

ARTICLE

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A multidecadal Bayesian trend analysis of harbor porpoise (*Phocoena phocoena*) populations off California relative to past fishery bycatch

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Abstract

Harbor porpoises, *Phocoena phocoena*, off California, comprise four recognized population stocks: Morro Bay (MOR), Monterey Bay (MRY), San Francisco-Russian River (SFRR), and Northern California-Southern Oregon (NCSO). The three southernmost stocks experienced substantial bycatch in gill net fisheries during the 1970s and 1980s. While the SFRR stock received full protection from gill nets in 1989, the MOR and MRY stocks continued to experience at least some bycatch through 2001–2002. We examined long-term population trends for these four harbor porpoise stocks, based on two sets of systematic, aerial line-transect surveys conducted off California during summer/fall of 1986–2017. We applied a Bayesian hierarchical framework to specify a process model of population density and an observation model of porpoise counts during line-transect surveys. Growth rates were estimated for periods with and without bycatch. Posterior distributions indicate the MOR, MRY, and SFRR stocks, respectively, grew at 9.6%, 5.8%, and 6.1% per year after gill nets were largely or fully eliminated for each stock. Abundance off northern California appears stable or slightly increasing. This study provides a first empirical estimate of maximum net reproductive rate for harbor porpoise (at least 9.6%), and demonstrates that porpoise populations can recover from substantial gill net impacts if bycatch is eliminated.

KEYWORDS

abundance, Bayesian hierarchical model, bycatch, California, harbor porpoise, maximum net productivity rate, Pacific, *Phocoena phocoena*, population recovery, population trends

1 | INTRODUCTION

Small cetaceans are known to be vulnerable to bycatch (i.e., incidental mortality in fishing gear) throughout the world (Read, et al., 1993; Reeves, et al., 2013). Bycatch has caused or contributed to population declines of dolphins and porpoises in diverse oceanic, neritic, and river systems, leading to extinction or near-extinction in the most extreme cases, such as the baiji (*Lipotes vexillifer*) and the vaquita (*Phocoena sinus*) (Benke et al., 2014; Burkhart & Slooten, 2003; Dawson et al., 2001; Gerrodette & Forcada, 2005; Slooten et al., 2013; Taylor et al., 2016; Turvey et al., 2007). Even when active monitoring programs have been implemented and steps have been taken to reduce bycatch, population recoveries have been difficult to achieve and document (e.g., Gerrodette & Forcada, 2005; Slooten & Davies, 2012).

The harbor porpoise, *Phocoena phocoena*, has been particularly vulnerable to impacts from fishing and other anthropogenic activities throughout its coastal, northern hemisphere range (Barlow & Hanan, 1995; Jefferson & Curry, 1994; Read et al., 1993; Teilmann & Carstensen, 2012; Tregenza et al., 1997). Gill net fisheries have been particularly problematic, as harbor porpoises are vulnerable to fatal entanglement. Population declines attributable to gill net fisheries have been documented or are suspected in several regions (Carlén et al., 2018; Jefferson & Curry, 1994; Osmek et al., 1996; Read et al., 1993). To our knowledge, population recoveries have not been documented, although harbor porpoises have recently expanded back into Puget Sound, Washington, and San Francisco Bay, California, from adjacent waters after decades of absence (Evenson et al., 2016; Stern et al., 2017).

Off California, harbor porpoises were anecdotally reported as bycatch in a large-scale California gill net fishery for white seabass (*Cynoscion nobilis*) that started in the 1930s and tapered off with the depletion of this fish stock in the 1970s (Barlow & Hanan, 1995; Methot, 1983). No estimates of total bycatch were made, but Norris and Prescott (1961) reported that 10 porpoises were caught within less than a week by a single sea bass fishing vessel operating out of Morro Bay. A gill net fishery for halibut (*Paralichthys californicus*) expanded in central California during 1970s and 1980s. Limited bycatch monitoring in that fishery facilitated the first rough estimates of harbor porpoise bycatch, revealing differences in the timing and intensity of bycatch in three fishing regions along the central California coast (Barlow & Hanan, 1995; Figure 1). Despite the uncertainty of these early estimates, the levels of mortality were sufficiently high to have caused an overall population decline in central California by 1989 (Barlow & Hanan, 1995).

A monitoring program was initiated in 1986 to assess population status and trends of California harbor porpoises (Forney et al., 1991). Aerial surveys were conducted annually from 1986 to 1991, biannually from 1993 to 1999, and every 3–5 years from 2002 to 2011. Genetic studies have revealed that there are multiple, genetically distinct populations off California (Chivers et al., 2002, 2007), and four distinct “population stocks” (henceforth, “populations” for simplicity) are currently recognized for management under the U.S. Marine Mammal Protection Act (Figure 2A–C; Carretta et al., 2019). The most recent abundance estimates, N , for these four populations (with population names, abbreviations used in this paper, and coefficients of variation, CV) are: Morro Bay (MOR; $N = 2,917$, $CV = 0.44$ during 2012), Monterey Bay (MRY; $N = 3,715$, $CV = 0.51$ during 2011), San Francisco-Russian River (SFRR; $N = 9,886$, $CV = 0.51$ during 2007–2011), and Northern California-Southern Oregon (NCSO; $N = 35,769$, $CV = 0.52$ during 2007–2011) (Carretta et al., 2019; Forney et al., 2014).

Between 2000 and 2017, additional aerial surveys were conducted within portions of central and northern California to assess the abundance and distribution of leatherback turtles. These surveys were flown along adaptive fine-scale transect lines, using the same data collection protocols and many of the same observers as the ongoing harbor porpoise surveys. Combined, the two aerial survey data sets offer a unique opportunity to examine

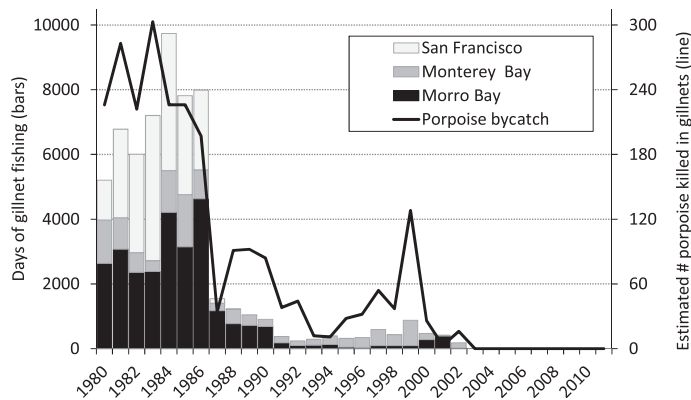


FIGURE 1 History of estimated harbor porpoise bycatch and set gill net fishing effort off central California, by porpoise population region. No commercial set gill net fishing has been allowed north of the Sonoma-Mendocino County line since at least 1915. Sources: Barlow & Forney (1994); Barlow & Hanan (1995); Carretta (2001, 2002); Carretta & Chivers (2003); Diamond & Vojtkovich (1990); Forney et al. (2001); Hanan et al. (1991); Konno (1991); Perkins et al. (1994); Wild (1990). In those studies, fishing effort was estimated from logbook data, and total porpoise bycatch was estimated by multiplying total effort times porpoise bycatch rates calculated from a subset of observed fishing trips.

multidecadal population trends for each California harbor porpoise population, relative to the timing and intensity of past gill net bycatch. In this study, we have conducted a trend analysis within a Bayesian hierarchical framework, which allows us to efficiently integrate the different data sets. Past trend analyses for California harbor porpoise were limited by low statistical power (Forney et al., 1991), whereas the Bayesian framework we apply here provides greater power to detect marine mammal population trends, even for rare species such as beaked whales (Moore & Barlow, 2013). Our goals are to (1) examine whether there is evidence for population recoveries in the three populations that experienced historical bycatch, compared to the northern California population that did not experience such mortality; and (2) empirically estimate post-bycatch growth rates, to increase our understanding of recovery capabilities and time-frames for this small cetacean species.

2 | METHODS

2.1 | Field methods

Survey effort along transects established to estimate harbor porpoise abundance and trends included a full series of replicated flights during 1986–1991, 1993, 1995, 1997, 1999, 2002, 2007 and 2011, and partial coverage during leatherback surveys during 2001, 2003–2006, and 2008–2017. These survey data were augmented with separate data from annually variable fine-scale surveys conducted during 2000–2017 in support of leatherback turtle and other harbor porpoise studies. All flights used the same data collection protocols, as described in Forney et al. (1991), with a few minor modifications. Dedicated harbor porpoise surveys were flown in a high-wing, twin-engine Partenavia P-68. Leatherback surveys were flown either in the same Partenavia aircraft or, in some years, a NOAA Twin Otter aircraft. All aircraft were outfitted similarly with lateral bubble windows and a belly viewing port, to accommodate two side observers and one belly observer. A data recorder documented information on survey conditions and sighting details. During 1986–1987, information was recorded on paper data sheets; beginning in 1988, all data were recorded into a laptop computer using custom survey software. Surveys were flown at 198–213 m altitude and 166–185 km/hr airspeed, from August 15 to November 15 of each year when weather conditions were forecast to be good (clear or mostly clear skies, light winds).

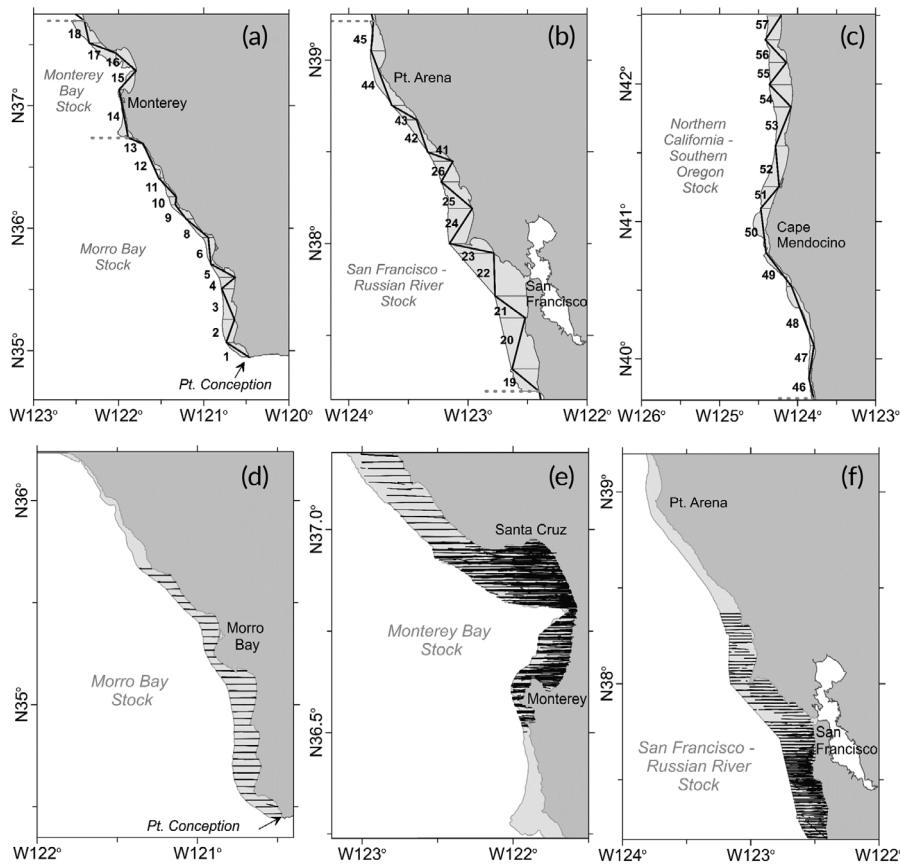


FIGURE 2 Summary of 1986–2017 aerial survey effort (black lines). Top panels: 1986–2017 harbor porpoise aerial surveys within the range of the (a) Morro Bay and Monterey Bay stocks, (b) San Francisco-Russian River stock, and (c) northern California portion of Northern California-Southern Oregon stock. Bottom panels: fine-scale survey effort within the range of (d) Morro Bay stock (flown in 2012), (e) Monterey Bay stock (2001–2013), and (f) San Francisco-Russian River stock (2002–2017). The light gray shaded area represents the survey area from coast to the 92-m isobath. In panels a–c, the individual transect strata defined for our analyses are labeled by transect number and separated by gray lines between transects. Area sizes for all strata are provided in Table S1.

Off California, harbor porpoises are primarily found in waters shallower than 92 m (50 fathoms) water depth (Forney et al., 2014), and the long-term harbor porpoise aerial survey transects (HPAS) followed a zig-zag pattern from the coast to the 92-m isobath (Figure 2a–c). Surveys were replicated up to 4–7 times during each full harbor porpoise survey year (except the areas north of the Russian River, which were only surveyed from 1989 onward). Leatherback surveys were conducted along portions of the same HPAS lines (Benson et al., 2007), and on adaptive, fine-scale east–west lines in areas where leatherback turtles and/or leatherback prey (Scyphomedusae) were encountered (Figure 2b–d) during 2000–2017.

2.2 | Data processing

We filtered the survey data to include only good weather conditions, defined as Beaufort sea states 0–2 and less than 25% cloud cover, before deriving transect-specific kilometers flown, number of porpoise sightings, and number of porpoises seen. Perpendicular sighting distances were extracted for all sightings, along with potential covariates

(sea state, glare, aircraft type, and group size). Each HPAS transect was considered to represent an along-shore stratum (Figure 2a–c). The adaptive fine-scale transects (Figure 2d–f) were assigned to the stratum within which they were located to allow the surveys to be combined into a single analysis. Any fine-scale effort that extended beyond the stratum boundaries was truncated.

2.3 | Bycatch and postbycatch periods

Based on independent bycatch estimates derived from fishing effort data and bycatch rates documented in observed gill and trammel net sets (Barlow & Forney, 1994; Barlow & Hanan, 1995; Carretta, 2001, 2002; Carretta & Chivers, 2003; Diamond & Vojkovich, 1990; Forney et al., 2001; Hanan et al., 1991; Konno, 1991; Perkins et al., 1994; Wild, 1990), the largest reduction in harbor porpoise bycatch occurred at the beginning of our population monitoring period in 1986–1987 (Figure 1). This reduction was a consequence of regulations implemented to protect seabirds and southern sea otters, *Enhydra lutris* (Wild, 1990). However, subsequent smaller reductions in bycatch also occurred during 1988–2003, and these were used to define distinct periods with extensive bycatch, low-moderate bycatch, or no bycatch for each region. For the Morro Bay population, gill net bycatch of harbor porpoises was mostly eliminated by 1991, when set gill net fisheries were prohibited in waters shallower than 56 m (30 fm) and fishing effort dropped by nearly 95% compared to the early 1980s (Figure 1). However, some estimated bycatch continued through late 2002, when set gill net fishing was permanently prohibited in waters shallower than 110 m (60 fm) off central California.¹ In the Monterey Bay region, a series of regulations restricting set gill nets in waters shallower than 27–37 m (15–20 fm) water depth caused fishing effort dropped by about half in 1987. However, harbor porpoise bycatch continued at moderate to high levels through 2000 (Figure 1), when a series of emergency closures were enacted. Gill net bycatch of harbor porpoises in the Monterey Bay Region was fully eliminated in 2002 when set gill net fishing was permanently prohibited in waters <110 m (60 fm; see Endnote 1). For the San Francisco-Russian River population, gill net and trammel net fishing was fully eliminated during 1987 because of concern over seabirds in that region (Wild, 1990).

Based on the above periods with greater harbor porpoise bycatch vs. little or no bycatch, we considered separate growth rates before and after 1991 and 2003 for MOR, and before/after 2000 and 2003 for MRY. For SFRR, we evaluated growth rates separately for 1986–1987 and 1988 onward. Porpoises in northern California were never exposed to commercial gill net fisheries, so a single growth rate was estimated in this region (noting that this population also ranges into southern Oregon, for which we did not have comparable survey data).

2.4 | Analytical methods

We conducted the trend analysis within a Bayesian hierarchical modeling framework using Markov Chain Monte Carlo (MCMC) simulations in R (v. 3.1.3; R Core Team, 2015) and OpenBUGS (v. 3.22; Lunn et al., 2009). The full model included a process model for population growth and an observation model of the distance sampling detection process during our surveys (Buckland et al., 2001). The approach is based on analyses of several California Current cetacean stocks conducted by Moore & Barlow (2011, 2013, 2014).

2.4.1 | Process model

For each harbor porpoise population, a Markov process model for population growth was specified as:

$$N_t = N_{t-1} \times \exp(r + \varepsilon_t) \times Sp$$

$$\varepsilon_t \sim \text{Normal}(0, \sigma_{\text{process}}^2),$$

where N_t is porpoise abundance in year t ; r is the expected annual rate of change for a population growing at its maximum potential rate (e.g., density-independent condition); S_p is the bycatch survival rate for porpoises in period p , i.e., $1 -$ the probability of dying from bycatch (with S_1 and S_2 representing this survival rate during and after the high-bycatch period, respectively); and ε_t is process error, assumed to be normally distributed on a log scale with a mean of zero and variance $\sigma^2_{\text{process}}$. Process variance is contributed by both demographic and movement processes. We set $S_2 = 1$, as this parameter is not separately estimable from the data. Thus, we make the model assumption that bycatch mortality does not occur during the low/no-bycatch period, though in reality some small level of bycatch mortality might occur. This implies that S_1 is in fact the survival relative to the true unknown S_2 , and that r is the maximum potential growth rate discounted by the true unknown S_2 . A density-dependent model was also attempted but would not converge for any stock (i.e., the simulations did not update and ran indefinitely); this is not entirely surprising, given that the aerial survey data do not contain information that would uniquely resolve the interlinked parameters r , N , and K .

The mean rate of actual population change during the course of the study differs from r . This realized mean annual growth rate for each time period, λ_p , was estimated as the geometric mean of the annual population changes, i.e., of the $\lambda_{t(p)} = N_{t(p)}/N_{t(p)-1}$. The posterior distribution for $\lambda_2 - \lambda_1$ was used to probabilistically assess support for a change in growth rates between the two periods.

Animal density is $D_t = N_t/A$, where A is the size of the total study area for each population (Table 1). However, density varies across space (strata) and—for purposes of linking the process and observation models—this must be modeled in the current analysis, because weather constraints resulted in uneven sampling of the within-population strata across years. Let the density of porpoise in stratum i at time t be thus described by: $D_{i,t} = D_t * c_i$. The stratum effect multiplier c_i was treated as a constant through time, implying that certain strata have persistently higher mean densities (better habitat) than others. Annual departures from this expectation were handled by allowing for overdispersion in the observation model below. We also defined stratum-area weights $w_i = a_i/A$, where a_i are the stratum areas, to allow estimation of the c_i (Table S1). The $c_i * w_i$ must sum to 1, so that overall density for the study area equals the area-weighted average of the stratum densities, i.e., $D_t = \sum_i D_{i,t} a_i / A = \sum_i D_{i,t} c_i w_i$. Also note that c_i must be less than or equal to its respective $1/w_i$ because if any $c_i = 1/w_i$ this implies that all animals in the population are in this single stratum. These constraints are important when specifying Bayesian priors for the c_i .

2.4.2 | Observation model

The observation model links the above process to the observed data, namely the counts of porpoises within each year and stratum. Following a distance sampling approach, the expected porpoise counts, $E[n_{i,t}] = \mu_{i,t}$, are:

$$E[n_{i,t}] = \mu_{i,t} = 2 \times L_{i,t} \times ESW \times g(0) \times D_{i,t}$$

where $L_{i,t}$ are the lengths of transect line (kilometers) surveyed within the strata, $g(0)$ is the probability of detecting a porpoise group that is on the transect line, and ESW is the effective strip half-width (kilometers). ESW was estimated from the porpoise observation data using Distance 6.2 (Thomas et al., 2010), evaluating both conventional and multivariate approaches to include potential weather and aircraft-type covariates. The detection function that minimized AIC was selected for subsequent analyses and included as an informative prior with a normal distribution in the model. The probability of detecting animals on the transect line, $g(0)$, was taken as 0.292 (CV = 0.366) from a study by Laake et al. (1997) that included both availability and perception bias. In our analysis, $g(0)$ was specified using a beta distribution corresponding to these values (alpha = 4.993, beta = 12.107).

TABLE 1 Summary of combined 1986–2017 survey effort (km), numbers of porpoises recorded (# porp.), and area sizes (km²), by harbor porpoise population region. Northern California represents only the California portion of the Northern California–Southern Oregon population (Carretta et al., 2019).

Year	Morro Bay population 1,848		Monterey Bay population 1,195		San Francisco-Russian River population 3,639		Northern California 3,559	
	Area size (km ²)	# porp.	Area size (km ²)	# porp.	Area size (km ²)	# porp.	Area size (km ²)	# porp.
1986	919	56	379	37	409	54	—	—
1987	1,000	30	353	32	225	5	—	—
1988	471	6	366	18	491	65	—	—
1989	445	12	386	71	418	42	240	27
1990	1,010	20	351	50	547	55	525	227
1991	567	12	297	59	198	10	408	149
1992	—	—	—	—	—	—	—	—
1993	1,105	17	677	67	919	92	631	196
1994	—	—	—	—	—	—	—	—
1995	827	30	603	119	678	68	304	144
1996	—	—	—	—	—	—	—	—
1997	1,276	59	671	131	733	136	530	214
1998	—	—	—	—	—	—	—	—
1999	1,135	106	525	69	922	200	669	319
2000	—	—	62	7	142	36	—	—
2001	—	—	980	176	343	51	—	—
2002	1,312	120	1,699	423	2,044	540	350	97
2003	—	—	1,884	593	1,642	426	—	—
2004	—	—	2,611	914	2,132	727	—	—
2005	—	—	990	339	660	540	—	—
2006	110	14	776	119	1,639	480	—	—
2007	517	96	821	234	1,143	146	320	193
2008	76	17	541	88	1,214	320	24	—
2009	—	—	594	202	1,572	356	—	—
2010	—	—	450	173	173	34	—	—
2011	542	68	1,396	473	974	185	390	179
2012	1,406	238	372	120	277	34	—	—
2013	—	—	488	202	1,174	141	—	—
2014	—	—	—	—	319	72	90	18
2015	—	—	—	—	—	—	—	—
2016	—	—	—	—	1,442	262	288	61
2017	—	—	—	—	978	187	—	—

The observed porpoise counts, $n_{i,t}$, were assumed to be negative binomially distributed using a Poisson-gamma specification:

$$\begin{aligned} n_{i,t} &\sim \text{Poisson}(\mu_{i,t} \times \rho_{i,t}), \\ \rho_{i,t} &\sim \text{gamma}(\alpha, \alpha). \end{aligned}$$

2.4.3 | Priors and estimation

For the process model, we used the following uniform priors: $r \sim \text{Uniform}(0.00, 0.15)$; $\sigma_p \sim \text{Uniform}(0, 1)$. Initial population sizes were specified as $N_0 \sim \text{Uniform}(0, 10,000)$, except for the larger northern California population, for which we specified $N_0 \sim \text{Uniform}(0, 40,000)$. [Note: we also evaluated alternate, nonuniform priors, and results were virtually identical, so we retained the simpler uniform specification for the analysis.] Prior specifications for the c_i were more complex, to conform to the constraints described above:

$$c_1 \sim \text{uniform}(0, 1/w_1)$$

$$c_i \sim \text{uniform}\left(0, \frac{1 - \sum_{j=1}^{i-1} c_j w_j}{w_i}\right),$$

for $i = 2, 3, \dots, k-1$, where k is the number of strata.

$$c_k = \frac{1 - \sum_{j=1}^{k-1} c_j w_j}{w_k}$$

For the observation model, ESW was specified based on the estimated detection function (see Results below): $ESW \sim \text{Normal}(0.1603, 0.004)$. The negative binomial overdispersion parameter, α , was specified as $\alpha \sim \text{Uniform}(0, 10)$.

Analyses were conducted separately for each the four porpoise populations, because our model did not require the estimation of any shared parameters, and this approach was computationally simpler for evaluating the different bycatch change years for MOR and MRY. For each of the four porpoise populations, we used two MCMC chains of 10,000 samples, with a thinning rate of 100 to minimize autocorrelation in the samples and a 5,000 step burn-in. Using this thinning rate, the effective sample size was 5,000 samples. Model convergence was ascertained visually (when chains were clearly stable and well-mixed, and posterior distributions had smoothed), and using diagnostics developed by Gelman and Rubin (1992) and Geweke (1992) using the R package *coda*. The Geweke method tests for equality of the means of the first and last parts of a Markov chain, while the Gelman score provides a measure of convergence (with scores in the 1.00–1.05 range indicating good convergence).

3 | RESULTS

Survey effort varied by year in each region (Table 1), with better coverage earlier in our study period for most areas. Harbor porpoise sighting rates were spatially and temporally variable. The available time series spanned 1986–2012, 1986–2013, 1986–2017, and 1989–2016, respectively, for MOR, MRY, SFRR and the northern California portion of NCSO. The detection function that minimized AIC was determined to be a simple half-normal function without covariates, resulting in an estimated ESW of 160.3 m ($SE = 4$). In all four analyses, the MCMC chains achieved convergence, as indicated by Gelman statistics within the recommended range of 1.00–1.05, and nonsignificant Geweke scores for the abundance estimates. The resulting estimates of population growth rates (Table 2) and abundance are summarized separately below for each harbor porpoise population. Posterior distributions for key parameters are shown in the Supplementary Materials.

3.1 | Morro Bay population (MOR)

The analysis indicated very strong support (100% chance that $\lambda_1 < \lambda_2$) for a change in annual population growth rate beginning in 1991 (when bycatch was mostly eliminated) with an estimated mean $\lambda = 0.734$ ($SE = 0.076$) during the

TABLE 2 Survey years for bycatch and postbycatch periods in each harbor porpoise population, with estimated annual population growth rates (λ) and associated standard error (SE) and 95% credible interval (CI), by bycatch period.

Population		Bycatch period	No/low bycatch period
Morro Bay	Years	1986–1990	1991–2012
	λ	0.734, SE = 0.076, 95% CI [0.596, 0.893]	1.096, SE = 0.017, 95% CI [1.062, 1.130]
Monterey Bay	Years	1986–2002	2003–2013
	λ	1.016, SE = 0.019, 95% CI [0.975, 1.054]	1.058, SE = 0.031, 95% CI [0.998, 1.124]
San Francisco-Russian River	Years	1986–1987	1990–2017
	λ	0.548, SE = 0.186, 95% CI [0.281, 0.969]	1.025, SE = 0.012, 95% CI [0.9992, 1.048]
Northern California	Years		1989–2016
	λ		1.018, SE = 0.017, 95% CI = [0.987, 1.055]

bycatch period of 1986–1990 and $\lambda = 1.096$ (SE = 0.017) from 1991 onward. There was less support (78.9%) for a change in growth rates beginning in 2003, when gill net bycatch was fully eliminated. Our analysis estimated a 99.9% probability that the population declined during 1986–1990, when bycatch of harbor porpoises in gill nets was known but virtually unmonitored. In contrast, the analysis indicated a 100% probability of population increase during 1991–2012. The lowest estimated median abundance for MOR was estimated to be 571 porpoises, 95% credible interval (CI) [252, 2,666], CV = 0.585, during 1990. Abundance increased to an estimated 4,191 porpoises, 95% CI [1,900, 11,971], CV = 0.561, during 2012, the most recent survey year. Combined, these results indicate a population decline during the bycatch years of 1986–1990, and a dramatic recovery of the population during the subsequent two decades (Figure 3a).

3.2 | Monterey Bay population (MRY)

There was similar support for a change in population growth rates in 2003 (87.6%), when bycatch was fully eliminated, compared to 2000 (86.2%), when bycatch was reduced. The mean annual growth rate estimates for the bycatch period of 1986–2002 ($\lambda = 1.016$, SE = 0.019) was lower than for the postbycatch period ($\lambda = 1.058$, SE = 0.031), but both periods exhibited positive growth, with a 98.8% chance of an increasing trend between 1986 and 2013 (Figure 3b). The lowest estimated median abundance for MRY harbor porpoises was about 1,486, 95% CI [670, 4,233], CV = 0.548, during 1987, while the most recent estimate during 2013 was 3,760 95% CI [1,686, 10,940], CV = 0.561.

3.3 | San Francisco–Russian River population (SFRR)

The analysis estimated a 98.9% probability that the growth rates differed before and after bycatch was fully eliminated during 1987. There is a 98.4% probability that this population exhibited a year-over-year decline between 1986 and 1987 ($\lambda = 0.548$, SE = 0.186), followed by 97.1% certainty that the annual population growth rate became positive ($\lambda = 1.025$, SE = 0.012). The lowest estimated median abundance for SFRR harbor porpoise was about 2,957, 95% CI [1,233, 9,048], CV = 0.622, during 1987. The population then appeared to increase to a peak estimated abundance of 13,530, 95% CI [6,215, 39,554], CV = 0.653 during 2005 before stabilizing at a lower abundance of about 7,000–8,000 during 2007–2017. The most recent estimate is 7,777, 95% CI [3,440, 22,610],

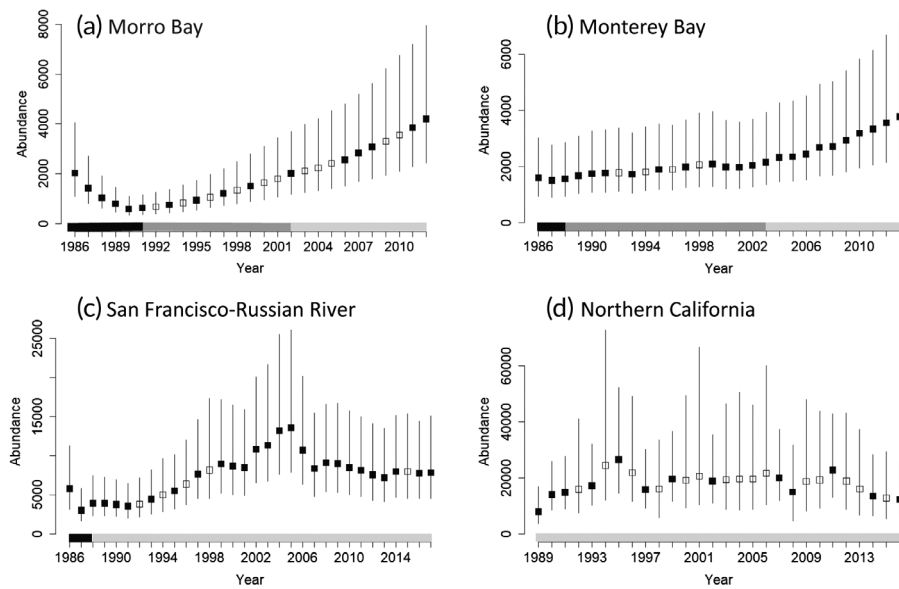


FIGURE 3 Population trends for harbor porpoises belonging to (a) Morro Bay, (b) Monterey Bay, (c) San Francisco-Russian River, and (d) Northern California-Southern Oregon stocks recognized under the Marine Mammal Protection Act (Carretta et al., 2019). Estimates represent median abundance (with 95% credible intervals) for years with survey effort (solid symbols) and without survey effort (open symbols). Shaded bars along the x-axes reflect the relative level of bycatch during each period: high bycatch (black), low-moderate bycatch (dark gray), or no bycatch (light gray).

CV = 0.620, during 2017 (Figure 3c). Given the leveling off of this population during 2006–2017, we conducted an additional simulation to estimate the growth rate during peak growth years (through 2005), yielding $\lambda = 1.061$ (SE = 0.021) as a maximum realized rate of growth.

3.4 | Northern California-Southern Oregon population (NCSO)

The surveys represented in this study only included the northern California portion of the currently designated Northern California-Southern Oregon population, so the estimated trends are only for a subset of this population's described geographic range. Although there is considerable uncertainty in the abundance estimates for northern California because of the limited survey effort in this region (Table 1), our analysis suggests a mostly stable population size of about 10,000–20,000 porpoises (Figure 3d). The overall annual population growth rate was estimated to be slightly positive, with $\lambda = 1.018$ (SE = 0.017), and an 85.1% probability of increase between 1989 and 2016. The most recent median abundance estimate was 12,160, 95% CI [4,471, 38,561], CV = 0.663 during 2016 (Figure 3d).

4 | DISCUSSION

The trends identified in this analysis are consistent with the existence of prior bycatch impacts on harbor porpoises off California, continued impacts on some populations early in our monitoring period, and a subsequent recovery of all three harbor porpoise populations exposed to gill net fisheries. In particular, the results of this trend analysis strongly suggest that the Morro Bay harbor porpoise population was more severely impacted prior to the 1980s than previously recognized. When gill net fishing effort was reduced to low levels in 1991, this harbor porpoise population was estimated to include only about 570 porpoises, but it has since rebounded to about 4,200 individuals.

Although there are opportunistic records of porpoise mortality in gill nets going back as far as the 1950s (Norris & Prescott, 1961), gill net fisheries that had potential to kill porpoises were not systematically monitored in this region until the early 1990s (Julian & Beeson, 1998). Given the large population increase after set gill net fishing was mostly eliminated in 1991, it is likely that unmonitored fisheries had a dramatic adverse impact on the Morro Bay population before monitoring of harbor porpoise began in 1986 (Diamond & Vojkovich, 1990). This population appears to be isolated from the Monterey Bay population by a section of coastline along Big Sur that has very steep bathymetry and little shallow-water habitat, and where very few porpoises have been recorded during our multidecadal aerial surveys. The estimated Morro Bay population growth rate during the postbycatch period, 9.6% per year, is very similar to the maximum possible growth rate of 9.4% estimated by Barlow & Hanan (1995) based on plausible life history parameters, despite some low levels of continued bycatch until 2002. To our knowledge, this represents the first time that a maximum net productivity rate has been estimated empirically for any harbor porpoise population in the world.

Population trends for the other three harbor porpoise populations are less clear. There was moderately strong support for a change in population growth rates for the Monterey Bay population associated with the end of gill net bycatch in 2003, and the estimated annual population growth rate after 2003 was 5.8% per year—much lower than for Morro Bay. This could suggest that (1) the population was not as heavily depleted by pre-1986 gill net bycatch; (2) the population had already partially recovered during the period of lower bycatch during the early 1990s (Figures 1 and 3), resulting in a slower growth rate after gill nets were fully eliminated in 2003; (3) there have been continuing factors slowing population recovery; (4) the intrinsic net productivity rate of this population is lower than for the Morro Bay population, or (5) the true growth rate was similar (e.g., $\lambda = 1.08$) but there is error in the estimates, as illustrated by the overlapping credible intervals (Figures S1a and S2a). The high documented levels of bycatch during the 1980s (Barlow & Hanan, 1995) make (1) unlikely, but continued fishery-related strandings of harbor porpoises, as well as fatal attacks on porpoises by bottlenose dolphins (Cotter et al., 2012; Wilkin et al., 2012) could have contributed to (3). The results of our analysis appear most consistent with (2), as the abundance estimates in Figure 3b show a slight population increase during the early 1990s, followed by leveling off during the period of greater bycatch in the late 1990s and then a more rapid growth after gill net bycatch was fully eliminated in 2003.

Trends for the San Francisco-Russian River population (Figure 3c) initially are similar to those for Morro Bay population, showing a decline followed by rapid postbycatch population growth between 1988 and 2005. After 2005, however, the population appears to level off at a slightly lower abundance (but with wide credible intervals) that is relatively stable through the end of our surveys in 2017. Given the large uncertainty in our abundance estimates during 2002–2007, it is plausible that the apparent peak and decline was caused by high sampling variation during the years when the population stabilized following a period of growth after 1988. Alternately, if this population decline is real and not artifact of the large uncertainty in our estimates, potential causes could include (1) unusual ocean conditions documented during 2005 (Petersen et al., 2006); (2) a change in the distribution of porpoises that would make them less likely to be sampled during our surveys; or (3) a population decline caused by other, unknown natural or anthropogenic factors. An offshore distribution shift is unlikely, as we have rarely encountered harbor porpoises in waters deeper than our study area during 2005–2016 fine-scale leatherback surveys that extended farther offshore (Benson et al., 2020). Beginning in 2009, however, hundreds of porpoises have regularly been seen in San Francisco Bay after decades of absence (Stern et al., 2017), and it is possible that a shift in their distribution towards the bay could have affected the number of animals available for detection along the outer coast transect lines in this region. A coordinated survey of both outer coast and inner bay waters could help resolve whether the population abundance has indeed changed. Further, although genetic differences were detected between the MRY and SFRR populations (Chivers et al., 2002, 2007), the precise boundary between these populations was inferred to be within a low-density region because of sparse sampling. As a result, some interchange of animals across this boundary is possible, which could potentially confound our trend analysis.

Abundance patterns for harbor porpoises off northern California suggest a stable population, consistent with our *a priori* expectation, given the absence of past commercial gill net bycatch. However, there is large

uncertainty in our estimates because of the low level of survey coverage in this area. Furthermore, genetic studies indicate that this population extends into southern Oregon (Chivers et al., 2007), and potential movement of individuals between Oregon and California could increase year-to-year variation in our northern California survey results.

Although statistical power to detect trends has historically been challenging for harbor porpoise along the U.S. West Coast (Forney, 1999; Forney et al., 1991), our analysis that combined different data sets within a Bayesian hierarchical framework enabled us to identify trends for four harbor porpoise populations relative to past gill net bycatch within each population's range. The results of this study confirm that harbor porpoise populations can recover if anthropogenic impacts are eliminated, but recovery takes many years or decades, underscoring the importance of long-term monitoring. Large adverse impacts on harbor porpoise populations can happen over relatively short periods of time, particularly in areas of continued gill net fishing or other activities known to affect harbor porpoises adversely, such as anthropogenic noise (e.g., Carstensen et al., 2006; Dähne et al., 2013; Forney et al., 2017; Lucke et al., 2009; Pirotta et al., 2014; Teilman & Carstensen, 2012; Thompson et al., 2013; Tougaard et al., 2009). Ongoing population monitoring, coupled with analytical approaches that maximize our ability to assess potential anthropogenic impacts and population trends, are essential for ongoing management of vulnerable coastal small cetaceans, such as the harbor porpoise. Our finding that three harbor porpoise populations did indeed recover when bycatch was eliminated or reduced gives hope that other depleted small cetacean populations worldwide can also recover if management actions are successful at mitigating anthropogenic impacts.

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AUTHOR CONTRIBUTIONS

Karin Forney: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing-original draft; writing-review and editing. **Jeffrey Moore:** Conceptualization; formal analysis; investigation; methodology; writing-original draft; writing-review and editing. **Jay Barlow:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; visualization; writing-review and editing. **James Carretta:** Data curation; investigation; methodology; project administration; writing-review and editing. **Scott Benson:** Conceptualization; data curation; investigation; methodology; project administration; writing-review and editing.

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ENDNOTE

- ¹ California Code of Regulations, Title 14, Section 104.1 (14 CCR 104.1).

REFERENCES

- Barlow, J., & Forney, K. A. (1994). *An assessment of the 1994 status of harbor porpoise in California in 1993* (NOAA Technical Memorandum NMFS-SWFSC-205). U.S. Department of Commerce.
- Barlow, J. & Hanan, D. (1995). An assessment of the status of harbor porpoise in central California. *Report of the International Whaling Commission, Special Issue 16*, 123–140.
- Benke H., Bräger S., Dähne M., Gallus A., Hansen, S., Honnef, C. G., Jabbusch, M., Koblit, J. C., Krügel, K., Liebschner, A., Narberhaus, I., & Verfuß, U. (2014). Baltic Sea harbour porpoise populations: Status and conservation needs derived from recent survey results. *Marine Ecology Progress Series*, 495, 275–290. <https://doi.org/10.3354/meps10538>
- Benson, S. R., Forney, K. A., Harvey, J. T., Carretta, J. V., & Dutton, P. H. (2007). Abundance, distribution and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. *Fishery Bulletin*, 105, 337–347.
- Benson, S. R., Forney, K. A., Moore, J. E., LaCasella, E. L., Harvey, J. T., & Carretta, J. V. (2020). A long-term decline in the abundance of endangered leatherback turtles, *Dermochelys coriacea*, at a foraging ground in the California Current Ecosystem [Manuscript submitted for publication]. Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration; Moss Landing Marine Laboratories, San Jose State University.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press.
- Burkhart, S. M., & Slooten, E. (2003). Population viability analysis for Hector's dolphin (*Cephalorhynchus hectori*): A stochastic population model for local populations. *New Zealand Journal of Marine and Freshwater Research*, 37(3), 553–566. doi: <https://doi.org/10.1080/00288330.2003.9517189>
- Carlén, I., Thomas, L., Carlström, J., Amundin, M., Teilmann, J., Tregenza, N., Tougaard, J., Koblit, J. C., Sveegaard, S., Wennerberg, D., Loisa, O., Dähne, M., Brundiers, K., Kosecka, M., Kyhn, L. A., Ljungqvist, C. T., Pawliczka, I., Koza, R., Arciszewski, B., Galatius A., Jabbusch M., Laaksonlahti J., Niemi J., Lyytinen S., Gallus A., Benke H., Blankett P., Skóra K. E. Acevedo-Gutiérrez, A. (2018). Basin-scale distribution of harbour porpoises in the Baltic Sea provides basis for effective conservation actions. *Biological Conservation*, 226, 42–53. <https://doi.org/10.1016/j.biocon.2018.06.031>
- Carretta, J. V. (2001). Preliminary estimates of cetacean mortality in California gillnet fisheries for 2000. Paper SC/53/SM9 presented to the International Whaling Commission, Scientific Committee, London, UK.
- Carretta, J. V. (2002). Preliminary estimates of cetacean mortality in California gillnet fisheries for 2001. Paper SC/54/SM12 presented to the International Whaling Commission, Scientific Committee, Shimonoseki, Japan.
- Carretta, J. V., & Chivers, S. J. (2003). Preliminary estimates of marine mammal mortality and biological sampling of cetaceans in California gillnet fisheries for 2002. Paper SC/55/SM3 presented to the International Whaling Commission, Scientific Committee, Berlin, Germany.
- Carretta, J. V., Forney, K. A., Oleson, E. M., Weller, D. W., Lang, A. R., Baker, J., Muto, M. M., Hanson, B., Orr, A. J., Huber, H., Lowry, M. S., Barlow, J., Moore, J. E., Lynch, D., Carswell, L., & Brownell, R. L., Jr. (2019). *U.S. Pacific Marine Mammal Stock Assessments: 2018* (NOAA Technical Memorandum NMFS-SWFSC-617). U.S. Department of Commerce.
- Carstensen, J., Henriksen, O. D., & Teilmann, J. (2006). Impacts of offshore wind farm construction on harbour porpoises: Acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series*, 321, 295–308.
- Chivers, S. J., Dizon, A. E., Gearin, P. J., & Robertson, K. M. (2002). Small-scale population structure of eastern North Pacific harbour porpoises, (*Phocoena phocoena*), indicated by molecular genetic analyses. *Journal of Cetacean Research and Management*, 4(2), 111–122.
- Chivers, S. J., Hanson, B., Laake, J., Gearin, P., Muto, M. M., Calambokidis, J., Duffield, D., McGuire, T., Hodder, J., Greig, D., Wheeler, E., Harvey, J., Robertson, K. M., & Hancock, B. (2007). *Additional genetic evidence for population structure of Phocoena phocoena off the coasts of California, Oregon and Washington* (Southwest Fisheries Science Center Administrative Report LJ-07-08). U.S. Department of Commerce.
- Cotter, M. P., Maldini, D., & Jefferson, T. A. (2012). "Porpicide" in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 28(1), E1–E15. <https://doi.org/10.1111/j.1748-7692.2011.00474.x>
- Dähne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krügel, K., Sundermeyer, J., & Siebert, U. (2013). Effects of pile-driving on harbor porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters*, 8, 025002. <https://doi.org/10.1088/1748-9326/8/2/025002>
- Dawson, S. D., Pichler, F., Slooten, E., Russel, K., & Baker C. S. (2001). The North Island Hector's dolphin is vulnerable to extinction. *Marine Mammal Science*, 17(2), 371–381.

- Diamond, S. L., & Vojkovich, M. (1990). Estimating total effort in the gill and entangling net fishery for California halibut, 1980–86. In C. W. Haugen (Ed.), *The California halibut, Paralichthys californicus, resource and fisheries* (pp. 265–279). California Department of Fish and Game, Fish Bulletin 174.
- Evenson, J. R., Anderson, D., Murphie, B. L., Cyra, T. A., & Calambokidis, J. (2016). *Disappearance and return of harbor porpoise to Puget Sound: 20 year pattern revealed from winter aerial surveys* (Technical report). Washington Department of Fish and Wildlife, Wildlife Program and Cascadia Research Collective.
- Forney, K. A. (1999). Trends in harbor porpoise abundance off central California 1986–95: Evidence for interannual changes in distribution? *Journal of Cetacean Research and Management*, 1, 73–80.
- Forney, K. A., Benson, S. R., & Cameron, G. A. (2001). Central California gillnet effort and bycatch of sensitive species, 1990–98. In E. F. Melvin & J. K. Parrish (Eds.), *Seabird bycatch: Trends, roadblocks and solutions* (pp. 141–160). University of Alaska Sea Grant Publication AK-SG-01-01.
- Forney, K. A., Carretta, J. V., & Benson, S. R. (2014). *Preliminary estimates of harbor porpoise abundance in Pacific Coast waters of California, Oregon and Washington, 2007–2012* (NOAA Technical Memorandum NMFS-SWFSC-537). U.S. Department of Commerce.
- Forney, K. A., Hanan, D. A., & Barlow, J. (1991). Detecting trends in harbor porpoise abundance from aerial surveys using analysis of covariance. *Fishery Bulletin*, 89, 367–377.
- Forney, K. A., Southall, B., Slooten, E., Dawson, S., Read, A. J., Baird, R. W., & Brownell, R. L., Jr. (2017). Nowhere to go: Noise impact assessments for marine mammal populations with high site fidelity. *Endangered Species Research*, 32, 391–413. <https://doi.org/10.3354/esr00820>
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–511.
- Gerrodette, T., & Forcada, J. (2005). Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Marine Ecology Progress Series*, 291, 1–25.
- Geweke, J. (1992). Evaluating the accuracy of sampling-based approaches to calculating posterior moments. In J. M. Bernardo, J. O. Berger, A. P. Dawid, & A. F. M. Smith (Eds.), *Bayesian statistics 4*. (pp. 169–193). Clarendon Press.
- Hanan, D., Beeson, M. J., & Konno, E. S. (1991). *Effort estimates of California gill net fisheries: Halibut-angel shark set net and shark-swordfish drift net for the 1988–89 fishing year (April 1, 1988 - March 31, 1989)*. Final Report submitted to NOAA Fisheries/National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA in partial fulfillment of Cooperative Agreements Nos. NA90AA-H-FC401 and NA86-ABD-00201.
- Jefferson, T. A., & Curry, B. E. (1994). A global review of porpoise (Cetacea: Phocoenidae) mortality in gillnets. *Biological Conservation*, 67, 167–183.
- Julian, F., & Beeson, M. (1998). Estimates of marine mammal, turtle and seabird mortality for two California gillnet fisheries: 1990–95. *Fishery Bulletin*, 96, 271–284.
- Konno, E. S. (1991). *Effort estimates of gill net fisheries in California that incidentally catch marine mammals, for the 1987–88 fishing year*. Final report submitted to National Marine Fisheries Service, Southwest Region, 200 South Ferry Street, Terminal Island, CA, in partial fulfillment of Cooperative Agreement NA-86-ABH00018.
- Laake, J. L., Calambokidis, J. C., Osmek, S. D., & Rugh, D. J. (1997). Probability of detecting harbor porpoise from aerial surveys: Estimating g(0). *Journal of Wildlife Management*, 61, 63–75.
- Lucke, K., Siebert, U., Lepper, P. A., & Blanckett, M. A. (2009). Temporary shift in masked hearing thresholds in a harbor porpoise (*Phocoena phocoena*) after exposure to seismic airgun stimuli. *Journal of the Acoustical Society of America*, 125, 4060–4070.
- Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009). The BUGS project: Evolution, critique and future directions. *Statistics in Medicine*, 28, 3049–3082.
- Methot, R. D. (1983). Management of California's nearshore fishes. In R. H. Stroud (Ed.), *Marine recreational fisheries* (pp. 161–172). Proceedings of the Eighth Annual Marine Recreational Fisheries Symposium, April 26 and 27, 1983.
- Moore, J. E., & Barlow, J. (2011). Bayesian state-space model of fin whale abundance trends from a 1991–2008 time series of line-transect surveys in the California Current. *Journal of Applied Ecology*, 48, 1195–1205.
- Moore, J. E., & Barlow, J. P. (2013). Declining abundance of beaked whales (Family Ziphiidae) in the California Current Large Marine Ecosystem. *PLoS ONE*, 8(1), e52770. <https://doi.org/10.1371/journal.pone.0052770>
- Moore, J. E., & Barlow, J. P. (2014). Improved abundance and trend estimates for sperm whales in the eastern North Pacific from Bayesian hierarchical modeling. *Endangered Species Research*, 25, 141–150. <https://doi.org/10.3354/esr00633>
- Norris, K. S., & Prescott, J. H. (1961). Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, 63(4), 291–402.
- Osmek, S., Calambokidis, J., Laake, J., Gearin, P., DeLong, R., Scordino, J., Jeffries, S., & Brown, R. (1996). *Assessment of the status of harbor porpoise, Phocoena phocoena, in Oregon and Washington waters* (NOAA Technical Memorandum NMFS-AFSC-76). U.S. Department of Commerce.
- Perkins, P., Barlow, J., & Beeson, M. (1994). *Report on pinniped and cetacean mortality in California gillnet fisheries: 1988–90* (Southwest Fisheries Center Administrative Report LJ-94-11). U.S. Department of Commerce.
- Peterson, W. T., Emmett, R., Goericke, R., Venrick, E., Mantyla, A., Bograd, S. J., Schwing, F. B., Hewitt, Lo, N., Watson, W., Barlow, J., Lowry, M., Ralston, S., Forney, K. A., Lavaniegos, B. E., Sydeman, W. J., Hyrenbach, D., Bradley, R. W.,

- Warzybok, P., ... Durazo, R. (2006). The State of the California Current, 2005–2006: Warm in the north, cool in the south. *California Cooperative Fisheries Investigations Report*, 47, 30–74.
- Pirotta, E., Brookes, K. L., Graham, I. M., & Thompson, P. M. (2014). Variation in harbour porpoise activity in response to seismic survey noise. *Biological Letters*, 10, 20131090. <https://doi.org/10.1098/rsbl.2013.1090>
- R Core Team. (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Read, A. J., Drinker, P., & Northridge, S. (2006). Bycatch of marine mammals in US and global fisheries. *Conservation Biology*, 20(1), 163–169.
- Read, A. J., Kraus, S. D., Bisack, K. D., & Palka, D. (1993). Harbor porpoises and gill nets in the Gulf of Maine. *Conservation Biology*, 7(1), 189–193.
- Reeves, R. R., McClellan, K., & Werner, T. B. (2013). Marine mammal bycatch in gillnet and other entangling net fisheries, 1990 to 2011. *Endangered Species Research*, 20, 71–97. <https://doi.org/10.3354/esr00481>
- Slooten, E., & Davies, N. (2012). Hector's dolphin risk assessments: Old and new analyses show consistent results. *Journal of the Royal Society of New Zealand*, 42(1), 49–60. <https://doi.org/10.1080/03036758.2011.606820>
- Slooten E., Wang J. Y., Dungan S. Z., Forney K. A., Hung, S. K. Jefferson, T. A., Riehl, K. N., Rojas Bracho, L., Ross, P. A., Wee, A., Winkler, R., Yang, S. C., & Chen, C. A. (2013). Impacts of fisheries on the Critically Endangered humpback dolphin *Sousa chinensis* population in the eastern Taiwan Strait. *Endangered Species Research*, 22, 99–114. <https://doi.org/10.3354/esr00518>
- Stern, S. J., Keener, W., Szczepaniak, I. D., Webber, M. A. (2017). Return of harbor porpoises (*Phocoena phocoena*) to San Francisco Bay. *Aquatic Mammals*, 43(6), 691–702. <https://doi.org/10.1578/AM.43.6.2017.691>
- Taylor, B. L., Rojas-Bracho, L., Moore, J., Jaramillo-Legorreta, A., Ver Hoef, J., Cardenas-Hinojosa, G., Nieto-Garcia, E., Barlow, J., Gerrodette, T., Tregenza, N., Thomas, L., & Hammond, P. S. (2016). Extinction is imminent for Mexico's endemic porpoise unless fishery bycatch is eliminated. *Conservation Letters*, 10(5), 588–595. <https://doi.org/10.1111/conl.12331>
- Teilmann, J., & Carstensen, J. (2012). Negative long term effects on harbor porpoises from a large scale offshore wind farm in the Baltic—evidence of slow recovery. *Environmental Research Letters*, 7, 045101.
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., & Burnham, K. P. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14. <https://doi.org/10.1111/j.1365-2664.2009.01737.x>
- Thompson, P. M., Brookes, K. L., Graham, I. M., Barton, T. R., Needham, K., Bradbury, G., & Merchant, N. D. (2013). Short-term disturbance by a commercial two-dimensional seismic survey does not lead to long-term displacement of harbour porpoises. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20132001. <https://doi.org/10.1098/rspb.2013.2001>
- Tougaard, J., Carstensen, J., Teilmann, J., Skov, H., & Rasmussen, P. (2009). Pile driving zone of responsiveness extends beyond 20 km for harbor porpoises (*Phocoena phocoena* (L.)) *Journal of the Acoustical Society of America*, 126, 11–14. <https://doi.org/10.1121/1.3132523>
- Tregenza, N. J. C., Berrow, S. D., Hammond, P. S., & Leaper, R. (1997). Harbour porpoise (*Phocoena phocoena* L.) by-catch in set gillnets in the Celtic Sea. *ICES Journal of Marine Science*, 54, 896–904.
- Turvey, S. T., Pitman, R. L., Taylor, B. L., Barlow, J., Akamatsu, T., Barrett, L. A., Zhao, X., Reeves, R. R., Stewart, B. S., Wang, K., Wei, Z., Zhang, X., Pusser, L. T., Richlen, M., Brandon, J. R., & Wang, D. (2007). First human-caused extinction of a cetacean species? *Biology Letters*, 3(5), 537–540. <https://doi.org/10.1098/rsbl.2007.0292>
- Wild, P. W. (1990). The central California experience: A case history of California halibut set net laws and regulations. In C. W. Haugen (Ed.), *The California halibut, Paralichthys californicus, resource and fisheries* (pp. 321–339). California Department of Fish and Game, Fish Bulletin 174.
- Wilkin, S. M., Cordaro, J., & Gulland, F. (2012). An unusual mortality event of harbor porpoises (*Phocoena phocoena*) off central California: Increase in blunt trauma rather than an epizootic. *Aquatic Mammals*, 38(3), 301–310.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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