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Swimming speed, respiration rate, and estimated cost of transport in adult killer whales

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ABSTRACT

The physiology of free-ranging cetaceans is difficult to study and as a consequence, data on the energetics of these animals are limited. To better understand the energetic cost of swimming in killer whales, total cost of transport (*COT*) was estimated from swimming speeds and respiration rates from wild adult northern resident killer whales (*Orcinus orca*) and reported values of oxygen consumption in captive whales. Respiration rate (breaths per minute) was positively correlated with swimming speed (meters per second), while mass-specific *COT* (Joules per kilogram per meter) decreased with speed. Lack of data on very fast-swimming animals hindered assessment of the exact speed at which *COT* was minimal. However, minimum mass-specific *COT* for killer whales in the present study approached those predicted by a previously published allometric equation for marine mammals, and corresponded to "optimal" swimming speeds of 2.6–3 m/s. Interestingly, the observed average swimming speed (1.6 m/s) was lower than predicted optimal swimming speed. Finally, females with dependent calves had higher respiration rates than females without calves. These findings could be due to synchronous breathing with calves or could result from increased costs of lactation and swimming with a calf in echelon formation. Consequently, females with calves may have much greater *COT* at optimal swimming speeds than females without calves.

Key words: activity budget, cetacean, cost of transport, energetics, marine mammal, metabolism, whale.

INTRODUCTION

Free-ranging cetaceans are less accessible to researchers than other marine vertebrates due to their large body size and fully aquatic lifestyle, and as a consequence, data on the energetics of these animals are limited. Unlike pinnipeds, cetaceans do not come ashore, which makes the use of doubly-labeled water techniques to estimate at-sea metabolic rates (for review of methods, see Costa 1987) difficult to apply to free-swimming cetaceans. Open-flow respirometry has been used to quantify resting metabolic rate (RMR) and metabolism of short activity periods in captive killer whales, dolphins, and porpoises (*e.g.,* Kasting *et al.* 1989, Williams *et al.* 1993a, Williams *et al.* 1993b, Kriete 1995, Otani *et al.* 2001), yet these methods can only provide rough estimates of field metabolic rates (FMR) of their free-ranging counterparts. This is because wild cetaceans swim almost continuously across a wide range of speeds that are difficult to replicate in captive experimental studies. However, swimming metabolism can be estimated from field observations of swimming speeds and respiration rates in combination with theoretical values for oxygen consumption, as has been done previously for baleen whales (Sumich 1983, Blix and Folkow 1995). Such calculations are obviously complex and difficult to validate. Few captive animals are available for research purposes, and the health and vigor of captive and free-ranging cetaceans may not be directly comparable. Despite the inherent difficulty in generating or validating even rough estimates of energetic demand of free-ranging cetaceans, these modeling exercises represent important first steps to understanding energy expenditure during swimming and FMRs, simply because there are few alternatives. It will always be difficult to obtain metabolic rate (MR) estimates directly for large and intractable study animals like whales.

Among cetaceans, killer whales (*Orcinus orca*) represent an important subject for application of alternative methods to estimate FMR, in part because their trophic level is the highest of any marine mammal (Pauly *et al.* 1998). Killer whale predation has been implicated in changes in the dynamics of marine mammal populations in the northeast Pacific (*e.g.,* Springer *et al.* 2003, Williams *et al.* 2004), although the role of killer whales in the collapse of marine mammal populations is controversial (*e.g.,* DeMaster *et al.* 2006). One component of the uncertainty includes energetic requirements of killer whales (Baird 1994, Kriete 1995, Williams *et al.* 2004, Williams *et al.* 2006). In addition, killer whales possess life-history attributes, such as small population size (Ford *et al.*, 2000) and social networks that are vulnerable to even low levels of anthropogenic mortality (Williams and Lusseau 2006), that make them inherently vulnerable to extinction. The northern resident killer whale (NRKW) population, which is the focus of this study, is composed of ~200 individuals and is listed as Threatened under Canada's Species at Risk Act (SARA). The adjacent southern resident (SRKW) population numbers fewer than 100 individuals and is listed as Endangered under both the US Endangered Species Act and SARA.

Reliable estimates of the metabolic cost of swimming in killer whales are needed both to understand the whales' energetic requirements and their influence in marine ecosystems. We use a novel approach to estimate energetic cost of the swimming behavior that we observed and measured in wild killer whales. This study used non-invasive techniques to estimate total metabolic cost of transport (*COT*—that is, the cost of basal metabolism plus the metabolic cost of swimming) in free-ranging killer whales. Specifically, we measured swimming speeds and respiration rates of free-swimming killer whales from a land-based observation site. We combined these with physiological data (oxygen consumption values) reported from captive killer whales to estimate the total cost of transport during routine swimming speeds in wild whales. We report novel estimates of the total metabolic cost of transport in adult killer whales and assess how these costs varied by the sex and reproductive status of individuals within the population.

METHODS

Field Methods and Data Processing

Data from northern resident killer whales were collected from a cliff in Johnstone Strait, British Columbia (BC), Canada (50°30′N, 126°30′W) during summer field seasons (1 July through 11 September) between 1995 and 2004. An electronic theodolite was used to record locations of whales via a laptop computer equipped with custom software (THEOPROG: see Williams *et al*. 2002). As whales entered the study area, a focal whale was identified by referencing photo-identification catalogues (Ford *et al.* 1994, 2000), which also provided information on age and sex for the animal, as well as the ages of all known offspring of adult females. All individuals in the population are identifiable. A theodolite was used to record the time and position of the focal whale at each surfacing (*i.e.,* breath), following methods of previous studies (Williams *et al.* 2002). Focal animals were tracked continuously for at least 15 min. Each period of continuous observation of a focal animal is referred to subsequently as a "track." Measurements of five behavioral variables (respiration rate, swimming speed, two measures of path linearity, and the rate of surface-active or aerial displays) were summarized for each track. Respiration rates and swimming speeds were averaged over each track, and each selected track (see below) was represented only once in the analyses. Previous analyses have shown that measurements recorded (and consequently swimming speeds inferred) by the theodolite used in this study were accurate to within ±3.5% at a distance of approximately 4 km from the observation cliff (Williams *et al.* 2002).

Our field methods involved selecting focal animals that were engaged in typical "travel/forage" activity (Williams *et al.* 2006). This was identified in the field by experienced observers using a consistent set of definitions in which activity state was scored as travel/forage when whales surfaced and dove independently, but all whales in the group were heading in the same general (east–west) direction. Focal animals were chosen such that individuals were usually >10 body lengths apart, in order to avoid mistaking a non-focal animal with the focal animal. The dive sequences of individuals showed regular patterns of several short dives followed by a long one, and whales swam at moderate speeds. This activity state's function likely includes both a travel and a foraging component—that is, traveling between feeding sites and searching for prey *en route* (Ford *et al.* 1994, Williams *et al.* 2006). Note that while activity state classification involved a somewhat subjective decision, all data analysis relied on variables (swimming speed and respiration rate) that were measured objectively.

Track Selection Criteria

Analyses were restricted to observations of adults because we wanted to estimate metabolic cost of transport without the confounding energetic costs of growth. Males that were 15 years old were considered to be adults (Bigg *et al.* 1990), because male body growth slows at 12–16 years postpartum and metabolic costs due to growth are likely to be negligible at this age (Duffield and Miller 1988). We considered females to be adults at age 13, which corresponds to the age of reproductive maturity (Ford *et al.* 2000). In addition, increased metabolic costs due to growth are likely negligible by age 13, because female body growth tends to slow by 9–12 years postpartum (Duffield and Miller 1988). Females were also further divided by reproductive status (females with calves ≤ 2 years of age and females with older or no offspring). Given that a census has been conducted of this population annually since the 1970s, the age of every individual born since the 1970s is known with certainty (Ford *et al.* 1994, 2000). Thus, every juvenile was excluded reliably from our analyses.

In an attempt to identify observations that best represented directed, straight-line routine swimming activity, while excluding other activities that impact respiration and MR, we removed several tracks from our analyses. Given that field methods prioritized selection of focal animals that were engaged in travel/forage activity (Williams *et al.* 2006), the first data censoring step removed observations when whales switched from travel/forage activity to resting, socializing, or beach-rubbing activities (Williams *et al.* 2006). Second, tracks were eliminated if they contained obvious feeding attempts as indicated by milling activity and frequent changes in direction (Ford 1989). Tracks were excluded if the average angle between adjacent surfacings was greater than 30°, or if the directness index (the ratio of beginning-to-end distance to cumulative surface-distance covered during the track) was less than 0.8, which was a typical value for the directness index when whales were engaged in travel/forage activity in a previous study (Williams *et al.* 2002). Third, tracks with observations of "porpoising" behavior, breaching, or spy-hopping were removed, because performance of surface-active behaviors such as breaching increases MR (Kriete 1995; D. Noren, unpublished data). If a breach occurred at the end of a track, then only the last few minutes were removed, rather than deleting the entire observation. Fourth, tracks with dive durations greater than 3 min were excluded, because of the potential for greater dive depths (Hastie *et al.* 2006) and durations (Hurley and Costa 2001) to reduce MR and also because of our inability to account for swim speeds and distances underwater. Tracks were eliminated from the analyses if a boat was observed within 1000 m of the focal animal at any point during the tracking session, because boat-avoidance activities can influence surfacing behavior (Williams *et al.* 2002, 2006). These censored tracks with observation durations of less than 10 min were also discarded, because short track durations can produce biased estimates of respiration rate (Kriete 1995).

The strict selection process provided a homogeneous set of observations for analyses of the energetic costs of transport. The final dataset included whales in travel/forage mode, traveling in a fairly straight path, generally at a constant speed, with short dive durations. Additional distances were not added to the surface distances to account for vertical distances traveled during dives (*cf.*, Kriete 1995) because all tracks with long dives (>3 min) were dropped from the analyses, and because killer whale dive depths are shallow and swimming velocity is steady during travel mode (Baird *et al.* 2003). While the selection criteria were designed to minimize bias due to uncertainty about animal behavior underwater, the swim speeds presented here may be slightly underestimated because we assumed straight-line movements between surfacings.

Tracks that satisfied all of the selection criteria above were categorized as having satisfied "strict" selection criteria. However, the known difficulty of tracking female killer whales (Williams *et al.* 2002) prompted us to relax some selection criteria to increase sample size for females. Specifically, some tracks in which boats were

Table 1. Morphology and oxygen consumption values used for calculating cost of transport in free-ranging, adult northern resident killer whales.

Sex	Body mass[a] (kg)	Activity level 1 mean oxygen consumption (L O_2/breath)[b]	Activity level 2 mean oxygen consumption (L O_2/breath)[b]	Activity level 3 mean oxygen consumption (L O_2/breath)[b]
M	3913	19.1	22.3	25.5
F	2800	10.4	11.9	13.7

[a] Body mass was estimated for the study animals in Kriete (1995) using an equation from Bigg and Wolman (1975).

[b] Mean oxygen consumption for a captive adult male (age 20) and an adult female (age 21) killer whale were calculated from maximum tidal volume (L) and mean oxygen extraction (% O_2 extracted per breath) measured from exhaled air collected after several trials at each of three activity levels (Kriete 1995). For these calculations, it was also assumed that the partial pressure of O_2 in air is 0.2095. [Correction added after publication online: values for oxygen consumption (L O_2/breath) in Table 1 were corrected to account for the partial pressure of O_2 in air] Activity levels were defined as follows. Activity level 1 was measured after resting for a 15-min period and at least 14 h after the last meal. Activity level 2 was measured after light to moderate activity for a period of at least 15 min. Activity level 3 was measured immediately after a show with high intensity activities, including several breaches. For activity levels 2 and 3, measurements were made after animals had been fed at least once within the previous 3 h. Due to logistical constraints, oxygen consumption for the male in activity level 2 was estimated as the average of levels 1 and 3 (Kriete 1995). Although this estimate is not ideal, data from the female subject indicate that this was a reasonable assumption. For all calculations of oxygen consumption (L O_2/breath), maximum tidal volumes were used because these volumes appeared to better estimate normal tidal volume values than mean volumes (Kriete 1995). Importantly, there were no significant differences in mean tidal volumes measured following the different activity states for either the male or the female (Kriete 1995).

observed between 100 and 1000 m, and/or the directness index was between 0.40 and 0.80 were included, because violation of these selection criteria was deemed least likely to impact respiration and MR. All other strict criteria were met for these additional tracks with "relaxed" selection criteria.

Metabolic Cost of Transport Calculations

The total cost of transport (*COT*) was estimated from the average swimming speed and respiration rate for each track. First, mean swimming speed (meters per second) and mean respiration rate (breaths per min) were used to calculate average breaths per meter for each track from killer whales, similar to methods used in gray whales *Eschrichtius robustus* (Sumich 1983). Second, oxygen consumption values (L O_2 per breath) measured in captive killer whales (Kriete 1995, Table 1) were used to convert respiration rate for each track to L O_2 per meter. These values were converted to units of total *COT* (Joules per meter) using the conversion factor of 20.1 kJ per 1 L O_2. Finally, total *COT* (Joules per meter) was divided by the body mass values of the captive killer whale subjects (Table 1) to attain the standard units of mass-specific *COT* (Joules per kilogram per meter). Although the body mass of the captive subjects were not measured, Kriete (1995) estimated their body mass from predictive equations of body mass based on body length determined from wild killer whales (Bigg and

Wolman 1975). The whales from the Bigg and Wolman (1975) study were members of the same killer whale ecotype and from the same geographic region from which the field data in the present study were collected. Hence, it is likely that the adult male and female animals in the northern resident killer whale population from which the respiration and swimming speed data were collected are similar in body size to the captive animals from the Kriete (1995) study.

Underlying Assumptions and Variability in COT

The calculations presented above are somewhat simplistic due to the difficulty of observing cetaceans swimming underwater and the paucity of data on their respiration physiology. Because of this, a number of explicit and implicit assumptions were made for our calculations of *COT* from respiration rates and swimming speeds of free-ranging whales and values of oxygen consumption per breath from captive whales.

Besides assuming that the wild killer whales swam in straight paths, we also assumed that currents would not significantly impact the results. We did not adjust our calculated swimming speeds for the effects of tidal currents. Such a correction could not be made because tidal currents were highly variable throughout the study area, and because the whales' orientation relative to the current was not always obvious. However, an extensive study of movement patterns of resident killer whales with respect to tidal currents (Felleman 1986) indicates that this assumption was unlikely to have introduced major bias. Traveling killer whales were found to be oriented with, against, or non-oriented with respect to tidal currents in approximately equal proportions (Felleman 1986). Thus, our inability to correct for orientation with respect to current was likely to have contributed to unmodeled heterogeneity, but was unlikely to have introduced systematic bias. This can be evaluated with future, directed field efforts.

Furthermore, for the *COT* calculations, we assumed both constant maximum tidal volume and fixed oxygen extraction per breath within an activity level. In reality, lung tidal volume and oxygen extraction can vary with individual breaths, and thus, whales may not always inspire their maximum tidal volume (Spencer *et al.* 1967, Kriete 1995). Yet, in light of Kriete's (1995) findings that maximum tidal volumes appeared to estimate normal tidal volumes better and that tidal volume did not increase with increasing activity level, we chose to incorporate the maximum tidal volume in all of our calculations. Although we incorporated a constant value of oxygen consumption for each breath, we did vary it with activity level because Kriete (1995) found that oxygen consumption increases with activity level. These assumptions also need evaluation, but until data are available on variability in tidal volume and O_2 extraction, this method is a reasonable starting point.

Additionally, we assumed that oxygen consumption is correlated with respiration rate in wild killer whales. This assumption is also valid because Kriete (1995) found that oxygen consumption was correlated with respiration rate in captive killer whales. In addition, it is unlikely that respiration rates and oxygen consumption values differed between the captive and wild killer whales due to temperature effects because the range of temperatures in the captive facilities (likely within the thermal neutral zone of killer whales) were similar to water temperatures experienced by wild killer whales (Kriete 1995).

Finally, we assumed that activity levels of cetaceans in captive experiments approximate behaviors observed in the wild. Though it is likely that activity levels of captive animals do not precisely correspond to behaviors observed in the wild, we concur with Kriete (1995) that routine swimming speeds of wild whales are most closely approximated by activity level 2 in the captive study (see Table 1 for description of activity levels). Consequently, for female killer whales, we used the oxygen consumption values from Kriete (1999) during activity level 2 for our quantification of *COT* (Joules per kilogram per meter). For males, we interpolated this value from the numbers reported by Kriete (1995) at higher and lower activity levels. Although oxygen consumption was not measured during activity level 2 in the captive male killer whale, Kriete (1995) estimated that the value would be midway between those measured during activity levels 1 and 3. This is a reasonable assumption given that data from the female killer whale show this pattern (Kriete 1995, Table 1). Due to the potential mismatch in wild and captive killer whale activity levels and corresponding oxygen consumption values, we also present *COT* (Joules per kilogram per meter) calculated from oxygen consumption values from Kriete's (1995) activity levels 1 and 3 (for both males and females) in order to provide a range of estimates for *COT* (Joules per kilogram per meter) expected across the swimming speeds observed. In reality, the elevated levels of oxygen consumption reported for activity level 3 are unlikely to be observed in wild whales that are swimming at the range of speeds presented here. Conversely, the oxygen consumption levels that Kriete (1995) measured from resting animals (activity level 1) are unlikely to occur in free-ranging swimming animals that are not engaged in resting behavior.

Despite the numerous assumptions made, the calculation methods presented here were expected to produce reasonable estimates of *COT* for free-ranging northern resident killer whales. First, the majority of assumptions are substantiated by results from previous studies. Second, we calculated *COT* from oxygen consumption values measured during three activity states (Kriete 1995) to provide a robust range of estimated *COT* values. Third, we compared our *COT* estimates to the predicted minimum mass-specific *COT* values from the allometric equation for marine mammals in Williams (1999) to assess the validity of our estimated *COT* curves.

Statistical Analysis

The average swim speed and respiration rate were calculated for each individual theodolite track, and these paired average values were represented only once in the analyses. Each pair was treated as an independent sample because: tracks were collected at different time periods over several years; focal animals were never studied more than once on a given day; and data were collected from focal animals across a wide range of swim speeds and respiration rates. A similar rationale has been used in studies investigating swimming mechanics in cetaceans using video clips (Fish 1993, Noren *et al.* 2006). Data were separated by sex, sorted in the order in which they were collected, and tested for serial autocorrelation. Durbin-Watson test statistics for males (1.9) and females (1.7) were within the range (1.5–2.5) generally considered to indicate independence (Systat 2004), so all subsequent analyses were conducted using each observation as an independent sample.

Adult male and female killer whale tracks were analyzed separately due to the large sexual dimorphism in body size and shape, which has the potential to affect swimming mechanics and energetics. After between-sex comparisons were made, females were separated into two groups for comparison of adult females with dependent calves (0–2 years old) to adult females with older or no offspring. These classifications were necessary to assess the potential energetic impacts of milk production during lactation (Fedak and Anderson 1982, Costa *et al.* 1986, Kriete 1995) and swimming in echelon (Weihs *et al.* 2006). The age of 2 years was chosen because killer whale calves, like other cetacean calves, often swim in "echelon position," slightly behind and to the side of the mother's dorsal fin (Mann 1997, and for review see Noren and Edwards 2006) up to the age of 2 years (Mann 1997, Ford *et al.* 2000). This swimming arrangement has the potential to increase drag, and consequently, the metabolic cost of swimming for females with young calves (Weihs *et al.* 2006, Noren 2008).

Graphical and regression analyses were conducted using SigmaPlot 8.0 Software for Windows (Systat Software Inc., San Jose, CA, USA, 2002). A Mann–Whitney *U* test was performed (GraphPad Software Inc., San Diego, CA, USA, 2005) to assess whether female tracks that satisfied the relaxed censoring conditions differed significantly in speed and directness of swimming paths from those that met the strict selection criteria. For females, 25 tracks satisfied the strict censoring criteria, and the remaining 11 satisfied the relaxed criteria, yet there were no significant differences in swimming speed (Mann–Whitney *U* test, $P = 0.229$) or swimming path directness (Mann–Whitney *U* test, $P = 0.595$), so data were pooled for subsequent analyses. All other statistical tests were performed by SYSTAT 10.2 Software (Systat Software Inc., San Jose, CA, USA, 2004). Means are reported ±SE.

RESULTS

Swimming Speeds and Respiration Rates

Data for the analyses were obtained from 18 adult males and 13 adult females (Table 2), which represents 31 individuals from a population that numbered 219 in 2004 (Ford and Ellis 2006). Minimum, maximum, and average swimming speeds (meters per second) and respiration rates (breaths per minute) are reported in Table 3. The apparent tendency for male killer whales to swim faster than females (1.7 *vs.* 1.5 m/s, Table 3) was not significant (Mann–Whitney *U* test, $P = 0.17$). The average swimming speed for all animals pooled was 1.6 m/s. It is important to note that slow swimming speeds reported here do not indicate an artifact of our data selection process. Fast swimming was rarely observed in the study area. The fastest swimming speed measured was one observation of 4 m/s, but this track was eliminated from the analysis because a boat approached the focal whale within 55 m, and the path directness index was approximately 0.30 (that is to say, the whale followed a highly convoluted path). Overall, respiration rate (breaths per minute) increased significantly with swimming speed (meters per second) according to a linear function for both males (Fig. 1A) and females (Fig. 1B). For any given speed, there was weak statistical evidence that females had higher respiration rates than males (ANCOVA, $F = 3.9$, $P = 0.051$).

Given the rarity of observing whales swimming at speeds faster than 3 m/s, the breaths per kilometer data could not be described by a U-shaped curve that was observed in gray whales (Sumich 1983). A power function was chosen over an exponential function for data from both males and females, because more variance was

Table 2. Summary of theodolite tracks from northern resident killer whales used for calculating cost of transport curves.

ID	Sex	Tracks	Year (number of tracks for the year)	Age
A5	M	5	1996 (5)	39
A6	M	4	1995 (1), 1996 (3)	31, 32
A13	M	10	1995 (1), 1996 (6), 2002 (1), 2004 (2)	17, 18, 24, 26
A27	M	2	1996 (2)	25
A31	M	2	1996 (2)	38
A32	M	4	1996 (3), 2004 (1)	32, 40
A33	M	12	1995 (2), 1996 (2), 1997 (1), 1998 (2), 2002 (3), 2004 (2)	24, 25, 26, 27, 31, 33
A37	M	3	1996 (1), 2004 (2)	19, 27
A38	M	3	1996 (2), 2004 (1)	26, 34
A39	M	6	1995 (1), 1996 (3), 2004 (2)	20, 21, 29
A46	M	1	2004 (1)	22
B2	M	2	1998 (2)	46
B8	M	1	1998 (1)	34
B10	M	5	1996 (3), 1998 (1), 2004 (1)	17, 19, 25
C9	M	3	1998 (3)	27
I41	M	11	1995 (3), 1996 (5), 1998 (2), 2004 (1)	15, 16, 18, 24
I43	M	2	2004 (2)	21
I46	M	1	2004 (1)	19
A12	F	2	1996 (1), 2002 (1)	55, 61
A23	F	6	1996 (6)	49
A25	F	6	1996 (6)	25
A30	F	3	1996 (3)	49
A34	F	2	1996 (1), 2004 (1)	21, 29
A36	F	6	1996 (6)	49
B7	F	2	1996 (2)	49
B14	F	1	2004 (1)	13
C10	F	2	1998 (2)	27
I4	F	2	1996 (2)	16
I15	F	1	1998 (1)	46
I16	F	2	2004 (2)	36
I27	F	1	1998 (1)	24

Table 3. Summary of swimming speeds and respiration rates in free-ranging adult killer whales from the selected sub-sample of tracks.

Sex	Average age	Number of tracks	Number of individuals	Min speed (m/s)	Max speed (m/s)	Mean speed ± 1 SE (m/s)	Min respiration rate (breaths/min)	Max respiration rate (breaths/min)	Mean respiration rate ± 1 SE (breaths/min)
Males	26	77	18	0.6	3.0	1.7 ± 0.1	0.9	2.5	1.6 ± 0.0
All females	39	36	13	0.7	2.7	1.5 ± 0.1	0.8	3.0	1.7 ± 0.1
Females without a calf	46	20	6	0.7	2.0	1.4 ± 0.1	0.8	2.1	1.6 ± 0.1
Females with a Calf	29	16	7	0.8	2.7	1.7 ± 0.2	1.3	3.0	1.9 ± 0.1

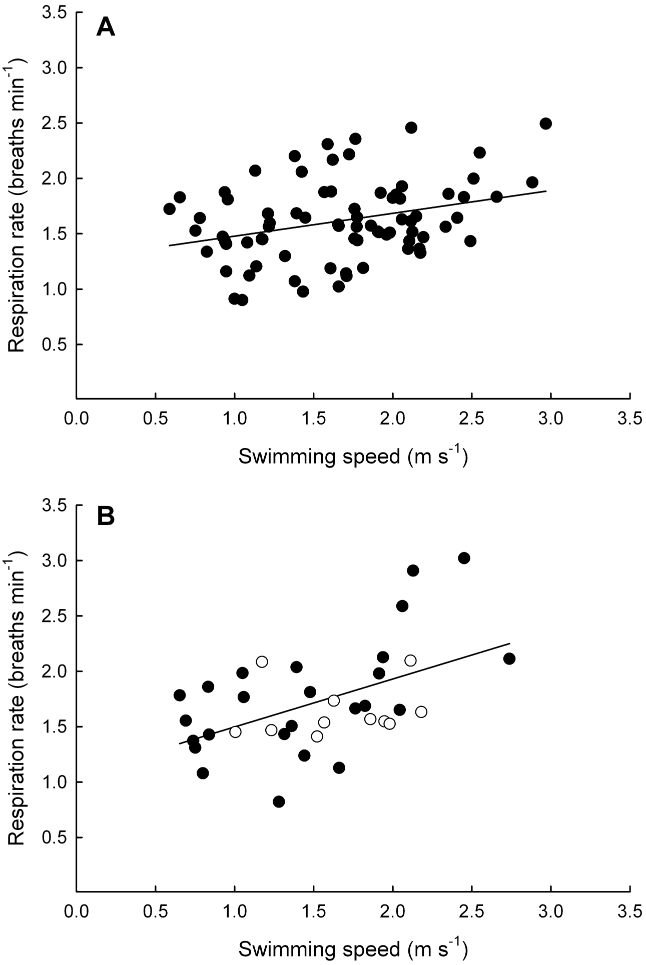

Figure 1. Respiration rate as a function of swimming speed in adult (A) male and (B) female killer whales. Respiration rates calculated from data for female tracks that satisfied "relaxed criteria" are designated by open circles. Observations that met either strict or relaxed censoring criteria did not differ significantly in terms of swimming speed (Mann–Whitney U test, $P = 0.229$) or swimming path directness (Mann–Whitney U test, $P = 0.595$), so data were pooled in subsequent analyses. Respiration rate increased with swimming speed according to the linear relationship for males, $R = 0.21S + 1.3$ ($F = 8.4$, $r^2 = 0.10$, $P = 0.0049$, $n = 77$), and for females, $R = 0.43S + 1.1$ ($F = 11.8$, $r^2 = 0.26$, $P = 0.0016$, $n = 36$). R is respiration rate in breaths per minute and S is swimming speed in meters per second. Least-squares regressions are denoted by solid lines.

explained. Breaths per kilometer decreased significantly with increased swimming speed according to a power function for both males (Fig. 2A) and females (Fig. 2B). The lowest values for breaths per kilometer occurred at speeds between 2.6 and 3 m/s, which corresponded to 10.4–9.1 breaths/km for males and 12.1–10.8 breaths/km for females (calculated from the regression equations from Fig. 2A, B).

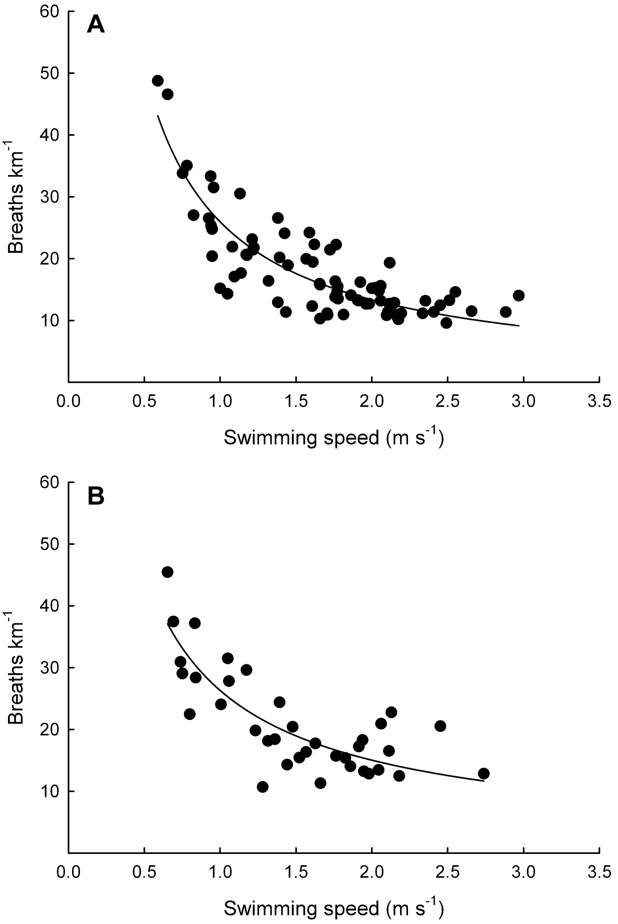

Figure 2. Breaths per kilometer as a function of swimming speed in adult (A) male and (B) female northern resident killer whales. Breaths per kilometer decreased with increased swimming speed (m/s) according to a power relationship for males (breaths/km $= 26.0S^{-0.96}$, $F = 210.7$, $r^2 = 0.74$, $P < 0.0001$, $n = 77$) and for females (breaths/km $= 26.3S^{-0.81}$, $F = 72.8$, $r^2 = 0.68$, $P < 0.0001$, $n = 36$). Least-squares regressions are denoted by solid lines. [Correction added after publication on-line: regression coefficients changed somewhat, but the exponents and regression statistics did not change]

Metabolic Cost of Transport

Mass-specific cost of transport (*COT*) ranged from 1.1–5.6 J/kg/m in males and 0.9–3.9 J/kg/m in females. Given that very fast swimming speeds were never observed in these animals at this location, it was not possible to fit a U-shaped *COT* curve, which is usually observed in swimming animals (Williams *et al.* 1993a), to the *COT* data. The curve did decline toward an asymptote, but data for fast speeds were lacking to detect an obvious inflection point beyond which costs were expected to increase again. For the data available, mass-specific *COT* (Joules per kilogram per meter) decreased significantly with increased swimming speed (meters per second) for both males (Fig. 3A) and females (Fig. 3B) according to a power function, which has

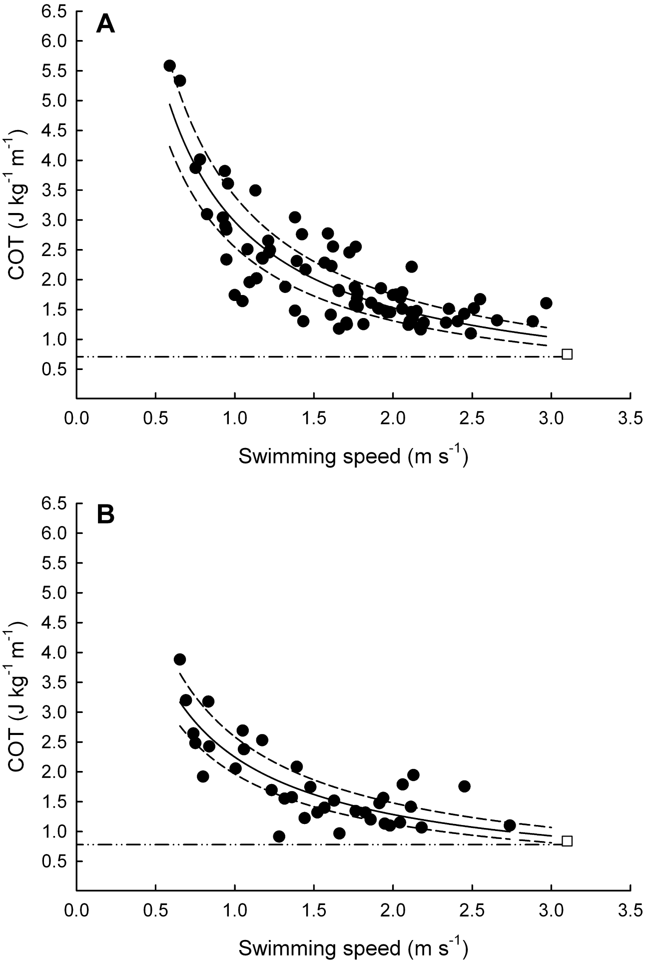

Figure 3. Mass-specific cost of transport (*COT*) as a function of swimming speed in adult (A) male and (B) female northern resident killer whales. Mass-specific *COT* calculated using oxygen consumption values for captive killer whales at activity level 2 decreased with increased swimming speed according to power relationships for males ($COT = 3.0S^{-0.96}$, $F = 210.7$, $r^2 = 0.74$, $P < 0.0001$, $n = 77$) and females ($COT = 2.2S^{-0.81}$, $F = 72.8$, $r^2 = 0.68$, $P < 0.0001$, $n = 36$). *COT* is cost of transport in Joules per kilogram per meter, and *S* is swimming speed in meters per second. Least-squares regressions are denoted by solid lines. The dashed lines below and above the solid regression line represent regressions for the relationships for mass-specific *COT* and swimming speed when mass-specific *COT* is calculated using oxygen consumption values for captive killer whales at activity level 1 (males: $COT = 2.5S^{-0.96}$ and females: $COT = 2.0S^{-0.81}$) and activity level 3 (males: $COT = 3.4S^{-0.96}$ and females: $COT = 2.6S^{-0.81}$), respectively. [Correction added after publication on-line: regression coefficients changed somewhat, but the exponents and regression statistics did not change] The dot-dot-dash lines denote the predicted minimum mass-specific *COT* from the equation in Williams (1999) for male (0.71 J/kg/m) and female (0.78 J/kg/m) killer whales with a mass of 3913 and 2800 kg, respectively. The square on each plot designates the cost of transport at the optimum swimming speed of 3.1 m/s for male and female killer whales reported by Kriete (1995).

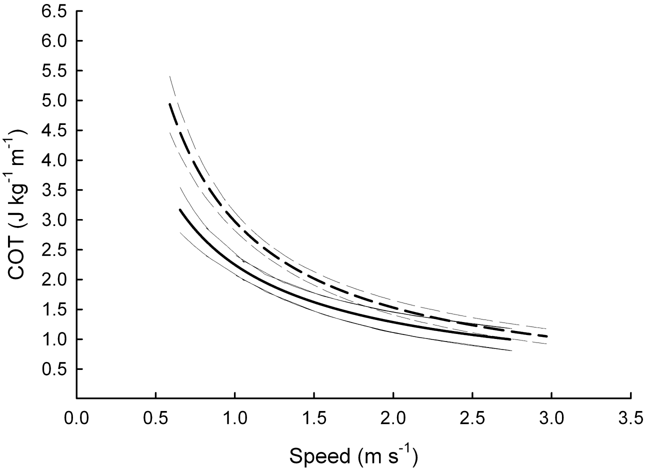

Figure 4. Regression lines and 95% confidence interval (CI) lines for mass-specific cost of transport (*COT*) as a function of swimming speed in adult male and female northern resident killer whales. *COT* is mass-specific cost of transport in Joules per kilogram per meter, calculated using oxygen consumption values for captive killer whales at activity level 2, and *S* is swimming speed in meters per second. The regression line (bold) and CI lines (hairline) for males and females are designated by long dashed lines and solid lines, respectively. Note that CI lines for males and females do not overlap at speeds ≤ 1.5 m/s, which could indicate that males have greater mass-specific *COT* than females at these speeds. [Correction added after publication on-line: regression coefficients changed, which shifted the regression lines somewhat]

previously been applied to swimming *COT* data (Peters 1983). Box-plots of residuals for each individual showed strong within-individual variability, but the confidence intervals spanned zero for all whales with large sample size. Overall, these diagnostic plots suggest that the model provided a good fit to the data and that there was no evidence for an individual effect.

The minimum *COT* lies between 2.6 and ≥ 3 m/s (Fig. 3A, B). Yet, due to the paucity of faster speeds in our data, these results preclude us from determining the true minimum *COT* speed for killer whales. Speeds of 2.6 and 3 m/s correspond to metabolic costs of 1.2 and 1 J/kg/m for males and 1 and 0.9 J/kg/m for females (calculated from the *COT* regression equations using activity level 2 oxygen consumption data from Fig. 3A, B). This range of speeds was only slightly less than the minimum *COT* speed of 3.1 m/s reported previously (Kriete 1995, Williams 1999, Fig. 3A, 3B). Our values for minimum mass-specific *COT* (Joules per kilogram per meter) were quite similar to previously reported values (Kriete 1995, Williams 1999) for females (Fig. 3B) while those of males were only slightly higher (Fig. 3A). Finally, males tended to have higher mass-specific *COT* (Joules per kilogram per meter) than females, but these differences do not appear to be significant at speeds greater than 1.5 m/s (Fig. 4).

Influence of Calf Presence on Female Cost of Transport

Mean swimming speeds of females with calves aged 0–2-years ranged from 0.8–2.7 m/s, while mean swimming speeds of females without calves ranged from

0.7–2 m/s (Table 3). Females with calves aged 0–2 years tended to swim faster than those without calves (Table 3), yet this difference was not statistically significant at the conventional level (Mann–Whitney *U* test, $P = 0.058$). Respiration rate ranged from 1.3–3 breaths/min in females with young calves and from 0.8–2.1 breaths/min in females without young calves. Yet, this trend for females with young calves to have relatively higher respiration rates compared to females without calves was not statistically significant ($F = 2.9$, $P = 0.095$, Table 3).

Mass-specific *COT* ranged from 0.9–3.9 J/kg/m in females without calves and from 1.1–3.2 J/kg/m in females with young calves aged 0–2 year. As anticipated, mass-specific *COT* (Joules per kilogram per meter) decreased significantly with increased swimming speed (meters per second) according to a power function for both females without (Fig. 5A) and with (Fig. 5B) calves. The mass-specific *COT* regression curve for females without calves (Fig. 5A) more closely approximated the minimum mass-specific *COT* previously reported for female killer whales (Kriete 1995, Williams 1999) than the curve for all females combined (Fig. 3B). Furthermore, females with calves had somewhat higher mass-specific *COT* (Joules per kilogram per meter) compared to females without calves (Fig. 6). For example, speeds of 2.6 and 3 m/s correspond to metabolic costs of 1.2 and 1.1 J/kg/m for females with calves and 0.9 and 0.8 J/kg/m for females without calves (calculated from the *COT* regression equations using activity level 2 oxygen consumption data).

The elevated *COT* values for females with calves relative to females without calves may be due to the higher respiration rates of females with calves (Table 3). With the removal of respiration rates (breaths per minute) from females with calves, respiration rates of females without calves did not differ from those of males at any given speed ($F = 0.001$, $P = 0.971$). Additionally, with the removal of swimming speeds from females with calves, swimming speeds of males were significantly faster than those of females without calves (Mann–Whitney *U* test, $P = 0.0286$). Furthermore, males tended to have higher mass-specific *COT* (Joules per kilogram per meter) than females without calves at speeds ≤ 2 m/s and females with calves at speeds ≤ 1.5 m/s (Fig. 6).

DISCUSSION

Swimming Speeds and Respiration Rates

For killer whales, strong sexual dimorphism in body size suggests that there should be considerable inter-sex variability in optimal swimming speed and diving behavior (Baird *et al.* 2005), foraging ecology (Ford and Ellis 2006), and MR (Kasting *et al.* 1989, Kriete 1995). The respiration rate data support these predictions. Respiration rate increased with swimming speed for both adult male and female killer whales, yet females tended to have greater respiration rates than males for any given speed. This finding suggests that females must expend more effort (on a mass-specific basis) than males to swim over the range of speeds studied, which is not surprising given the large difference in body size between male and female killer whales (Peters 1983).

In addition to inter-sex differences in respiration rates, females with calves had higher respiration rates than those without calves. This elevated respiration rate in females with young calves may be due to an increase in energetic costs of milk production during lactation (Fedak and Anderson 1982, Costa *et al.* 1986, Lockyer 1993, Kriete 1995) and/or an increase in swimming costs due to drag caused by calves swimming in echelon formation (Weihs *et al.* 2006, Noren 2008).

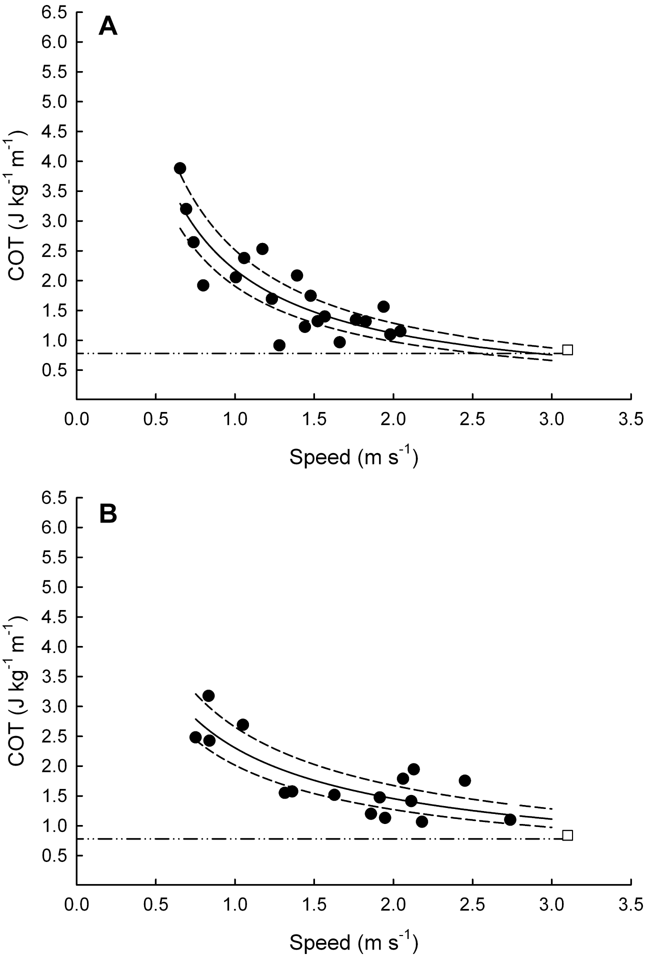

Figure 5. Mass-specific cost of transport (*COT*) as a function of swimming speed in adult female northern resident killer whales (A) without young calves and (B) with calves aged 0–2 years. Least-squares regressions are denoted by solid lines. Mass-specific *COT* decreased with increased swimming speed according to a power relationship for females without young calves ($COT = 2.2S^{-0.97}$, $F = 51.8$, $r^2 = 0.74$, $P < 0.0001$, $n = 20$) and females with calves aged 0–2 years old ($COT = 2.3S^{-0.66}$, $F = 28.7$, $r^2 = 0.67$, $P = 0.0001$, $n = 16$). *COT* is mass-specific cost of transport in Joules per kilogram per meter, calculated using oxygen consumption values for captive killer whales at activity level 2, and *S* is swimming speed in meters per second. The dashed lines below and above the solid regression line represent regressions for the relationships for mass-specific *COT* and swimming speed when mass-specific *COT* is calculated using oxygen consumption values for captive killer whales at activity level 1 (females without calves: $COT = 1.9S^{-0.97}$, females with calves: $COT = 2.0S^{-0.66}$) and activity level 3 (females without calves: $COT = 2.5S^{-0.97}$, females with calves: $COT = 2.7S^{-0.66}$), respectively. [Correction added after publication on-line: regression coefficients changed somewhat, but the exponents and regression statistics did not change] The dot–dot–dash line denotes the predicted minimum mass-specific *COT* of 0.78 J/kg/m calculated from the equation in Williams (1999) for female killer whales with a mass of 2800 kg. The square on each plot designates the cost of transport at the optimum swimming speed of 3.1 m/s reported for female killer whales by Kriete (1995).

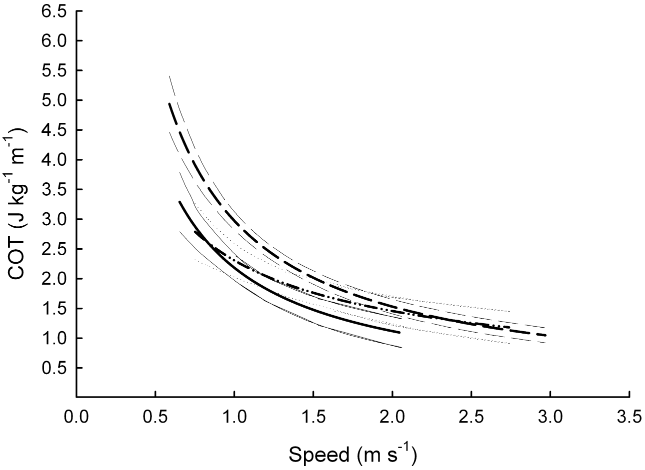

Figure 6. Regression lines and 95% confidence intervals (CI) lines for mass-specific cost of transport (*COT*) as a function of swimming speed in adult males, females with calves, and females without calves. *COT* is mass-specific cost of transport in Joules per kilogram per meter, calculated using oxygen consumption values for captive killer whales at activity level 2, and *S* is swimming speed in meters per second. All regression lines are plotted in bold, and all CI lines are shown in hairline with the same line type for sex classes: males, long dashed lines; females without calves, solid lines; females with calves, dot–dot–dashed (regression), and dotted lines (CIs). Note that CI lines for males do not overlap with those of either group of females at speeds ≤ 1.5 m/s, which could indicate that both female groups have lower mass-specific *COT* than males for these speeds. Although there is a trend for females with calves to have greater mass-specific *COT* than females without calves, there is overlap throughout the range, which may be a result of low statistical power. [Correction added after publication on-line: regression coefficients changed, which shifted the regression lines somewhat]

Metabolic Cost of Transport

Our data suggest that the speed for minimum cost of transport (optimum swimming speed) in killer whales falls between 2.6 and $\geq$ 3 m/s. These results fit well with predictions, because Kriete (1995) reported that 3.1 m/s was the optimum swimming speed for killer whales. Although we found that mass-specific *COT* may be higher for males than females at slower speeds, mass-specific *COT* was roughly similar for both sexes near optimal swimming speeds. For example, the mass-specific *COT* for female killer whales swimming at 2.8 m/s are approximately 88% (all females combined), 73% (females without calves), and 105% (females with calves) of the mass-specific *COT* for adult male killer whales swimming at the same speed. Despite these potential differences in swimming capabilities, their social structure ensures that age-sex classes of animals with very different physiological constraints remain together throughout their lives (Ford *et al.* 2000).

Killer whales are capable of traveling over a range of speeds with minimal changes in metabolic costs. For example, the range of swimming speeds with minimal mass-specific *COT* (2.6–3 m/s) only represents a 9–13% change in *COT* in adult male and female killer whales. A fairly wide range of optimum swimming speeds has also been reported in several other marine mammal species (Williams *et al.* 1993b, Otani *et al.* 2001, Davis *et al.* 1985). The optimal swimming speed for a traveling cetacean is at the minimum *COT* speed because the energetic expenditure is minimized per distance traveled. Thus, it is not surprising that the range of speeds we present here for minimal *COT* in killer whales (2.6–3 m/s) includes the average swimming speed observed at the water's surface for "traveling" northern resident killer whales (2.9 m/s, Ford 1989). Similarly, the minimum *COT* speed reported for bottlenose dolphins, *Tursiops truncatus* (2.1 m/s) was well within their range of observed mean cruising speeds (Williams *et al.* 1993a). In comparison, a hydrodynamic model based on the analysis of films of captive cetaceans swimming below the water's surface suggests that the maximum efficiency for killer whales and bottlenose dolphins occur at swimming speeds of 6.5 and 3.8 m/s, respectively (Fish 1998). However, the minimum *COT* speeds reported in the present study and in Williams *et al.* (1993a) are likely to reflect more accurately speeds that wild animals can sustain for extended periods, particularly when swimming near the water's surface, rather than submerged.

The "transient" killer whale population consumes marine mammal prey species (Ford *et al.* 1998), which are also adapted to swim optimally across a wide range of speeds. Our estimate of optimum swimming speed (2.6–3 m/s) for killer whales is greater than those reported for a variety of prey species of mammal-eating killer whales (harbor seals, *Phoca vitulina*, 0.85–1.4 m/s, Davis *et al.* 1985; juvenile Steller sea lions, *Eumetopias jubatus*, 1.7–2.1 m/s, Rosen and Trites 2002; harbor porpoise, *Phocena phocena*, 1.3–1.5 m/s, Otani *et al.* 2001; gray whales, 2–2.2 m/s, Sumich 1983; and bottlenose dolphins, 2.1 m/s, Williams *et al.* 1993a). Minimum *COT* speeds for killer whales also fall within the range of normal swimming speeds for Dall's porpoise, *Phocenoides dalli* (1.6–3.4 m/s, Law and Blake 1994). Of course, the body size of killer whales is orders of magnitude larger than many of these marine mammal species, and optimal swimming speed increases with increasing body size (Peters 1983; Culik *et al.* 1994). In contrast, the minimum *COT* speed for minke whales, the second smallest rorqual, is 3.25 m/s (Blix and Folkow 1995), which is similar to that of killer whales. This wide disparity in swimming abilities among marine mammal species, ignoring sprinting and other anti-predator evasive tactics, may explain from a purely physiological perspective why harbor and Dall's porpoise, harbor seals, Steller sea lions, and gray whales are preferred prey items for mammal-hunting killer whales in the northeast Pacific (Baird 1994, Jefferson *et al.* 1991, Ford *et al.* 1998), while minke whales are only occasionally consumed (Ford *et al.* 2005), and coordinated attacks by killer whales on the large and fast balaenopterids are rare (Jefferson *et al.* 1991). Although data on burst speed capabilities may better describe physiological correlates in some predator–prey interactions, maximum speeds also tend to scale with body size (Peters 1983). Consequently, larger predators may benefit from their ability to swim for long durations at fast speeds. In fact, it has been proposed that killer whales rely on endurance to catch tuna rather than on sprinting speed (Guinet *et al.* 2007). Thus, the greater swimming efficiency at fast speeds (see Fish 1998) and large body size of killer whales pre-adapts them to prey on smaller pinnipeds and delphinids. These results make sense in an ecological context: killer whales can efficiently (Fish 1998) and cost-effectively (present study) swim at faster speeds than most of their prey, and they do not readily prey on species that can swim at faster speeds.

Ecological Implications

Knowing how energetic expenditure changes with swimming speed will be critical to determining daily energetic expenditure in wild animals. For example, if we assume that in general, killer whales travel at a speed of 2.8 m/s (mean of our estimated range of minimum *COT* speeds) for 24 h a day, the estimated daily metabolic rate (calculated from the *COT* regression equation using activity level 2 data and average body mass for adult male (4088 kg) and female (2441 kg) killer whales from Clark *et al.* (2000)) is 7.3, 5.7, 4.7, and 6.8 times Kleiber (1975) predicted basal metabolic rate (BMR) for males, all females combined, females without calves, and females with calves, respectively. However, these calculations may not accurately represent daily energetic requirements for killer whales, because northern resident killer whales are in the long-range "travel" activity state for only 4.2% of their time (Ford 1989). Data for this study were collected from northern resident killer whales in what we call the travel/forage state, an activity state in which they are engaged for 60–66.5% of their time (Williams *et al.* 2006). The average swimming speed reported in the current study (1.6 m/s) agrees well with the average foraging speed of 1.7 m/s observed at the water's surface by Ford (1989) and the mean travel/forage speeds of 1.8 and 1.3 m/s for males and females, respectively, reported by Williams *et al.* (2002). These speeds are significantly slower than the optimum swimming speeds estimated by the present study (2.6–3 m/s) and determined by Kriete (3.1 m/s, 1995). Studies on killer whales in the Strait of Gibraltar have also found that the mean observed swimming speed of killer whales chasing tuna were well below the range of maximum sustainable velocities estimated by an energetics model (Guinet *et al.* 2007). Guinet et al. (2007) offered several explanations for whales' swimming below their capabilities, but one explanation, which may also apply to the Northern resident killer whales in this study, was that killer whales adjust their swimming velocity in relation to the size of the prey they chase to remain aerobic and consequently reduce the metabolic cost of the chase. In general, killer whales will expend less total energy while swimming at slower speeds. For example, if we assume that killer whales swim at a speed of 1.6 m/s for 24 h a day, then the estimated daily metabolic rate (calculated as above) is 7.2, 5.1, 4.6, and 5.6 times Kleiber (1975) predicted BMR for males, all females combined, females without calves, and females with calves, respectively. Interestingly, on a mass-specific basis, the daily metabolic rates predicted for killer whales swimming at 1.6 m/s in the travel/forage behavior state are similar to at-sea field metabolic rates (FMR) of foraging otariids and bottlenose dolphins (approximately five to six times Kleiber (1975) predicted BMRs—calculated from Costa *et al.* 1991, Costa 2002).

The regression equations presented in this study can be used to estimate total *COT* for traveling whales that are swimming over the range of speeds we observed (0.6–3 m/s), but should not be used to extrapolate *COT* for speeds beyond the scope of this study. For example, whales that are observed swimming at speeds slower than 0.6 m/s may actually be traveling against the tide or potentially in a resting state, and thus, expected total *COT* at these speeds cannot be calculated using the equations presented here. Similarly, these equations should not be used to calculate total *COT* for killer whales swimming faster than 3 m/s. This is because the *COT* curve is expected to be U-shaped (Williams *et al.* 1993a), and consequently, the energetic cost of swimming is expected to increase at speeds greater than the minimum *COT* speed. We do not have sufficient data to estimate the shape of the curve at speeds beyond the minimum *COT*. This is for several reasons, including the fact that after a "cross-over speed," cetaceans no longer swim underwater with regular "rolling" surfacing patterns to breathe, but instead, leap out of the water as a means to reduce energetic costs (Au and Weihs 1980, Blake 1983, Law and Blake 1994). The predicted "crossover speed" for killer whales is 5.7 m/s (Blake 1983). Thus, the shape of the *COT* curve may change at 5.7 m/s for killer whales, in a manner similar to changes in the *COT* curve when horses change gaits (from walk to trot to gallop) with increasing speed (Hoyt and Taylor 1981).

These results provide preliminary evidence that females with calves may have higher mass-specific *COT* compared to females without calves, however more data are needed to confirm this finding. There is reason to suspect increased energetic costs to females with calves due to milk production during lactation (Fedak and Anderson 1982, Costa *et al.* 1986, Lockyer 1993, Kriete 1995) and swimming in echelon with their calves (Weihs *et al.* 2006, Noren 2008). On the other hand, our *COT* estimates for females with calves may be biased high. We based our calculations of mass-specific *COT* on respiration rates, which may have been elevated in females for other reasons, such as surfacing at shorter intervals in synchrony with their calves (Waite 1988), which have reduced swimming (Noren *et al.* 2006) and breath-holding (Noren *et al.* 2002, Noren *et al.* 2004) capacities relative to adults (for review, see Noren and Edwards 2006). It is possible that although females with calves may be breathing at a higher rate, there is no actual increase in energetic demand because they may not be using maximum tidal volumes every time they surface (Spencer *et al.* 1967). As a consequence, we may have overestimated mass-specific *COT* for all females combined and for females with young calves. Furthermore, reproductive status is confounded with age. Females with calves were on average 17 years younger than females without calves. It is beyond the scope of this study to assess changes in swimming speed, respiration rates, and mass-specific *COT* with reproductive status and age in adult female killer whales, but this remains a fruitful area for future research.

Wider Implications

Once appropriate data are collected under other behavioral conditions, the methods presented here can be used to determine the cost of transport for speeds during other activity states and eventually model the total energetic needs of adult killer whales. This modeling exercise can be conducted in a sensitivity-analysis framework, to assess how uncertainty in individual requirements affects population-level estimates, and vice-versa. This study points us to a new line of research questions about the ideal speed of movement as a trade-off between the swim speed that is optimal for long-distance transport and that which is optimal for prey detection and capture. Future research should also explore the cost to females of having a calf swimming in echelon formation, as well as the cost of swimming at speeds <0.6 and >3 m/s and of performing surface-active behaviors such as breaching. In wider terms, we see the methods adopted here as being broadly applicable to a range of large, free-living vertebrates that are not amenable to traditional methods for estimating metabolic rate, but for which some data exist from captive animals. The use of a theodolite to measure swim speed and respiration rate in lone or individually recognizable animals provides a benign way to collect data for energetics modeling, which is especially attractive for work on endangered populations.

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LITERATURE CITED

AU, D., AND D. WEIHS. 1980. At high speeds dolphins save energy by leaping. Nature 284:548–550.

BAIRD, R. W. 1994. Foraging behavior and ecology of transient killer whales (*Orcinus orca*). Unpublished PhD thesis in Zoology. Simon Fraser University, Vancouver. 159 pp.

BAIRD, R. W., M. B. HANSON, E. E. ASHE, M. R. HEITHAUS AND G. J. MARSHALL. 2003. Studies of foraging in "Southern Resident" killer whales during July 2002: Dive depths, bursts in speed, and the use of a "Crittercam" system for examining sub-surface behavior. Unpublished report prepared under order number AB133F-02-SE-1744 for the National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, WA. 17 pp.

BAIRD, R. W., M. B. HANSON AND L. M. DILL. 2005. Factors influencing the diving behaviour of fish-eating killer whales: Sex differences and diel and interannual variation in diving rates. Canadian Journal of Zoology 83:257–267.

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.

BIGG, M. A., P. F. OLESIUK, G. M. ELLIS, J. K. B. FORD AND K. C. BALCOMB. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission Special Issue 12:383–405.

BLAKE, R. W. 1983. Energetics of leaping in dolphins and other aquatic animals. Journal of the Marine Biological Association of the United Kingdom 63:61–70.

BLIX, A. S., AND L. P. FOLKOW. 1995. Daily expenditure in free-living minke whales. Acta Physiologica Scandinavica 153:61–66.

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. 1987. Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. Pages 43–66 *in* A. C. Huntley D. P. Costa, G. A. J. Worthy, and M. A. Castellini, eds. Marine mammal energetics: The society for marine mammalogy special publication no. 1. Allen Press, Lawrence, KS.

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., 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.

CULIK, B. M., R. P. WILSON AND R. BANNASCH. 1994. Underwater swimming at low energetic cost by pygoscelid penguins. Journal of Experimental Biology 197:65–78.

Davis, R. W., T. M. Williams and G. L. Kooyman. 1985. Swimming metabolism of yearling and adult harbour seals *Phoca vitulina*. Physiological Zoology 58:590–596.

DeMaster, D. P., A. W. Trites, P. Clapham, S. Mizroch, P. Wade, R. J. Small and Ver Hoef J. 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.

Fedak, M. A., and S. S. Anderson. 1982. The energetics of lactation: Accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). Journal of Zoology, London 198:473–479.

Felleman, F. L. 1986. Feeding ecology of the killer whale (*Orcinus orca*). Unpublished MS thesis, University of Washington, Seattle, WA. 163 pp.

Fish, F. E. 1993. Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). The Journal of Experimental Biology 185:179–193.

Fish, F. E. 1998. Comparative kinematics and hydrodynamics of odontocete cetaceans: Morphological and ecological correlates with swimming performance. Journal of Experimental Biology 201:2867–2877.

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 and K. C. Balcomb. 1994. Killer whales. UBC Press, Vancouver, Canada.

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 and K. C. Balcomb. 2000. Killer whales. 2nd Edition. UBC Press, Vancouver, Canada.

Ford, J. K. B., G. M. Ellis, D. R. Matkin, K. C. Balcomb, D. Briggs and A. B. Morton. 2005. Killer whale attacks on minke whales: Prey capture and antipredator tactics. Marine Mammal Science 21:603–618.

Guinet, G. C., P. Domenici, R. de Stephanis, L. Barrett-Lennard, J. K. B. Ford and P. Verborgh. 2007. Killer whale predation on bluefin tuna: Exploring the hypothesis of the endurance-exhaustion technique. Marine Ecology Progress Series 347:111–119.

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 and Ecology 336:163–170.

Hoyt, D. F., and C. R. Taylor. 1981. Gait and the energetics of locomotion in horses. Nature 292:239–240.

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*). Journal of Experimental Biology 204:3273–3281.

Jefferson, T. A., P. J. Stacey and R. W. Baird. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. Mammal Review 21:151–180.

Kasting, N. W., S. A. L. Adderley, T. Safford and H. K. Gilbey. 1989. Thermoregulation in beluga (*Delphinapterus leucas*) and killer (*Orcinus orca*) whales. Physiological Zoology 62:687–701.

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

Kriete, B. 1995. Bioenergetics in the killer whale, Orcinus orca. Unpublished PhD thesis, University of British Columbia, Vancouver, B.C. 138 pp.

Law, T. C., and R. W. Blake. 1994. Swimming behaviours and speeds of wild Dall's porpoises (*Phocoenoides dalli*). Marine Mammal Science 10:208–213.

LOCKYER, C. 1993. Seasonal changes in body fat condition of northeast Atlantic pilot whales, and their biological significance. Report of the International Whaling Commission Special Issue 14:323–350.

MANN, J. 1997. Individual differences in bottlenose dolphin infants. Family Systems 4:35–49.

NOREN, S. R. 2008. Infant carrying behaviour in dolphins: Costly parental care in an aquatic environment. Functional Ecology 22:284–288.

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, S. R., G. LACAVE, R. S. WELLS AND T. M. WILLIAMS. 2002. The development of blood oxygen stores in bottlenose dolphins (*Tursiops truncatus*): Implications for diving capacity. Journal of Zoology, London 258:105–113.

NOREN, S. R., V. CUCCURULLO AND T. M. WILLIAMS. 2004. The development of diving bradycardia in bottlenose dolphins (*Tursiops truncatus*). Journal of Comparative Physiology B 174:139–147.

NOREN, S. R., G. BIEDENBACH AND E. F. EDWARDS. 2006. Ontogeny of swim performance and mechanics in bottlenose dolphins (*Tursiops truncatus*). The Journal of Experimental Biology 209:4724–4731.

OTANI, S. Y. NAITO, A. KATO AND A. KAWAMURA. 2001. Oxygen consumption and swim speed of the harbor porpoise *Phocoena phocoena*. Fisheries Science 67:894–898.

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.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

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

SPENCER, M. P., T. A. GORNALL AND T. C. POULTER. 1967. Respiratory and cardiac activity of killer whales. Journal of Applied Physiology 22:974–981.

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.

SUMICH, J. L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. Canadian Journal of Zoology 61:647–652.

SYSTAT SOFTWARE. 2004. SigmaPlot® 9.0 user's guide, Point Richmond, CA.

WAITE, J. C. 1988. Alloparental care in killer whales (*Orcinus orca*). MS thesis, University of California, Santa Cruz, CA. 65 pp.

WEIHS, D., M. RINGEL AND M. VICTOR. 2006. Aerodynamic interactions between adjacent slender bodies. AIAA Journal 44:481–484.

WILLIAMS, R., A. W. TRITES AND D. E. BAIN. 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: Opportunistic observations and experimental approaches. Journal of Zoology, London 256:255–270.

WILLIAMS, R., AND D. LUSSEAU. 2006. A killer whale social network is vulnerable to targeted removals. Biology Letters 2:497–500.

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.

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., W. A. FRIEDL AND J. E. HAUN. 1993a. The physiology of bottlenose dolphins (*Tursiops truncatus*): Heart rate, metabolic rate and plasma lactate concentration during exercise. Journal of Experimental Biology 179:31–46.

WILLIAMS, T. M., W. A. FRIEDL, J. E. HAUN AND N. K. CHUN. 1993b. Balancing power and speed in bottlenose dolphins (*Tursiops truncatus*). Sympoisum of the Zoological Society of London 66:383–394.

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.

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