



Passive acoustic monitoring of the decline of Mexico's critically endangered vaquita

Armando Jaramillo-Legorreta,* ¶ Gustavo Cardenas-Hinojosa,* † Edwyna Nieto-Garcia,* Lorenzo Rojas-Bracho,* Jay Ver Hoef,‡ Jeffrey Moore,§ Nicholas Tregenza,** Jay Barlow,§ Tim Gerrodette,§ Len Thomas,†† and Barbara Taylor§

*Instituto Nacional de Ecología y Cambio Climático/SEMARNAT, Coordinación de Investigación y Conservación de Mamíferos Marinos, CICESE Camper 10, Carretera Ensenada-Tijuana 3918, Zona Playitas, Ensenada, B.C., 22860, México

†Departamento de Biología de la Conservación, Centro de Investigación Científica y Educación Superior de Ensenada, Carretera Ensenada-Tijuana 3918, Zona Playitas, Ensenada, Baja California, CP 22860, México

‡Alaska Fisheries Science Center, NOAA Fisheries, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Building 4, Seattle, WA 98115, U.S.A.

§Southwest Fisheries Science Center, NOAA Fisheries, Protected Resources Division, 8901 La Jolla Shores Dr., La Jolla, CA 92037, U.S.A.

**Chelonia Limited, The Barkhouse, Mousehole TR196PH, U.K.

††University of St Andrews, Centre for Research into Ecological and Environmental Modelling, The Observatory, Buchanan Gardens, St Andrews, Fife KY16 9LZ, U.K.

Abstract: *The vaquita (Phocoena sinus) is the world's most endangered marine mammal with approximately 245 individuals remaining in 2008. This species of porpoise is endemic to the northern Gulf of California, Mexico, and historically the population has declined because of unsustainable bycatch in gillnets. An illegal gillnet fishery for an endangered fish, the totoaba (Totoaba macdonaldi), has recently resurged throughout the vaquita's range. The secretive but lucrative wildlife trade with China for totoaba swim bladders has probably increased vaquita bycatch mortality by an unknown amount. Precise population monitoring by visual surveys is difficult because vaquitas are inherently hard to see and have now become so rare that sighting rates are very low. However, their echolocation clicks can be identified readily on specialized acoustic detectors. Acoustic detections on an array of 46 moored detectors indicated vaquita acoustic activity declined by 80% between 2011 and 2015 in the central part of the species' range. Statistical models estimated an annual rate of decline of 34% (95% Bayesian credible interval -48% to -21%). Based on results from 2011 to 2014, the government of Mexico enacted and is enforcing an emergency 2-year ban on gillnets throughout the species' range to prevent extinction, at a cost of US\$74 million to compensate fishers. Developing precise acoustic monitoring methods proved critical to exposing the severity of vaquitas' decline and emphasizes the need for continual monitoring to effectively manage critically endangered species.*

Keywords: extinction, *Phocoena sinus*, population decline, statistical modeling

Monitorización Acústica Pasiva del Declive de la Críticamente Amenazada Vaquita de México

Resumen: *La vaquita (Phocoena sinus) es el mamífero marino en mayor peligro de extinción, con aproximadamente 245 individuos existentes en 2008. Esta especie de marsopa es endémica de la parte norte del Golfo de California, México, e históricamente su población ha declinado por causa de la captura accidental en redes agalleras. La pesca ilegal con redes agalleras de un pez en peligro, la totoaba (Totoaba macdonaldi), ha resurgido recientemente en la zona de distribución de la vaquita. El lucrativo y oculto mercado de fauna con China, por la vejiga de la totoaba, probablemente ha incrementado la mortalidad por captura accidental de la vaquita en una cantidad desconocida. El monitoreo preciso de la población por medio de censos visuales*

¶email ajaramil@cicese.mx

Paper submitted April 21, 2016; revised manuscript accepted June 17, 2016.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

es difícil porque las vaquitas son difíciles de ver por naturaleza y actualmente se han vuelto tan raras que las tasas de avistamiento son muy bajas. Sin embargo, sus chasquidos de eco-localización pueden ser identificados certeramente con detectores acústicos especializados. Las detecciones acústicas obtenidas en una malla de 46 detectores anclados al fondo indicaron que la actividad acústica de la vaquita declinó en un 80 % entre 2011 y 2015 en la parte central de la distribución de la especie. Dos modelos estadísticos estimaron una tasa anual de declive del 34 % (intervalo de credibilidad bayesiano al 95% de -48 % a -21 %). Con base en los resultados del 2011 al 2014, el gobierno de México promulgó, y está haciendo cumplir, una prohibición de emergencia de 2 años para el uso de redes agalleras en toda la distribución de la especie para prevenir su extinción, con un costo de \$74 millones de dólares para compensar a los pescadores. El desarrollo de métodos precisos de monitorización acústica resultó ser crítico para exponer la severidad del declive de la vaquita y enfatiza la necesidad de una monitorización continua para manejar efectivamente a especies críticamente amenazadas.

Palabras Clave: declive poblacional, extinción, modelado estadístico, *Phocoena sinus*

Introduction

The global bycatch of marine mammals in fishing nets is estimated to be over 600,000 animals/year and is a great threat to many species (Read et al. 2006; Reeves et al. 2013). Fishery bycatch contributed substantially to the extinction of the Yangtze River dolphin (*Lipotes vexillifer*) in China (Turvey et al. 2007) and threatens several species and subspecies of dolphins and porpoises (Reeves et al. 2013). This unsustainable bycatch occurs often in developing countries, even those with sophisticated fisheries management programs, given that small-scale fisheries receive little attention from managers (Reeves et al. 2013). Solutions that could prevent extinctions are not being implemented in many countries due to a lack of political will, of convincing evidence of unsustainable bycatch rates, and sometimes of viable alternative fishing gear (Reeves et al. 2013).

The vaquita (*Phocoena sinus*) is a small porpoise endemic to the northern Gulf of California, Mexico (Rojas-Bracho & Reeves 2013). Its geographic distribution is entirely within an 11,594 km² area with high fish and shrimp productivity and with easy access for small-scale fisheries. Vaquitas have been subject to a long history of unsustainable bycatch (Rojas-Bracho & Reeves 2013). The species was listed as endangered under the U.S. Endangered Species Act in 1985 and Mexico's equivalent law in 1994 and as critically endangered by the International Union for Conservation of Nature and Natural Resources in 1996. Vaquita bycatch occurs in entangling nets used by small fishing vessels for shrimp and finfish (D'Agrosa et al. 2000). Fishing income is critical to the economy for the 2 villages adjacent to the range of the species (Blanco-Orozco 1998) (Fig. 1). A long-standing illegal fishery for an endangered fish species, the totoaba (*Totoaba macdonaldi*) (Fig. 2), has boomed in this area within the past 3 years, fueled by a new and lucrative illegal trade with China for totoaba swim bladders (Valenzuela-Quiñonez et al. 2015; EIA 2016). Fishers have reported receiving up to US\$5,000 on the black market in recent years for the swim bladder of a large totoaba

(Valenzuela-Quiñonez et al. 2015). Of the documented 128 vaquitas caught in gillnets from 1985 to 1992, 65% were caught in totoaba nets, which have a mesh size from 20.0 to 30.5 cm (Vidal 1995). The reported boom in illegal totoaba fishing increased the risk of bycatch to vaquitas, but the secretive nature of the fishery made direct estimation of the impact impossible.

Initially, the decline in vaquita abundance was inferred from the high estimated bycatch (D'Agrosa et al. 2000) relative to the low estimated population size (Jaramillo-Legorreta et al. 1999). Later, it was measured directly from visual surveys in 1997 (567 individuals, 95% Confidence Interval 177–1073) and 2008 (245 individuals, 95% Confidence Interval 68–884) that showed a total decrease of 57%, corresponding to an average annual rate of change of -7.6% (Gerrodette et al. 2011). Vaquitas echolocate nearly continuously to find prey, which makes acoustic signals a viable metric to detect trends in abundance. Anchored boat-based acoustic detectors deployed at random sites from 1997 to 2007 throughout the range of vaquitas revealed a -7.6%/year rate of change in acoustic encounters (total decline of 58%) (Jaramillo-Legorreta 2008). The congruence of the visual and acoustic inference over the same period supports our assumption that acoustic detection rates are proportional to population abundance.

In response to the estimated decline (Jaramillo-Legorreta 2008), the government of Mexico implemented a recovery plan in 2008 (described in Rojas-Bracho & Reeves [2013]) that included a fishing ban inside the Vaquita Refuge (including compensation for fishers) (Fig. 1) and a reduction of fishing with gillnets based on a buy-out program (compensation for cancellation of fishing permits and boats). Approximately 50% of the total population occurred in the refuge (Gerrodette & Rojas-Bracho 2011). Although enforcement appeared effective within the refuge during the 2008 survey, the pilot study for our acoustic-monitoring program lost 9 of 15 acoustic detectors within the refuge from 30 October 2010 to 3 March 2011 during the shrimping season. Few detectors were lost when monitoring occurred in summer months

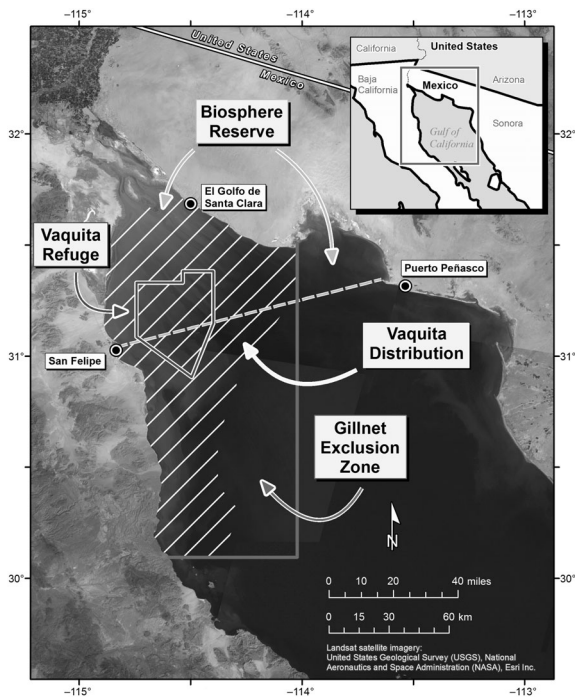


Figure 1. Gillnet exclusion zone in the upper Gulf of California, which includes all the distribution area of vaquitas (hatched area).

when there is little fishing. Therefore, it is likely that illegal fishing within the refuge was common prior to the recent 2-year ban. Based on the preliminary results of this monitoring study, the government of Mexico implemented an emergency ban on gillnet fishing throughout the known range of the vaquita in May 2015 (Fig. 1). Enforcement of the temporary 2-year ban is coordinated by the Mexican Navy. To facilitate enforcement, the gillnet exclusion zone was given simple oceanic boundaries (a southern line just north of 30°N and an eastern line near 114°W) (Fig. 1).

Infrequent and expensive visual sighting surveys (in 1997 and 2008) proved an ineffective monitoring tool for the increasingly rare vaquita. In contrast, an early acoustic-monitoring program (1997–2007) was cost-effective and produced reasonably precise estimates of trends in acoustic detections (Rojas-Bracho et al. 2010). Therefore, starting in 2011, we conducted an expanded, 5-year, passive acoustic-monitoring program for the Vaquita Refuge. Initial examination of the acoustic monitoring data from 2011 to 2013 indicated a severe decline in vaquita and pointed to the need for strong management actions. However, the loss of some detectors meant that survey effort was not uniform over space and time within or between seasons, meaning that simplistic interpretation of the data could be biased. An expert statistical panel was formed in 2014 to provide analytical expertise and generate robust inferences from the data collected from 2011 to 2015.



Figure 2. Totoaba (being held) and vaquita atop gillnet (photo by Omar Vidal).

Methods

Acoustic Data Collection and Processing

The expected intrinsic growth rate for vaquita, based on estimates for closely related species (Reilly & Barlow 1986; Barlow & Boveng 1991; 1986; Slooten & Lad 1991; Woodley & Read 1991), is 4%/year. Accordingly, the goal was to design an acoustic monitoring program that could detect a vaquita population growth rate of this magnitude over 5 years (Rojas-Bracho et al. 2010). Variance in detection rates from earlier acoustic monitoring in 2008 indicated that approximately 5000 sampling days/year would yield the precision needed to meet the monitoring goal (Rojas-Bracho et al. 2010). To achieve this, we established a systematic array of 48 acoustic detectors in the refuge and 14 buoys around the perimeter that recorded transient signals (clicks) continuously for 3 months in each season. Detectors in all perimeter buoys and 2 deployed in the 48 sites inside the refuge were lost each year, and their deployment ended in 2013, resulting in data from 46 sites (Fig. 3). Results from 2008 indicated that, after testing several autonomous acoustic detectors, C-PODs (Tregenza et al. 2016) had the best detection distance (approximately 200 m) and the necessary battery life to obtain the quantity of data needed to meet our objectives (Rojas-Bracho et al. 2010). A C-POD stores temporal sequences of marine ultrasound (clicks) between 20 and 160 kHz, which are subsequently processed by pattern-recognition software (Castellote et al. 2012; Roberts & Read 2014; Tregenza et al. 2016). This algorithm (KERNO in C-POD software version 2.044) looks for coherent sequences of more or less regularly spaced clicks (i.e., click trains). All click trains identified as likely belonging to vaquita were visually inspected on screen and validated by experienced analysts using the guidelines provided by C-POD designer (available from <http://www.chelonia.co.uk/downloads/Validating%20cetacean%20detections.pdf>).

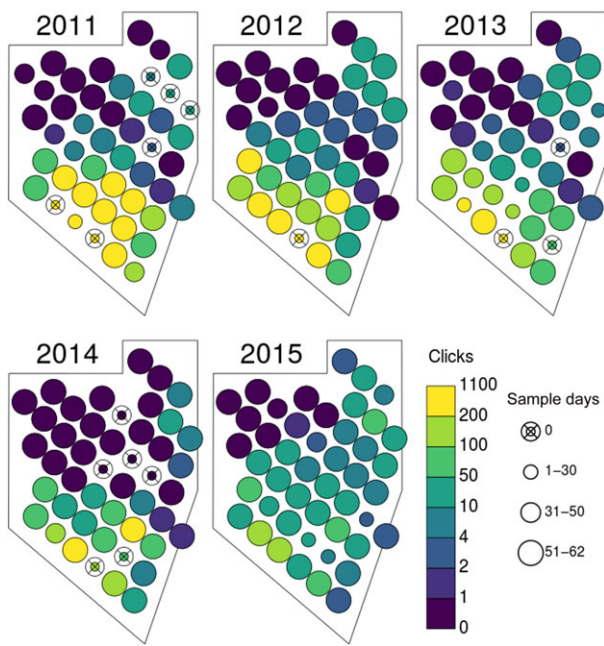


Figure 3. Estimated mean number of clicks per day predicted by the spatial model of vaquita acoustic activity for the 46 sampling sites with data for at least 1 year. Values in the key are posterior medians (log scale). Some sites (circle with an x) were missing in the indicated year. Sample days is the number of days with data in each site and year.

Although the sampling grid was designed to give equal coverage in space and time, in practice sampling was uneven due to shifts in the annual deployment of detectors and loss of data toward the end of deployment. To increase the robustness of the trend analysis (see below), we truncated the data set to a core sampling period within which at least 50% of the detectors were operating across all 5 years (details given in Supporting Information). Vaquita acoustic behavior may vary; thus, comparisons of detection rates between years could be confounded. We considered 3 factors related to sampling effort: season, time of day, and state of the tide (the northern Gulf of California has a tidal range of over 10 m). Use of the same core period for all years helped reduce any seasonal effects, and use of total acoustic counts per day averaged out diurnal effects. Tidal regimes among years were compared based on the number of hours sampled at each vertical tide speed component in intervals of 0.1 m/h with a Kruskal-Wallis analysis of variance test.

Acoustic Metric

Click trains have been quantified in various ways, including attempts to identify encounters of animals by breaks in click sequences and counts of clicks over defined periods (e.g., detection positive minutes [DPMs]) (Carlström 2005; Scheidat et al. 2011; Roberts & Read 2014). We

based our analysis on the total number of identified clicks in 24 h (i.e., daily click rates) for 2 reasons. First, this is the most direct form of detection data and does not require aggregation over time intervals such as minutes. Second, click rates are more likely to be proportional to animal density than metrics such as DPMs, which saturate at high density. For this last reason, click rates are frequently used as input to passive acoustic-density estimates (Marques et al. 2013).

Relating trends in click rates to trends in abundance assumes that there is no systematic change in animal vocal behavior. Checking this directly, for example, through focal follows or animal-borne tags is not feasible for vaquita. However, we undertook 2 simple exploratory diagnostics. First, we compared the distribution of the number of identified clicks per DPM between years to determine whether click rates changed over time. Second, we grouped clicks into encounters (periods of detected clicks with gaps of no longer than 30 min) and compared the relationship between encounter length and number of DPMs for each year to see whether there was any indication of changes in the patterns of clicking.

Trend Analyses

We used statistical modeling to make inferences about trends in click rate over time; the models accounted for nonuniform sampling over space and time. We explored several models: generalized additive models (GAMs) (e.g., Ruppert et al. 2003), where the covariates were the spatial coordinates; time series models (e.g., Brockwell & Davis 2013); spatial statistical models (geostatistical models) (e.g., Cressie 1993); spatiotemporal models (Cressie & Wikle 2011); and poststratification mixture models (Little & Rubin 2014). Initial fits for estimating annual trend among all sampling sites showed that all models gave similar results. We concentrated on models that were highly responsive to annual changes, so we discarded all time-series and spatiotemporal models, which smooth over time. The spatial GAM was substantially similar to the geostatistical model. The poststratification mixture model had connections to classical sampling methods and differed substantially in assumptions from the geostatistical model. We performed detailed analyses using the geostatistical and poststratification mixture models (full description of both models given in Supporting Information). Rather than choose between these 2 models, we used a simple average of their predictions. We did not formally weight models (e.g., Hoeting et al. 1999; Burnham & Anderson 2002) because the spatial model was based on a log transformation, which made likelihood-based weighting difficult, and because we wanted the results to be robust to model choice and not dominated by either model. Both models drew on the strength of the systematic sampling design, which

is efficient for spatially dispersed natural populations (Thompson 1992).

In the following, W_{it} is the mean number of clicks per day for i th site ($i = 1, \dots, 46$) in the t th year ($t = 2011, \dots, 2015$) and S_{it} is an estimate of W_{it} when acoustic-detector data are missing, or smoothed spatial estimates, or stratum means, depending on the method. An annual index of acoustic activity based on the click data is then

$$B_t = \frac{1}{K} \sum_{i=1}^K S_{it} \quad (1)$$

for $K = 46$ sampling sites. Annual changes in acoustic activity were computed as B_{t+1}/B_t . For the 5-year trend, we used the geometric mean of the annual changes, which simplified to $\lambda = (B_{2015}/B_{2011})^{1/4}$. Both geostatistical and poststratification mixture models were fitted under a framework of Bayesian analysis sampling from the posterior distributions. For this operation, we used Markov chain Monte Carlo methods and the software packages WinBugs and OpenBugs (Lunn et al. 2000). For both models, we discarded the first 10,000 samples (burn-in) and continued with 1,000,000 further iterations. Every 100th sample was retained for posterior distribution summaries.

Spatial Model

Spatial statistical models are used increasingly for wildlife data (Ver Hoef 2008). They are often used in hierarchical models (e.g., Cressie et al. 2009) that separate the noisy observation process from a smoother spatial surface (Royle et al. 2007). The number of clicks encountered at a sampling site was considered a noisy sample of an underlying use surface because of the stochastic movements of vaquitas. There was also unequal effort at sites because some sites had no data in some years. The hierarchical spatial model partitioned variability into a spatially smooth surface and into independent random error, where the variance of the independent part decreased proportionally as effort increased (number of sampling days). The estimated surface of vaquita use, then, was the predicted spatial surface. Each year was treated independently for predictions, but autocorrelation parameters were estimated by pooling across years.

The spatial model was a lognormal mixed model (i.e., data assumed normal on log scale) with a spatially autocorrelated random effect. We transformed data by adding 1 and taking the log of the values (i.e., $Y_{it} = \log[W_{it} + 1]$) because some $W_{it} = 0$. The transformed data had reasonable variance:mean properties for a Gaussian model (details given in Supporting Information). The transformed data were modeled as

$$Y_{it} | \mu_t, Z_{it}, \sigma_\varepsilon^2, n_{it} \sim \text{Normal}(\mu_t + Z_{it}, \sigma_\varepsilon^2 / n_{it}), \quad (2)$$

where μ_t is the expected mean number of clicks per day across sites in year t , Z_{it} is a spatially autocorrelated random effect allowing the number of clicks per day at each site within a year to depart from the overall mean (with sites in closer proximity to each other expected to have more similar departures from the overall mean), and σ_ε^2 is the variance for spatially independent random error weighted by variable sampling effort (number of site-days, n_{it}) across sites. We used an exponential model for spatial autocorrelation among Z_{it} within year (Chiles & Delfiner 2009). All parameters had noninformative priors (Supporting Information). The Markov chain Monte Carlo samples from the posterior distribution of $\mu_t + Z_{it}$ formed the estimates for $S_{it} = \exp(\mu_t + Z_{it}) - 1$ and subsequently the posterior distributions for B_t and λ , our primary quantities of interest.

Poststratification Mixture Model

Mixture models have been applied to diverse types of ecological analyses to deal with overdispersed data (Martin et al. 2005; Rhodes 2015). The basic concept is to treat the data as having arisen from a mixture of processes rather than a single process. Here, the values of W_{it} within a year were assumed to arise from a mixture of negative binomial processes. Within a generalized linear mixed model framework, we assigned individual sites probabilistically to 1 of $V = 3$ strata based on the level of detections they received across the 5 years of sampling (i.e., each site is assumed to be in a consistently high click-rate, medium click-rate, or low click-rate stratum [data provided strong evidence for these consistencies]). Estimates of S_{it} for individual sites within each year were the estimated means for the strata to which the sites are assigned.

We used $\theta_{v[i],t}$ (the mean click rate in year t for each of the V strata to which site i was attributed) as the main parameter to infer acoustic activity rates. We let X_{it} be the total number of clicks recorded at i in year t (i.e., $W_{it} * n_{it}$). Because X_{it} was overdispersed for a Poisson model, it was treated with a negative binomial distribution, and the expected value was the product of the estimated $\theta_{v[i],t}$ and effort n_{it} :

$$X_{it} \sim \text{negative binomial}(p_{it}, r_{v[i],t}), \quad (3)$$

where p_{it} and $r_{v[i],t}$ are negative binomial parameters and $\theta_{v[i],t} n_{it} = r_{v[i],t} (1-p_{it})/p_{it}$ is the expected value of X_{it} . Thus, variable sampling effort across sampling sites was addressed through its effect on the expected value and variance of X_{it} .

Individual sampling sites were probabilistically assigned to the 3 click-rate strata v based on the data recorded at i across the years during which site i had data, which were given a multinomial distribution,

$$v[i] \sim \text{multinomial}(\mathbf{s}_{vi}), \quad (4)$$

where \mathbf{s}_{vi} is the vector of estimated probabilities for i being in stratum v . The vector \mathbf{s}_{vi} was assumed to have a Dirichlet prior distribution (Supporting Information). The degree of certainty in assigning a site to a particular stratum depended on how correlated detections were at that site through time. Sites with consistently low or high levels of detections (relative to others within a year) were assigned to a stratum with greater confidence, and, all else being equal, sites with 5 years of data were assigned more confidently to a stratum than sites with fewer years of data. For purposes of calculating B_t , $S_{it} = \theta_{v[i],t}$. Thus, uncertainty in group assignment was propagated through to estimates of B_t and λ . Information across years was shared for the purpose of assigning each sampling site to a particular group v , but the means and variances for each $\theta_{v[i],t}$ were independent. Predicted estimates for sites in years with missing data were based on the probability of belonging to group v and the conditional mean and variance for $\theta_{v[i],t}$. Further prior distributions for the model are given in Supporting Information.

Results

Acoustic Data and Metric

After truncating days in which <50% of the detectors were operating, the remaining core sampling period was 62 days (19 June through 19 August). The number of sample days per year per site is shown in Fig. 3. The distribution of tide speeds in the core sampling period did not differ significantly among years (Kruskal-Wallis $H=1.425$, $df = 4$, $n = 7440$, $p = 0.84$). We were therefore confident in proceeding without accounting for any effect of tide on detections.

We found no evidence that acoustic behavior changed over time. The distribution of clicks/DPM was very similar between years. Means were from 48 to 53 (SD 76–82), whereas the relationship between encounter duration and number of DPMs was approximately linear with a very similar slope in each year (0.22 and 0.28 DPM/min). Detailed results are provided in Supporting Information as is the entire acoustic data set.

Trend Analyses

Model-averaged estimates of annual rates of change in acoustic activity were -17% , -3% , -46% , and -35% between successive years from 2011 to 2015. The geometric mean for the annual rate of decline from 2011 to 2015 was -34% /year (95% posterior Credibility Interval -48% to -21%) (Fig. 4). If acoustic activity is proportional to abundance, it was certain that the population declined (100% of the posterior distribution for the 2011–2015 average rate of change was < 0) (Fig. 4), and there was a 98% probability that it declined more

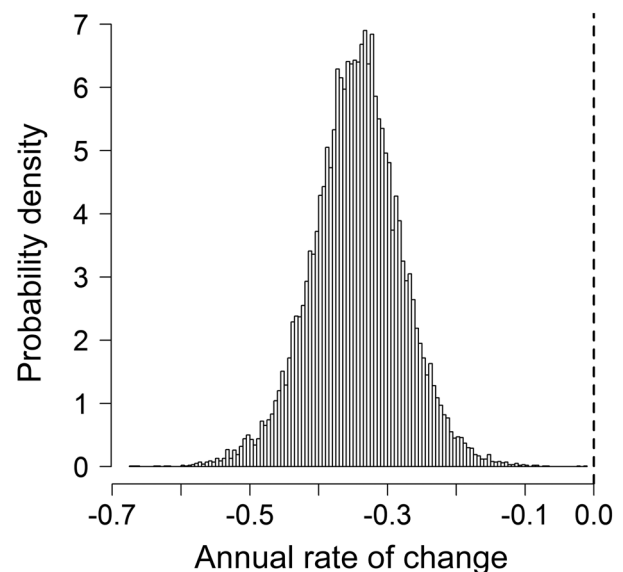


Figure 4. Posterior probability distribution for annual rate of change in mean clicks per day of vaquita from the pooled spatial and nonspatial mixture models. The vertical broken line is at the level of zero population growth, and 100% of the distribution is within the area of population decline.

than 20%/year. The estimated total decline for 2011–2015 was 80% (95% Credibility Interval 62–93%). Site-specific estimates of mean click rate from the spatial model showed that in the southern portion of the refuge, where vaquita acoustic activity was highest, acoustic activity rates decreased throughout the study period (Fig. 3), and the most notable decline occurred after 2012.

Discussion

A robust acoustic monitoring program revealed a catastrophic decline of the vaquita population over 4 years, following decades of already steep decline (figure 7A in Gerrodette & Rojas-Bracho [2011]). The accelerated collapse—with vaquita numbers decreasing by 34%/year relative to 7.6%/year from 1997 to 2008—illuminates the drastic impact of the illegal totoaba fishery (Valenzuela-Quiñonez et al. 2015, EIA 2016). Our preliminary analyses of these data in 2014 (CIRVA 2015) motivated the Mexican government to enact and enforce a 2-year gillnet ban and to compensate fishers and processors for US\$74 million in lost income. As noted repeatedly by the international recovery team (CIRVA 2015), alternative fishing gears need to replace gillnets to allow both fishing and vaquitas to coexist.

Our interpretation that the observed decline in acoustic activity represents a population decline is broadly

plausible, given that trends from independent visual and acoustic surveys have been nearly identical in the past. This interpretation depends on 2 key assumptions. First, acoustic activity is proportional to abundance within the monitored area (i.e., the Vaquita Refuge). Second, the proportion of the population within the monitored area during the sampling period shows no systematic trend. Acoustic monitoring was only possible in areas and at times with limited gillnet and trawl fishing, which in practice meant inside the Vaquita Refuge from June through September. Experiments with replica acoustic detectors outside the Refuge resulted in loss of nearly all equipment.

Regarding the first assumption, the acoustic measure we used, click rate, is proportional to abundance if 3 factors remain constant: average animal click production rate, effective click-detection range, and false-positive rate (Marques et al. 2013). We could not measure click production rate. However, it is essential for foraging and navigation, and we have no reason to suppose it varied systematically between years. We found no pattern in the acoustic metrics we examined, such as the number of clicks per detection-positive minute (although we recognize this gives only a partial picture). Factors that may affect acoustic behavior such as moon phase were balanced between years, and the same 62 calendar days were used in each year. Effective detection ranges were also not measured, but again there is no reason to expect systematic changes in click source level, click propagation, or background noise among years. For false-positive rate, manual screening of detections ensured that this was negligible in all years.

Regarding the second assumption (constant proportion of the population monitored), the spatial pattern of acoustic detections remained relatively constant within the Refuge across years (Fig. 3), giving some indication that spatial distribution did not change. Moreover, the spatial distribution of vaquitas was remarkably constant both within and outside the Refuge between the 1997 and 2008 visual surveys; vaquita density outside the Refuge was low (Rojas-Bracho et al. 2010). Further evidence comes from a 2015 combined visual (waters 20–50 m deep) and acoustic survey of vaquitas throughout their plausible range (Supporting Information). Nearly all sightings and all but a few acoustic detections from that survey were within the Vaquita Refuge (Supporting Information). No sightings were made to the south or east of the Refuge, indicating the distribution of vaquitas has not shifted to that area to account for the large decline observed within the refuge (i.e., monitoring) area. However, visual data from 1997, 2008, and 2015 show a slight contraction of distribution from the southern portion of the range (B. T., personal observation). Hence, the rate of decline could be slightly underestimated.

Our work is an example of the importance of conducting well-designed, cost-effective, and precise monitoring

to provide undeniable evidence of population decline and thereby prompt government action. Our approach may be useful as a template for monitoring other critically endangered species, which are often difficult to monitor precisely through visual or other conventional means. The use of an external statistical panel of international leaders in their field proved valuable for expediting data analysis, because these experts specialized in the modeling needed for this particular data set. Also, the composition of the panel minimized politically motivated debate concerning the credibility of results, given that they were not directly connected to conservation strategies for vaquita. Two experts took 2 very different modeling approaches that yielded very similar results, which increases confidence in the result that vaquitas have declined rapidly.

Given that we estimated the population to have declined by 80% in 4 years and that vaquitas numbered around 200 at the start of this period, the emergency gillnet ban was clearly needed to save vaquitas. Should gillnetting resume at recent levels that resulted in an annual loss of 34%, vaquitas could quickly go extinct, and Mexico would lose its largest endemic mammal. Vaquitas are not the only cetacean species close to extinction. The most endangered populations of porpoises and dolphins in the world suffer from similar gillnet threats, plus additional threats of habitat loss and degradation (Reeves et al. 2013). Mexico has taken a progressive step by temporarily banning gillnets and moving toward replacing shrimp gillnets with alternative vaquita-friendly gear (DOF 2013). But long-term actions are urgently needed if the vaquita is to be saved. Mexico can shine as a world leader by solving the cetacean-gillnet crisis in its waters or follow China in being the next to lose an endemic cetacean species.

Acknowledgments

Different institutions and agencies provided funding during the development and implementation of the acoustic monitoring program. We are especially grateful to the U.S. Marine Mammal Commission for their support from the very early stages of the acoustic monitoring, in particular T. Ragen, R. Lent, and P. Thomas. O. Vidal and E. Sanjurjo from World Wildlife Fund (WWF) Mexico supported our program through different grants. B.L.T. provided some personal funding. We thank Le Equipe Cousteau, The Ocean Foundation, Fonds de Dotation pour la Biodiversité, MAAF Assurances (Save Your Logo), WWF-US, and Opel Project Earth. The Southwest Fisheries Science Center, NOAA Fisheries, supported several coauthors' time and the ship time for the 2008 survey to test acoustic equipment. We also thank L. Ballance for marshalling NOAA support and A. Henry for logistical support throughout. We express our sincere thanks to the Mexican Secretaría del Medio Ambiente y Recursos

Naturales (SEMARAT), the Instituto Nacional de Ecología (INE), Comisión Nacional de Áreas Naturales Protegidas (CONANP), and the Directorate of the Reserva de la Biósfera del Alto Golfo de California y Delta del Río Colorado. Many thanks to our field staff J. Osuna, P. Valverde, R. Arozamena, and all the fishers who deployed and recovered the equipment. We thank R. Pitman, K. Forney, and anonymous reviewers for helpful comments and improvements to the manuscript. Finally, we dedicate this paper to the memory of J. Campoy, former director of the Biosphere Reserve, who championed the conservation of the upper Gulf of California. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of the U.S. National Oceanic and Atmospheric Administration or the Department of Commerce.

Supporting Information

Details of the examination of the data for potential effects of tide, time of day, season, and acoustic metric and detailed descriptions and results from the spatial model and the poststratification model (Appendix S1) and the full acoustic data set (Appendix S2) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than the absence of the material) should be directed to the corresponding author.

Literature Cited

- Barlow J, Boveng P. 1991. Modelling age-specific mortality for marine mammal populations. *Marine Mammal Science* **7**:84–119.
- Blanco-Orozco ML. 1998. Pobreza y explotación de recursos pesqueros en el Alto Golfo de California. *Comercio Exterior* **48**:1002–1011.
- Brockwell PJ, Davis RA. 2013. *Time series: theory and methods*. Springer Science & Business Media, New York.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media, New York.
- Carlström J. 2005. Diel variation in echolocation behavior of wild harbor porpoises. *Marine Mammal Science* **21**:1–12.
- Castellote M, Leeney RH, O’Corry-Crowe G, Lauhakangas R, Kovacs K, Lucey W, Krasnova V, Lydersen C, Stafford KM, Belikov R. 2012. Monitoring white whales (*Delphinapterus leucas*) with echolocation loggers. *Polar Biology* **36**:493–509.
- Chiles JP, Delfiner P. 2009. *Geostatistics: modeling spatial uncertainty*. John Wiley & Sons, New York.
- CIRVA (Comité Internacional para la Recuperación de la Vaquita). 2015. Report of the Sixth meeting of the Comité Internacional para la Recuperación de la Vaquita (CIRVA-VI). Annex L, appendix 2. Report of the 66a meeting of the Scientific Committee. International Whaling Commission, Cambridge, United Kingdom.
- Cressie N. 1993. *Statistics for spatial data*. John Wiley & Sons, New York.
- Cressie N, Calder CA, Clark JS, Ver Hoef JM, Wikle CK. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications* **19**:553–570.
- Cressie N, Wikle CK. 2011. *Statistics for spatio-temporal data*. John Wiley & Sons, New York.
- D’Agrosa C, Lennert-Cody CE, Vidal O. 2000. Vaquita bycatch in Mexico’s artisanal gillnet fisheries: driving a small population to extinction. *Conservation Biology* **14**:1110–1119.
- DOF (Diario Oficial de la Federación). 2013. Norma Oficial Mexicana NOM-002-SAG/PESC-2013. Secretaría de Agricultura, Ganadería, Pesca y Alimentación. DOF 11 July, Mexico City.
- EIA (Environmental Investigation Agency). 2016. Briefing to the 66th Standing Committee of CITES: January 11–15. Dual extinction: the illegal trade in the endangered totoaba and its impact on the critically endangered vaquita. EIA, London. Available from <https://eia-international.org/wp-content/uploads/EIA-Dual-Extinction.pdf> (accessed August 2016).
- Gerrodette T, Rojas-Bracho L. 2011. Estimating the success of protected areas for the vaquita, *Phocoena sinus*. *Marine Mammal Science* **27**:E101–E125.
- Gerrodette T, Taylor BL, Swift R, Rankin S, Jaramillo-Legorreta AM, Rojas-Bracho L. 2011. A combined visual and acoustic estimate of 2008 abundance, and change in abundance since 1997, for the vaquita, *Phocoena sinus*. *Marine Mammal Science* **27**:E79–E100.
- Hoeting JA, Madigan D, Raftery AE, Volinsky CT. 1999. Bayesian model averaging: a tutorial. *Statistical Science* **14**:382–401.
- Jaramillo-Legorreta AM. 2008. Estatus actual de una especie en peligro de extinción, la vaquita (*Phocoena sinus*): una aproximación poblacional con métodos acústicos y bayesianos. PhD dissertation. Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico.
- Jaramillo-Legorreta AM, Rojas-Bracho L, Gerrodette T. 1999. A new abundance estimate for vaquitas: first step for recovery. *Marine Mammal Science* **15**:957–973.
- Little RJ, Rubin DB. 2014. *Statistical analysis with missing data*. John Wiley & Sons, New York.
- Lunn DJ, Thomas A, Best N, Spiegelhalter D. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* **10**:325–337.
- Marques TA, Thomas L, Martin SW, Mellinger DK, Ward JA, Moretti DJ, Harris D, Tyack PL. 2013. Estimating animal population density using passive acoustics. *Biological Reviews* **88**:287–309.
- Martin TG, White BA, Rhodes JR, Kuhnert PM, Field SA, Low-Choy SJ, Tyre AJ, Possingham HP. 2005. Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. *Ecology Letters* **8**:1235–1246.
- Read AJ, Drinker P, Northridge S. 2006. Bycatch of marine mammals in U.S. and Global Fisheries. *Conservation Biology* **20**:163–169.
- Reeves RR, McClellan K, Werner TB. 2013. Marine mammal bycatch in gillnet and other entangling net fisheries, 1990 to 2011. *Endangered Species Research* **20**:71–97.
- Reilly SB, Barlow J. 1986. Rates of increase in dolphin population size. *Fishery Bulletin* **84**:527–533.
- Rhodes JR. 2015. Mixture models for overdispersed data. Pages 284–306 in Fox GA, Negrete-Yankelevich S, Sosa VJ, editors. *Ecological statistics: contemporary theory and application*. Oxford University Press, Oxford, United Kingdom.
- Roberts BL, Read AJ. 2014. Field assessment of C-POD performance in detecting echolocation click trains of bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science* **31**:169–190.
- Rojas-Bracho L, et al. 2010. Assessing trends in abundance for vaquita using acoustic monitoring: within refuge plan and outside refuge research needs. Workshop report—October 19–23, 2009. Technical memorandum NOAA-TM-NMFS-SWFSC-459. National Oceanic and Atmospheric Administration, La Jolla, California.
- Rojas-Bracho L, Reeves RR. 2013. Vaquitas and gillnets: Mexico’s ultimate cetacean conservation challenge. *Endangered Species Research* **21**:77–87.
- Royle JA, Kéry M, Gautier R, Schmid H. 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs* **77**:465–481.

- Ruppert D, Wand MP, Carroll RJ. 2003. Semiparametric regression (No. 12). Cambridge University Press, Cambridge, United Kingdom.
- Scheidat M, Tougaard J, Brasseur S, Carstensen J, van Polanen Petel T, Teilmann J, Reijnders P. 2011. Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. *Environmental Research Letters* **6**:1–10.
- Slooten E, Lad F. 1991. Population biology and conservation of Hector's dolphin. *Canadian Journal of Zoology* **69**:1701–1707.
- Thompson SK. 1992. Sampling. John Wiley & Sons, New York.
- Tregenza N, Dawson S, Rayment W, Verfuss U. 2016. Listening to echolocation clicks with PODs. Pages 163–206 in Au WWL, Lammers MO, editors. *Listening in the ocean, modern acoustics signal processing*. Springer, New York.
- Turvey ST, et al. 2007. First human-caused extinction of a cetacean species? *Biology Letters* **3**:537–540.
- Valenzuela-Quñonez F, Arreguín-Sánchez F, Salas-Márquez S, García-De León FJ, Barza JC, Román-Rodríguez MJ, De-Anda-Montañez JA. 2015. Critically endangered totoaba *Totoaba macdonaldi*: signs of recovery and potential threats after a population collapse. *Endangered Species Research* **29**:1–11.
- Ver Hoef JM. 2008. Spatial methods for plot-based sampling of wildlife populations. *Environmental and Ecological Statistics* **15**:3–13.
- Vidal O. 1995. Population biology and incidental mortality of the vaquita, *Phocoena sinus*. Report of the International Whaling Commission (Special Issue 16):247–272. International Whaling Commission. Cambridge, United Kingdom.
- Woodley TH, Read AJ. 1991. Potential rates of increase of a harbour porpoise (*Phocoena phocoena*) population subjected to incidental mortality in commercial fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:2429–2435.

