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Likely annual calving in the vaquita, *Phocoena sinus*: A new hope?

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The ability of a small population to recover after a severe decline is strongly influenced by its reproductive biology.

Unfortunately, little is known about many key reproductive parameters of the vaquita (*Phocoena sinus*), a small porpoise that is nearly extinct due to entanglement in fishing nets, many of which were set illegally (Thomas et al. 2017). Improved knowledge of key life history parameters of this critically endangered species would improve our understanding of its potential for recovery.

Calving intervals of five other phocoenids have been described, including: harbor porpoise, (P. phocoena), Dall's porpoise (Phocoenoides dalli), Burmeister's porpoise (P. spinnipinis), and Indopacific finless porpoise (Neophocaena phocaenoides) and the sunameri finless porpoise subspecies (Neophocaena asiaorientalis sunameri). In general, these porpoises fall on the fast end of the odontocete life history continuum. In particular, females are capable of postpartum estrus and are thus able to produce calves annually (Read 1990). For example, the pregnancy rate of mature female harbor porpoises in the Gulf of Maine was 0.95, indicating an annual pattern of reproduction (Read and Hohn 1995). Similar findings of annual reproduction have been reported for Dall's porpoise

(Ferrero and Walker 1999) and Burmeister's porpoise (Reyes and Van Waerebeek 1995). In these three species, annual calving is accompanied by lactation periods of <1 yr (Gaskin et al. 1984).

Kasuya (2017) noted that the sunameri finless porpoises may have reproductive cycles of 1, 2, or more years and Amano (2017) states that females are believed to calve every 2 yr.

In contrast, the ovaries of nine adult female vaquitas taken as bycatch between February and May in 1985-1993 (Brownell et al. 1986, Vidal 1995) were interpreted by Hohn et al. (1996) as indicating a 2 yr calving interval. Herein we examine photographic evidence that suggests annual calf production in vaquitas is possible, leading us to reexamine the conclusions of Hohn et al. (1996).

On 18 October 2017 a group of three vaquitas was sighted off San Felipe, Baja California Norte, Mexico, as part of an effort to capture vaquitas and bring them into human care, (Rojas-Bracho et al. 2019). Two of the vaquitas were photographed together at 1037 (local time) (Fig. 1a). The third individual was not photographed. Nine minutes after the photograph of the two vaquitas was taken, a single female

vaquita was captured (V01F). The captured vaquita (Fig. 1b) had a total length of 105 cm and most of its teeth were erupted. The animal was estimated to be approximately 6 mo old, assuming a calving season in March-April (Hohn et al. 1996). The pair photographed together moments before the capture included the calf and a larger animal presumed to be her mother, based on photographs of their close association. The presumed mother did not match any of the animals photographed previously by Jefferson et al. (2009) or by any of the photographers involved in the 2017 capture efforts. Unfortunately, no genetic samples are available from the larger animal to determine its sex. Following the capture of V01F, the field team spent the next 2 h attempting to capture the presumed mother (Fig. 1c), but the vaquita(s) in the area successfully evaded the gill nets. V01F did not respond well to being held in a net pen and 4 h after capture was released in the area where the presumed mother had last been seen.

Almost a year later, on 26 September 2018 (during a dedicated effort to obtain photographs and/or biopsies), a pair of vaquitas was observed off San Felipe 10 km from where V01F

was first seen a year earlier. The pair was visually tracked for 1 h with no other vaquitas observed in the vicinity. The pair stayed within a body length of each other for the entire period, during which more than 30 surfacing intervals were observed. Due to their prolonged close association and their relative body and dorsal fin sizes, the pair was assumed to be a mother and calf. The presumed mother in 2018 photographically matched the presumed mother of V01F taken in 2017, based on a distinctive protrusion along the trailing edge of the dorsal fin, with a distinctive notch above and an indentation below (Fig. 1d) The dorsal fin of V01F (Fig. 1b), measured directly during capture, was used as the basis for estimating dorsal fin heights from field photographs. The dorsal fin height (DH) from the base (a line drawn from the anterior insertion of the fin to the posterior insertion of the fin) to the tip for V01F was measured as 12.5 cm during capture. We used V01F's measured DH as a scale to measure the distance from the tip of the presumed female's dorsal fin to the distinctive protrusion visible in Fig. 1a (5.8 cm), the best available photo of the pair. This partial fin measure was then used as a scale to estimate the total DH of

15.25 cm from the full-fin photo of the presumed female in Fig. 1c. The ratio of the calf's DH to the presumed female's DH is 0.82. Assuming the presumed mother's DH remained constant from one year to the next, the measure of the distance from the distinctive protrusion to the fin tip was used as a scale for the measurements of the photo (Fig. 1d) taken of her with the 2018 presumed calf (C18), resulting in an estimated DH of 11.2 cm for C18, and a DH ratio of C18 to the presumed female of 0.73.

Previous measurements (Table 1) suggest that VO1F had expected fin height for a calf, with the ratio of DH to average adult female DH in the expected range (Fig. 2). We also measured the fin height of two calves relative to their presumed mothers for two pairs of vaquitas photographed in October 2008 when calves are about 6 mo old (Jefferson et al. 2009). These calves had ratios of 0.87 and 0.88.

C18 was smaller than V01F had been in 2017 and we conclude that the former was a younger calf associating with the adult that we photographed in 2017 and 2018. The larger porpoise was photographed with V01F at a time when the vaquitas were in the

presence of many boats, which vaquitas generally avoid and may have perceived as a threat. Under such conditions, we expect that calves will stay close to their mothers, which makes it seem likely that the larger porpoise was, indeed, the mother of VO1F. The identity of the third animal observed at the start of the encounter remains unknown. If VO1F and C18 are indeed calves of the same distinctive mother, then these photographs indicate that vaquitas can calve annually.

Recognizing that the information available to us is incomplete, we used structured expert decision making (Burgman 2015) to quantify the likelihood that these photographs represented evidence of annual calving. We consulted eleven experts, who have been employed as observers in at least two vaquita surveys, with an average of 4 yr of experience observing vaquitas, and 18 yr observing porpoises. The experts were asked to distribute 10 likelihood points between the following categories with the probability values given in parentheses: false (0), very unlikely (between 1% and 25%), unlikely (between 26% and 50%), likely (between 51% and 75%), very likely (between 76% and 99%), certain (100%). We provided these experts the

information above independently and asked them two questions:

(1) Was the pair observed in 2018 a mother/calf pair? and (2)

Was the individual seen in the photograph with V01F the mother of that calf? Their responses indicated a probability of 90% (CV = 12.1) that the 2018 pair was a mother and calf, an 88% probability (CV = 10.6) that the individual seen with V01F was her mother. No likelihood points were given to categories from false through unlikely. Taken together and assuming independence in these estimates, there is a combined probability of 79% (very likely) that these photographs represent an example of annual calving.

We then reexamined the evidence for a 2 yr calving interval presented in Hohn et al. (1996). These authors made the reasonable assumption that the life history of the vaquita is similar to that of the better-studied harbor porpoise.

Specifically, they assumed that (1) gestation lasts for 10.6 mo (Read 1990, Learmonth et al. 2014, Norman et al. 2018) and (2) the duration of lactation is <1 yr (Read 1990). Temporal synchrony in the sizes of calves examined and the seasonality of male testicular activity led the authors to conclude that, like

harbor porpoises, vaquitas have a single calving season with a peak in March, and that most ovulation and conception occur in mid-April. Carcasses were found primarily during the totoaba spawning season between February and May. Visual surveys and photographic efforts rely on calm winds and have occurred between August and December. Although views are generally distant, neonates were not noted during the fall, which is consistent with the single calving season noted by Hohn et al. (1996). Table 2 presents data taken from table 3 of Hohn et al. (1996) but places individuals in order of sampling date by month. We excluded the 21-yr-old female that appeared to be nonreproductive. It is immediately apparent that both females sampled before March were pregnant and all examined after March 1 were lactating, which is consistent with a pattern of annual calving. We added a column indicating whether there was evidence for ovulation in successive years. Three individuals ovulated in successive years. Four animals died in March, and did not have evidence of ovulation in the current year. However, if these animals were examined immediately around parturition, assuming calving occurs in March (see above), then it is possible that

the postpartum estrus was still to occur that year, so lack of an observed ovulation scar does not imply that ovulation would not occur that year. Thus, we scored these animals in Table 2 as "data not available, na" to make a definitive statement on ovulation frequency. Two of these four animals had not, however, ovulated in successive prior and past years, suggesting a two year calving interval for these two individuals in those years. Thus, these data are consistent with a pattern of annual reproduction for some individuals, as is the case for other porpoises for which we have sufficient reproductive data. It is impossible to draw any stronger inference, because most of the sampled animals died in the month of peak calving when it was likely too early to detect postpartum ovulation.

Some past models projecting expected abundance trajectories of the vaquita have assumed that calving occurs every 2 yr, with a maximum growth rate of 4%/yr. For example, Gerrodette and Rojas-Bracho (2011) used an informative prior that limited growth rate to less than 8% based on the Hohn et al. (1996) paper. The growth rate for the apparently very similar harbor porpoise is now estimated to be up to 11.6% (upper 90%

probability interval, Moore and Read 2008). Jaramillo-Legorreta (2008) created a Bayesian model of vaquita population dynamics that did not assume the 2 yr calving interval and had a maximum rate of 11.7%, which is very similar to that for harbor porpoises.

However, if we use model trajectories assuming a mean growth rate of 8% or even 11%, the simple model (Jaramillo-Legorreta et al. 2007) still shows that fishing mortality has been at unsustainable levels since at least 1997. Projecting from 1997 to 2007 assuming a growth rate of 4%/year, the best estimate in 2007 was 150 vaquitas, which falls within the values observed from the survey in 2008 (245 animals, 95% CI 68-884, Gerrodette et al. 2011). When we assume an annual rate of increase of 8% or 11%, the estimated abundance in 2007 increases to 185 or 257, respectively, which is closer to the observed best estimate. Thus, even with annual calving the amount of fishing mortality that can be sustained is trivial, reinforcing the need to eliminate gillnets from their habitat. If these critically endangered porpoises can reproduce annually, the potential growth rate could provide more hope for recovery if

mortality in gill nets can be halted.

The presumed 2 yr calving interval seems anomalous given the ability of most other porpoises to calve annually and similar values of longevity across species (Read 1990, Learmonth et al. 2014, Norman et al. 2018). Maximum age in several populations of P. phocoena is just over 20 yr (Hohn and Brownell 1990, Read and Hohn 1995, Learmonth et al. 2014, Norman et al. 2018) and in sunameri the maximum age is 23 yr (Kasuya 1999). Note, however, that Jefferson et al. (2002) documented finless porpoises in southern China (N. phocaenoides), where exploitation levels may be less intense, living 33 yr. These values are similar to those of the vaquita (Hohn et al. 1996). The habitat of vaquitas is a highly productive area (Brusca et al. 2017) and vaquitas examined at necropsy have presented excellent body condition with no signs of malnutrition (Vidal 1995). Vaquitas seen during research efforts, including the one in September 2018, have all been robust with no signs of malnutrition (BLT, LRB) and this was also the case for vaquita taken as bycatch in the 1980s (RLB). Thus, a prolonged interbirth interval based on nutritional limitation seems very

unlikely.

To determine conclusively whether the vaquita is capable of annual calving (beyond the ability to ovulate annually demonstrated in Hohn et al. 1996), we recommend that further research efforts should focus on photo-identification of adult females and their dependent calves. Future efforts should consider including laser photogrammetry in the field (Webster et al. 2010), as an adjunct to provide a noninvasive way of discriminating between individuals of different sizes bearing similar marks, measuring individuals, and possibly assigning them to general age categories. The acoustic monitoring program (Jaramillo-Legorreta et al. 2017, Thomas et al. 2017) can provide near-real-time vaquita locations that are critical for such photo-identification efforts and also can provide knowledge about the distribution of remaining vaquitas to support the targeted removal of illegal nets and improved enforcement. Unlike some other porpoises, many adult female vaquitas are well-marked, providing an opportunity to monitor them from year to year (Jefferson et al. 2009).

In addition to demonstrating the potential of annual

calving, our observations provide additional hope for the future of the vaquita. This small field effort confirmed that there were at least six vaquitas surviving including one and likely two calves. If the female was the mother of V01F, she eluded capture while pregnant and is raising an apparently healthy calf. We suggest that the survivors of the 90% decline that occurred between 2011 and 2016 (Thomas et al. 2017) are experienced in avoiding capture in nets, as a result of a strong behavioral selection. These surviving animals will form the basis of any future recovery of the species.

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Figure 1. Dorsal fin photographs used to match the presumed mother of two calves in successive years. Digital measurements of relative dorsal fin heights were calibrated against the measurement for V01F. (a) Presumed mother and V01F photographed together on 18 October 2017. Presumed mother is identifiable from distinctive tissue protrusion on trailing edge of dorsal fin, indicated by white arrow. (b) V01F on 18 October 2017 after capture. (c) Presumed mother on 18 October 2017 showing full fin

including distinctive notch above and indentation below tissue protrusion, as additional identifying features. (d) Presumed mother and C18 on 26 September 2018. Dorsal fin bases for measurements indicated by white lines.

Figure 2. Total length of calves and adult females (Table 1) with respect to the dorsal fin height (a) and ratio of calf dorsal fin height to the average dorsal fin height for adult females (b). Observed values for VO1F are also given.

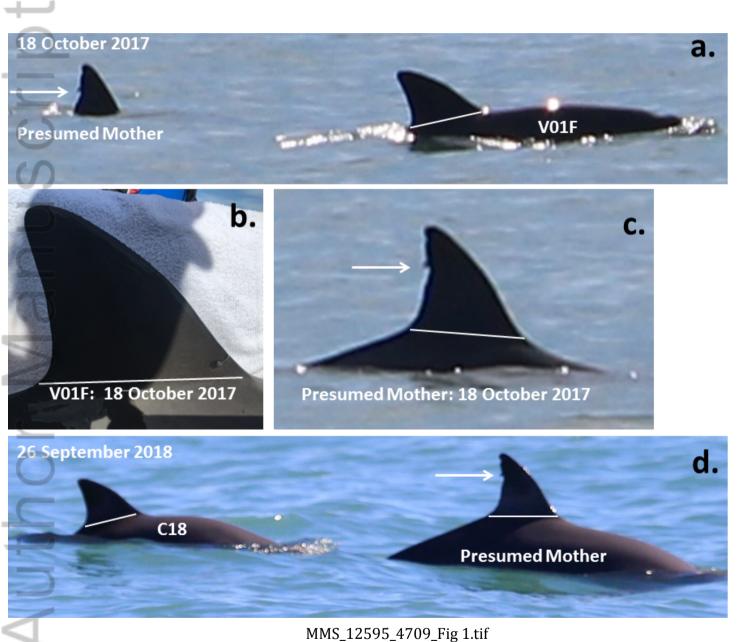
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Table 1. Total length (TL) in cm, sex (F, M) and maturity (adult or immature), and dorsal fin height (DH) in cm for vaquitas necropsied by R. L. Brownell, L. Torres, and O. Vidal (Brownell et al. 1986, Vidal 1995).

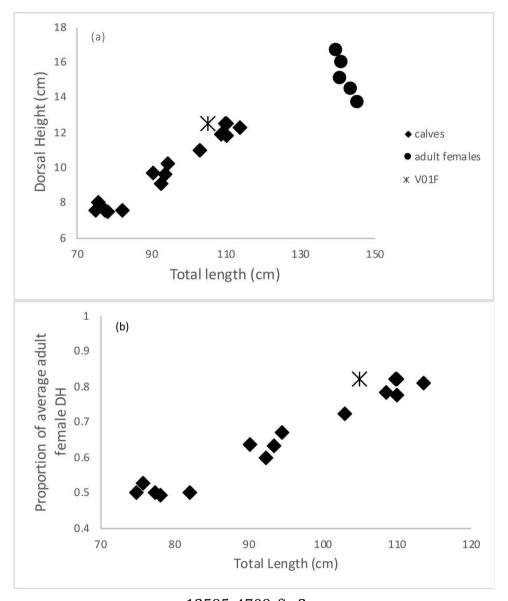
Date	${ m TL}$	Sex	DH
14 May 1985	143.5	F ad	14.5
31 March 1991	140.5	F ad	15.1
24 February 1991	140.9	F ad	16
6 February 1993	145.2	F ad	13.7
13 March 1991	139.7	F ad	16.7
12 May 1985	110	F im	11.8
12 March 1990	74.9	F im	7.6
12 March 1985	108.6	F im	11.9
14 May 1985	90.3	F im	9.7
27 February 1990	109.8	F im	12.5
19 May 1991	92.5	F im	9.1
12 March1985	103	M im	11
17 May 1985	110	M im	12.5
14 May 1985	93.5	M im	9.6
14 May 1985	94.5	M im	10.2
8 April 1990	78.2	M im	7.5
11 April 1990	75.8	M im	8
26 May 1990	113.7	M im	12.3
9 April 1991	77.5	M im	7.6
21 April 1991	82.2	M im	7.6
18 October 2017	105	V01F	12.5

Table 2. Data from table 3 of Hohn et al. 1996 reordered by month and day. The added column on whether the individual had evidence for ovulating in successive years is "incomplete" if all years did not have data to evaluate the question and "na" if the date of death was in March before the current year could be reliably evaluated.

		_	History of recent ovulations			_
Date of death (mo d yr)	Age (yr)	Current reproductive status	Prior year	Past year	Current year	Ovulating in successive years
02 06 93	13	Pregnant	N	Y	?	incomplete
02 24 91	14	Pregnant	Y	Y	?	Y
03 13 85	12	Lactating	;	Y	?	na
03 13 85	11	Lactating	;	Y	?	na
03 13 91	11	Lactating	N	Y	N	na
03 31 91	7	Lactating	N	Y	N	na
04 08 90	13	Lactating	Y	Y	N	Y
05 14 85	15	Lactating	3	Y	Y	Y



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