Energetic cost of behaviour in *Ornicus orca*: a non-invasive acoustic study.

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Research Paper

Abstract

Estimating metabolic rate from the behavioural states of free-ranging individuals, by combining acoustic cue data from the field with oxygen consumption and tidal volume information from captive individuals, allows for the non-invasive study of the marine mammals, in particular cetaceans. The endangered Southern Resident *O.Orca*'s are perfect model organisms for this study as their behaviour and physiology have been studied both in captive and free-ranging settings. In this study the acoustic cues used are respiratory blow, measured in source level SEL$_{dB}$ re 20μpa^{2}s. Respiratory blows are a good measurement, as they have to be performed be all individuals, across al behaviours. Results of this preliminary study indicate that unlike in captive settings females hold significantly high average estimated metabolic rate than males, across all behaviours statistically analysed. Resting held the highest metabolic rate of all behaviours with milling holding the lowest; again this was contrary to captive studies, suggesting more complex energetic associations with social system.

Key words: Orcinus Orca, Killer whale, Sound exposure level, Energetics, Acoustic cues

Introduction

The Salish Sea ecosystem supports a great plethora of marine obligates, including Cetaceans, which have evolved highly adapted physiology and behaviour to utilize this environment and the challenges it presents. The killer whale (*Ornicus orca*) is the largest cetacean in the Delphinidae family. There are three distinct ecotypes of *O. orca* in this area: offshores, transients, and residents (Holt 2008). Each ecotype is distinct in terms of typical behaviour, ecology, vocalisations and social structure. From 1995 to 2001 the population size of the Southern Resident community had decreased from a high 98 individuals to a low of 79 animals, representing a reduction of 20% of the entire population in only 6 years (Bain 2002). While we do not fully understand the reason for this decline, several contributing factors have been reported, such as prey availability through a decrease in salmon stocks, exposure to toxic chemicals, as well as the increase in commercial and private vessels mostly for whale watching over the last 10 years (Bain 2002).

Whale watching is sighted as a factor due to studies that have documented the impact of vessel traffic on different whale ecotypes. Studies have concluded that the animals change their behaviour in the presence of boats (Kriete 2002). In the Northern Resident killer whales it was shown that the whales swim significantly faster, increasing the angle between successive dives or choosing less direct paths in their swimming direction in order to avoid boats when vessels were in the vicinity (Williams et al 2002, Kriete 2002). Trites and Bain (2000) estimated theoretically that the male killer whales added an extra 13% in traveling distance when followed by boats and thus performed less resting behaviours. Boats have also been linked to a loss in feeding opportunities and this could result in a substantial (18%) estimated decrease in energy intake. Whales may also adopt less predictable paths of movement (Williams et al 2002, Holt 2008) and endure compromised immune system levels due to stress and energy expenditure (Simmons and Dolman 2000). Although behavioral impacts have been demonstrated in this population, few direct measurements of energetic costs have been conducted, therefore an estimation of the longer-term impact upon population levels is difficult to achieve.

The impacts of energetic stress affect the sexes differently due to variation of metabolic efficiency and size variation. In *O. orcas*, males are approximately 4,500Kg whereas females are 3,400Kg (Noren 2010). As body size increases, the surface area to volume ratio decreases and thus the surface exchange of heat is proportionally lower. This results in a lower heat loss rate and thus greater metabolic efficiency. When traveling in mixed groups all activities will carry an energetic cost and will possibly affect group cohesion and survival success.

The emphasis of acoustic studies on killer whales have been on pulsed calls or whistle vocalisations and their relationship to social organization, genealogy, and behaviour (Ford 1991, Deecke et al. 2010). These are all acoustic signals, however very little work has been done on acoustic cues, especially in marine mammals. Acoustic cues are sounds produced as a result of physiological or locomotive needs, and are not produced to provide a benefit to either the sender or receiver (Wood review 2010). In *O. orcas*, and other marine mammals, the obligation to breathe at the surface provides a measurable cue from the blow as they exhale. Not only can these cues be measured, but they can also provide information about the biology of both the individual and the species, particularly in relation to their energetics. Energetics efficiency is important as it affects fitness and ultimately survival. Survival is largely a function of the amount of energy expended while in motion and the amount of energy gained through food consumed. While gravity is the primary force behind the energetic cost of locomotion in terrestrial mammals, in marine mammals it is a combination of hydrostatic pressure, body drag, effort and buoyancy (Williams 2001). Reliable measurements of energetic cost in marine mammals are difficult to obtain in the wild, however this previously unutilized area of acoustic cues could help to shed light on the energetics of *O.orca*. Estimated metabolic rate in this study will be calculated from the volume of air exchanged in a period of time. This is a good measure as it represents effort, without requiring direct intervention with the animals in the study.

In order to truly understand these complex energetics the cost of each behaviour state must be assessed. The following questions are posed: does blow amplitude, and thus air volume exchanged and energy used, vary with behavioural state? Are longer dives more energetically costly? To test these questions the Sound Exposure Levels (SEL) at the source of a blow (air exhalation) were measured by analysing the received level and estimating sound attenuation from the source to give source volume. SEL is a measurement of the energy of a sound, which is calculated by integrating the squared instantaneous sound pressure over a stated time interval (Richardson et al 1995). In this study, in order to use the measurement for energetic profiling, the volume of air exhaled needs to be implied. SEL will allow for blows of different amplitude and duration to hold the same value, as they will involve the same amount of air exchanged. The assumption being that the higher the SEL value the higher the volume of air exchanged. A single SEL value can be assigned to a short, high amplitude blow and a long, low amplitude blow. Both allowed for the same amount of air to be exchanged. This assumption was also analysed; do shorter blows have higher amplitude and vice versa? Distance from the site of the blow to the microphone will also affect the amplitude of the recorded blow; therefore, the spreading loss was included in calculations of SEL to control for distance effects.

The above technique allowed for the following hypotheses to be tested;

1) Foraging, travel and play will have a higher estimated metabolic rate than resting and milling.
2) As dive length increases so will the keep to perform that dive, and thus blow SEL will increase.
3) SEL is an appropriate measurement for this study. Shorter blows will have a higher intensity (measured as watts/m^2) than longer blows.

Methods

Data collection:

Acoustic measurements and surface behaviour observations of the Southern Resident ecotype were performed in the Greater Puget Sound region. Data acquisition occurred over a five-week period, from 13th September to 23rd October 2010. Data analysis was continuous throughout this period as well as for one week upon return to land. Data acquisition occurred on the fore deck of the Gato Verde, a 42' long sailing catamaran. During all study periods the Be Whale Wise Guidelines and The State Law were followed, to limit observer error due to interference.

When the whales were within 300m of the boat the study period was initiated. At the start of each study period a GPS way point was taken, in order to allow for cross reference to identification photos. If the focal animal was not identified at the time of surface recording, photographs of each focal animal were taken and the time frame on the camera was documented for each blow series recorded. The Center for Whale Research ID Guide, 2009 edition was then later employed to identify individuals from the photographs (Ellifrit et al 2009).

All acoustic recordings were taken using an Earth Works QTC40 omni directional microphone with a flat frequency response from 4Hz to 40KHz recording to a Marantz professional solid state recorder PMD660 (PCM-44.1K recording wave files to a 1.0GB compact flash dish). The microphone was mounted with a parabolic dish to aid directionality and boost the signal to noise ratio of the recordings. During recording the time, distance, sex, behaviour state and orientation to the boat were audibly noted. Time was read from a watch sychronised to the GPS and cameras used. Distance was determined using a Newcon Optik x9; LRM 2000PRC laser range finder. Sex was determined from visual observations (based on dorsal fin shape characteristic of different sexes), and the decision finalized based on identification photo analysis in order to limit error due to juvenile males appearing similar to females.

Five behaviours were used: foraging, milling, resting, traveling and playing. I will be using the following definitions:

Foraging	**Traveling**	**Resting**	**Milling**	**Play**
Erratic high-speed swimming, lunging, rapid circling and chasing fish at the surface. Includes feeding or searching for food. It Is the most common activity. The pod is usually spread out with small subpods that are generally swimming together. There are usually 2-3 short dives made, followed by a loner diver (1-3 minutes). Foraging is thought to compromise 65% of the Southern Resident behavior.	Traveling is defined as when a group of whales is consistently swimming in a specific direction. Usually there is a tight formation, and there cannot be ay signs of feeding or searching for food. They usually travel faster than when they forage, and they often surface and dive simultaneously. They are usually Very vocal while traveling.	This behavior is very easily recognized because the whales swim slowly, in a tightly knit group, usually abreast. While swimming abreast, the offspring usually surround their mother. They are very quiet and make longer dives. Resting is thought to make up 13% of southern resident behavior.	Repeated, non-linear orientation; nondirectional; any distance, slow or medium speed.	Many different physical interactions, displays, and percussive events. Socializing behavior includes sexual interactions, kelping, aerial displays (breaching, tail slapping, spyhopping, etc.) This is thought to account for 15% of the Southern Resident's time.

Table 1. Behaviour categories adapted from NOAA 2004, Barrett-Lennard et al 2004.

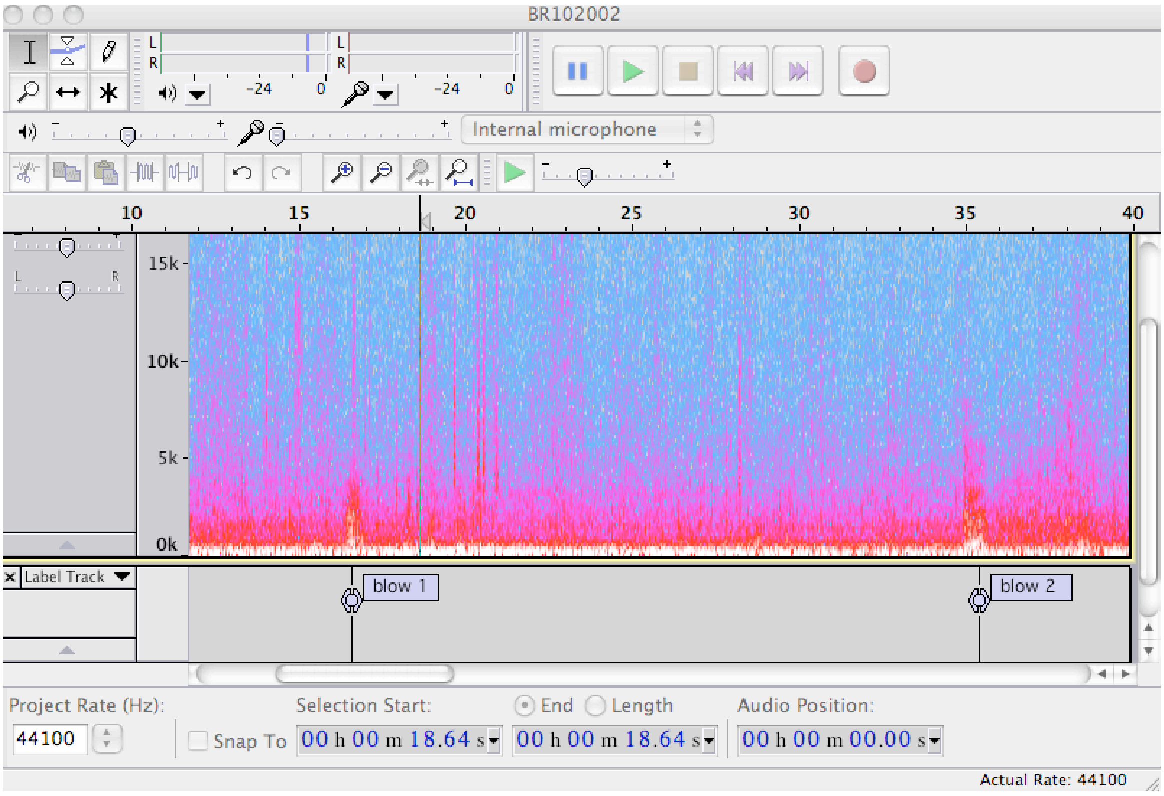
Orientation to boat was determined using a clock face template, with 12o’clock at the bow and time continuing clockwise around the boat to 6o’clock at the stern (See appendix figure 1 for diagram). Orientation was important for identification and cross-referencing behaviours with hand written data.

The recordings were continuous over 6-10 blows for an individual selected based on the following criteria; within focal range of microphone, surfacing alone (i.e. out of sync with group if there are many individuals) and performing one behaviour during the whole recording. All juveniles were excluded from this study as their metabolic rate is affected by growth and thus their energetic cost is not directly comparable to adults. A new recording was started for each new individual or behaviour.

All behaviours reported audibly during recording were compared to the written behaviour data sheet taken at the same time. Time is matched by using the same watch for both the written and the recorded data. In the event of discrepancy the observation made during recordings on the sound file was taken to be correct.

Data Analysis:

Data files were analysed using a MacBook Pro laptop computer running both Windows 7 and Mac OS X (version 10.5.8) software. Wav files were analysed using the Audacity 1.3 Beta software. Each blow was listened to, and viewed in both waveform and spectrogram. A spectrogram was computed for both the blow being analysed and the background noise before the blow (not after due to a dramatic increase in background noise because of camera clicks and movement around the boat in some cases) (figure 1).



Project Rate (Hz): 44100

☐ Snap To

Selection Start: 00 h 00 m 18.64 s

● End ○ Length: 00 h 00 m 18.64 s

Audio Position: 00 h 00 m 00.00 s

Actual Rate: 44100

Figure 1. Screen shot illustration of Audacity analysis spectrogram. The figure shows a snap shot of two blows from the same individual. X-axis is time, with Y-axis showing frequency. Apnea was calculated as the time between each blow, which can be read from the start and end of selection bar. White represents the loudest amplitude, with red intermediate and pink quietest.

This was then exported into an excel file. All results were calibrated using a dB recording actual received levels for comparison. Acoustic attenuation was also analysed using the regression line plotted in the spreading model created for the microphone used (figure 2) and then included with the calibration to calibrate audacity exports, then calculate SEL$_{dB}$ re 20µpa^{2}s from SEL energy. Formula 1 was used.

(1) $dB_{SEL} = 10\log \quad SEL_{ENERGY}/SEL_0$

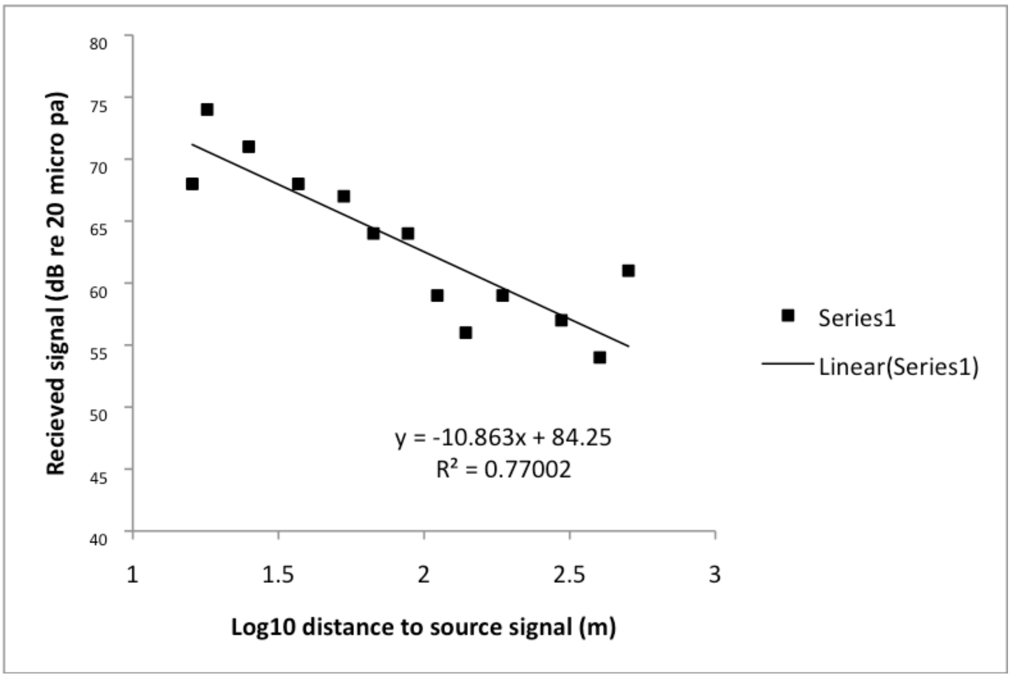


Figure 2. Spreading model for in air signal in study area in wind condition of less than 15Knts. Spreading is taken to be 10.836, and thus shows cylindrical spreading.

This calculation of source level SEL was then instrumental in achieving an estimate of mass specific metabolic rate using the following series of equations. First SEL was compared to tidal volume for each behaviour categorised by a captive study (see appendix Table 1)(Kriete 1995). Only Kriete’s data from Hyak (a 4733 kg adult male) and Yaka (a 2800 kg adult female) were used, rather than values for both adult and sub-adult subjects, because data on the sub-adult female were thought to be unreliable, and juveniles were excluded in this study. The regression line formula in figure 4 was used. The tidal volume for each blow was then integrated in to formula 2 to calculate mean metabolic rate (Litres of oxygen/s) and finally mass specific metabolic rate:

(2) Mean metabolic rate (MMR)= (Tidal Volume x [% oxygen consumed])/apnea

Where: Mean metabolic rate is in litres of O_2/s, Tidal Volume is in lires, % of oxygen taken from Kriete (2002) and apnea is measured in seconds.

(3) Metabolic rate = (MMR x 20.1)*1000

Where: Metabolic rate is in J/Kg/minute, 20.1 is the conversion factor (20.1KJ per $1LO_2$)

This was then divided by body mass (Kg), which was calculated, from ID's of individuals. Variations in saddle-patch coloration and dorsal fin characteristics were employed to identify individuals. Comparisons were made with the Center for Whale Research ID Guide, 2009 edition of southern resident killer whales (Ellifrit et al 2009). Individuals were identified and correlated with a particular time and orientation. Once ID was complete the age given for that individual was compared a graph of age versus weight to gain an estimate of weight (Kg) (figure 3).

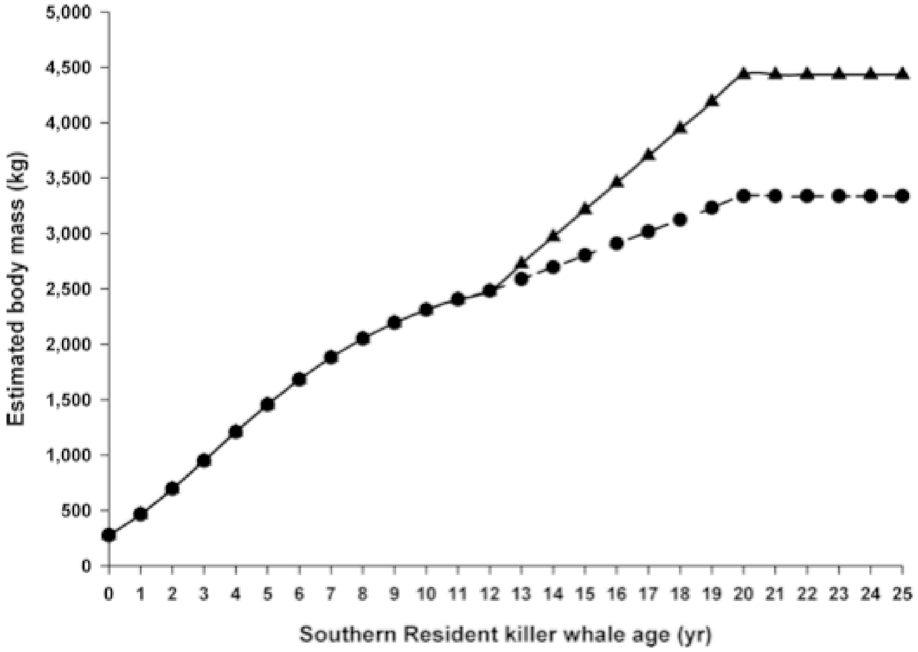


Figure 3) *Figure 1.* Taken from Noren 2010, Relationship between body mass and age in years for male and female killer whales. The growth curves for male (triangles) and females (circles) killer whales are denoted by the solid and broken lines respectively.

The results were then converted to J/Kg/Hr, and all results for estimated metabolic rate are presented are presented in this format. All SEL values refered to are source level SEL$_{dB}$ re 20μpa^{2}s.

Statistics

The collated information was subsequently statistically analysed using SigmaPlot 11.0 statistical analysis package. A Two Way ANOVA was performed with interaction for behavioural state, gender and estimated metabolic rate for the purpose of testing hypothesis 1 - behaviour alters estimated metabolic rate. Hypothesis 2, dive length vs SEL, was analysed using a linear regression line. Hypothesis 3, intensity vs duration was also analysed using a linear regression line.

Results

General observations

40 of the total blow samples collected were suitable for analysis; these were sampled from 8 individuals taken from 11 separate days over the 5-week study period. The samples were broken into foraging (14), traveling (16), resting (6), milling (4). Blow recordings on days with high wind had a poor signal to noise ratio (winds above 15Knts) and thus did not undergo further analysis.

Groups had a tendency to hold a set behavior for most individuals in the group. Males appear to split from the group more frequently and travel faster than females. Resting often resulted in synchronized surface behavior. On the two occasions when resting behavior was observed it was both preceded and followed by periods of travelling or socializing. Socializing is problematic to record due to the nature of the interactions, and thus it does not appear in the results.

The SEL values were then taken to represent tidal volume in a field setting, and as such were plotted against tidal volume measured in a captive study (kriete 2002) for the similar behavioural state (Figure 4). The negative correlation seen in females (R^2 = 0.15) was unexpected but was verified, and thus was taken to be correct. This result may be due to little variation for female tidal volume in the source study (kriete 1995)

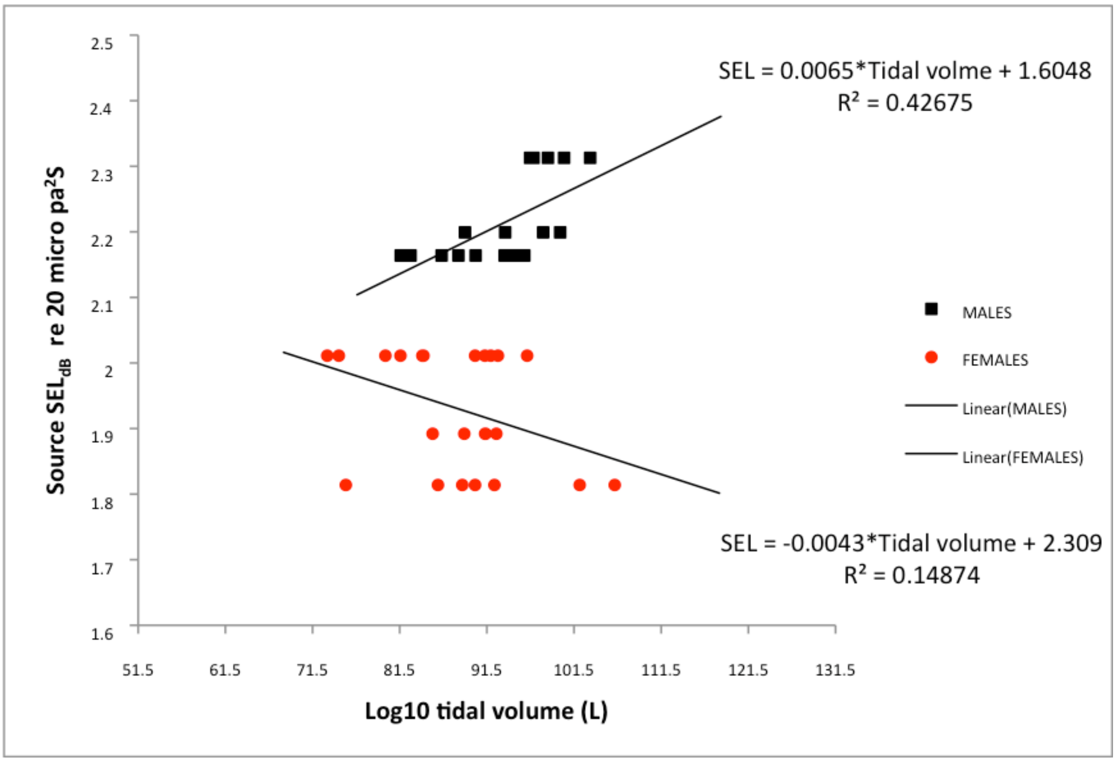


Figure 4. SEL plotted against tidal volume. Regression equation used to calculate tidal volume for each blow recording (n=41). X axis is logged account for log scale values in SEL. (See appendix for behavioural groupings of reference paper, figure 2) Axes scale is adapted to allow for ease of viewing.

Hypothesis 1: Energetic cost of behavioural states

Mass specific metabolic rate was graphically shown to vary with behaviour (Figure 5). There was a positive trend from foraging through traveling to resting, which held the highest metabolic cost. In females milling was also recorded and this held the lowest metabolic cost (24.69 J/Kg/Hr) (Figure 5).

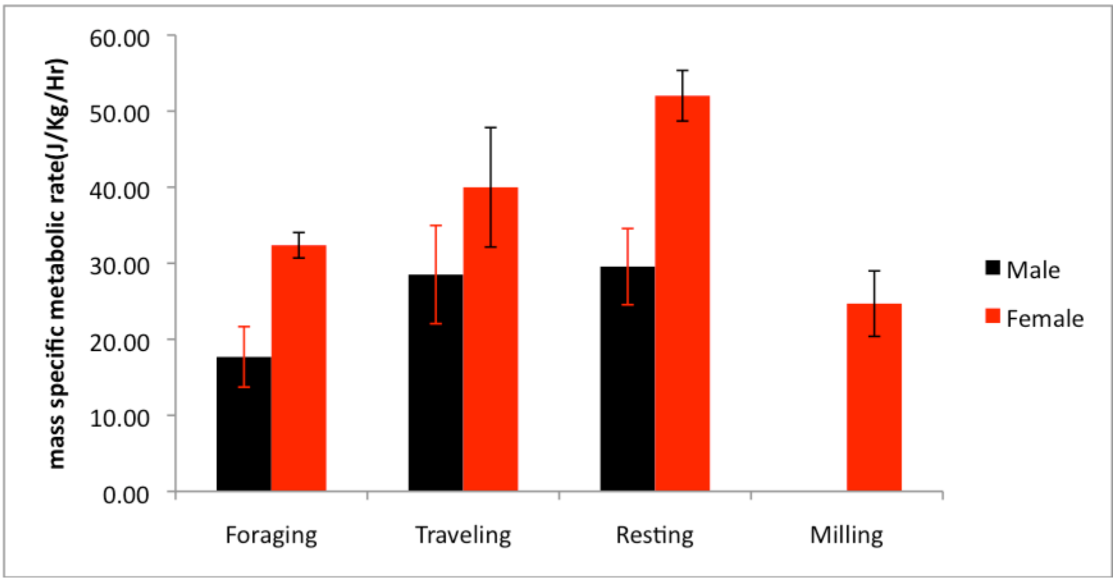
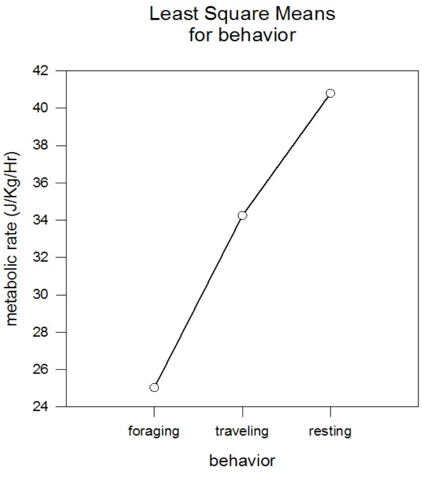


Figure 5. Mean mass specific metabolic rate (J/Kg/Hr) presented as a function of both behavior and gender. All values are presented as means ± S.E.M (n=40).

No significant difference was found between behavioural states (P=0.181, $F_{2,\,35}$ = 1.809), the power of the performed test was 0.05000:0.168. A less than significant result indicates that the differences observed may be due to random sampling variability or the low power of performance in which case any negative results should be viewed with caution. However a trend can again be seen in the profile plots of results (figure 6). In all statistical tests, milling behaviour is excluded as sample associations cannot be analysed unless there is data in both categories, and no data for males milling was suitable for analysis. Hypothesis 1, Foraging, travel and play is more energetically costly than resting and milling, is not supported by statistical analyses performed, however strong trends can be found within the data.

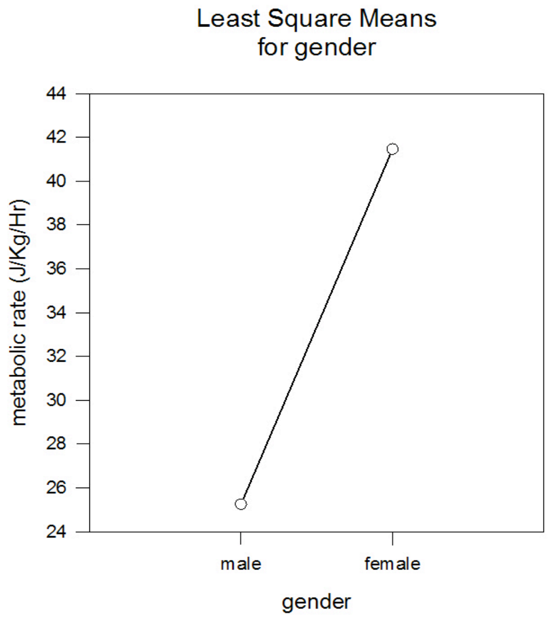
Figure 6. Profile plot of One way Anova results for SigmaPlot analysis on behaviour states.



Estimate of metabolic rate as a function of gender

Gender differences across behavioural state and metabolic range were a key part of data analysis, though no hypothesis regarding this were originally tested. There was a significant difference between males and females, which was indicated by preliminary visual analysis (figure 5), and supported by statistical analysis ($P=0.023$, $F_{1,\,35} = 5.739$)(figure 7). This suggests that differences in gender metabolic rate are greater than would be expected by chance after allowing for effects of differences in behaviour. The profile plots created on these results support both the trends seen and the level of significance with ~16 J/Kg/Hr difference between genders (figure 6). The multipairwise analysis for where significance lies was inconclusive due to small data set, however figure 5 suggests a larger difference between genders for resting and foraging than traveling, with milling excluded from analysis due to a lack of data for males.

Figure 7. Profile plot of One way Anova results for SigmaPlot analysis on gender.



Hypothesis 2: Dive length and energetic effort

Divelength is not used in the calculation of SEL but is important for determining metabolic rate and thus was plotted against SEL, not only to test the second hypothesis , dive length and SEL are positively correlated, but also to analyse further results (figure 8). Variation in dive length (Apnea), does not apear to have a significant effect on SEL, with a weak negative correlation (R^2 = 0.02). The hypothesis that as dive length increase so will the energetic effort to perform that dive, and thus blow SEL will increase, can not be supported.

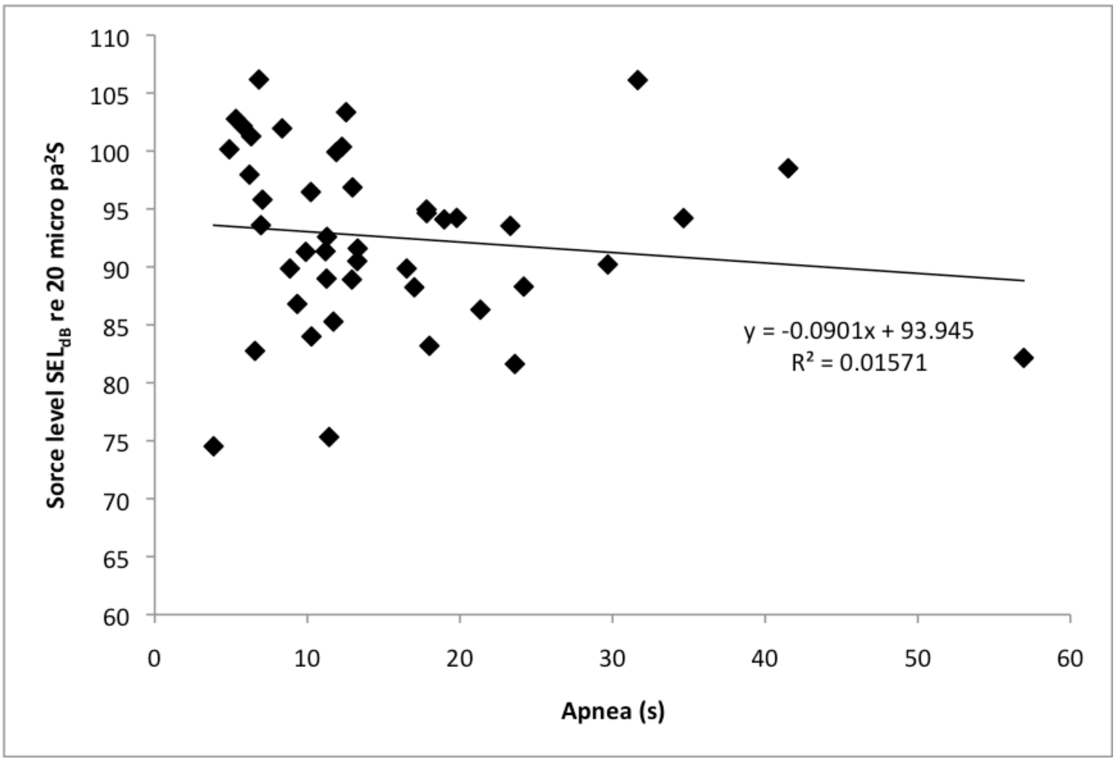


Figure 8. Variation in source level SEL as a function of Apnea over all samples used to calculate SEL (n = 40). X axis scale is adapted to allow for ease of viewing.

Hypothesis 3: Assessment of SEL as an appropriate measurement

As SEL is an important factor used to calculate the metabolic rate, it is necessary to analyse the data used to calculate this parameter. The changes in mean signal received intensity and blow length will affect the calculation of SEL, as it is dependent upon these parameters. It is therefore important to understand how these vary for each individual and the ranges they occupy (Figure 9). A weak positive correlation seen ($R^2 = 0.0025$), this suggests there is little increase in blow length with increased mean received signal intensity. Mean received signal intensity varies from $3.02x10^5$-$4.95x10^7$ (order of magnitude ≈ 100) and blow length varies from 0.1-1.19 (order of magnitude ≈ 10) with the majority of points between 0.3-0.9 (order of magnitude ≈ 3). This indicates that much of the variation in SEL presented is the result of variation in the mean received signal intensity rather than blow length.

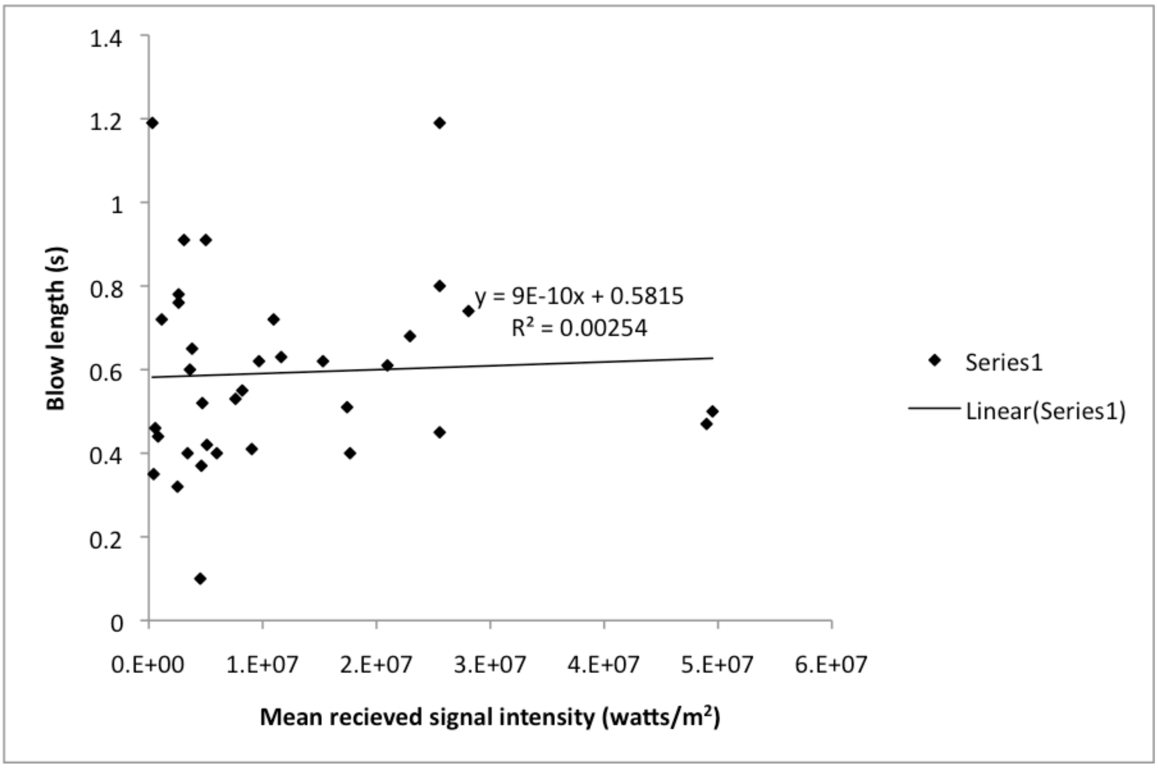


Figure 9. Variation in Blow length and Mean signal power over all samples used to calculate SEL (n = 40). Outliers were checked and verified as appropriate.

Discussion

Estimate of metabolic rate as a function of behaviour

There was no significant change in metabolic rate as a function of behaviour, however a trend was seen which is worth serious consideration. Firstly, resting carried the highest metabolic rate based on SEL. Resting in a previous study has been classified as the least energetically costly behaviour (Kriete 1995). The key difference between this previous study and the current one is state (captive vs free ranging) of the individuals. The difference may lie in the fact that when the blow recordings were take the whales had just (within 3-7minutes) finished a traveling event and after a short period of resting began highly active socialising behaviour. This opens up the question of what the whales are doing during behaviour characterized as resting? The whales could be replenishing an oxygen deficit built up during an extended period of traveling and possible aerobic respiration. This could result in a high source level SEL, as the mean signal power is high. This is a recognised theory in other species, which would be missed in captivity due to the need to control behavioural states. However it was noted in Kriete (1995), that there were differences in the respiration rate of individuals resting at night (when this behaviour was performed for long periods of time) and in the day when respiration rates were higher. A decreased respiration rate in resting periods in wild killer whales was observed in a different study (Osborne 1986). However, this study did not look blow intensity, which is a major driving factor through SEL in this study (figure 9). The resting differences seen by Kriete may have been due to a wider range of behaviours being performed during the day and thus a larger deficit being built up than at night.

Traveling is the second most energetic behaviour, and this is as expected as both this and foraging have shown a moderate to high metabolic cost in previous studies (Kriete 1995). The fact foraging in this study carries a relatively low metabolic rate is unexpected; this may also be explained by short shallow breaths during a foraging event to maximise foraging time (i.e time under water) followed by a resting period with more energy intensive blows.

Estimate of metabolic rate as a function of gender

There was a significant change in metabolic rate as a function of gender; females had a significantly higher metabolic rate than males in three behaviours (traveling, foraging, resting). This makes physiological sense. As body size increases, the surface area to volume ratio decreases and thus the surface exchange of heat is proportionally lower. This results in a lower heat loss rate and thus greater metabolic efficiency in large individuals. Males are larger than females (Noren 2010). Females have been shown to have a higher basal metabolic rate than males in other species (Selman et al 2001). The difference may also be explained by the inherent complexity of the social structure of *O.orca* groupings. When traveling in mixed groups all activities will carry an energetic cost, however, this will vary between individuals. Lusseau 2007, reported that in Bottlenose dolphin groups males often initiate traveling behaviour whilst females cease it. This could be happening across traveling and foraging in orca. As such, males may be pushing females above their optimum metabolic efficiency, which in turn will put a greater oxygen demand on females when performing the same behaviour. This would produce a greater deficit and thus a higher metabolic for females during resting.

Dive length and energetic effort

As dive length increases so will the energetic effort to perform that dive, and thus blow amplitude will increase; this was not supported. The most questionable factor in dive length analysis is the SEL of the blow. The researcher cannot be certain the exhilation is consistent across all dives and individuals. Individuals doing deep dives may exhale some air under water and thus the surface blow will be lower that would be expected for longer dives. More dive, travel path and inhilation data are needed to analyse dive length effects further.

SEL as an appropriate tool for Metabolic studies

SEL is a novel way of obtaining tidal volume to calculate metabolic rate for free ranging individuals. It takes into account inter-individual differences and thus is more representative than the standard blow amplitude measurement (dB re 20 micro pa). Oxygen demand is an effective way to measure metabolic demand, and any use of this to develop a non-invasive analysis technique should be pursued.

Comparisons of overall data points obtained show promise of method, as Kriete obtained a range of 7.1-9.8 (Kcal/Kg/d) (12.38-17.08 J/kg/Hr [metric used in this study]) and this study found a range of 11.125-12.25 (Kcal/Kg/d), this indicates that results are falling in a similar range as other studies and thus SEL calculations are not affecting range. This is especially true as free-ranging metabolic rates are shown to be 25-33% higher than captive studies (Kriete 1995); this is a similar range to that seen listed above.

Shorter blows do not, however, have a significantly higher amplitude (measured as Sound Pressure Levels in dB re 20µPa) than longer blows, as was originally hypothesised. However this does not mean SEL is not acceptable as a measure. The lack of significance, i.e trend seen, may be due to the error of analysis. This may be explained by the sampling method. When exporting the spectrogram of the blow the signal envelope may have be inaccurately sampled due to signal to noise ratio. If the signal to noise ratio is high the trail ends of the blow may have been masked by background and thus not counted, resulting in a shorter blow length. This analysis should be repeated.

Sources of error during data collection and analysis

Small sample size (n = 41) may have been a source of error not only from this data set but also the studies used to get tidal volumes (n=2) and weight estimates also have a low sample size this would compound the error.

Observer error during data collection must also be considered. Whilst only one observer took behavioural data throughout the data collection, to avoid inter-obsever error, error in wrong categorization still exists. Foraging and milling are difficult to identify and thus define. This could have resulted in a lower metabolic rate due to the inclusion of milling blows within the foraging category. This may also explain a lack of milling data for both males and females. Young males and females look very similar, whilst the likelihood of miss identification is low due to the cross referencing from three independent sources, it may still have occurred and thus is worth considering. If young males were included in the data set then their metabolic rate would be higher than expected for females, due to growth demands on metabolism in juveniles.

Resting animals have a tendency to surface in unison. When blows were selected, group surfacing was excluded and only blows that were identified as individuals surfacing on their own were used, however background blows may have altered results. This is unlikely to have been the case as the amplitude of blow was consistent across all six resting blows used, suggesting there were not extra individuals in some of the samples skewing the mean.

Travel data was not controlled for by speed. This could have skewed the travel data seen, as the speed of travel can vary dramatically, and the will have a large effect on metabolic rate not accounted for in this study. The ranges are described as slow travel is 3-6 Km/h and traveling is >6 Km/h (Barrett-Lennard et al 2004). The spread of data points seen in Traveling and thus the overlap of error bars may have corresponded with not only different travel speeds but also different gaits as seen in terrestrial organisms (Schmidt-Nielsen 1990).

Further study

It has always been considered difficult, to study physiological and behavioural aspects of free ranging marine mammals, and whilst there are still many technological advances to be made, the amalgamation of scientific fields will allow for vital studies on Cetaceans. Firstly the data used in this study should be extended to improve accuracy of results and reduce error. Cost of transport analysis (COT) could also be added to the data set, by the inclusion of measurements of locomotory speed. Another variable to consider is the inclusion of inhilation in the data set (only achieved with an increase in microphone gain). This may shed light on whether individuals are exhaling under water during long dives, and thus skewing metabolic rate results observed in this study.

Once the data set is completed it should be used to build behaviour-based models of metabolic rate. The key requirement is that the energetic cost of a variety of activity states must be known. The best way will be to map all behaviours when ‘free’ swimming in captivity and then map this against the longer term study in free ranging individuals. This integration has been done for wintering great cormorants (Gremillet et al., 2003). The difficulty of obtaining useful data for Cetaceans in the past has made this approach extremely challenging. However, these data are available readily for many Pinniped species that come ashore for moulting or breeding. If these data sets are used alongside *O.orca* data obtained using SEL, it can quickly and non-invasively be used to assess whether the magnitude of change is likely to be large enough to justify investing resources into more sophisticated studies.

Further studies can then incorporate data across many marine mammal species in order to create a model for marine mammals acoustic cues and energetics (obligates and amphibious), like those done for terrestrial animals (R. Williams 2006).

Concluding statements

Estimating metabolic rate from the behavioural states of free-ranging individuals, by combining acoustic cue data from the field with oxygen consumption and tidal volume information from captive individuals, allows for the non-invasive study of the marine mammals, in particular cetaceans. The endangered Southern Resident *O.orca*’s are perfect model organisms for this study as their behaviour and physiology have been studied both in captive and free-ranging settings. Results of this preliminary study indicate that unlike in captive settings females hold significantly high average estimated metabolic rate than males, across all behaviours statistically analysed. Resting held the highest metabolic rate of all behaviours with milling holding the lowest; again this was contrary to captive studies, suggesting more complex energetic associations with social system that needs further investigation.

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Appendix

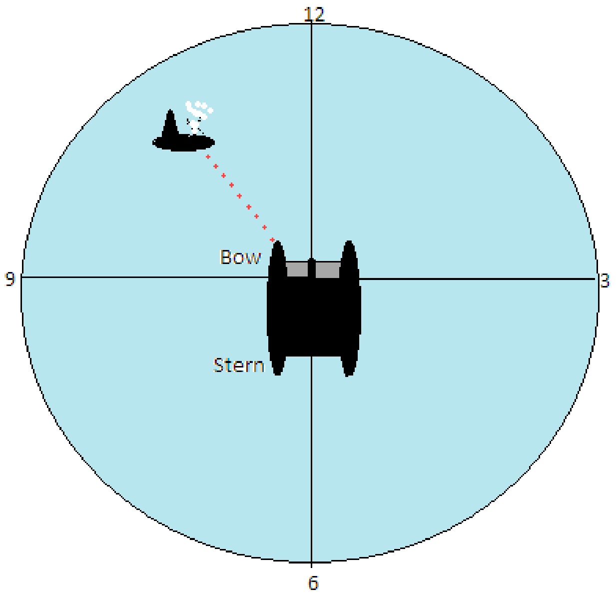

Figure 1,)Clock orientation of whales to the Gato Verde during behaviour observations.

Energetic cost (Kriete, 1995)	**Behavioural state (this study)**	**Definition**
1	Resting	Whales were swimming at slow speed with highly predictable sequences of several short (30 s) dives followed by a long dive of 3–5 min. This activity state was characterised by the absence of surface-active behaviour (e.g., breaching or tail-slapping)
2-3	Travelling/ Foraging	Whales surfaced and dove independently but all whales in the group were heading in the same general (east–west) direction. The dive sequences of individuals showed regular patterns of several short dives followed by a long one, and whales swam at moderate speeds
3	Socialising	Animals surfaced in tight groups with individuals engaged in tactile behaviour; whales showed irregular surfacing and diving sequences and swim speeds; irregular direction of movement; and high rates of surface- active behaviour

Table 1) Behavioural states used in this study with their equivalent energetic cost categories defined by Kriete (1995). Probable functional roles for activity states are inferred from earlier studies of behaviour and feeding ecology in Killer whales (NOAA 2004, Ford et al 2000, Barrett-Lennard et al 2004)