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From: mmsci@megalink.net

To: ben_becker@nps.gov

Cc:

Subject: Marine Mammal Science - Editorial Decision for MMSCI-2668.R1

Body: 28-May-2008

Dear Dr. Becker:

I am very pleased to inform you that your revised Article entitled "MODELING THE EFFECTS OF EL NIÑO, DENSITY-DEPENDENCE, AND DISTURBANCE ON HARBOR SEAL (PHOCA VITULINA) COUNTS IN DRAKES ESTERO, CALIFORNIA: 1997 - 2007" has been accepted for publication in Marine Mammal Science.

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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

BENJAMIN H. BECKER[1]

Pacific Coast Science and Learning Center

Point Reyes National Seashore

1 Bear Valley Road

Point Reyes Station, CA 94956

ben_becker@nps.gov

DAVID T. PRESS

Inventory and Monitoring Program

Point Reyes National Seashore

1 Bear Valley Road

Point Reyes Station, CA 94956

SARAH G. ALLEN

Point Reyes National Seashore

1 Bear Valley Road

Point Reyes Station, CA 94956

[1] Author to whom correspondence should be addressed.

ABSTRACT

Harbor seal (*Phoca vitulina*) haulout site presence may be affected by natural or anthropogenic factors. Here, we use an 11-year (1997 – 2007) study of a seal colony located near an oyster mariculture operation in Drakes Estero, California to test for natural (El Niño-Southern Oscillation (ENSO), density-dependence, long-term trends) and anthropogenic (disturbance related to oyster production activities) factors that may influence the use of haul out subsites. During the study period there was a strong ENSO in 1998, a U-shaped pattern of oyster production, and increasing levels of disturbance related to oyster operations. Using generalized linear models (GLM) ranked by best fit and Akaike's Information Criteria, ENSO and oyster production best explained the patterns of seal use of one subsite (OB) within the oyster lease (pseudo $R^2 = 0.48$). The total number of seals at OB increased with time after the 1998 ENSO, and then decreased with increasing oyster harvest. Conversely, density-dependence (seal counts in the lower Estero outside of the oyster lease) and linear trend effects poorly explained the counts at OB. The best model from OB had very high predictive power ($r^2 = 0.87$) for seal counts at another nearby site, UEF, suggesting that model development was robust and similar processes were occurring at both sites. Comparison of counts at OB during 2002 – 2004 (prior to increasing oyster harvest, but after ENSO effects had tapered off) with 2005 – 2007 indicates an 57% decline in use by adults and 54% decline by pups at subsite OB. We conclude that ENSO and disturbance related to mariculture best explain the patterns of seal haulout use during the breeding/pupping season at the two seal haulout sites closest to oyster activities.

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

INTRODUCTION

The Pacific harbor seal (*Phoca vitulina richardii*) ranges along the eastern Pacific from Baja California to Alaska, and in north-central 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 latitude 37.0° and 37.5° N[2]. Much of the Point Reyes coastal zone remains relatively pristine in 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.* 1987, Seuront and Prinzivalli 2005). During the pupping and molting

[2] LOWRY, M.S., J. V. CARRETTA and K.A. FORNEY. 2005. Pacific harbor seal, *Phoca vitulina richardsi*, census in California during May-July 2004. NMFS NOAA –SWFSC Administrative Report LJ-05-06. 38p.

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 (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[3] (Sydeman and Allen 1999). 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 an oyster lease. We tested four *a priori* hypotheses

[3] ALLEN, S., S. WABER, W. HOLTER and D. PRESS. 2004. Long-term monitoring of harbor seals at Point Reyes, California: five year annual report 1997-2001. National Park Service Technical Report. 66 p.

that could explain trends in seal counts: (1) year as a linear trend, (2) number of seals at other subsites within the Estero (to search for a density-dependent effect), (3) years since the last ENSO event, and (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 is on the north central California Coast and extends from Tomales Bay (Lat. 38° 30'N) south to Bolinas Lagoon (Lat. 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 "haulout 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 haulout sites within a limited geographic area. Drakes Estero and Estero de Limantour encompass a complex of eight subsites where seals haulout (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-middle portions of the Estero that are isolated from the mainland, and consequently from humans

and predators, and Limantour Spit was primarily used by non-breeding seals during the breeding season, including immatures and males (Allen Miller 1988).

Human access to the seal haulout sites within Drakes Estero was limited because it is part of a national park and a congressionally designated wilderness area. During the breeding and molt seasons (March 1-July 1), no boats were allowed within the Estero except for the non-conforming (to wilderness) uses by a commercial oyster operation. Three of the subsites where seals haul out are proximate to this commercial oyster operation (UEF, OB, and UEN). Subsite OB is within the oyster lease but was not used much for oyster culture in the recent past, subsite UEN was adjacent to the lease, and subsite UEF is in a navigational channel that bisects a gap in the oyster lease where oyster boats traverse 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 include oyster racks (measuring approximately 3 x 30 m each), stakes, and bags (each measuring 0.5 x 1 m). In 2007, most of the racks were distributed in the upper portion of the estuary and > 1000 oyster bags (est.) were distributed along the margins of the estuary, on intertidal sandbars in the middle of the bay and in Home and Creamery Bays (Fig. 1)[4]. Oyster production levels were high between 1981 and 1998 (annual production ranged from 3 - 9 million oysters per year) and reduced between 1999 and 2005 (annual production < 2 million oysters per year). Production then increased to about 3.5 million (~136,000 kg) oysters in 2006, and was estimated at ~9 million (~340,000 kg) oysters for 2007 (Figs. 2A and B)[5,6].

[4] Brown, D. and B.H. Becker. 2007. Trip Report - Drakes Estero eelgrass, oyster bag, and oyster rack assessment. Unpublished NPS report.
[5] California Department of Fish and Game. 2007. Unpublished report on Oyster Landings in Drakes Estero from 1950 - 2006. Available from Tom Moore, CDFG Biologist. Bodega Bay, California.

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Surveys

The National Park Service conducted surveys of harbor seals throughout the year from 1997 – 2007, but surveys were more frequent during breeding (March through May) and molting (June to August) seasons (2-4 times per week, depending on weather).
140 Surveys were conducted by trained volunteers at medium to low tides (below 2.5 ft (0.76 m)) during the day. Surveys were not conducted in heavy fog because of poor visibility or in the rain because harbor seals haul out in lower numbers in the rain. Surveys prior to 1997 were collected by other agencies and organizations, and were summarized in various reports; subsite survey data were collected in these studies but not analyzed
145 (Allen Miller 1988).

Surveys were designed to capture the seasonal peak numbers at all of the Point Reyes colonies, including the Drakes Estero/Limantour colony, and to detect disturbances that might affect seasonal peak numbers at each colony. Survey periods last at least two hours, with counts occurring every half-hour. Each sub-site was surveyed separately, and
150 added to other sub-sites to obtain a total for the entire colony. All sub-sites 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.
155 Consequently, pup numbers were reliable only from March 1 to June 1. Surveys were

[6] Personal Communication, Tom Moore, Biologist, California Department of Fish and Game, Bodega Bay, California.

conducted with binoculars and a 40-50x 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 towards water, or flush into water. Disturbance data is only included for the years 2000 to 2007 because the subsite specific disturbance data prior to 2000 has not been converted to current data standards. We tested for differences in mariculture related disturbance rate before and after the increase in harvest rates (2000 - 2005 versus 2006 - 2007) using binomial tests comparing mariculture related disturbances versus human related (but non-mariculture) disturbances. We also tested the statistical power of these tests based on the sample sizes and differences in means (Crawley 2005).

Data Preparation

Data on disturbance events at each subsite were compiled and classified based on whether they were caused by oyster vessels or other activities related to mariculture ("mariculture related" and "non-mariculture related" disturbances). We only analyzed events that resulted in head alerts or flushing toward or into water. 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. Disturbance data from the entire year were analyzed for 2000 – 2006, but ended on July 31 in 2007, although the majority of the surveys in each year occurred between April – June.

Prior to population analyses, survey data from Drakes Estero collected from 1997 – 2007 were filtered to remove: (1) data from observers with less than one year 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 are standardized to the Golden Gate Bridge, San Francisco (PST). To ensure that variation in tide levels ≤ 2 ft (0.61 m) did not affect counts, we tested for correlations between tide level and counts at each 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 $r < 0.5$). A subset of the data from all 104 surveys used in this analysis was checked for accuracy against the raw data forms and by comparing subsite data with the sum of counts from the full Estero. We then selected the data within the peak of the pupping season (April 15 – May 15) for each year for analyses of trends in counts over time and between subsites. Between 6 and 15 surveys (mean = 9.5 ± 2.9) were completed in each year during this period. We also compare pupping season counts with the five other primary local harbor seal sites within 30 km of Drakes Estero from 2000 – 2007 to provide a regional context.

Analyses

We hypothesized that there could be four potential effects on counts at OB and UEN: (1) year as a trend through time, (2) total seal counts in the rest of the Estero, since density-dependent effects might be related to use of an individual subsite, (3) years since

the last ENSO event (1991-1992 and 1997-1998; http://www.pmel.noaa.gov/tao/elnino/), and (4) oyster aquaculture activity measured as the weight of oysters harvested ($x10^5$ lbs) the following year. The last factor was chosen *a priori* with a 1-year time lag since time from oyster spat outplanting to harvest is about 18 months and any effects due to harvest levels should begin to be felt sometime during the 18 months prior to harvest[7,8]. The oyster harvest factor is assumed related to boat traffic, human activity, and oyster bag placement that may displace or disturb seals. Candidate models included between 1 and 3 of the above factors; year and ENSO were not used in the same models since both represent time.

For analyses of total counts at subsites OB and UEN, we built generalized linear models (GLM). Counts were overdispersed (*i.e.,* variance greater than the mean and increasing with the mean) and we therefore used a negative binomial distribution to model the counts (Venables and Ripley 2002, Insightful 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 theta (mean and variance parameter for the negative binomial distribution) for both UEN and OB using the glm.nb function in S-Plus (Venables and Ripley 2002). These values (1.0 for OB and 1.6 for UEN) were subsequently used in all GLM models since theta must be kept constant to compare maximum likelihood (and hence AIC_c)

[7] PAULEY, G.B., B. VAN DER RAAY and D. TOUTT. 1988. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)-Pacific Oyster. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.85). U.S. Army Corps of Engineers, TR EL-82.4. 28pp.
[8] Personal Communication, Tom Moore, Biologist, California Department of Fish and Game, Bodega Bay, California.

between models using the same dataset (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.

225 As a comparison to traditional AIC_c model selection, we also used generalized linear mixed-models (GLMM) with penalized quasi-likelihood (glmmPQL function in the MASS package in S-Plus) to explore effects of considering year and seals counts in the rest of the Estero as random effects (Venables and Ripley 2002). Thus, glmmPQL models any lack of independence (pseudoreplication) of the within-year seal counts at a
230 single subsite and seal counts in the rest of the Estero. All GLM and GLMM analyses were done with S-Plus 6.2 (Insightful 2003).

To validate the best model at OB, we used the best fitting GLM model parameters to predict counts at UEF by using a scaling parameter that divided the mean counts at UEF from 1997-2007 (26.4) by the mean counts at OB (83.6) for the same period (ratio =
235 0.32). We then compared the predicted and actual counts at UEF for each year using r^2. We also tested for mean differences between adults and pup counts at OB for the 2002 - 2004 and 2005 - 2007 breeding seasons using paired t-tests when the counts could be normalized using a square-root transformation and non-parametric Mann-Whitney U tests on non-Gaussian raw counts of adults and pups.

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RESULTS

Seal attendance declined in upper Drakes Estero related to both environmental factors and human activities between 1997 and 2007; however, the amount of change varied amongst the subsites. At subsite OB after 1997, both the maximum and mean

counts for seals and pups were lower from 1998 – 2001, higher from 2002 – 2004, and then lower for 2004 – 2007. Oyster harvesting showed a U-shaped pattern, declining in the early part of the study period and increasing in 2005 (Fig. 2A). Binomial tests indicated there was strong statistical power to detect changes in mariculture related disturbance rates ($1\text{-}\beta > 0.91$ at $\alpha = 0.05$) which were significantly higher in 2006 - 2007 (7 of 14 human disturbances) than for 2000 – 2005 (0 of 22 human disturbances; $\chi^2 = 10.65$, $df = 1$, $P < 0.002$) (Fig. 2B, Table 1; subsites OB, UEN, UEF). The nearly 100% increase in average annual human related disturbance in the upper estero (from 3.7 yr to 7/yr) from maricuture related disturbance between 2000-2005 and 2006-2007 was entirely accounted for by mariculture activities (Table 1). Lastly, disturbances in the lower estero whose subsites are generally closer or attached to the mainland have suffered higher annual human disturbance rates when compared to the island sandbars of the upper estero.

The best GLM model to explain seal counts at OB ($w_i = 0.75$) included years since ENSO and oyster harvest (Table 2, Fig. 3A). The coefficients indicated that seal counts had a positive relationship with years since ENSO and a negative relationship with oyster harvest (Table 3). The second ranked model (Seals+ENSO+oyster) was similar to the first with the inclusion of seals as a non-significant variable ($w_i = 0.25$). Thus, the top two models had a total w_i of 1.00 and consisted primarily of years since ENSO and oyster harvest. Pseudo R^2 was high (0.48) for these two best models and declined rapidly thereafter to <0.29 for the remaining models. The predicted and actual counts for the best model at OB were quite close in most years. Predicted counts at UEF using the scaled best fit/lowest AIC_c model from OB fit remarkably well ($r^2 = 0.87$, $P < 0.001$), strongly

suggesting that similar processes (ENSO and oyster harvest) are driving the counts at both OB and UEF (Fig. 3A). Models for subsite UEN, which is farther from the oyster operations, all had poor fit (all pseudo $R^2 < 0.19$), and there was no clear best (lowest AIC_c) model (Fig. 3B, Table 2). The generalized linear mixed-models (glmmPQL) also found the same best fitting models and/or approximate significance of factors (ENSO and Oyster harvest) for OB. Thus, the random factors "year" and "seals" did not have an affect on significance of ENSO and Oyster.

The square root of total counts (adults + pups) was lower at OB from 2005 – 2007 than during 2002 – 2004 ($t_{58} = 4.2$, $P < 0.001$). Similarly, mean adult counts declined from 122 ± 70 to 53 ± 38 ($U = 731.5$, $P < 0.001$), and pup counts dropped from 46 ± 31 to 21 ± 14 ($U = 694.0$, $P < 0.001$) during this time (Fig. 4). Counts at subsite UEF showed no significant change (all $P > 0.15$) during these two selected time periods since it appears that declines did not begin there until 2006. However, counts were significantly lower at UEF during 2006 – 2007 than the previous 3 years ($U = 462.5$, $P < 0.04$) (Fig. 3B).

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 Lagoon, Tomales Bay, and Duxbury Reef (which is only a molting site, not a breeding/pupping site) showed stable populations during the time series. The Double Point haulout site suffered from an aggressive male elephant seal (*Mirounga augustirostrus*) in 2003 that killed approximately 40 (mostly female) and chronically harassed 100s of other harbor seals throughout the breeding season. The Tomales Point

290 colony showed a small increase over time. Finally, Drakes Estero showed a total population decline of about 25% from 2003 to 2007.

DISCUSSION

Pinnipeds, and harbor seals in particular, are vulnerable to human disturbance at
295 haulout sites where they rest and raise their young (Seuront and Prinzivalli 2005, Grigg *et al.* 2002, Perry *et al.* 2002, Suryan and Harvey 1999, Allen *et al.* 1984, Kenyon 1972). 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
300 account for factors such as density-dependence on long-term trends of populations (Johnson and Acevedo-Gutierrez 2007, Perry *et al.* 2002, Grigg *et al.* 2002).

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
305 evidence that from 1997 – 2007 seal counts at Drakes Estero subsites OB and UEF increased since the last ENSO and then declined with an increase in oyster harvesting activities since 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
310 foraging (Lee *et al.* 2007, Grigg *et al.* 2004, Benson *et al.* 2002, Sydeman and Allen 1999, Trillmich and Ono 1991).

Oyster operations began increasing by 2005 to generate the increases in harvesting seen in 2006 and 2007, as time from oyster spat outplanting to harvest is around 18 months in Drakes Estero. 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, unpubl. data). Conversely, as of 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 are hauled out, surveys that count seals and record disturbance events are only completed during a small fraction of the year (< 50 days per year, each survey 2-4 hours), so all types of disturbance are likely underestimated here. Studies from Washington state found that disturbance events that flush seals into the water only result in a return to previous numbers 39% of the time (Suryan and Harvey 1999), and results from nearby Bolinas Lagoon indicate similar results (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 occur (Lucas and Stobo 2000, Suryan and Harvey 1999, Stein 1989). Such disturbance events in Drakes Estero at OB and UEF appear to have produced effects that are detectable during the entire pupping season via reduced seal counts.

The similar count pattern and excellent model fit observed at subsite UEF (Fig. 3A) suggests that similar factors are driving counts at OB and UEF. The lack of a clear

335 best model for UEN and the generally poor fit of all UEN models includes the possibility that seals here are either not influenced by oyster harvesting during the pupping season or that other unmodeled factors (including interactions among subsites) may affect counts. Additional processes that might influence the seal counts at UEN include that seals here are typically farther from oyster operations than those at OB and UEF and thus less 340 susceptible to disturbance, or that some seals may have moved from OB and 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 (Johnson and Acevedo-Gutierrez 2007, Suryan and Harvey 1999, Allen *et al.* 1984). Furthermore, changes in sandbar morphology affect counts in the lower Estero, and any 345 changes in counts in that area may affect counts in the middle-upper Estero due to redistribution of seals. For example, counts at subsite A in the lower estero (Fig. 1) declined dramatically from 2004 - 2007, due to a naturally shifting sandbar that allowed predator (coyote – *Canis latrans*) access to the site. These displaced seals appeared to move to other subsites in the estero (for example, subsite A1 increased dramatically as A 350 declined), and this process may have also had a confounding impact on the counts at UEN. Clearly, the variation at UEN is not well explained by our candidate models and unknown processes such as interactions among subsites in the Estero may be partially driving counts at UEN.

The variable "seals" which represented total number of seals in Drakes Estero 355 (excluding subsite OB or UEN, in their respective models) was designed to control for density-dependent effects within the estero. This variable should also control for larger scale regional impacts such as the poorly understood oceanographic anomalies in the

California Current 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 the "Seals" variable should have presented a better (more parsimonious) explanation of the data than "ENSO" and "Oyster" (Table 2). This would similarly address any covariation of counts in Drakes Estero with other harbor seal haulout sites in north central California due to unexplained interannual variation (Fig. 5). While total harbor seal counts in Drakes Estero increased from 2000 – 2003 (from ~700 – 1000 individuals), and then declined from 2003 – 2007 (down to ~ 750 individuals), ENSO and oyster harvesting still explained the data much better than total seal counts in the Estero. The significant decline in adults and pups after 2004 (Fig. 4) suggests that oyster harvesting influenced these numbers; however, the GLM models were fit to actual data, so it would be inappropriate to predict if OB would have continued to increase or asymptote after 2004 in the absence of increasing oyster harvesting. Nonetheless, while long-term studies in Washington and Oregon State noted density-dependence effects at harbor seal colonies (Brown *et al.* 2005, Jeffries *et al.* 2005), the data for subsite OB in Drakes Estero are most consistent with the hypothesis that significantly reduced counts during 2005 – 2007 are related to the increase in oyster harvesting.

In summary, patterns observed in Drakes Estero at subsites OB and UEF are best explained by ENSO and increased disturbance from oyster harvest activities at subsite OB and that oyster activities reduced the OB and UEF counts during the pupping season from 2005 - 2007. The excellent 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. Because the UEF model predictions were built without any data from the UEF site, this appears to be a very powerful explanatory model. Conversely, counts at subsite UEN, which is further away from oyster operations, showed no clear response to year, density-dependence, ENSO, or 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 suffered no such physical changes that we are aware of other than an increase in nearby mariculture use.

The results of the 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 farming in coastal waters off Australia reduced use by bottlenose dolphins (*Tursiops* sp.) even though the facility had open areas that presumably would allow them to pass. Such conflicts may increase in the future if mariculture replaces wild ocean harvesting due to the decline in wild fish stocks worldwide (Worm *et al.* 2006).

The results of these analyses illustrate the benefits of long-term studies for understanding multiple anthropogenic and environmental factors that can affect pinniped populations and productivity (Thompson *et al.* 2001, Richardson *et al.* 1995). The study also demonstrates how chronic disturbance activities, in this case associated with a mariculture operation, can lead to long term displacement of seals at haulout 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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Table 1. Mean annual human disturbances at Drakes Estero subsites and percentage of human disturbances that were mariculture related (in parentheses). See results for sample sizes and statistical tests.

Subsite	**2000 - 2005**	**2006**	**2007**
Upper Estero			
OB	0.5 (0%)	2 (0%)	2 (100%)
UEF	1.3 (0%)	3 (33%)	1 (100%)
UEN	1.8 (0%)	2 (0%)	4 (75%)
Total	3.7 (0%)	7 (14%)	7 (86%)

Lower Estero	**2000 - 2007**
A	6.5 (0%)
A1	4.6 (0%)
L	8.6 (0%)
DEM	3.6 (0%)
DBS	2.0 (0%)
Total	25.4

Table 2. Ranking of candidate models at subsites OB and UEN by AIC_c and Akaike weights (w_i). Dependent variable is the count of total seals at subsite OB and independent variables are year as linear trend (Year), Sum of all other seals in estero (Seals), years since last El Niño event (ENSO), and lbs. of oysters harvested in following year (Oyst). Column headings are: Log Likelihood (LogLik), number of model parameters (K), small sample AIC (AICc), distance from best model (Δi), likelihood of model given the data ($\mathcal{L}(g|x)$), and Akaike weight (w_i). N = 104 for all models.

Model	LogLik	K	AIC_c	Δ_i	$\mathcal{L}(g\|x)$	w_i	pseudo R^2
Subsite OB							
ENSO+Oyst	-156.72	4	321.84	0.00	1.00	0.75	0.48
ENSO+Oyst+Seals	-156.70	5	324.01	2.17	0.34	0.25	0.48
Year+Seals	-165.40	4	339.20	17.36	0.00	0.00	0.24
ENSO	-167.06	3	340.36	18.52	0.00	0.00	0.25
Year+Oysters	-167.19	4	342.78	20.94	0.00	0.00	0.25
Seals+ENSO	-167.29	4	342.98	21.14	0.00	0.00	0.29
Year	-169.42	3	345.08	23.24	0.00	0.00	0.18
Seals	-171.72	3	349.68	27.84	0.00	0.00	0.11
Seals+Oyst	-171.72	4	351.84	30.00	0.00	0.00	0.11
Null model (y ~ 1)	-174.78	2	353.68	31.83	0.00	0.00	0.00
Oyst	-174.76	3	355.76	33.92	0.00	0.00	0.00
Subsite UEN							
Year+Seals	-155.17	4	318.75	0.00	1.00	0.31	0.18
ENSO+Oyst	-155.18	4	318.77	0.03	0.99	0.30	0.18
Seals+ENSO+Oyst	-155.17	5	320.95	2.20	0.33	0.10	0.18
ENSO	-157.44	3	321.13	2.38	0.30	0.09	0.11
Year	-157.75	3	321.75	3.00	0.22	0.07	0.10
Seals+ENSO	-156.80	4	322.00	3.26	0.20	0.06	0.13
Year+Oyst	-157.21	4	322.82	4.08	0.13	0.04	0.12
Null model (y ~ 1)	-160.99	2	326.10	7.35	0.03	0.01	0.00
Seals	-159.94	3	326.12	7.37	0.03	0.01	0.04

Seals+Oyst	-158.99	4	326.38	7.64	0.02	0.01	0.07
Oyst	-160.56	3	327.36	8.61	0.01	0.00	0.01

Table 3. Coefficients of the best two AIC_c ranked models for OB and UEN from Table 2.

Subsite:Model	Coefficient	Standard Error	t	p<0.05
Subsite OB				
Model: ENSO+Oyst				
Constant	2.947	0.175	16.883	*
ENSO	0.445	0.051	8.780	*
Oyst	-0.323	0.056	-5.785	*
Model: Seals+ENSO+Oyst				
Constant	2.905	0.337	8.628	*
Seals	0.000	0.000	0.157	
ENSO	0.440	0.059	7.453	*
Oyst	-0.319	0.063	-5.101	*
Subsite UEN				
Model: Year+Oyst				
Constant	-187.284	48.724	-3.844	*
Year	0.096	0.024	3.946	*
Oyst	-0.046	0.031	-1.502	
Model: ENSO+Oyst				
Constant	4.519	0.111	40.542	*
ENSO	0.181	0.033	5.551	*
Oyst	-0.120	0.036	-3.316	*

Figure Legends

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 "middle to upper Estero". Subsites A, A1, DBS, DEM, and L are in the lower Estero and not subject to disturbance from mariculture. All surveys were completed from the bluffs indicated by the "survey location" marker.

Figure 2. (A) Mean (±1 SE) counts of harbor seals at Drakes Estero subsite OB and oysters harvested from Drakes Estero during 1997 – 2007. 1998 was an El Niño year. Time from oyster planting to harvest is approximately 18 months. (B) Proportion of human-related seal disturbances in the middle-upper estero attributed to oyster operations and pounds of shucked oysters harvested from the estero from 2000 - 2007. No disturbances were solely attributed to oyster operations during 2000 – 2005 in this area. See text for power analysis, sample sizes and statistical tests. See table 1 for summary of disturbance data.

Figure 3. (A) Predicted and actual (from the best fitting generalized linear model at OB) mean counts of pups and adults from 1997 – 2007 at subsite UEF. The model shows very good prediction ($r^2 = 0.87$). (B) Mean (±1 SE) seal counts from 1997 – 2007 at subsite UEN during the April 15 – May 15 pupping season.

Figure 4. Comparison of the mean (±1 SD) counts of pups and adults during the pupping season (April 15 – May 15) from 2002 - 2004 and 2005 - 2007 at subsite OB. Counts are significantly lower (all $P < 0.001$; see text for statistical tests) for both age classes during 2005 – 2007. There were 31 surveys from 2002 – 2004 and 29 surveys from 2005 – 2007.

Figure 5. Mean (±1 SE) counts of pups and adults during the pupping season (April 15 – May 15) from 2000 – 2007 at six regional sites (including Drakes Estero) within 30 km of Drakes Estero. Note that a Northern elephant seal harassed 100s of seals and killed about 40 (mostly female) harbor seals at Double Point in 2003, causing a marked decline. Drakes Estero is an important haul out site in the region, generally hosting between 750 – 1000 seals during the pupping season in recent years.

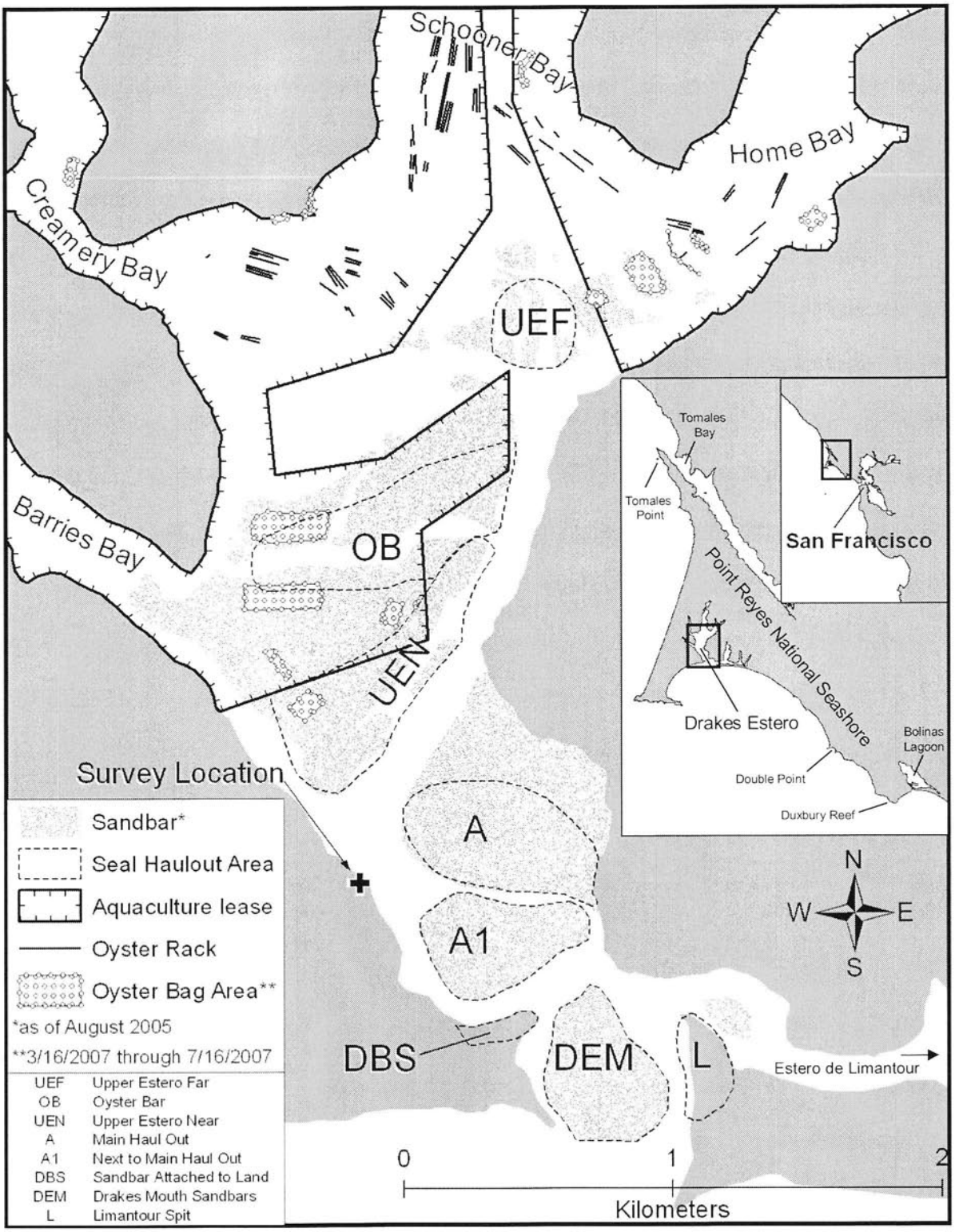
Schooner Bay
Home Bay
Creamery Bay
Barries Bay
UEF
OB
UEN
A
A1
DBS
DEM
L
Survey Location
Estero de Limantour
Tomales Bay
Tomales Point
San Francisco
Point Reyes National Seashore
Drakes Estero
Bolinas Lagoon
Double Point
Duxbury Reef
N
W
E
S
Sandbar*
Seal Haulout Area
Aquaculture lease
Oyster Rack
Oyster Bag Area**
*as of August 2005
**3/16/2007 through 7/16/2007
UEF Upper Estero Far
OB Oyster Bar
UEN Upper Estero Near
A Main Haul Out
A1 Next to Main Haul Out
DBS Sandbar Attached to Land
DEM Drakes Mouth Sandbars
L Limantour Spit
0
1
2
Kilometers

Fig. 1

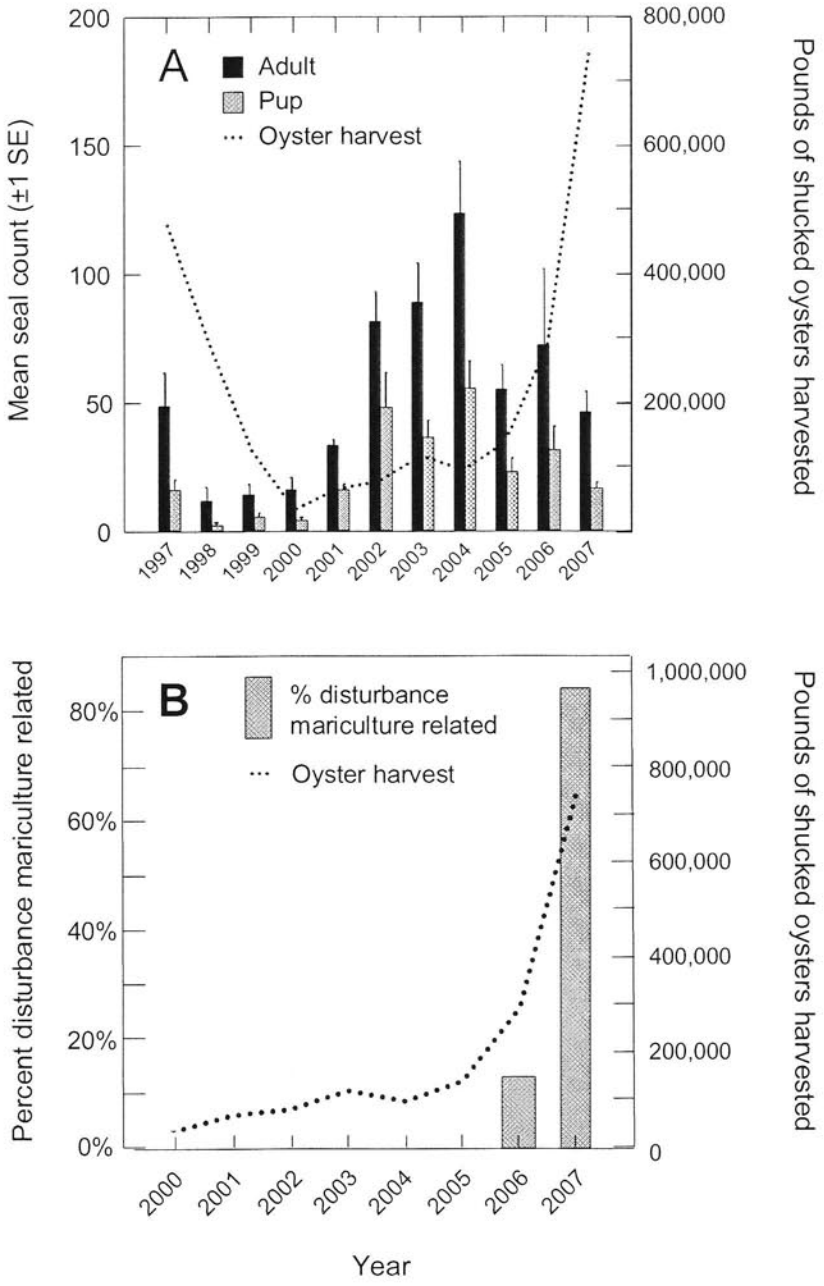
A
Adult
Pup
Oyster harvest
Mean seal count (±1 SE)
Pounds of shucked oysters harvested
200
150
100
50
0
800,000
600,000
400,000
200,000
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
B
% disturbance mariculture related
Oyster harvest
Percent disturbance mariculture related
80%
60%
40%
20%
0%
1,000,000
800,000
600,000
400,000
200,000
0
2000
2001
2002
2003
2004
2005
2006
2007
Year

Fig. 2

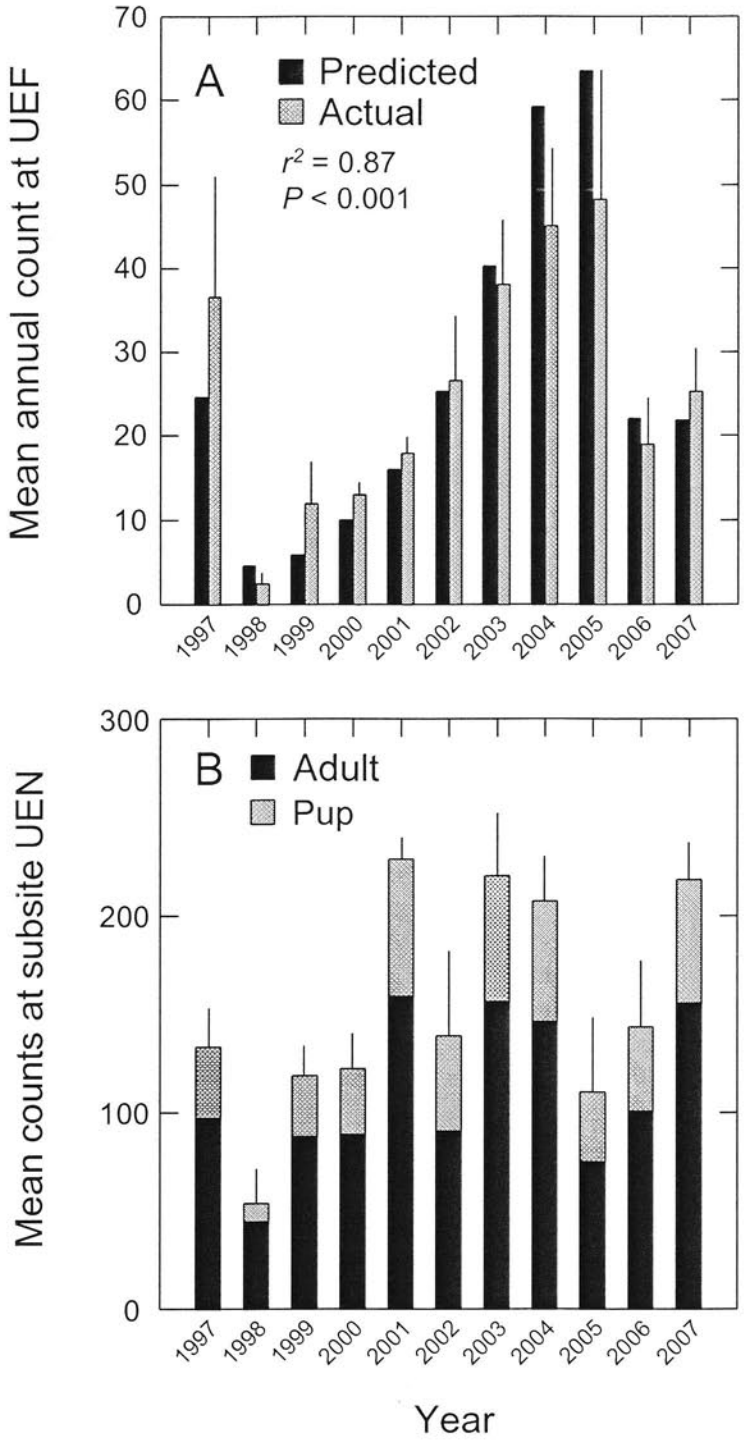
A
Predicted
Actual
r^2 = 0.87
P < 0.001
Mean annual count at UEF
0
10
20
30
40
50
60
70
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
B
Adult
Pup
Mean counts at subsite UEN
0
100
200
300
Year

Fig. 3

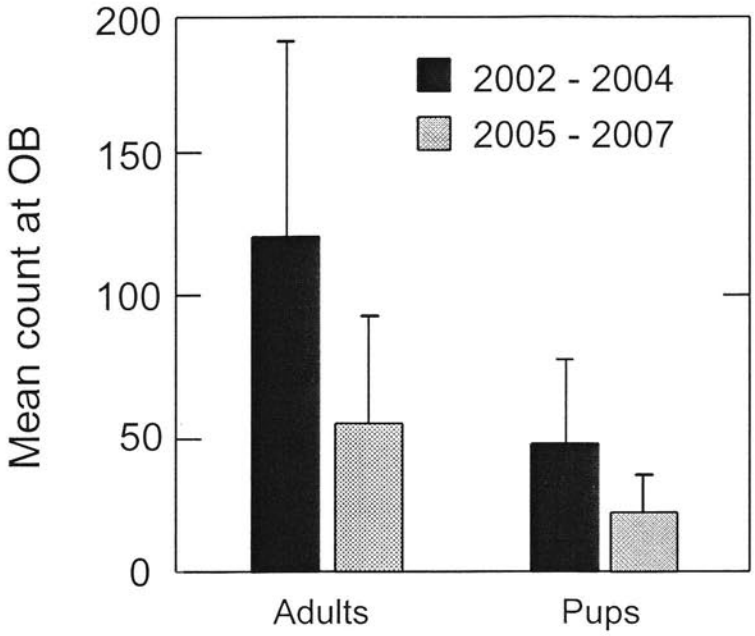
200
150
100
50
0
Mean count at OB
2002 - 2004
2005 - 2007
Adults
Pups

Fig. 4

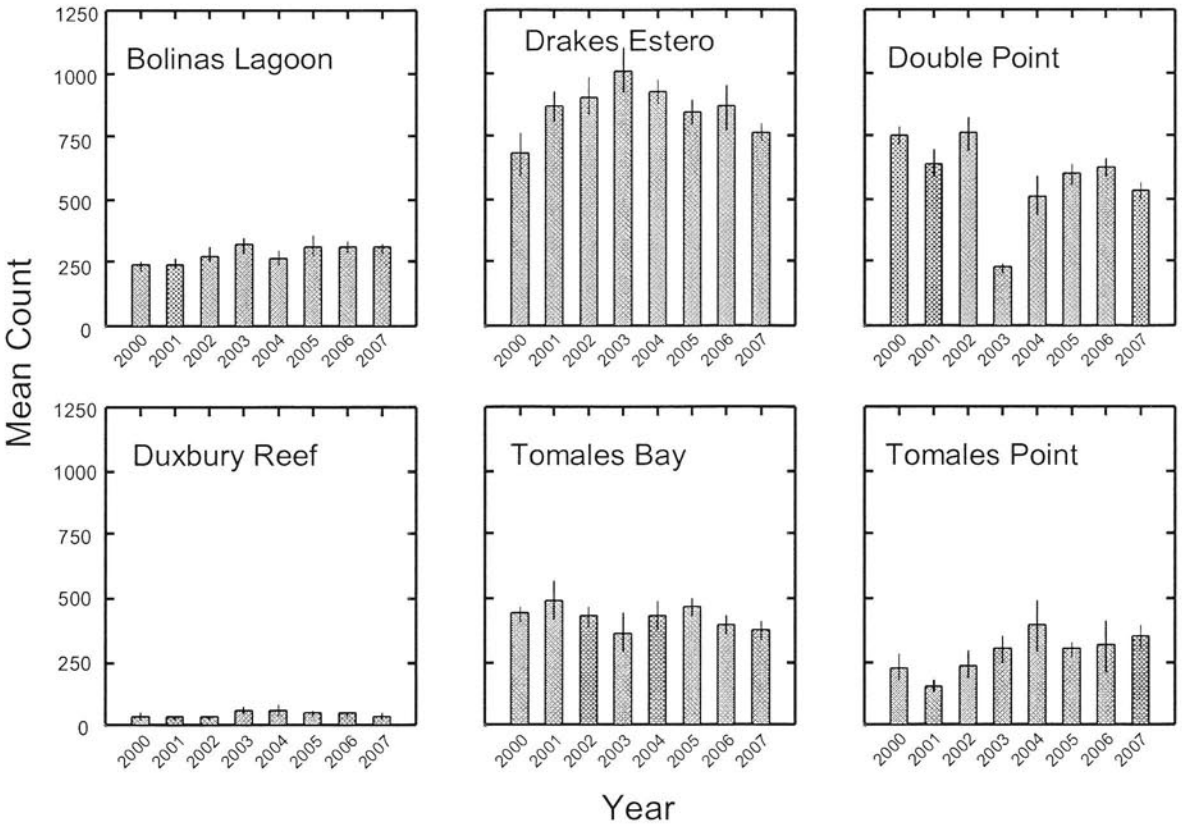
Bolinas Lagoon
Drakes Estero
Double Point
Duxbury Reef
Tomales Bay
Tomales Point
Mean Count
Year
0
250
500
750
1000
1250
2000
2001
2002
2003
2004
2005
2006
2007

Fig. 5