Estimated field metabolic rates and prey requirements of resident killer whales

DAWN P. NOREN

National Oceanic and Atmospheric Administration,
National Marine Fisheries Service,
Northwest Fisheries Science Center,
Marine Mammal Ecology Team,
2725 Montlake Boulevard East,
Seattle, Washington 98112, U.S.A.
E-mail: dawn.noren@noaa.gov

ABSTRACT

Killer whales are large animals that often feed in groups and thus have the potential to deplete prey populations. Determining predator energy requirements is essential to assessing whether prey availability is sufficient. This is important because one risk factor facing the endangered Southern Resident killer whale distinct population segment is limited prey availability. Body mass, field metabolic rate (FMR), and daily prey energy requirements (DPERs) were estimated for each individual in the population. FMRs were calculated from body mass, assuming they range from five to six times Kleiber-predicted basal metabolic rates. FMRs of adults were also calculated from resident killer whale activity budgets and the metabolic cost of swimming at speeds associated with daily activities. These two methods yielded similar results. Total FMRs varied by age and sex, which is partly due to the long developmental period and sexual dimorphism in killer whales. FMRs for males (465–4,434 kg) ranged from 35,048 to 228,216 kcal/d while FMRs for females (465–3,338 kg) ranged from 35,048 to 184,444 kcal/d. DPERs were calculated from FMRs assuming a standard digestive efficiency. Corresponding DPERs ranged from 41,376 to 269,458 kcal/d and 41,376 to 217,775 kcal/d, respectively.

Key words: energetics, *Orcinus orca*, killer whale, marine mammal, metabolism, prey consumption.

The daily energetic needs and prey consumption rates of apex predators are important areas of research, particularly because of their potential impact on ecosystems. Killer whales (*Orcinus orca*) represent the highest trophic level of any marine mammal (Pauly *et al.* 1998), and as a consequence, their energetic requirements and resulting prey consumption rates could be significant. However, these values are difficult to quantify. For example, the proposed impact of transient killer whale predation on marine mammal populations in the Northeast Pacific has resulted in considerable debate (*e.g.*, Springer *et al.* 2003, Williams *et al.* 2004, DeMaster *et al.* 2006, Trites

et al. 2007, Wade *et al.* 2007, Springer *et al.* 2008, Estes *et al.* 2009, Wade *et al.* 2009). One component of uncertainty is a basic understanding of the energetic requirements of killer whales (see Maniscalco *et al.* 2007). Indeed, for cetaceans in general, there is a paucity of information on energetic requirements and prey consumption rates. A key component in studying predator–prey interactions is an understanding of daily energy requirements of individual members of the population as well as the total energy requirements of the entire population.

Previous studies have used several different methods to assess the daily energy expenditure and prey consumption rates of adult resident (Kriete 1995, Williams *et al.* 2006) and transient (Baird and Dill 1996, Williams *et al.* 2004, Maniscalco *et al.* 2007) killer whales. For example, Williams *et al.* (2004) extrapolated field metabolic rates of adult transient killer whales from an allometric relationship of at-sea metabolic rates for marine mammals (Costa and Williams 1999). Other researchers (Kriete 1995, Williams *et al.* 2006, Maniscalco *et al.* 2007) estimated field metabolic rates of adult resident and transient killer whales from daily activity budgets of free-ranging animals and metabolic rates measured in captive killer whales performing behaviors that approximated wild killer whale activity states (from Kriete 1995). Baird and Dill (1996) estimated the rate of energy intake from observations of prey intake by wild transient killer whales. Alternatively, Barrett-Lennard *et al.* (1995) estimated daily caloric intake of transient killer whales based on daily fish ingestion by smaller, relatively sedentary captive whales with a correction factor of 25% to account for the difference in activity levels of captive and wild animals.

All of the previous studies have merit, yet additional approaches are warranted for several reasons. First, the estimates of daily field metabolic and prey consumption rates from some studies are similar, while the results of others differ significantly (for comparisons between studies see Williams *et al.* 2004, Williams *et al.* 2006, Maniscalco *et al.* 2007). Thus, there is some degree of uncertainty in our ability to estimate FMRs and prey consumption rates of killer whales, and therefore, other methods to calculate these values are needed. Second, only two previous studies estimated daily field metabolic or prey consumption rates of immature killer whales (Barrett-Lennard *et al.* 1995, Osborne 1999). Because a population of killer whales can be composed of a significant number of immature individuals, these segments of the population should not be ignored when modeling killer whale field metabolic rates, prey consumption rates, and potential impacts to the ecosystem. Third, none of the previous studies determined prey consumption rates for an existent population of killer whales with a known population size, including the number of individuals within each age and sex class. Because killer whales travel in family groups, refined estimates of daily prey requirements that are based on the demographics (*e.g.*, age and sex structure) of existent killer whale populations are essential to determining potential impacts on prey populations in an ecosystem.

Estimating daily prey energy requirements on the level of a marine mammal population is not a trivial task, particularly because so many variables impact daily energetic expenditure. Metabolic rates are influenced by age, body size, growth, reproductive status, activity level, and environmental conditions (Kleiber 1975, Costa *et al.* 1986, Kriete 1995, Costa 2002, Noren 2002, Williams *et al.* 2006, Maniscalco *et al.* 2007, Williams and Noren 2009, D. Noren, unpublished data). Furthermore, for marine mammals, metabolic rates are further affected by dive depth and duration, activity, and swimming speed (Webb *et al.* 1998, Hurley and Costa 2001, Rosen and Trites 2002, Hastie *et al.* 2006, 2007, Fahlman *et al.* 2008, Williams and Noren 2009). Thus, the proportion of time killer whales spend swimming at

different speeds during distinct activity states will impact FMRs, and consequently daily energetic needs.

The objective of this study was to estimate the daily energy expenditure and prey requirements for the entire distinct population segment of Southern Resident killer whales (SRKWs). These whales, which inhabit the eastern Pacific Ocean, ranging from central California to the northern Queen Charlotte Islands of British Columbia, suffered a 20% population decline from 1996 to 2001 (Krahn *et al.* 2004). This decline as well as several risk factors led to the population being listed as Endangered under the U.S. Endangered Species Act and Canada's Species at Risk Act. Because low abundance of their preferred prey, Chinook salmon (*Oncorhynchus tshawytscha*; Ford *et al.* 1998, Ford and Ellis 2006, Hanson *et al.*, in press), is linked to high mortality (Ford *et al.* 2009) and low fecundity (Ward *et al.* 2009), it is imperative that we have estimates of daily prey energy requirements for all members of the SRKW population. Resident killer whales travel in large matriarchal groups, so understanding the daily energetic needs on the level of the population, rather than on the level of the individual, is necessary to inform decisions regarding the conservation of SRKWs, the conservation of salmon, and the management of fishing activities which may limit Southern Resident killer whale prey resources.

<center>METHODS</center>

Body masses, field metabolic rates (FMRs), and daily prey energy requirements (DPERs) were estimated for all individuals in the SRKW population (November 2008 census data, Center for Whale Research, http://www.whaleresearch.com), with the exception of calves aged 0–<1 yr old because delphinids at this age are primarily dependent on their mothers for nourishment (for review see Noren and Edwards 2006). Although many delphinid calves may nurse for up to 3 yr after birth (for review see Noren and Edwards 2006), wild killer whale calves can consume fish by 1-yr postpartum (Heyning 1988). Thus, for simplicity, FMRs and DPERs for 2- and 3-yr-old calves were calculated with the assumption that 100% of their daily energetic requirements are met through the consumption of prey, rather than milk.

Estimating Killer Whale Body Mass

There is no simple method to measure the body mass of free-swimming killer whales. Although body mass can be estimated from body length (Bigg and Wolman 1975), there are limited data on body lengths of wild killer whales, and not all age classes are represented. Similarly, there is a paucity of information on relationships between age and length and age and body mass of killer whales (for review see Clark *et al.* 2000). Because of this, a combination of published values and equations were used to estimate body masses of SRKWs.

For both male and female SRKWs 1–12 yr of age, body mass for each year of life was estimated using a Gompertz function that predicts female killer whale body mass from age in days (Clark *et al.* 2000). The growth rate of these captive-born animals through the age of 6 yr (36.0 cm/yr, Clark *et al.* 2000) was similar to the value (36.6 cm/yr) reported by Bigg (1982) for wild male and female killer whales, including southern and northern resident ecotypes, from the eastern North Pacific.

Because adult Atlantic killer whales (Christensen 1988, Duffield and Miller 1988) tend to be smaller than adult Northeast Pacific killer whales (Bigg and Wolman

1975, Bigg 1982), the growth curve from Clark *et al*. (2000), which was constructed almost exclusively from measurements made on Icelandic whales, was not used to estimate body masses for whales aged 13–≥20 yr. Instead, terminal body masses for adult male and female SRKWs were based on values from adult male and female Northeast Pacific resident killer whales reported by Bigg and Wolman (1975). Similar to body growth curves from Icelandic killer whales (Christensen 1988) and patterns of growth and food consumption rates in captive killer whales (Kastelein *et al.* 2000, 2001, 2003*a*), it was assumed that both male and female SRKWs complete their body growth and food consumption rates level off by approximately 20 yr of age.

Terminal body masses of adult female and male SRKWs were set to equal the largest estimated body masses of female and male Northeast Pacific resident killer whales that were taken by the live-capture fishery (Bigg and Wolman 1975). This is because the live-capture fishery focused primarily on smaller animals, thus the majority of masses reported by Bigg and Wolman (1975) were for juvenile animals. The terminal body mass for female SRKWs ≥20 yr old was set at 3,338 kg (estimated from Bigg and Wolman 1975). Due to a lack of data on changes in body mass with age in sexually mature female SRKWs, it was assumed that female body mass changes at a constant rate of approximately 107 kg/yr from the mass of 2,482 kg at the age of 12 (estimated according to methods from above) to the terminal mass of 3,338 kg for all adult females ≥20 yr of age (Fig. 1).

Killer whales are highly sexually dimorphic. Adult males have longer body length, larger body mass, greater girth, and larger flukes and fins than adult females (Nishiwaki and Handa 1958, Jonsgård and Lyshoel 1970, Bigg and Wolman 1975,
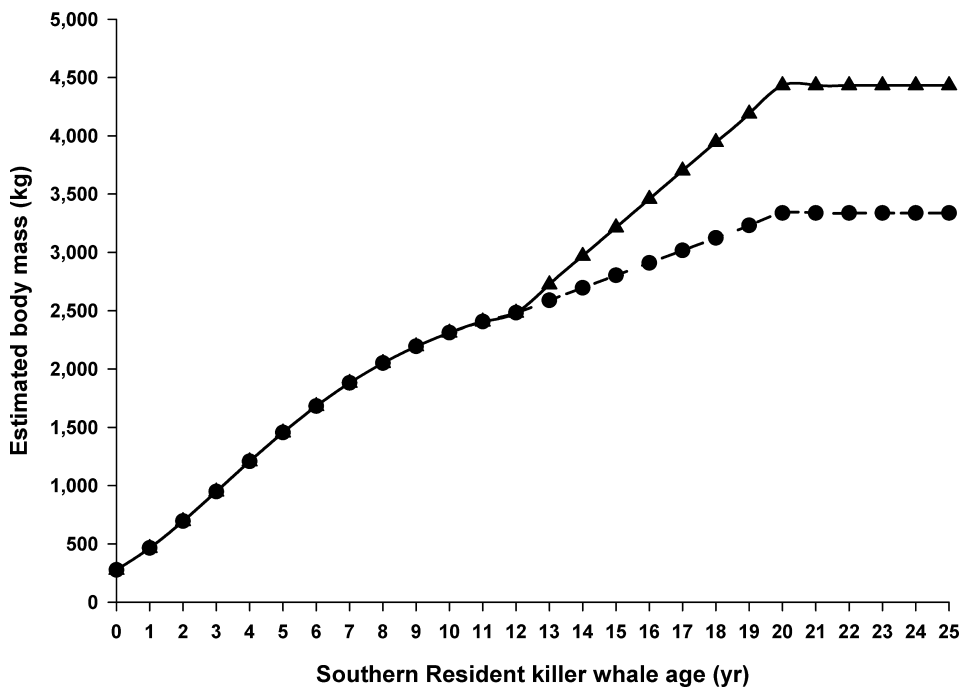

Figure 1. Relationship between body mass and age in years for male and female killer whales. The growth curves for male (▲) and female (●) killer whales are denoted by the solid and broken lines, respectively.

Clark and Odell 1999). Thus, the terminal body mass for male SRKWs ≥20-yr old was set at 4,434 kg (estimated from Bigg and Wolman 1975). To reach this large body size, male killer whales undergo a period of rapid growth, which begins at 13–14 yr of age (Christensen 1988). Due to a lack of data on changes in body mass with age in adolescent male SRKWs, it was assumed that male body mass changes at a constant rate of approximately 244 kg/yr from the mass of 2,482 kg at the age of 12 (estimated according to methods from above) to the terminal mass of 4,434 kg for all adult males ≥20 yr of age (Fig. 1).

Although it may be preferable to express SRKW male and female growth patterns as single nonlinear functions, there were insufficient data to do so. As more data become available, SRKW growth curves can be refined. In the meantime, this approach was deemed reasonable because realistic SRKW juvenile growth rates and adult body masses were incorporated into the estimates, which resulted in growth curves (Fig. 1) that are nearly identical in shape to growth curves of wild male and female Norwegian killer whales (Christensen 1988).

Estimating Field Metabolic Rates (FMRs)

The potential range of field metabolic rates (FMRs, the total metabolic cost of all physiological processes and activities of an animal in the wild) for killer whales of all age and sex classes were calculated from body mass assuming that daily metabolism ranges from five to six times Kleiber (1975) predicted BMR, according to the following equations:

$$\text{Lower bound FMR} = 350 M_b^{0.75} \tag{1}$$

$$\text{Upper bound FMR} = 420 M_b^{0.75} \tag{2}$$

where FMR is in kcal/d and M_b is body mass in kg.

This method was deemed appropriate for adult (≥20 yr of age) killer whales because FMRs of adult otariids and bottlenose dolphins (*Tursiops truncatus*) range from five to six times Kleiber-predicted BMR (calculated from Costa *et al.* 1991, Costa and Williams 1999, Costa 2002). For comparison, Williams *et al.* (2004) used the equation FMR = $406 M_b^{0.756}$ for adult transient killer whales in Alaska, which is near the upper bound of FMRs presented above.

It is plausible that the cost of reproduction in females and growth in juveniles may affect individual FMRs. However, results from previous studies on marine mammals suggest that energetic costs of gestation and lactation in females and growth in juveniles do not increase FMR values. For example, FMRs of lactating California sea lions (*Zalophus californianus*) range from five to six times Kleiber-predicted BMR (calculated from Costa *et al.* 1991), which are comparable to those of nonlactating otariids and delphinids (Costa and Williams 1999, Costa 2002). Similarly, resting metabolic rates do not differ between reproductive and nonreproductive female California sea lions during the late pregnancy or lactation periods (Williams *et al.* 2007).

Body size changes rapidly in young animals, so FMRs of immature animals (1–12-yr old), "sprouting" adolescent males (13–19-yr old), and young adult females (13–19-yr old) were estimated for each yr of life. Although body growth has the potential to increase daily metabolic rates, there is a paucity of information on how

the cost of growth affects FMRs in cetaceans. Data from juvenile sea lions suggest that these costs may not represent a large portion of daily energy expenditure. For example, the energy required for growth in immature Steller sea lions is small relative to their total energy needs (Winship *et al.* 2002). Furthermore, energetic costs of swimming juvenile sea lions (calculated from Feldkamp 1987, Williams *et al.* 1991, and Rosen and Trites 2002) range from three to six times Kleiber-predicted BMR. Thus, it was deemed reasonable to assume that FMRs of juvenile killer whales could also be calculated using Equations 1 and 2, similar to adult killer whales. Although the multiplier values for juveniles, adolescents, and adults are identical, the fact that FMR is proportional to $M_b^{0.75}$ means that smaller, younger individuals have significantly higher mass-specific FMRs than larger, older individuals, which is the typical mammalian pattern.

Comparing Predicted FMRs with FMRs Calculated from Daily Activity Budgets

To help determine whether FMRs calculated by the above methods are reasonable, FMRs were also calculated for adult (age $\geq$20 yr) male and female resident killer whales using cost of transport (*COT*) curves developed for killer whales (Williams and Noren 2009) and daily activity budgets that identified the proportion of time Northeast Pacific resident killer whales were engaged in each activity state in addition to the average swimming speed for each activity state (Northern Residents from Ford 1989, Southern Residents from Noren *et al.* 2009 and D. Noren, unpublished data). Specifically, FMRs were calculated with the assumption that whales swam at a constant speed specific to each activity state for the entire duration (proportion of a 24 h day) they were engaged in each activity state. The total metabolic cost of swimming during each activity state was calculated from *COT* curves from Williams and Noren (2009). Daily FMRs were then calculated by summing the total metabolic costs of swimming for all activity states that whales were engaged in daily (Table 1, 2).

These calculations are rather simplistic because the *COT* curves from Williams and Noren (2009) were constructed from speed and respiration rate data collected from Northern Resident killer whales during one activity state (travel/forage), and it is possible that *COT* curves may differ when whales are engaged in other activity states. However, Williams and Noren (2009) selected their data using strict criteria in an attempt to determine *COT* for swimming only, while excluding other associated costs of foraging (*e.g.*, diving and performing surface active behaviors). Thus, the *COT* curves from Williams and Noren (2009) should provide good estimates for the energetic costs associated with swimming over a range of speeds, and be applicable across most activity states. Although the energetic costs of surface active behaviors (*e.g.*, breaches, tail slaps, *etc.*) will not be accounted for in these calculations, these behaviors do not make up a substantial portion of Southern Resident killer whales' daily activity budgets (Noren *et al.* 2009). Furthermore, tail slaps, which are the predominant surface active behaviors performed (Noren *et al.* 2009), are not associated with high energetic costs (D. Noren, unpublished data). Consequently, the performance of surface active behaviors is not expected to significantly affect daily FMRs.

Estimating Daily Prey Energy Requirements (DPERs)

Digestive efficiency for killer whales is approximately 84.7% (Williams *et al.* 2004). This means that killer whales must consume more kcal/d than their predicted

Table 1. FMRs for adult male and female Northern Resident killer whales calculated from daily activity budgets.

Activity state[a] (% of 24 h day engaged in activity, mean swimming speed during activity)	Daily adult male (4,434 kg) FMR[b]	Daily adult female (3,338 kg) FMR[c]
Foraging (66.5%, 1.7 m/s)	780.7 MJ (186,585.8 kcal)	428.7 MJ (102,462.8 kcal)
Travelling (4.2%, 2.9 m/s)	50.4 MJ (12,038.8 kcal)	27.5 MJ (6,575.9 kcal)
Resting (13.2%, 0.8 m/s)	150.4 MJ (35,936.6 kcal)	83.2 MJ (19,883.7 kcal)
Socializing (11.6%, 1.1 m/s)	133.8 MJ (31,985.5 kcal)	73.8 MJ (17,641.3 kcal)
Beach-rubbing (4.5%, speed not available but assumed to be 0.8 m/s [speed for resting], since beach rubbing whales do not move through the area very quickly and rubbing behavior was often accompanied by resting among nearby animals ([Ford 1989]).	51.3 MJ (12,251.1 kcal)	28.4 MJ (6,778.5 kcal)
Total daily energy budget (24 h)	1,166.5 MJ (278,797.8 kcal)	641.6 MJ (153,342.2 kcal)
Daily energy budget relative to Kleiber (1975) predicted basal metabolic rate (BMR) values	7.3× Kleiber	5.0× Kleiber

[a]Percentage of time Northern Resident killer whales were observed in five activity states and mean swimming speed during each activity from Ford (1989). Ford (1989) reported percentages based on 416 total h of observations collected on 93 d. For this illustration, these percentages were also assumed to apply to a 24 h activity budget.

[b]Energy expenditure was calculated using the speed for each activity state from Ford (1989) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult males from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

[c]Energy expenditure was calculated using the speed for each activity state from Ford (1989) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult females without calves from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

FMR (Equations 1 and 2) to meet their daily energy demands. The estimated potential range of daily prey energy requirements (DPERs) for all killer whales takes digestive efficiency into account and was calculated from body mass, according to the following equations:

$$\text{Lower bound DPER} = 413.2 M_b^{0.75} \qquad (3)$$

$$\text{Upper bound DPER} = 495.9 M_b^{0.75} \qquad (4)$$

where DPER is in kcal/d and M_b is body mass in kg.

Table 2. FMRs for adult male and female Southern Resident killer whales calculated from daily activity budgets.

Activity state[a] (% of 24 h day engaged in activity, mean swimming speed during activity)	Daily adult male (4,434 kg) FMR[b]	Daily adult female (3,338 kg) FMR[c]
Foraging	242.3 MJ	133.6 MJ
(21%, 1.1 m/s)	(57,904.7 kcal)	(31,936.9 kcal)
Travelling	835.0 MJ	457.4 MJ
(70.4%, 2.2 m/s)	(199,576.1 kcal)	(109,314.2 kcal)
Resting	77.5 MJ	42.9 MJ
(6.8%, 0.8 m/s)	(18,512.8 kcal)	(10,243.1 kcal)
Socializing	19.7 MJ	11.0 MJ
(1.8%, 0.3 m/s)	(4,711.9 kcal)	(2,632.8 kcal)
Total daily energy budget (24 h)	1174.5 MJ	644.9 MJ
	(280,705.5 kcal)	(154,126.9 kcal)
Daily energy budget relative to Kleiber (1975) predicted basal metabolic rate (BMR)	7.4× Kleiber	5.0× Kleiber

[a]Percentage of scan samples collected on a 10-min interval ($n = 571$ sampling intervals) that Southern Resident killer whales were observed in four activity states (Noren *et al.* 2009, D. Noren, unpublished data). The mean swimming speed for each activity state was calculated from speeds of individual male and female focal whales recorded during each state (D. Noren, unpublished data). Data were collected during daylight hrs only, but for this illustration, it is assumed that the percentages approximate percentages of a 24 h activity budget.

[b]Energy expenditure was calculated using the speed for each activity state (D. Noren, unpublished data) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult males from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

[c]Energy expenditure was calculated using the speed for each activity state (D. Noren, unpublished data) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult females without calves from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

It is possible that food consumption increases to compensate for the energetic costs of gestation, lactation, and growth. Results from the few studies conducted on marine mammals demonstrate that food intake can increase during some, but not all of these life processes. For example, food intake rates of captive killer whales (Kriete 1995, Kastelein *et al.* 2003*a*) and bottlenose dolphins (Kastelein *et al.* 2002, 2003*b*) do not increase significantly during gestation. Thus, it is also likely that DPERs of pregnant free-ranging killer whales do not increase. In contrast, food consumption is likely to increase during lactation. For instance, food consumption in lactating female California sea lions is greater than that of nonlactating females (Williams *et al.* 2007). Though, due to confounding energetic demands associated with the annual molt, which also increased food consumption in non-lactating females during the lactation period (Williams *et al.* 2007), it is not possible to determine the proportion of consumed prey that is attributed to lactation demands alone. Data on lactating odontocetes are also inadequate to establish an appropriate level of increased food

consumption for lactating, free-ranging killer whales. For example, lactating captive killer whales (Kriete 1995, Kastelein *et al.* 2003*a*) and bottlenose dolphins (Kastelein *et al.* 2002, 2003*b*) increase food intake rates by 1.5–2 times baseline levels, but food consumption rates are highly variable across individuals, across different lactation periods in females that have given birth more than once, and within a single lactation period (Kriete 1995, Kastelein *et al.* 2002, 2003*a*, *b*). In general, food intake rates increase only after the first month following birth but then decrease by the third or fourth month of lactation (Kastelein *et al.* 2003*b*). Several researchers have investigated lactation costs in terrestrial mammals, but it would be inappropriate to apply their results to lactating cetaceans because energy expenditure and caloric intake during lactation in mammals varies by several factors, including allometry, life history, phylogeny, and individual variation (Gittleman and Thompson 1988).

Given that pregnant captive delphinids do not increase food intake rates and data on food intake rates during lactation are equivocal, it was deemed appropriate to use Equations 3 and 4 to estimate DPERs of free-ranging pregnant and lactating killer whales. Similarly, Equations 3 and 4 were also used to estimate DPERs of growing juvenile and adolescent killer whales. This is because energy intake required for growth in immature captive killer whales (Kriete 1995) and free-ranging Steller sea lions (Winship *et al.* 2002) is negligible relative to total energy intake.

RESULTS

Comparing Predicted FMRs with FMRs Calculated from Daily Activity Budgets

FMRs calculated from *COT* curves and daily activity budgets range from 5.0 to 7.4 times Kleiber (1975) predicted basal metabolic rates for adult resident killer whales (Table 1, 2). Even though the percentage of time spent in different activity states differs somewhat between Northern and Southern Resident killer whales, the resulting daily FMRs are very similar (Table 1, 2).

The results of these calculations suggest that FMRs of female killer whales are five times Kleiber (1975) predicted BMR values, which is the predicted lower bound FMR (Equation 1), and FMRs of males are 7.3–7.4 times Kleiber (1975) predicted BMR values, which is slightly greater than the predicted upper bound FMR (Equation 2). Relatively higher mass-specific FMRs for adult males (Table 1, 2) are likely due to the finding that mass-specific *COTs* at slower speeds are slightly higher in males compared to females (Williams and Noren 2009). In contrast, there is no sex difference in mass-specific *COTs* at faster speeds (Williams and Noren 2009). It is probable that differences in mass-specific *COTs* at slower speeds are artifacts of the methods used by Williams and Noren (2009) to determine *COT*, rather than a true elevation of mass-specific *COTs* in males relative to females. The elevated mass-specific FMR values for males (Table 1, 2) are likely due to the fact that the majority of speeds in the daily activity budgets are <2.0 m/s and do not necessarily indicate that mass-specific FMRs of adult males are higher than those of adult females.

Given that several assumptions were made during the construction of the *COT* curves (see Williams and Noren 2009) and that activities that reduce (*e.g.*, long-duration diving, rest) and increase (*e.g.*, social, surface active behaviors) metabolism were not accounted for in the calculations, FMRs estimated from *COT* curves and daily activity budgets were not expected to be identical to those estimated from Equations 1 and 2. However, the similarity is encouraging and provides some evidence to suggest
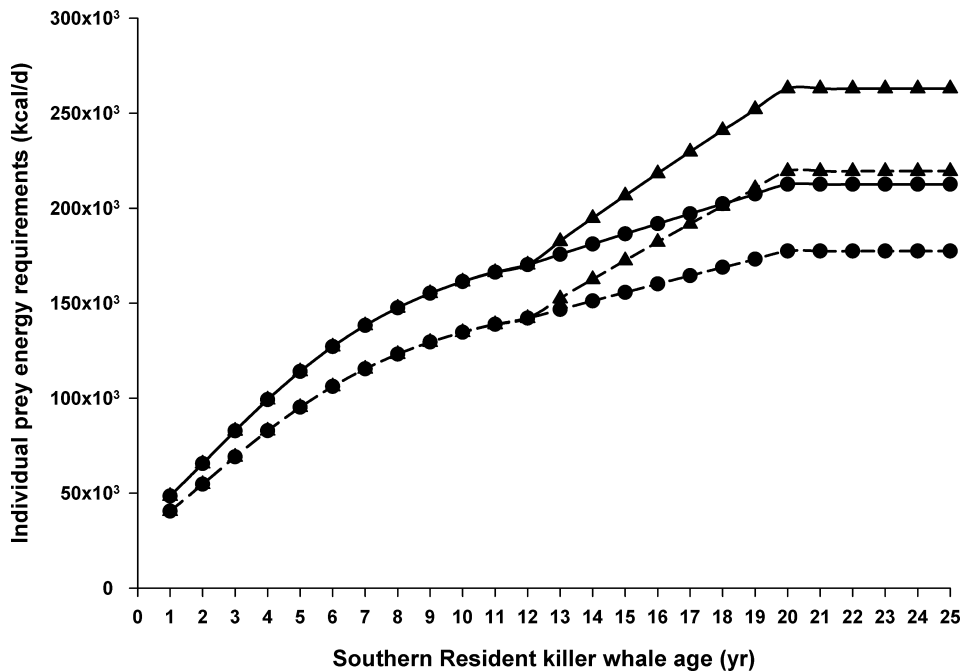
Figure 2. Relationship between daily prey energy requirements (DPERs) and age in years for male and female killer whales. Lower bound (broken lines) and upper bound (solid lines) estimates of DPERs (kcal/d) are presented for male (▲) and female (●) killer whales.

that FMRs of resident killer whales are likely to fall within the range of five to six times Kleiber (1975) predicted BMR, similar to other marine mammals.

Field Metabolic Rates (FMRs) and Daily Prey Energy Requirements (DPERs)

As expected, total FMRs and DPERs differ widely across Southern Resident killer whale age and sex classes (see online Table S1, Fig. 2). Not surprisingly, juvenile animals have the lowest total FMRs and DPERs, while adult males have the highest. Although males >12 yr old have higher lower and upper bound FMRs and DPERs than females of comparable age, there is some overlap in the range of values for males and females aged 13–18 yr old (Fig. 2). However, by 19 yr of age, FMRs and DPERs of males surpass those of females (Fig. 2).

Yet, when considering DPERs of the entire Southern Resident killer whale population, it is not the males, but the females that collectively have the highest total DPER. This is because 34.9% of the November 2008 population of SRKWs were older adult females (≥20 yr old), and thus a large portion of the population's total DPER is attributed to this segment (Fig. 3a, b). Specifically, the DPERs of all older adult females combined represent 40.5% of the population's total DPER (12,980,019–15,577,908 kcal/d). Although the number of adult males (≥20-yr old) in the November 2008 population was relatively small (7.2% of the population), and comparable to the number of animals in some of the juvenile/immature age classes, their larger body size ensures that the combined DPERs of all adult males is the second largest portion (10.4%) of the population's total DPER (Fig. 3a, b).
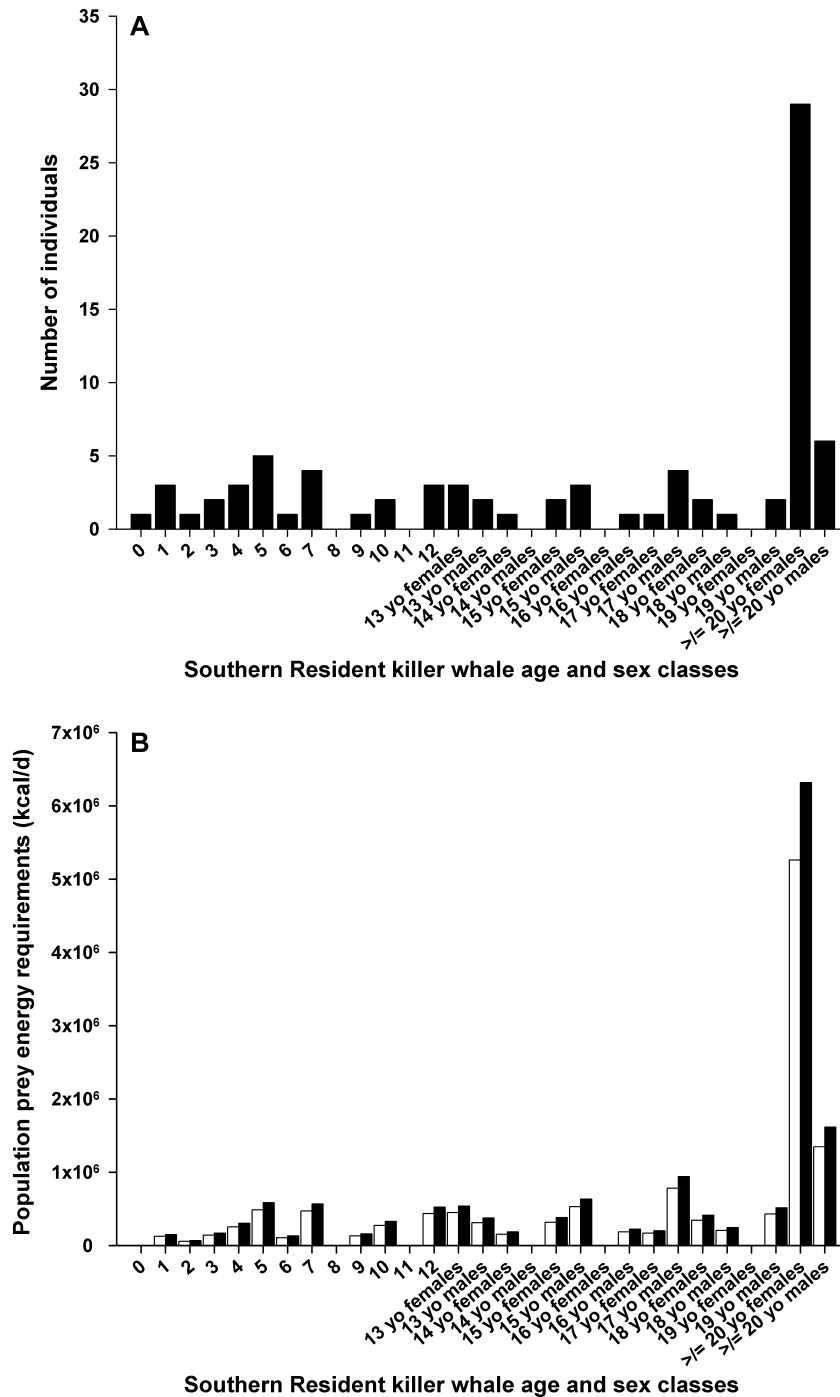
Figure 3. Number of individuals within each age and sex class (a) and total daily prey energy requirements (DPERs) for all killer whales combined within each age and sex class (b) from the Southern Resident killer whale population in November 2008 (Center for Whale Research, http://www.whaleresearch.com). Lower bound (white bars) and upper bound (black bars) estimated DPERs are presented. It is assumed that calves <1 yr of age receive all of their daily energy requirements through their mothers' milk, not *via* ingestion of fish.

DISCUSSION

Because of the multitude of uncertainties associated with estimating body mass and field metabolic rates (FMRs) in free-ranging killer whales, it is not appropriate to provide point estimates of FMR and daily prey energy requirements (DPERs). Thus, upper and lower bounds for daily FMRs and DPERs were used to estimate a reasonable range of FMRs and DPERs for Southern Resident killer whales. Upper bound FMRs and DPERs are approximately 20% greater than lower bound FMRs and DPERs, respectively, for all age and sex classes.

The concurrence between FMRs calculated from Equations 1 and 2, which assumed that FMRs of resident killer whales are five to six times Kleiber-predicted BMR (similar to other marine mammals), and FMRs calculated from killer whale daily activity budgets and *COT* curves suggests that FMRs and DPERs of free-ranging killer whales fall within the ranges presented in the current study. Furthermore, the estimated FMRs and DPERS of adult male (FMRs: 43–51 kcal/kg/d, DPERs: 51–61 kcal/kg/d) and female (FMRs: 46–55 kcal/kg/d, DPERs: 54–65 kcal/kg/d) killer whales from the present study are similar to those reported previously for other adult killer whales (Kriete 1995, Baird and Dill 1996, Osborne 1999, Williams 1999, Williams *et al.* 2004, Williams and Noren 2009). Interestingly, these mass-specific FMRs are also similar to those of adult harbor porpoises (*Phocoena phocoena*), which were calculated from swimming speeds and estimates of partitioned daily activity levels (Yasui and Gaskin 1986).

As additional information on SRKW body size and cetacean energetics become available, FMR and DPER estimates should be refined. Given that the calculations are based on body mass, deviations from true body mass values will inevitably lead to errors in these estimates. For example, a 10% increase in body mass results in a 7% increase in both FMR and DPER values. Thus, accurate assessments of body mass are critical to improving FMR and DPER estimates. Also, as mentioned previously, the energetic costs of growth in young animals and adolescent males and lactation in females could increase DPERs, though the effect of these costs on DPERs is unclear. Until these can be better quantified, it is probably best to use DPERs calculated from the upper bound equation (Equation 4), which are 1.2 times greater than DPERs calculated from the lower bound equation (Equation 3), for growing and lactating whales. If, for example, upper bound DPERs were used to estimate prey consumption rates in lactating females over the course of 1 yr, the 3–4 mo (Kastelein *et al.* 2003*b*) of 1.5–2 times increased prey consumption rates (Kriete 1995, Kastelein 2002, Kastelein *et al.* 2003*a*, *b*) would be accounted for.

Although discrepancies between the estimated and actual DPERs of an individual lactating female killer whale may arise from using the above methods, these discrepancies will negligibly impact the accuracy of the SRKW population's total estimated annual DPER. This is because there are only a small number of lactating females with calves <1 yr of age in the population at any given time (number of calves <1 yr of age in November 2008: 1, average number ± SD of calves born per year: 3.1 ± 0.8, average percent ± SD first year survival of calves: 64.6 ± 30.8%, data from 1998 through 2008, Center for Whale Research, http://www.whaleresearch.com). Similarly, only 15.7% of the population were adolescent males (aged 13–19 yr old) in November 2008 (census data, Center for Whale Research, http://www.whaleresearch.com), so if the DPERs of these growing animals were slightly underestimated, the total SRKW population DPER would only be slightly underestimated.

Table 3. Comparison of daily prey energy requirements predicted for Southern Resident killer whales by Osborne (1999) and the present study.

Age and sex class[a]	DPER (kcal/d)[a]	Lower bound DPER (kcal/d)[b]	Upper bound DPER (kcal/d)[b]
Immature (1–6 yr)	85,000	41,376–108,525	49,657–130,246
Juvenile (7–12 yr)	100,000	118,019–145,299	141,640–174,380
Female >12 yr	160,000	149,972–181,458	179,988–217,775
Male >12 yr	200,000	155,885–224,521	187,085–269,458

[a]From Osborne (1999).

[b]From the present study.

This is the first study to estimate FMRs and DPERs of killer whales from all segments of a population during each yr of life until physical maturity (20 yr of age when body growth ceases). In contrast, Osborne (1999) presented distinct DPER estimates for immature (1–6 yr of age), juvenile (7–12 yr of age), male (>12 yr of age), and female (>12 yr of age) killer whales (Table 3). The results of this study suggest that there is a wide range of DPERs within each of the four groups (Table 3) defined by Osborne (1999). For example, DPERs of immatures (1–6-yr old) and juveniles (7–12-yr old) increase 2.6- and 1.2-fold over a 5-yr span in age, respectively. Similarly, DPERs increase 1.4-fold during the male growth spurt from the age of 13–20-yr old. These findings differ significantly from those of Osborne (1999) and are due to the prolonged developmental period and associated changes in body mass with age in killer whales. These comparisons demonstrate the importance of keeping life history patterns in mind when estimating daily prey energy requirements.

Estimating FMRs and DPERs are first steps in determining prey consumption rates (PCRs) for the Southern Resident killer whale population. The next step for management purposes is to know how many individual fish are consumed by these whales per year. From a mathematical perspective, converting DPERs (kcal/d) to fish/year is a relatively straightforward task, as long as the caloric densities of the fish consumed are known.

However, determining the number of fish consumed per year by the Southern Resident killer whale population is not a simple undertaking for several reasons. First, the caloric densities of fish vary by species, age, size, percentage lipid content, geographic region, and season (Brett 1995). Second, although SRKWs prefer to consume relatively rare Chinook salmon in the summer (Ford *et al.* 1998, Ford and Ellis 2006, Hanson *et al.,* in press), the diet composition of SRKWs during other seasons is not as well known. Data suggest that diets of resident killer whales not only change seasonally (Ford and Ellis 2006, Hanson *et al.*, in press), but that even within the summer season, killer whales may predominantly consume different species of salmon during particular months (Ford and Ellis 2006, Hanson *et al.*, in press). Third, differences in prey selectivity across pod members of different age and sex classes are not well understood (Ford and Ellis 2006).

Given the limited data on SRKW prey selectivity, it would be difficult to estimate annual PCRs for every prey item that is consumed by this population. However, to illustrate how diverse species-specific consumption rates can be, PCRs for Chinook and chum (*Oncorhynchus keta*) salmon were calculated. Specifically, lower and upper bounds for PCRs of Chinook and chum salmon were calculated from DPERs (kcal/d)

of Southern Resident killer whales and caloric densities (kcal/fish) of Chinook (average value for adults from the Fraser River: 16,386 kcal/fish)[1] and chum (average value for adults from the Puget Sound: 3,877 kcal/fish)[1] salmon, assuming a single-species diet (for simplicity). Chinook and chum salmon were used for this example because they are the two most prevalent salmon species in the diets of Northern and Southern Resident killer whales (Ford *et al.* 1998, Ford and Ellis 2006, Hanson *et al.*, in press). When subsisting only on Chinook, the daily consumption rate for the 82 animals ≥1 yr of age in the 83-member SRKW population ranges from 792 to 951 fish/d (289,131–347,000 fish/yr). Fish consumption increases significantly to 3,348–4,018 fish/d (1,222,003–1,466,581 fish/yr) when the population consumes only chum.

It is not surprising that Chinook salmon is the preferred prey of resident killer whales (Ford and Ellis 2006), given its larger size and greater mass-specific caloric content compared to other salmonid species (Groot and Margolis 1991). As a consequence, fewer Chinook salmon need to be consumed by killer whales to meet their DPERs. However, because PCR values are sensitive to assumptions about the size and caloric density of the fish consumed, they should be refined as additional data on prey selectivity become available.

Although coarse estimates for the number of individual fish consumed per day are presented here, the actual number of prey items available in the ocean will have to be much greater to ensure that the population of SRKWs meets their DPERs. This is because prey resources can be patchy and ephemeral. Thus, a much larger prey base will need to be available to SRKWs when the total area of the foraging ground and the energetic cost of searching for prey are considered. Consequently, upper bound PCR estimates likely represent a minimum starting point for how many prey need to be available to meet the metabolic demands of the SRKW population. Future studies on the foraging efficiency of resident killer whales should be conducted to provide additional information to improve these estimates.

In conclusion, this study provides the first estimates of body mass, FMRs, and DPERs for all members of an existent cetacean population. These estimates were based on the best available data and should be refined as additional data become available. In the meantime, however, the estimated DPERs presented here can be combined with data on salmon availability and SRKW foraging selectivity and efficiency to assess the degree to which SRKWs may be prey limited.

LITERATURE CITED

Baird, R. W., and L. M. Dill. 1996. Ecological and social determinants of group size in *transient* killer whales. Behavioral Ecology 7:408–416.
Barrett-Lennard, L. G., K. Heise, E. Saulitis, G. Ellis and C. Matkin. 1995. The impact of killer whale predation on Steller sea lion populations in British Columbia and Alaska. Report to the North Pacific Universities Marine Mammal Research Consortium, Vancouver,

[1] Personal communication from Sandra O'Neill, NOAA Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, August 2009.

British Columbia, Canada (unpublished). Available at http://www.marinemammal.org/pdfs/Barrett_etal1995-killer.pdf.

Bigg, M. A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, B.C. Report of the International Whaling Commission 32:655–666.

Bigg, M. A., and A. A. Wolman. 1975. Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington waters, 1962–1973. Journal of Fisheries Research Board Canada 32:1213–1221.

Brett, J. R. 1995. Energetics. Pages 1–68 *in* C. Groot, L. Margolis and W. C. Clark, eds. Physiological Ecology of Pacific Salmon. UBC Press, Vancouver, B.C.

Christensen, I. 1988. Growth and reproduction of killer whales, *Orcinus orca*, in Norwegian coastal waters. Report of the International Whaling Commission (Special Issue 6):253–258.

Clark, S. T., and D. K. Odell. 1999. Allometric relationships and sexual dimorphism in captive killer whales (*Orcinus orca*). Journal of Mammalogy 80:777–785.

Clark, S. T., D. K. Odell and C. T. Lacinak. 2000. Aspects of growth in captive killer whales (*Orcinus orca*). Marine Mammal Science 16:110–123.

Costa, D. P. 2002. Energetics. Pages 387–394 *in* W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. Encyclopedia of marine mammals. Academic Press, San Diego, CA.

Costa, D. P., and T. M. Williams. 1999. Marine mammal energetics. Pages 176–217 *in* J. E. Reynolds III and S. A. Rommel, eds. Biology of marine mammals. Smithsonian Institution Press, Washington, DC.

Costa, D. P., B. J. Le Boeuf, A. C. Huntley and C. L. Ortiz. 1986. The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. Journal of Zoology, London 209:21–33.

Costa, D. P., G. A. Antonelis and R. L. Delong. 1991. Effects of El Niño on the foraging energetics of the California sea lion. Pages 156–165 *in* F. Trillmich and K. A. Ono, eds. Pinnipeds and El Niño responses to environmental stress. Springer-Verlag, Berlin, Germany.

DeMaster, D. P., A. W. Trites, P. Clapham, S. Mizroch, P. Wade, R. J. Small and J. Ver Hoef. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. Progress in Oceanography 68:329–342.

Duffield, D. A., and K. W. Miller. 1988. Demographic features of killer whales in oceanaria in the United States and Canada, 1965–1987. Rit Fiskideildar 11:297–306.

Estes, J. A., D. F. Doak, A. M. Springer, T. M. Williams and G. B. Van Vliet. 2009. Trend data *do* support the sequential nature of pinniped and sea otter declines in the North Pacific Ocean, *but* does it really matter? Marine Mammal Science 25:748–754.

Fahlman, A., R. Svärd, C. Wilson, D. A. S. Rosen and A. W. Trites. 2008. Activity and diving metabolism correlate in Steller sea lion *Eumetopias jubatus*. Aquatic Biology 2:75–84.

Feldkamp, S. D. 1987. Swimming in the California sea lion: Morphometrics, drag and energetics. Journal of Experimental Biology 131:117–135.

Ford, J. K. B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67:727–745.

Ford, J. K. B., and G. M. Ellis. 2006. Selective foraging by fish-eating killer whales (*Orcinus orca*) in British Columbia. Marine Ecology Progress Series 316:185–199.

Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C. Balcomb. 1998. Dietary specialisation in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

Ford, J. K. B., G. M. Ellis, P. F. Olesiuk and K. C. Balcomb. 2009. Linking killer whale survival and prey abundance: Food limitation in the oceans' apex predator? Biology Letters 6:139–142.

Gittleman, J. L., and S. D. Thompson. 1988. Energy allocation in mammalian reproduction. American Zoologist 28:863–875.

Groot, C., and L. Margolis, eds. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, BC.

Hanson, M. B., R. W. Baird, J. K. B. Ford, J. Hempelmann-Halos, D. M. Van Doornik, J. R. Candy, C. K. Emmons, G. S. Schorr, B. Gisborne, K. L. Ayres, S. K. Wasser, K. C. Balcomb, K. Balcomb-Bartok, J. G. Sneva and M. J. Ford. In press. Species and stock identification of prey consumed by endangered "southern resident" killer whales in their summer range. Endangered Species Research.

Hastie, G. D., D. A. S. Rosen and A. W. Trites. 2006. The influence of depth on a breath-hold diver: predicting the diving metabolism of Steller sea lions (*Eumetopias jubatus*). Journal of Experimental Marine Biology 336:163–170.

Hastie, G. D., D. A. S. Rosen and A. W. Trites. 2007. Reductions in oxygen consumption during dives and estimated submergence limitations of Steller sea lions (*Eumetopius jubatus*). Marine Mammal Science 23:272–286.

Heyning, J. E. 1988. Presence of solid food in a young calf killer whale (*Orcinus orca*). Marine Mammal Science 4:68–71.

Hurley, J. A., and D. P. Costa. 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). The Journal of Experimental Biology 204:3273–3281.

Jonsgård, Å., and P. B. Lyshoel. 1970. A contribution to the knowledge of the biology of the killer whale *Orcinus orca* (L.). Nytt Magasin for Zoologi 18:41–48.

Kastelein, R. A., S. Walton, D. Odell, S. H. Nieuwstraten and P. R. Wiepkema. 2000. Food consumption of a captive female killer whale (*Orcinus orca*). Aquatic Mammals 26:127–131.

Kastelein, R. A., J. Kershaw, E. Berghout and P. R. Wiepkema. 2001. Food consumption and suckling in Killer whales (*Orcinus orca*) at Marineland Antibes. International Zoo Yearbook 38:204–218.

Kastelein, R. A., N. Vaughan, S. Walton and P. R. Wiepkema. 2002. Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. Marine Environmental Research 53:199–218.

Kastelein, R. A., J. Kershaw, E. Berghout and P. R. Wiepkema. 2003*a*. Food consumption and suckling in killer whales *Orcinus orca* at Marineland Antibes. International Zoo Yearbook 38:204–218.

Kastelein, R. A., C. Staal and P. R. Wiepkema. 2003*b*. Food consumption, food passage time and body measurements of captive Atlantic bottlenose dolphins (*Tursiops truncatus*). Aquatic Mammals 29:53–66.

Kleiber, M. 1975. The fire of life: An introduction to animal energetics. 2nd edition. Robert E. Kreiger Publishing, Huntington, NY.

Krahn, M. M., M. J. Ford, W. F. Perrin, P. R. Wade, R. P. Angliss, M. B. Hanson, B. L. Taylor, G. M. Ylitalo, M. E. Dahlheim, J. E. Stein and R. S. Waples. 2004. 2004 status review of southern resident killer whales (*Orcinus orca*) under the Endangered Species Act. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-62. 73 pp.

Kriete, B. 1995. Bioenergetics in the killer whale, *Orcinus orca*. Doctoral dissertation, University of British Columbia, Vancouver, BC. 138 pp.

Maniscalco, J. M., C. O. Matkin, D. Maldini, D. G. Calkins and S. Atkinson. 2007. Assessing killer whale predation on Steller sea lions from field observations in Kenai Fjords, Alaska. Marine Mammal Science 23:306–321.

Nishiwaki, M., and C. Handa. 1958. Killer whales caught in the coastal waters off Japan for recent 10 years. Scientific Reports of the Whales Research Institute, Tokyo 13:85–96.

Noren, D. P. 2002. Thermoregulation of weaned northern elephant seal (*Mirounga angustirostris*) pups in air and water. Physiological and Biochemical Zoology 75:513–523.

Noren, S. R., and E. F. Edwards. 2006. Physiological and behavioral development in delphinid calves: Implications for calf separation and mortality due to tuna purse-seine sets. Marine Mammal Science 23:15–29.

Noren, D. P., A. H. Johnson, D. Rehder and A. Larson. 2009. Close approaches by vessels elicit surface active behaviors by southern resident killer whales. Endangered Species Research 8:179–192.

Osborne, R. W. 1999. A historical ecology of Salish Sea "resident" killer whales (*Orcinus orca*): With implications for management. Doctoral dissertation, University of Victoria, Victoria, BC. 262 pp.

Pauly, D., A. W. Trites, E. Capuli and V. Christensen. 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science 55:467–481.

Rosen, D. A. S., and A. W. Trites. 2002. Cost of transport in Steller sea lions, *Eumetopias jubatus*. Marine Mammal Science 18:513–524.

Springer, A. M., J. A. Estes, G. B. Van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences 100:12223–12228.

Springer, A. M., J. A. Estes, G. B. Van Vliet, T. M. Williams, D. F. Doak, E. M. Danner and B. Pfister. 2008. Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: A reply to the critics of Springer *et al.* 2003. Marine Mammal Science 24:414–442.

Trites, A. W., V. B. Deecke, E. J. Gregr, J. K. B. Ford and P. F. Olesiuk. 2007. Killer whales, whaling, and sequential megafaunal collapse in the north Pacific: A comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. Marine Mammal Science 23:751–765.

Wade, P. R., V. N. Burkanov, M. E. Dahlheim, N. A. Friday, L. W. Fritz, T. R. Loughlin, S. A. Mizroch, M. M. Muto, D. W. Rice, L. G. Barrett-Lennard, N. A. Black, A. M. Burdin, J. Calambokidis, S. Cerchio, J. K. B. Ford, J. K. Jacobsen, C. O. Matkin, D. R. Matkin, A. V. Mehta, R. J. Small, J. M. Straley, S. M. McCluskey, G. R. VanBlaricom and P. J. Clapham. 2007. Killer whales and marine mammal trends in the North Pacific—a re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. Marine Mammal Science 23:766–802.

Wade, P. R., J. M. Ver Hoef and D. P. DeMaster. 2009. Mammal-eating killer whales and their prey—trend data for pinnipeds and sea otters in the North Pacific Ocean do not support the sequential megafaunal collapse hypothesis. Marine Mammal Science 25:737–747.

Ward, E. J., E. E. Holmes and K. C. Balcomb. 2009. Quantifying the effects of prey abundance on killer whale reproduction. Journal of Applied Ecology 46:632–640.

Webb, P. M., R. D. Andrews, D. P. Costa and B. J. Le Boeuf. 1998. Heart rate and oxygen consumption of northern elephant seals diving in the laboratory. Physiological Zoology 71:116–125.

Williams, T. M. 1999. The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. Philosophical Transactions of the Royal Society London B 354:193–201.

Williams, T. M., J. A. Estes, D. F. Doak and A. M. Springer. 2004. Killer appetites: Assessing the role of predators in ecological communities. Ecology 85:3373–3384.

Williams, T. M., G. L. Kooyman and D. A. Croll. 1991. The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. Journal of Comparative Physiology B 160:637–644.

Williams, R., and D. P. Noren. 2009. Swimming speed, respiration rate and estimated cost of transport in adult killer whales. Marine Mammal Science 25:327–350.

Williams, T. M., M. Rutishauser, B. Long, T. Fink, J. Gafney, H. Mostman-Liwanag and D. Casper. 2007. Seasonal variability in otariid energetics: Implications for the effects of predators on localized prey resources. Physiological and Biochemical Zoology 80:433–443.

Williams, R., D. Lusseau and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133:301–311.

Winship, A. J., A. W. Trites and D. A. S. Rosen. 2002. A bioenergetic model for estimating food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Marine Ecology Progress Series 229:291–312.

Yasui, W. Y., and D. E. Gaskin. 1986. Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). Ophelia 25:183–197.

SUPPORTING INFORMATION

The following supporting information is available for this article online:

Table S1. Field metabolic rates (FMRs) and daily prey energy requirements (DPERs) for Southern Resident killer whales.