Measuring body length of male sperm whales from their clicks: The relationship between inter-pulse intervals and photogrammetrically measured lengths

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Sperm whales (Physeter macrocephalus) emit short, broadband clicks which often include multiple pulses. The time interval between these pulses [inter-pulse interval (IPI)] represents the two-way time for a pulse to travel between the air sacs located at either end of the sperm whale’s head. The IPI therefore, is a proxy of head length which, using an allometric relationship, can be used to estimate total body length. Previous studies relating IPI to an independent measure of length have relied on very small sample sizes and manual techniques for measuring IPI. Sound recordings and digital stereo photogrammetric measurements of 21 individuals were made off Kaikoura, New Zealand, and, in addition, archived recordings of whales measured with a previous photogrammetric system were reanalyzed to obtain a total sample size of 33 individuals. IPIs were measured automatically via cepstral analysis implemented via a software plug-in for PAMGUARD, an open-source software package for passive acoustic monitoring. IPI measurements were highly consistent within individuals (mean CV = 0.63%). The new regression relationship relating IPI (I) and total length (T) was found to be $T = 1.258I + 5.736$ ($r^2 = 0.77$, $p < 0.001$). This new regression provides a better fit than previous studies of large (> 11 m) sperm whales.

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I. INTRODUCTION

The broadband clicks that are characteristic of sperm whales often display a decaying, evenly spaced multiple-pulse structure (Backus and Schevill, 1966). Norris and Harvey (1972) proposed that the interpulse interval (IPI) is an indication of the time taken for a click to travel posteriorly from its source at the front of the head (the museau de singe), through the spermaceti organ to be reflected off the frontal air sac at the front of the skull and back along the spermaceti organ and then emitted from the front of the head. Recently, the “bent-horn” model of sound production (Mohl et al., 2003) has been developed which better explains click production and structure. Nevertheless, the key point of Norris and Harvey that IPI represents the two-way travel time taken for the energy in a click to travel between sound reflectors at opposite ends of the Spermaceti organ, remains unaltered. Because spermaceti sac length and total body length of a sperm whale are allometrically related, IPI can be used to estimate whale body length.

Several researchers have noted that typically only a small fraction of clicks within a recording show the clear multi-pulse structure illustrated by Backus and Schevill (1966), and thus are suitable for measuring IPI (Alder-Fenchel, 1980; Mohl et al., 1981; Gordon, 1991; Rhinelander and Dawson, 2004). The bent horn model (Mohl et al., 2003), explained why: the orientation of the vocalizing whale relative to that of the hydrophone influences the pulse structure of the click. Clicks recorded on-axis, either behind or in front of the whale display a regular multi-pulsed structure whereas clicks recorded off-axis have a pulse which occurs at some time-delay that varies depending on the off-axis angle of the click (Zimmer et al., 2005). Aspect-dependent pulses would be expected to arrive at different times as the whale’s orientation changes. However, the whale’s “true” IPI will be present in every click, even if it is masked by the other aspect dependent pulses.

Teloni et al. (2007) applied this idea, developing a new method for extracting consistent IPI measurements from recordings in which the whale’s orientation is unknown. Their approach averages the cepstrum of a large number of clicks, which, in most recordings, will have been recorded from varying aspects, ranges, and depths with respect to the hydrophone (Teloni et al., 2007). By averaging all the...
cepstrums of all the clicks the aspect-dependent pulses tend to cancel, while the pulse at the “true” IPI is reinforced. The time of the highest peak of the ensemble average of click cepstrums is left as the best estimate of the IPI and thus is an estimator of the whale’s spermaceti sac length (Teloni et al., 2007). As a best practice, they recommended using on the order of 1000 clicks to obtain a stable estimate of IPI. Antunes et al. (2010) explored additional signal processing and statistical methods for estimating IPI with as few as 52 clicks. Miller (2010) streamlined and fully automated the method described by Teloni et al. (2007) by writing an IPI plug-in for PAMGUARD (Gillespie et al., 2008). This freely available plugin takes audio (either from a hydrophone or a digital file) as input and outputs an estimate of IPI, requiring no user intervention or knowledge of computer programming. It runs quickly on a standard computer, and allows IPIs to be calculated from a much larger sample of clicks than would be feasible to measure manually. Prior to this development, published measurements of IPI, used various signal processing methods but were either essentially manual, measuring one click at a time by hand (Gordon, 1991; Goold, 1996; Pavan et al., 2000; Rendell and Whitehead, 2004; Rhinelander and Dawson, 2004; Drouot et al., 2004; Marcoux et al., 2006; Jaquet, 2006), or semi-automated, requiring separate programs for audio processing, click detection, and IPI measurement, as well as knowledge of computer programming (Teloni et al. 2007; Antunes et al. 2010).

Three studies have attempted to relate IPI estimates to independent measurements of whale length. Gordon (1991) analyzed the IPIs of 11 individuals that he measured from photographs taken at a known height above the sea surface. Since Gordon was working with nursery groups in the Azores and Sri Lanka, most of the whales he measured were small (only one was > 12 m). Rhinelander and Dawson (2004) recorded sperm whales at Kaikoura, New Zealand and made independent measurements of whale length with a stereo photogrammetric system (Dawson et al., 1995). They showed that within individuals IPIs were stable over short periods, but increased significantly over periods of years, consistent with expected growth of animals. Their sample size of 12 measured whales included larger whales (up to 15.3 m) than had been previously measured. A third study by Jaquet (2006) used a single camera combined with a laser rangefinder to measure fluke width. Using data from whaling and strandings, she developed a relationship between fluke width and total length. She then compared IPI and estimates of total length for five males from Kaikoura and six females/immatures from the Gulf of California.

As methods of measuring IPI have improved, so have photogrammetric methods (Mikhail et al. 2001). Digital photography and the availability of off-the-shelf photogrammetric software have increased stereo photogrammetry’s precision and accuracy and dramatically improved its ease of use. Here we apply digital stereo photogrammetry, and the cepstral analysis approach of Teloni et al. (2007) to develop a new, more robust, empirical relationship between IPI and total length of sperm whales off Kaikoura New Zealand.

II. METHODS

Data for this project were collected over two 3–4 week field seasons (19 June – 9 July 2009; 14 Nov. – 9 Dec. 2009). Additionally, sound recordings made between 1996 and 2000 by Rhinelander and Dawson (2004) were reanalyzed. Research was conducted aboard a 6.6 m outboard-powered rigid-hull inflatable boat. Almost all field work was within a 10 by 20 nautical mile block located south of the Kaikoura peninsula [see Fig. 1 in Rhinelander and Dawson (2004)]. Remaining data were collected in the Kaikoura Canyon or Conway Trough, nearby, but outside of the 10 by 20 nautical mile area. This area overlies the Kaikoura canyon and depths range from between 50–1500 m. Data collection was limited to sea states of Beaufort 4 and below.

A custom-built directional hydrophone was used to find and track individual whales. A digital photogrammetric system [an updated version of the film-based system of Dawson et al. (1995)] was used to measure the distance between the blowhole and dorsal fin. When a whale surfaced, the research vessel was maneuvered alongside for photogrammetry as described by Dawson et al. (1995), and then the vessel was maneuvered behind the whale while a stereo hydrophone array was deployed (depth of deepest hydrophone either 65 or 105 m) to record the diving whale’s vocalizations. When the whale fluked, fluke identification photographs (Arnbom, 1987; Childerhouse et al., 1995) were taken using either a Nikon D1H or D3 SLR with a AF Nikkor 300 mm f2.8 lens or a AF Nikkor 80–200 mm f2.8 lens.

Clicks from the target whale were recorded until (a) at least 15 min of continuous recording was completed, (b) the target whale was judged to be too faint, or (c) other whales appeared to be closer to the hydrophone array and louder.
than the target whale. This last criterion was only necessary for archived recordings made with a single hydrophone. Search effort and sightings were logged via custom written software running on a palmtop computer connected to a GPS navigator. To assess the stability of camera orientation, at the start of each day an object of known length (2.67 m floating PVC pipe) was photographed floating in the water.

Sperm whale vocalizations were recorded with a custom-built stereo hydrophone array (Barlow et al., 2008) attached to an Edirol R4 hard drive recorder (fs = 96 kHz, 16 bit). The hydrophone array had a frequency response that varied by ±4 dB over the range of 1–40 kHz. Archived digital audio tape (DAT; fs = 48 kHz, 16 bit) recordings were made using a Sonatech 8178 hydrophone and a Sony TCDD10-PROII recorder.

Recordings were analyzed using the Pamguard IPI plugin with parameters identical to those described by Miller (2010). The IPI plugin employed the IPI estimation method developed by Teloni et al. (2007), using cepstrum analysis (Bogert et al., 1963) to detect the time delay between repeated patterns in a broadband signal. The cepstrum of each click was computed using the equation

\[ C_t = \left[ \text{FFT}^{-1} \left[ \log(\text{FFT}(x_t)) \right] \right], \]

where \( x_t \) is the digital recording represented in the time domain. FFT is the fast Fourier transform and FFT\(^{-1}\) is the inverse fast Fourier transform. The cepstrums of all clicks belonging to the target whale were averaged, and the peak value was located and the time delay of the peak kept as the IPI (Teloni et al., 2007).

Clicks could be attributed to the target whale because at Kaikoura sperm whales usually surface alone and other whales, when present, are usually spaced at least one mile apart (Childerhouse et al., 1995). Therefore, the target whale was always closest to the hydrophone array and produced the most intense vocalizations when the recording began. Additionally, Pamguard has two built-in features which allow other whale’s clicks to be filtered out: (a) a built-in click detector allows detection thresholds to be altered, rejecting all but the most intense clicks and (b) computation of bearings to the sound sources allows signals from shallow bearings (i.e., from whales further away) to be excluded. Both options (a) and (b) are used with recordings made via the stereo array. For recordings made via a single hydrophone, option (b) cannot be used.

IPIs were used to estimate the head lengths (H) of whales using the equation

\[ H = 0.5Ic_s, \]

where \( c_s \) is the speed of sound in spermaceti. A value of 1430 m/s was used for \( c_s \), which corresponded to spermaceti between 28–30°C and a pressures between 0–4551 kPa (Goold et al., 1996). These choices correspond to temperatures measured from spermaceti in recently dead whales [Clarke (1978): 28.5–29.7°C] and dive depths measured with a 3D hydrophone array off Kaikoura [Miller (2010): average dive depth 400 m].

Stereo photographs were used for measurement only if they were in-focus, both the blowhole and the posterior emargination of the dorsal fin were clearly visible and the measured angle of the whale relative to the camera system was less than 15° from parallel. The distance between the blowhole and posterior emargination of the dorsal fin (B) was measured three times for each stereo pair using the photogrammetry software AUSTRALIS (version 6.01, Photometrix Pty., Ltd., Australia) and whale’s total length (T) estimated using the regression equation \( T = 1.399B + 1.587 \) (n = 215; \( r^2 = 0.985; \) p-value < 0.001; see the Appendix).

### III. RESULTS

From our recent fieldwork, a total of 172 digital stereo pairs of images were available to measure the distance between the blowhole and the posterior emargination of 21 whales. Each individual whale was encountered an average of 2.9 times (range: 1–8) and the average number of measured photographs per whale was 8.2 (range: 2–17). Eighty three percent of photographs were taken at distances less than 50 m (max = 67 m). The mean number of recordings obtained per whale was 3 (range: 1–8) and mean number of clicks analyzed per whale was 645 (range: 83–1618).

Measurement in the field of the PVC calibration target demonstrated consistent camera alignment (mean CV = 0.23%). Repeated photogrammetric measurement of individual whales throughout a field season showed mean (and median) coefficient of variation (CV = standard deviation/mean) of 1.57% (range: 0.56%–3.32%) which represents a mean error of ±21.7 cm. IPI measurements from individual whales recorded in the same field season had a mean CV of 0.63% (range: 0.16%–3.13%) which represents an average error of ±0.04 ms. The IPI measurements were less variable compared to total length estimates derived from stereo photogrammetry. Of the 21 whales which were acoustically and photogrammetrically measured in 2009, 12 had both sets of measurement data collected in the same encounter on more than one day (Fig. 1).

Recordings made by Rhinlander and Dawson (2004) were re-analyzed using the PAMGUARD IPI plugin. These new estimates, along with the corresponding photogrammetric estimates of Rhinlander and Dawson (2004) were pooled with the more recent data collected by us in 2009. This increased the sample size of whales to 33 for which both independent measures of IPI and total length (T) were obtained. The weighted linear regression of IPI vs total length was computed in accordance with York et al. (2004) to account for errors in both variables. The regression fit was highly significant at the 95% confidence level (0.58 < \( r^2 = 0.77 < 0.88 \), Fig 2), resulting in the equation

\[ T = 1.257I + 5.736. \]
Mean lengths were not significantly different (t-test; p-value = 0.67, degrees of freedom (d.f.) = 32).

Differences among the published equations and that above are relatively small (Table I). Notably, Gordon’s (1991) equation gives larger length estimates at IPIs larger than 5 ms, while the equation of Rhinelander and Dawson (2004) gives smaller length estimates for all but the most extreme IPIs measured.

The relationship between IPI-derived head length and photogrammetric total length was not significantly different (ANCOVA: F = 0.8791; d.f. = 1203; p-value = 0.3496) from measures of head and total body length made during whaling (Matthews 1938; Fujino 1956; Clarke and Paliza 1972) (Fig. 3). A least-squares regression of the whaling data gave the equation $H_{\text{whaling}} = 0.486T_{\text{whaling}} - 2.025$ ($r^2 = 0.9668$; p-value < 0.001) and this study via photogrammetry and IPI (open circles and solid line; $H_{\text{photo}} = 0.498T_{\text{IP}} - 2.223; r^2 = 0.8779$; p-value < 0.001).

IV. DISCUSSION

Errors associated with measuring the distance between the blowhole and posterior emargination were small (the mean CV of multiple measurements of the same whale was 1.57%), and a substantial improvement over the previous photogrammetric techniques measuring the same body dimensions [Dawson et al. (1995): CV = 4.35%; Gordon (1990): CV = 5.1%]. Jaquet (2006) used a single camera and laser-rangefinder combination to measure fluke width, and reports a smaller CV (1.3%) in re-measurements of the same whale. The method developed here should be a better estimate of total length for two reasons; the distance between the blowhole and posterior emargination (Fig. 4; n = 215; $r^2 = 0.98$) is a better predictor of total length than fluke width [Jaquet (2006): n = 102; $r^2 = 0.87$ after removal of 10 outliers], and is supported by more data, over a larger range of whale sizes.

Within individuals, IPIs computed via the cepstrum method were less variable than digital photogrammetric length estimates of the same whales (mean CVs = 0.63 and 1.57%, respectively). This is likely to be due to two causes. First, whales are inherently flexible, which will affect photogrammetric accuracy (Dawson et al., 1995). Second, some imprecision is inevitable in locating the same points to measure each time from the stereo pairs. IPI estimates from this study were less variable than all previous studies that have attempted to correlate this feature to an independent measure

<table>
<thead>
<tr>
<th>IPI (ms)</th>
<th>TL, Gordon (1991) (m)</th>
<th>TL, Rhinelander and Dawson (2004) (m)</th>
<th>TL, this study (m)</th>
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<tr>
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</tr>
<tr>
<td>$r^2$</td>
<td>0.98</td>
<td>0.76</td>
<td>0.77</td>
</tr>
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</table>
of length [median CV = 5.6%, Gordon (1991); mean CV = 0.82%, Rhinelander and Dawson (2004); median CV 1.9% Jaquet (2006)]. This confirms the reliability of the method for measuring IPI of Teloni et al. (2007).

For our data the best fit between IPI and total length was found with a linear regression. Previous studies have used power functions (Fujino, 1956; Clarke, 1972) or second order polynomials (Gordon, 1991; Rhinelander and Dawson, 2004) to account for the fact that the head length (and hence IPI) increases proportionally more than the total length. While this may be true for smaller whales, upon reinspection of the data from Matthews (1938), Fujino (1956), and Clarke (1972) we propose that a linear relationship exists between head length and total length for whales larger than 10 m (Fig. 3). Gordon (1991) and Rhinelander and Dawson (2004) found that a second order polynomial provided a good fit to their data. However, the coefficient of the squared term from Gordon’s equation was so small as to render the fit effectively linear over the range of physically realizable IPIs, and the fit provided by Rhinelander and Dawson actually shows total length increasing in proportion to IPI (and thus head length), which is opposite to the trend reported from whaling data. The larger sample size in this study affords us a more parsimonious equation that provides a better fit than previous studies and is consistent with physical measurements collected during whaling.

The reanalysis of recordings from Rhinelander and Dawson (2004) produced IPI values that differed only slightly from their original estimates. Combining the recently collected data with the re-analyzed data of Rhinelander and Dawson (2004) provided the largest sample size yet available from which to estimate the relationship between IPI and total length. A weighted regression using only the 21 individuals measured in this study had an \( r^2 = 0.81 \) with 95% confidence interval between 0.59 and 0.92. While the value of \( r^2 \) was higher using only the recently collected data, the confidence interval was larger than the one obtained using all of the data, indicating that the regression with more data points is a more reliable model despite its lower coefficient of determination.

The sperm whales of Kaikoura offer some profound advantages for testing hypotheses about how the multi-pulse structure of sperm whale clicks relates to whale size, chiefly because the same individuals can be recorded repeatedly over periods from days to decades. To date (June 2010), the longest re-sighting in this project is of NN20, which has been identified more than 120 times over 18 years. The main disadvantage of Kaikoura, and of other study sites beyond about 40° North or South, is that females and immatures are very seldom encountered. Data reported here contain no whales small enough to be females (Rice, 1989). Thus the relationship developed here may not be appropriate for estimating the size of small whales from their IPIs.

**APPENDIX**

In 1990, Best presented a short paper to the International Whaling Commission illustrating that the total length of the whale (\( T \)) and the distance between the blowhole and the posterior emargination of the dorsal fin (\( B \)) followed a linear relationship for sperm whales. This result was derived from measurements of male and female sperm whales taken during whaling as reported by Fujino (1956) and Clarke and Paliza (1972). Here we also include data from Matthews (1938), which brings the sample size to 215 individuals. The relationship, \( T = 1.399B + 1.587 \) (\( r^2 = 0.985; p\text{-value} < 0.001 \); Fig. 4), is nearly identical to the one presented by Best (\( T = 1.38B + 1.721; r^2 = 0.97 \)).

![Graph showing the relationship between total length and blowhole distance](image-url)

**FIG. 4.** Relationship between total length (\( T \)) and the distance between the blowhole and posterior emargination of the dorsal fin (\( B \)) derived from whaling data (Matthews, 1938; Fujino, 1956; Clarke and Paliza, 1972). The linear regression has the form \( T = 1.399B + 1.587 \) (\( n = 215; r^2 = 0.985; p\text{-value} < 0.001 \)).


