Population size of humpback whale, *Megaptera novaeangliae*, in waters off the Pacific coast of Mexico

Jorge Urbán R.
Departamento de Biología Marina
Universidad Autónoma de Baja California Sur
Ap. Post 19-B
La Paz, B.C.S. 23081 México
E-mail: jurban@calafia.uabcs.mx

Carlos Alvarez F.

Mario Salinas Z.
Laboratorio de Mamíferos Marinos
Universidad Nacional Autónoma de México
Ap. Post 70-572
México, D.F. 04510 México

Jeff Jacobsen
P.O. Box 4492
Arcata, California 95521

Kenneth C. Balcomb III
Center for Whale Research
1359 Smugglers Cove Road
Friday Harbor, Washington 98250

Armando Jaramillo L.
Departamento de Biología Marina
Universidad Autónoma de Baja California Sur
Ap. Post 19-B
La Paz, B.C.S. 23081 México

Paloma Ladrón de Guevara P.

Anelio Aguayo L.
Laboratorio de Mamíferos Marinos
Universidad Nacional Autónoma de México
Ap. Post 70-572, México, D.F. 04510 México

Abstract.–The humpback whale (*Megaptera novaeangliae)* is a cosmopolitan species whose stocks were drastically decreased by commercial whaling practices prior to 1967. The North Pacific population was estimated to be between 15,000 and 20,000 animals before the practice of whaling. At the time of the commencement of its international protection in 1967, this population may have been reduced to fewer than 1000 individuals. The Pacific coast of Mexico and the Revillagigedo Archipelago constitute one of the main breeding and calving areas for North Pacific humpback whales. The objective of this paper is to present an estimation of abundance of humpback whales in this region based on photographic identification of individual animals. Estimates of population size were obtained by using mark and recapture models for both closed and open populations, with each year representing a capture occasion. A total of 1184 humpback whales were identified in Mexican waters between 1986 and 1993. The best estimates of population size for the Mexican stocks were those provided by the modified Jolly-Seber method: 1813 (95% CI: 918–2505) for the coastal stock in 1992, and 914 (95% CI: 590–1193) for the Revillagigedo stock in 1991.

Humpback whales, *Megaptera novaeangliae*, make seasonal migrations between low-latitude wintering areas used for mating and calving and high-latitude feeding areas. The general distribution of feeding areas in the North Pacific covers coastal waters in the western North Pacific from northern Japan throughout the Bering Sea and in the eastern North Pacific as far south as southern California. During the winter breeding season, these whales congregate in three geographically isolated tropical areas: the Ryukyuan, Bonin, and Mariana Islands south of Japan; the islands of the Hawaiian Archipelago; and the Pacific coast of Mexico and the Revillagigedo Archipelago (Rice, 1974; Johnson and Wolman, 1984).

Manuscript accepted 15 January 1999.
Fish. Bull. 97:1017–1024 (1999).

Humpback whales have been listed as endangered since severe reduction of all stocks worldwide by commercial exploitation (Rice, 1974; Gambel, 1976). The number of these whales were estimated to be between 15,000 and 20,000 animals before whaling depleted them during the first half of the 20th century; at the time of its international protection in 1967 this population may have been reduced to fewer than 1000 individuals (Rice, 1974, 1978). However, the reliability of these figures is unknown.

The extent of the recovery in the North Pacific population over the last 25 years is debatable. Estimates of abundance with mark and recapture techniques based upon photo-identification data have been made for different areas of this ocean, but there has been much debate regarding the reliability of such estimates (Darling et al., 1983; Baker et al., 1986; Darling and Morowitz, 1986; Baker and Herman, 1987; Alvarez et al., 1990; Calambokidis et al., 1990; Cerchio, 1998; Calambokidis et al.[1]). There is currently insufficient evidence to assess whether a significant change in abundance has occurred since whaling ceased.

Three main wintering aggregations of humpback whales are recognized off the Pacific coast of Mexico: the Baja California Peninsula; the mainland coast of Mexico (including, Isabel Island, Tres Marias Islands, and the mainland coast); and the Revillagigedo Archipelago (including Socorro, San Benedicto, Roca Partida, and Clarion Islands) (Rice, 1979; Urbán y Aguayo, 1987).

The comparison of photo-identified humpback whales in these wintering grounds showed that there was a greater affinity between whales off Baja California and those off the mainland coast of Mexico than those off either Baja California or the mainland coast and those off the Revillagigedo Archipelago (Urbán et al., 1989; Ladrón de Guevara et al., 1993; Jaramillo, 1995) (Table 1). From these results, two different population units of humpback whales during winter in Mexican waters were previously proposed: the coastal Stock (including Baja California and mainland coast of Mexico), and the Revillagigedo stock (Alvarez et al., 1990; Urbán et al.[2]) (Fig. 1).

Table 1

Matches (above the diagonal) and interchange index[1] (below the diagonal) among the three main wintering aggregations in the Mexican Pacific. Sample size in parentheses.

	Baja California Peninsula (471)	Mainland coast of Mexico (383)	Revillagigedo Archipelago (450)
Baja California Peninsula	—	64	20
Mainland coast of Mexico	0.38	—	23
Revillagigedo Archipelago	0.12	0.18	—

[1] Index of interchange.
This index quantify the degree of interchange among two samples (among regions) that accounted for sample size:

$$\textit{Index of interchange} = (m_{12}/(n_1 \times n_2)) \times 1000,$$

where n_1 = whales identified (captured) in sample 1;
n_2 = whales identified in sample 2; and
m_2 = captured whales from sample 1 recaptured in sample 2.

(see Baker et al. 1985; Cerchio et al., 1998).

This division of winter aggregations is also supported by mitochondrial DNA lineage analyses (Medrano-Gonzalez et al., 1994, 1995a, 1995b); however, because the waters off California, Oregon and Washington are the primary feeding destination of the whales observed in Baja California and the mainland coast, the migratory destination of the whales seen around the Revillagigedo Islands is still unknown (Urbán et al. 1987; Urbán et al.[3]).

Previous estimates of humpback whale abundance in Mexican waters are the following: 500–600 for Socorro Is. (Campos, 1987); 200–400 for Isabel Is. (Alvarez, 1987); 600–700 for the mainland coast (Alvarez et al., 1990); and 1200–1700 for all the Mexican Pacific (Urbán et al., 1989). However, it is recognized that these estimates were based on limited data and on assumptions that generally were not tested.

In our study we present an analysis of photographic data obtained during the winter breeding and calving seasons from 1983 to 1993 in the different assembly areas of the Mexican Pacific. We use this analysis to calculate reliable independent estimates of abundance of humpback whales for the coastal and the Revillagigedo stocks.

[1] Calambokidis, J., G. H. Steiger, J. Straley, T. J. Quinn II, L. M. Herman, S. Cerchio, D. Salden, M. Yagamuchi, F. Sato, J. Urbán R., J. K. Jacobsen, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dahlheim, N. Higashi, S. Uchida, J. K. B. Ford, Y. Miyamura, P. Ladrón de Guevara P., S. A. Mizroch, L. Shlender, K. Rasmussen. 1977. Abundance and population structure of humpback whales in the North Pacific basin. Final Rep. to Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, La Jolla, CA, 72 p.

[2] Urbán R., J., J. C. Salinas V., A. Guillén G., and E. Vázquez M. 1997. La ballena jorobada *Megaptera novaeangliae* en al Península de Baja California Sur, México. Final Report to the Biodiversity National Commission (CONABIO). Contract H035, 41 p.

[3] Urbán R., J., A. Jaramillo L., A. Aguayo L., Paloma Ladrón de Guevara P., M. Salinas Z., C. Alvarez F., L. Medrano G., J. Jacobsen, K. C. Balcomb, D. E. Claridge, J. Calambokidis, G. H. Steiger, J. M. Straley, O von Ziegesar, S. Mizroch, .M. Dahlheim, J. M. Waite, J. D. Darling, and C. S. Baker. 19xx. Migratory destination of the Mexican Pacific humpback whales. Universidad Autónoma de Baja California Sur, Ap. Post. 19-B, La Paz, Baja California Sur, Mexico.

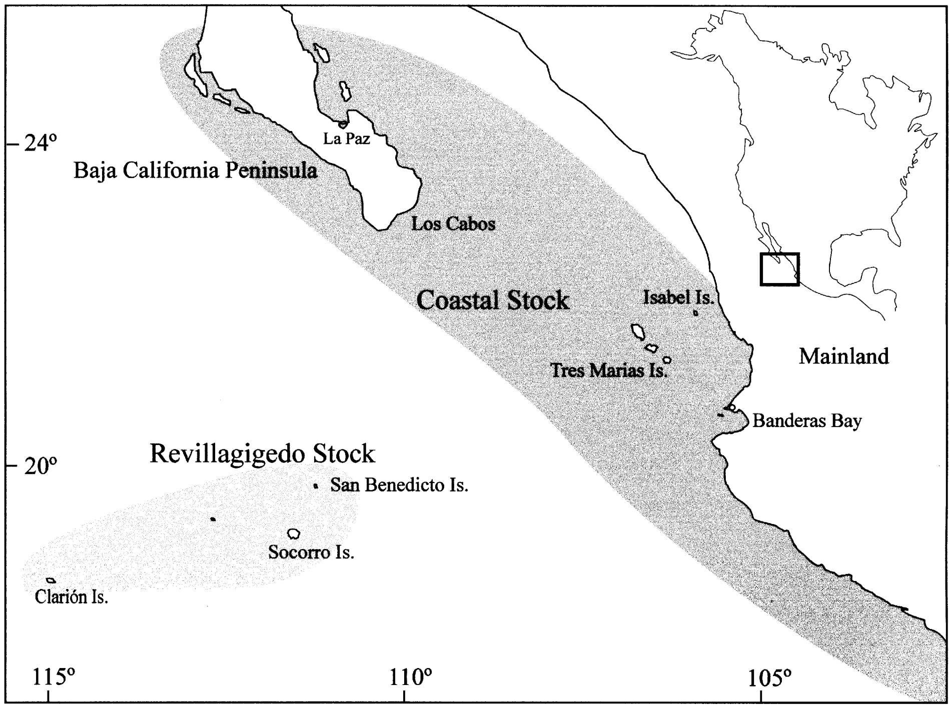

Figure 1

Study area showing, by shading, the distribution of the Revillagigedo and coastal stocks.

Materials and methods

Individual identification

Humpback whales were individually identified from photographs taken by different institutions from approximately December to March, along the mainland coast of Mexico (1983–92), from mid-January to March in Baja California (1987–93), and at the Revillagigedo Archipelago (1986–92) (Table 2).

Although photo-identification data have been available for the coastal stock since 1983 and for the Revillagigedo stock since 1985, efforts before 1986 were limited in time and space, and also lacked continuity. Beginning in 1986, surveys were conducted off Socorro Island for the Revillagigedo stock, and near San José del Cabo or the mainland coast (or both) for the coastal stock. No data were obtained for either Revillagigedo or the mainland in 1993.

The whales were identified individually through photographs of the black and white pigmentation patterns on the ventral surface of their flukes (see Katona and Whitehead, 1981). Photographs were obtained with 35-mm cameras equipped with 200–300 mm lenses. Although the film used varied by region and season, most photographs were taken with black and white Kodak Tmax 400 ISO pushed to 1600 ISO, ensuring shutter speeds as high as 1/1000 of a second.

On the basis of focus, angle, and light conditions, all fluke photographs were judged to be either good, fair, or of poor quality; only photos in the first two categories were included in this study. Within these quality levels, the whales showed at least 50% of each fluke at a sufficiently vertical angle to allow the shape of the trailing edge to be distinguished. Calves were excluded from the analysis owing to their tendency to show changes in pigmentation patterns during the first year of life (Carlson et al., 1990). Selected photographs were compared visually by at least three persons with experience in matching humpback whales flukes photographs from both Universidad Nacional Autonoma de Mexico and Universidad Autonoma de Baja California Sur.

Abundance estimation

Abundance estimates were obtained by using an eight-year period for the coastal stock, from 1986 to 1993, and a seven-year period for the Revillagigedo stock, from 1986 to 1992.

Estimates of population size were obtained by using mark and recapture models for both closed and open populations, with each year representing a capture occasion. The time span of the study was seven years; consequently, although calves were not included in the analysis, it is inevitable that additions

Table 2

Study periods and data sources for each of the regions. UNAM = Universidad Nacional Autonoma de Mexico; UABCS = Universidad Autonoma de Baja California Sur; CWR = Center for Whale Research; CS =Cousteau Society.

Region	Season	Study period	Source
	1986	20 Dec 85–4 Mar 86	UNAM
	1987	25 Dec 86–20 Mar 87	UNAM
	1988	22 Jan 88–8 Feb 88	UNAM
	1989	24 Jan 89–5 Mar 89	UNAM
	1990	25 Nov 89–21 Mar 90	CWR, UABCS, UNAM
	1991	28 Nov 90–26 Feb 91	UNAM
	1992	26 Dec 91–6 Mar 92	UNAM
Baja California Peninsula	1987	10 Feb 87–5 Mar 87	CWR, UABCS
	1988	6 Feb 88– 8 Mar 88	CWR, UABCS
	1989	23 Jan 89–25 Mar 89	CWR, UABCS
	1990	20 Feb 90–31 Mar 90	CWR, UABCS
	1991	24 Jan 91–23 Mar 91	UABCS
	1992	20 Jan 92–2 Apr 92	UABCS
	1993	15 Jan 93–5 Apr 93	UABCS
Revillagigedo Archipelago	1986	16 Jan 86–20 Feb 86	UNAM
	1987	20 Jan 87–5 Mar 87	UNAM
	1988	1 Feb 88–9 Mar 88	UNAM
	1989	16 Jan 89–7 Mar 89	UNAM
	1990	31 Jan 90–20 Mar 90	UNAM
	1991	15 Jan 91–25 Apr 91	UNAM
	1992	25 Apr 92–7 May 92	UNAM, UABCS, CS

to the population were occurring in the form of animals born in previous years that became identifiable as they grew. Also, some individuals died. Because we would therefore expect to be studying an open population, we chose the Jolly-Seber mark and recapture model. One of the critical assumptions of this method is the highly unlikely condition that all animals have the same capture probabilities at the moment of the sample (Seber, 1982). If heterogeneity in capture probabilities is present, the open population models will underestimate population size to a greater extent than closed population models (Carothers, 1973; Pollock et al., 1990). Given that there was no way to account for such problems with open population models (Hammond, 1986), we decided to use closed population models to test for variations in capture probabilities.

Closed population estimates were obtained and assumptions were tested by using the software program CAPTURE developed by Otis et al. (1978), which included an algorithm to select the appropriate model after the hypothesis testing procedure. The conceptual basis for this selection procedure is a tradeoff between precision and bias. If a simple model, such as the null model M_o in Otis et al. (1978), is used to estimate parameters from data that violates in any way the assumption of equal capture probability, then significant biases are introduced in parameter estimates and sampling variances will be artificially small. On the other hand, if a more complex model is used, such as M_{th} of Otis et al.. (1978), that allows capture probabilities to vary with time and among individuals, biases may be reduced but the sampling variance will be greater than it should be. The selection procedure takes into account the individual goodness-of-fit tests performed for specific models on the data and the confrontation of related models (i.e. where one model is a particular case of a general one). The significance levels for all these tests are combined in a standard discriminant analysis and the resulting statistic is standardized so that its value ranges from 0 to 1, 1 being the score that indicates the appropriate model (Otis et al., 1978).

The basic or null model M_o can be applied to the general case of multiple recaptures in a closed population, where all animals have equal capture probabilities, and where this probability remains constant in time. The model that allows the capture probability to vary in time, simultaneously permitting individuals to have unequal capture probability (Chao et al., 1991: model M_{th} in Otis et al., 1978) was selected for estimation of both stock sizes. In addition, abundance was also estimated for the coastal stock by using the model that only allows relaxation of the requirement for constant capture probability in time (Darroch, 1958: model M_t in Otis et al., 1978). Model M_{th} provides the estimator of population size for a situation where capture probabilities vary in time and among individuals. Model M_t provides the estimate of population size when capture probabilities are the same among individuals but vary in time (Otis et al., 1978).

Outputs from CAPTURE were used only as a "screening technique," as suggested by Menkins and Anderson (1988) to investigate departures from the assumption of equal catchability. The test for population closure within CAPTURE was ignored because its power is low (Otis et al., 1978).

Open population estimation was done through the software program RECAP[4] This program provides estimates of parameters under the basic Jolly-Seber model where all individuals have equal capture probabilities and survivorship, but these were allowed to vary between sampling occasions. Also, it incorporates a modification of the Jolly-Seber model (modified J-S model) that constrains estimates to feasible values, stabilizing them and providing more reliable confidence intervals (Buckland, 1980). Open population estimates were also obtained by using the software program JOLLY described by Pollock et al. (1990). Of particular interest is the goodness-of-fit tests performed for this program to investigate how well our data are explained by the Jolly-Seber model or any of the variants included in the program. The results obtained under such variants were also very useful because they allowed for the estimation of more precise parameters when either capture probabilities or survivorship (or both) were kept constant. Even in the case when the more general Jolly-Seber model was chosen (model A), observation of survivorship estimates under model 2 (temporary trap response model) were useful to look for the amount of transit within the areas occupied by each stock.

Results and discussion

Photo identification

A total of 1184 humpback whales were identified in Mexican waters between 1986 and 1993. Of the total, 733 individuals were observed in the area occupied by the coastal stock, 412 in Revillagigedo, and 39 in both areas (a summary of the number of individuals identified in each area is provided in Table 3).

Table 3

Number of humpback whales identified in Mexican waters from 1986 to 1993.

Region	1986	1987	1988	1989	1990	1991	1992	1993
Coast								
Animals caught	74	71	74	83	218	109	180	92
Newly caught	74	65	61	67	174	91	140	61
Revillagigedo								
Animals caught	26	41	73	106	48	189	36	
Newly caught	26	37	64	86	33	143	23	

Table 4

Estimates of population size (*N*) with closed population models (see "Materials and methods" section for descriptions of the models).

Model	*N*	95% CI	Capture prob. *P*
Coastal stock			
M_o	2039	1728–2194	0.05
M_t[1]	1828	1660–2076	0.06 average
M_{th}[1]	2188	1861–2612	0.05 average
Revillagigedo stock			
M_o	1078	807–1169	0.0687
M_t	874	762–1020	0.084 average
M_{th}[1]	1308	1043–1684	0.057 average

[1] Selected models.

Abundance estimation

The closed population estimators showed that heterogeneity and variations in capture probabilities in time are present in both stocks. However, the confidence intervals built for models M_t and M_{th} overlap to a greater extent in the coastal estimates than in the Revillagigedo estimates, indicating that both models M_{th} and M_t are equally good for the coastal stock (Table 4). These relatively small capture probabilities estimated with the closed models are consistent with a positive bias in the population size estimates because, as will be discussed, the populations were open through the period of study. Therefore, the closed population models were useful in showing that the assumption of equal catchability is not met.

[4] Contact Stephen Buckland, Mathematical Institute, North Haugh, University of St Andrews, St. Andrews, Fife KY169SS, U.K.

Table 5

Estimates of population size (N) with the program JOLLY, model A (general) (see "Materials and methods" section for descriptions of the models).

Year	N	95% CI	Capture prob. P
Coastal stock[1]			
1987	771	119–1424	0.08
1988	484	215–753	0.14
1989	791	382–1220	0.10
1990	1247	682–1811	0.17
1991	1660	610–2712	0.06
1992	1702	488–2917	0.10
Average	1109	793–1425	0.11
Revillagigedo stock[2]			
1987	134	13–256	0.25
1988	367	125–609	0.18
1989	593	288–897	0.17
1990	456	179–733	0.10
1991	1569	–140–3277	0.12
Average	623	268–980	0.16

[1] χ^2 Goodness-of-fit model A x = 5.968 P = 0.8754
χ^2 Goodness-of-fit model 2 x = 1.132 P = 0.8892

[2] χ^2 Goodness-of-fit model A x = 13.23 P = 0.0667
χ^2 Goodness-of-fit model 2 x = 0.448 P = 0.799

Table 6

Estimates of population size (N) with the program RECAP, modified Jolly-Seber model (see "Materials and methods" section for descriptions of the models).

Year	N	95% CI	Capture prob. P
Coastal stock			
1987	822	425–1142	0.09
1988	580	327–931	0.13
1989	825	519–1229	0.10
1990	1120	824–1613	0.19
1991	1813	1168–2686	0.06
1992	1813	918–2505	0.10
Average	1162	889–1406	
Revillagigedo stock			
1987	167	49–484	0.25
1988	414	215–691	0.18
1989	610	388–825	0.17
1990	606	359–891	0.08
1991	914	590–1193	0.21
Average	642	373–677	

The Jolly-Seber analysis indicated that the open population model explained in a better way the data for both Revillagigedo and coastal stocks (Table 5). In the Revillagigedo stock the goodness of fit χ^2 test on model A (general model) did not reject the null hypothesis (P=0.0667), but the result showed that data are better explained (P=0.799) by model 2 (temporary trap response model), assuming that survival rates of newly captured animals differ from those of previously captured animals. In other words, this test indicates that some animals may have moved into the capture site and once captured, they could have left and even re-entered the sampling area. This inference an be supported by the fact that data for this stock were collected only in Socorro Island and that some animals may have a preference for anther island, such as Clarion, far away from the sampling area (Fig. 1). For the coastal stock, the goodness-of-fit χ^2 tests indicate that the model A (P=0.8754) and model 2 (P=0.8892) are almost equally good in explaining the data. Although sampling coverage was wider for this stock, allowing a better collection of photographs for moving animals, this problem still remained, but had a smaller effect on the estimates.

Having accepted that the Jolly-Seber model explained the data well for the two stocks, population-size estimates were obtained with the software program RECAP. Results show that the modified estimator (modified J-S model) provided more stable estimates and narrower and more realistic confidence intervals (Table 6).

Because capture probabilities are larger than those obtained by the closed population methods, and considering that the Jolly-Seber estimates may be negatively biased given heterogeneity, population size are likely overestimated by the closed population methods.

In light of the above arguments, we conclude that the best estimates of population size for the Mexican stocks, using the data at hand, are those provided by the modified Jolly-Seber model of program RECAP. Estimates obtained with closed population methods are not recommended when data are pooled for the whole extension of the study; however, it may be worth obtaining estimates with pairs of years with models testing for heterogeneity and capture probabilities varying with time, although certain information and precision may be sacrificed.

Estimates for each year show an apparent trend towards increase for both stocks. Such a trend was considered an artifact of a reduction in the bias caused by heterogeneity in capture probabilities after sample size increased with time. Consequently, we consider that the best estimates for the stock sizes were those obtained for the last years and are 1813 (95% CI: 918–2505) for the coastal stock in 1992, and 914 (95% CI: 590–1193) for the Revillagigedo stock in 1991.

Acknowledgments

We would like to thank Jeff Laake for valuable advice and fruitful discussions. Judith Zeh, Jay Barlow, Phil Clapham, and two anonymous reviewers provided helpful suggestions for the improvement of the paper. This work was supported by the Dirección General de Investigación Científica y Superación Académica (DGICSA), C88-01-0414 (1988–90), Earthwatch (1988–90), and the Consejo Nacional de Ciencia y Tecnología, CONACyT (1991–92). We worked under the permits of the Instituto Nacional de Ecologia, SEDUE, SEMARNAP.

Literature cited

Alvarez, F. C.
1987. Fotoidentificación del Rorcual jorobado (*Megaptera novaeangliae*, Borowski, 1781), en las aguas adyacentes a Isla Isabel, Nayarit, México (Cetacea: Balaenopteridae). Professional thesis, Facultad de Ciencias, UNAM, 107 p.

Alvarez, C. A., Aguayo L., R. Rueda, and J. Urbán R.
1990. A note on the stock size of humpback whales along the Pacific coast of México. Rep. Int. Whal. Comm. Spec. Issue 12:191–193.

Baker, C. S., and L. M. Herman.
1987. Alternate population estimates of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. Can. J. Zool. 65:2, 818–2,821.

Baker, C. S., L. M. Herman, A. Perry, W. S. Lawton, J. M. Straley, and J. H. Straley.
1985. Population characteristics and migration of summer and late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Mar. Mamm. Sci. 1:304–323.

Baker, C. S., L. M. Herman, A. A. Wolman, H. E. Winn, J. Hall, G. Kaufman, J. Reinke, and J. Ostman.
1986. The migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. Mar. Ecol. Prog. Ser. 31:105–119.

Buckland, S. T.
1980. A modified analysis of the Jolly-Seber capture-recapture model. Biometrics 36:419–435.

Calambokidis, J., J. C. Cubbage, G. H. Steiger, K. C. Balcomb, and P. Bloedel.
1990. Population estimates of humpback whales in the Gulf of the Farallones, California. Rep. Int. Whal. Comm. Spec. Issue 12:343–48.

Campos R., R.
1987. Fotoidentificación y comportamiento del Rorcual jorobado, *Megaptera novaeangliae* (Borowski, 1781), en las aguas adyacentes al Archipiélago de Revillagigedo, México. (Cetacea: Balaenopteridae). Professional thesis, Facultad de Ciencias, UNAM, 134 p.

Carlson, C. A., C. A. Mayo, and H. Whitehead.
1990. Changer in the ventral fluke pattern of the humpback whale, *Megaptera novaeangliae*, and its affect on matching. Rep. Int. Whal. Comm. Spec. Issue 12:105–112.

Carothers, A. D.
1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29:79–100.

Cerchio, S.
1998. Estimates of humpback whale abundance off Kauai, Hawaii, 1989 to 1993: evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. Mar. Ecol. Prog. Ser. 175:23–34.

Cerchio, S., C. M. Gabriele, T. F. Norris, and L. M. Herman.
1998. Movements of humpback whales between Kauai and Hawaii: implications for population structure and abundance estimation in the Hawaiian Islands. Mar. Ecol. Prog. Ser. 175:13–22.

Darling, J. D., K. M. Gibson, and G. K Silber.
1983. Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui, Hawaii, 1977–79. *In* R. Payne (ed.), Communication and behavior of whales, p. 201–22. Westview Press, Boulder.

Darling, J. D., and H. Morowitz.
1986. Census of "Hawaiian" humpback whales (*Megaptera novaeangliae*) by individual identification. Can. J. Zool. 64:105–111.

Gambel, R.
1976. World whale stocks. Mar. Rev. 6:41–53.

Hammond, P. S.
1986. Estimating the size of naturally marked whale population using capture–recapture techniques. Rep. Int. Whal. Comm. Spec. Issue 8:253–282

Jaramillo L., A.
1995. Fotoidentificación del Rorcual jorobado (*Megaptera novaeangliae*, Borowski, 1781), en las aguas adyacentes a Isla Isabel, Nayarit, México. (Cetacea: Balaenopteridae). Professional thesis, Facultad de Ciencias, UNAM, 107 p.

Johnson, J. H., and A. A. Wolman.
1984. The humpback whale, *Megaptera novaeangliae*. Mar. Fish. Rev. 46:30–37.

Katona, S. K., and H. P. Whitehead.
1981. Identifying whales using their natural markings. Polar Rec. 20:439–444.

Ladrón de Guevara, P., J. Urbán R., M. Salinas Z., J. Jacobsen, K. C. Balcomb, A. Jaramillo L., D. Claridge, and A. Aguayo L.
1993. Relationships among winter aggregations of humpback whales, *Megaptera novaeangliae*, in the Mexican Pacific. *In* Abstracts of the XVIII Reunion Internacional para el Estudio de los Mamiferos Marinos, La Paz, Mexico, May 4–7, 1993, p. 26.

Medrano-Gonzalez, L., L. Aguayo L., J. Urbán R., and C. S. Baker.
1995a. Diversity and distribution of mitochondrial DNA lineages among humpback whales, *Megaptera novaeangliae*, in the Mexican Pacific. Can. J. Zool. 73:1,735–1,743.

Medrano-Gonzalez, L. J. Urbán R., and C. S. Baker.
1994. Sex and maternal lineage identities of humpback whales in the Mexican Pacific. *In* Abstracts of the Int. Symposium of Marine Mammal Genetics, La Jolla, CA, 23–24 September 1994.
1995b. Short and long term population structure of humpback whales in the eastern North Pacific: the definition of management units and evolutionary significant units revisited. *In* abstracts of the XX Reunion Internacional para el Estudio de los Mamiferos Marinos, La Paz, Mexico. 18–22 April 1995, p. 35.

Menkins, G. E., Jr., and S. H. Anderson.
1988. Estimation of small-mammal population size. Ecology 69:1,952–1,959.

Otis, D. L., K. P. Burnham, C. G. White, and D. R. Anderson.
1978. Statistical inference from captures data on closed animal populations. Wildl. Monogr. 62, 135 p.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines.
1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107, 97 p.

Rice, D. W.
1974. Whales and whales research in the Eastern North Pacific. *In* W. E. Schevill (ed.), The whale problem, p. 170–195. Harvard. Univ. Press, Cambridge, MA.
1978. The humpback whale in the North Pacific: distribution, exploitation, and numbers. *In* K. S. Norris and R. Reeves (eds.), Report on a workshop on problems related to humpback whales (*Megaptera novaeangliae*) in Hawaii, p. 29–44. U.S. Marine Mammal Commission, Washington, D.C.

Seber, G. A. F.
1982. The estimation of animal abundance and related parameters, 2nd ed. MacMillan, New York, NY, 654 p.

Urbán R., J., and A. Aguayo L.
1987. Spatial and seasonal distribution of the humpback whale, *Megaptera novaeangliae,* in the Mexican Pacific. Mar. Mamm. Sci. 3(4):333–344.

Urbán R., J., A. Aguayo, L., M. Salinas, Z., R. Campos, R., K. C. Balcomb, J. K. Jacobsen, P. Ladrón de G. and C. Alvarez F.
1989. Abundance and interactions of the humpback whale, in the Mexican breeding grounds. *In* Abstracts of the 8th Biennial Conference on the Biology of Marine Mammals. Monterey, CA.

Urbán R., J., K. C. Balcomb, C. Alvarez, P. Bloedel, P. Cubbage, J. Calambokidis, J. Steiger, and A. Aguayo L.
1987. Photo-identification matches of humpback whales (*Megaptera novaeangliae*) between Mexico and central California. *In* Abstracts of the 17th Biennial Conference on the Biology of Marine Mammals, Miami, FL.