Acoustically derived growth rates of sperm whales ( Physeter macrocephalus ) in Kaikoura, New Zealand

Brian S. Miller and Abraham Growcott
Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand

Elisabeth Slooten
Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Stephen M. Dawson
Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand

(Received 21 June 2012; revised 12 December 2012; accepted 14 December 2012)

A non-invasive acoustic method for measuring the growth of sperm whales was developed based on estimating the length of individuals by measuring the inter-pulse interval (IPI) of their clicks. Most prior knowledge of growth in male sperm whales has come from fitting growth curves to length data gained from whaling. Recordings made at Kaikoura, New Zealand, were used to estimate the length and growth of 32 photographically identified, resident whales that have been recorded repeatedly between 1991 and 2009. All whales recorded more than six months apart ( n = 30) showed an increase in IPI. Using established relationships between IPI and total length, it was found that the average growth rate in the Kaikoura population is lower, especially for smaller whales (13–14.5 m), than that derived from historical whaling data from other populations. This difference may be due to ecological differences among populations but might also reflect upward bias in measurements gained in whaling. The ability to track growth of individuals through time is only possible via non-lethal means and offers a fundamentally different kind of data because differences among individuals can be measured. © 2013 Acoustical Society of America.

PACS number(s): 43.80.Ka, 43.64.Tk, 43.80.Jz, 43.64.Yp [JJF] Pages: 2438–2445

I. INTRODUCTION

Measuring the length of individuals and quantifying their growth are fundamental to answering many ecological questions. Size, as well as being an indicator of physical maturity, can indicate age (e.g., Gaskin and Cawthorn, 1973). Length distributions can be used to estimate population parameters (e.g., Waters and Whitehead, 1990), and patterns of growth potentially provide insight into ecological differences among populations, habitats, and, in the case of sexually dimorphic species, between the sexes.

Whales, because of their great mass and marine habitat, are among the most difficult animals to measure alive. For this reason, most measurement data have come from dead whales measured at whaling stations or on factory ships (e.g., Fujino, 1956; Clarke and Paliza, 1972). In some cases, such data have been deliberately biased (Cooke et al., 1983; Best, 1989; Kasuya, 1999). Nevertheless, whaling data have been useful in quantifying the basic growth parameters of species (e.g. Kasuya, 1991). Previous studies of growth in male sperm whales (Nishiwaki et al., 1963; Gaskin and Cawthorn, 1973; Lockyer, 1981) are few in number and rely upon age and length data from various 20th century whaling catches. However, many of the most interesting ecological questions require individuals to be measured repeatedly throughout their lives, which is impossible in whaling. While various photogrammetric approaches have been applied to the task of measuring free-ranging whales (e.g. Cubbage and Calambokidis, 1987; Best and Ruther, 1992; Gordon, 1991, Dawson et al., 1995; Jaquet, 2006), none have been applied sufficiently often, and over a long enough period, to provide much useful information on growth. New developments in the theory of how sperm whales make their clicks (Mohl et al., 2003) facilitate measurement of individual whales acoustically and by recording the same individuals over many years, enable quantification of their growth.

The typical vocalizations of sperm whales are broadband echolocation clicks that often show a multiple pulse structure (Backus and Schevill, 1966). Norris and Harvey (1972) hypothesized that this multiple pulse structure arises from a single impulsive sound, created at the museau de singe, that is reflected within the head of the whale and hence that time interval between these pulses represents the time taken for sound to travel the length of the spermaceti sac. Hence the hypothesis predicts that due to allometric relationships between head length and whale length, the inter-pulse interval (IPI) can be used as a measure of whale length. Rhinelander and Dawson (2004) showed that IPIs are stable within individuals over short periods and vary among individuals of different length, confirming that IPIs are a reliable measure of whale length. Gordon (1991) and Rhinelander and Dawson (2004) used simple photogrammetric techniques to measure whale length and quantified the relationship between photogrammetrically measured length and IPI. Gordon derived this relationship mostly from
juvenille and female whales, while Rhinelander and Dawson measured pubertal and mature male sperm whales between 12.5 and 15.2 m in length. Growcott et al. (2011), using a new digital stereophotogrammetric system, has extended the number of individuals with independent measures of IPI and length, facilitating a new regression equation for IPI ($L$ measured in ms) and photogrammetric length ($L$ measured in meters) (Growcott et al., 2011)

$$L = 1.257 \times I + 5.736;$$

($n = 33, r^2 = 0.77, \text{SE0.0201 m/ms and 0.1239 m})$.

(1)

Methods of computing IPI have also advanced recently. Adler-Fenchel (1980), Gordon (1991), Goold (1996), Rendell and Whitehead (2004), and Rhinelander and Dawson (2004) computed IPI from recorded sperm whale clicks using various signal processing techniques and classification criteria but from a small number of carefully selected individual clicks. Large numbers of clicks were considered unsuitable for analysis and discarded because they did not show the multipulse structure clearly.

After investigating the radiation pattern of sperm whale clicks, Möhl et al. (2003) proposed the bent-horn model of sound production, which is a refinement of the original Norris and Harvey model. The new theory explains why many clicks do not appear to contain a clear multi-pulse structure (Zimmer et al., 2005a). According to the bent horn model, only on-axis clicks, recorded either directly in front of or behind the acoustic axis of the whale, exhibit a clear-multi pulse structure. The time delay between pulses of an on-axis click corresponds to the acoustic propagation delay as sound travels from the museum de singe reflects off the frontal sac and travels forward out of the anterior surface of the junk. In off-axis clicks, these pulses are present but obscured by interference arising from the off-axis angle of the whale (Zimmer et al., 2005a). In the earlier studies of sperm whale IPI mentioned in the preceding text, the discarded clicks were most likely to have been recorded off-axis.

A new approach to IPI computation, based on the bent horn model of sound propagation, was proposed by Teloni et al. (2007). They postulated that the ensemble average of the cepstrum of hundreds of clicks should yield a consistent estimate of IPI. Using statistical bootstrapping, Antunes et al. (2010) were able to supplement and adapt the methods of Teloni et al. (2007) to estimate IPIs from recordings containing as few as 50–400 clicks. Antunes et al. found that autocorrelation methods of IPI computation were the most reliable for IPI computation; however, they found that when using small number of clicks occasionally cepstral methods converged when autocorrelation did not. The advance offered by the Teloni et al. (2007) method is considerable; it is not only objective, which facilitates automation, but also requires fewer assumptions than previous criteria for computing IPI and hence allows for analysis of additional recordings not previously considered suitable for IPI measurement, thus increasing sample size.

The acoustic data set from Kaikoura contains dozens of individuals that have been recorded many times, and over many years (maximum 14.7 yr), and most of the audio recordings in this data set come from photographically identified whales. Growcott et al. (2011) described the relationship between IPI and length. Here we build upon that knowledge, implementing the approach of Teloni et al. (2007) to IPI measurement to quantify growth of individuals recorded repeatedly over many years. To our knowledge, this is the first application of passive acoustic methods to measure growth in any marine mammal.

II. METHODS

A. Data collection

Data for this project were collected from 1990 to 2009 as part of a long-term research program of Kaikoura, New Zealand, conducted by Otago University’s Marine Mammal Research Group. In brief, data collection involved making acoustic recordings of photographically identified whales (Ambom, 1987; Childerhouse et al., 1996). Field work from 1990–2000 was previously described by Rhinelander and Dawson (2004). All recordings analyzed in the original study by Rhinelander and Dawson (2004) were made directly behind whales after they fluked up to ensure that the first 8 min of recordings contained clicks that were largely parallel to the main acoustic axis as the whale descended.

Additional photographic and acoustic data collection occurred in 2002 and between 2005 and 2009. The 2002 recordings were made with the same Sonatech 8178 hydrophone, Sony TCDD10-PROII digital audio tape recorder, and protocols for acoustic recording and photographic identification from 1996 to 2000. Recordings from 2005 were made with a custom-built stereo hydrophone array similar to that described by Barlow et al. (2008) and a laptop running iMSMAEL software with a National Instruments DAQ6062E data acquisition card (2005–2006) or an Edirol R4 hard disk recorder (2006–2009). Hydrophones in the stereo hydrophone array were not individually calibrated, but an identical array had a reasonably flat (+4 dB) frequency response from 2 to 40 kHz (Barlow et al., 2008). The Edirol R4 and National Instruments 6062E were set to 96 kHz sample rate and had a flat frequency response from 10 Hz to 40 kHz (−3 dB). A pinna producing a tone of 10.100 kHz was used to check that sampling rates were accurate, and an adjustment was applied to data recorded using the NI 6062E to correct for discrepancies between the requested and actual sampling rate. The 6062E data acquisition card sampled with 12-bit precision, while the Edirol R4 was set to either 24- or 16-bit precision. PAMGUARD (version 1.6) was only capable of using 16-bit wave files, so 12- and 24-bit recordings were converted to 16-bit wave files before analysis. The hydrophone elements on the stereo array were spaced 5 m apart and the deepest element was deployed to a depth of either 65 or 105 m.

B. Data analysis

A custom software plug-in implementing the IPI computation method from Teloni et al. (2007) was developed for the computer program PAMGUARD (version 1.6). PAMGUARD is
freely available, open source software for passive acoustic monitoring (Gillespie et al., 2008). The IPI plug-in presented here depends on the basic functionality provided by PAMGUARD core modules. Existing PAMGUARD plug-ins used in this study include the hydrophone array manager, multichannel data acquisition (both from live input and archived audio files), bandpass filters, and click detection.

Acoustic data were first high-pass filtered with an eighth order Butterworth filter using PAMGUARD’s IIR filter module with the corner frequency set to 1.5 kHz. Filtered data were then input into PAMGUARD’s built-in click detector. For single hydrophone recordings, the click detection threshold was set so that detected clicks correspond to those from the target whale (which was typically the loudest in a recording). For stereo recordings, the click detection threshold was usually set lower, and the built-in angle vetoes of the click detector adjusted so that only clicks coming from the target whale were kept. The angle veto works by excluding clicks from further analysis if they have a bearing that is dramatically different than that of the target whale. The time window for detected clicks was set to 40 ms with 10 ms preceding the detection and 30 ms following the detection. Detected clicks were then used as input into the IPI computation plug-in.

IPI measurement followed the methods outlined by Teloni et al. (2007) and to a lesser extent Rhinelander and Dawson (2004). Before IPI measurement, the IPI plug-in filtered any clicks that had more than three consecutive samples within 90% of the full scale amplitude to exclude clicks that had been clipped, as the cepstrum of a clipped waveform could be distorted by artifacts. Next, the cepstrum of each individual click was computed as

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

where \( x_t \) is the digital representation of the time domain waveform and \( FFT \) and \( FFT^{-1} \) are the fast Fourier transform and inverse fast Fourier transform, respectively, as in Teloni et al. (2007). The time delay at the peak of the cepstrum was stored as the IPI of that click and used to create a histogram of IPI for each recording. On a basic level, this IPI histogram was similar to the methods used by Rhinelander and Dawson (2004), who estimated the IPI from the autocorrelation function of individual clicks and then computed the mean and standard error of all IPIs.

In addition to constructing the IPI histogram, the plug-in also computed the ensemble average of the cepstrum from all detected clicks. The peak value of the ensemble average of the cepstrum was located and the time delay of the peak kept as the ensemble IPI as described by Teloni et al. (2007). The ensemble IPI computation allows analysis of recordings that were made from arbitrary locations with respect to the whale. Implementing both methods in the module required little extra processing, and facilitated comparison of the methods (see Sec. III).

The peak width of the ensemble IPI was used as the measure of uncertainty for each recording. Peak widths were measured at 75% of the maximum value, a value that was empirically shown to give reasonable results. A threshold width of 1 ms was used to exclude measurements with high uncertainty (typical IPI values ranged from 5 to 8 ms). Of 279 analyzed recordings, only two were excluded due to high uncertainty. We compared the IPI histogram and ensemble IPI results from the PAMGUARD plug-in to the IPIs of 36 recordings from the same data set that had been analyzed previously by Rhinelander and Dawson (2004).

For computation of growth rates, all recordings of each individual whale were considered for analysis if the total time between first and last recordings spanned 6 months or more. IPIs from these recordings were obtained using the PAMGUARD IPI plug-in, and the mean of all recordings made within 6 months of each other was taken as an average measure of IPI for each individual during the years that they were recorded. Average growth rates, \( g(t) \), were then computed for each consecutive pair of mean IPIs as

\[ g(t) = \frac{L(t_{n+1}) - L(t_n)}{t_{n+1} - t_n}, \]

where \( t_n \) is the time of the average measurement and \( L \) is the length derived from the average IPIs using Eq. (1).

Direct comparison among growth rates in Kaikoura to those obtained from whaling data was not possible due to the lack of age data on individuals in Kaikoura. Furthermore, no analytical functions (e.g., von Bertalanffy growth curves) were fitted to whaling data by their original authors. Nishiwaki et al. (1963) and Lockyer (1981) published only hand-drawn curve fits without the raw data, and Gaskin and Cawthorn (1973) published a subset of their data along with their hand-drawn curve fit. To compare our results with measurements made during whaling, we compared growth as a function of length. A piecewise polynomial smoothing spline was fit to digitized growth curves published by Nishiwaki et al. (1963), Gaskin and Cawthorn (1973) and Lockyer (1981), and instantaneous growth rate was computed via differentiation and plotted as a function of whale length (Fig. 3). These instantaneous growth rates were then comparable to the average growth rates estimated in this study.

III. RESULTS

A. Comparison of IPI computation methods

There was good correspondence between the ensemble IPI and IPIs measured manually by Rhinelander and Dawson (2004) for all 36 recordings, and the mode of the IPI histogram had good correspondence between paired measurements for 34 of the 36 recordings. For all of these recordings, the number of detected clicks used by the PAMGUARD plug-in for IPI measurement ranged from 105 to 2604, while the number of clicks used by Rhinelander and Dawson ranged from 6 to 45. Linear regression between the ensemble IPI estimate, I, and those computed by Rhinelander and Dawson (2004), \( x \), reveal an excellent one-to-one relationship (I = 1.01 * x + 0.0096; \( r^2 = 0.952 \); solid line Fig. 1). The relationship between the modal value of the IPI histogram, \( H \), did not show as good a relationship with the Rhinelander and Dawson measurements (\( H = 1.21 * x - 1.65; r^2 = 0.368 \); dashed line Fig. 1), indicating that the
ensemble IPI method provides the most similar results to those of Rhinelander and Dawson (2004).

B. Acoustically measured growth rates from Kaikoura

Thirty-two whales were recorded over multiple field seasons, and all whales showed an increasing or stable IPI over time (Table I). Nine whales were recorded on several occasions over time spans of more than 8 yr, and all of these whales showed an increase in IPI over the total time, although not every whale showed growth over all consecutive recordings (Fig. 2). There was not a strongly predictive relationship between growth rate and length for whales measured in this study; however, the growth rates of the fastest-growing whales were almost all lower than the average growth rates measured during industrial whaling (Fig. 3; see Sec. IV).

IV. DISCUSSION

Both the ensemble IPI, and the mode of the IPI histogram, as computed by the PAMGUARD plug-in, provide an automated estimate of IPI that is very similar to the manual measurement methods used by Rhinelander and Dawson (2004); however, the ensemble IPI appears to be slightly more robust than the IPI histogram (Fig. 1). The automated nature of the analysis greatly reduces the time required to estimate IPI; however, automated analysis should be used with caution when multiple whales have been recorded simultaneously. In these cases, the threshold for click detection should be adjusted, or preferably other Pamguard modules, such as angle vetoes, should be used to remove clicks from other whales.

Reanalysis of the Rhinelander and Dawson data shows that the automated method works surprisingly well even with as few as 105 clicks. Teloni et al. (2007) suggested using at least 1000 clicks for stable results. The present results indicate that fewer clicks can be used under some circumstances, e.g., when using high quality recordings made directly behind the whale after fluke up. Antunes et al. (2010) found a similar result when investigating semi-automated approaches for computing IPI given a small number of recorded clicks. While they suggest additional statistical and signal processing methods, these methods were deemed unnecessary because our recordings had large numbers of loud clicks (median of 744 clicks/recording), and the ensemble average showed little uncertainty with all our recordings.

By applying the PAMGUARD plug-in to a long term data set, we were able to observe an increase in IPI over time for 30 of 32 whales in Kaikoura. The two whales that showed no increase in IPI were both seen only on two occasions less than 6 months apart. The only parsimonious explanation for increase in IPI over time is individual growth. The fact that no individuals showed fluctuation in IPI over time provides further validation of the IPI computation method described by Teloni et al. (2007) and, incidentally, further supports the bent horn model of sound production.

Applying Eq. (1) to these IPI estimates allows us to estimate whale length (Table I; second vertical axis in Fig. 2).
We estimated growth rates for all whales that had both identification photographs and recordings that were made greater than 6 months apart. This is the first time that acoustic estimates of whale length have been used to derive measurements of the growth of individual whales. In contrast to growth rate measurements made during whaling (Nishiwaki et al., 1963; Gaskin and Cawthorn, 1973; Lockyer, 1981) or from stranded animals (e.g., Evans and Hindell, 2004), this technique is not only non-lethal but also completely non-invasive.

While growth of individuals could be measured using photogrammetric techniques only (e.g., Durban and Parsons, 2006; Rowe and Dawson, 2008; Webster et al., 2010), there are several advantages to the acoustic methods presented here. Stereo photography requires manoeuvring alongside of the whale (Dawson et al., 1995), which can cause the whale to turn away or dive early, especially when other vessels (such as whale watching boats) are present (Richter et al., 2006). Additionally, identification photographs of the whale must be taken from directly behind the whale, requiring additional manoeuvring. In contrast, audio recordings of the whale can be made from any position, including behind the whale, which compliments rather than conflicts with the photogrammetric identification efforts. Stereo photogrammetry presently requires a somewhat cumbersome system of two cameras on either end of a 2.4 m bar, attached, at eye height, to a short mast. Analysis of the image requires expensive proprietary software. IPI measurements can be made using a single hydrophone, field recorder, and free open source software. Furthermore, IPI measurements have been demonstrated to be more precise than all of the photogrammetric techniques reported in Growcott et al. (2011).

There are some inherent limitations when measuring growth rates of sperm whales acoustically. Unless the researcher is able to track individual whales at depth using a hydrophone array, the approach will be more difficult to use when multiple whales are diving in close proximity. Hence it is more practical at higher latitudes, where whales are typically spaced further apart (Gaskin, 1970); however, it should be noted that most of the IPI measurements reported by Antunes et al. (2010) came from low latitudes. In nursery groups where many whales are closely grouped together and dive in synchrony, it is unlikely that IPIs could successfully be matched to particular individuals. It should be noted that the limitation stated above arises from the inability to match photographs with acoustic records for nearby individuals and not from any inherent limitation in the PAMGUARD IPI plug-in.

Lockyer (1981) noted continued growth in male sperm whales until they reached physical maturity (at an average length of 15.85 m). Most of the whales recorded repeatedly in Kaikoura were between 13 and 15 m and still growing. This suggests that these whales are socially mature but not yet physically mature. Age-length keys from Nishiwaki et al. (1963) and Gaskin and Cawthorn (1973) give age estimates of approximately 17–30 yr for this length range, while Lockyer (1981) estimates 25–35 yr. The fact that some of the whales in this study have been seen at Kaikoura for at least 19 yr (e.g., NN20, MLS100, HL40) is in accord with these age estimates.

Growth rates at Kaikoura (Fig. 3) appear well below those derived from whaling in the Southeast Pacific (Lockyer, 1981), and most are lower than those from whaling in the North Pacific (Nishiwaki et al., 1963). Perhaps unsurprisingly, our acoustically measured growth rates match most closely with those derived from whaling in Cook Strait (a superset of our study area) in 1963 and 1964 (Gaskin and Cawthorn, 1973), although they still appear to be slightly lower. Because Gaskin and Cawthorn published neither error estimates nor raw data for their growth curve, it is not possible to say whether these differences are
statistically significant. However, assuming that these differences are real, they could be driven by differing measurement methodology (e.g., measuring tape vs IPI), bias in whaling data, differences among populations, or density dependent changes.

Our measurement methods, which rely on the relationship between IPI and photogrammetrically measured lengths, could hardly be more different from measuring dead whales killed in whaling. Variability in our photogrammetric estimates arises chiefly from the difficulty of locating exactly the same point to measure from, and the fact that whales are inherently flexible (Dawson et al., 1995; Growcott et al., 2012). Gaskin and Cawthorn’s estimates of growth, like those of Lockyer (1981) and Nishwaki et al. (1963), are based on lengths measured from dead whales and ages estimated from counting growth layer groups in teeth. The specific criteria used for aging were not published by these authors; however, Evans et al. (2002) reveal substantial differences in the number of growth layers counted among different readers. Also, tooth wear often removes outer growth layers making older (larger) individuals appear to be younger than they truly are. Thus caution is required when comparing the age-length data from dental growth layers (e.g., Nishiwaki et al., 1963; Gaskin, 1973; Lockyer, 1981) to the acoustically derived growth rates.

Wholesale misreporting of whale catches occurred during post-WWII whaling (Zemsky et al., 1995). More subtle distortion of recorded data also occurred (e.g., Best, 1989; Kasuya, 1999). Sperm whale catches were managed in part via minimum length limits. The Russian and Japanese data from the 1960s and 1970s show a knife-edge distribution of body lengths at the minimum allowable length (Allen, 1980; Cooke et al., 1983). This feature is also seen in length data from the Taiji land station in Japan, (Kasuya, 1999) and also in data from Durban in South Africa (Best, 1989). Assuming that the data were not entirely falsified, and that the gunners were not almost supernaturally gifted at estimating the length of whales before they harpooned them, it appears that whalers routinely recorded exaggerated lengths for whales that were under the limit (Cooke et al., 1983; Best, 1989; Kasuya, 1999). Hence it is possible that the growth curves published from whaling data are biased. Exaggeration of lengths recorded from whales near the length limit would have the effect of overestimating growth at this life-stage.

It is also possible that growth rate varies among populations. If true, either the whales that repeatedly return to Kaikoura are not growing as fast as the whales caught during whaling, or the Kaikoura population does not grow as large as those taken during whaling. Gaskin and Cawthorn (1973) published the lengths of 238 male sperm whales caught in the Cook Straight area (which includes our study site) from 1963 to 1964. They reported a mean length of 14.09 m with a minimum length of 10.7 m and a maximum of 16.8 m. The mean of the initial lengths, $L_0$ in our study was 13.96 m, and the mean of the final lengths, $L_f$ was 14.44 m, both of which are very similar to the mean reported by Gaskin and Cawthorn; however, the distributions of lengths were significantly different (Fig. 4; Kolmogorov-Smirnov test; maximum difference between distributions, $D = 0.2877$ m; $p = 0.0145$). The discrepancy between length distributions is likely explained by our study area being much smaller, and there may have been some size selectivity on behalf of the whalers in 1963 to 1964.

Both Kasuya (1991) and Kahn et al. (1993) suggested that density dependent effects on sperm whale size resulted from the removal of large numbers of whales during commercial whaling. Kasuya (1991) noted an increase in the length distribution of males and attributed this change to an increase in available food (or decrease in competition for food). Similarly, Kahn et al. (1993) found differences in

---

**FIG. 3.** Average growth plotted for measurements with the longest time span (a) and for each consecutive measurement period (b) and for all individuals. Lengths are derived from interpulse intervals (IPI) using Eq. (1). The dashed, dotted, and solid lines show growth of male sperm whales derived from Nishiwaki et al. (1963), Lockyer (1981), and Gaskin and Cawthorn (1973), respectively.
ACKNOWLEDGMENTS

length distribution of females off the West coast of South America. Both of these studies observed changes five to ten years after the end of the intensive whaling effort. Sperm whales were hunted in the Southwest Pacific around New Zealand from the 1830s until as recently as 1970 with whales were hunted in the Southwest Pacific around New Zealand from the 1830s until as recently as 1970 with

V. CONCLUSION

Coupling new analysis techniques with long-term monitoring efforts (in the form of photographic identification and audio recordings) has provided a unique opportunity to measure acoustically the growth of individual sperm whales in Kaikoura, New Zealand.

While the idea of acoustic measurement of sperm whale whale length is not new (Gordon, 1991; Goold, 1996; Rhinelander and Dawson, 2004; Mathias et al., 2009), this study does represent the first application of this non-lethal technique to measure growth of individual whales. It is hoped that the freely available software presented here will enable more researchers to add acoustic length estimates to their analysis toolbox. The plug-in features fully automated IPI estimation, the ability to work with real-time input as well as post-processing of archived data. Contact the authors for a copy of the IPI plug-in.

ACKNOWLEDGMENTS

We thank our colleagues who collected data, Olaf Jaeke, Lesley Douglas, Quinn Rhinelander, Christoph Richter, Miranda van der Linde, Eleanor Hutchison, and Will Rayment. Thanks to Ross Vennell for his comments on the manuscript. This project was part of a long-term research program in Kaikoura that has received funding from the New Zealand Lottery Board, World Wide Fund for Nature (NZ), Telecom NZ Ltd., the University of Otago, Department of Conservation, and the New Zealand Whale and Dolphin Trust.


