DISCUSSION OF: ESTIMATION OF FETAL GROWTH AND GESTATION IN BOWHEAD WHALES

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I thank the authors for a stimulating article on Bayesian growth curve modeling with only one data point per curve. This article fits squarely into a growing literature of statistical methods developed for use in managing populations of whales and other large marine mammals.

My own involvement in whale research began in 1996, when I took a sabbatical at the Bioacoustics Laboratory at Cornell, to assist with various projects involving the annual census of blue and finback whales off the coast of California, and as well as other whale studies.

I will address 2 points in this discussion: some features of bowhead whale studies which make them particularly of interest for statisticians (and particularly amenable to Bayesian methods) and some comments on the Bayesian growth modeling done by the authors.

Estimation of size of whale populations is of interest for a number of reasons: environmental concerns, management of marine resources, and setting quotas for aboriginal subsistence whaling. The latter (and the possibility of resuming commercial whaling of some species) has been a topic of hot controversy in recent years due to requests from various aboriginal groups for whaling permits, and due to the efforts of some countries (most notably Japan and Norway) to remove the ban on commercial whaling of some species.

Estimates of the sizes of whale populations for various species and stocks are available from the web site of the International Whaling Commission (http://ourworld.compuserve.com/homepages/iwcoffice). These estimates are not universally accepted. Although some of the discussion reflects political rather than scientific concerns, the main problem is data quality. It is difficult to estimate the number of animals in species that travel widely throughout the world's oceans, often at great depths, and which spend a large portion of the year in Arctic or Antarctic waters or in the open ocean, which are inimical to human observers.

Up until the mid-1980s most whale counts were done by visual censusing, either from shoreline observation stations or aerial surveys. A major problem in interpreting the data was in estimating the proportion of animals not detected at the shortest distance from the observation point or transect, as well as estimating the number of animals beyond the detection limits or passing through the area when observation was not possible. (The environmental conditions which obstruct viewing, might also limit whale movement.) The literature on the whale census, especially the annual reports of the Internation Whaling Commission, abounds with statistical papers which forward the methodology to improve estimates from ship and aerial transect counts, by use of multiple viewers, estimation of behavioral parameters, Bayesian methods and so on. Much of this literature is summarized and extended in the text on distance sampling by Buckland et al.

Since the mid-1980s, visual detection has been supplemented by underwater acoustic detection which extends the detection area and provides data at night and when weather conditions are adverse for visual detection. Acoustic data are provided by both stationary arrays of hydrophones, and towed arrays (Clark and Fristrup 1997, Fristrup and Clark, 1997). While the addition of acoustic data has greatly improved our ability to detect whales, there are still many unknowns about why whales vocalize. Hence, it is not known whether some biologically important groups of animals (e.g. females, immature males and so on) may vocalize more or less than others, and hence have differing detection probabilities.

An annual visual and aerial census for the Bering-Chukchi-Beaufort Seas stock of bowhead whales was established in 1978. Since 1984 this has been supplemented by an acoustic survey using stationary undersea hydrophones attached to the shorefast ice. Clark and Ellison (2000) provides an overview of the effort..

This stock of bowheads is particulary amenable to acoustic monitoring, because, as indicated by Reese, bowheads migrate along well-defined paths between the Bering, Chukchi and Beaufort Seas. The passage through the the waters close to Point Barrow, and the short duration of the migration, provides a convenient window in time and space for handling the census. The spring migration is ideal for visual counts, as daylight is continuous. As indicated by Clark and Ellison (2000) the acoustics of the Arctic waters are ideal for locating whales from their vocalizations. Raftery and Zeh (1998) also provide a very nice summary of the visual and acoustic survey methods, as well as of the sophisticated statistical methods employed in the census.

The visual data is strongly affected by environmental conditions including ice-cover, weather, and light. However, the number of animals spotted is fairly unambiguous. By contrast, the hydrophones can pick up animals at great distance and are not affected by surface conditions. For example, using the U.S. Navy's Integrated Undersea Surveillance System, blue whale sounds can be detected at ranges of up to 1000 kilometers (Clark, 1995). However, although identifying bowhead vocalizations is relatively straightward (for example, see the information at http://birds.cornell.edu/BRP/WhaleSounds.html and Clark, Ellison and Beeman, 1986), individual animals are not readily identified. Hence, for each vocalization it is necessary to locate the source, and then cluster the sources into tracks representing individual animals. The directional bias imposed by the migration path aids determining plausible tracks. Tracking algorithms were developed by Sonntag et al 1986 and 1988. An interesting sequence of papers by Raftery, Zeh and other collaborators discuss Bayesian methods for track estimation. These are summarized in Raftery and Zeh (1998).

Dual acoustic and visual censusing of other stocks of great whales are performed using ship-based observers and towed linear hydophone arrays. (Fristrup and Clark, 1997, Clark and Fristrup, 1997). These may also be supplemented by aerial surveys. Data quality of the ship-based visual observations is affected by visibility as well as ship movement which make triangulation subject to error. Away from the Arctic regions, layering of the ocean water by temperature and salinity produces reflections and refractions of the acoustic signals which make source location very imprecise. Towed arrays are linear which means that each signal produces a pair of possible source locations (one on each side of the array). As well, whales detected during these surveys do not have a preferred direction of movement. Species such as blue whales have highly monotone vocalizations, so that it can be difficult to determine whether calls received at different hydrophones originated from the same source. As a result, bioacoustics researchers are in the process of developing Bayesian tracking algorithms that take into account both ocean acoustics and plausible whale movements (Fristrup, Dunsmore, 2001, personal communication). As in growth modeling, Bayesian modeling is preferred in this context due to the existence of biological and physical parameters with relatively well defined distributions that can be used to formulate proper priors (for example, the distribution of swimming speeds and accelerations, the properties of the hydrophone array, and the propagation of sound through ocean water) to supplement data that is either sparse (in the case of fetal growth) or very noisy (in the case of whale tracking).

Once a tracking algorithm is available, it is expected that the methods developed by Raftery and Zeh and their collaborators for the bowhead census can be extended to other species, and will thus improve the accuracy of the assessment of the population size. It may also be used with stationary hydophone arrays anchored to the ocean floor in some areas.

While tracking the size of the population is important for establishing whether or not a species is endangered, "recovering" or stable, this may not be sufficient information for management purposes. Information about the population age structure, age of maturity, fertility and habitat use are essential if informed policies are to be implemented. Surprisingly little about life history is known for the great whales. A summary of what is currently known for the Bering-Chuchki-Beaufort stock of bowheads is available in Shelden, and Rugh (1999). However, this information is not well-established. For example, anecdotal evidence suggested that bowheads have a life-span of about 60 years. However, the recovery of harpoon points over 100 years old in the blubber of bowheads killed since 1981 suggests a much longer lifespan; dating of tissue from several large males suggests ages of well over 100, and possibly up to 200 years or more for one animal (Raloff, 2000; George and Bada, 1999).

The contribution of the authors to the literature on bowhead life history is substantial, giving improved estimates of conception date, gestation length and birth date (and correspondingly, locations at these times). The use of Bayesian modeling to account for differences in growth curves among the individuals, the elicitation of the priors from the experts, and the use of sensitivity analysis to determine the effects of the priors are beautifully done.

I do wish to comment, however, on one point not addressed by the authors. It is well-known that parametrization is important in maximum likelihood estimation, due to numerical problems in finding the maximum. The Bayesian situation is somewhat different. If the parameters are characterized by a full multivariate prior, reparametrization induces a transformation of the prior. The subsequent posterior distributions will also be transformed accordingly. Thus, a Bayesian analysis should be be much affected by the choice of parametrization.

However, it is very difficult to elicit a multivariate prior. More commonly, marginals are elicited, as the authors have done here. This ignores potential associations among random variables. For example, it is quite likely that the gestation date, and parturition date are correlated, the mean and variance of the fetal birth length are correlated, and so on. Multivariate priors with the same marginals can lead to different posterior inferences as discussed in Lavine, Wasserman and Wolpert (1991), so that parametrization can have a large effect.

One way to avoid the need to elicit joint priors is to choose a parametrization in which the prior distributions of the parameters are independent. In multi-stage models such as used by the authors, it is difficult to assess which parameters should be independent. However, independence of the parameters at the highest level of the hierarchy is more readily achieved.

The highest level parameters of the model are the conception dates, birth dates, fetal birth lengths and the growth rate (relative to the birth length). Conception date and birth date are likely highly correlated. By contrast, conception date and gestation length are unlikely to be correlated and should be independent of birth length and growth rate. (Of course, one can imagine scenarios in which environmental factors induce corrrelation.) I therefore reparametrized the model replacing birth date by gestation length. This is summarized in Table. 1.

Table 1: *The mean and standard deviation of gestation length as a function of model parametrization.*

parametrized by	mean gestation length	standard deviation
parturition date	424 days	35.2 days
gestation length	437 days	27.5 days

The main thing to note is the higher mean and smaller standard deviation for the posterior distribution of gestation length when the model is parametrized by gestation length, rather than by parturition date. I hypothesis that the smaller standard deviation is due to the positive correlation between parturition date and conception date. The higher mean may be due to the choice of hyperprior mean (425 days). The sensitivity analysis should be redone using the alternative parametrization.

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