., & Nieuwstraten, S. H. (1997). Blubber thickness in harbour porpoises (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (1st ed., pp. 179-199). Woerden, the Netherlands: De Spil Publishers.
- Kastelein, R. A., van der Elst, C. A., Tennant, H. K., & Wiepkema, P. R. (2000b). Food consumption and growth of a female dusky dolphin (*Lagenorhynchus obscurus*). *Zoo Biology*, 19, 131-142. [http://dx.doi.org/10.1002/1098-2361\(2000\)19:2<131::AID-ZOO4>3.0.CO;2-P](http://dx.doi.org/10.1002/1098-2361(2000)19:2<131::AID-ZOO4>3.0.CO;2-P); [http://dx.doi.org/10.1002/1098-2361\(2000\)19:2<131::AID-ZOO4>3.0.CO;2-Y](http://dx.doi.org/10.1002/1098-2361(2000)19:2<131::AID-ZOO4>3.0.CO;2-Y)
- Kastelein, R. A., Vaughan, N., Walton, S., & Wiepkema, P. R. (2002). Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. *Marine Environmental Research*, 53(2), 199-218. [http://dx.doi.org/10.1016/S0141-1136\(01\)00123-4](http://dx.doi.org/10.1016/S0141-1136(01)00123-4)
- Kastelein, R. A., Ford, J., Berghout, E., Wiepkema, P. R., & van Boxsel, M. (1994). Food consumption, growth and reproduction of belugas (*Delphinapterus leucas*) in human care. *Aquatic Mammals*, 20(2), 81-97.
- Kastelein, R. A., Walton, S., Odell, D., Nieuwstraten, H., & Wiepkema, P. R. (2000c). Food consumption of a captive female killer whale (*Orcinus orca*). *Aquatic Mammals*, 26(2), 127-131.
- Kastelein, R. A., McBain, J., Neurohr, B., Mohri, M., Saijo, S., Wakabayashi, I., & Wiepkema, P. R. (1993). The food consumption of Commerson's dolphins

- (*Cephalorhynchus commersonii*). *Aquatic Mammals*, 19(2), 99-121.
- Kasting, N. W., Adderley, S. A. L., Safford, T., & Hewlett, K. G. (1989). Thermoregulation in beluga (*Delphinapterus leucas*) and killer (*Orcinus orca*) whales. *Physiological Zoology*, 62(3), 687-701.
- Logerwell, E. A., & Schaufler, L. E. (2005). New data on proximate composition and energy density of stellar sea lion (*Eumetopias jubatus*) prey fills seasonal and geographic gaps in existing information. *Aquatic Mammals*, 31(1), 62-82. <http://dx.doi.org/10.1578/AM.31.1.2005.62>
- Noren, D. P. (2011). Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science*, 27(1), 60-77. <http://dx.doi.org/10.1111/j.1748-7692.2010.00386.x>
- R Development Core Team. (2011). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Retrieved 24 June 2013 from www.R-project.org.
- Rechsteiner, E. U. (2012). *Resting metabolism, energetics, and seasonal distribution of Pacific white-sided dolphins* (Master's thesis). The University of British Columbia, Vancouver.
- Rechsteiner, E. U., Rosen, D. A. S., & Trites, A. W. (2013, online). Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetics model. *Journal of Mammalogy*, 94(4). <http://dx.doi.org/10.1644/12-MAMM-A-206.1>
- Robeck, T. R., Steinman, K. J., Greenwell, M., Ramirez, K., Van Bonn, W., Yoshioka, M., . . . O'Brien, J. K. (2009). Seasonality, estrous cycle characterization, estrus synchronization, semen cryopreservation, and artificial insemination in the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). *Reproduction Research*, 138, 391-405. <http://dx.doi.org/10.1530/REP-08-0528>.
- Rosen, D. A. S., & Trites, A. W. (1999). Metabolic effects of low-energy diet on Steller sea lions, *Eumetopias jubatus*. *Physiological Zoology*, 72, 723-731. <http://dx.doi.org/10.1086/316705>
- Scholander, P. F., Irving, I., & Grinnell, S. W. (1942). On the temperature and metabolism of the seal during diving. *Journal of Cellular and Comparative Physiology*, 19, 67-78. <http://dx.doi.org/10.1002/jcp.1030190107>
- Trites, A. W. (2003). Food webs in the ocean: Who eats whom and how much? In M. Sinclair & G. Valdimarsson (Eds.), *Responsible fisheries in the marine ecosystem* (pp. 125-143). Wallingford, UK, and Rome: CABI Publishing and Food and Agriculture Organization of the United Nations (FAO). <http://dx.doi.org/10.1079/9780851996332.0125>
- Trites, A. W., Christensen, V., & Pauly, D. (1997). Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fishery Science*, 22, 173-187. <http://dx.doi.org/10.2960/J.v22.a14>
- Van Pelt, T. I., Piatt, J. F., Lance, B. K., & Roby, D. D. (1997). Proximate composition and energy density of some North Pacific forage fishes. *Comparative Biochemistry and Physiology*, 118, 1393-1398. [http://dx.doi.org/10.1016/S0300-9629\(97\)00240-5](http://dx.doi.org/10.1016/S0300-9629(97)00240-5)
- Winship, A. J., Trites, A. W., & Rosen, D. A. S. (2002). A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Marine Ecology Progress Series*, 229, 291-312. <http://dx.doi.org/10.3354/meps229291>
- Worthy, G. A. J. (1991, December). *Thermoregulatory implications of the interspecific variation in blubber composition of odontocete cetaceans*. Proceedings of the 9th Biennial Conference on the Biology of Marine Mammals, Chicago, IL.
- Worthy, G. A. J. (2001). Nutrition and energetics. In L. A. Dierauf & F. M. D. Gulland (Eds.), *CRC handbook of marine mammal medicine: Health, disease, and rehabilitation* (2nd ed., pp. 791-827). Boca Raton, FL: CRC Press. <http://dx.doi.org/10.1201/9781420041637.ch36>
- Worthy, G. A. J., & Edwards, E. F. (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*). *Physiological Zoology*, 63, 432-442.
- Worthy, G. A. J., Innes, S., Braune, B. M., & Stewart, R. E. A. (1987). Rapid acclimation of cetaceans to an open-system respirometer. In A. C. Huntley, D. P. Costa, G. A. J. Worthy, & M. A. Castellini (Eds.), *Approaches to marine mammal energetics* (Special Publication No. 1, pp. 115-126). Lawrence, KS: Society for Marine Mammalogy.