Technical Report

ONR BAA N00014-16-R-BA01

A Population Consequence of Acoustic Disturbance Model for Cuvier's beaked whale (Ziphius cavirostris) in Southern California:

Photo-ID and Tag Data Components

April 2018

Erin A. Falcone, Erin L. Keene, and Gregory S. Schorr

Marine Ecology and Telemetry Research
2468 Camp McKenzie Tr NW
Seabeck, WA 98380
(206) 931-4638
efalcone@marecotel.org

Table of Contents

BACKGROUND

Cuvier's beaked whales (*Ziphius cavirostris*) are the most broadly distributed beaked whale species, but like most beaked whales, many basic aspects of their life history remain poorly understood. This is despite the fact that beaked whale research has increased dramatically since the late 1990's, when Cuvier's and other beaked whale species were first observed stranded in unusual numbers following military sonar use at several locations worldwide (Balcomb III and Claridge, 2001; D'Amico et al., 2009; Filadelfo et al., 2009; Frantzis, 1998). Much subsequent research has focused on the subsurface behavior of the species (Schorr et al., 2014; Tyack et al., 2006), and specifically on how behavior changes following sound exposure might predispose these whales to harm (DeRuiter et al., 2013; Falcone et al., 2017; Harris et al., 2017). However, while it is clear that military sonar use has caused Cuvier's beaked whale to strand in some regions, the species also occurs in places where these same sound sources are regularly used during routine training exercises, most notably off the coast of Southern California (Falcone et al., 2009, 2017; Schorr et al., 2014). This has underscored the need to look beyond the immediate behavioral changes of whales in this area, to the implications of the cumulative sonar exposures these whales presumably experience, as individuals, and as a population as a whole (New et al., 2013). Such models require many additional inputs, and these can be notoriously difficult to obtain from beaked whales, given their generally offshore distribution and limited surface time. Key among these are demographic parameters, like the birth interval, the time to weaning, the calf survival rate, and the ratio of adult females to calves in the population, all of which require extensive, long-term individual sighting histories.

Adult Cuvier's beaked whales are generally well suited to photo-identification studies (Rosso et al., 2011), though mark-rates, and thus the ability to resight individuals, vary considerably among age and sex classes. It has long been known that mature males can be differentiated from other age and sex classes by the presence of erupted teeth at the tip of the mandible and extensive scarring from intraspecific aggression (Heyning and Mead, 2009; Mead, 1984), but the ability to reliably differentiate among other classes of living whales appears to vary regionally. In Hawaii and other tropical regions, for example, Cuvier's beaked whales co-occur with cookie-cutter sharks throughout their lives, and the accumulation of cookie-cutter shark bite scars is a strong indication of age that can be used to reliably differentiate adult females from subadults (McSweeney et al., 2007). These same marks are uncommon on whales in Southern California (Falcone et al., 2009) and absent on whales in the Mediterranean (Rosso et al., 2011). This leaves few options to reliably differentiate living adult females in these regions, beyond association with a calf or genetics, and thus precludes the assessment of demographic parameters that rely on an accurate assessment of the number of adult females in the population, such as the female to calf ratio.

To address the fact that early descriptions of age- and sex-specific pigmentation patterns in Cuvier's beaked whales, derived from small numbers of stranded individuals, were often vague or equivocal, Coomber at al. (2016) conducted a detailed investigation into natural markings of known-sex adults in the Mediterranean Sea. The authors assessed the incidence of four pigmentation patterns in their sample of well-photographed, known-sex adults: (1) "dark crescents" - transverse stripes slightly posterior to the blowhole; (2) "dark ovals" - dark pigmentation among the pale coloration of the melon; (3) the length and distinctiveness of a pale "cape" that extends from the head along the topline of the back and flanks; (4) flank pigmentation color. An analysis based on these features parsed animals into two clusters strongly associated with cape pigmentation: “soft” (low contrast compared to the back and flanks), and “sharp” (high contrast, resulting in a nearly homogenous depigmented cape). No adult males were assigned to the “soft” cluster, which has been historically associated with females and subadults, but nearly one-third of females were placed in a “sharp” cluster along with all adult males. Thus, sex cannot be determined by pigmentation alone, and attempting to do so likely results in an overestimation of males in the population (Coomber et al., 2016; Rosso et al., 2011).

Since pigmentation patterns alone were not a reliable indicator of sex for whales in their study population, Coomber et al. (2016) also conducted a quantitative analysis of linear scarring rates (i.e. the prevalence of scars likely to result from intraspecific aggression). Assuming the dorsal fin width at the base is approximately one-seventh the distance from the blowhole to the dorsal fin insertion (Heyning, 1989), they defined up to thirteen regions of interest (ROIs) from the tip of the rostrum to the end of the peduncle (Figure 1) and measured the density of scarred tissue within each ROI for known-sex adults. Several scarring metrics were strongly indicative of sex. While it was not surprising that fully-mature males and females would differ starkly in the total amount of scarring, the ability to derive robust sex-associated scarring thresholds, both overall and across specific ROIs, also provided support for differentiating adult females from larger subadults using photos alone. It also potentially allows for reasonable estimation of the sex of subadults themselves. For example, Coomber et al. (2016) found that males have a bimodal peak in scarring along the body near the cranial and dorsal regions, whereas the peak scarring density of females falls half way between the rostrum and fluke. This pattern develops quite early, often before subadult males have fully developed the “sharp” pigmentation associated with male sexual maturity. Ultimately, a systematic assessment of both pigmentation and scarring patterns from photographs correctly predicted the sex of Cuvier’s beaked whales in the Mediterranean 85-90% of the time (Coomber et al. 2016).

The purpose of this study was to adapt and apply this method of age and sex determination to Cuvier’s beaked whales photographed at and near the Southern California Anti-Submarine Warfare Range (SOAR). The Mediterranean study used ideal, full-body photo sequences to analyze the pigmentation and scarring differences in a sub-set of known-sex whales; we needed to use those findings to age and sex a complete catalog of individuals. Many whales in our catalog do not have complete, perpendicular photo sequences from the rostrum to the caudal peduncle at each sighting, so a preliminary step was to assess an alternate method of collecting standardized scarring metrics when a full-body photo sequence was not available. Further, it was not known if thresholds derived from one population could be applied to whales outside that region. Our second step was thus to examine scarring thresholds from a subset of known-sex individuals in our population, and adjust the sex-specific thresholds derived by Coomber et al. (2016), if necessary. With these steps in place, each whale photographed in our study was assigned to a putative age and sex class on a sighting-by-sighting basis, with a confidence rating based on the level of available support for each designation. Finally, these updated age and sex class data were used to characterize the population structure for an ongoing effort to model the Population Consequences of Disturbance (PCoD) associated with repeated exposure to military sonar in this region.

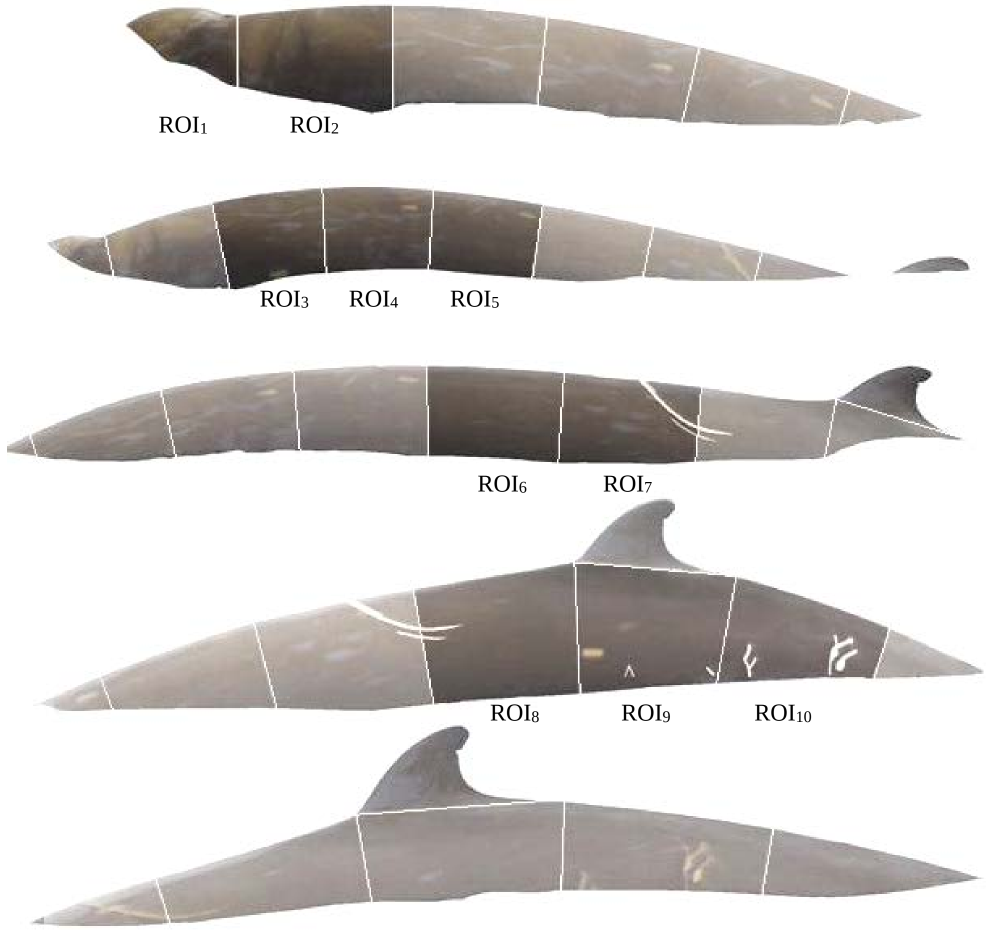


Figure 1. An example of Region of Interest (ROI) determination from an ideal photo sequence, after the method described by Coomber et al. (2016).

METHODS

Photo Selection

We reviewed the complete set of images from each Cuvier's beaked whale encounter since data collection began in 2006 to select the most appropriate set of images of each group member. The goal was to capture a perpendicular view of one entire side of the body from rostrum to caudal peduncle. In addition to coverage, image series were selected for good exposure and resolution. Ideally, each series included one picture that showed the dorsum from the blowhole to the dorsal fin: the ROI determination photo following the method used by Coomber et al. (2016). If an otherwise-suitable series did not include a single ideal ROI determination photo, two sequential images from the series could be joined in a composite to create one (Figure 2), assuming the whale had sufficient marks on the body to align the images. Alternately, a good view from the blowhole to the dorsal fin could be selected from another surface series could be used for this purpose. Finally, if a whale was never completely photographed along one side from rostrum to caudal peduncle, the best views of the rostrum and the region of the dorsum surrounding the dorsal fin (the typical part of the body used for photo-ID) were each selected separately.

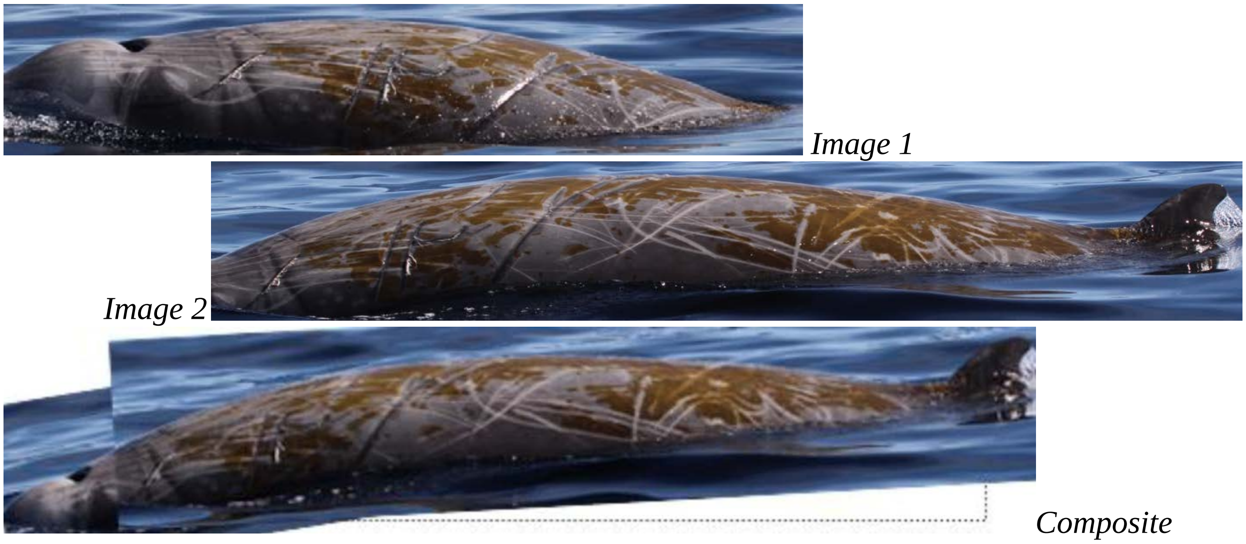


Figure 2: Example of a composite ROI Determination Image (displaying the rostrum to the blowhole) that was created by joining two sequential images from the same surfacing series.

Data Collection

A custom database was built in MS Access (Microsoft, Redmond, WA) for viewing photos and managing associated data. Prior to scarring measurement, the selection of photos from each sighting of each whale was assessed for measurement suitability and used to describe the general appearance of the whale via a series of standardized descriptors. When the best available photos series was not suitable for scarring measurement, the reason why images could not be used was noted (Table 1).

Table 1. Quality faults that prevented the systematic measurement of all or part of an image series from a sighting.

Quality Fault	Description
Can't make ROIs	ROIs can’t be accurately placed across photos, usually due to lack of scarring
Heavy Diatoms	Diatom film obscures markings
Indistinguishable Scars	Scars have repigmented, or are too numerous to trace individually.
Low in Water	Body of the whale is exposed less than height of the dorsal.
Obstructed View	Body of the whale is obstructed by water or another whale.
Poor Quality	Multiple quality faults prevent accurate scar tracing
Too Angled	Whale is too angled for accurate ROI placement

General appearance was characterized using the set of features that were diagnostic of age and sex in Coomber et al. (2016). These included visible dentition (Figure 3), the presence and appearance of pigmentation “ovals” on the melon (Figure 4), the presence of “crescents” (transverse bands of pigmentation) just posterior to the blowhole (Figure 5), and the color, sharpness, extent, and uniformity of the cape (Figure 6).


Not Erupted

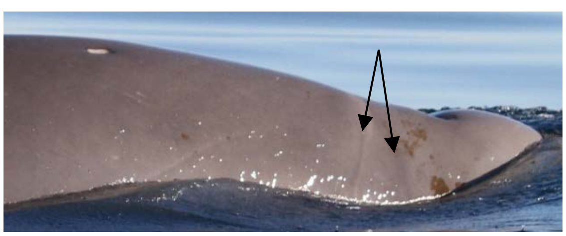

New, Erupting


Well Developed


Well Developed (covered with stalked barnacles)

Figure 3. Examples of dentition scores from high-quality images of the rostrum.


Figure 4. Whale with gray “oval” patches on the melon.


Faint cresecents


Dark crescents

Figure 5. Examples of faint and dark “crescent” markings behind the blowhole. Note that for very pale whales, the upper part of the crescents may disappear.

Sharp, Uniform Cape

Soft, Uniform Cape

Sharp, Variable Cape

Soft, Variable cape

Figure 6. Examples of cape types.

The program ImageJ (https://imagej.nih.gov/ij) was used to define ROI partitions, trace scars, and measure scarring density data. For whale sightings with a single ROI Determination Photo, the Bezier Curve tool was used to trace the topline of the whale's back from the blowhole to the insertion of the dorsal fin. Next, a custom macro was used to divide the curve into seven equal segments. The point-to-point distance along this curve was used to manually place additional points posterior to the dorsal fin in later photos from the surface sequence. The Angle Bisector tool was used to place a vertical dividing line down the side of the body at each of the division points based on the curvature of the topline between the adjacent points. The position of dividing lines in any other images from the surface series to be measured were placed based on the layout of the ROI Determination Photo, using natural markings as points of reference.

A subset of whale sightings that were measured using the standard ROI determination approach described above, were also measured using an alternate method where ROIs were based on the width of the dorsal fin at insertion. Once it was determined that scarring density metrics from the same sighting of an individual did not differ significantly based on the ROI determination method, this dorsal-fin-width method was used to derive ROI data for all sightings of whales that did not include an ideal ROI determination photo. In this method, a single line was drawn from the leading to trailing insertion points of the dorsal fin in the most complete and perpendicular photo of an individual from a given sighting. Then additional lines of equal length were placed end to end along the top of the back, extending as far anterior and posterior of the dorsal fin insertions as possible. Vertical division lines were placed using the Angle Bisector tool as described for the standard ROI Determination approach.

A combination of the line, Bezier curve, and paint brush tools were used to exactly trace all linear and curvilinear scars in the best available image of each delineated ROI. Once all scars were traced, the Polygon tool was used to select the boundaries of each ROI and the background outside the ROI polygon of interest was cleared. The Measurement tool was used to determine the area of the complete polygon in pixels. Next, either the Color Threshold selection tool or the Versatile Wand tool (depending on the scarring density) was used to select, then measure, all scarred pixels within each ROI polygon, and both these measurements were stored in the database. The process was repeated until total polygon area and scarred area measurement data were collected from all ROIs from each sighting of each whale. Scarring density was calculated by dividing the area of scarred pixels by the total ROI area.

Data analysis

General appearance and scarring density data were integrated with sighting history and genetic data for individual whales. A subset of independently confirmed adult females were selected based on having been sighted with a calf in close association or genetically derived sex, and a subset of known adult males were selected based on the presence of erupted teeth in the mandible or genetic sex. The general appearance scores and maximum scarring density at each measured ROI were summarized for these individuals, and compared to published values from the Mediterranean to determine if published thresholds could be used to sex whales in our study, or if region-specific scarring densities would be needed.

Once appropriate scarring thresholds were determined, they were used in combination with general appearance scores to assign each whale in the study to a putative age and sex class each time it was sighted. The one exception to this were calves, which were classified as such based on close association with an adult female. Because not all sightings yielded a complete set of appearance and scarring data, classifications were made iteratively from the most to least confident assignments. Resulting age and sex classification data were used to derive sex ratios at several levels (e.g. population, group, year), as well as other demographic parameters required for population modeling.

RESULTS AND DISCUSSION

Data collection and assessment of sex-associated differences

A total of 322 sightings of 200 unique individuals were included in the analysis. While all sightings were scored for general appearance, 178 (55%) were also measured for scarring density; ultimately, 133 of 200 individuals had scarring density measurements from at least one sighting. This sample included 19 adult females and 24 adult males that were independently sexed, and measured in at least one sighting. Not all of these 43 whales were completely measured along the body, but each had measurements at a minimum of 4 ROIs (mode = 11). All 43 were measured at ROI 8 (immediately below the dorsal fin), 42 were also measured at ROIs 7 and 9, 39 were measured at ROI 6, and 38 at ROIs 3-5 (Figure 1).

Scarring densities at ROIs 7-9, the most completely measured for both the known-sex individuals and in the overall study, were well-differentiated by sex (Table 2, Figure 7). The mean scarring density for males at these three ROIs were 15-20 times higher than for females, and the maximum values from females and minimum values from males were also well differentiated. The pattern in scarring rates across ROIs also varied by sex, with females displaying an increase in scarring density from ROI 2 (just behind the blowhole) to ROI 9 (just posterior to the dorsal fin), but males showing an overall decrease along the body, with peak scarring densities near the head and just anterior to the dorsal fin (Table 3). These are consistent with the patterns described for whales in the Mediterranean (Coomber et al., 2016).

Table 2. Scarring density statistics at the most completely measured ROIS (7-9) for males and females that were sexed independent of scarring.

Sex	Measured Individuals	Mean-7	Min-7	Max-7	SD-7	Mean -8	Min-8	Max-8	SD-8	Mean -9	Min-9	Max-9	SD-9
Female	19	0.01	0.00	0.05	0.01	0.01	0.00	0.04	0.01	0.01	0.00	0.04	0.01
Male	24	0.27	0.05	0.57	0.14	0.24	0.07	0.46	0.12	0.17	0.07	0.39	0.10

Table 3. ROI-specific scarring density thresholds derived from measurements of whales whose sex was confirmed independently of appearance. These maximum (female) and minimum (male) thresholds were used to assign sex to other measured whales based on appearance.

		ROI									
Sex	**Stat**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Female	Mean + SD	0.025	0.012	0.011	0.016	0.026	0.029	0.022	0.022	0.020	0.025
Male	Mean - SD	0.074	0.088	0.101	0.090	0.106	0.108	0.127	0.119	0.066	0.071

The frequencies of pigmentation category scores also varied by sex (Tables 4 A-E), though less consistently than scarring density scores. The number of independently sexed individuals that could be scored for general appearance varied among categories (e.g. quality faults precluded confident assessment of some pigmentation categories for the same sighting but not others). Adult males fell exclusively into the sharp cape contrast category, and all had capes that extended beyond ROI 4. Adult females fell predominantly into the soft cape contrast category, but some females also had sharp capes. Likewise, the majority (~60%) of females had short capes, stopping before ROI 4, but the remainder had extensive capes like males. Cape uniformity varied both within and between sexes, with females having predominantly, but not exclusively, variable cape pigmentation (i.e. that faded in and out along the extent of the cape), and males predominantly, but not exclusively, uniform cape color. All adults of both sexes displayed crescent marks posterior to the blowhole, though like cape contrast, females were more likely to have faint crescents that were not starkly differentiated from the cape color than males. Finally, all females with adequate photos of the melon bore oval marks, while these were present on only about 30% of adult males. Males with oval marks also tended to have variable cape pigmentation.

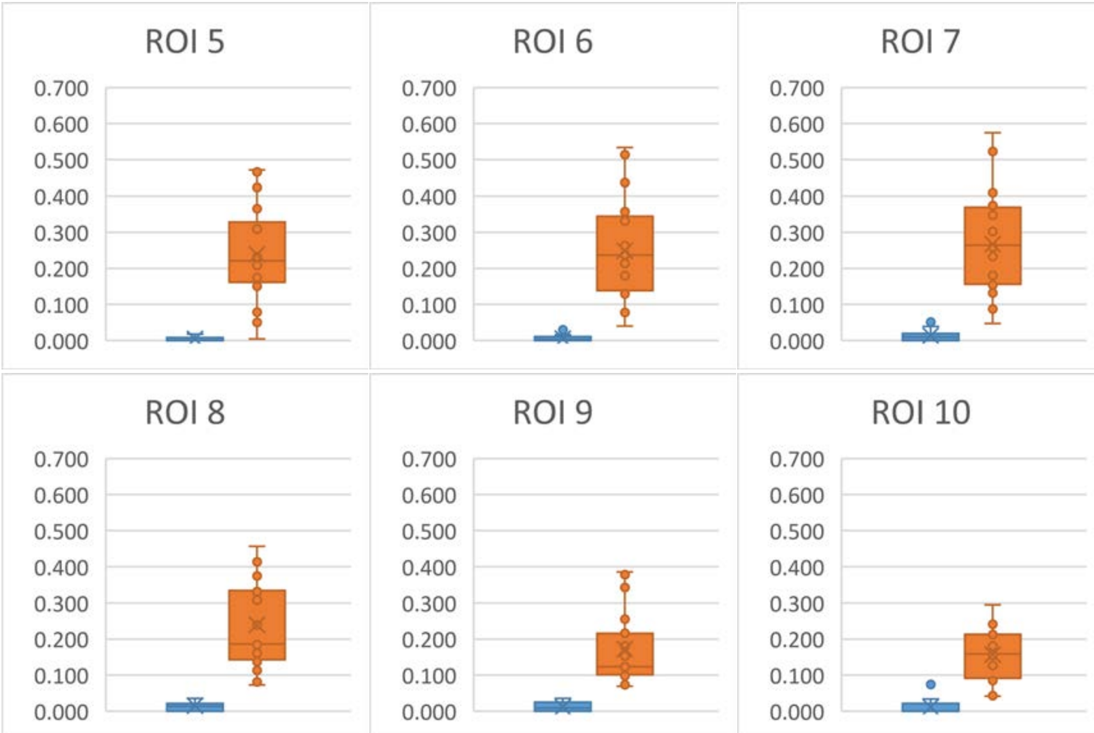


Figure 7. Box plots of scarring density data for independently sexed females (blue) and males (orange) at six Regions-of-Interest (ROI) along the body. “X” indicates mean value, circles are data points.

Individual whales that were not independently sexed were assigned to putative age and sex classes using a combination of scarring density and general appearance scores, with criteria based on the sex-specific statistics derived above. Age and sex classes were assigned on a sighting-by-sighting basis, generally moving from the most to least confident (i.e. well-supported) classifications. This iterative process is described in Appendix 1.

Tables 4 A-E. Pigmentation category score frequencies among the sample of independently sexed individuals that could be assessed for each characteristic.

A. Cape Contrast

Sex	IDs	Low	High
Female	17	0.76	0.24
Male	29	0.00	1.00

B. Last ROI of Cape

Sex	IDs	<=3	>=4
Female	16	0.63	0.38
Male	24	0.00	1.00

C. Cape Uniformity

Sex	IDs	Variable	Uniform
Female	14	0.71	0.29
Male	28	0.25	0.75

D. Post-Blowhole Crescents

Sex	IDs	Faint	Dark
Female	18	0.56	0.44
Male	27	0.15	t0.85

E. Ovals on the Melon

Sex	IDs	No	Yes
Female	11	0.00	1.00
Male	19	0.68	0.46

Individual age and sex classifications, maturity rates

Of the 200 individuals included in the study, 184 (92%) were assigned to at least one age class, with varying degrees of confidence (Table 5A). Sex was assigned to 149 (75%) of the whales in the study (Table 5B). This included 83 females and 66 males (1.26:1), though males were generally sexed with higher confidence than females (Table 5B), so uncertainty in sex could influence this ratio, particularly if some adult females were actually subadult males. The sex ratio of adults only (including all confidence levels) was more biased toward females at approximately 1.55:1, whereas subadults were biased towards males (1.9:1). One whale classified as a subadult female was initially sighted as juvenile; no other juveniles or calves were sexed.

Ten whales transitioned from subadult to adult classification, and one whale from juvenile to subadult classification, based on changes in appearance over time. While whales were classified as calves as long as they were sighted in obvious association with their mother, some calves associated with their mothers were similar in appearance (size and pigmentation) to juveniles that were sighted independently. Young calves usually lacked permanent marks, making it nearly impossible to identify them after they have separated from their mothers, and no older calves (i.e. that had attained permanent marks while still associated with their mothers) have been resighted independently as of yet. However, seven of 21 mother-calf photographed during the study were sighted together on more than one day. The spans across which these mother-calf pairs were sighted ranged from one to 734 days, or just over two years (Table 6).

Five of the whales that transitioned through age classes during the study were presumed to be female, including the one sighted as a juvenile (ID 75), and the remaining five male. The sighting histories of these ten whales provide insights into sexual maturation rates, and are provided in Appendix 2. ID 75 retained juvenile appearance from 2009 through 2013, with the first signs of cape differentiation, including faint crescents, first appearing in 2014. A second female, ID 104, was sighted as a possible subadult in 2011 and 2013 (heavy diatom coverage and low light in both these sightings caused uncertainty in the classification), but had attained adult pigmentation at her next sightings in 2015, when she was sighted with a calf. Combined with evidence that calves remained associated with their mother for two years, the sighting histories of these two whales suggest females may begin to sexually mature around age seven, and transition to adulthood at approximately age ten.

Two of the five males that transitioned during the study were sighted as subadults in more than one year. ID 41 was classified as a subadult in 2008 and 2011, and as an adult in 2016. In 2008, the whale had an extensive soft, variable cape and moderately high scarring rates, in 2011 the whale's teeth had not erupted but the cape had sharpened; in 2016 his teeth were well developed and his cape brighter and less variable. This whale steadily accrued linear scars during this time, and though presumably a young male in 2011, was heavily scarred by 2016. In contrast, ID 81 was first sighted in 2010 with a well-differentiated cape, minimal linear scarring, and no visible teeth, and was visually indistinguishable from a pale adult female. However, the whale was seen the following year with a modest increase in scarring, and again in 2015 with well-developed teeth but only a few more scars. The timing and degree of pigmentation and dentition development suggest that these two young males are likely similar in age, but their scarring rates differed drastically. ID 41 apparently began engaging in agonistic behavior long before erupting teeth; ID 81 had barely reached the minimum scarring threshold for an adult male even with teeth in place.

A subset of known-sex whales were measured at the same ROI on the same side in more than one year, including eight adult females, six adult males, and three males seen as subadults. Scarring increased at less than 0.01% per year, on average, in adult females (n = 83 repeat measurements), at 1.3% per year for adult males (n = 41 repeat measurements), and at 1.4% per year for males sighted as subadults (n = 36 repeat measurements). Scarring acquisition rates for both adult and subadult males varied considerably from whale to whale.

Tables 5A-5C. Age class and sex assignments at the most recent sighting of all 200 individuals included in the study. Juveniles were animals that lacked pigmentation differentiation but were not obviously associated with a particular adult female when sighted. Whales were considered calves when they were sighted in clear association with an adult female presumed to be their mother.

A.	**Confidence**				
Age Class	**High**	**Med**	**Low**	**Total**	**Percent**
Adult	76	21	23	120	56%
Subadult	4	16	9	29	14%
Juvenile	8	4	1	13	6%
Calf	21	1	0	22	10%
Unknown				20	9%

B.	**Confidence**				
Sex	**High**	**Med**	**Low**	**Total**	**Percent**
Female	39	20	24	83	39%
Male	53	10	3	66	31%
Unknown				51	24%

C.	**Age Class**				
Sex	**Adult**	**Subadult**	**Juvenile**	**Calf**	**Unknown**
Female	73	10			
Male	47	19			
Unknown			13	22	16

Table 6. Mother-calf pairs sighted during the study, with the first and last day each pair was sighted together and the total span of days between.

Year	ID-Mom	ID-Calf	Date-First	Date-Last	Span
2008	23	59	10/24/2008	10/24/2008	0
2008	35	36	8/2/2008	8/2/2008	0
2008	45	44	8/3/2008	8/3/2008	0
2008	46	55	8/3/2008	10/23/2008	81
2008	50	51	10/22/2008	10/23/2008	1
2011	102	227	5/1/2011	5/1/2011	0
2011	103	158	5/2/2011	5/2/2011	0
2011	108	109	9/24/2011	9/24/2011	0
2013	112	No ID	9/11/2013	9/11/2013	0
2013	126	159	1/5/2013	5/20/2013	135
2013	127	160	1/5/2013	1/9/2015	734
2014	103	149	1/6/2014	1/7/2015	366
2014	153	192	1/7/2014	1/7/2014	0
2015	104	170	1/5/2015	1/9/2015	4
2015	175	176	1/7/2015	1/7/2015	0
2015	183	228	1/7/2015	1/7/2015	0
2015	184	185	1/8/2015	1/8/2015	0
2015	186	229	1/9/2015	1/9/2015	0
2016	126	207	11/11/2016	11/11/2016	0
2016	187	205	4/5/2016	1/14/2018	649
2017	218	221	7/24/2017	7/24/2017	0
2017	219	225	7/22/2017	7/22/2017	0

Calving rates

The 75 adult females sighted in the course of the study produced a total of 22 calves. Two females produced two calves each. ID 103 was sighted with her first calf, which had the proportions, head shape, and brownish color typical of younger calves, in May 2011. She was then sighted without a calf in January 2012 and March 2013. She was with a second calf in January 2014 and remained associated with this calf in January 2015. While this calf appeared more mature than her first calf did on its only known sighting, it appeared too young in 2014 to have been the same calf. The second female to bear two calves during the study was ID 126. She was sighted with her first calf, which was no longer brownish and thus a somewhat older calf, in January 2013, and was still associated with this calf three months later. ID 126 was not sighted again until November 2016, when she had a new calf in attendance.

The intervals from the first sighting of the first calf to the first sighting of the second calf were 980 days (2.7 years) for ID 103 and 1,406 days (3.6 years) for ID 126. However, given that ID 103 was still associated with her second calf one year after it was first sighted, and that two other calves remained associated with their mothers at two years after their initial sighting (Table 6), it is possible that her first calf did not survive, and thus her calving interval may be artificially low.

In addition to being one of only two females to bear more than one calf during the study, ID 103 was also the most frequently sighted whale, having been photographed in seven of eight consecutive years. Given the paucity of data on calving intervals from other females in the study, another way to estimate calving rates from these data are to look at the sighting histories of adult females that were sighted in more than one year (n=12), and the minimum number of calves they produced (Appendix 3) during that time. For nine females that were sighted in more than 50% of the years within the span of their sighting histories, the average number of calves per year was 0.25, or approximately one calf every 4 years. Taken with the weaning data previously presented, this suggests females may lactate for up to two years, become pregnant in the third year when the previous calf separates, then bear a new calf in the fourth year.

Sex ratios

There were 99 groups sighted in the San Nicolas Basin from 2006 through 2017- the focal study area where effort was most consistent and the vast majority of the photo data were collected. The average group size for these sightings was 3.4 individuals (SD 2.0). Groups numbering 1-4 whales occurred with similar frequency, larger groups (max = 10) were much less common and decreased in frequency as group size increased (Figure 8).

All group members were identified in 70 of these sightings, and these provided information on the sex composition of groups. Solitary individuals (n = 18 of 70 fully identified sightings) were most often adult males (9), followed by adult females (6), and immature individuals (one subadult female and 2 juveniles of unknown sex). All but six of the remaining 53 groups with more than one individual included at least one adult female. Pairs (n = 17) usually consisted of an adult female and a calf or a juvenile. There were four exceptions to this: one adult female was seen paired with an adult male, one subadult female was seen paired with a subadult male, one subadult female was seen paired with an unsexed juvenile, and two adult males were sighted together. All trios (n = 11) included at least one adult female and three were comprised of two adult females and one calf. Four of the remaining eight trios with one adult female included a single adult male and a calf, two had one adult and one subadult male, and one had two subadult males.

For larger groups that were fully identified (containing four to eight whales, n = 24), the likelihood of including a calf was low and decreased as group size increased: only three of these groups included a calf, the largest of which had five members. Larger groups often included multiple adult and/or subadult males. There were nine large groups where the ratio of males to females was equal and six with more confirmed males than females present. The largest of these groups consisted of three adult males, three subadult males, an apparent subadult female, and an individual whose age and sex could not be determined due to photo quality, but was most likely another younger female.

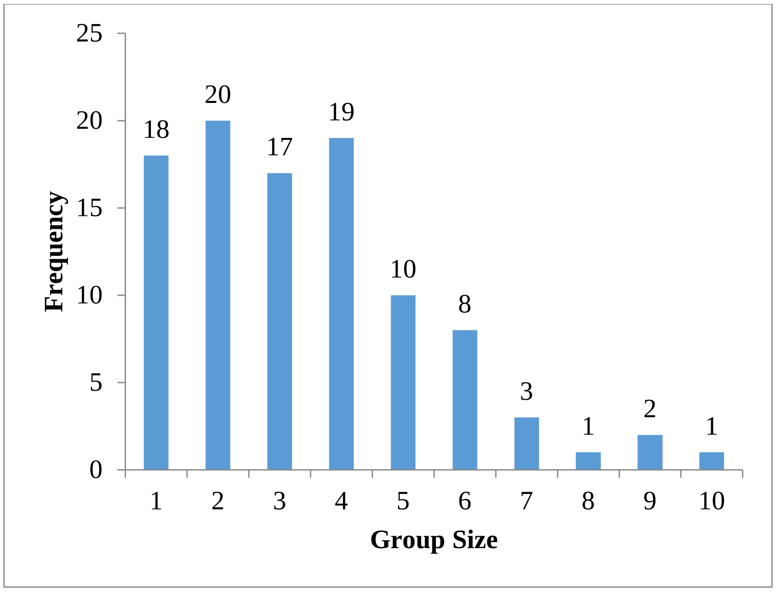


Figure 8. Histogram of group size for Cuvier's beaked whales encountered in the San Nicolas Basin.

Another way to estimate the age and sex ratio in the population is to look at the annual sample of identified individuals. Certain age classes are more likely to be incorrectly identified in different years due to lack of markings- namely females and young whales- but can be reliably differentiated within a year. Table 7 provides data on the age-sex class distribution of the sample of unique whales identified in the San Nicolas Basin each study year.

The annual ratio of calves to adult females identified was highly variable. The total number of calves identified each year ranged from zero to seven, and while two of the three years in which no calves were seen had below average total whales, one of them was among the highest number of whales- so this is not necessarily an artifact of low sample size. The average number of calves per adult female identified each year was 0.25 (SD 0.21), which may be associated with the apparent calving interval of four years in this population. If a number of females in the population are in reproductive synchrony, for example, if extrinsic factors tend to cause a high number of reproductive failures in the same year and females that lost calves had their calving interval effectively "reset" to the same schedule, this could explain some of the extreme variability in annual calving rates.

Table 7. Annual sex and age class distribution of unique individuals identified in the San Nicolas Basin for each study year with more than ten individuals identified.

Year	Unique IDs	Adult-Female	Adult-Male	Subad-Female	Subad-Male	Juv	Calf	Unk	Calf: AdFem	Adult-F % Total ID	Adult-M % Total ID	Calf % Total ID	Immature/Unk % Total ID
2007	28	7	8	4	4	0	0	5	0.00	25%	29%	0%	46%
2008	24	8	4	2	2	2	5	1	0.63	33%	17%	21%	29%
2010	17	4	6	3	4	0	0	0	0.00	24%	35%	0%	41%
2011	22	8	5	2	2	2	2	1	0.25	36%	23%	9%	32%
2012	13	4	5	1	2	0	0	1	0.00	31%	38%	0%	31%
2013	28	10	8	1	3	3	2	1	0.20	36%	29%	7%	29%
2014	18	7	4	1	1	1	3	1	0.43	39%	22%	17%	22%
2015	33	17	5	0	1	3	7	0	0.41	52%	15%	21%	12%
2016	26	8	7	1	4	2	2	2	0.25	31%	27%	8%	35%
2017	19	7	6	1	1	1	2	1	0.29	37%	32%	11%	21%
Median	23.0	7.5	5.5	1.0	2.0	1.5	2.0	1.0	0.25	35%	28%	8%	30%
Mean	22.8	8.0	5.8	1.6	2.4	1.4	2.3	1.3	0.25	34%	27%	9%	30%
SD	6.1	3.7	1.5	1.2	1.3	1.2	2.3	1.4	0.21	8%	8%	8%	10%

TAG DATA COMPONENTS

Throughout the time these photographic data were collected, 22 dive-recording satellite tags were deployed on whales in this population. Data from these tags have been published (Falcone et al., 2017; Schorr et al., 2014), and also provided to the M3R program for direct use in estimating relevant parameters for the PCoD model.

CONCLUSIONS

The relatively low cost, low-impact approach of photo-ID continues to provide some of the most important metrics of population health for whales. Here, we have applied a published method for determining the age and sex of individual Cuvier's beaked whales from photographs alone, adapting it for use in a new population and in cases where ideal photographic sequences are not available. While these results represent the best available demographic data for use in PCoD modeling, they also demonstrate the importance of long-term photographic sampling for acquiring enough data to inform these models in a species with sighting rates as low as this one. Ultimately, the PCoD approach needs data from another similar population of whales that is not subject the impact of interest for comparison. These methods should be applied to other populations of Cuvier's beaked whales that are being studied via photo-ID in the future.

ACKNOWLEDGEMENTS

This work was conducted in collaboration with the M3R program at the Naval Undersea Warfare Center, Newport, RI, particularly Dave Moretti, Stephanie Watwood, Ron Morrissey, Susan Jarvis, and Nancy DiMarzzio. This work would not have been possible without the support of SCORE, particularly Heidi Nevitt, Robert Tahimic, and the rest of the SCORE personnel. Thanks to Jane and Frank Falcone for access to their house, truck, and shop and continued support of our field work and to Kelly Robertson and the Southwest Fisheries Science Center Marine Mammal Genetics Program for providing genetic sex from biopsy samples. For support and help with photo-ID we thank Drew Xitco. We also thank Cascadia Research for support on this project. Funding for this work was provided by the Office of Naval Research (award No. N00014-15-2899 and N00014-16-1-3068), with additional funding via the Navy's Living Marine Resources (LMR) program (contract No. N29340-16-C-1870 and grant No. N00244-10-1-0050), LMR & the US Navy's Pacific Fleet (contract No. N6660-14-C-0145), and ESTCP (contract No. N66604-14-C-2438). Work was conducted under NOAA permits No. 540-1811, 19091, 15330 and 16111 and covered under Cascadia Research's IACUC.

LITERATURE CITED

Balcomb III, K., Claridge, D., 2001. A mass stranding of cetaceans caused by naval sonar in the Bahamas. Bahamas J. Sci. 8, 2–12.

Coomber, F., Moulins, A., Tepsich, P., Rosso, M., 2016. Sexing free-ranging adult Cuvier's beaked whales (*Ziphius cavirostris*) using natural marking thresholds and pigmentation patterns. J. Mammal. 97, 879–890. https://doi.org/10.1093/jmammal/gyw033

D'Amico, A., Gisner, R.C., Ketten, D.R., Hammock, J.A., Johnson, C., Tyack, P.L., Mead, J., 2009. Beaked whale strandings and naval exercises. Aquat. Mamm. 34, 452–472. https://doi.org/10.1578/AM.35.4.2009.452

DeRuiter, S.L., Southall, B.L., Calambokidis, J., Zimmer, W.M., Sadykova, D., Falcone, E.A., Friedlaender, A.S., Joseph, J.E., Moretti, D., Schorr, G.S., Thomas, Len, Tyack, Peter L, 2013. First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. Biol. Lett. 9, 2–6.

Falcone, E., Schorr, G., Douglas, A., Calambokidis, J., Henderson, E., McKenna, M., Hildebrand, J., Moretti, D., 2009. Sighting characteristics and photo-identification of Cuvier's beaked whales (*Ziphius cavirostris*) near San Clemente Island, California: a key area for beaked whales and the military? Mar. Biol. 156, 2631–2640. https://doi.org/10.1007/s00227-009-1289-8

Falcone, E.A., Schorr, G.S., Watwood, S.L., DeRuiter, S.L., Zerbini, A.N., Andrews, R.D., Morrissey, R.P., Moretti, D.J., 2017. Diving behaviour of Cuvier's beaked whales exposed to two types of military sonar. R. Soc. Open Sci. 4. https://doi.org/10.1098/rsos.170629

Filadelfo, R., Pinelis, Y.K., Davis, S., Chase, R., Mintz, J., Wolfanger, J., Tyack, P.L., Ketten, D.R., D'Amico, A., 2009. Correlating whale strandings with Navy exercises off Southern California. Aquat. Mamm. 35, 445–451. https://doi.org/DOI 10.1578/AM.35.4.2009.445

Frantzis, A., 1998. Does acoustic testing strand whales? Nature 392, 29. https://doi.org/10.1038/32068

Harris, C.M., Thomas, L., Falcone, E.A., Hildebrand, J., Houser, D., Kvadsheim, P.H., Lam, F.-P.A., Miller, P.J.O., Moretti, D.J., Read, A.J., Slabbekoorn, H., Southall, B.L., Tyack, P.L., Wartzok, D., Janik, V.M., 2017. Marine mammals and sonar: dose-response studies, the risk-disturbance hypothesis and the role of exposure context. J. Appl. Ecol. 00, 1–9. https://doi.org/10.1111/1365-2664.12955

Heyning, J.E., 1989. Cuvier's beaked whale, Ziphius cavirostris (G. Cuvier, 1823), in: Handbook of Marine Mammals (S. H. Ridgway and R. S. Harrison, Eds.). Academic Press, London, pp. 289–308.

Heyning, J.E., Mead, J.G., 2009. Cuvier's beaked whale: Ziphius cavirostris., in: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals. Second Edition. Academic Press, San Diego, CA, pp. 294–295.

McSweeney, D.J., Baird, R.W., Mahaffy, S.D., 2007. Site fidelity, associations, and movements of Cuvier's (Ziphius cavirostris) and Blainville's (Mesoplodon densirostris) beaked whales off the island of Hawai 'i. Mar. Mammal Sci. 23, 666–687.

Mead, J.G., 1984. Survey of reproductive data for the beaked whales (Ziphiidae). Rep Int Whal CommSpecial Issue 6, 91–96.

Moretti, D., Thomas, L., Marques, T., Harwood, J., Dilley, A., Neales, B., Shaffer, J., McCarthy, E., New, L., Jarvis, S., Morrissey, R., 2014. A Risk Function for Behavioral Disruption of Blainville's Beaked Whales (Mesoplodon densirostris) from Mid-Frequency Active Sonar. PLoS ONE 9, e85064. https://doi.org/10.1371/journal.pone.0085064

New, L.F., Moretti, D.J., Hooker, S.K., Costa, D.P., Simmons, S.E., 2013. Using Energetic Models to Investigate the Survival and Reproduction of Beaked Whales (family Ziphiidae). PLoS ONE 8, e68725. https://doi.org/10.1371/journal.pone.0068725

Rosso, M., Ballardini, M., Moulins, A., Würtz, M., 2011. Natural markings of Cuvier's beaked whale *Ziphius cavirostris* in the Mediterranean Sea. Afr. J. Mar. Sci. 33, 45–57. https://doi.org/10.2989/1814232X.2011.572336

Schorr, G.S., Falcone, E.A., Moretti, D.J., Andrews, R.D., 2014. First Long-Term Behavioral Records from Cuvier's Beaked Whales (Ziphius cavirostris) Reveal Record-Breaking Dives. PLoS ONE 9, e92633. https://doi.org/10.1371/journal.pone.0092633

Tyack, P.L., Johnson, M., Soto, N.A., Sturlese, A., Madsen, P.T., 2006. Extreme diving of beaked whales. J. Exp. Biol. 209, 4238–4253. https://doi.org/10.1242/jeb.02505

Appendix 1. Criteria used to iteratively assign whales to age and sex classes based on sighting history and appearance.

		Criteria						Classification			
Step	**Class**	**Teeth**	**Cape**	**Last ROI**	**Crescents**	**Scarring Density at ROI 7-9**	**Additional Factors**	**Age**	**Age Confidence**	**Sex**	**Sex Confidence**
1	Adult females by reproductive history	No or Unknown					Mother, used to derive female criteria for later steps	Adult	High	Female	High
2	Calves by size and association with mother	No or Unknown					Calf	Calf	High	Unknown	
3	Adult males by dentition	Erupted					Used to derive male criteria applied in later steps	Adult	High	Male	High
4	Juveniles by appearance	No or Unknown	No	NA	No	Any	Rostrum, cape area, and flank gray or dark gray	Juvenile	High	Unknown	
5	Adult males by appearance, with ROI measurements	Unknown	High contrast	>4	Yes	>= Mean - SD for known adult males (by dentition)		Adult	High	Male	High
6	Adult females by appearance, with ROI measurements	No or Unknown	High or low contrast	Any	Yes	<= Mean + SD for known adult females (by calf assoc)		Adult	High	Female	High
7	Adult male at a subsequent sighting	Unknown	High contrast	Unknown	Unknown	NA	Heavily scarred, unable to measure due to image quality	Adult	High	Male	High
8		No	High contrast	Any	Yes or Unknown	NA or below threshold for adult males	Not heavily scarred	Subadult	High	Male	High
9		Unknown	Any	Any	Any	NA or less than in later sightings		Subadult	Med	Male	High
10	Adult female at a subsequent sighting	No or Unknown	No or Low contrast	< later sightings	No	NA or less than in later sightings	Grayish head, cape	Subadult	Med	Female	High
11	Subadult at a subsequent sighting	No or Unknown	No	NA	No	NA or less than in later sightings	Amount of time between sightings and appearance change evaluated	Subadult or Juvenile	Med	Unknown	
12	Unclassified whales with partial appearance scores and ROI measurements from at least one sighting	Unknown	High contrast or unknown	>4 or unknown	Yes or Unknown	>= Mean - SD for known males	Pigmentation details used to inform age	Adult or Subadult	Med	Male	Med
		No	High or low contrast	Any	Yes	Near upper boundary of threshold between adult male/female		Subadult	Med	Male	Med
		No	High or low contrast	Any	Yes	Near lower boundary of threshold between adult male/female		Adult	Low	Female	Low
13	Unclassified whales with partial appearance scores and no ROI measurements	Evaluated on a case by case basis, using change over time as an indicator									

Appendix 2. Sighting history of whales that transitioned through more than one age class during the study.

Sex	ID	AgeClass	First Date	Last Date	MinimumYears in Class	Maximum Years in Transition
Female	**22**	Subadult	10/25/2007	10/25/2007	0.0	6.2
		Adult	1/4/2014	1/11/2014	0.0	
	42	Subadult	8/3/2008	8/5/2008	0.0	3.4
		Adult	1/14/2012	11/7/2016	4.8	
	75	Juvenile	7/20/2009	3/28/2013	3.7	0.8
		Subadult	1/6/2014	1/6/2014	0.0	
	99	Subadult	1/6/2011	1/6/2011	0.0	5.1
		Adult	2/24/2016	11/11/2016	0.7	
	104	Subadult	7/23/2011	3/30/2013	1.7	1.8
		Adult	1/5/2015	1/9/2015	0.0	
Male	**15**	Subadult	10/24/2007	10/26/2007	0.0	6.0
		Adult	11/1/2013	11/1/2013	0.0	
	41	Subadult	8/3/2008	1/5/2011	2.4	5.2
		Adult	4/2/2016	4/2/2016	0.0	
	66	Subadult	8/23/2009	8/23/2009	0.0	3.9
		Adult	7/28/2013	7/28/2013	0.0	
	81	Subadult	6/28/2010	9/24/2011	1.2	3.3
		Adult	1/3/2015	1/3/2015	0.0	
	203	Subadult	4/5/2016	4/5/2016	0.0	1.0
		Adult	4/7/2017	4/7/2017	0.0	

Appendix 3. Annual reproductive status for adult females sighted in more than one year. For females sighted with a calf in more than one year, a single asterisk (*) denotes a sighting with her first calf in attendance, and a double asterisk (**) a sighting with a second calf.

	Annual Reproductive State												**Years Sighted**	**Span (Years)**	**Calves**	**% Years Assessed**	**Calves/Yr**
ID	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**					
19	AD						AD						2	7	0	29%	0.00
23	AD	MO		AD									3	4	1	75%	0.25
32		AD					AD			AD		AD	4	11	0	36%	0.00
46		MO			AD			AD				AD	4	11	1	36%	0.09
50		MO								AD			2	9	1	22%	0.11
103					MO*	AD	AD	MO**	AD	AD		AD	7	8	2	88%	0.25
104					SA?		SA?		MO				3	5	1	60%	0.20
105					AD		AD			AD		AD	4	8	0	50%	0.00
112					AD		MO						2	4	1	50%	0.25
126							MO*			MO**			2	4	2	50%	0.50
127							MO*		MO*				2	3	1	67%	0.33
187									AD	MO*	MO*	MO*	4	4	1	100%	0.25