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MARINE MAMMAL SCIENCE, 16(3):664–676 (July 2000)

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MEASURING SIZES OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) BY UNDERWATER VIDEOGRAMMETRY

Measurements of body sizes of living humpback whales (*Megaptera novaeangliae*) can aid significantly in the understanding of important aspects of their biology and behavior, such as age-related demographics of the population, social organization, reproductive behaviors and strategies, and calf growth rates. We report here on a new inexpensive technique we call underwater videogrammetry for measuring sizes of whales that, at the same time, offers opportunities for gathering data on individual identification, behavior, social role, and sex. We demonstrate the accuracy and reliability of the technique by measuring objects of known size. We also provide size data on female humpback whales (“mothers”) accompanied by their calf, and on male whales acting as single escorts to mother-calf pairs (Herman and Antinoja 1977). We obtained both data sets during the annual winter assembly of humpback whales in Hawaiian waters.

During the approximate first half of the 20th century, whaling biologists provided data for killed animals on the range of size by sex and the relation of size to reproductive state (see summaries in True 1904; Matthews 1937; Macintosh 1942; Chittleborough 1955, 1965; Omura 1955; Tomilin 1967). Scientists continue to gather information on whale body size by analyzing archival whaling data (Clapham *et al.* 1997) or by examining stranded whale carcasses (Stevick 1999). Whaling records must be treated with some caution, however, because of documented occurrences of errors in reporting of sizes or variability in procedures, such as the deliberate overestimation of lengths of

whales that were near the minimum legal size (Cooke *et al.* 1983), failure to follow standardized techniques for length measurements (Best 1989), and apparent differences in sizing procedures across whaling nations or whaling fleets (Clark 1983). Nonetheless, the data, on average, can provide a guide against which to gauge the reasonableness of the sizing of live animals obtained by non-invasive techniques.

Currently available non-invasive techniques rely on photogrammetry obtained from aircraft or ship platforms. All photogrammetric techniques estimate the sizes of the animals by applying a scaling factor or scaling object to the animal's image on obtained photographs. A scaling object may be something of known size that is included within the photograph of the whale. For example, Whitehead and Payne (1981) photographed southern right whales (*Eubalaena australis*) from a fixed-wing aircraft while a boat carrying a white disk of known size ran parallel to the whales. Other aircraft-based photogrammetric studies of whales have relied on barometric or radar altimeters to eliminate the need for a scaling object. Knowledge of the focal length of the camera lens (a still camera is used) together with the measured distance to the whale obtained from altimeter readings, is sufficient to compute the dimensions of the field of view of the camera lens at the measured distance. The whale's size is then obtained from the proportion of the field of view occupied by its full body image, as measured on individual frames by a device such as a binocular microscope (Ray *et al.* 1984, Calambokidis *et al.* 1989, Ratnaswamy and Winn 1993) or a stereo comparator (Best and Ruther 1992, Perryman and Westlake 1998). Photogrammetric techniques employing altimeter readings have been used to measure sizes of bowhead whales (*Balaena mysticetus*) (Ray *et al.* 1984, Cabbage and Calambokidis 1987); right whales (Best and Ruther 1992); blue (*Balaenoptera musculus*) and humpback whales (Calambokidis *et al.* 1989); fin whales (*Balaenoptera physalus*) (Ratnaswamy and Winn 1993); beluga whales (*Delphinapterus leucus*) (Ray *et al.* 1984); common dolphins (*Delphinus delphis*), striped dolphins (*Stenella coeruleoalba*), and spinner dolphins (*Stenella longirostris*) (Perryman and Lynn 1993, Perryman and Lynn 1994, Perryman and Westlake 1998).

Scott and Winn (1980) estimated the body length of humpback whales from aerial photographs by using non-linear regression analysis of the allometric growth relationships between morphological dimensions and total body length. A shortcoming of this procedure, however, is that humpback whales may show substantial variability in the ratios of partial body lengths to full body length (Tomilin 1967). For example, rostrum to blowhole distances in Tomilin's data range from 16.6% to 25.8% of total body length.

Boat-based techniques have also been used to estimate whale size. Gordon (1990) photographed sperm whales (*Physeter macrocephalus*) from a ship's mast rising approximately 10 m above sea level. Distance to the whale was estimated from the angle subtended by the whale and the horizon. Gordon then calculated the blowhole-to-dorsal-fin length of the whales from measurements on the obtained negatives, and from this partial length extrapolated total body length using inferences from allometric data on killed sperm whales. Dawson *et al.* (1995) also used photographs taken from a boat to derive blowhole-to-

dorsal-fin lengths of sperm whales. These researchers used two cameras separated laterally and synchronized to photograph at the same instant. Scale was derived from the known camera separation and the resulting separation of the images as measured with a stereo plotter. Extrapolation of total body length from the partial length measurements was then made, as was the case for Gordon (1990). Allometric measurements for male and for female sperm whales (Tomilin 1967, Berzin 1972) seem less variable than for humpbacks.

Finally, Glockner and Venus (1983) attempted to determine the sizes of 12 humpback whale calves through underwater photography, using a still camera. They compared the length of the calf to the length of its mother, which was swimming parallel to the calf. For the mother's length, they simply used the average length of sexually mature females as reported in whaling data (Nishiwaki 1959). Calf length was then calculated from the ratio of the calf's length to its mother's length as derived from the photographs. Inasmuch as there can be considerable variation in the sizes of sexually mature females (Nishiwaki 1959, Tomilin 1967), there can be considerable error in these calculations.

Although many of these various photogrammetric techniques provide reasonably accurate measurements of whale length, they are often expensive and may be limited in the degree to which they can provide ancillary data on individual identification, behavior, social role, and sex.

In our videogrammetric technique, we use a Sony DCR TRV-7 digital video camera in a JAY-MAR VM-6000 underwater housing to obtain full-body images of a whale and a hand-held Speedtech Depthmate sonar device to measure the distance from camera to whale. The Speedtech sonar uses a 200-kHz signal with a beam width of 24° and a range of approximately 100 m. The 200-kHz frequency is well above the vocal range and estimated hearing range of humpback whales (Payne and Payne 1985, Frankel *et al.* 1995). No responses of the whales to the sonar signal have been observed. A lighted digital read-out on the sonar device indicates the distance to the nearest 0.1 m at ranges of less than 6.1 m and to the nearest 0.3 m at greater ranges. Ninety-nine percent of our sonar measurements were obtained at distances of 29 m or less. The maximum distance for any single measurement was 36 m.

To obtain videogrammetric data, a swimmer wearing mask, snorkel, and fins, and carrying the digital video camera and sonar device, is deployed opportunistically from our boat when a whale or group of whales becomes stationary, mills, or sufficiently reduces its rate of travel. The snorkeler swims towards a whale and remains at the surface. To obtain the best video image, the swimmer positions himself or herself perpendicular to the submerged whale's longitudinal axis and near its midline. Whales at depths of up to 30 m can be suitable subjects under most conditions in Hawaiian waters. While videotaping with the camera set at maximum angle of view and the whale centered within the field of view, the snorkeler points the sonar device at the whale and takes one or more distance measurements. A click sound made by the switch of the sonar device at the moment of activation is recorded on the videotape and marks the exact moment when the sonar reading is made. The sonar read-out, once obtained, is held briefly in front of the camera to create a permanent record of the measured distance on the videotape. Multiple in-

dependent measurements are obtained when the snorkeler moves relative to a stationary whale, when the whale moves and the snorkeler repositions himself or herself, or when the whale swims off and then slows down, presenting another opportunity for the boat to approach and deploy the snorkeler. Any or all of these conditions may occur with a given whale.

The captured video images are subsequently reviewed on an Apple Power Macintosh G3 computer using DV Tools PPC software. Individual frames on which the click sounds from the sonar device are heard are scrutinized to judge the suitability of the captured image. To qualify for measurement, the full body of the whale must be visible, there must be no curvature of the body, and the camera axis must be perpendicular, or nearly so, to the whale's body and as close to the body midline as possible. When a suitable frame is identified, the accompanying sonar distance is noted, and the PICT image of the whale is imported into Adobe Photoshop and displayed on the computer screen. The sonar distance and the calibrated angle of view of the camera lens at a fixed focal length (the widest angle of the camera lens was used in all of our work) allow for the calculation, in meters, of the field of view of the camera at the measured distance. The field of view exactly fills the horizontal dimension of the software window (720 pixels). The X-Y coordinates of the tip of the rostrum and of the notch at the center of the tail flukes are measured in pixels using the Marquee tool. Image length is then calculated in pixels as

$$L_i = [(X_1 - X_2)^2 + (Y_1 - Y_2)^2]^{1/2} \quad (1)$$

where L_i = length of the whale's image (in pixels), and the pairs X_1, Y_1 and X_2, Y_2 represent the coordinates (in pixels) of the anterior and posterior ends of the whale's image, respectively. The whale's length in meters is then given as

$$L_e = (F * L_i)/720 \quad (2)$$

where L_e = the measured whale length (in meters), F = field of view of the camera at the sonar-measured distance (in meters), and L_i = length of the whale's image (in pixels).

To calibrate the system, we first measured the angle of view of the digital camera in the Jay-Mar housing using two different techniques. For the first technique, the camera was positioned in a 50-m pool perpendicular to parallel lane ropes spaced every 2.44 m. The angle of view was measured at distances of 11.15, 14.54, and 18.76 m. The camera lens was set at its widest angle, and marks were made on the lane ropes to define the edges of the camera's field of view at each of the three indicated distances. The distance between the marks was then measured by tape, and Equation 3 was used to calculate the angle of view, \emptyset , of the camera lens at each distance, D , from the camera lens to the center of the marked lane rope.

$$\emptyset_i = 2 * \arctan\{(F/2)/D_i\} \quad (3)$$

The angle of view of the camera was also calculated using a computer-generated grid. A black-on-white grid (40 × 56 cm) consisting of 2-cm

squares was affixed in front of the camera in its underwater housing and perpendicular to the lens. The distance from the center of the grid to the nodal point of the camera's wide angle lens was 38.85 cm. The entire camera-grid apparatus was submerged in a saltwater tank and an image of the grid was video-recorded. The recorded image was then captured and measured on a computer screen, using the software described earlier, to determine the field of view at the fixed distance. Again, the measured field of view and distance were applied to Equation 3 to calculate the angle of view of the camera system underwater.

The mean angle of view over the two procedures at the four different distances was 66.25° (SD = 1.69, CV = 2.5%, range = 64.87° – 68.56°). With \emptyset determined, the field of view, F , at any measured distance to the whale could be calculated.

The image of the grid was then used to calculate the amount of distortion existing at different points in the field of view due to the curvature of the lens. Using Adobe Photoshop, the width (in pixels) of each 2-cm square along three horizontal lines was measured across the field of view. The mean width of all squares was 28.6 pixels (SD = 1.05, CV = 3.7%, range = 26–30) with squares toward the center of the field of view occupying more pixels than squares near the edge. The true size of squares near the center of the image was slightly overestimated by the videogrammetric technique, and those near the edge were slightly underestimated. A regression equation ($r^2 = 0.999$) was derived from these data to convert measured image length (x) into expected image length (y) and is given as

$$y = 0.00009x^2 + 0.9335x + 1.6349 \quad (4)$$

As can be seen from Equation 4, the non-linear component is very small. Nonetheless, the quadratic equation minimized the distortion of the captured image arising from the curvature of the lens and was applied to all calibration and field measurements.

We field tested the accuracy of two Speedtech sonar devices in clear waters off Lahaina, Maui. A 6.1-m-long white polyvinylchloride (PVC) pipe, 5.1 cm in diameter, was placed on the flat, firm, sandy ocean bottom at three different locations, each of a different depth. A snorkeler positioned at the surface directly above the pipe obtained six measurements with each sonar device of the distance to the pipe, alternating the two devices over the total of 12 measurements at each depth. The obtained measurements were then compared with direct measurements of depth using a weighted line held plumb to the bottom whose length was then determined by tape measure. Table 1 compares the mean of the sonar-measured depths with the tape-measured depths, using the combined 12 measurements from the two sonar devices. The sonar-measured means differed from the tape-measured means by only 1.52%, 4.16%, and 0.06%, respectively, from the shallowest depth to the deepest. Precision of measurement was high, with CVs ranging from 0% to 1.91%. There was little or no difference between the means of the six measurements obtained with each of the two sonar devices at each of the three depths. At the two

Table 1. Calibration of sonar devices. All measurements in meters.

Tape-measured distance	Sonar-measured distance					
	<i>n</i>	Mean	Median	SD	Range	CV %
5.92	12	5.83	5.79	0.11	5.73–5.98	1.91
10.82	12	10.37	10.37	0.00*	10.37–10.37	0.00
17.34	12	17.33	17.38	0.18	16.77–17.38	1.02

CV = Coefficient of variation.

* All 12 measurements were 10.37 m.

shallowest depths the two sonar means were identical (5.83 m at the 5.92-m depth, and 10.37 m at the 10.82-m depth). At the 17.34-m depth, one sonar device yielded a mean measured depth of 17.28 m and the other a mean of 17.38 m. We can conclude, therefore, that the sonar devices are highly reliable, interchangeable, and introduce little error, with perhaps only a slight underestimation of true depth.

Additionally, 12 video images of the 6.1-m-long PVC pipe were acquired during the 12 sonar-distance measurements at each depth, and the length of the pipe was computed using the videogrammetric technique. Also, to better approximate the size of an adult humpback whale, we made measurements of a rope grid we affixed to the side of a sunken ship at 28-m depth in waters off Honolulu, Hawaii. The above-ground portion of the ship's hull was approximately 30-m long and 6-m high. The side of the ship's hull was flat. Two ropes were tied vertically to the side of the ship spaced 13.72 m apart forming a simple grid. Twenty underwater videogrammetric measurements of the grid were taken by a SCUBA diver using the sonar device and the digital video camera. The diver was positioned at approximately the same depth as the top of the ship's hull. The sonar signal was reflected off the side of the hull at distances ranging from 11.9 m to 14.6 m as the diver changed position.

Table 2 (rows a, b, c) compares the mean of the videogrammetric measurements of pipe length at each distance with the true pipe length (6.1 m). The

Table 2. Videogrammetric measurements of objects of known length using obtained sonar distances. All measurements in meters.

Object	Sonar measured distance*	True length	Videogrammetric measured length					
			<i>n</i>	Mean	Median	SD	Range	CV %
a. Pipe	5.73–5.98	6.10	12	6.07	6.07	0.090	5.94–6.19	1.48
b. Pipe	10.37	6.10	12	6.05	6.04	0.051	5.96–6.12	0.84
c. Pipe	16.77–17.38	6.10	12	6.16	6.16	0.068	6.07–6.28	1.10
d. Ship	11.89–14.63	13.72	20	13.09	13.08	0.565	12.00–13.94	4.32

CV = Coefficient of variation.

* Indicates lower and upper bounds (range) of distance measurements obtained over indicated number of trials (*n*).

Videogrammetric length for each trial based on sonar distance obtained on that trial.

Table 3. Length measurements (in meters) for humpback whale mothers and escorts obtained by underwater videogrammetry.

Social role	No. independent measures	<i>n</i>	Mean	Median	SD	Range	Mean CV %
Mother	2	14	12.73	12.73	0.484	12.07–13.85	3.59
	≥3	12	12.60	12.56	0.633	11.70–13.67	2.49
	Total	26	12.67	12.65	0.550	11.70–13.85	3.08
Escort	2	9	11.80	11.89	0.332	11.25–12.24	2.59
	≥3	10	11.65	11.64	0.243	11.27–12.02	2.55
	Total	19	11.72	11.67	0.291	11.25–12.24	2.57

CV = Coefficient of variation. Data for Mean, Median, SD, Range and Mean CV are based on the individual CVs calculated for each whale.

differences between the measured and true pipe lengths were small, -3 cm, -5 cm, and $+6$ cm, respectively, at each successively increasing distance. No consistent bias was apparent. The length measurements were highly precise at each distance (CVs = 1.5%, 0.8%, and 1.1%, respectively, at the three distances).

Row d of Table 2 shows that the mean of the twenty videogrammetric measurements of the rope grid on the ship's hull underestimated true size by 0.63 m (4.59% on average). The individual videogrammetric lengths were also generally underestimates of true length. Precision of measurements was good (CV = 4.3%).

During March and April of 1997, February–April of 1998, and January–April of 1999, we made opportunistic videogrammetric measurements of body lengths of humpback whales in waters off the island of Maui, Hawaii. The same system was used as in the calibration studies, with the lens of the camera again set at its widest angle. Our goal was to obtain body size data on a variety of whales in various social groupings and engaged in various types of behaviors. Table 3 summarizes size measurements on 26 “mothers,” identified by the presence of a closely accompanying calf, and 19 single escorts accompanying a mother-calf pair. Only those whales for which we obtained at least two independent videogrammetric observations are listed in Table 3. Data are shown separately for those cases when only two independent measurements were obtained and those cases when we obtained three or more. The difference between the mean sizes obtained with two versus three or more measurements was not significant for mothers ($F[1, 24] = 0.37, P = 0.55$) or escorts ($F[1, 17] = 1.30, P = 0.27$). Thus the videogrammetric technique can be useful even when opportunities for many multiple independent measurements of a whale are infrequent. Table 3 shows that the mean of the individual CVs for the 26 mothers and for the 19 escorts are small (3.08% and 2.57%, respectively). Figure 1 shows the distribution of individual CVs for the 12 mothers and 10 escorts measured three or more times. CVs for mothers ranged from

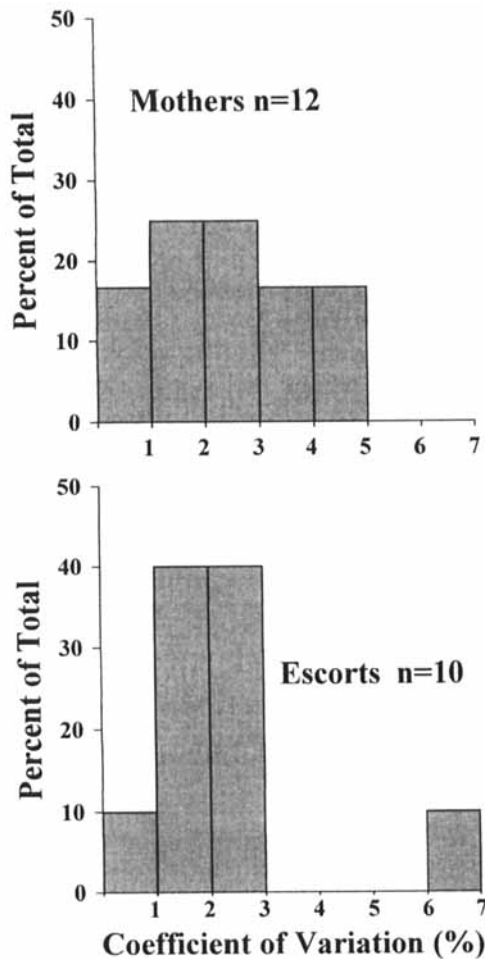


Figure 1. Percentage of 12 mothers (Top) and 10 escorts (Bottom) having coefficients of variation (CVs) falling within each unit range shown (0–0.99, 1–1.99, etc.). Three or more independent videogrammetric measurements of total length obtained for each of 12 mothers and 10 escorts.

0.68% to a maximum of 4.70%. CVs were 2.79% or less for eight of the 12 mothers. CVs for escorts ranged from 0.94% to 2.91% for nine of the ten individuals, with one outlier yielding a CV of 6.75%. Clearly, precision of measurement was good and compares favorably with CV values reported for individual whales in several photogrammetric studies. For example, Best and Ruther (1992) provided a histogram similar to Figure 1 of this paper showing the distribution of CVs for the body length of 31 female right whales measured multiple times by aerial photogrammetry. Extrapolating from the histogram, it appears that 28 females had CVs of 3.99% or less; one individual fell within the range 5.00%–5.99%, a second in the range 6.00%–6.99% and a third in the range 9.00%–9.99%. Dawson *et al.* (1995), using boat-based stereo pho-

togrammetry, reported CVs ranging from 0.9% to 11.3% for multiple measurements of blowhole to dorsal fin emargination of 12 sperm whales. Nine of the 12 CVs were between 3.1% and 5.5%.

The overall mean size of 12.67 m for the 26 mothers we measured by underwater videogrammetry and the range of 11.70–13.85 m (Table 3) compare well with measurements of North Pacific humpbacks obtained from whaling operations. Nishiwaki (1959) reported a mean length of 13.20 m and a range of 10.98–15.24 m for 70 sexually mature females, and Omura (1955) listed a mean length of 12.93 m and a range of 11.28–13.72 m for 68 sexually mature females. Nishiwaki (1962) gave additional data for 35 sexually mature females, listing a mean length of 13.11 m and a range of 11.59–15.24 m. The upper bound (15.24 m) of the ranges given by Nishiwaki (1959, 1962) was in each case based on a single female.

The mean length of 11.72 m and the range of 11.25–12.24 m for the 19 escorts we measured also compare well with whaling data. Nishiwaki's 1959 report gave a mean length of 12.07 m and a range of 10.98–14.33 m for 77 sexually mature males; his 1962 report listed a mean length of 12.38 m and a range of 10.98–13.72 m for 25 sexually mature males. Omura's (1959) data for 59 sexually mature males gave a mean length of 12.11 m and a range of 10.98–12.80 m.

Observations of genital areas (Glockner 1983) and biopsy data (Clapham *et al.* 1992) have confirmed that escorts are males. The whaling data clearly show that sexually mature females are on average larger than sexually mature males. Our data are consistent with this trend; the 26 females we measured significantly exceeded the mean length of the 19 escorts ($F[1,43] = 47.99$, $P < .0001$). The functional role of the single escort is speculative, as is its reproductive state; while it is often assumed that it may be prospecting for mating opportunities, mating has never been observed (Mobley and Herman 1985, Clapham 1996).

In summary, the videogrammetric technique we have described provides the first non-invasive measurements of the sizes of living humpback whales in conjunction with determination of sex and social role. The results of the calibration studies using objects of known length demonstrated that the underwater videogrammetric technique yielded highly accurate length measurements. Error estimates using a PVC pipe of known length ranged from 0.49% to 0.98%. The largest error estimate (4.59%) was derived from the measurements of the rope grid affixed to the side of a sunken ship. A strong current, the use of SCUBA gear at depth, and the presence of schooling fish made these calibrations particularly challenging, so we consider this number to be an approximation of the outer limit for videogrammetric error. There was no consistent tendency across calibration procedures for the technique to underestimate or overestimate true length. Precision was consistently high (means of individual CVs ranged from 0.84% to 4.32%).

The precision of repeated videogrammetric size measurements of individual whales, as measured by mean CV values, was good, 3.08% for mothers and 2.57% for single escorts. These CV values compare well with mean or median

CVs of 1.29%–4.56% for aircraft-based measurements of right whales (Best and Ruther 1992), 5.1% for sperm whales measured by Gordon's (1990) boat-based morphometric technique, and 4.38% for sperm whales measured by the boat-based morphometric technique of Dawson *et al.* (1995) using stereo photogrammetry. The CV of 0.59% reported by Cubbage and Calambokidis (1987) for eight independent measurements of one bowhead whale is very low but not substantially different from CVs reported for some individual whales by others (Best and Ruther 1992, Dawson *et al.* 1995) or by ourselves (Fig. 1). Cubbage and Calambokidis report, however, that the high cost of their aerial technique makes it prohibitive as a generally useful method. Occasional high CVs for repeated measurements are also reported in some of these same studies. For example, Best and Ruther (1992) list a CV of 9% for a right whale cow and 11% for a right whale calf. Dawson *et al.* list a CV of 11.3% for a sperm whale of 7.39 m length measured five times. Our largest CV for an individual humpback measured three or more times was 4.7% for a mother of 13.01 m mean length and 6.75% for an escort of 11.27 m mean length.

The underwater videogrammetric technique offers several advantages. First, it is relatively inexpensive to obtain field data, requiring only a small boat, a digital video camera in an underwater housing (*ca.* US\$4,000–\$6,000), and a portable sonar device (US\$150.00). Photogrammetric techniques that require a large boat, helicopter, or fixed-wing aircraft can be much more expensive. Also, both the aerial and the boat-based photogrammetric techniques can be limited in the information that can be gathered on the behavior, sex, and individual identity of the whales being measured. In contrast, the underwater videogrammetric technique allows one to obtain size measurements concurrently with the collection of data on surface and underwater behavior and interactions, individual identities, social roles, and sex. The pooling of these data enables inferences to be made on the relation of body size to behavior. The technique is limited by the accessibility of the individual whale or dolphin to approach by a swimmer and requires the water to be clear enough for good video images. These conditions characterize the Hawaiian winter grounds of the humpback whale and may be found as well in other tropical areas frequented by whales or dolphins (*e.g.*, the Bahamas Banks, Herzing 1997).

ACKNOWLEDGMENTS

This research was supported by grants to L. M. Herman and A. A. Pack from Earthwatch and its Research Corps and from The Dolphin Institute and its members. We gratefully acknowledge hardware and software donations from APPLE Computer, Inc., and Adobe, and equipment, supplies, and services donations from Budget Rent-A-Car, Motorola Corp., Shaklee, Trimble Navigation, Valley Isle Marine, No Ka Oi Marine, and AAA Storage. We thank Alison Craig for her review of an earlier version of this manuscript, and Andrea Coombs, Mark Deakos, Kirk Duplessis, David Glickman, Catherine Hadfield, Molly Hurst, Carrie Southgate, Alison Stimpert, and our Earthwatch volunteers and short-term participants for their assistance in data collection during the 1997, 1998, and 1999 field seasons. Mark Deakos and Matthias Hoffmann-Kuhnt were especially helpful with the calibration phase of the study, and we greatly appreciate Malcom Northcott's advice for correcting the lens' distortion. We also thank

Mark Robinson for donating the use of his boat *Nuki* in 1998, and Bruce Mate for the opportunity to rent his boat in 1999. John Cook, Dee Kiamy, and Kenwal Sharma provided valuable assistance with hardware and software for the videogrammetric computer analysis. This research was carried out under Federal Scientific Research Permit No. 941 and Hawaii State Permits SCP97-31, MP-SCP98-2, and MP-1999-52.

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MARINE MAMMAL SCIENCE, 16(3):676–681 (July 2000)
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RELATIONSHIP BETWEEN APNEA DURATION AND RATE OF OXYGEN CONSUMPTION IN CAPTIVE FEMALE GRAY SEALS WHILE SLEEPING OR RESTING ON LAND

Phocid seals undergo voluntary apnea while resting or sleeping on land, during which time they experience physiological changes that are similar to those that occur while diving. For instance, the onset and depth of bradycardia (Castellini *et al.* 1994), changes in hematocrit (Castellini *et al.* 1986), and reduction in their rate of oxygen consumption ($\dot{V}O_2$) (Boily and Lavigne 1996, Hansen and Lavigne 1997) exhibited during both conditions are very similar. While the occurrence of a reduction in $\dot{V}O_2$ during apnea is well documented, the quantitative relationship between $\dot{V}O_2$ and apnea duration (AD) is not. Two previous studies on freely diving seals, by Reed *et al.* (1994) on gray seals (*Halichoerus grypus*) and by Castellini *et al.* (1992) on Weddell seals (*Leptonychotes weddelli*), reported a gradual decrease in $\dot{V}O_2$ as apnea or diving duration increased. However, such information is not available for seals resting or sleeping on land under controlled laboratory conditions. We examined if the reported decrease in $\dot{V}O_2$ as a function of apnea duration in freely diving seals also occurs in seals resting or sleeping on land, when animals are not diving and there is no potentially confounding factor such as activity, feeding, or thermoregulation.

Measurements of $\dot{V}O_2$ were obtained from five female Northwest Atlantic gray seals, two wild-caught adults (no. 89–7 and 89–17) and three captive-born juveniles (no. 75, 195, 200) as part of a previous study (Boily and Lavigne 1997), which detailed the general care of these animals and the facilities in which they were housed at the University of Guelph (Ontario). These animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. Briefly, $\dot{V}O_2$ was measured on animals resting or sleeping on land using open-flow respirometry. Two different respiratory cham-