MARINE MAMMAL SCIENCE, 16(3):530–544 (July 2000)

SEASONAL AND DIURNAL TRENDS OF CHORUSING HUMPBACK WHALES WINTERING IN WATERS OFF WESTERN MAUI

WHITLOW W. L. AU
Hawaii Institute of Marine Biology,
University of Hawaii,
46-007 Lilipuna Road,
Kaneohe, Hawaii 96744, U.S.A.

JOSEPH MOBLEY
Social Sciences,
University of Hawaii-West O'ahu,
Ala Ike 96-043,
Pearl City, Hawaii 96782, U.S.A.

WILLIAM C. BURGESS
Greeneridge Sciences, Inc.,
4512 Via Huerto,
Santa Barbara, California 93110, U.S.A.

MARC O. LAMMERS
PAUL E. NACHTIGALL
Hawaii Institute of Marine Biology,
University of Hawaii,
46-007 Lilipuna Road,
Kaneohe, Hawaii 96744, U.S.A.

ABSTRACT

A portable data logger controlled by a Tattletale 7 microcontroller was used to record humpback whale choruses during the 1998 humpback whale winter season in Hawaii. The data logger sampled the sounds for four minutes every half hour using a digitizing rate of 2 kHz, and the data were stored on a hard disk. The results between January and April showed a peak in the sound pressure level between mid-February and mid-March. This peak of approximately 120 dB re 1 μPa coincided with the peak in the number of whales sighted by aerial survey on 7 March 1998. The choruses had spectral peaks at 315 Hz and 630 Hz. Some of the sounds at 630 Hz were second harmonics of the 315 Hz peak and others were not. The data also indicated a diurnal pattern in the sound pressure level, with levels at night significantly louder than the daytime levels. The sound levels began to increase during sunset and remained relatively high until sunrise, when they progressively decreased to a minimum. The nighttime peak occurred within an hour before and after midnight, and the daytime minimum occurred between 1100 and 1500. That more humpback whales appear to sing at night may reflect a switch to sexual advertisement as the primary male mating strategy at this time. It may also indicate that daylight and vision play key roles in the formation of competitive groups. It is suggested that the relative number of humpback whales in a given locale may be estimated by monitoring changes in sound pressure levels.

Key words: humpback whale, *Megaptera novaeangliae*, chorusing sounds, data logger, ambient noise.

The winter song of humpback whales (*Megaptera novaeangliae*) has been described as the most complex display in the animal kingdom (Wilson 1975). Since its initial description by Payne and McVay (1971) it has become the most studied of any baleen whale sound. From the many studies of humpback whale songs, we can summarize some general properties of songs and singing whales. Singers mostly appear as lone, stationary males (Winn and Winn 1978, Tyack 1981), yet some have been documented as singing in groups (Baker and Herman 1984) and while moving (Frankel *et al.* 1995). Singing has been recorded on the Alaskan (McSweeney *et al.* 1989) and Gulf of Maine (Mattila *et al.* 1987) feeding grounds and during migration (Clapham and Matilla 1990), yet appears to be most prevalent on the winter breeding grounds. Humpback whale songs show clear structure based on aural analysis, with smaller repetitive units called "phrases" organized into larger "themes" which tend to occur in specific sequence (Payne and McVay 1971, Guinee *et al.* 1983). The structure of song changes over the course of a winter season, yet at any given time all singers appear to be singing the same version of a song (Guinee *et al.* 1983, Payne *et al.* 1983, Payne and Payne 1985). Estimates of broadband source levels of song include 174 dB re 1 μPa (Frankel 1994) and 155.4 dB re 1 μPa (Levenson 1972).

Helweg *et al.* (1992) presented a detailed summary of current hypotheses regarding the role of humpback whale song, but its role is still far from certain. A number of possible functions of song have been proposed, including sexual advertisement to females (Payne and McVay 1971, Winn and Winn 1978, Tyack 1981), maintenance of spacing among singing males (Winn and Winn 1978, Tyack 1981, Frankel *et al.* 1995), inducement or synchronization of ovulation in females (Baker and Herman 1984), and a navigational "beacon" for migrating whales (Winn and Winn 1978). Helweg *et al.* (1992) proposed that song may provide both a "stay away" message to males, and a "come hither" message to females.

Songs of humpback whales are typically recorded close to a whale in order to maximize the signal-to-noise ratio. However, when sounds are recorded at large distances from any whale, one is likely to hear a number of whales singing as in a chorus, although they do not sing in unison on the same portion of a song. Whereas much attention has been given to the characteristics of songs, little attention has been given to the chorusing by multiple whales. Thompson and Friedl (1982) over several years studied low frequency sounds from several species of whales, including humpback whales, off the island of Oahu, Hawaii. They taped recorded sounds detected by two bottom-mounted hydrophones that were 11.6 km apart at a depth of 400 fathoms (~738 m) in the waters off the northernmost point of Oahu. They found that humpback whale daytime chorusing peaked during the winter months, between February and May, with song detections as early as November and as late as June. However, sound pressure levels were not presented with their data.

In another study, humpback sounds were recorded over a season (25 January–1 June 1988) from a fixed bottom-moored hydrophone located at a depth of about 1,560 m and about 13 km from shore off the island of Kauai (Helweg 1989, Helweg and Herman 1994). Recordings were made for five minutes every two hours around the clock. The data indicated that the number of singing whales did not vary with time of day. Unfortunately, the system was not calibrated, so absolute levels were not measured. Also, the number of singers as a function of days within the humpback winter season was not reported.

In order to obtain a better understanding of the characteristics of humpback whale choruses, we made recordings from a beach location throughout the humpback whale season (January–April). The goals of this project were to obtain calibrated measurements of humpback whale choruses at a single location during regular intervals during each day, to characterize the chorus sounds, and to determine the feasibility of long-term, nearly constant monitoring of humpback whale sounds from a beach location. Recordings were made in nearshore waters off Puamana Beach Park (20°21′N, 156°39.5′W) adjacent to the town of Lahaina, Maui, in Hawaii (see Fig. 1).

Methods

A compact acoustic probe (CAP) data acquisition instrumentation package, originally developed by Burgess *et al.* (1998) to be attached to migrating elephant seals, was used to monitor the humpback whale choruses. The CAP package contained a HTI-94-SSQB preamplified hydrophone from High-Tech, Inc. with a sensitivity of −170 dB re 1V/μPa, a "Tattletale 7" (TT7) microcontroller board from Onset Corporation, and an 814 Mb hard disk drive. The TT7 had four 12-bit analog-to-digital (A/D) conversion channels, although only one of the channels was used. A real-time clock with a dedicated crystal provided time stamps for all data collected, and the entire process of sampling and sleeping was controlled by the TT7 in conjunction with the real-time clock.

A custom amplification and filtering circuit conditioned the hydrophone signals before they were digitized at a rate of 2 kHz. An initial gain stage amplified the signal by 0–31 dB of trimpot adjustable gain. The acoustic signals passed through a Linear Technolgies LTC-1164-6 switch capacitor el-

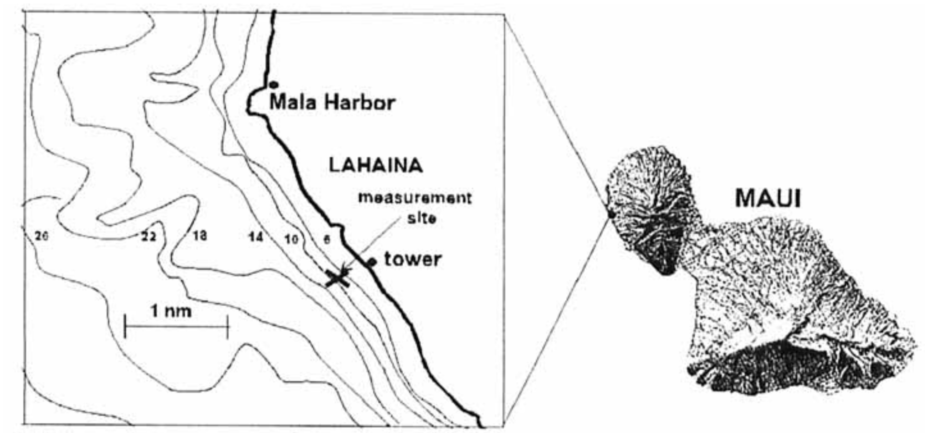

Figure 1. Map of Maui and location of experimental site.

liptical anti-aliasing filter set at 700 Hz. Au and Green (2000) used a system with 20 kHz bandwidth to measure humpback whale chorusing in the same area as the present study. Their results indicated that humpback whale chorusing sounds measured close to shore have most of their energy below 700 Hz. A final gain stage of 20 dB additional gain was used to boost the acoustic signal before digitizing. A total of 36 dB of gain was realized by the amplifier circuit. The digitized data were buffered with 2 Mb of pseudostatic RAM and 180 kb of static RAM. The power consumption of the data acquisition package was 6 W while spinning up the hard disk, 3 W when writing to the disk, 150 mW when sampling sounds at 2 kHz, and 5 mW when idle. Power for the CAP was provided by a bank of alkaline and lithium D-cell batteries. The entire assembly was housed in a watertight anodized aluminum container that measured 10.8 × 7.6 × 16.6 cm and weighed about 2.4 kg.

The data acquisition package was placed on the bottom of the ocean, approximately 0.8 km off shore in 7 fathoms (13 m) of water. The bottom was relatively flat and consisted mainly of sand with the benthic algae *Halimeda* sp. covering approximately 10% of the area. The CAP was secured to a concrete cinder block, but the hydrophone portion was above the edge of the block.

Acoustic signals were digitized for a four-minute period on the hour and half-hour. At this sampling interval and with a 2 kHz sampling rate, the hard disk storage limit of 814 Mb was reached after 23 d. The CAP was retrieved after six days following the first deployment and at intervals of 15–17 d thereafter. Upon retrieval, the data were downloaded to a 1 Gb Iomega Jaz disk and the batteries replaced before the next deployment. All of the data were eventually transferred to a CD ROM disk for archival purposes.

The data were analyzed using Cool Edit 96 and two programs written in Matlab. The first program determined the average and standard deviation of the root-mean-square sound pressure level. The program could analyze the data in a number of ways from a single data file consisting of a single recording

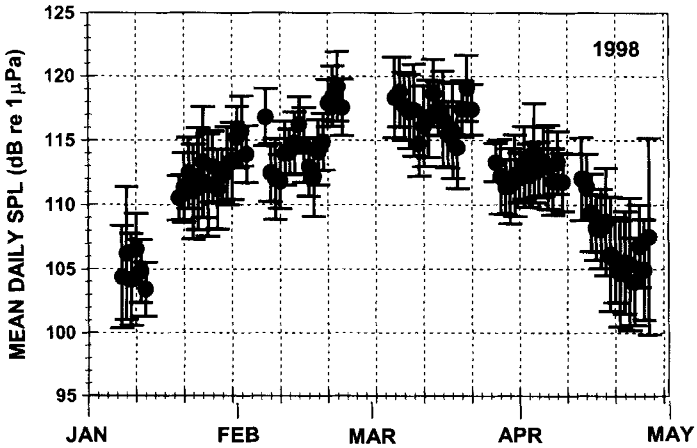

Figure 2. Mean and standard deviation of daily received sound pressure level in dB as function of time. Each data point represents 5,760 one-sec measure of rms sound pressure level.

interval of four minutes, to any number of data files. The data could also be separated in specific time intervals during a day. The second program determined the ⅓-octave band spectra of the data by computing the Fourier transform of the data in blocks of 2,048 points. A Hanning window (Brigham, 1988) was applied to the data before the fast Fourier transform was computed. As with the first program, the ⅓-octave band program analyzed data in a number of ways, from determining the average and standard deviation in each ⅓-octave band for a single file, a number of files, over specific time periods, and in whatever manner desired to consolidate or separate the data.

Results

Data were collected for 85 d between 7 January and 28 April 1998. The mean daily root mean square (rms) sound pressure levels (SPL) from 7 January to 28 April are shown in Figure 2. The rms SPL was calculated using the equation (Spiegel 1961)

$$\text{SPL} = 20 \log_{10} \sqrt{\left(\frac{1}{T} \int_0^T p^2(t)\, dt\right)} \approx 20 \log_{10} \sqrt{\left(\frac{1}{N} \sum_{i=1}^{N} p_i^2\right)} \qquad (1)$$

where $p(t)$ is the acoustic pressure, p_i is the digitized version of $p(t)$, T is the duration over which the rms values was calculated, and N is the number of points over which the summation was taken. Each 4-min sampling period was divided into 1-sec blocks so that T = 1 sec and N = 240 points. The values plotted in the figure are for the mean and standard deviation of the SPL given in dB and were presented in this manner so that the standard deviations would be symmetrical about the mean. In early January the SPL was relatively low, varying between 103 and 107 dB re 1 µPa. The mean SPL gradually rose

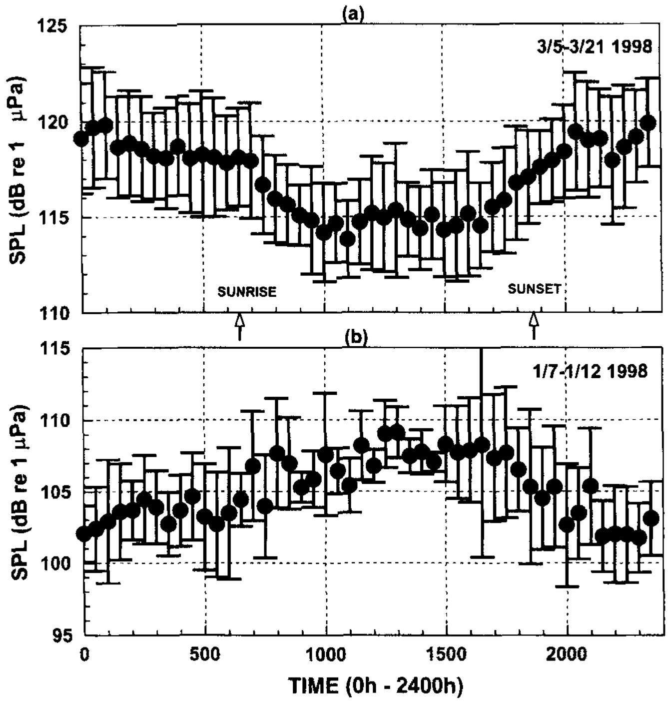

Figure 3. Diurnal variation of received sounds for 5–21 March and 7–12 January 1998. Mean and standard deviation of received SPL in dB plotted. Each point represents 4,080 one-sec measure of received rms SPL for 5–21 March period and 1,200 one-sec measure for 7–12 January period.

after the second week of January into a broad peak from about the last week in February until the third week of March with mean SPL varying between about 114 and 119 dB. From the end of the third week of March, the mean SPL decreased steadily until the levels during the third week of April were similar to the levels during the early part of January. The standard deviations were very similar from day to day, suggesting that the amount of variation in the SPL was relatively uniform. There were two multiday gaps in the data (14–18 January and 25 February–5 March). One was caused by battery problems and the other by rough weather which made it difficult to safely deploy the CAP.

The diurnal variation of the recorded signals during the period between 5–21 March, representing a period of high recorded sound levels, is shown in Figure 3a. This graph can be contrasted with the diurnal variation of sounds measured 1–12 January, a period of low recorded sound levels. Figure 3a clearly shows higher sound levels at night than during the day. The SPL began to rise about 1730, about an hour before sunset, reaching a peak close to midnight and then began to decrease about 0730, about an hour after sunrise. Sunrise occurred at about 0630 and sunset at about 1845. The difference between the SPL at 0600 and at 0800 was significantly different at the 0.01

level (2 tailed *t*-test). Similarly, the SPLs at 1700 and at 1900 were significantly different at the 0.01 level (2 tailed *t*-test). The averaged nighttime SPL from 1900 to 0700 was 118.5 ± 2.7 dB compared to 114.7 ± 2.5 dB for the averaged daytime SPL between 0900 and 1700. The nighttime and daytime SPLs were also significantly different at the 0.01 level (2 tailed *t*-test). Minimum SPL was recorded between 1000 and 1600.

The diurnal variation during the 7–12 January time period showed an opposite trend. Lower levels of sounds were measured during the night between 2100 and 0600 with a minimum at midnight and a peak at noon. The higher day and lower night SPL may be attributed to human activities such as boat traffic close to shore and to other biological sounds such as snapping shrimp. The minimum in the sound levels during the 5–21 March period was higher than the maximum during the 7–12 January period, suggesting that the contribution of humpback whale chorusing sounds to the overall noise or sound environment was relatively small during the 7–12 January period. The data from the 13–27 April deployment also had relatively low SPLs (Fig. 1) and a similar diurnal pattern as the data from the first deployment (7–12 January period).

In order to gain a better understanding of the noon peak during the 7–12 January period, spectrograms for the midnight recording session on 1 March were computed and compared with the spectrogram for the noon period on 7 January. The spectrogram for the midnight recording session is shown in Figure 4a and for the noon session in Figure 4b. The midnight spectrogram consisted mainly of humpback whale chorusing sounds (based on subjective aural analysis) and showed several broad peaks; one between 100 and 150 Hz, another between 250 and 350 Hz and a third between 600 and 650 Hz. The band between 600 and 650 Hz contained some signals that were second harmonics of the signals in the lower band, but there were also many other signals in the higher band that were not harmonics. This could be seen by expanding the time axis to obtain a more detailed look at the spectrogram. The noon spectrogram was devoid of humpback whale choruses but contained many lines or tonal sounds which may be attributed to boat engine and propeller noise.

Examples of the ⅓-octave band spectrum for data collected early in the season (7–12 January) and near the peak (5–21 March) are shown in Figure 5. The spectrum near the peak of the season had higher SPL levels, and the mean values varied from a low of about 79 dB to a high of 109 dB, a span of 30 dB. The 5–21 March spectrum also showed a distinct peak at approximately 315 Hz with another peak at 630 Hz, which could be a second harmonic of the first peak. In contrast, the spectrum for the 7–12 January data is relatively flat with mean SPL values varying from a low of 76 to a high of 95 dB, a 19-dB-amplitude span. The 7 January spectrum did not exhibit any specific peak. The mean SPLs for both spectra were similar for frequencies below approximately 80 Hz, suggesting that the chorusing sounds began to contribute to the total noise in the environment at frequencies greater than approximately 80 Hz. Finally, the ⅓-octave band results indicated that

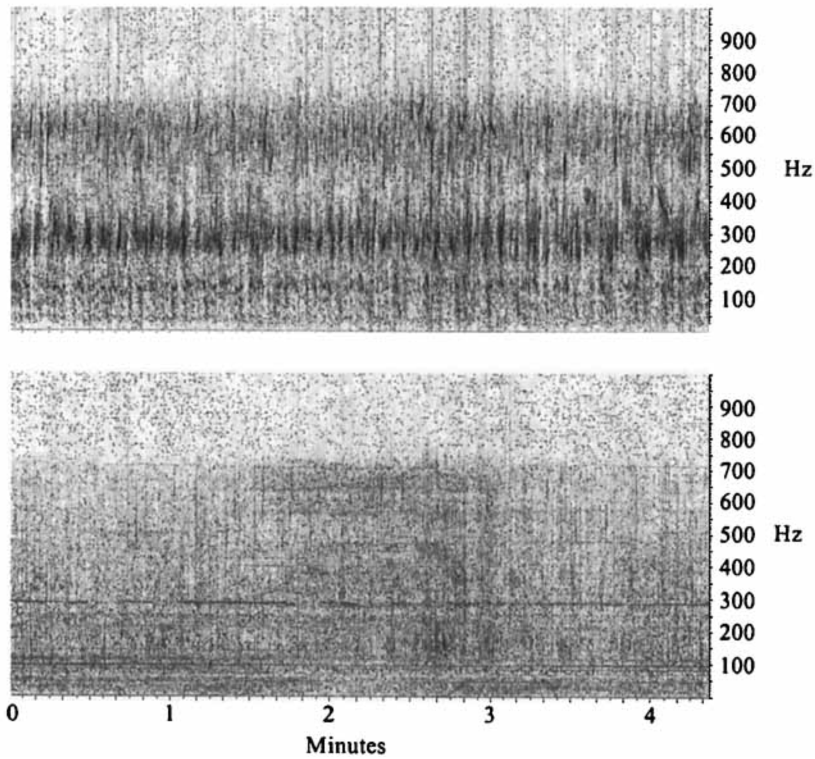

Figure 4. Spectrograms of recorded sounds (top) midnight of 5 March and (bottom) noon of 7 January 1998.

the amount of fluctuation in the measured sound levels in January was almost twice as much as for the sounds measured in March.

Discussion

The results in Figure 2 showing the change of the SPL with time throughout the winter humpback whale season are similar to the results obtained by Thompson and Friedl (1982) with the major differences being the calibrated nature of our measurements and the location of the hydrophones. The peak in the SPL towards the end of February to mid-March corresponds well with the prevailing understanding that the population of humpback whales in Hawaii tends to peak between mid-February and mid-March (Herman *et al.* 1980, Mobley *et al.* 1999). The data also correspond well with the results of aerial surveys of humpback whales performed by the marine mammal research component of the ATOC (Acoustic Thermometry of Ocean Climate) program that are shown in Figure 6 (Mobley *et al.* 1999). The greatest number of humpback whale sightings was on 7 March. Although the aerial survey results are consistent with our acoustic data, the long intervals between surveys makes a more definitive comparison impossible.

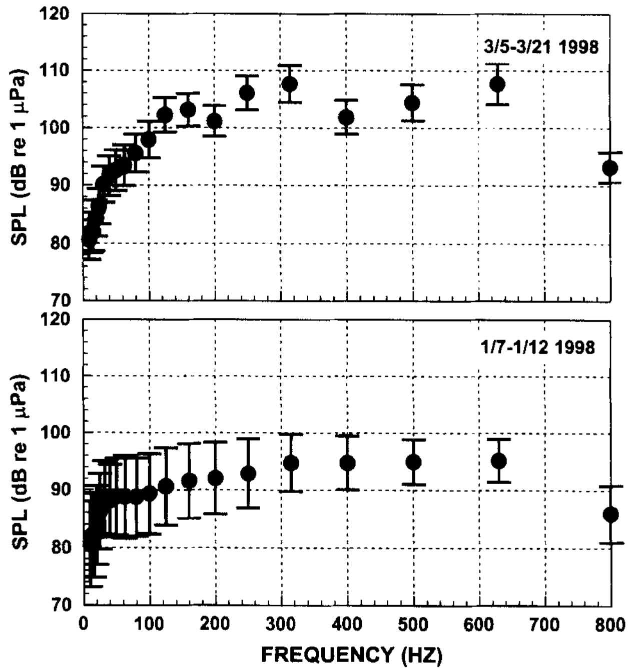

Figure 5. One-third-octave band spectra of received sounds for 5–21 March and 7–12 January 1998. Mean and standard deviation of received SPL in dB are plotted.

The seasonal peak in the SPL towards the end of February–mid-March could be caused by (1) a larger number of singers moving into the vicinity of the CAP, (2) singers emitting louder sounds, or (3) singers moving closer to shore. We believe that the seasonal and diurnal changes in sound pressure levels primarily reflect changes in received levels of chorusing humpback whales based on the following arguments: (1) subjective aural analysis throughout the

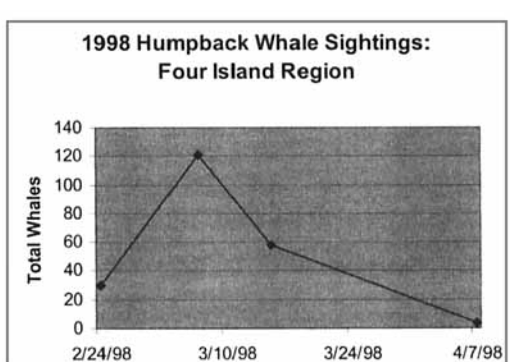

Figure 6. Results of aerial survey for humpback whales from the marine mammal research phase of the ATOC program.

period revealed that the signals were dominated by multiple singing whales, (2) the overall changes in sound pressure levels closely tracked the influx of whales into the area based on the aerial survey results of Figure 6, and (3) the recorded signals showed peak frequencies (*ca.* 100, 300, and 600 Hz) consistent with past descriptions of humpback whale songs (Payne and Payne 1985).

The late-February–early-March peak in SPL is not only consistent with previous reports of peaks in pod membership changes (Mobley and Herman 1985), it is also consistent with timing of aggressive encounters (Baker and Herman 1984). Both set of behaviors presumably relate to reproductive success on the wintering grounds. If males are singing in order to enhance their reproductive success (Tyack 1981, Helweg *et al.* 1992) it would be adaptive for peaks in singing activity to coincide with peak numbers of ovulating females. Nishiwaki (1959), reporting on North Pacific humpback whales harvested in the Ryukyuan wintering grounds, found maximum numbers of ovulating females between early January and late February, a period largely overlapping with the increases in SPL that we observed.

The levels of the humpback choruses measured by Au and Green (2000) on 9 March 1996 were about 4–5 dB higher than the levels indicated in Figure 2. The peak in their ⅓-octave band spectra at 315 Hz was also much sharper than the peak in Figure 5. The differences in the spectra may be due to differences in sound propagation. Au and Green (2000) were about a mile farther off shore and their hydrophone was close to mid-depth, whereas in this study the hydrophone was anchored to a cement block on the bottom. Nevertheless, the results of both studies indicated peaks at 315 and 630 Hz in the spectra of the humpback whale chorusing sounds. The difference in levels may also be attributed to differences in propagation and perhaps to the number of singing whales.

The results in Figure 2 suggest that a single hydrophone at a fixed location can be used to obtain a relative measure of the number of singers in a given area throughout the winter season and from year to year. If the ratio of the number of singers to total number of whales is relatively constant, then estimates of the relative abundance of humpback whales can also be made from acoustic monitoring. However, the notion of using a single hydrophone could be strengthened by performing a simultaneous acoustic and visual observation program in the same area of the ocean. Simultaneous observations could provide further "ground truthing" of the acoustic monitoring technique (*cf.* Clark and Fristrup 1997, Fristrup and Clark 1997).

A single hydrophone at one location could also be used to make estimates of the absolute number of singers in an area if additional information could be obtained. Besides the three alternatives mentioned in the beginning of this section, the SPL measured by a hydrophone for a given location will also depend on the propagation condition pertaining to a specific body of water. Important information can be obtained by performing some type of localization measurements so that the number and location of singing whales can be determined for a specific area and at a specific time and the results compared with the measured SPL of a single monitoring hydrophone. The localization measurement would need to be done only during a short period of approximately several days so that the propagation conditions and the number of singing whales could be related to the single monitoring hydrophone results. Determining the number of singing whales and their locations could be done with a horizontal array of hydrophones or by having two or three directional hydrophones that can sweep in azimuth so that the azimuthal positions of a singing whale can be encoded by each directional hydrophone. Then the location of the singers could be determined by a simple triangulation technique.

The diurnal variations in the received SPL in Figure 3a seem to be initiated at sunrise and sunset. Diurnal variations could be observed only when the levels of the chorusing sounds increased above approximately 110 dB and dominated the other sources of ambient noise. For the time period associated with Figure 3a, sunrise occurred at approximately 0630 and sunset at about 1845 The highest SPLs were recorded at night followed by a decrease at about 0700 The lowest SPL were recorded during the day and the SPL began to increase at about 1630 and reached the same level as the 0700 measurement by 1900. It is not clear why the levels were louder at night, but the data suggest that the variations were caused either by individual whales singing louder at night, more whales singing at night, or whales moving closer to shore (and to the CAP) at night. In order to investigate these two possibilities, some type of acoustic localization must be performed so that the location of each singer can be determined.

In light of past claims of the association of singing with reproduction among humpbacks (Tyack 1981, Helweg *et al.* 1992), a likely interpretation is that singing may be just one of several alternate strategies available to males interested in mating (Frankel 1994). Assuming that song indeed functions primarily as a sexual advertisement, the significantly higher levels of singing recorded at night may provide an important clue regarding the conditions and constraints under which different male mating strategies are favored. More whales are evidently singing at night, suggesting that fewer males are engaging in direct competition for females at this time. This further suggests that competitive group formation occurs primarily during the day, and that daylight and vision play key roles in such intrasexual interactions. In the more constraining environment of darkness, males may switch to advertisement as the primary mating strategy. During the day, when visual cues are possible, males may choose to compete with each other directly through physical aggression, which has been observed in the context of surface-active groups (Baker and Herman 1984, Clapham *et al.* 1992). At night, acoustic communication (singing) becomes the sole alternate strategy. This explanation assumes that the increased SPLs at night represent increased numbers of singing whales.

McCauley *et al.* (1996) in studying the impact of vessel noise on humpback whales in Hervey Bay, Queensland, Australia, found a similar diurnal variation in singing at a particular location in Hervey Bay, where whale songs were recorded in 90% of all samples taken. The data were analyzed by an observer scoring the number of singers and relative loudness. There was a low point in singing during the middle of the day with more singing at night. From 923 samples, each 41 sec in duration, taken approximately 15 min apart over a 10-d period, they found a minimum number of singers between 1110 and noon and a maximum at about 1800. This finding is additionally supported by observations in the West Indies, where there appear to be more humpback whales singing at night.[1]

The diurnal variation we observed was opposite to that observed off the island of Kauai, Hawaii (Helweg 1989, Helweg and Herman 1994). Helweg (1989) estimated the number of singers by having an observer listen to tape recordings and counting them (choruses were considered as a single whale). Helweg and Herman (1994) reported that the number of singing whales did not vary with time of day. They further concluded that "the lack of a diel rhythm in the number of singers suggests that song is not directly involved in physical competition among males." The data were obtained with a bottom-mounted hydrophone located at a depth of about 700 m in mid-channel between the Islands of Kauai and Niihau, about 10–14 mi offshore (Helweg 1989, Helweg and Herman 1994). Differences in methodology, distance off shore and water depth, as well as possible regional differences, may contribute to the discrepancies between our results. The sounds we measured were almost totally choruses, whereas in deeper offshore waters individual singing whales can be recorded. Aerial surveys by Mobley *et al.* (1999) suggested that most humpback whales around the Hawaiian Islands are found where the bottom depth is less than 100 fathoms (182 m). Therefore, the apparent lack of a diurnal variation in humpback whale singing off Kauai may also be explained by the a low number of humpback whales in mid-channel, too few to precipitate much direct intrasexual competition.

Diurnal variations in sound production by odontocetes have been reported by a number of investigators. Powell (1966) found peaks at sunrise and sunset, and Moore and Ridgway (1996) found minimum sound production between midnight and 0400 for captive Atlantic bottlenose dolphins (*Tursiops truncatus*). Moore and Ridgway (1996) also found minimum sound production at 2300–0700 and 1000–1100 for captive common dolphins (*Delphinus delphis*). Goold (2000) found a peak in sound production of wild common dolphins off the West Wales coast of the British Isles between 2100 and midnight, with a minimum between noon and 1500. Higher sound production at night has been reported for striped dolphins (*Stenella coeruleoalba*) in the Mediterranean Sea (Notarbartolo di Sciara and Gordon 1997), and for pantropical spotted dolphins (*S. attenuata*) and the pelagic dolphins in the Gulf of Mexico (Stienessen 1998).

It is difficult to relate the diurnal pattern of sound production in odontocetes with that in humpback whales. Sound-production patterns of captive dolphins can be greatly influenced by activities around the animals' enclosures and by regular daily feeding routines (Powell 1966). The high levels of sound production at night for wild dolphins are often associated with feeding (No-

[1] Personal communication from P. J. Clapham, Northwest Fisheries Science Center, Woods Hole, MA 02543, December, 1999.

tarbartolo di Sciara and Gordon 1997, Goold 2000). Since humpback whales apparently do not feed during their winter stay at lower latitudes, their song production should not have any association with feeding behavior.

Conclusions

Singing humpback whales contribute a significant amount of sound to the acoustic environment along the west coast of Maui from mid-January to mid-April. During this time period, the choruses of humpback whales are essentially continuous and are the most dominant source of steady long-duration noise. The high level of chorusing could be used to monitor and estimate the relative abundance of male humpback whales in any given locale. Estimates of absolute numbers may be possible by monitoring a single hydrophone if more information about propagation conditions and the behavior of whales in a particular locale can also be determined. It would seem reasonable to consider having hydrophones located at vital spots off each island in the Hawaiian chain, so that a gross estimate of the total number of humpback whales wintering in Hawaiian waters could be obtained. Such a system would probably provide a more accurate estimate of the number of whales than visual observations. However, such a monitoring technique would require a better estimate of the ratio of singers to non-singing whales and a better understanding of the relationship between received sound levels and the actual number of singers. It would also be important to measure humpback singing simultaneously several miles offshore and inshore in the same body of water in order to obtain a better appreciation of how chorusing sounds propagate into inshore waters.

Acknowledgments

The authors would like to acknowledge and express their appreciation to Dr. Burney Le Boeuf of the University of California, Santa Cruz, for loaning us the CAP, to Eric Brown of the University of Hawaii for regularly placing the CAP at its underwater location and retrieving it, to Dr. Peter Tyack of Woods Hole Oceanographic Institute for the loan of a Macintosh computer with a Nu-bus, and to the University of Hawaii Research Council for its financial support. Our thanks to Mr. William Friedl of the National Defense Center of Excellence in Ocean Sciences, Dr. Adam Frankel of the Bioacoustics Research Program, Cornell University, and Dr. David Helweg of the Space Warfare Systems Command for their comments on this manuscript. Finally, the authors would also like to express their appreciation to one of the reviewers, Dr. Phillip Clapham, for his thoughtful and helpful comments and suggestions. This is HIMB contribution number 1092.

Literature Cited

Au, W. W. L., and M. Green. 2000. Acoustic interaction of humpback whales and whale watching boats. Marine Environmental Research. In press.

Baker, C. S., and L. M. Herman. 1984. Aggressive behavior between humpback whales (*Megaptera novaeanglaie*) wintering in Hawaiian waters. Canadian Journal of Zoology 62:1922–1937.

BRIGHAM, E. O. 1988. The fast Fourier transform and its application. Prentice Hall, Englewood Cliffs, NJ.

BURGESS, W. C., P. L. TYACK, B. J. LE BOOEUF AND D. P. COSTA. 1998. A programmable acoustic recording tag and first results from free-ranging northern elephant seals. Deep-Sea Research II 45:1327–1351.

CHAPHAM, P. J., AND D. K. MATTILA. 1990. Humpback whale songs as indicators of migration routes. Marine Mammal Science 6:155–160.

CLAPHAM, P. J., P. J. PALSBØLL, D. K. MATTILA AND O. VASQUEZ. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour 122:182–194.

CLARK, C. W., AND K. M. FRISTRUP. 1997. Whales '95: A combined visual and acoustic survey of blue and fin whales off southern California. Report of the International Whaling Commission 47:583–600.

FRANKEL, A. S. 1994. Acoustic and visual tracking reveals distribution, song variability and social roles of humpback whales in Hawaiian waters. Doctoral dissertation, University of Hawaii, Manoa. 142 pp.

FRANKEL, A. S., C. W. CLARK, L. M. HERMAN AND C. M. GABRIELE. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae,* off Hawaii, determined using acoustic and visual techniques. Canadian Journal of Zoology 73:1134–1146.

FRISTRUP, K. M., AND C. W. CLARK. 1997. Combining visual and acoustic survey data to enhance density estimation. Report of the International Whaling Commission 47:933–936.

GOOLD, J. C. 2000. A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis.* Marine Mammal Science 16:240–244.

GUINEE, L. N., K. CHU AND E. M. DORSEY. 1983. Changes over time in the songs of known individual humpback whales (*Megaptera novaeanglaie*). Pages 59–80 *in* R. Payne, ed. Communication and behavior of whales. Westview Press, Boulder, CO.

HELWEG, D. A. 1989. Daily and seasonal patterns of behavior and abundance of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. M.A. thesis, University of Hawaii at Manoa, Honolulu, HI.

HELWEG, D. A., AND L. M. HERMAN. 1994. Diurnal Patterns of behavior and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Ethology 98:298–311.

HELWEG, D. A., A. S. FRANKEL, J. R. MOBLEY JR. AND L. M. HERMAN. 1992. Humpback whale song: Our current understanding. Pages 459–481 *in* J. A. Thomas, R. A. Kastelein and A. Ya. Supin, eds. Sensory abilities of aquatic mammals. Plenum Press, New York NY.

HERMAN, L. M., P. H. FORESTELL AND R. A. ANTINOJA. 1980. The 1976/77 migration of humpback whales into Hawaiian waters: Composite description. Report MMC-77/19 to U.S. Marine Mammal Commission. 55 pp. Available from Marine Mammal Commission, 4340 East-West Highway, Bethesda, MD 20814, U.S.A.

LEVENSON, C. 1972. Characteristics of sound produced by humpback whales (*Megaptera novaeangliae*). NAVOCEANO Technical Note NO. 7700-6-72. Naval Oceanographic Office, Washington, DC. 41 pp.

MCCAULEY, R. D., D. H. CATO AND A. F. JEFFERY. 1996. A study of the impacts of vessel noise on humpback whales in Hervey Bay. Report for Queensland Department of Environment and Heritage, James Cook University Marine Biology Department. 137 pp. Available from Centre for Marine Science and Technology, Curtin University, GPO Box U1987, Perth 6845, Australia.

MCSWEENEY, D. J., K. C. CHU, W. F. DOLPHIN AND L. N. GUINEE. 1989. North Pacific humpback whale songs: A comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. Marine Mammal Science 5:139–148.

MATTILA, D. K., L. N. GUINEE AND C. A. MAYO. 1987. Humpback whale songs on a North Atlantic feeding ground. Journal of Mammalogy 68:880–883.

MOBLEY, JR., J. R., AND L. H. HERMAN. 1985. Transience of social affiliations among hump-back whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. Canandian Journal of Zoology 63:762–772.

MOBLEY, JR., J. R., R. A. GROTEFENDT, P. H. FORESTELL AND A. S. FRANKEL. 1999. Results of aerial surveys of marine mammals in the major Hawaiian Islands (1993–98): Final report to the Acoustic Thermometry of Ocean Climate Marine Mammal Research Program (ATOC MMRP). 39 pp. Available from Social Sciences, University of Hawaii-West O'ahu, 96-129 Ala Ike, Pearl City, HI 95782, U.S.A.

MOORE, S. E., AND S. H. RIDGWAY. 1996. Patterns of dolphin sound production and ovulation. Aquatic Mammals 22.3:175–184.

NISHIWAKI, M. 1959. Humpback whales in Ryukyuan waters. Scientific Reports of the Whales Research Institute, Tokyo 14:49–86.

NOTARBARTOLO DI SCIARA, G., AND J. C. D. GORDON. 1997. Bioacoustics: A Tool for the conservation of cetaceans in the Mediterranean Sea. Marine and Freshwater Behaviour and Physiology 30:1215–1246.

PAYNE, K., AND R. PAYNE. 1985. Large scale changes over 19 years in songs of humpback whales in Bermuda. Zeitschrift für Tierpsychologie 68:89–114.

PAYNE, K., P. TYACK AND R. PAYNE. 1983. Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. Pages 333–358 *in* R. Payne, ed. Communication and behavior of whales. Westview Press, Boulder, CO.

PAYNE, R. S., AND S. MCVAY. 1971. Songs of humpback whales. Science 173:585–597.

POWELL, B. A. 1966. Periodicity of vocal activity of captive Atlantic bottlenose dolphins: *Tursiops truncatus.* Bulletin of the Southern California Academy of Sciences 65:237–244.

SPIEGEL, M. R. 1961. Theory and problems of statistics. McGraw Hill, New York, NY.

STIENESSEN, S. C. 1998. Diel, seasonal and species specific trends in vocalization of dolphins in the Gulf of Mexico. M.Sc. thesis, Texas A&M University. 73 pp.

THOMPSON, P. O., AND W. A. FRIEDL. 1982. A long term study of low frequency sounds from several species of whales off Oahu, Hawaii. Cetology 45:1–19.

TYACK, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral and Ecological Sociobiology 8:105–116.

WILSON, E. O. 1975. Sociobiology: The new synthesis. Belknap Press, Cambridge, MA.

WINN, H. E., AND L. K. WINN. 1978. The song of the humpback whale, *Megaptera novaeangliae,* in the West Indies. Marine Biology 47:97–114.

Received: 7 June 1999
Accepted: 18 January 2000