Letters

Inference from limited data: A response to Lonergan

TIM GERRODETTE,[1] NOAA National Marine Fisheries Service, Southwest Fisheries Science Center, 3333 North Torrey Pines Court, La Jolla, California 92037, U.S.A.; LORENZO ROJAS-BRACHO, Instituto Nacional de Ecología, Centro de Investigación Científica y de Educación Superior de Ensenada, 107 Carretera Ensenada-Tijuana, Ensenada, Baja California 22860, Mexico.

Lonergan (2012) criticized the analysis of Gerrodette and Rojas-Bracho (2011), who estimated the success of three possible protected areas for the critically endangered vaquita (*Phocoena sinus*) proposed under the Action Plan for the Conservation of Vaquitas. We fitted a Bayesian population model to the limited data available for this rare cetacean. Lonergan asserted that the data were not sufficient to reach the conclusions that we reported. In one sense, Lonergan's concern is understandable: it *is* amazing that useful conclusions can be drawn from such sparse data. But that was not due to unreasonable assumptions or model structure as Lonergan claimed. Rather, our analysis demonstrated the remarkable power of modern statistical methods.

Some of the criticisms of Lonergan (2012) were misstatements about what the model of Gerrodette and Rojas-Bracho (2011) did or assumed. Lonergan incorrectly stated that the parameter for scaling the partial 1993 abundance estimate was not linked to other data, but the parameter was directly estimated by the 1997 data. Lonergan incorrectly stated that we used a single acoustic detection rate in all years. What we assumed was that the rate (acoustic vaquita detections per hour) was proportional to abundance. Observed acoustic rates decreased between 1997 and 2007 (fig. 7 of Gerrodette and Rojas-Bracho 2011), which we interpreted as evidence of a decline in vaquita abundance. Lonergan incorrectly stated that our model assumed that the decline in abundance was exponential. The change in vaquita abundance each year depended on bycatch, which in turn depended on fishing effort (eq. 1, 2 in Gerrodette and Rojas-Bracho 2011). Fishing effort increased between 1993 and 2007, then decreased sharply in 2008 and 2009, so changes were not exponential. Lonergan thought that the high vaquita bycatch in 1993 was "difficult to reconcile

[1] Corresponding author (e-mail: tim.gerrodette@noaa.gov).

with the population having been stable at that time." We did not assume that the vaquita population was stable in 1993; it had been declining for decades before that (Jaramillo-Legorreta 2008). Lonergan's comment may have been prompted by a slightly misleading description of the prior used for the initial (1992) abundance in the model. We described the prior as informative because it used pre-1992 data. In fact, the variance of the prior was large (table 2 in Gerrodette and Rojas-Bracho 2011), so the prior was only minimally informative. A uniform prior for initial abundance gave virtually identical results.

Other inconsistencies that Lonergan claimed to find were the result of inappropriate comparisons. For example, Lonergan found that the conclusion that the Vaquita Refuge Area (Option 1) had an 8% chance of succeeding was "hard to reconcile" with the estimate that there was an 11% chance that the unprotected population increased between 1997 and 2008. However, the 11% estimate was based on comparing 1997 and 2008 point estimates only (Gerrodette *et al*. 2011), while the 8% estimate was based on the 2008 data combined with other available data in a population model (Gerrodette and Rojas-Bracho 2011). The other available data were two previous population estimates (one of them partial) over a 16 yr period, a single partial estimate of vaquita bycatch during that period, 22 d of acoustic monitoring over 8 yr, and some limited data on the amount and spatial distribution of fishing effort. Using these additional data led to more certainty about the decline of the vaquita population. Instead of 11%, the probability that the unprotected population increased between 1997 and 2008 was <0.01% (table 3 in Gerrodette and Rojas-Bracho 2011). In fact, even using only line-transect data from 1997 and 2008, *i.e.*, without using additional data in a population model, the probability that the vaquita population increased between 1997 and 2008 was <0.01% in the core area of vaquita distribution (Gerrodette 2011).

The relative contributions of different data can be illustrated by comparing the precision of three estimates of 2008 vaquita abundance based on (1) 2008 line-transect data alone, (2) the population model using all data except the 2008 line-transect data, and (3) the population model with all data (Fig. 1). The estimate of 2008 abundance based on the population model with all data was more precise than the estimate based on the line-transect data alone. The median of the posterior distribution of 2008 abundance from the population model was also lower (214) than the point estimate based on line-transect data alone (245).

It is worth noting that there are two kinds of estimates shown in Figure 1. The plot on the left shows a standard point estimate and confidence interval; the other two plots summarize probability distributions by showing the median and central 50% and 95% probability intervals. Bayesian posterior probability intervals are also called credibility intervals. Frequentist confidence intervals are often incorrectly interpreted as Bayesian credibility intervals (*i.e.*, as an interval containing the true value with the given probability), but confidence intervals are conceptually quite different (Johnson 1999, Gerrodette 2011).

Lonergan perceptively noted that the prior distributions for the proportions of the vaquita population in protected areas 1 and 2 were not entirely consistent with each other. Area 1 was contained within area 2, yet both priors were Uniform(0,1). Since
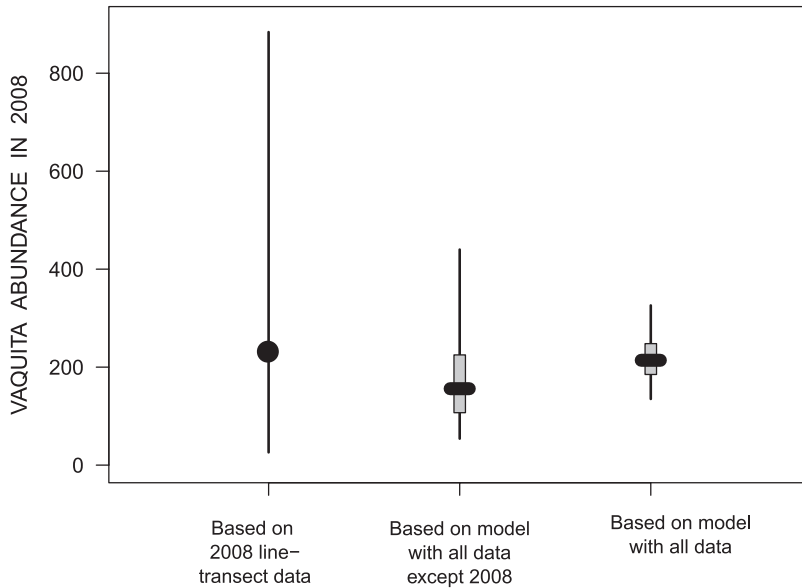
Figure 1. Three estimates of 2008 vaquita (*Phocoena sinus*) abundance, with measures of uncertainty. Left: Point estimate and 95% lognormal confidence interval based on visual and acoustic line-transect data collected in 2008 (Gerrodette *et al.* 2011). Center: Posterior distribution from a Bayesian population model (Gerrodette and Rojas-Bracho 2011) but excluding the 2008 line-transect data. Right: Posterior distribution from the same population model with all data. The posterior distributions are summarized by medians (thick horizontal lines), and central 50% (gray rectangles) and 95% (vertical lines) intervals of probability.

the proportion in area 2 must logically be greater than or equal to the proportion in area 1, a better formulation might have been to model the proportion in area 2 as the proportion in area 1 plus another unknown fraction to be estimated. Nevertheless, the consequences of using uniform priors for both parameters were negligible. The uniform priors did not imply, as Lonergan claimed, that there were no animals in area 2 not protected in area 1. The likelihoods of the two parameters were independent, so estimating the success of Option 1 did not require estimating the proportion in area 2, and *vice versa*.

Lonergan pointed out that the estimated probability of success of complete protection from fishing mortality (Option 3) was too high because it was based on the assumption that bycatch was the only factor inhibiting population growth. In our paper we discussed several assumptions that probably made our estimates of success too high, including the one Lonergan mentioned. Other rather optimistic assumptions were that protected areas would be perfectly enforced, that Option 3 would include the entire range of the vaquita, and that all fishers displaced under Option 2 would stop fishing in the vaquita's range. Even with no mortality in fishing nets, competition with artisanal fisheries for food, disturbance of the benthos by trawling, and effects of the reduction in flow of the Colorado River could reduce the vaquita population growth rate. However, the dominant factor in vaquita population

dynamics is bycatch in gill nets (Rojas-Bracho and Taylor 1999), so we focused on modeling that effect.

After listing the many perceived failings of our analysis, Lonergan suggested that "A simpler approach to the problem is to estimate the reduction in bycatch that would be necessary to reverse the estimated decline in the population." We did that. Figure 4 of Gerrodette and Rojas-Bracho (2011) showed that bycatch would have to be reduced between 60% and 70% to have equal probability that the population would increase or decrease. Lonergan's calculation that bycatch would have to be reduced by about two-thirds came to the same conclusion. Our approach was not as simple as what Lonergan suggested because we estimated the effects of multiple levels of bycatch reduction as well as the uncertainty associated with each.

Let us now examine the deeper question of how it was possible to achieve the dramatic gain in precision shown in Figure 1 for the estimate of 2008 vaquita abundance, as well as the probabilities of success of the three fishery closure area options, the main objective of the paper. The conclusions of Gerrodette and Rojas-Bracho (2011) from limited data were possible primarily because of two features of the analysis: (1) the unified framework of a population model to allow different kinds of data to work together for stronger inference, and (2) informative priors to supplement sparse data. The first is a general feature of modern statistical analysis, while the second is a feature of the Bayesian approach.

Analyzing data within a single likelihood framework is one of the most important developments in modern statistics. It forces the model to confront (in the sense of Hilborn and Mangel 1997) all of the data simultaneously, enforces consistency among the parameters, and accounts for uncertainty comprehensively. Combining multiple sources of data led to stronger inference on manatee survivorship (Goodman 2004). The benefits of this approach are well recognized in the fisheries literature (Fournier and Archibald 1982, Maunder 2003), in ecological modeling (Buckland *et al.* 2007), and in many other fields as diverse as archaeology, medicine, and physics (Draper *et al.* 1993).

For vaquitas, the gain in inference based on combining visual sightings, acoustic detections, bycatch mortality, and fishing effort within a population model is clear from Figure 1. Lonergan's calculation that the increase in precision shown in Figure 1 was approximately equal to a 17-fold increase in 2008 survey effort may be correct from a frequentist perspective, but this does not seem to be a helpful way of thinking about the analysis. Within the likelihood structure of the model, different kinds of data contribute multiplicatively rather than additively to inference. Furthermore, the model itself represents a kind of information that strengthens inference.

Because data were limited, Gerrodette and Rojas-Bracho (2011) attempted to model vaquita population dynamics and the main sources of uncertainty with a minimum number of parameters. The main structural assumptions of the model were that the vaquita population would grow exponentially in the absence of by-catch, that bycatch was proportional to gill net and vaquita density, that gill net fishing effort was proportional to the number of boats, and that the relative spatial distributions of vaquitas and fishing effort remained constant. As with all models, these assumptions were simplifications of reality. However, we think that they were
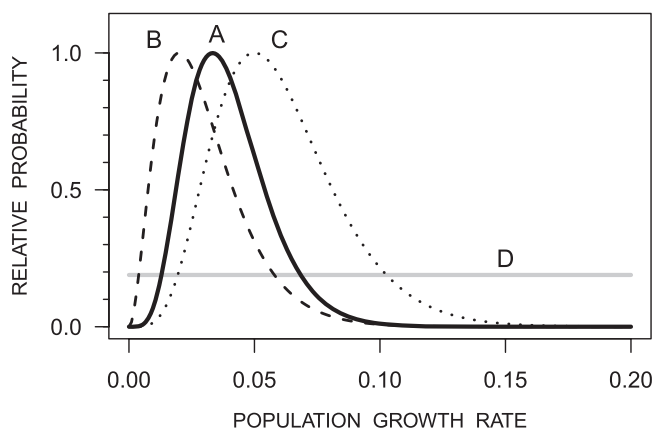
Figure 2. Some possible prior distributions of annual population growth rate for vaquitas. (A) Gamma(6,150) with mean 0.04, the distribution used in Gerrodette and Rojas-Bracho (2011). (B) Gamma(3,100) with mean 0.03. (C) Gamma(6,100) with mean 0.06. (D) Uniform(0,0.2), scaled to have the same area as A.

reasonable simplifications that captured the essential features of vaquita population dynamics. Projecting forward from the 1997 abundance estimate of 567, the model was able to predict 2008 abundance quite well (Fig. 1).

Because the number of parameters was relatively small (6–8, depending on the protected area scenario), the data were sufficient to estimate all parameters except the annual population growth rate and the proportional error in fishing effort (table 2 of Gerrodette and Rojas-Bracho 2011 and appendix S1 at http://onlinelibrary.wiley.com/doi/10.1111/j.1748–7692.2010.00449.x/suppinfo). While the proportional error in fishing effort had little effect on our results, the population growth rate had a strong effect on predicting the success of the three protected area options, the central goal of the paper. Yet we had no direct information about the population growth rate of vaquitas. Furthermore, the data that we did have was not indirectly informative either (the posterior was the same as the prior).

This is where the Bayesian use of an informative prior came in. Despite the lack of direct data, we could make some sensible assumptions about population growth rates for vaquitas on the basis of previous studies and general knowledge of cetacean reproduction. Given single annual births and different combinations of calf and adult survival rates, population growth rates for dolphins are unlikely to be above 10% per year (Reilly and Barlow 1986). To represent possible population growth rates for vaquitas, Gerrodette and Rojas-Bracho (2011) used a gamma distribution with a mean of 4% (Fig. 2, curve A). This distribution implied that annual growth rates as low as 1% or as high as 9% were possible but not very probable. Using a distribution rather than a single value for population growth rate allowed the uncertainty about the true value of the parameter to be propagated through the analysis. As noted in the paper, we did not include additional variation due to process error—that is, annual variation in the true growth rate. Some colleagues who read drafts of the paper,

noting some limited data that vaquitas may reproduce only in alternate years (Hohn *et al*. 1996), thought lower values of the growth rate were more reasonable (Fig. 2, curve B). Others, noting the lack of direct information, thought higher values should be allowed (Fig. 2, curve C). A uniform prior (Fig. 2, curve D), which is sometimes assumed to represent lack of information about a parameter, would have implied that a growth rate of 10% or 15% was as probable as a growth rate of 4%, which is certainly not a reasonable assumption for cetaceans.

In the end, we used the intermediate curve A and investigated the sensitivity of our results to this assumption. The probabilities of success of the three protected area options were 0.08, 0.35, and 0.99 when curve A was the prior. The probabilities of success were 0.05, 0.24, and 0.94 when curve B was the prior, and 0.20, 0.50, and 1.00 when curve C was the prior. Thus results were sensitive to the prior of population growth rate, but the basic conclusion that it is unlikely that the vaquita population will recover under the protection of the existing Vaquita Refuge (the first probability in each set of numbers) was not changed.

Lonergan noted that priors are "most problematic in the analysis of small data sets." We agree, but we would add " . . . and that is also where they are most useful." Of course, unreasonable assumptions can lead to unreliable results for any analysis, but a reasonable choice of an informative prior based on results from other studies may allow analysis to proceed in the face of limited data. We maintain that our choice of a prior for the annual population growth rate for vaquitas (Fig. 2, curve A) was carefully considered and reasonable. All analyses involve assumptions and subjective choices. Our job as scientists is to make those assumptions and choices clear, and to investigate the sensitivity of our results to them.

Because marine mammals are difficult to study, marine mammal scientists are often faced with limited data. It is therefore important to analyze data in ways that allow the strongest possible inference. The problem is particularly acute for a species like the vaquita, where critical decisions, which may determine whether a species goes extinct, have to be made on the basis of incomplete and imprecise data. Combining multiple sources of data within a statistical model and supplementing sparse data with carefully chosen informative priors are two analytical techniques that allow useful conclusions to be drawn from limited data, while respecting the uncertainty of the data.

Literature Cited

Buckland, S. T., K. B. Newman, C. Fernández, L. Thomas and J. Harwood. 2007. Embedding population dynamics models in inference. Statistical Science 22:44–58.
Draper, D., D. P. Gaver, P. K. Goel, J. B. Greenhouse, L. V. Hedges, C. N. Morris and C. Wa-ternaux. 1993. Combining information: Statistical issues and opportunities for research. Contemporary Statistics, Volume 1. American Statistical Association, Alexandria, VA.
Fournier, D., and C. P. Archibald. 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences 39:1195–1207.
Gerrodette, T. 2011. Inference without significance: Measuring support for hypotheses rather than rejecting them. Marine Ecology 32:404–418.

Gerrodette, T., and L. Rojas-Bracho. 2011. Estimating the success of protected areas for the vaquita, *Phocoena sinus*. Marine Mammal Science 27:E101–E125.

Gerrodette, T., B. L. Taylor, R. Swift, S. Rankin, A. Jaramillo-Legorreta and L. Rojas-Bracho. 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.

Goodman, D. 2004. Methods for joint inference from multiple data sources for improved estimates of population size and survival rates. Marine Mammal Science 20:401–423.

Hilborn, R., and M. Mangel 1997. The ecological detective: Confronting models with data. Princeton University Press, Princeton, NJ.

Hohn, A. A., A. J. Read, S. Fernandez, O. Vidal and L. T. Findley. 1996. Life history of the vaquita, *Phocoena sinus* (Phocoenidae, Cetacea). Journal of Zoology, London 239:235–251.

Jaramillo-Legorreta, A. M. 2008. Estatus actual de una especie en peligro de extinción, la vaquita (*Phocoena sinus*): Una aproximación poblacional con métodos acústicos y bayesianos [Current status of a species in danger of extinction, the vaquita (*Phocoena sinus*): A population model using acoustic and Bayesian methods]. Ph.D. thesis, Universidad Autónoma de Baja California, Ensenada, Mexico. 108 pp.

Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

Lonergan, M. 2012. Insufficient data are available to predict the success of protected areas for the vaquita (*Phocoena sinus*): A critique of Gerrodette and Rojas-Bracho (2011). Marine Mammal Science.

Maunder, M. N. 2003. Paradigm shifts in fisheries stock assessment: From integrated analysis to Bayesian analysis and back again. Natural Resource Modeling 16:465–475.

Reilly, S. B., and J. Barlow. 1986. Rates of increase in dolphin population size. Fishery Bulletin 84:527–533.

Rojas-Bracho, L., and B. L. Taylor. 1999. Risk factors affecting the vaquita (*Phocoena sinus*). Marine Mammal Science 15:974–989.