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Modeling the effects of El Niño, density-dependence, and disturbance on harbor seal (*Phoca vitulina*) counts in Drakes Estero, California: 1997–2007

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ABSTRACT

Harbor seal (*Phoca vitulina*) haul-out site use may be affected by natural or anthropogenic factors. Here, we use an 11-yr (1997–2007) study of a seal colony located near a mariculture operation in Drakes Estero, California, to test for natural (El Niño-Southern Oscillation (ENSO), density-dependence, long-term trends) and anthropogenic (disturbance or displacement related to oyster production activities) factors that may influence the use of haul-out subsites. Annual mariculture related seal disturbance rates increased significantly with increases in oyster harvest ($r_s = 0.55$). Using generalized linear models (GLMs) ranked by best fit and Akaike's Information Criteria, ENSO and oyster production (as a proxy for disturbance/displacement) best explained the patterns of seal use at all three subsites near the mariculture operations, with effects being stronger at the two subsites closest to operations. Conversely, density-dependence and linear trend effects poorly explained the counts at these subsites. We conclude that a combination of ENSO and mariculture activities best explain the patterns of seal haul-out use during the breeding/pupping season at the seal haul-out sites closest to oyster activities.

Key words: information-theoretic, AIC, *Phoca vitulina*, harbor seal, disturbance, Point Reyes, Drakes Estero, El Niño, density-dependence, mariculture.

The Pacific harbor seal (*Phoca vitulina richardii*) ranges along the eastern Pacific from Baja California to Alaska, and in north-central coastal California, they are the dominant and only year-round resident pinniped (Sydeman and Allen 1999, Burns 2002). The population at Point Reyes, California, represents the second largest concentration of harbor seals in the State of California, accounting for about 20% of the mainland breeding population, and the most seals per haul-out site in the state occur between 37.5° and 38.0°N.[1] Much of the Point Reyes coastal zone remains relatively pristine within a national park, and provides diverse marine and terrestrial habitat for seals to rest, molt, feed, and breed where human encroachment is minimal, in contrast to urbanized locations nearby such as San Francisco Bay (Sydeman and Allen 1999, Grigg *et al.* 2004).

Harbor seals are unusual for a large marine predator because they occur almost exclusively in nearshore habitats, and as a pinniped, they come onshore at traditional terrestrial sites to breed and rest (Burns 2002). Typically, seals attend haul-out sites year round and spend about 33%–55% of their time onshore (Yochem *et al.* 1987, Allen Miller 1988). The number of seals present at any given haul-out site is influenced by several factors including time of day, tide level, current direction, weather, season, year, disease outbreaks, disturbances from other wildlife, and human activities (Allen *et al.* 1984, Yochem *et al.* 1987, Suryan and Harvey 1999, Thompson *et al*. 2001, Grigg *et al.* 2004, Hayward *et al.* 2005, Seuront and Prinzivalli 2005). During the pupping and molting seasons, attendance is usually higher than at other times of the year (Yochem *et al.* 1987, Grigg *et al.* 2004), but females and pups may also react more strongly to disturbances, depending on the source (Perry *et al.* 2002). Environmental factors such as El Niño-Southern Oscillation (ENSO) events can affect attendance and reproduction (Allen *et al.* 1989, Trillmich and Ono 1991, Sydeman and Allen 1999), as can density-dependent factors (Brown *et al*. 2005, Jeffries *et al.* 2005), interspecific competition (Bowen *et al.* 2003), predation (Lucas and Stobo 2000), and epizootic outbreaks (Thompson *et al.* 2001). Human activities can disturb seals at haul-out sites, causing changes in seal abundance, distribution, and behavior, and can even cause abandonment (Allen *et al.* 1984, Suryan and Harvey 1999, Grigg *et al.* 2002, Seuront and Prinzivalli 2005, Johnson and Acevedo-Gutierrez 2007). Given all of these potential factors, it can be difficult to determine which are the most important ones affecting seal attendance at haul-out sites. This pitfall was aptly noted by Richardson *et al.* (1995) by the statement: "it is uncommon to have a series of reliable counts long enough to quantify the numerical change, let alone determine the cause."

To explore how environmental and anthropogenic factors affect seal use of colonies, we examined a long-term study of harbor seals at Drakes Estero, Point Reyes, California. The purpose of the study was to determine changes in population size, reproductive success, and anthropogenic or environmental factors that may affect trends in counts (Sydeman and Allen 1999, Allen *et al*. 2004). Here, we present an analysis of the seal population at three of eight subsites in Drakes Estero that were exposed to varying levels of human related disturbances associated with a mariculture operation. We tested four *a priori* hypotheses that could explain trends in seal counts: (1) year as a linear trend, (2) number of seals at subsites in the middle-lower estero (to search for a density-dependent effect), (3) years since the last ENSO event, and

[1]Lowry, M. S., J. V. Carretta and K. A. Forney. 2005. Pacific harbor seal, *Phoca vitulina richardii*, census in California during May–July 2004. NMFS NOAA-SWFSC Administrative Report LJ-05-06. 38 pp.

(4) the level of mariculture operations in the estuary as measured by the magnitude of annual oyster harvesting.

METHODS

Study Area

The Point Reyes peninsula, along the north-central California Coast, extends from Tomales Bay (38°30′N) south to Bolinas Lagoon (37°30′N). The peninsula is located within the Point Reyes National Seashore and adjacent to the Gulf of the Farallones National Marine Sanctuary. The topographic diversity of this coastal zone provides a broad range of substrates for harbor seals to haul-out of the water. These include tidal mud flats, offshore and onshore rocky tidal ledges, and sandy beaches. A "haul-out site" is defined as a terrestrial location where seals aggregate for periods of rest, birthing, and suckling of young (Harvey 1987). A colony site may be a collection of haul-out sites within a limited geographic area. Drakes Estero and Estero de Limantour encompass a complex of eight subsites where seals haul-out (Fig. 1), which are referred to collectively as the Drakes Estero/Limantour colony. Seals use the subsites at various times of the year depending upon their reproductive status, molting condition, and the level of disturbance encountered (Allen Miller 1988). All subsites are used during the breeding and molt seasons, and some are used regularly year-round. Females with pups have disproportionately used the sand bars exposed at low tide in the upper and middle portions of the estero that are isolated from the mainland, and consequently from humans and predators. Limantour Spit was mostly used by non-breeding seals during the breeding season (Allen Miller 1988). Subsites in the middle-lower estero, which are generally closer or attached to the mainland, have historically suffered higher human disturbance rates when compared to the isolated island sandbars of the upper estero.

Human access to the seal haul-out sites within Drakes Estero was limited because it is part of a national park and a congressionally designated wilderness area. During the breeding season (1 March to 1 July), no boats were allowed within the estero except for the non-conforming (to congressionally designated wilderness) uses by a commercial oyster operation. Three of the subsites where seals haul-out were proximate to this commercial oyster operation (UEF, OB, and UEN). Subsite OB was within the oyster lease but was not used much for oyster culture in the recent past (1999–2004), portions of subsite UEN were within or adjacent to the lease, and subsite UEF was in a navigational channel that bisects a gap in the oyster lease where oyster boats traversed Drakes Estero (Fig. 1).

Oyster production and oyster culture methods used within the estuary have varied over the past 50 yr. However, the primary methods included oyster racks (measuring approximately 3×30 m^2 each), stakes, and bags (each measuring 0.5×1 m^2). In 2007, most of the racks were distributed in the upper portion of the estuary and >1,000 oyster bags (estimated) were distributed along the margins of the estuary, on intertidal sandbars in the center of the bay and in Home and Creamery Bays (Fig. 1).[2] Oyster production levels were high between 1981 and 1998 (annual production ranged from 3 to 9 million oysters per year) and reduced between 1999

[2]Brown, D., and B. H. Becker. 2007. Trip report—Drakes Estero eelgrass, oyster bag, and oyster rack assessment. Unpublished National Park Service report.

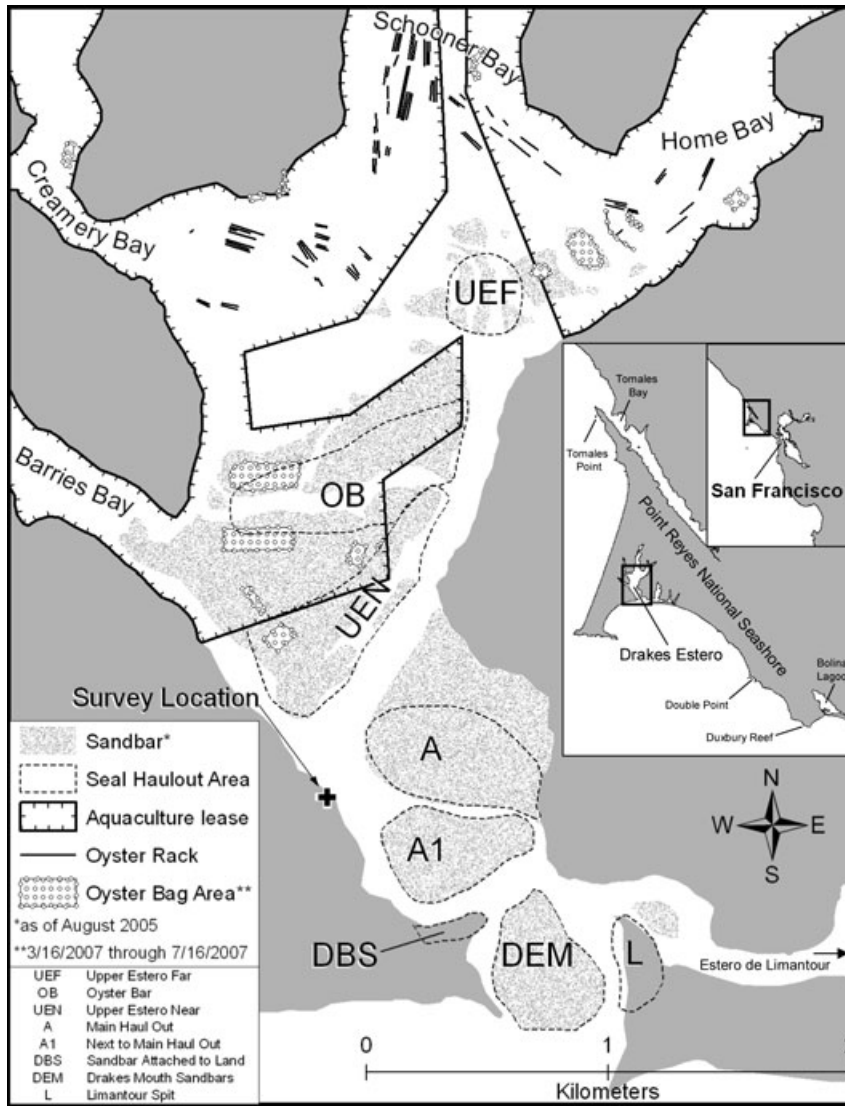

Figure 1. Oyster bag areas (mapped in spring of 2007), oyster racks, and the eight seal haul out subsites (*e.g.*, OB) in Drakes Estero. UEF, OB, and UEN are considered upper estero. Subsites A, A1, DBS, DEM, and L are in the middle-lower estero and not subject to disturbance from mariculture. All surveys were completed from the bluffs indicated by the "survey location" marker.

and 2005 (annual production <2 million oysters per year). Production then increased to about 3.5 million (~136,000 kg) oysters in 2006, and ~211,000 kg oysters for 2007 (Fig. 2A, B).[3,4]

[3]California Department of Fish and Game. 2007. Unpublished report on oyster landings in Drakes Estero from 1950 to 2006. Available from Tom Moore, CDFG Biologist, Bodega Bay, CA.

[4]Tom Moore, Biologist, California Department of Fish and Game, Presentation to the National Research Council Panel on Mariculture in Drakes Estero, 4 September 2008.

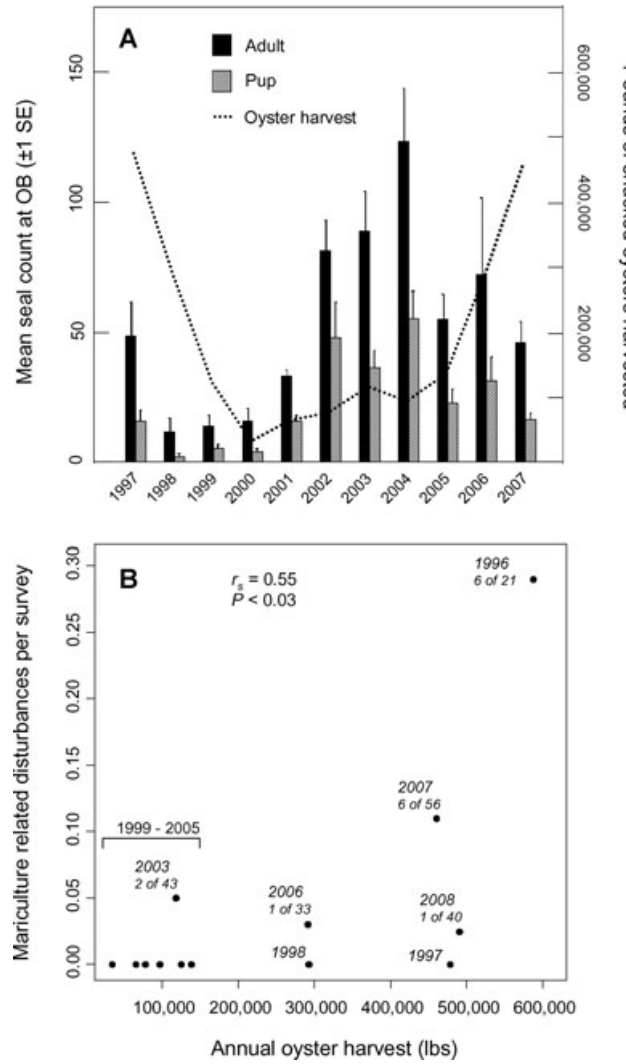

Figure 2. (A) Mean (±1 SE) counts of harbor seals at Drakes Estero subsite OB and oysters harvested from Drakes Estero during 1997–2007. The year 1998 was an El Niño year. (B) Relationship between annual oyster harvest and mariculture related disturbance rate from 1996 to 2008. Text adjacent to points indicates the year, the number of disturbances in that year, and the number of surveys. Between 37 and 50 surveys were conducted each year from 1997 to 2005. During 1997–1998, oyster harvest rate was rapidly declining which may have diminished some of the factors that lead to disturbance.

Surveys

The National Park Service (NPS) conducted surveys of harbor seals throughout the year from 1996 to 2007, but surveys were more frequent during breeding (1 March to 30 May) and molting (1 June to 1 August) seasons (two to four times per week, depending on weather). Trained volunteers and NPS staff conducted surveys at medium to low tides (below 2.5 ft [0.76 m]) during the day. Surveys were

not conducted in heavy fog or rain because of poor visibility. NPS data collection began in 1996 but we were not able to completely discern all subsite count data in that first year since a few subsites were grouped on some surveys. We therefore analyzed disturbance data from 1996 to 2008, and count data from 1997 to 2007.

Surveys were designed to capture the seasonal peak numbers at several of the Point Reyes seal colonies, including the Drakes Estero/Limantour colony, and to detect disturbances that might affect seasonal peak numbers at each colony. Survey periods lasted at least 2 h, with counts occurring every half-hour. Each subsite was surveyed separately, and added to other subsites to obtain a total count for the entire colony. All subsites were visible from one survey location. For each subsite, the observer recorded the total number of adult/immature seals, pups, and dead pups present. Because of the difficulty in distinguishing adult from immature seals, these two groups were combined. Pups were the young of the year and, after weaning, were difficult to distinguish from yearling seals. Consequently, pup numbers were reliable only from 1 March to 1 June. Surveys were conducted with binoculars and a 40–50× monocular spotting scope from a bluff on the western edge of Drakes Estero (Fig. 1).

Disturbances of the seals were recorded during each survey, and within a survey, multiple disturbances could occur. We defined disturbance as any activity that elicited a reaction by the seals; which was either a head alert, a flush toward water, or flush into water. Disturbance rate (# disturbance events/# surveys during March–July of each year) was analyzed from 1996 to 2008 for the upper estero subsites and we tested for a correlation in mariculture related disturbance rate in relation to annual oyster harvest using a 1-tailed Spearman ranks test. We also used a non-parametric Wilcoxon rank test to see if oyster harvest differed in years with or without mariculture related disturbances. To be conservative, if two or more activities (*e.g.*, oyster boat and a kayak) appeared to cause a seal disturbance, the event was categorized as "non-oyster" related.

Data Preparation

We selected count data from Drakes Estero within the historical peak of the pupping season (15 April to 15 May) during 1997–2007. These data were then filtered to remove: (1) data from observers with less than 1 yr of survey experience, (2) observations at tide levels above +2 ft (+0.61 m) (MLW) when fewer seals would be present because some subsites might be submerged (Allen Miller 1988, Grigg *et al.* 2004), and (3) observation dates where weather reduced visibility. Tide level and tide time were standardized to the Golden Gate Bridge, San Francisco (PST). To ensure that variation in tide levels $\leq$ 2 ft (0.61 m) did not affect counts, we tested for correlations between tide level and counts at all of the eight subsites and found no relationships (Spearman ranks test, all $r_s < |0.24|$, $n = 104$). Temporal autocorrelation plots of means by year indicated no significant autocorrelations at any time lag (all $r < 0.5$). The data from all 104 surveys used in this analysis were checked for accuracy against the raw data forms and by comparing subsite data with the sum of counts from the full estero. Between 6 and 15 surveys (mean = 9.5 ± 2.9) were completed in each year during this period. We also graphically compared pupping season counts with the five other primary local harbor seal colonies within 30 km of Drakes Estero from 2000 to 2007 to provide a regional context.

Analyses

We hypothesized that there could be four potential effects on counts at two of the subsites closest to the mariculture operation in the upper estero (OB and UEN): (1) year as a linear trend through time, (2) density-dependence, defined as total seal counts in the middle-lower estero away from mariculture operations (L, A, A1, DEM, DBS), (3) years since the last ENSO event (1991–1992 and 1997–1998; http://www.pmel.noaa.gov/tao/elnino/), and (4) mariculture activity measured as the weight of oysters harvested ($\times 10^5$ lbs) during the same year. We assumed that the oyster harvest variable represented the combined effects from boat traffic, human activity, and oyster bag placement that may displace or disturb seals. Candidate models included between one and three of the above factors; year and ENSO were not used in the same models since both represent time and they were correlated. Density-dependence data was limited to the middle-lower estero counts since the upper estero subsites were being modeled as dependent variables and including them would lead to lack of independence between independent and dependent variables. For example, if oyster harvest was impacting any of the upper estero subsite counts, then using those counts as independent variables in the model would lead to a lack of independence. This could result in using overlapping data in both the independent and dependent variables.

To investigate the robustness of the models to how density-dependence was calculated, we also investigated density-dependence effects on an annual (mean) basis (in addition to daily, as described above). Similarly, we also investigated modeling oyster harvest with a 1-yr time lag. Since time from oyster planting to harvest is about 18 mo, any effects due to harvest levels could potentially begin to be expressed sometime during the 18 mo prior to harvest (Pauley *et al.* 1988). However, in Drakes Estero, most oyster related activity occurs near seal haul-out sites OB and UEN for only 3–4 mo prior to harvest. Consequently, we focus on *same* year oyster harvest effects in the analyses and results. Lastly, we considered lowest tide height during the survey as an additional covariate. Linear mixed-effects models were also tested using ENSO as a random effect.

For analyses of total counts at subsites OB and UEN, we built generalized linear models (GLMs). Daily counts were overdispersed (*i.e.,* variance greater than the mean and increasing with the mean), and therefore, we used a negative binomial distribution to model the data (Venables and Ripley 2002, Insightful Corp. 2003, Crawley 2005) and ranked each model using Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). Lower AIC_c values indicate a more parsimonious model that better explains the pattern in the data while penalizing the addition of trivial parameters. For the negative binomial distribution, we used a maximum likelihood estimation of θ (shape parameter for the negative binomial distribution) for both UEN and OB using the glm.nb function in S-Plus (GLM with negative binomial distribution) (Venables and Ripley 2002). These values (1.0 for OB and 1.6 for UEN) were subsequently used in all GLM models because θ must be kept constant to compare maximum likelihood (and hence AIC_c) between models using the same data set (Venables and Ripley 2002). We report the ΔAIC_c value, Akaike weights (w_i), and pseudo r^2 (Maddalla 1983) to present the level of confidence in each model.

To validate the best model at OB, we used the best fitting GLM model parameters to predict counts at UEF using a scaling parameter that divided the mean counts at UEF from 1997 to 2007 (26.4) by the mean counts at OB (83.6) for the same

period (ratio = 0.32). We then compared the predicted and actual counts at UEF for each year using a Pearson correlation. Lastly, we constructed a regression tree with the software program R to illustrate and test the interactions between independent variables (year, ENSO, density-dependence, and oyster harvest in the same year) on combined OB and UEF harbor seal counts. Statistical analyses were done with S-Plus 6.2 (Insightful Corp. 2003) or R 2.7.2 (R Development Core Team 2008) using the MASS library (Venables and Ripley 2002).

Results

Seal attendance varied at all three upper Drakes Estero subsites from 1997 to 2007; however, the amount of change varied amongst the subsites. At subsite OB, both the maximum and mean counts for seals and pups were lower from 1998 to 2001, higher from 2002 to 2004, and then lower for 2005–2007. Oyster harvesting showed a U-shaped pattern, declining in the early part of the study period and increasing in 2005 (Fig. 2A).

Disturbance rates in the upper estero (subsites OB, UEF, UEN) significantly increased with oyster harvest ($r_s = 0.55$, $P < 0.03$) (Fig. 2B). This correlation is highly robust to sample size. For example, there was still a significant positive correlation ($r_s = 0.53$, $P < 0.04$) of disturbance rate with oyster harvest even when removing the 2006 disturbance, four of the 2007 disturbances (including two disturbances on 1 day in 2007 that the mariculture company challenged), and four of the 1996 disturbances (nine total) from the analysis. Similarly, oyster harvest levels in years with oyster related disturbances were significantly higher ($U = 43$, $n = 13$, $P_{1-\text{tail}} < 0.04$). Only one mariculture related disturbance was recorded in the middle-lower estero during the study. This was at subsite A in 2003 and was likely due to a state mandated water quality testing trip.

The best GLM model to explain seal counts at OB ($w_i = 0.65$) included years since ENSO and oyster harvest (Table 1). The coefficients indicated that seal counts had a positive relationship with years since ENSO and a negative relationship with oyster harvest (Table 2). The second ranked model (oyster + ENSO + density-dependence) was similar to the first model with the inclusion of density-dependence as a non-significant variable ($w_i = 0.32$). Thus, the top two models had a total w_i of 0.97 and consisted primarily of years since ENSO and oyster harvest. Pseudo r^2 was moderate (0.37–0.38) for these two best models and declined rapidly thereafter to <0.29 for the remaining models.

Predicted counts at UEF using the scaled best fit/lowest AIC_c model from OB fit well ($r = 0.66$, $P < 0.04$), strongly suggesting that similar processes (ENSO and oyster harvest) were driving the counts at both OB and UEF (Fig. 3A). In fact, all years except the highest oyster harvest years (1997, 2006, 2007) fit extremely well. The only significantly correlated ($P < 0.05$) variables were year and ENSO ($r_s = 0.89$), and ENSO and subsite OB counts ($r_s = 0.64$). Daily density-dependence was not correlated with counts at OB ($r_s = -0.12$), but mean annual density-dependence was using ranks tests ($r_s = 0.65$) but not Pearson tests ($r_p = 0.43$, $P > 0.18$).

Using density-dependence as an annual mean rather than a daily value and/or oyster harvest with a 1-yr lag effect still resulted in oyster harvest (with a significant negative coefficient) being included in all of the best (lowest AIC_c/highest r^2) models at OB. For example, if considering density-dependence on an *annual* mean basis (not shown in tables) the best model included density-dependence, ENSO and oyster

Table 1. Ranking of candidate models at subsites OB and UEN by AIC_c and Akaike weights (w_i). The dependent variable is the count of total seals at subsite OB and independent variables are year as linear trend (Year), density-dependence (DenDep: daily sum of seals in the middle-lower estero), years since last El Niño event (ENSO), and lbs of oysters harvested in the same year (Oyst). Column headings are: small sample AIC (AIC_c), distance from best model (Δ_i), and Akaike weight (w_i); $n = 104$ for all models.

Model	AIC_c	Δ_i	w_i	r^2
Subsite OB				
Oyst + ENSO	332.96	0.00	0.65	0.37
Oyst + ENSO + DenDep	334.38	1.42	0.32	0.38
ENSO	340.36	7.40	0.02	0.25
ENSO + DenDep	340.70	7.74	0.01	0.28
Year	344.90	16.53	0.00	0.19
DenDep	353.16	20.20	0.00	0.07
Oyst	353.22	20.26	0.00	0.05
Oyst + DenDep	353.42	20.47	0.00	0.11
Null	353.68	20.72	0.00	0.05
Subsite UEN				
Oyst + ENSO	320.19	0.00	0.41	0.16
Year	321.68	1.49	0.20	0.10
Oyst + ENSO + DenDep	322.34	2.15	0.14	0.16
ENSO + DenDep	322.66	2.47	0.12	0.12
ENSO	323.20	3.01	0.09	0.11
Null	326.10	5.90	0.02	0.00
DenDep	327.66	7.47	0.01	0.01
Oyst	328.22	8.02	0.01	0.00
Oyst + DenDep	329.81	9.61	0.00	0.01

Table 2. Coefficients of the best two AIC_c ranked models for OB and UEN from Table 1. w_i is Akaike weight. Asterisk indicates coefficient is significant at $P < 0.05$.

Subsite: Model	Coefficient	Standard error	t	$P < 0.05$
Subsite OB				
Model 1 ($w_i = 0.65$)				
Constant	3.530	0.185	19.099	*
Oyst	−0.240	0.063	−3.821	*
ENSO	0.261	0.035	7.563	*
Model 2 ($w_i = 0.32$)				
Constant	3.269	0.366	8.928	*
Oyst	−0.229	0.066	−3.447	*
ENSO	0.251	0.036	6.911	*
Density-dependence	0.001	0.001	0.914	
Subsite UEN				
Model 1 ($w_i = 0.41$)				
Constant	4.720	0.117	40.292	*
Oyst	−0.105	0.040	−2.631	*
ENSO	0.119	0.022	5.436	*
Model 2 ($w_i = 0.20$)				
Constant	−140.463	36.041	−3.897	*
Year	0.073	0.018	4.038	*

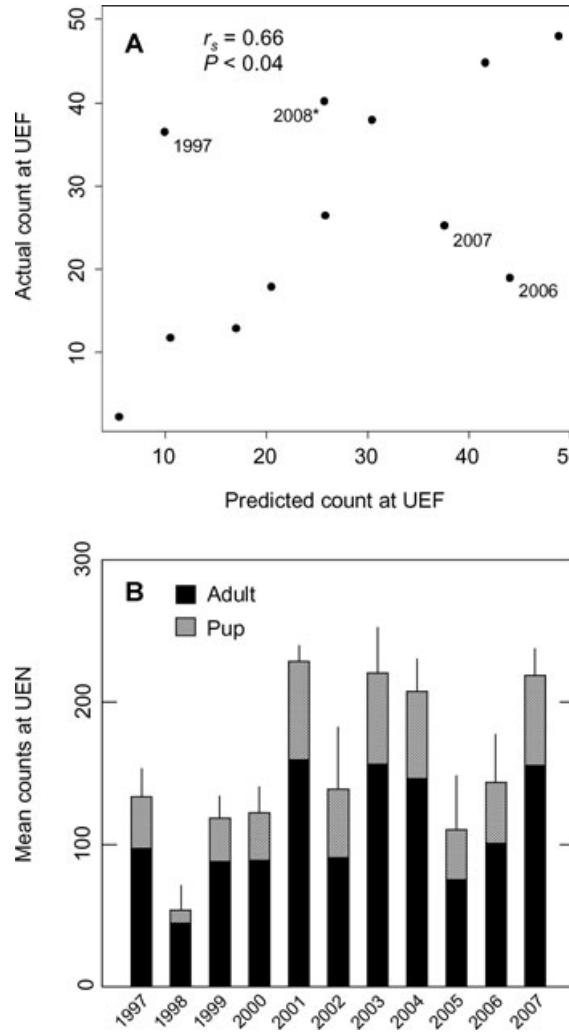

Figure 3. (A) Predicted and actual (from the best fitting GLM at OB) mean counts of pups and adults from 1997 to 2007 at subsite UEF. The 2008 data point is not derived from the model (it is actual data) or used in the correlation test. It is only shown to illustrate that seals in 2008 appear to be returning to more normal covariation between OB and UEF. (B) Mean seal counts from 1997 to 2007 at subsite UEN during the 15 April–15 May pupping season. Error bars represent the standard error for the total count.

harvest (same year) all as significant ($P < 0.004$) variables and oyster harvest still had a negative coefficient similar to that in Table 2. However, removing oyster harvest from the model increased AIC by ~6.7, indicating that failing to consider oyster harvest results in a model with much lower confidence (Burnham and Anderson 2002). Tide height effects were not important in any models and did not appear in the highest-ranking models. Linear mixed-effects models (termed non-nested or

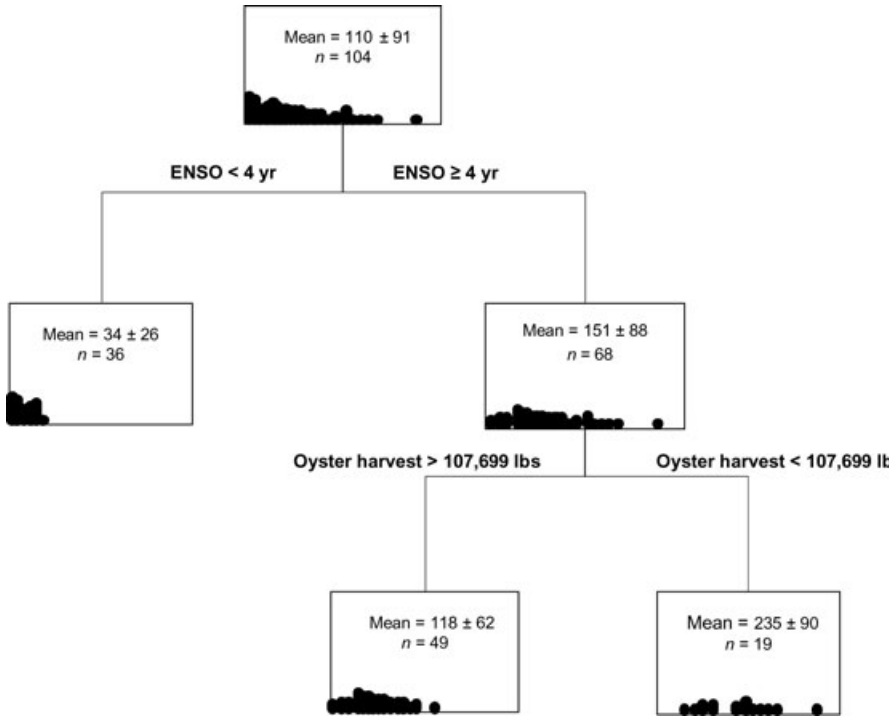

Figure 4. Regression tree illustrating how ENSO and oyster harvest interact to best explain seal counts at subsites UEF and OB. The number of seals for each survey is represented by a dot histogram along the *x*-axis in each box, with points at the origin indicating a zero count and points to the right of the box indicating larger counts. This model agrees closely with the GLM results in Table 1.

crossed random effects) (Faraway 2006) using ENSO as a random factor also resulted in a significant negative oyster harvest coefficient. Model results were also not affected by including components for temporal autocorrelation. Residual plots for the GLMs showed no issues with homoscedasticity or increasing variance.

Models for subsite UEN, which is farther from the oyster operations, all had poorer fit than OB (all pseudo $r^2 < 0.17$), but oyster harvest and ENSO were once again in the best (lowest AIC_c) model with an Akaike weight of 0.41 (Fig. 3B, Table 1). However, the model containing only year as an explanatory variable ranked second and had an Akaike weight of 0.20, which partially reduces our confidence in the top model.

The regression tree for counts at OB and UEF combined also confirmed the patterns found by the GLMs. ENSO explained much of the variation, and an increase in oyster harvest explained the significantly lower counts (from 255 ± 90 seals down to 118 ± 62) once ENSO effects had subsided (Fig. 4). The tree was grown until additional nodes had a negligible (<5%) additional reduction in model deviance. Residual plots of the regression tree model indicated that the model was sound.

Five other colonies in the region showed a different pattern than Drakes Estero subsites UEF, UEN, and OB, as well as Drakes Estero as a whole (Fig. 5). Bolinas

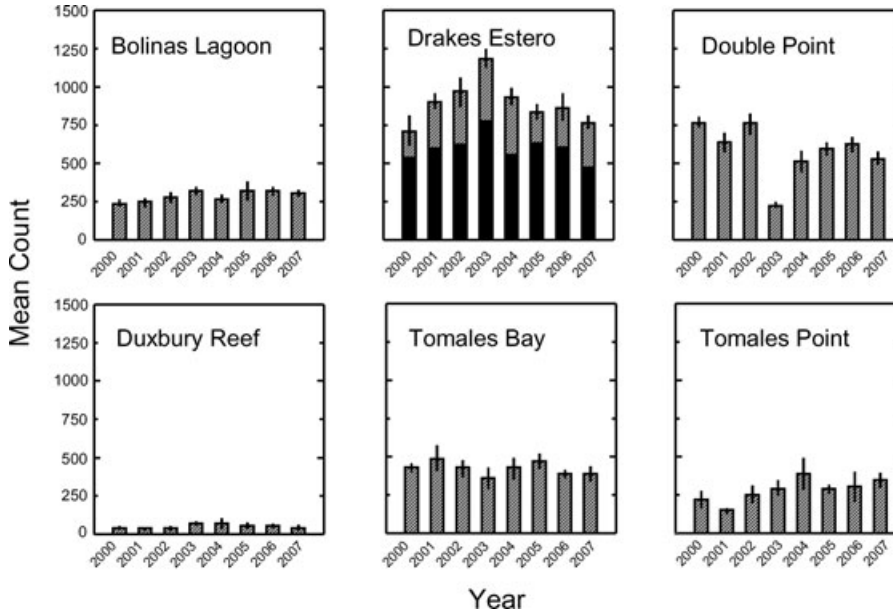

Figure 5. Mean (±1 SE) counts of pups and adults during the pupping season (15 April–15 May) from 2000 to 2007 at Drakes Estero and five regional sites within 30 km. Dark bars on the Drakes Estero panel represent only the middle-lower estero counts used for calculating density-dependence in the GLM and regression tree models.

Lagoon, Tomales Bay, and Duxbury Reef showed stable populations during the time series. The Double Point colony suffered from an aggressive male elephant seal (*Mirounga augustirostrus*) in 2003 that killed approximately 40 (mostly female) and chronically harassed hundreds of harbor seals throughout the breeding season. Coincidentally, the Drakes Estero colony had an abrupt peak in 2003, possibly due to movement of some of the seals from Double Point. The Tomales Point colony showed a small increase over time. Finally, middle-lower Drakes Estero counts (used to analyze density-dependence in this paper: subsites A, A1, DEM, DBS, and L) were relatively stable from 2000 to 2006, and similar to the entire estero, had a 1-yr peak in 2003 that may have been related to the displaced seals from nearby Double Point, and then a small decline in 2007.

Discussion

Pinnipeds, and harbor seals in particular, are vulnerable to human disturbance at haul-out sites where they rest, molt, and raise their young (Kenyon 1972, Allen *et al.* 1984, Suryan and Harvey 1999, Grigg *et al.* 2002, Perry *et al.* 2002, Seuront and Prinzivalli 2005). Determining the level of effect from human activities, though, is difficult because of confounding factors such as environmental variables and multiple disturbance sources. Additionally, many studies are of short duration, focusing on short-term issues, and do not account for factors such as density-dependence on

long-term trends of populations (Grigg *et al.* 2002, Perry *et al.* 2002, Johnson and Acevedo-Gutierrez 2007).

This study illustrates the utility of concurrently modeling anthropogenic and environmental factors using *a priori* hypotheses and information-theoretic (*i.e.*, AIC) model selection to explain observed patterns in wildlife counts. Here, we provide evidence that from 1997 to 2007 seal counts at Drakes Estero subsites OB and UEF increased after the last ENSO and then declined with an increase in mariculture activities around 2005. The strong ENSO in 1998 had widespread ramifications for many upper trophic level predators in the California current, and in harbor seals, who may forego breeding and pupping in years of low available forage while spending more time foraging (Trillmich and Ono 1991, Sydeman and Allen 1999, Benson *et al*. 2002, Grigg *et al.* 2004, Lee *et al.* 2007). The upper estero subsites were used mainly for pupping and molting because they are islands, and therefore generally have lower human and natural disturbance rates.

Mariculture operations likely began increasing by 2005 to generate the increases in harvesting seen in 2006 and 2007, as time from oyster planting to harvest is typically around 18 mo in Drakes Estero, with the latter 3–4 mo being in areas closer to seal haul-out sites OB and UEF. This is consistent with observations that there was little or no oyster equipment (*e.g.,* bags) near the OB sandbars from the summer of 2002 to the summer of 2004 (DTP, unpublished data). Also, aerial imagery from August of 2005 showed oyster bags on the west end of sandbar OB. By April 2007, there were extensive oyster equipment arrays and bags in this area (Fig. 1). The disturbance data and oyster landings (Fig. 2B, Table 1) suggest that increasing mariculture activities resulted in some combination of increased disturbance from boat traffic, human presence on sand bars, and/or physical displacement of seals from the sandbars by oyster growing equipment. While disturbance would likely occur primarily at low tides when seals were hauled out, surveys that count seals and record disturbance events were only completed during a small fraction of the year (typically <50 d per year, each survey 2–4 h), so all types of disturbance were likely underestimated here. Studies from Washington found that disturbance events that flush seals into the water only resulted in a return to previous numbers 39% of the time (Suryan and Harvey 1999), and results from nearby Bolinas Lagoon were similar (Allen *et al.* 1984). Other studies have indicated that females with pups may be more vigilant and sensitive to disturbance, and this also may have contributed to the sharp decline of seals at the subsite (OB) in Drakes Estero where mostly females and pups occurred (Stein 1989, Suryan and Harvey 1999, Lucas and Stobo 2000). Such disturbance events in Drakes Estero at OB and UEF appear to have produced effects that were detectable during the entire pupping season via reduced seal counts. However, simple displacement due to mariculture activities or equipment without actual direct disturbance events may equally be driving the patterns observed at OB and UEF.

The similar count pattern and good model fit observed at subsite UEF (Fig. 3A) suggests that the same factors were driving counts at both OB and UEF. However, the predictive model also showed that the subsites appeared to decouple when oyster harvest was high (1997, 2006, 2007, and perhaps 2008). This suggests that UEF and OB covary strongly in the absence of high oyster harvest levels. Conversely, it appears that when oyster harvest was high, the subsites (OB and UEF) fell out of sync due to mariculture related disturbance or displacement events. Curiously, there is no consistent directionality in this decoupling pattern (Fig. 3A). Alternatively, this decoupling could be related to poorer model fit at the beginning and end of the

time series, but because time (year) was not a variable selected or used in the model, this seems unlikely.

Counts at subsite UEN, which is slightly further away from mariculture operations, nonetheless showed a significant, but muted response to ENSO and oyster harvesting. While several other subsites in the estero vary with changes in sandbar morphology, disturbance, predators, and other environmental factors, subsites OB and UEF (and UEN) suffered no such physical changes other than an increase in nearby mariculture use. The generally poor fit for all of the UEN models suggests that other unmodeled factors (including interactions among subsites) may affect counts there more than ENSO, density-dependence, or oyster harvest. Additional processes that might influence the seal counts at UEN include: (1) seals are typically farther from oyster operations than those at OB and UEF and thus less susceptible to disturbance, and/or (2) some seals may have moved from OB or UEF to UEN upon being displaced by oyster operations. Distance from a disturbance source has often been documented as contributing to whether seals respond to a human activity (Allen *et al.* 1984, Suryan and Harvey 1999, Johnson and Acevedo-Gutierrez 2007). Furthermore, changes in sandbar morphology in the middle-lower estero, might also have affected counts in the upper estero because of redistribution of seals. For example, counts at subsite A in the middle estero (Fig. 1) declined dramatically from 2004 to 2007, due to a naturally shifting sandbar that allowed predator (coyote, *Canis latrans*) access to the site. The displaced seals appeared to move to other subsites in the estero (*e.g.*, subsite A1 increased dramatically as A declined), and this process may have also had a confounding impact on the counts at UEN. Clearly, the variation at UEN is not very well explained by our candidate models and unknown processes such as interactions among subsites in the estero may be partially driving counts there. Additionally, variation in tidal height should not affect the counts since all surveys were conducted at low tides, and multiple counts were conducted during each survey, with only the highest count recorded and analyzed here.

Modeling density-dependence should also control for larger scale regional impacts such as the poorly understood oceanographic anomalies in the California Current reported in 2005 and 2006 that depressed food for many seabirds (Barth *et al.* 2007). For example, if ocean conditions depressed seal density in Drakes Estero and this in turn caused less use of OB or UEF due to density-dependent effects, then density-dependence should have presented a better (more parsimonious) explanation of the data than "ENSO" and "Oyster" (Table 1). This would similarly address any covariation of counts in Drakes Estero compared to other harbor seal haul-out sites in north-central California due to unexplained interannual variation (Fig. 5). While mean total harbor seal counts in all of Drakes Estero increased from 2000 to 2003 (from ~700 to 1,200 individuals), and then declined from 2003 to 2007 (back down to ~750 individuals), ENSO and oyster harvesting still explained the data much better than density-dependence (Table 1, 2). This is likely because the middle-lower estero counts were somewhat more stable (Fig. 5). The 1-yr spike in 2003 was likely due to displaced seals from Double Point moving to Drakes Estero. There was also a small, unexplained decline in 2007.

The significant decline in adults and pups at OB after 2004 suggests that oyster harvesting influenced these numbers; however, the GLM models were fit to actual data, so it would be inappropriate to predict if seals at OB would have continued to increase or asymptote after 2004 in the absence of increasing oyster harvesting. In fact, a square-root (diminishing effects) transformation for ENSO may have also

been a reasonable *a priori* test. Nonetheless, while long-term studies in Washington and Oregon noted density-dependence effects at harbor seal colonies (Brown *et al.* 2005, Jeffries *et al.* 2005), the data for subsite OB in Drakes Estero were most consistent with the hypothesis that a significant portion of the reduced seal count during 2005–2007 was related to the increase in oyster harvesting.

Further evidence for the negative effect of oyster harvest levels on counts at subsites OB and UEF comes from the limited data available for 1996. These counts were not used in the GLM or tree models due to incomplete data; however, five surveys during the peak pupping season showed a mean count for OB of only 47 ± 39 (similar to 1997, 2005, and 2007) during the highest oyster harvest year (587,000 lbs) and the highest disturbance rate during the study (Fig. 2B).

The 2008 pupping season presented an opportunity to investigate the immediate effect of a change in oyster operations. In 2008, the California Coastal Commission (CCC) imposed a seal protection zone that restricted some use of the lateral channel adjacent to OB by oyster boats during the pupping season. Thus, boat use in the lateral channel in 2008 may have been curtailed from use levels during 2005–2007, and concurrently, mean counts at OB increased from about 61 ± 10 (SE) in 2007 to 81 ± 12 in 2008 despite a nominal increase in oyster harvest, from 466,000 lbs in 2007 to a projected 493,000 lbs in 2008. The restriction of oyster operations also coincided with one mariculture related disturbance detected in the upper estero in 2008 (*vs*. six in 2007) (Fig. 2B), suggesting that conditions that previously reduced pupping season seal counts may have partially abated due to CCC restrictions.

We therefore suggest that an adaptive management approach for oyster operations be investigated since apparently reducing activity in the area close to seals may have had immediate positive effects. This also suggests that while oyster harvest was a good proxy for impacts on seal counts in the upper estero for 1997–2007, changes in operations such as those experienced in 2008 may make the oyster harvest proxy less useful in the future. For this reason, it is not appropriate to include the 2008 data in the models because of this large change in management.

In conclusion, patterns observed in Drakes Estero at upper estero subsites OB and UEF (and potentially UEN) are best explained by ENSO and increased disturbance from oyster harvest activities. The ability of the OB model to predict counts at subsite UEF suggests that similar processes are occurring at both subsites and that the modeling techniques are robust. The results of this study also contribute to a limited body of literature on the potential negative effects of mariculture on marine mammals. Watson-Capps and Mann (2005) found that oyster operations in coastal waters off Australia reduced use by bottlenose dolphins (*Tursiops* sp.) even though the facility had open areas that presumably would allow dolphins to pass. Such conflicts may increase in the future if mariculture replaces wild ocean harvesting due to the worldwide decline in wild fish stocks (Worm *et al.* 2006).

This study illustrates the benefits of long-term studies for understanding multiple anthropogenic and environmental factors that can affect pinniped populations and productivity (Richardson *et al.* 1995, Thompson *et al.* 2001). It also demonstrates how chronic disturbance activities, in this case associated with a mariculture operation, can lead to displacement of seals at haul-out sites, resulting in animals either shifting to alternate subsites or leaving the area. Kenyon (1972) noted for the monk seal (*Monachus schauinslandi*) that such losses likely led to net population losses because of the lack of suitable breeding habitat. If harbor seals in the region are at environmental carrying capacity, then loss of pupping sites within Drakes Estero also might conceivably lead to population loss. Finally, our results suggest that an

important part of managing for protection of pinnipeds may be to provide a higher level of protection around breeding habitat which is not currently protected under the U.S. Marine Mammal Protection Act (www.nmfs.noaa.gov/pr/laws/mmpa).

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