Beaked whale abundance trends in the California Current, 1991 – 2008

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Abstract:
The Southwest Fisheries Science Center (NOAA) conducted ship line-transect cetacean abundance surveys in the California Current (to 300 nmi, 556 km, offshore of the US mainland, from the border with Mexico to the Canadian border) in 1991, 1993, 1996, 2001, 2005, and 2008. We used a Bayesian hierarchical modeling approach to estimate abundance and population trends of beaked whales using sightings data from these surveys. The model partitions the state process of interest (i.e., population density modeled as a function of covariates and random process terms) from the observation process (i.e., observed counts modeled as a function of population density and detection probability using distance sampling theory). Bayesian posterior summaries for trend parameters provide strong evidence of declining beaked whale abundance in the California Current study area over the survey period. Specifically, the probability of negative trend for Cuvier's beaked whale (*Ziphius cavirostris*) during 1991 – 2008 was 0.84, with 1991 and 2008 estimates of ≈ 10800 (CV = 0.51) and ≈ 7500 (CV = 0.55), respectively. The probability of decline for *Mesoplodon* (pooled across species) was 0.96, with 1991 and 2008 estimates of ≈ 2200 (CV = 0.46) and ≈ 800 (CV = 0.65). The mean posterior estimates for average rate of decline were 2.9% and 7.0% per year. There was no evidence of abundance trend for Baird's beaked whale (*Berardius bairdii*), for which annual abundance estimates in the survey area ranged from ≈ 900 to 1300 (CV ≈ 1.3). Causes of apparent declines are unknown; we discuss some hypotheses.

Keywords: anthropogenic noise, fisheries bycatch, distance sampling, ecosystem change, hierarchical Bayesian, navy sonar, Ziphiidae

INTRODUCTION

Beaked whales (Family Ziphiidae) are one of the most diverse groups of marine mammals, comprising 21 (24%) of the 87 extant cetacean species recognized by the Society of Marine Mammalogy (Committee on Taxonomy 2012). Among all marine mammal taxa, only the family Delphinidae is more speciose. Yet, the ecology and conservation status of ziphiids are the least understood for all marine mammal groups, owing to their deep-water existence and cryptic behavior. According to the IUCN Red List, approximately 40% of marine mammal species are considered Data Deficient (Davidson et al. 2012). For the Ziphiidae, all but two (90%) species are Data Deficient.

The NOAA Southwest Fisheries Science Center (SWFSC) has systematically conducted vessel line-transect surveys for marine mammals in the California Current (survey area, $A \approx 1.142 \times 10^6$ km²) since 1991, allowing for investigation of abundance trends that could be used to help assess conservation status of beaked whales in this part of the eastern North Pacific. Beaked whale species known to occur in the study area (Fig. 1) include Cuvier's beaked whale (*Ziphius cavirostris*), Baird's beaked whale (*Berardius bairdii*), and several species of the genus *Mesoplodon* that cannot be easily distinguished in the field – *M. densirostris*, *M. perrini*, *M. peruvianus*, *M. stejnegeri*, *M. gingkodens*, and *M. carlhubbsi* (Carretta et al. 2010). Cetacean abundance trends can be notoriously difficult to estimate because of typically low precision in the abundance estimates (Taylor et al. 2007, Jewell et al. 2012), but Moore and Barlow (2011) demonstrated for fin whales the value of hierarchical Bayesian modeling to improve inference about abundance trends based on line-transect data. Here, we report on the results of a similar analysis of beaked whale data from the SWFSC cruise surveys.

METHODS

Methods generally follow those described by Moore and Barlow (2011) in their analysis of fin whale abundance trends. A brief description is provided here.

Surveys

Shipboard line-transect surveys for marine mammals were conducted in the California Current by the SWFSC in summer/autumn of 1991, 1993, 1996, 2001, 2005, and 2008 (Fig. 1). The study area has been consistently divided into four strata from north to south: Oregon-Washington (OW), Northern California (NC), Central California (CC), and Southern California (SC). However, because of small sample sizes for beaked whales, the survey strata were collapsed into a single study area for this analysis. Waters off the coast of Oregon and Washington ($\approx$ 28 % of the study area) were not surveyed in 1991 or 1993 (implications of this discussed in Results – Sensitivity analysis). Transects followed a uniform grid pattern anchored to a different random starting point each survey year. Observers used 25x binoculars to sight cetacean groups. Group sizes and perpendicular distances from the group center to the transect lines were calculated from estimated radial distances and measured sighting angles, and various covariates associated with each detection were recorded (e.g., visibility measures, environmental conditions). For additional details on survey methodology, see Kinzey et al. (2000) and Barlow & Forney (2007).

Detections and effort occurring during sea state conditions of Beaufort 0 – 5 were included in the analysis (although there were no detections in Beaufort 0 conditions, which rarely occur in the region). Distance data were truncated to only include observations < 4 km from the transect line; this eliminated 17% (4 of 24) of *Berardius* groups and 6% (7 of 112) of groups of *Ziphius, Mesoplodon*, and unidentified beaked whales (which belonged to either *Ziphius* or *Mesoplodon*). These data truncations are consistent with recommendations by Buckland *et al*. (2001). Total survey effort (on-effort transect length) and counts of beaked whale groups in the full study area are summarized in Table 1.
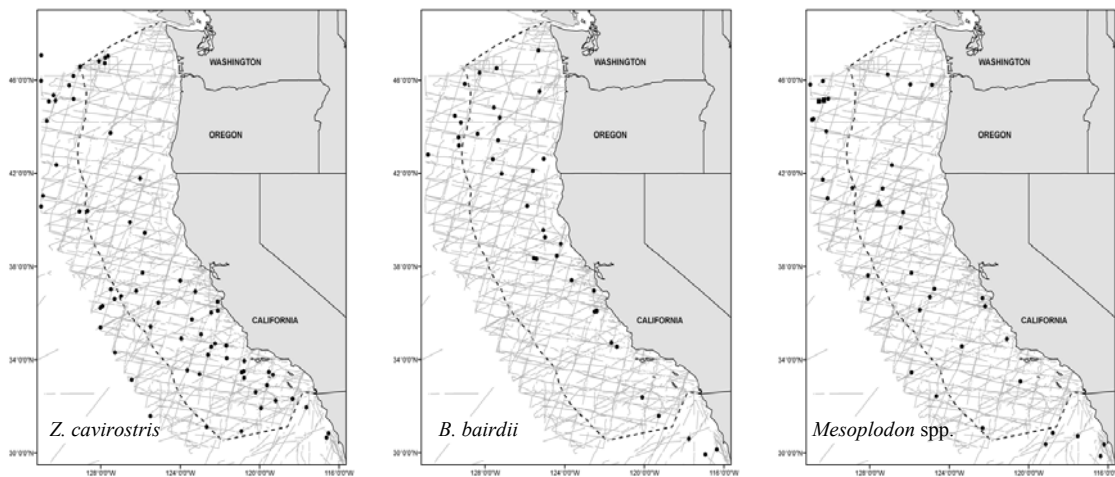

Fig. 1. Study area ($A \approx 1.142$ x 10^6 km^2) demarcated by extent of on-effort transect lines, US EEZ boundary (dotted line), and sighting locations of Cuvier's beaked whale (*Z. cavirostris*), Baird's beaked whale (*B. bairdii*), and *Mesoplodon* spp., from 1991-2008 (from US Marine Mammal Stock assessments, Carretta et al. 2011).

Table 1. Number of beaked whale groups detected, and total km of survey effort (L_t) in each year of cetacean line-transect surveys. Only whale groups < 4 km from the transect line, and only survey effort during Beaufort sea state ≤ 5 are included

	1991	1993	1996	2001	2005	2008
L_t (km)	10,025*	6235*	14,674	9537	10,838	11,564
Berardius bairdii	2	3	5	2	3	5
Ziphius cavirostris	18	12	9	5	3	10
Mesoplodon spp.	6	7	15	0	3	1
unidentified ziphiid	0	3	3	2	4	4

* Only includes effort from three survey strata (i.e., Oregon-Washington stratum not surveyed in these years)

Analytical methods

Process and Observation Models

Models were developed separately for Baird's beaked whale, Cuvier's beaked whale, a single *Mesoplodon* species group, and a group of unidentified ziphiids (which were either *Ziphius* or *Mesoplodon*), although sighting distance data were pooled across these groups for purposes of estimating parameters of the detection function. Recognizing that *Berardius* are more easily detectable than other ziphiids, the detection model included covariates for inter-species differences (see below).

Following Moore and Barlow (2011), the model for each species group is partitioned into process and observation components. The process model describes how population density changes through time. Abundance, $N_t = D_t * A$. The most general model we considered describes variation in animal density simply as a function of a single temporal trend parameter and a stochastic component (random variable) for each year (t). Small sample sizes precluded more complex (e.g., geographically stratified) models. If the population is changing exponentially, the full density model is:

$$D_t = \exp(\beta_0 + \beta_1 t + \gamma_t), \tag{1}$$

$$\gamma_t \sim \text{Normal}(0, \sigma).$$

The observation model links the state process to the observed data. Following line-transect sampling theory (Buckland et al. 2001), and treating the observed counts of groups each year as a Poisson random variable (Moore and Barlow 2011):

$$n_t \sim Pois(E[n_t]),$$

$$E[n_t] = \frac{D_t}{s} \cdot \frac{2L_t g_t(0)}{f_t(0)}, \tag{2}$$

where n_t is number of groups detected; s is a mean group size estimate for the species (there was no evidence of annual variation) with overdispersed Poisson variance; $f_t(0)$ is the value at distance $y=0$ of $f(y)$, which is the pdf of the detection probability function $g_t(y)$, with $g_t(0)$ being the detection probability on the transect line; and L_t is the on-effort transect length (km), considered to be measured without error (Table 1). Poisson overdispersion in the counts is handled implicitly by process error terms in equation 1 (i.e., γ_t in reality should capture process + extra-Poisson sampling error if the latter is not estimated separately). A more intuitive expression of equation 2 is:

$$E[n_t] = \frac{D_t}{s} \cdot 2L_t w \cdot q_t, \tag{3}$$

where w equals the data truncation distance and q_t is the average detection probability of a group within the surveyed area $2L_t w$. Equation 3 thus indicates that the expected number of groups detected equals the group density, multiplied by the area surveyed, multiplied by detection probability. By substitution, $q_t = g_t(0)/f_t(0) \cdot 1/w$. In other

words, q_t is the "effective strip half-width" $[g_t(0)/f_t(0)]$ divided by the total distance from the vessel within which searching takes place. The effective strip half-width is mathematical re-interpretation of the distance-decay function $g_t(y)$ into a single theoretical distance from the transect line within which groups have a detection probability of 1 and beyond which the probability is zero.

Detection probability varies with Beaufort sea state. Thus the estimate of q_t in equation 3 is:

$$\overline{q_t} = \frac{\sum_{b=1}^{5} q_b L_{b,t}}{\sum_{b=1}^{5} L_{b,t}} \ ,$$

where $L_{b,t}$ is the amount of survey effort in each of 5 Beaufort classes (b = 0 & 1, 2, …5) in year t, and $q_b = g_b(0)/f_b(0) \cdot 1/w$. Note, the estimate for $\overline{q_t}$ is calculated from the effort-weighted mean of the ratio $[g_{b,t}(0)/f_{b,t}(0)]$, not the ratio of the means $\overline{g_{b,t}(0)} / \overline{f_{b,t}(0)}$. Based on previous analyses in our case study system (Barlow & Forney 2007) we assume a half-normal detection function for $g_b(y)$:

$$g_b(y) = \exp\left(\frac{-y^2}{2\sigma_{h,b}^2} \right),$$

where h denotes half-normal parameters. We estimated the shape parameter $\sigma_{h,b}$ and hence $f_b(0)$ as a function of covariates (Marques & Buckland 2004), assuming the following model:

$$\sigma_{h,b} = \exp[\beta_{h0} + \beta_{h1}(b) + \beta_{h2}[\log(\bar{s})]], \tag{4}$$

where β_{h0} is the intercept; and β_{h1} and β_{h2} are the coefficients for Beaufort sea state and mean group size for the species, respectively. The covariate model is based on the one used by Barlow and Forney (2007), the main difference being that we did not include a categorical variable for the ship on which observations occurred. Preliminary analyses did not reveal this variable to have much importance, while it complicated the weighted-mean estimation of $\overline{q_t}$. Species group (*Berardius* vs. other/smaller species) was considered as a covariate as well (and was included in a Sensitivity analysis – see Results), but the sample size for *Berardius* was small (Table 1); preliminary analyses suggested that group size was a more useful variable overall and sufficiently acted as a proxy for *Berardius* since they usually occur in larger groups. As sample sizes for *Berardius* increase with future surveys, a separate variable for them should be included. The parameters for equation 4 were estimated from data for individual detections:

$$\sigma_{h,i} = \exp[\beta_{h0} + \beta_{h1}(b_i) + \beta_{h2}[\log(s_i)]],$$

where i denotes each observed group (all species detections pooled).

Trackline detectability, $g_b(0)$, for *Ziphius* and *Mesoplodon* beaked whales declines strongly with deteriorating Beaufort sea state conditions. Barlow and Forney (2007) reported estimates of $g_b(0)$ for Beaufort states 0 – 1 (from Barlow 1999); these account for the combination of perception bias and availability bias. Estimates for these and Beaufort 2 – 5 (Barlow, unpublished data) are included in Table 2. The CVs of the $g_b(0)$ estimates are based on Beaufort 0 and 1 conditions (based on Barlow 1999); this CV was used for the other sea state levels as well.

Table 2. Estimates of trackline detection probability, g(0), for each beaked whale genus, as a function of Beaufort sea state. Estimates for sea state 0 – 1 and CV are from Barlow (1999). Estimates for *Ziphius and Mesoplodon* in sea states 2+ are from unpublished data (J. Barlow).

Beaufort sea state	*Berardius*	*Ziphius*	*Mesoplodon*
0 & 1	0.87*	0.230	0.450
2		0.148	0.290
3	assumed as	0.110	0.215
4	above	0.043	0.085
5		0.024	0.048
CV	0.23	0.35	0.23

* Barlow (1999) reported a point estimate of 0.96. Value reported here is the mean of Barlow's bootstrap distribution, for compatibility with the reported CV.

Parameter Estimation

Parameter estimation was conducted using a Bayesian MCMC approach in WinBUGS 1.4.3 (Lunn *et al*. 2000; Spiegelhalter *et al*. 2007). Likelihoods were Poisson for the n_t data, overdispersed Poisson for group size (s_i) data, and truncated half-normal for the distance (y_i) data. See Moore and Barlow (2011: Appendices S1 and S2 in Supporting Information for example WinBUGS code and likelihood expressions). Vague priors were used on all parameters except for $g_b(0)$, for which informative Beta priors were used for $g_1(0)$ corresponding to Beaufort 0 and 1 estimates in Table 2, and g(0) for the other sea state levels were calculated to preserve the ratios in Table 2. Normal priors with mean = 0 and large variance (e.g. 10,000) were used for most intercept and slope coefficients (e.g. β's). Positive uniform distributions (e.g., U[0, 10]) were used for standard deviations of random effects. For each model, MCMC runs consisted of two chains with a burn-in of 25,000 samples and a posterior distribution based on 75,000 samples for each chain thinned by 4 (i.e., posterior distributions constructed from 37,500 samples total); this was sufficient to achieve low Monte Carlo errors (< 5% of MCMC sample standard deviation) and $\hat{R} \approx 1$ for key parameters.

Abundance of "unidentified" beaked whales

The abundance of the "unidentified" group was modeled as a separate species; but these animals were believed to belong to either *Mesoplodon* or *Ziphius*. Therefore, q_t for the unknown group was estimated as a weighted average of q_t for *Mesoplodon* and *Ziphius*, with weights at each MCMC sample given by the posterior estimates of relative abundance for these two groups. These weights were also used to proportionally attribute abundance estimates for the unidentified group to *Mesoplodon* and *Ziphius*, thus providing revised estimates of annual abundance and trends.

RESULTS

Group size and Detection

Mean (and SD) of the Bayesian posterior distributions for group sizes (*s*) across all surveys were 9.6 (8.7) for *Berardius*, 1.81 (0.13) for *Ziphius*, 1.77 (0.17) for *Mesoplodon*, and 1.51 (0.20) for unidentified ziphiids. The smaller mean group size for the unidentified ziphiids may indicate that smaller groups in the field are less likely to be identified, or that groups not seen well enough to identify also tend to be underestimated in size, or the difference could be due to chance. The estimates for *Mesoplodon* and *Ziphius* were slightly lower than the average of previously reported estimates using data from the same surveys (Barlow and Forney 2007, Barlow 2010). For both groups, the mean group size in our full dataset (Beaufort 0 – 5 observations) was approximately 1.8, compared to 2.0 and 2.2 for *Mesoplodon* and *Ziphius*, respectively, in the earlier studies, which used Beaufort 0 – 2 observations

only. Differences could reflect sampling error, since we estimated group size from a larger dataset. Alternatively, group size estimates recorded in rougher seas could be biased low, driving down our estimates, although a *post hoc* linear regression of group size vs. Beaufort sea state suggested this possible bias only for the *Ziphius* data.

Detection probability, $g(y)$, decreased strongly as Beaufort sea state level increased and appeared to increase some with group size, as indicated by posterior distributions for detection model coefficients (Table 3, Fig. 2). Average sea-state conditions and thus detection probability estimates for *Ziphius* and *Mesoplodon* declined over the course of the study, and the average probability (q_t) of detecting a *Ziphius* or *Mesoplodon* group present within the 4-km truncation distance from the vessel was $0.03 - 0.05$ (CV ≈ 0.36) and $0.07 - 0.10$ (CV ≈ 0.25), respectively (Fig. 3). For *Berardius*, estimates of average detection probability declined slightly over the course of the study (due to trend in $f_t(0)$ but not $g_t(0)$) from 0.49 in 1991 to 0.43 in 2008 (CV ≈ 0.27).

Table 3. Posterior distribution summaries for coefficients of the covariate-dependent detection function (see equation 4 in text).

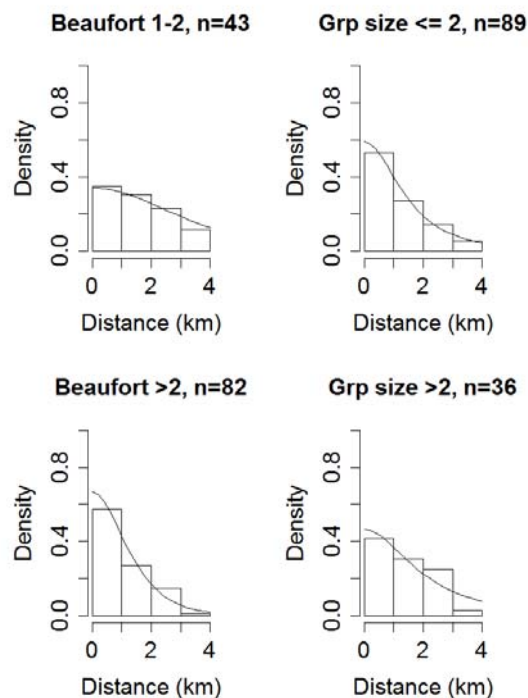|	Mean	SD	95% CRI
β_{h0} [Intercept]	1.63	0.37	0.99, 2.46
β_{h1} [Beaufort sea state]	-0.39	0.10	-0.60, -0.22
β_{h2} [log(groupSize)]	0.16	0.11	-0.04, 0.40

Figure 2. Histograms of beaked whale group detection distances and mean probability density curve, $f(y)$, of the observations, based on coefficient estimates in (Table 3). Plots are shown for observations in calm (Beaufort $1 - 2$) and rough (Beaufort 3+) sea state conditions, and for small (1 or 2 individuals) and larger (3+ individuals) groups
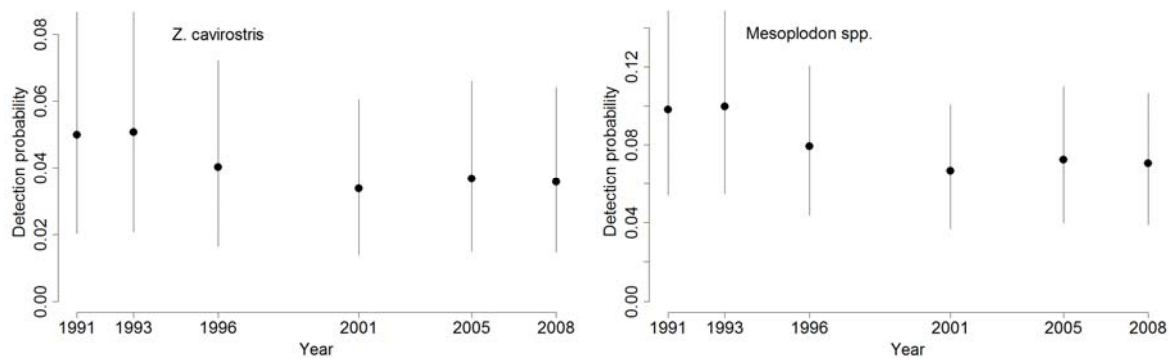
Figure 3. Average detection probability of Cuvier's beaked whale and *Mesoplodon* groups occurring within the truncation distance (4 km) of the research vessel. Plotted values are the medians and 95% CRI of the Bayesian posterior distributions

Abundance and Trends

Based upon analysis of four separate groups (i.e., including unidentified ziphiids counted as a separate group), the posterior mean estimates for the trend parameters (β_1) indicated annual rate of change of –4.5% per year (95% CRI: −11.5% to +2.2%) for *Ziphius* and −8.4% (95% CRI: −18.9% to +0.3%) for *Mesoplodon* over the period 1991 – 2008. The probabilities of declining trend (e.g., Prob[$\beta_1 < 0$]) were 0.92 and 0.97, respectively.

No trend was evident for *Berardius* (posterior mean trend estimate = +0.8% per year, 95% CRI: −7.6% to +9.8%; probability of decline = 0.44).

The 'unidentified ziphiid' group showed evidence of increasing trend (mean trend = +5.0% annually; 95% CRI: −4.8% to +16%), with mean abundance estimates of ≈ 700 (CV = 0.76) in 1991 and ≈ 2000 (CV = 0.65) in 2008. One explanation for this is that, since observing conditions coincidentally worsened with each survey, there was an increasing trend in the number of sighted groups that could not be identified to genus. Assuming the abundance estimates for unidentified ziphiids comprised a mixture *Ziphius* and *Mesoplodon*, proportionally allocating the estimates to the two species groups and re-estimating the trend parameters weakened the evidence slightly for *Ziphius* and *Mesoplodon* decline. The revised annual growth rate estimate for *Ziphius* was –2.9% per year (95% CRI: −8.8% to +3.3%) and for *Mesoplodon* was −7.0 % (95% CRI: −16.7% to +1.0%). The revised estimates for probability of negative trend were 0.84 and 0.96, respectively. Abundance estimates that include prorating from the unidentified ziphiid group are in Fig. 3.

Sensitivity analysis

We conducted a *post hoc* analysis to make sure that our trend results for *Ziphius* and *Mesoplodon* were not an artifact of pooling data across all survey strata even though the Oregon-Washington stratum had not been surveyed in 1991 and 1993. Conceivably, if this stratum had lower beaked whale densities than the California strata, this could reduce the overall density (and hence abundance) estimates for 1996 – 2008 surveys, relative to the 1991 and 1993 surveys, leading to a potentially spurious trend result. Therefore, we repeated the analysis using count (n_t) and effort (L_t) data in all years from only the three California strata to estimate annual average detection rates (q_t), density, and abundance. All data were still used to estimate the detection function parameters (e.g., model for $\sigma_{h,b}$) and group size. We also included an indicator variable for *B. bairdii* in the detection covariate model, in case the trend estimates were sensitive in any way to how data pooling across species affects the detectability estimates.

This revised analysis did not fundamentally change our inference about trends for any species, including the unidentified group. The probabilities of declining trend for *Ziphius* and *Mesoplodon*, after pro-rating the abundance and trend estimates by those of the unidentified ziphiid group, were 0.86 and 0.96, respectively, virtually identical to in the primary analysis. Posterior mean estimates for the trend parameters were actually slightly more

negative in this *post hoc* analysis (−4.2% and −8.3%, respectively). Given this result, we proceed with discussion based on our primary results, to take advantage of precision and inference from the full dataset.
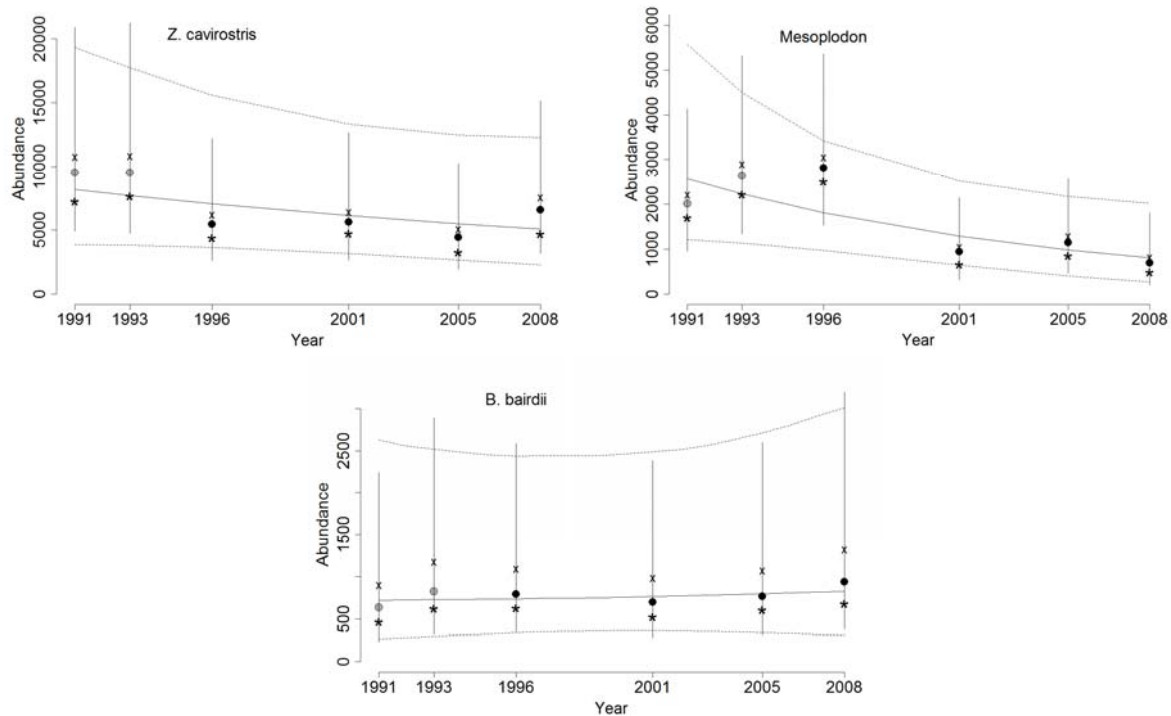

Fig. 3. Abundance and trend estimates for three species groups (*Z. cavirostris*, *Mesoplodon* spp., and *B. bairdii*) in the California Current from 1991 – 2008. *Z. cavirostris* and *Mesoplodon* estimates are pro-rated to include a proportion of the abundance estimated for the "unidentified ziphiid" group. For each year, the Bayesian posterior median (●), mean (X) and mode (*) abundance estimates are shown, along with 90% CRIs. Trend lines depict median and 90% CRI estimates of fitted abundance without process error (e.g., equation 1, with $\gamma_t = 0$). Gray points for median estimates in 1991 and 1993 denote that the total abundance estimate for the study area reflects extrapolated density estimates to the Oregon-Washington survey stratum.

DISCUSSION

Comparison with previous estimates

We compared our estimates with those of Barlow and Forney (2007) and Barlow (2010), who analyzed data from the same surveys. The most noteworthy difference is that our estimates were much more stable from year to year. Just as one example, Barlow and Forney's point estimates for *Berardius* ranged from 0 to 1591, reflecting strong sensitivity to the small number of groups observed in a particular year, whereas our estimates varied only by a few hundred individuals from year to year (Fig. 3). A key feature of the hierarchical modeling process is to treat the observations as random variables and borrow from the strength of information in the whole dataset to improve individual year estimates, shrinking them more toward the mean trend estimate in more data-poor years and thus improving the precision of each. This enables improved inference about population trends. For example, if we run a simple regression analysis on the log of Barlow and Forney's annual population density estimates vs. time, no significant trends for *Ziphius* and *Mesoplodon* are revealed (p-value$_{Ziphius}$ = 0.17; p-value$_{Mesoplodon}$ = 0.21). This comparison to our analysis is not entirely appropriate, in part because ours made use of a larger dataset by including observations in rougher sea conditions, and we did not account in the simple regression for covariance in the abundance estimates (from pooling of data to estimate detection parameters) or sample-weighted variances. On the

other hand, many abundance trend analyses are similarly conducted using simple regression techniques. Our general point is that efforts to maximize use of the available information through improved modeling and taking a probabilistic (Bayesian) approach to inference seem to allow for better assessment of population status than guidelines based on conventional power analyses suggest we could expect. Taylor et al. (2007) noted that when using simple regression and a null hypothesis-testing paradigm with significance criteria α = 0.05, even *annual* surveys (for 15 years) of a species would fail half the time to detect a 5% rate of decline when the abundance estimate CV = 0.34. Our annual CVs for for *Ziphius* and *Mesoplodon* were substantially higher (0.4 – 0.65). Thus, our analysis suggests we might be more optimistic about our ability to assess trends using methods such as those presented here.

On average, the population density estimates for *Ziphius*, *Mesoplodon* (before allocating abundance from the unidentified group) and the group of unidentified ziphiids were higher from our analysis than those reported by Barlow and Forney. Specifically, the average of our median population density estimates across all survey years were 21%, 34%, and 45% higher, respectively, than the average of Barlow and Forney's estimates. For *Berardius*, the estimates were more similar; the average of our median estimates was 17% lower than theirs, but the average of our posterior mean estimates was 17% higher. Many factors could explain these differences. We used a larger dataset that included observations in Beaufort ≤ 5, whereas the previous analyses were based on observations in Beaufort ≤ 2. Fewer observations could have simply introduced higher sampling error in their analysis. For observations in Beaufort 2, we used a lower estimate of *g*(0) than did Barlow and Forney; this would lead to higher abundance estimates in our analysis, all else equal. Underestimating *g*(0) for higher Beaufort states relative to the *g*(0) estimate in Beaufort 0 & 1 would also lead to higher abundance estimates. In contrast, our slightly lower group size estimates would decrease our abundance estimates. Finally, a suite of differences in how we modeled the detection function (covariates used, species-pooling decisions) could have all affected the results in different ways.

Hypotheses for declining trends

Our analysis strongly suggests that beaked whale abundance in the California Current has declined over the 18-year study period: 1991 – 2008. The evidence is particularly strong for the genus *Mesoplodon*, although we cannot say which species are driving the observed pattern. We do not know whether the apparent declines in the study area reflect trends for the whole populations or large-scale shifts in distribution to outside of the study area; either scenario is worrisome. Alternatively, temporal movement dynamics of beaked whales could have changed over the study period such that the timing of surveys coincided with higher animal abundance in the study area during the first years of the survey; however, beaked whales are not known to be migratory. Given limited information about the spatial ecology of beaked whales in the eastern North Pacific, it seems prudent to be precautionary and interpret the apparent declines as real based on the best available information. Causes of the apparent declines are unknown, but we consider three hypotheses: effects of incidental mortality from fishing; impacts of anthropogenic noise, particularly Navy sonar; and ecosystem changes.

Effects of direct mortality from fishing

Bycatch mortality of beaked whales has been reported worldwide, particularly in high-seas driftnet fisheries (e.g., Northridge 1996, Julian and Beeson 1998, Baker et al. 2006; see additional references in Carretta et al. 2008). The California large mesh drift gillnet fishery is the only fishery known to interact with beaked whales in the California Current within the US EEZ. Based on U.S. fishery observer program data, annual bycatch mortality estimates from 1990 – 1995 were 0 – 6 for *Berardius*, 0 – 44 for *Ziphius*, 0 – 29 for *Mesoplodon* whales, and 0 – 15 unidentified ziphiids (based on observer coverage levels of 4.4% to 17.9%; Julian and Beeson 1998). Comparing the mean 1990 – 1995 bycatch estimates to our 1991 and 1993 abundance estimates, the mean estimated mortality rate would have been less than 0.005 for both *Ziphius* and and *Mesoplodon*. Using the 20th percentile abundance estimates (in line with estimation of Potential Biological Removal under the US Marine Mammal Protection Act), the average bycatch mortality rate would have been as high as 0.008 for *Mesoplodon* in 1991.

Since mid-1996, acoustic pinger deterrents have been used in the California driftnet fishery; this effectively eliminated beaked whale bycatch (Carretta et al. 2005, Carretta et al. 2008). A declining trend in fishing effort (Appendix 1 in Carretta et al. 2011) and additional regulation of the fishery (reviewed in Moore et al. 2009) − including a large time-area closure (central California to Oregon) in effect for 4 months each year since 2001 to protect leatherback sea turtles − have likely reduced the potential for fishery-beaked whale interactions even further.

In summary, it seems unlikely that apparent beaked whale trends in the California Current can be explained by fishery-related mortality inside the US EEZ. Estimated bycatch during the early 1990s appears to have been low relative to abundance estimates, and bycatch of beaked whales since 1996 (inclusive) has presumably been trivial.

Navy sonar and other anthropogenic noise

The ocean has gotten much louder (Tyack 2008). Numerous studies and reviews in the past decade or so have described the potential impacts and threats posed to beaked whales and other cetaceans by anthropogenic noise. Of primary concern for beaked whales is noise caused by navy sonar activities, although noise associated with varied sources such as ship traffic and seismic exploration may also be an issue (e.g., Hildebrand 2005, Cox et al. 2006, Soto et al. 2006, Weilgart 2007, Parsons et al. 2008, Tyack et al. 2011, Wright et al. 2011).

Ziphius and *Mesoplodon* are the two beaked whale genera known to suffer impacts from navy sonar activities. They exhibit strong behavioral responses to certain types of active sonar, resulting in altered movements and space use for prolonged periods after exposure (e.g., several days; McCarthy et al. 2011, Tyack et al. 2011). In more extreme cases there can be physiological consequences leading to death or stranding (Jepson et al. 2003, Fernández et al. 2004, Cox et al. 2006).

Although the threats from naval acoustic activity have been described, population-level impacts have not been quantified. Mass strandings of beaked whales worldwide have been associated with offshore military activity. However, estimates of total mortality associated with these types of impacts do not exist, although they are sure to exceed levels that have been recorded, since the probability of observing dead whales is generally low, probably especially for deep-water species (Faerber and Baird 2010, Williams et al. 2011). Indirect impacts associated with chronic stress are even more difficult to document, although it could be hypothesized that frequent intense stressors that alter behavior and displace individuals from their habitat could reduce fitness via mechanisms such as reduced foraging efficiency, failed reproduction, increased calf mortality, etc. (Wright et al. 2007, 2011).

Ambient noise off the coast of California has increased many-fold over the past several decades (Andrew et al. 2002, McDonald et al. 2006). West of San Clemente Island in the Southern California bight, beaked whales are subject to sonar activities in the vicinity of the U.S. Navy's Southern California Anti-Submarine Warfare Range (SOAR). This area appears to support relatively high abundance of Cuvier's beaked whales (Falcone et al. 2009).

Evidence to implicate noise from naval activity or other acoustic sources as a cause of apparent beaked whale declines in the California Current is equivocal. If Navy activities at SOAR are responsible, one might expect declines to be localized to the southern California portion of the study area, or even restricted to the SOAR area, depending on beaked whale home range size and movement patterns. Unfortunately, the data do not support a formal evaluation of spatial variation in beaked whale abundance trends.

Navy ranges seem to support high densities of beaked whales. Apart from seemingly high density of Cuvier's beaked whales in the SOAR area (Falcone et al. 2009), the Navy's AUTEC sonar test facility in the Tongue of the Ocean (The Bahamas) supports the highest densities of *M. densirostris* that have ever been estimated (Moretti et al. 2006, Marques et al. 2009). High densities do not rule out the possibility that declines have occurred in these areas, or that Navy ranges occur in high-quality beaked whale habitat and could be acting as population sinks. On the other hand, observations of high whale densities in Navy ranges are not obviously consistent with a hypothesis that declines are due to military sonar. Densities of *M. densirostris* in the Abaco Island area, > 100 km north of the AUTEC range, appear to have remained stable from 1998 – 2011 (Claridge and Durban 2012), suggesting that, at least for this species in the Bahamas region, any potential negative effects of navy sonar may have a limited geographic reach. However, major differences in deepwater canyon bathymetry and spatial dynamics of naval operations between AUTEC and SOAR make it difficult to extend inference for *Mesoplodon* in the Bahamas to *Mesoplodon* and *Ziphius* in the California Current.

Ecosystem change

Beaked whale feeding ecology is poorly known. Stomach content analyses from stranded animals suggest many beaked whale species feed primarily on cephalopods as well as some mid-water and demersal fishes in the

deep ocean. *Mesoplodon* whales utilize smaller prey and more fish than *Z. cavirostris*, which seems to feed mainly on larger cephalopods (MacLeod et al. 2003). *B. bairdii* may feed mostly on demersal fishes, although cephalopods may be important as well (MacLeod et al. 2003, Ohizumi et al. 2003).

We do not know how preferred beaked whale prey abundance in the California Current may have changed over recent decades, so it is not possible to make conclusions in this paper about impacts of ecosystem change on apparent beaked whale declines in the region. However, it is important to acknowledge the possibility that prey abundance or composition could have changed, either as a consequence of fishing (e.g., mid-water and demersal trawling) or oceanographic changes associated with changing climate or other physical forces. For example, Ohizumi et al. (2003) documented strong overlap between *B. bairdii* diet species and those targeted by bottom-trawl fisheries in Japan. Major changes in bottomfish assemblages have been documented over the continental shelf of the U.S. Pacific coast, indicating the potential for bottom-trawl fisheries to impact food resources for bottom-feeding predators (Levin et al. 2006). Deep ocean oxygen levels in the California Current have decreased in recent decades, and climate models predict further decreases over the coming century; these have been linked to changes in mid- and deepwater animal communities (e.g., Bograd et al. 2008, Koslow et al. 2011, Seibel 2011), including those possibly associated with range expansion of jumbo squid (*Dosidicus gigas*) (Zeidberg and Robison 2007, Field et al. 2007). These are just a few anecdotes to highlight the potential viability of a hypothesis for ecosystem change in the deepwater environment as a driver of apparent beaked whale declines in our study system. A review beyond the scope of this paper is needed to thoroughly evaluate the evidence for changing demersal prey community composition and abundance in the California Current.

Summary and research recommendations

The abundance of *Mesoplodon* and *Ziphius* beaked whales appears to have declined in the California Current since the early 1990s. Drivers of these apparent declines are unknown. Fisheries impacts can probably be ruled out. Impacts from anthropogenic noise and ecosystem change are plausible explanations, but additional research is required to evaluate these hypotheses. Dedicated survey effort to estimate trends in the SOAR area and in additional control areas would help test hypotheses concerning the effects of navy sonar on trends. Data on individual movement patterns would provide complementary insight about the potential geographic reach of local impacts at SOAR to other areas of the system. Hypotheses related to ecosystem change could possibly be evaluated through dedicated surveys in areas differently affected by deepwater oxygen depletion, demersal fishing, jumbo squid range expansion, etc., combined with research on spatial or temporal variation in beaked whale diets (e.g., via stomach content and/or stable isotope analysis of stranded animals). Increased use of acoustic methods to improve the amount of abundance information collected during surveys would be valuable. Additional large-scale surveys (especially augmented by acoustic data) will be useful for increasing sample sizes and the length of the time series to eventually permit geographically stratified analysis (ideally in relation to large-scale variation in ecosystem characteristics) and to ensure that the declines estimated to date are not the result of random sampling error; although our best inference based on the current information is that they are not.

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