Report peer review documentation for:

Becker, B. H., D. T. Press, and S. G. Allen. 2010. Spatial use of Drakes Estero, California, by harbor seals correlated to anthropogenic disturbance and natural variation during 1982-2009. National Park Service Report, Point Reyes National Seashore. 48 p.

Project Manager: Don Neubacher, Superintendent, Point Reyes National Seashore.

Primary Peer Review Manager: Ray Sauvajot, Chief of Natural Resources Programs, Pacific West Region, National Park Service.

Secondary Peer Review Manager: Ben Becker, Marine Ecologist, Point Reyes National Seashore with oversight of incorporation of review comments by the Project Manager (Neubacher) and Primary Peer Review Manager (Sauvajot).

Report Classification: "Informative Scientific or Scholarly Information": One or more peer reviews required.

Summary of Peer review:

Reviewer #1: USGS Scientist – Completed: comments and suggestions incorporated.
Reviewer #2: NOAA scientist /Statistician– Completed: comments and suggestions incorporated.
Reviewer #3: Academic Statistician – Not completed after 2+ months.
Reviewer #4: USGS Scientist/Statistician – Completed: Comments and suggestions incorporated.
Park review and ensure incorporation of peer review comments: D. Neubacher, Park Superintendent – Completed.
Regional review and ensure incorporation of peer review comments: R. Sauvajot, Regional Chief of Natural Resource Programs – Completed.
Regional Chief Scientist Review: D. Graber – Completed.

Level of Peer review required: Following the NPS "Interim guidance document governing code of Conduct, Peer review, and information quality for natural park service cultural and natural resource disciplines" dated January 31, 2008, we determined that this report under review did not meet the "influential" level of scientific or scholarly information (see p. 11 in the NPS interim guidance) because it would not be the principal basis for a decision that affects significant numbers of private sector entities outside parks. Additionally, reports from the National Research Council (NRC 2009) and the Marine Mammal Commission (in progress) will serve as additional scholarly information, thus rendering this report not a "principal basis" for a decision. Therefore, this report for review was deemed to be "Informative Scientific or Scholarly Information"

Peer Review Process: This review will have the Project Manager (Neubacher) and the Primary Peer Review Manager (Sauvajot) ensure that peer review comments are adequately addressed by the Secondary Peer Review Manager (Becker) by approving the reviews and responses. Then two regional NPS scientists (Graber and Sauvajot) would provide a final review. We determined that peer reviews by Reviewers #1, #2, and #3, would provide an appropriate level of peer review. All are Ph.D.'s with extensive vertebrate ecology and/or statistical expertise. Reviewer #1 is an ecologist with USGS; Reviewer #2 is an associate editor at an academic journal, a marine mammal ecologist and statistician; and Reviewer #3 is a biostatistician, program director at a prominent

marine science institution, and affiliated with the National Research Council. When the latter (#3) did not return a review in a timely manner (~2 mos.), we contacted Reviewer #4 (USGS – Ecologist/Statistician) to complete an additional statistical review. Additionally, David Graber, Chief Scientist for the Pacific West Region of the NPS also reviewed the paper. Regional review was performed by the Primary Peer Review Manager (Ray Sauvajot).

Peer review timelines organized by reviewer

NPS Peer review request

11/09/09 - Sent to Jay Goldsmith (NPS – Pacific West Regional Office) to send out to subject matter experts for blind peer review.

Mid-November 2009 – All potential peer reviewers approached by Jay Goldsmith declined due to time constraints or potential conflicts of interest as they might be on the MMC panel reviewing the Drakes Estero harbor seal data at a later date.

STATUS: Ray Sauvajot (PWR) indicates that we can manage our own peer review with Neubacher as Project Manager, Ray as the Primary Peer Review Manager and Becker as Secondary Peer Review Manager. Neubacher and Sauvajot will ensure that the peer reviewer comments are addressed and then two regional reviewers will perform a final review. We proceed.

Reviewer #1

11/05/09: Sent for peer review.

11/13/09: Returns comments. Finds no logical errors, indicates that we need to reduce repetition and caveats in discussion, cite more literature in the discussion, and reduce the figures and tables. All comments are incorporated. Text significantly reduced and repetition removed. Figures reduced. Updated draft sent to Reviewers #2 and #3 on 11/15/09.

STATUS: COMPLETED

Reviewer#2

11/03/09 – Agrees to take a look, but can't promise in-depth review.

11/05/09 – Sent the 11-04-09 draft.

11/15/09 – Sent the 11-15-09 draft that incorporated Reviewer #1's Comments.

11/16/09 – Indicates he/she hopes to do comments week of Thanksgiving.

12/03/09 – Sent "ModelDetails" that was prepared for Reviewer #3 (see below).

12/03/09 – Indicates that he/she still hasn't had a chance to look at the paper

01/05/2010 –Delivers review with several minor suggestions (asking for clarification, adding citations, discusses use of P-values in correlations, which we keep following Zuur 2009). Indicates that he/she does not see any major flaws and that GEE modeling structure seems appropriate. All suggestions are addressed.

STATUS: COMPLETED

Reviewer #3

10/28/09 –Agrees to review.

11/05/09 – 11-04-09 draft sent.

11/15/09 – Sent the 11-15-09 draft that incorporated Reviewer # 1's comments.

11/30/09 – reviewer #3 requests additional statistical model details.

12/01/09 – Additional 2-page "ModelDetails" file sent.

12/01/09 – reviewer #3 indicates will have comments in a "day or two".

12/16/2009 – Additional status inquiry emails (also 12/07/09 and 12/10/09) get no response.

01/04/2010 – Becker sends another status inquiry email. No response.

01/15/2010 – After thorough statistical review received from Reviewer # 4 (see below), Becker left phone message for reviewer #3 indicating that we now had three other reviews and we were proceeding without his review. Also thanked him/her for their time.
STATUS: CLOSED WITHOUT COMPLETION

REGIONAL REVIEW: David Graber (NPS)
11/24/09 – 11-24-09 draft sent to Dave Graber for review.
12/01/09 – Graber email comments – Suggests submitting to journal and need for documented peer reviews prior to any public release. This includes final review by superintendent and region.
STATUS: After reviews by Reviewers #2 and/or #3 (#1 already done) are completed and comments addressed, Neubacher and the Region should review the document before public release.

Update 01/04/2010:

Still no review from Reviewers #2 or #3. So contacted Reviewer #4 and he/she agrees to do a peer review. Reviewer #2 review comes in the next day 01/05/2010.

Reviewer #4
01/04/2009 – Sent the 01-05-10 draft (only minor changes since the 12/10/09 draft) and supplementary figures. Agreed to review within a "week or two".
01/14/2010 – Received a very thorough statistical review. We implemented or addressed all of his/her suggestions and comments. Reviewer approved of GLMM models, GEE models, and GLMs for the 3 scales. Included a reanalysis of the subsite disturbance data within the estero which changed the interpretation when using a random slope and intercept model. We implemented suggestion to rank subsite models by AIC and use likelihood ratio tests. Explained that we cannot model sandbar changes though time (although it would be nice to), and that we felt binomial models were appropriate based on feedback from others and previous use of direct counts in Becker et al. 2009. Also, since the regional sites are pooled, transition probabilities among those sites are not important so we feel we meet the assumptions of the binomial model. In response to comments about binomial vs. count models to deal with density dependence, we included regional population size in both the colony and regional analyses which we consider a great improvement. This combination of binomial (proportional models) with density dependence should address the reviewers concerns.
STATUS: COMPLETED

FINAL CHECKLIST

01/22/2010 – Sent to Don Neubacher and Ray Sauvajot for final park and regional reviews and to ensure that all peer review comments addressed.

01/25/2010 - Project Manager Approval for Release Pending Regional Review

Final regional review and approval by: Ray Sauvajot, Regional Chief of Natural Resources on 02/03/2010. He OK's release of paper, approves the incorporation of peer review comments, and provides several minor language suggestions that are addressed.
Can release after final read by Becker and Allen. Completed 02/05/2010
Final version Sent to MMC and Interested Parties by Graber on 02/06/2010.

BHB RESPONSE IN CAPS

Reviewer #2 – REDACTED
NO HARDCOPY COMMENTS FROM REVIEWER #2

I've had a brief look and have a few comments/questions:
>
> line 25-6: the sentence says proportion but the number given is -61?
FIXED
> line 135: why use maximum counts only for regional effects? why not use
> all? if you have a reason for this selection, mention it. - CLARIFIED
> line 155: are the same models used when the response variable is a count
> and when it is a ratio? I must not be reading this correctly ...OK,
CLARIFIED
> about 20 years ago REDACTED and I documented the demographic
> consequences of disturbance of REDACTED: CITE REDACTED
> I'm not familiar with GEE but from your description it seems an
> appropriate model. I liked the presentation of the results as effect in
> terms of number of seals, in addition to the regression statistics.
> In my quick read, I thought you were using oyster harvest as a
> categorical variable (high/low) and continuous but wasn't sure I saw the
> results for the continuous case. I THINK THIS IS CLEAR.
> I would be careful about using P values, such as in statements like
> "ENSO and oyster harvest (high/low) were not correlated (P > 0.89)." P
> values indicate the probability of the data given an hypothesis (usually
> of no difference, or zero effect), and do not say anything the truth or
> falsity of the hypothesis - in this case, the hypothesis that ENSO and
> oyster harvest are correlated.
OK, WILL REWORD TO COLLINEAR. TRUE BUT I STILL THINK THE P-VALUE REPORTING HELPDS THE READER KNOW THAT BOTH VARIABLES WERE NOT SELECTED DUE TO ANY COLLINEARIRY. NOT SURE HOW ELSE TO REPORT THIS AND IT SEEMS STANDARD IN ZUUR 2009 AND CRAWLEY 2007.
> In my brief look I didn't see any major flaws (from follow up email).

> I hope these brief comments are a little help.
>
> NAME REDACTED

Reviewer #1 – REDACTED

You explain pretty well the pros and cons of what you have done in the Methods, and again in the Results. Look to reduce redundancies in those two sections. By the Discussion, you should be discussing what you found, and largely ignoring the qualifiers. The way it stands now, you hedge so much, the ms is not compelling because the reader begins to wonder if even you believe what you are saying. You need to emphasize your strongest points in the Discussion, not the weak stuff. The reader needs to finish thinking, wow that is really great stuff. OK, REPETITION REMOVED THROUGHOUT.

Also, the Discussion does not relate your data to much except the Becker et al. 2009 ms. Can you tie in other studies a bit more? DONE, EXTENSIVE LIT ADDED AND DISCUSSED IN CONTEXT, BOTH IN INTRODUCTION AND DISCUSSION.

Suggesting other work that could be done is OK, just don't present it so that it looks like a weakness of your work. OK.

You have made great strides working with the seal data. I don't want to suggest otherwise. I just want to nag you into presenting the data in as compelling of a fashion as possible. Not everyone is going to like the ms, but no one else has better or more relevant data. So, make the most of it and don't apologize for it.

REVIEWER #1 (NAME REDACTED)
ALSO SEE HARDCOPY COMMENTS FOLLOWING

Reviewer #1 [redacted]

All comments incorporated.

Intra- and inter-colony spatial use of Drakes Estero by harbor seals related to disturbance, mariculture activity, and natural variation during 1982-2009

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Abstract

Resilience of marine mammal populations is desirable in the face of climate change, urbanization, and other anthropogenic and natural impacts. To better understand harbor seal vulnerability to these effects in a National Park, we used a 15-year dataset collected between 1982 – 2009 to assess potential mechanisms which may affect the proportion of Point Reyes (California) harbor seals (*Phoca vitulina*) selecting sites within a major colony (Drakes Estero), and utilization of that colony for pupping in relation to other nearby colonies. There was no detectable relationship between human-related disturbance rate and the maximum number of seals hauled out within the estuary. However, pup:adult ratios decreased with increasing disturbance, suggesting that mothers with pups avoided chronically disturbed areas. Within Drakes Estero, after controlling for El Niño effects, the proportion of seals hauled out near mariculture activities declined during years of higher oyster harvest. This pattern also was manifested at larger estero-wide and regional scales. *A priori* models ranked by quasi-AIC indicated that oyster harvest (either binary low/high or continuous harvest level), the counts at a nearby colony, and the gradual loss of a major haul out site in Drakes Estero, best explained pup and total seal use of Drakes Estero. After accounting for these two other factors, the data suggest increased oyster harvest reduced the proportion of Point Reyes area seals using

Drakes Estero by -0.07 ± 0.02 for seal pups (-65 ± 18 total pups), and -0.05 ± 0.02 for total counts (-192 ± 58 total seals). When considering mass of harvested oyster ~~harvest weight~~ as a continuous variable with a linear relationship to proportional seal use, there was an estuary-wide decline in seal use of -19 ± 6 pups and -71 ± 25 total seals for every 100,000 lb. increase in oyster harvest. We suggest mechanisms whereby the interplay between naturally fluctuating seal haul out availability may interact with anthropogenically limited habitat (i.e., mariculture activities) to potentially reduce the proportion of Marin County seals (particularly pups) using Drakes Estero. These results are intended to guide future research questions, provide a baseline for future analyses, and highlight the insights that can be gained by testing multiple competing hypotheses with monitoring data.

Key Words

QAICc, Phoca vitulina, mariculture, disturbance, harbor seal.

Introduction

Wursig and Gailey (2002) ~~suggested~~ state that there is a "need to consider potential loss of feeding and breeding habitat from shellfish and finfish farms, particularly given predicted increases in these facilities in nearshore environments." Similarly, the recent findings that oyster harvest activities may have "potential negative interactions" with harbor seal use (*Phoca vitulina*) at two subsites near the mariculture operations in Drakes Estero (NRC 2009, Becker et al. 2009) and that is it "likely that visits to these areas by oyster farm workers (within 500 m of seals) can be expected to lead to short term disturbance of

any seals using these haul-out areas at the time" (NRC, P. 49), leads to the questions of (1) whether such potential negative interactions are still detected with additional years of monitoring data, (2) if females and pups are proportionately more affected by negative interactions, and (3) if any negative effects might be manifested throughout the entire estuary's breeding and pupping season population relative to surrounding areas.

The National Research Council (NRC) reported that the National Park Service (NPS) pinniped monitoring program provides "as yet untapped potential for assessing trends in the abundance of harbor seals in Drakes Estero in relation to wider regional trends" (NRC 2009, p. 84). Based on the NRC's suggestions, we expanded the Becker et al. 2009 analysis of seal use within Drakes Estero in response to mariculture by 1) adding 4 additional years of data (1982-1983 and 2008-2009), and 2) testing multiple factors that may be related to seal use (total seals and pups) at two spatial scales. The spatial scales ranged from subsite level within Drakes Estero, to colony level for the entire Drakes Estero and to regional level in relation to the other colonies at Point Reyes Peninsula (Fig. 1). A regional effect would be somewhat surprising, since mariculture chiefly occurs in a limited area in the upper/middle sandbars of Drakes Estero. However, cascading spatial effects are not uncommon in marine and terrestrial ecosystems (ADD CITES) and reduced seal use of individual subsites where breeding/pupping occurs could lead to overall reduced use of the estero, and increased out-migration to other less disturbed colonies. Furthermore, females with pups proportionately use the upper/middle intertidal sandbars that are isolated from the mainland and proportionately have more females than the sandbars attached to the mainland near the mouth of the estero (Allen 1988). There are potentially numerous other factors, in addition to mariculture activities, that

could influence seal use of Drakes Estero as well, including disturbance at other colonies, habitat changes and climate effects. Here, we present a preliminary analysis by modeling plausible factors that could be related to the variation in harbor seal use of Drakes Estero.

We made several predictions that scaled from subsite to estero-wide to region-wide scales. At the subsite scale, we predicted that human-induced disturbance would not reduce the number of seals using subsites (since more seals could also lead to more opportunity for disturbance), but disturbance would reduce use of sandbars by females with pups, as measured by the pup:adult ratio. At the estero-wide scale, we predicted that increased mariculture activity (as measured by harvest level) would shift seal use away to other unaffected haul-outs. Lastly, at the region-wide scale, we predicted that relative use of Drakes Estero compared to other seal colonies would be influenced by (1) within site dynamics (e.g., natural loss of a major pupping subsite), (2) nearby colony dynamics (disturbance at a nearby colony that could send more seals to Drakes Estero), and (3) if seals were displaced locally by mariculture activity, but had reduced options for haul out areas due to the factors 1 and 2, then mariculture would partially explain overall use of Drakes Estero in relation to other regional colonies. Because disturbance should increase with population size, we predicted that overall Drakes Estero disturbance rates would not be related to overall seal use. Finally, we tested for effects of ENSO on seal use of Drakes Estero as a while, but had no prediction that ENSO would affect other colonies differently than Drakes Estero.

move

define

Methods

Datasets

Survey methods are described in Becker et al. (2009). Disturbance rate was derived from number of human related disturbances that resulted in a head alert, a flush or a flush of seals into the water during March-May of each year, divided by the number of surveys conducted during that time period. Surveys were typically of similar time duration throughout the study period (~ 2 hrs), except for a few all day surveys in 1982-83.

Two types of seal count data were used. When modeling population level effects, we used the maximum counts of pups and adults from the maximum total count day of the breeding season. Values for Drakes Estero were compared with pooled maximum counts (of pups and adults) at the other 6 colonies in the region (Tomales Bay, Tomales Point, Point Reyes Headlands, Double Point, Bolinas Lagoon, and Duxbury Reef) (Fig. 1). When ~~we were interested in~~ assessing intra-estero variation in use, we used the daily counts at each subsite for all surveys during the peak breeding season (April 15 – May 15 of each year). For data from 1997 – 2009, QA/QC was identical to that used in Becker et al. 2009. We augmented this NPS database with additional subsite data from 1982 – 1983 derived from field notes of SGA, and annual maximum colony counts from Allen and Huber (1983, 1984).

Oyster harvest data was from the California Department of Fish and Game (1997 – 2006), the National Research Council (2007 – 2008), and was roughly estimated as ~450,000 lbs for 2009, based on recent harvest values for 2007-2008. We also explored the use of the oyster harvest value as a binary high/low factor, rather than a continuous variable, so we could treat the functional form (e.g., linear, curvilinear, etc.) of the relationship (if any) between oyster harvest activity and seal haul out behavior as unknown.

Will this need to be metric?

Analyses

Subsite counts and pup:adult ratios related to disturbance rate - Linear mixed-effect models (the "lmer" function in R) were used with subsite as a random effect to test if disturbance rate was related to annual maximum seal counts, maximum pup counts, and pup:adult ratios within subsites and across all subsites between 1997 - 2009. The count models were modeled as quasi-Poisson, and the ratio model as binomial. Models were checked to ensure randomly distributed residuals. Since there were only two covariates ("disturbance rate" and the grouping factor "subsite", we did not use model selection techniques (i.e., AIC) and simply report p values and model coefficients.

Subsite use in Drakes Estero related to mariculture - These models were designed to test if variation in the proportion of seals using the upper/middle (near mariculture) versus lower (away from mariculture) were related to ENSO events or oyster harvest level. The upper/middle intertidal sandbars are isolated from the mainland and historically have had more females than the sandbars attached to the mainland or near mouth of the estero (Allen 1988) (Fig. 2). We improved the analysis in Becker et al. (2009) in two significant ways. First, we used a form of Generalized Linear Models known as Generalized Estimating Equations (GEE) (Venables and Ripley 2002, Faraway 2006, Zuur et al. 2009) that explicitly model the temporal autocorrelation of multiple harbor seal counts taken during the breeding season within each year. GEEs are therefore a form of mixed-effects (or hierarchical) modeling (Gelman and Hill 2009). The GEEs also

allow flexible distributions for the entire dataset and for the within year counts, neither of which are normally distributed. Second, the GEEs were run as binomial models comparing the three subsites near mariculture (OB, UEN, UEF) against the five subsites farther away from mariculture (A, A1, L, DEM, DBS). This removes the need for any density dependence effects since proportions are modeled rather than counts. We also compared the proportion of seals at the two sites closest to mariculture (OB and UEF) versus the rest of the estuary with a similar binomial model.

We modeled "years since ENSO" as *log(years since ENSO+1)* because both observational and theoretical evidence suggest that any ENSO effects should taper off and not be linear. GEEs were run in the software R 2.9.2 using the "geeglm" function in the "geepack" library with year as the grouping variable to account for within year autocorrelation of counts at the same subsite. The correlation structure was set as autoregressive since the counts were during a one month period in each year and counts closer together should have higher correlation since seal counts generally rise, peak, and decline during the April 15 – May 15 pupping period.

Models were tested for combinations of ENSO, and high/low oyster harvest for effects on pup and total (adults + pups) counts. Nested models (e.g., ENSO + oyster vs. ENSO only) were tested for differences with the "anova" model comparison function in R. We then transformed the model logit coefficients (Crawley 2007) to calculate the proportional change in seals using the three subsites near mariculture, and multiplied the proportion by the mean seal count (pups and total) in the estuary during the time series to estimate a change in the number of seals using those subsites.

Drakes Estero compared to surrounding colonies - We examined regional anthropogenic effects during the breeding season by comparing maximum seal counts (pups and total) in Drakes Estero, and all other Point Reyes colonies combined (Tomales Bay, Tomales Point, Point Reyes Headlands, Double Point, Bolinas Lagoon, and Duxbury Reef) (Fig. 1).

The goal of explaining the proportion of seals using Drakes Estero is made somewhat more difficult by several factors in addition to process and sampling variation. During the time series, two potentially confounding events occurred. First, a major subsite in Drakes Estero (subsite A) connected to the mainland in 2004 and was essentially lost due to predation and disturbance pressure from a coyote (*Canis latrans*). Furthermore, this subsite appeared to lose importance throughout the study period (from 1982 – 2009 in a gradual but steady decline (Fig. 5). Second, a nearby major colony (Double Point ~ 12km away) was severely disrupted in 2003 by an elephant seal (*Mirounga angustirostris*) that killed and disturbed many harbor seals, reducing the counts at Double Point and potentially causing a relocation of some harbor seals to Drakes Estero or other colonies in the region.

To address these potential confounding factors, we examined the following variables in relation to the proportion of seals (total seals and pups only) using Drakes Estero compared to the sum of those using the other six Point Reyes area colonies (Fig. 4A):

- Null model.
- Year, to search for a time trend.
- Annual oyster harvest. 2009 was estimated to be similar to 2007-2008, but could easily be higher or lower (Tom Moore, pers. comm.).

- Five-year and six-year periods of lowest oyster harvest (2000-2004 and 1999-2004). Presumably, there was reduced activity and\or potential displacement by mariculture equipment near seal islands during these times (Table 1).
- Proportion of Drakes Estero seals using subsite A (which attached to the mainland ~ 2004).
- Maximum annual count and annual proportional change in seals at nearby Double Point colony.
- Overall spring (March-May) human related disturbance rate (disturbances/surveys) during in Drakes Estero.
- Time since the last major El Niño – Southern Oscillation (ENSO). need to define at first use

As noted above, in addition to the raw oyster harvest metric, we also explored an alternative measure of potential disturbance/displacement: the lowest 5 or 6 years (2000-2004 or 1999 - 2004) of oyster harvest (Fig. 4B). This binary value may be useful for two reasons. First, we do not have an official estimate for 2009 yet (~~and even~~ if we ~~did~~) the 2008 estimate departed from the actual harvest by 12%, indicating that some caution is needed when using estimates. Second, while the use of total annual oyster harvest in the estuary was negatively correlated with nearby seal haul out use (Becker et al. 2009, NRC 2009), total oyster harvest is surely not a perfect measure of oyster activity near the seals. It's activity, not oyster activity The number and distribution of oyster farming equipment (bags) on sandbars for extended time periods is another potential measure. Bags need to be tended, potentially causing disturbance, and the simple presence of the bags themselves may cause seal

displacement. Thus, the oyster harvest metric might not be linear, and using a binary measure eliminates assumptions of any ~~particular functional form~~ underlying distribution; however, we did have to make a decision as to where the cut-off point was for high/low and we did this based on the inferences in Table 1 regarding increased presence of oyster equipment at sites near seal haul out sites.

Aerial images confirm that oyster bags were present in proximity to seal haul out sites in 2005 – 2009. Personal observations (DTP) during regular fieldwork indicate that there were few or no bags on the seal islands from 2002-2004. We infer from the oyster harvest records that there were few or no bags in 2000-2001 since the harvest was relatively low, and that there were likely bags/infrastructure from 1997-1998. Unfortunately, 1999 is difficult to categorize based on the available data. Thus, we modeled the oyster harvest covariate for 1999 in two ways (as both a high and low oyster harvest year) (Table 1).

Modeling the pups and the total population was done separately because there is potential to have a greater disturbance/displacement effect on females having pups that may 1) be more sensitive to disturbance or 2) seek out more isolated haul out sites. This may also hold true for the loss of subsite A, as well as impacts from the Double Point elephant seal disturbances in 2003. We did not combine any covariates in a single model if the Variance Inflation Factors (VIFs) were above 3 (Zuur et al. 2009). VIFs were calculated from models without the complementary covariate. For example, the VIF for low/high oyster was calculated without "oyster", since these would never be used in the same model.

This sentence is hard to follow

DRAFT

We used binomial generalized linear models (GLM) which modeled the probability that any random seal is found in Drakes Estero (success) versus somewhere else in Point Reyes (failure). We bound "Drakes Estero" and "non-Drakes Estero" seal maximum counts for each breeding season into a single matrix (pups or total) for use as the dependent variable in this model. Because of overdispersion issues (variance larger than expected for binomially distributed data), we used a quasi-binomial family to assess *P* values and overdispersion, and the binomial distribution to derive log-likelihoods to rank models using an overdispersion adjusted Akaike's Information Criteria for small sample sizes (QAICc; Burnham and Anderson 2002). QAICc has a severe penalty for overdispersion and small sample size and is therefore particularly good at making sure such models are not over fit (Burnham and Anderson 2002). Further, binomial models often exhibit overdispersion, since there is no variance parameter, so overdispersion is not necessarily a sign of model inadequacy (Gelman and Hill 2009). According to the "n/3" (where n is the number of data points) guideline for the maximum number of covariates to simultaneously model (Burnham and Anderson 2002, we could model up to 5 covariates since we have 15 years of data. However, we preferred to typically model only 1-3 covariates at a time to ensure we did not over fit models ~~(although the QAICc severely penalizes extra parameters)~~. We also bootstrapped the best ranking models 2000 times to gain unbiased standard errors for the oyster harvest variable. We report models and QAICc values for both the oyster harvest and the low/high oyster models, but only consider the low/high variable when reporting Akaike weights and model averaging. To assess the overall effect of oyster harvest levels, we used the weighted (by Akaike weights) model coefficients (back transformed from binomial logits to proportions) of the

noted above

top models (within 4 QAICc units) for the *low oyster* effect multiplied by the mean number of pups or total seals in the Marin County seal population during the study period. All analyses were done in R 2.9.2 (www.r-project.org).

Results

Seal counts, pup:adult ratios and disturbance rate – Neither subsite pup counts (P > 0.38) nor total seal subsite counts (P > 0.28) were related to spring anthropogenic disturbance rate in Drakes Estero (Figs. A1A and A1B). However, spring disturbance rate was negatively related to a pup:adult ratios at seal haul outs within Drakes Estero (n = 104, groups = 8, $P < 0.001$) (Fig. 3). Residuals for all models were normally distributed (Figs. X and X) and within subsite variance was 0.17. The binomial coefficient for disturbance rate was -0.98 which when compared to the intercept (-0.71) suggests (when the binomial logits were back transformed) that the overall mean pup:adult ratio for 1997 – 2009 was 0.33 and that this value declines on average by 0.16 for every 100% increase in disturbance rate.

don't need

Drakes Estero Subsite Models - The more robust GEE modeling methodology using a binomial distribution and the extended time series adding four years of data gave similar results to Becker *et al.* 2009. Both ENSO and oyster harvest best explain seal use at sites closest to mariculture activity (Table 2). ENSO and oyster harvest (high/low) were not correlated (P > 0.89). Residual plots versus model predictions showed no model fitting issues with the GEE model (Figs. A4 & A6). Within year autocorrelation was moderate (0.45 - 0.60), indicating that GEEs are an appropriate tool for this dataset. An nested

ANOVA indicated the Oyster + ENSO binomial model was a better fit over the ENSO only binomial model for both pups (X^2= 6.7, p < 0.005) and total seals (X^2 = 8.1, P < 0.02) seals.

After accounting for the ENSO effect, the best models estimated 17 ± 4 fewer pups and 62 ± 15 fewer total seals in the three "near mariculture" subsites during the higher oyster harvest years (Table 2). Models for just the two sites closest to mariculture (OB and UEF), report similar results. If an interaction between ENSO and oyster harvest is included, it is also highly significant (and oyster harvest alone remains significant), but we do not report interactions here.

Drakes Estero compared to surrounding colonies - The proportion of pups and adult seals using Drakes Estero versus the other Point Reyes colonies varied throughout the study period, with a peak from 2003-2004. The pup and adult time series were generally similar, with the exception in 1997, when relative pup presence in Drakes Estero was low, but adult use was high (Fig. 4A). It thus appears that 1997 was an outlier for the adult and/or pup proportion of seals in Drakes Estero and we therefore weighted the total seal count model for 1997 by the ratio of the proportions using Drakes Estero of pups to adults in that year (0.3) (Venables and Ripley 2002). We felt this was reasonable since there was an anomalous harbor seal die-off of adults that began during the breeding season in 1997 that did not appear to affect pups, and appears to have affected other sites (specifically Double Point) more than Drakes Estero (D. Grieg and F. Gulland, The Marine Mammal Center, Pers. Comm.), although the sampling from that study was not random.

nearly significant is still not significant. It would not say nearly sig.

Oyster harvest was classified as low during 2000 – 2004 (Fig. 4B). Seal use of subsite A in Drakes Estero was high from 1997 – 2004, and dropped rapidly thereafter when the island connected to the mainland (Fig. 5). Seal use of Double Point increased from 1997 – 2002, dropped rapidly in 2003 due to an aggressive elephant seal, and then rebounded in 2004 – 2005, followed by another smaller decline after 2005 (Fig. 2).

too vague, were there issues or not?

Spearman rank correlations indicated few issues with collinearity among the variables in the models tested, but total counts at Double Point and the low oyster harvest metrics were nearly significant (Table 3a, Fig. 5)). ~~However,~~ variance inflation factors (VIF), which tests for collinearity within the models, found no evidence of collinearity as long as year and subsite A and ENSO and subsite A were not modeled together (VIFs = ~4 - 9) (Table 3b). Since VIFs change slightly when used with the oyster versus low oyster and Double Point counts versus Double Point change models, we only report the higher VIF here, but they were generally within 0.1 of each other.

Quasi-binomial GLMs ~~reported~~ showed that models of the proportion of seals in Drakes Estero were moderately over dispersed for the seal pup "global" model (4.85) and somewhat more over dispersed for the total seal count global model (8.5). We used these values to calculate the QAICc for all the pup models. Binomial models almost always have some degree of overdispersion with count data ~~since~~ because there is no variance parameter in the model (Gelman and Hill 2009).

Among the models tested for pups, the two and three-way combinations of *low oyster* + *Double Point* + *subsite A* (always containing low oyster) models had an Akaike weight of 0.71), and the r^2 for the top model had a good fit (r^2 = 0.46 - 0.63) (Table 4). Annual change at Double Point, disturbance rate, and year were poor predictors of seal

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use in Drakes Estero. ENSO appeared in model 6, but we did not ~~calculate~~ include it in the model averages since the Akaike weight was only 0.09. A similar pattern occurred for the total seal count model, with the exception that ENSO did not appear at all in the top models. (Table 4). Bootstrapped estimates of the oyster standard errors were smaller than those reported by model fitting alone, indicating robust and conservative estimates (Table 5). We note that low oyster harvest alone had an r^2 of 0.26 ~~–~~ and 0.29 for pups and total counts, respectively.

After controlling for the effects of Double Point and subsite A, the best fit weighted coefficients for low/high oyster harvest suggests that there were 65 ± 18 fewer seal pups and 192 ± 58 fewer seals overall using Drakes Estero (Table 5, Figs. 6, 7, A7, & A8). The multimodel results suggest that the increase in oyster harvest activity is related to nearly twice the total reduction in seals in Drakes Estero as Subsite A. Furthermore, subsite A had a non-intuitive affect: when subsite A was more important in Drakes Estero, the overall proportion of Point Reyes area seal in the estero was *lower* (Figs 6 & 7, A7 & A8). Double Point's overall effect size was the smallest, which is ~~intuitive~~ expected since the main effect was likely due to only one year (2003). Double Point is scaled on the order of per 100 seals, so the effect is somewhat difficult to directly compare to the other factors.

Discussion

The analyses are most consistent with the hypothesis that during high oyster harvest years (1997 – 1999, 2005 – 2009), a smaller proportion of seals (pups and total) use upper/middle Drakes Estero when compared to the lower estero. We estimate that these proportions result in about 62 (17 pups) fewer seals in the upper/middle estero, and

192 (65 pups) fewer in the overall estero. We caution that these results are based on only 15 years of data and that there are certainly other unmodeled factors affecting seal use during the breeding/pupping season. Nonetheless, these analyses provide ~~some clues as to the potential~~ useful insights about processes controlling harbor seal use of Drakes Estero. ~~These~~ Our data do not indicate that the seals are lost from the overall population (although that is possible), but rather assume a closed population and indicate a proportional shift in seal use both within the estero and between the estero and other Point Reyes area colonies.

~~This exploratory~~ Our analysis is intended to guide future research questions and has identified potential relationships between high oyster harvests in Drakes Estero and, less convincingly, counts at the nearby Double Point colony. Care needs to be exercised to avoid over interpreting the results because it is possible that an unmodeled factor happens to covary with oyster harvest and is actually driving the reduced proportion of seals using both the upper/middle estero, and Drakes Estero as a whole. Nonetheless, we have attempted to model all potential known factors and would be eager to address additional plausible and logical *a priori* hypotheses.

Limitations of the dataset – The three nearly concurrent events (changes in oyster harvest, availability of subsite A, and the elephant seal disturbance event at Double Point in 2003) all occurred in close temporal proximity (2003-2005), making it difficult to tease apart effects ~~with this short time series~~. Further, our assumption that low oyster harvest (2000-2004) is related to little oyster activity near the seal islands needs to be corroborated. We are confident that there were no or few oyster bags/structures on the islands from 2002-2004 (DTP pers. obs.), and presume that a similar pattern occurred during the other low harvest years (2000-2001), but additional data would be useful in

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supporting this covariate. ~~Actual~~ Years that oyster bags/structures were ~~not~~ present or not on the seal haul sites are not precisely known. If it were less, say only 2001-2004 or 2002-2004, then the "low oyster" fit becomes much better (results not reported here) and overdispersion also declines.

Modeling low oyster versus oyster harvest – Becker et al. (2009) found that oyster harvest and time since the last ENSO were correlated with total seal haul out use near the oyster bag areas. In the current analysis for the entire estero, we focused on low versus high oyster production, but also report nearly identical results when using the continuous linear covariate. The methods presented here are also ~~a great~~ an improvement of the methods in Becker et al. (2009) because they use mixed modeling approaches, within year autoregression of counts, a binomial distribution ~~framework~~ that should eliminate the effects of changing population size, a flexible distribution structure for the within and between year counts, and explicit modeling of the overdispersion. The low/high variable is somewhat more conservative in that it does not assume ~~the~~ a particular functional form (i.e., linear) ~~of the relationship~~ between oyster harvest and seal response. However, the low/high variable could suffer from errors in our assessment of the likelihood of bag presence (Table 1). This new high/low oyster proxy is more of a threshold type model (yes/no) rather than a continuous effect (as with Oyster Harvest). The threshold model might be more appropriate if the mere presence of oyster equipment bags caused seal displacement, rather than the frequency of visits. It does fit slightly better, possibly indicating a threshold effect. Further, because of the use of various parts of the Estero by the oyster growers, the oyster harvest value and activity near the seals need not be linear. Therefore, a simple high-low metric may be more valuable, and appears to fit in this

believe

exploratory analysis. We ~~hope~~, therefore, that the low oyster covariate is a more informative covariate than harvest alone.

Potential Scenario of Process – As expected, we found that the proportional reduction in seal use was larger for the upper/middle estero (-0.09 pups and -0.08 total) versus the estero as a whole (-0.07 pups and -0.05 total counts). However, these proportional values, when scaled up from the Drakes Estero population to the entire Point Reyes population, suggests more individual seals were displaced from the overall estero than those simply displaced from the upper/middle estero alone. Perhaps the effects of the impacts at Double Point, and increased oyster activity in the upper/middle estero led to the pronounced reduced counts for the entire estero. Curiously, as subsite A lost habitat during the study period, this could have *increased* the proportion of seals using the upper/middle estero, but then increased mariculture activity from 2005 – 2009 forced seals back away from the upper/middle estero, and without the resilience of subsite A and the upper estero availability now diminished, the overall proportion of seals using Drakes Estero declined. In early years (the 1980s) when subsite A was dominant, mariculture use was also high so perhaps this large sandbar was able to support some of the animals displaced from the upper estero. However, the proportion of Point Reyes seals was still low back in 1982-83 when Subsite A was well represented and mariculture activity was high. Finally, difficulties in modeling the concurrent ~~events of~~ changes at Double Point, Subsite A, and Oyster harvest with 15 years of data, may have led to statistical artifacts compounding the calculated effects at the population level (i.e., making it seem larger than it actually is). Nonetheless, despite the caveats of a limited time series and multiple

possible factors (including unmodeled ones) affecting seal use in the estero, there is ~~reasonable~~ evidence here that oyster equipment ~~presence~~ (or tending) near seal haul out sites is negatively related to harbor seals distribution and presence in Drakes Estero. While additional monitoring and a longer time series are desirable to help confirm or refute these patterns, it is still useful to discuss ~~potential~~ mechanisms that might lead to mariculture affects on Drakes Estero seals.

~~This apparent~~ The interaction between subsite A, Double Point, and Oyster harvest fits a model where ecosystem resilience is a function of both natural and anthropogenic influences. Specifically, the impacts at Double Point and subsite A were natural reductions in available habitat. ~~A cursory look at~~ Time series ~~of~~ counts suggests that ~~it is possible that~~ disturbed seals moved from Double Point to Drakes Estero in 2003. Such ~~buffers~~ options appear to be less available if additional habitat is ~~lowered in quality~~ degraded by the presence of oyster equipment and oyster harvest activities.

It is likely that proximate impacts of oyster harvest activities (or other disturbances) ~~do~~ disturb seals and potentially cause ~~seals~~ them to move away from the subsites in Drakes Estero and elsewhere (NRC 2009, Becker et al., 2009, Allen and Huber 1984). This would ~~in effect~~ reduce available habitat for hauled out seals on either short or long time scales, depending on the length and frequency of the disturbance / displacement. Affected seals might ~~then~~ choose to haul out nearby, or leave the Estero ~~entirely~~ for other areas. If the seals simply moved to other areas within the Estero, the ratios reported here for the entire estero compared to the rest of Point Reyes would not have changed. But, if there was some competition for space or preferential use of lost areas (such as subsites A,

OB, etc.) by females with pups, it could cause crowding on limited sand bar sites, and lead to a cascading effect causing some seals ~~forego using~~ to not use the estuary.

Concurrent with this scenario, Drakes Estero ~~essentially~~ lost the historical pupping habitat at subsite A in 2003-4 when it attached to the mainland and predatory coyotes could access the sandbar. This loss of a major subsite did not appear to reduce pup numbers in Drakes Estero (Table 4), but may have caused adults and pups to occupy other subsites (seals move around between subsites, but females with pups prefer subsites that are detached from the mainland) (Fig. 2). It is possible that ~~any~~ movement from Double Point in 2003 was absorbed by the upper/middle estero islands (UEN, OB UEF), that were released from oyster ~~displacement/~~ farming disturbance during the low harvest years of ~2000-2004. Then, in 2005 with the continued loss of subsite A and newly placed mariculture bags at subsites OB and UEN and near UEF, space was again limited and overall pup counts in Drakes Estero declined. This scenario, while consistent with the available data, is still somewhat conjectural without ~~detailed~~ tracking studies of individuals.

~~An additional potential mechanism to explain redistribution of seals within Drakes Estero, albeit similarly difficult to test with this dataset, could be~~ It is possible that subsite recolonization takes ~~a matter of~~ years, while abandonment due to displacement/ disturbance is rapid. For example, the recolonization of subsite OB could have been delayed after oyster harvest declined in the late 1990s, and then rapidly declined when oyster harvest increased again in 2005 and oyster harvest equipment and disturbances ~~(mostly disputed by the oyster company)~~ also increased. The *a priori* modeling suggested that an ENSO effect may have explained some of the delayed recolonization in the

middle/upper estero, but perhaps ~~simple time~~ delayed movement into the area is also partially responsible. Such a model would then have a lag effect for recolonization as oyster harvest declined, but no lag as it increased, similar to seal response to coyotes at subsite A. Such a test on the upper/middle estero subsites at this point would be data dredging, but this hypothesis would be interesting to test *a priori* at other subsites or a colony that had high disturbance which then abated. delete

Two ~~potential~~ examples of rapid abandonment and slow recovery come from Drakes Estero in the mid-1990s, and Hog Island in Tomales Bay between the mid-1990s and 2007. Drakes Estero had a decline in pup counts during increasing kayak use in the mid-1990s, and then a slow rebound after kayaking was prohibited during the pupping season (SGA, pers. obs.). Similarly, Hog Island in Tomales Bay (Fig. 1) was abandoned by harbor seals in the mid-1990s coincident with increasing numbers of kayakers landing on the east side of the island. Prohibition of kayak landing coincided with a gradual resumption of use by seals. The seal counts had remained low (< 20) for several years until recently when the island had over 100 seals in the fall of 2009 (SGA, pers. obs).

The decline of harbor seals at subsites OB and UEF in ~~the~~ upper Drakes estero follow~~s~~ this pattern, where after oyster harvest declined around 1999-2000, it took a few years (until 2002) for counts to greatly increase, and then the counts (and proportion of seals using the subsites) rapidly declined again with increased mariculture in 2005. Unfortunately, it is not possible to ~~conclusively~~ tease apart the ENSO ~~signal~~ effects from this delayed recolonization ~~hypothesis~~ pattern within Drakes Estero. ~~but comparisons with other areas may help assess the robustness of the proposed process.~~

~~Finally, this paper~~ Our data focused on processes within Drakes Estero and a major nearby colony (Double Point). Additional processes occurring at other colonies in the SF Bay Area could also affect the patterns we observed ~~here~~. This might include excessive disturbance or displacement, or newly available habitat at other colonies, as well as immigration or emigration from the entire study area. However, the fact that our models ~~do~~ explain much of the intra- and inter-colony patterns observed, suggests that these mechanisms should be taken seriously and are not likely to be spurious correlations.

Conclusion - ~~These exploratory~~ Our results highlight the importance of building and preserving resilience in natural systems. We have demonstrated natural and ~~apparently~~ anthropogenically driven colony dynamics both within Drakes Estero and between Drakes Estero and other colonies in ~~the rest of~~ the Point Reyes area ~~colonies~~. Human encroachment on sandbars may not have a detectable effect on harbor seals until natural fluctuations occur which further limit habitat and cause ~~thereby causing~~ additional competition for limited space resources, ~~especially those areas that are safe from predators or persistent disturbance~~. At a scale even larger than the Point Reyes area ~~colonies modeled here~~, seals transit between San Francisco Bay and the Point Reyes Area (Kopec and Harvey 1995, Grigg et al. 2009), thus anthropogenic impacts on the Marin Coast may indirectly affected the mobility of seals displaced at other colonies in San Francisco Bay or elsewhere. This may be particularly true for ~~the largest colonies such as~~ Drakes Estero which ~~is~~ supports one of the largest breeding colonies in the state and the largest in Marin County (CITE). There may not be sufficient available habitat elsewhere in the region to easily accommodate displaced seals from Drakes Estero.

This analysis is a response and first step toward addressing the NRC's recommendation that the NPS Pinniped monitoring program be used to test for colony-wide ~~variation in~~ response to natural and anthropogenic factors. Specifically, ~~they~~ NRC suggested that patterns in Drakes Estero be compared to region-wide patterns. ~~The~~ our results ~~reported here~~ show a logical series of steps from disturbance being related to lower pup:adult ratios at the subsite scale, to mariculture being related to an intra-estuarine spatial shift in seal use of subsites, and finally an apparent cascading effect to lower overall regional population use of Drakes Estero in relation to other local colonies. These analyses are intended to be a foundation for future research questions addressing ~~plausible~~ mechanisms governing ~~some of the variation in~~ seal use of and productivity in Drakes Estero.

You need a reference here since most of this is not from this ms

As shown in the disturbance vs. pup:ratio data, disturbances by park visitors, aircraft, kayaks, wildlife and predators also may drive spatial use dynamics in the Point Reyes colonies. The effects of disturbance ~~rate~~ on seal ~~counts~~ (*not* pup:adult ratios) may prove to be a difficult ~~variable~~ to investigate ~~in any meaningful way~~ without focused study since higher numbers of seals would likely be related to increased disturbance rates, since disturbance is necessarily zero when seals are absent. However, analyzing the effects of disturbance ~~rate~~ on the use of haul outs by mothers with pups may be a promising avenue of research. Because this monitoring dataset does not constitute an experiment, it can only highlight potential patterns and mechanisms, but additional research or modeling that could test for these affects (if any) would be useful for management.

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Wursig and Gailey (2002)

Additional references to be included

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Table 1. Sources and inferences for level of oyster harvest activity on or near OB, UEF, and/or UEN.

Year	Oyster harvest (lbs)	Mariculture use of sandbars near seals	Source
1982	360,004	Higher	inferred from harvest data, 1987 image
1983	440,139	Higher	inferred from harvest data, 1987 image
1997	476,791	Higher	inferred from harvest data and disturbance data
1998	292,188	Higher	inferred from harvest data
1999	125,749	Modeled high & low	slightly higher than 2000-2004, declining phase
2000	34,094	Lower	inferred from harvest data lower than 2002-2004
2001	65,676	Lower	inferred from harvest data lower than 2002-2004
2002	78,064	Lower	DTP, pers. obs, harvest data
2003	118,643	Lower	DTP, pers. obs, harvest data
2004	96,754	Lower	DTP, pers. obs, harvest data (checking notes)
2005	138,958	Higher	aerial image of bags, increasing activity
2006	291,538	Higher	increasing harvest, bags in '05
2007	468,000	Higher	aerial image of bags
2008	438,000	Higher	aerial image of bags
2009	450,000*	Higher	aerial image of bags

*Estimate based on 2007-2008. Official data likely available in mid-2010.

Table 2a. Binomial Generalized Estimating equation (GEE) for proportion of Drakes Estero Seals using the upper (OB, EUF + EUN) vs lower estero. Effect size is proportion * mean Drakes Estero population size for time series.can be interpreted as the change from the long-term average number of seals. The mean of the maximum seal counts for 1982-83 & 1997-2009 was 770 total and 187 for pups.

	Pups				Total seals			
Model	**Coefficient**	**Proportion**	**Effect size**	**P**	**Coefficient**	**Proportion**	**Effect size**	**P**
Intercept	-1.53 ± 0.34			< 0.001	-1.54 ± 0.23			< 0.001
log(ENSO)	0.72 ± 0.19			< 0.001	0.58 ± 0.13			< 0.001
Oyster high/low	-0.46 ± 0.18	-0.09 ± 0.02	-17 ± 4	< 0.01	-0.43 ± 0.15	-0.08 ± 0.02	-62 ± 15	< 0.005

Table 2b. Binomial Generalized Estimating equation (GEE) for proportion of Drakes Estero Seals using the OB + EUF vs. the rest of the estero.

	Pups				Total seals			
Model	**Coefficient**	**Proportion**	**Effect size**	**P**	**Coefficient**	**Proportion**	**Effect size**	**P**
Intercept	-3.43 ± 0.54			< 0.001	-3.28 ± 0.37			< 0.001
log(ENSO)	1.11 ± 0.30			< 0.001	0.94 ± 0.22			< 0.001
Oyster high/low	-0.75 ± 0.25	0.06 ± 0.02	-11 ± 4	< 0.003	-0.68 ± 0.24	0.05 ± 0.02	-40 ± 15	< 0.005

Table 3a. Spearman rank correlations between independent variables. We only used two variables in the same model if their r_s was < 0.51 and not significant. Significant (P < 0.05) correlations are in bold. Some caution should be used in interpreting any models with both dp.tot and oyster values. N = 15. If adjusted for multiple comparisons using Holm's method, only the three oyster vaues are correlated and the Double Point counts with Double Point change.

	Low oyster harvest 2000-2004	Low oyster harvest 1999-2004	Spring Disturbance rate	Annual change at Double Point	Proportion of seals at subsite A	Maximum counts at Double Point
Low oyster 1999-2004	**0.87**					
disturbance rate	0.23	0.13				
Change at Double Point	-0.20	-0.35	-0.09			
Prop. seals at subsite A	-0.11	-0.17	-0.10	0.00		
Counts at Double Point	0.46*	0.50**	-0.21	**0.78**	0.29	
Year	0.00	0.09	-0.02	-0.08	**-0.92**	-0.24

*p = 0.09
**p = 0.06
oyst + tot.dp: r = -0.59, P = 0.02

Table 3b. Variance inflation factors from full models. VIFs of less than 3 represent no ~~issues with~~ collinearity (Zuur et al. 2009)

	Variance inflation factor	
Covariate	**Pups**	**Total**
Oyster harvest	1.39	1.27
Low oyster 2000-2004	1.17	1.12
Prop. seals at subsite A	1.23	1.05
Counts at Double Point	1.21	1.21
Change at Double Point	1.10	1.13
El Nino	1.09	1.06
Disturbance rate	1.13	1.14

This is hard to read. I would rather like to see just a list of variables in each model. For example Model 1 would be oyster 00-04, Δcount

Table 4. *A priori* models ranked by QAICc for the proportion of Point Reyes seal pups using Drakes Estero. An "x" indicates the coefficient was selected in the model. Δi indicates QAICc distance from the best model and wi indicates model weight. "Low oyster 1999-2004" and "Oyster harvest" are only included for reference and not included in akaike weights. Models ranking within the lowest 4 QAICc units are shaded grey and used for multimodel inference in table 5.

		Oyster related			Major nearby colony		Internal colony effects							
Age class	Model	Low oyster 2000-2004	Low oyster 1999-2004	Oyster harvest	Double Point Counts	Double Point annual Change	Drakes Estero disturbance rate	Seals at A in Drakes Estero	ENSO	Year	Null	Δi	wi	r^2
Pup	1	x			x							0.0	0.35	0.51
	2			x	x			x				1.3		0.63
	3	x			x			x				1.3	0.18	0.63
	4	x						x				1.4	0.18	0.46
	5			x	x							1.5		0.46
	8	x							x			2.6	0.09	0.42
	7		x		x							3.3	.	0.40
	8	x										3.3	0.07	0.26
	9			x				x				3.4	.	0.40
	10		x					x				4.2	.	0.36
	11									x		5.0	0.03	0.20
	12	x					x					5.6	0.02	0.32
	13		x									6.3	.	0.16
	14	x			x		x	x				6.3	0.02	0.66
	15				x					x		6.4	0.01	0.29
	16			x								6.5	.	0.15
	17	x				x						7.1	0.01	0.26
	18				x							7.3	0.01	0.12
	19										x	7.7	0.01	0.00
	20								x			7.7	0.01	0.11
	21							x				8.2	0.01	0.09
	22				x				x			9.1	0.00	0.19
	23			x			x					9.2	.	0.19
	24				x			x				9.8	0.00	0.17
	25						x					10.6	0.00	0.01
	26					x						10.8	0.00	0.00
	27				x		x					11.0	0.00	0.13
	28					x		x				11.9	0.00	0.10
	29						x	x				11.9	0.00	0.09
	30					x	x					14.2	0.00	0.02
Total	1	x			x							0.0	0.55	0.54
	2	x			x			x				2.4	0.16	0.61
	3			x	x							2.5	.	0.47
	4		x		x							2.5	.	0.47
	5			x	x			x				3.8	0.08	0.57
	6	x						x				3.9	0.08	0.42
	7	x										4.3	0.06	0.29
	8	x					x					4.5	0.05	0.41
	9		x					x				6.0	.	0.36
	10	x			x		x	x				6.1	0.02	0.67
	11	x							x			6.3	0.02	0.35
	12		x									6.8	.	0.22
	13			x				x				7.5	.	0.32
	14	x				x						8.1	0.01	0.30
	15									x		8.5	0.01	0.17
	16			x								8.8	.	0.16
	17				x					x		9.6	0.00	0.25
	18			x			x					9.6	.	0.24
	19				x							10.4	0.00	0.11
	20										x	10.9	0.00	0.00
	21							x				11.7	0.00	0.07
	22						x					12.4	0.00	0.05
	23								x			12.6	0.00	0.05
	24				x			x				13.0	0.00	0.15
	25				x		x					13.2	0.00	0.14
	26				x				x			13.4	0.00	0.14
	27					x						13.9	0.00	0.01
	28						x	x				14.4	0.00	0.11
	29					x		x				15.3	0.00	0.08
	30					x				x		15.5	0.00	0.07

see Table 4

Table 5. Multimodel weighted coefficients of all models within 4 QAICc of the best model or pups and total harbor seals in Drakes Estero. Models represent an Akaike weight (wi) of 0.71 - 0.79. Number in parentheses after the "low oyster" coefficients represent the bootstrapped standard error estimate of 2000 replicates. Effect sizes based on mean seal counts of all Point Reyes area colonies during the study period.

	Logit Coefficients		Proportional change		Effect Sizes	
Variable	**Pups**	**Total**	**Pups**	**Total**	**Pups**	**Total**
Intercept	-0.26 ± 0.19	-0.37 ± 0.16				
Low oyster (low/high)	-0.27 ± 0.08 (0.05)	-0.23 ± 0.07 (0.03)	-0.07 ± 0.02	-0.05 ± 0.02	-65 ± 18	-192 ± 58
Double Point (per 100 seals)	-0.04 ± 0.02	-0.04 ± 0.02	-0.010 ± 0.005	-0.010 ± 0.005	-10 ± 5	-36 ± 18
Subsite A (low to high)	-0.43 ± 0.22	-0.11 ± 0.07	-0.09 ± 0.05	-0.03 ± 0.02	-91 ± 51	-106 ± 71
Oyster (per 100,000 lbs)*	-0.06 ± 0.02	-0.08 ± 0.03	-0.019 ± 0.006	-0.020 ± 0.007	-19 ± 6	-71 ± 25

*not multimodel: from Oyster + Double Point count model.

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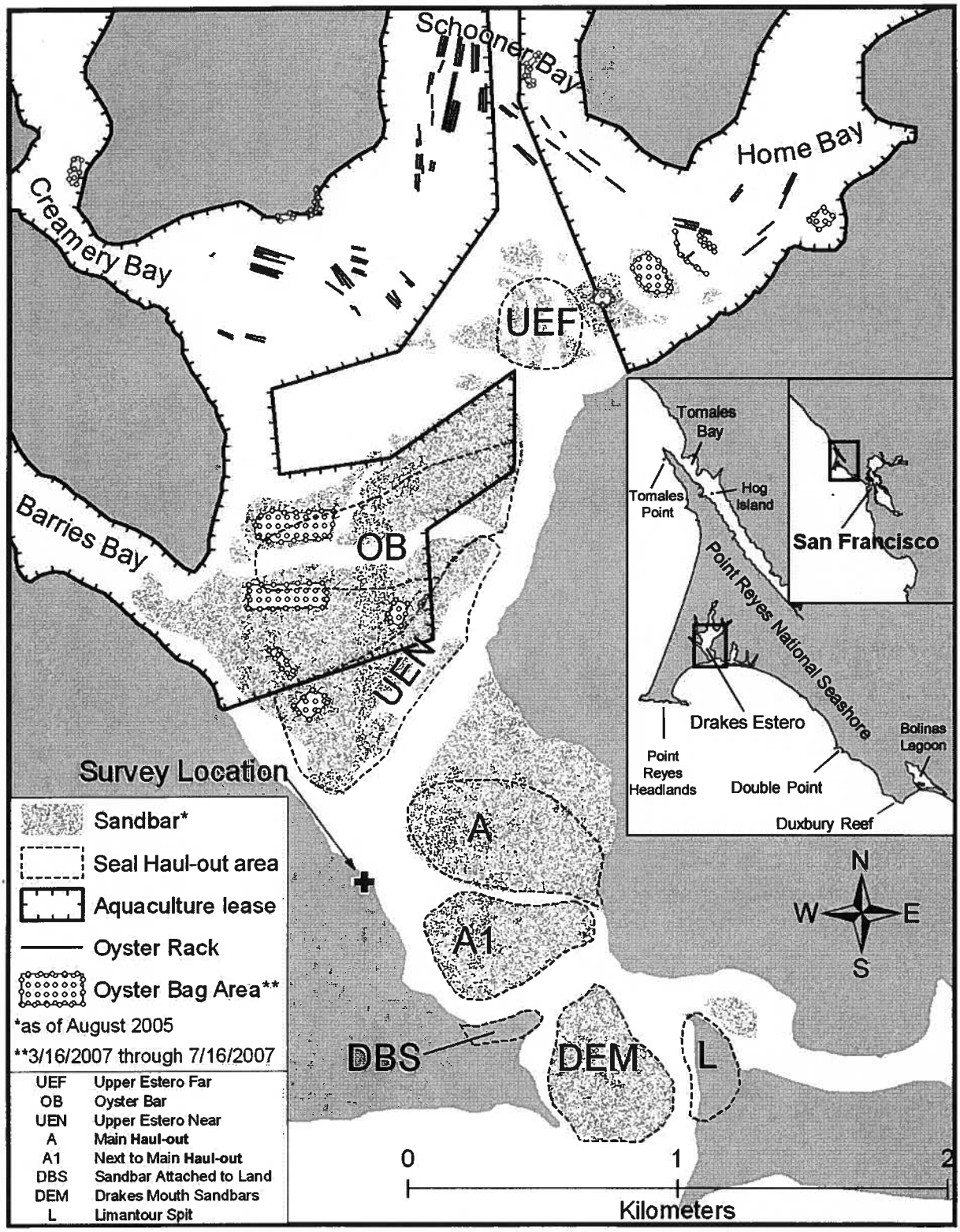

Figure 1. Drakes Estero and the eight labeled seal haul out subsites. Subsites UEF, OB, and UEN are considered "near" mariculture, while A, A1, DBS, DEM, and L are considered "away" from mariculture. Inset shows all the Point Reyes area colonies: Tomales Bay, Tomales Point, Point Reyes Headlands, Drakes Estero, Double Point, Duxbury Reef, and Bolinas Lagoon. Figure modified from Becker et al. (2009).

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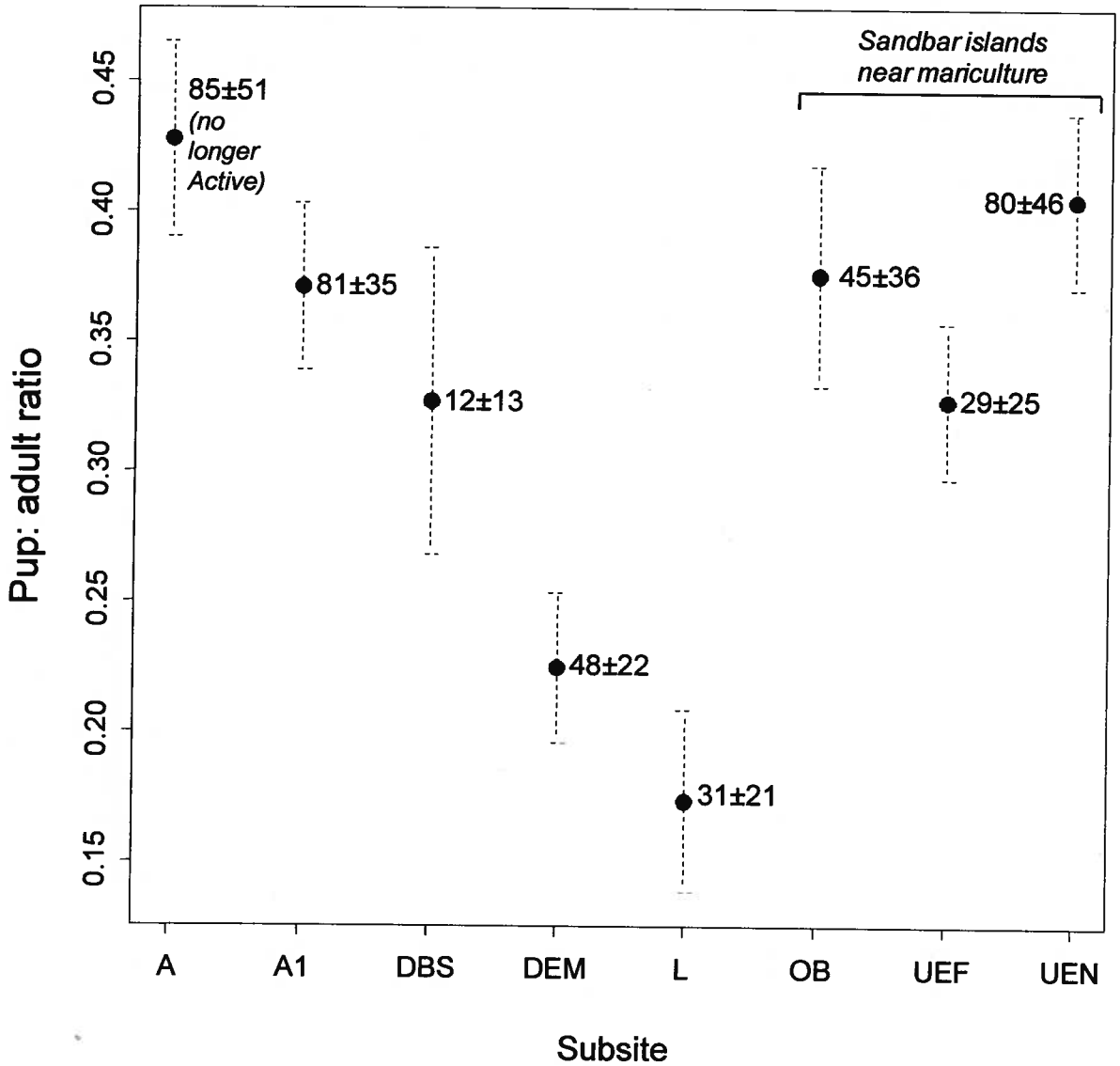

Figure 2. Mean (± SE) pup:adult ratio by subsite in Drakes Estero, 1997 - 2009. *Numbers next to points represent the mean (±SD) of the maximum annual pup counts at that subsite from 1997 – 2009.* The ratios at the estero mouth (DEM and L) are significantly lower than the other six subsites and UEF is lower than A. Furthermore, DBS has very low seal counts and pup production (~12/yr) indicating it is a minor site even though its pup ratio is high. Since 2004, seals have abandoned subsite A due to attachment to the mainland subsequent predator access. This currently leaves site A1 and the three sites near mariculture as the most important (considering pup:adult ratio and pup production) pupping sites in the estero.

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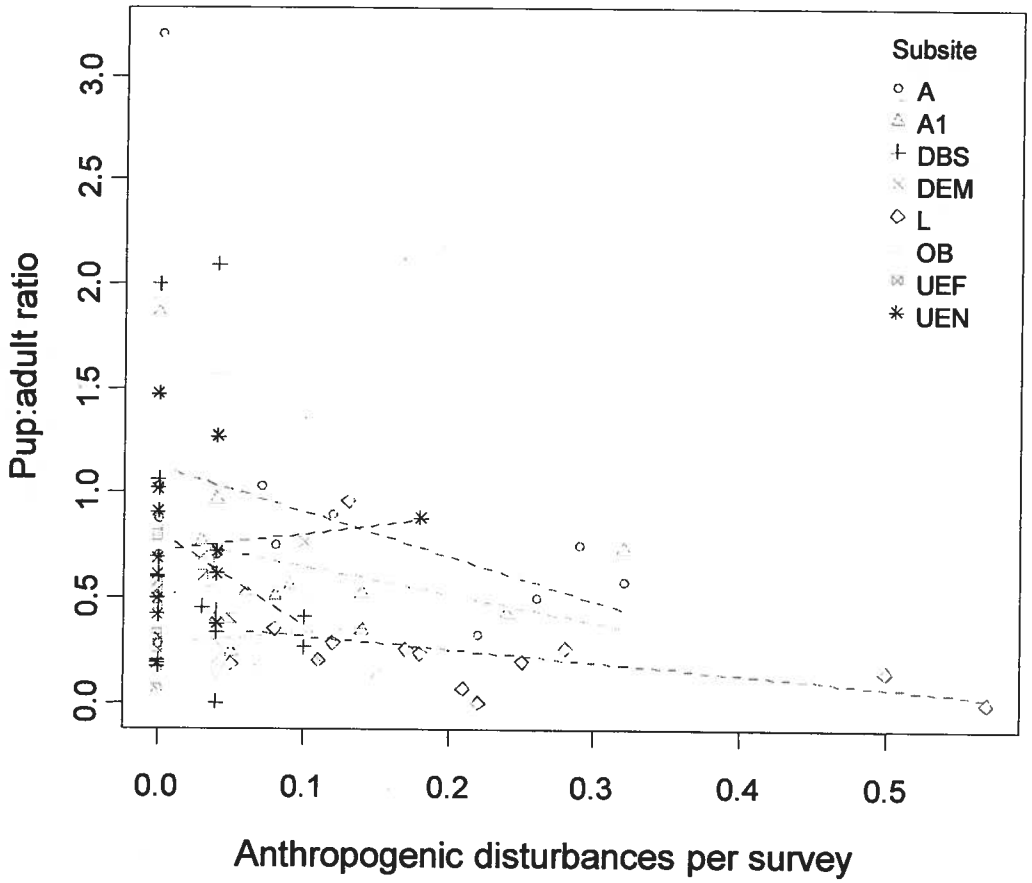

Figure 3. Pup:adult ratio within subsites declines with increasing spring disturbance rate ($P < 0.001$).

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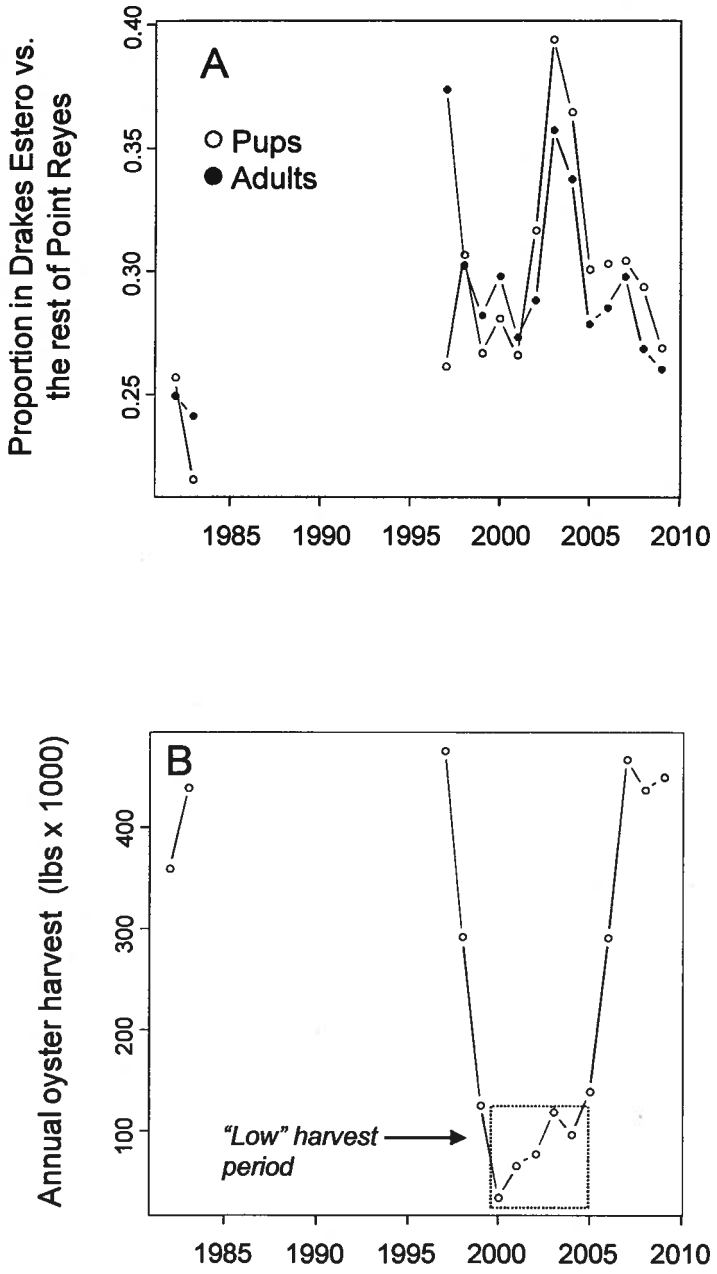

Figure 4. 1982 – 2009 time series of (A) proportion of Point Reyes area pup and adult harbor seals in Drakes Estero during the breeding/pupping season and (B) oyster harvest in Drakes Estero. The 2009 oyster harvest is estimated.

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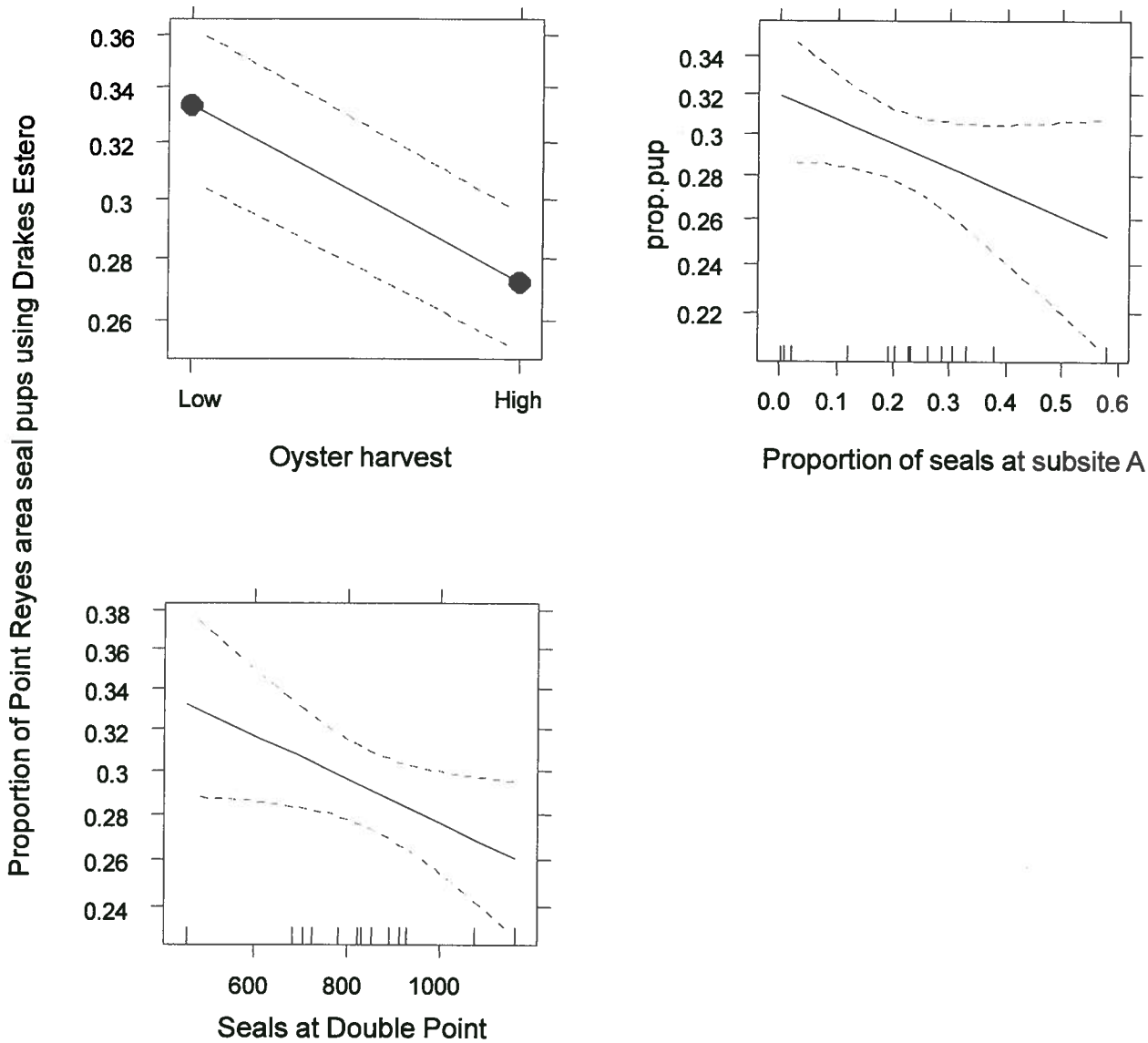

Figure ~~A7~~ 5. Model effects plots with standard errors for the proportion of Point Reyes area seal pups using Drakes Estero.

~~create~~

~~so figs.~~
Fig 5

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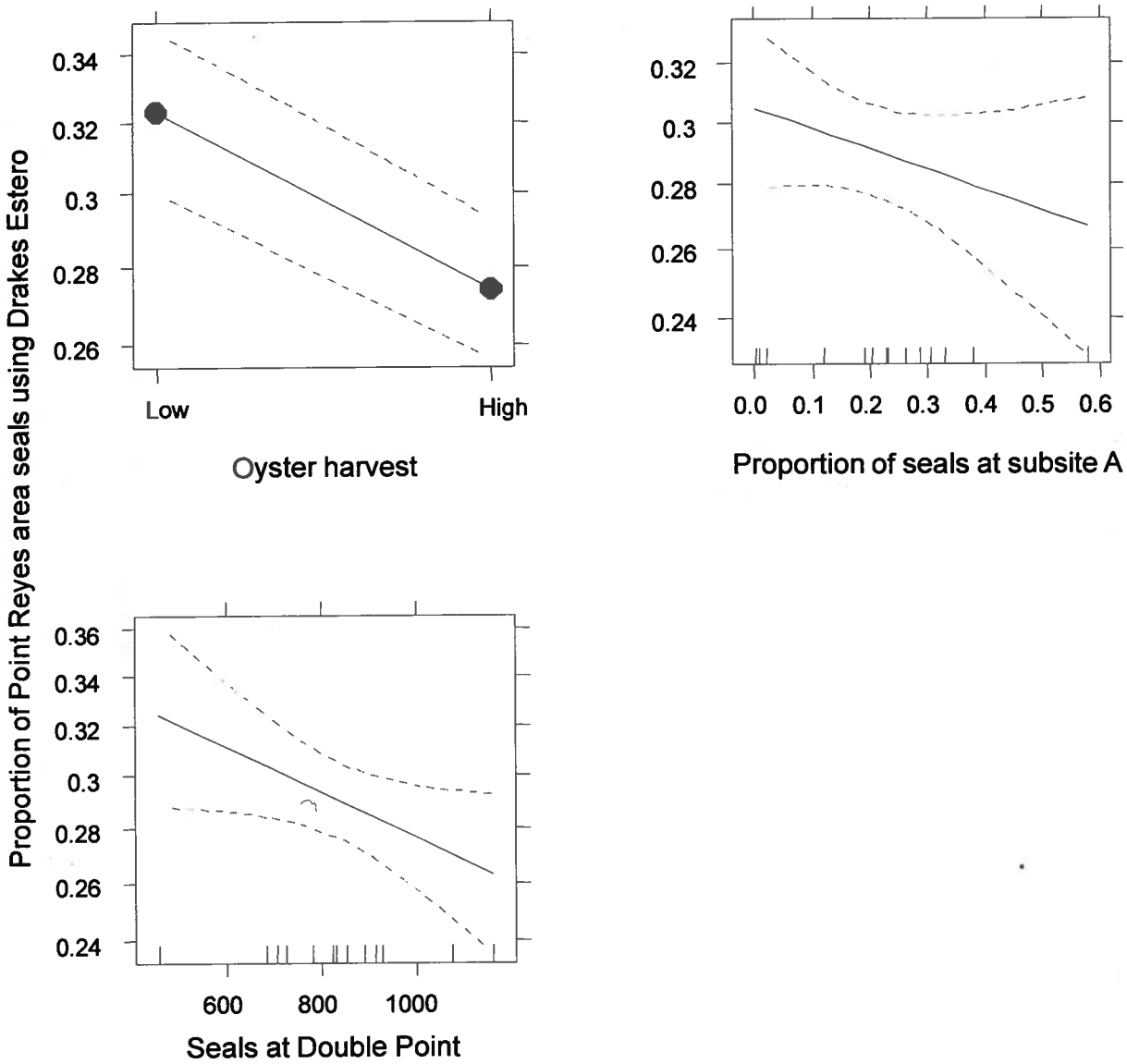

Figure ~~A8~~ 6. Model effects plots with standard errors for the proportion of Point Reyes area seals using Drakes Estero.

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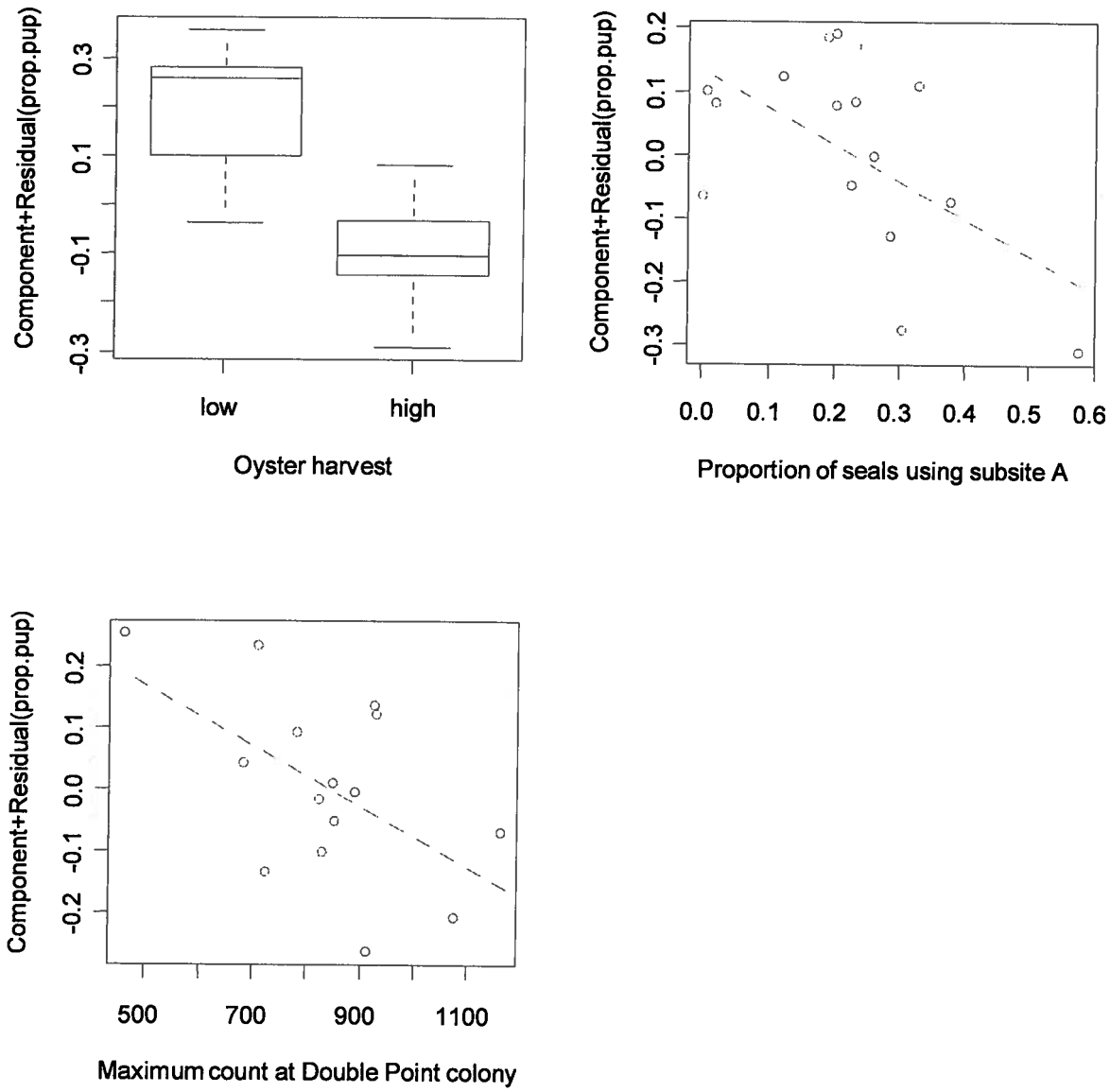

to supplement.

Figure 6. Component- residual plots for the best fitting model explaining the proportion of seal pups using Drakes Estero versus the rest of the Point Reyes area.

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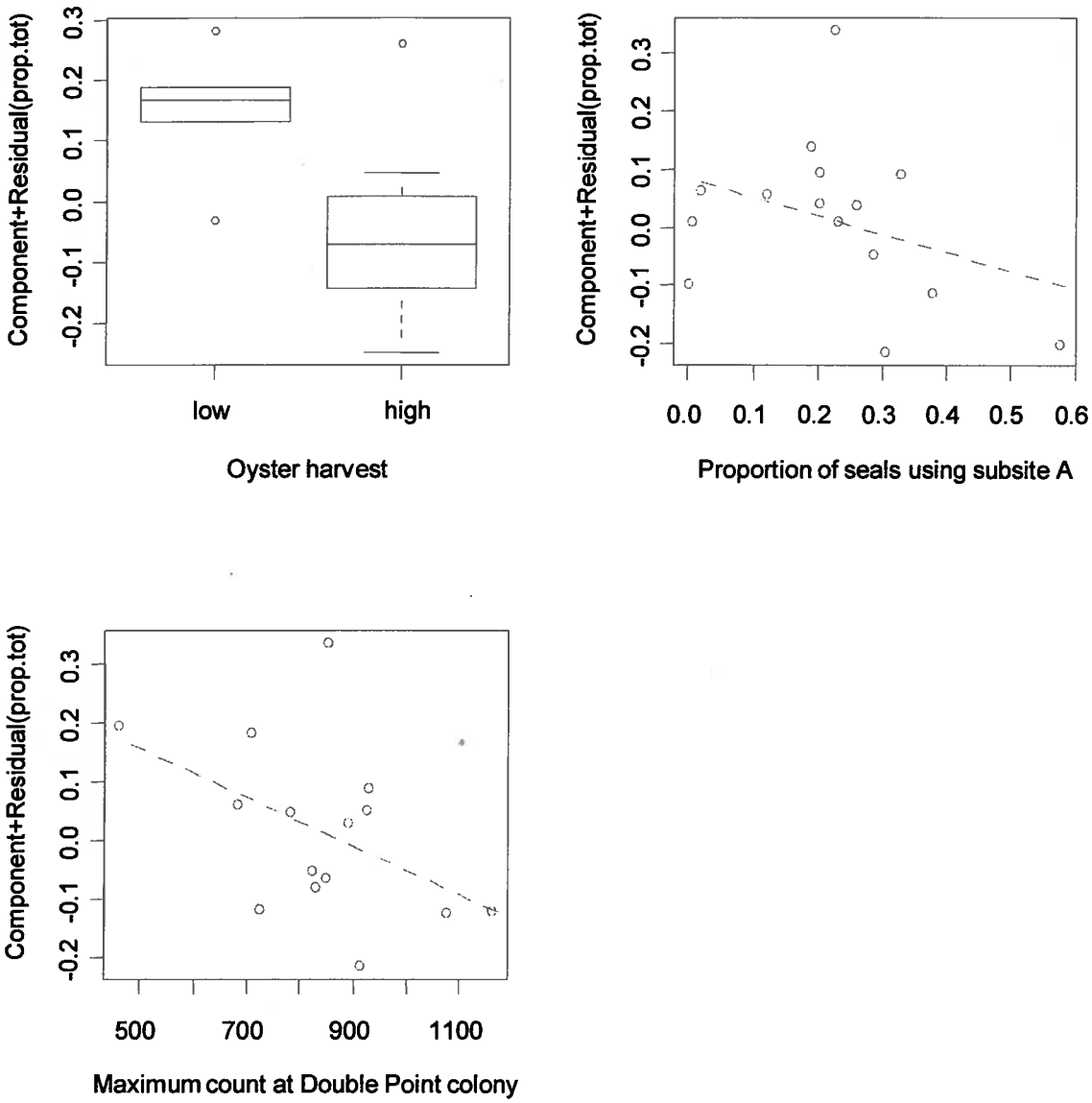

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~~Figure 7~~ Component- residual plots for the best fitting model explaining the proportion of total seals using Drakes Estero versus the rest of the Point Reyes area.

Supplementary Figures A1 – A9 follow

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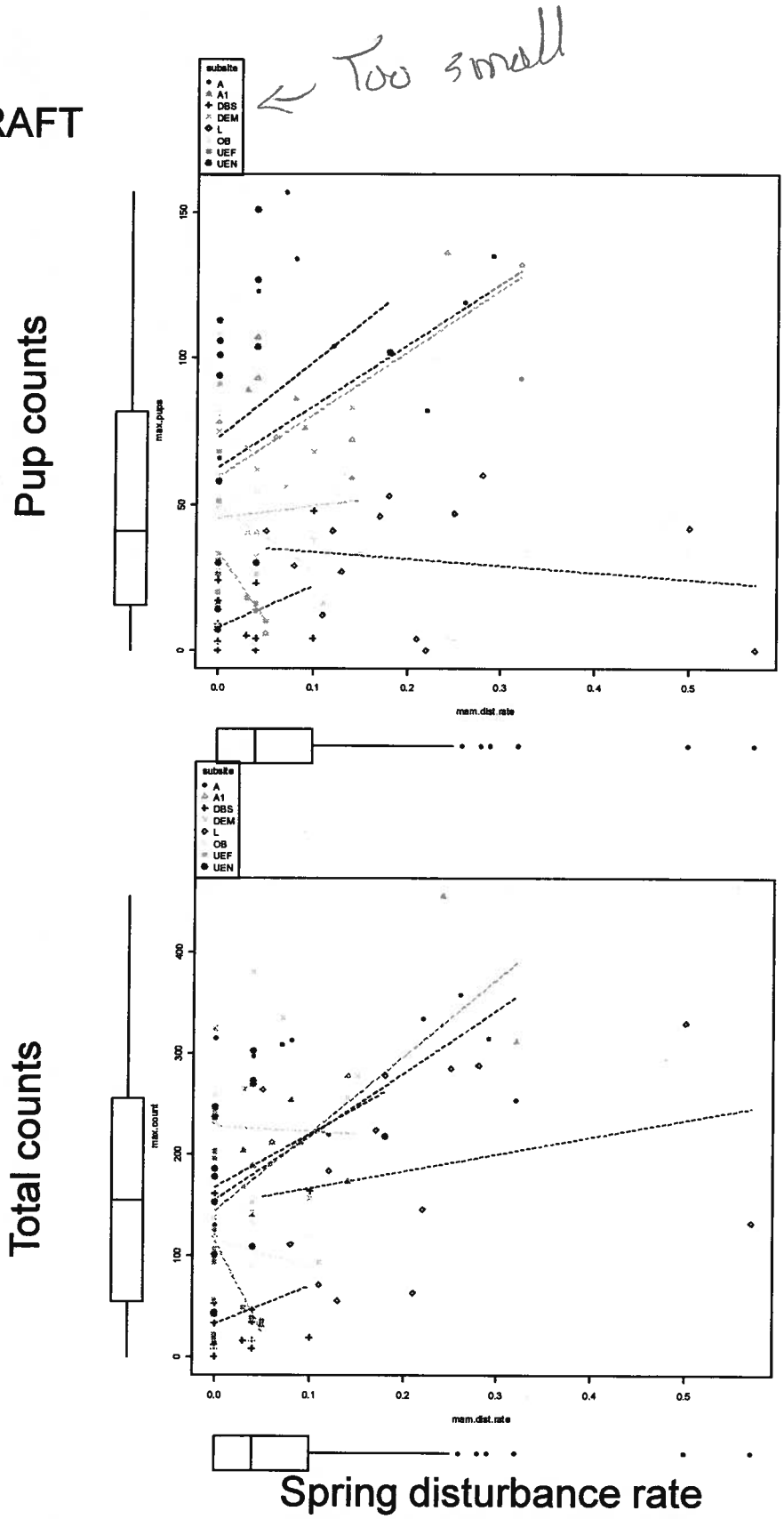

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Figure A1. There is no significant relationship between Spring anthropogenic disturbance rate and (A) pup counts at individual drakes estero subsites (P > 0.38) or (B) total counts at individual Drakes Estero subsites (P > 0.28) for 1997 – 2009. Regression lines and the model were grouped by subsite.

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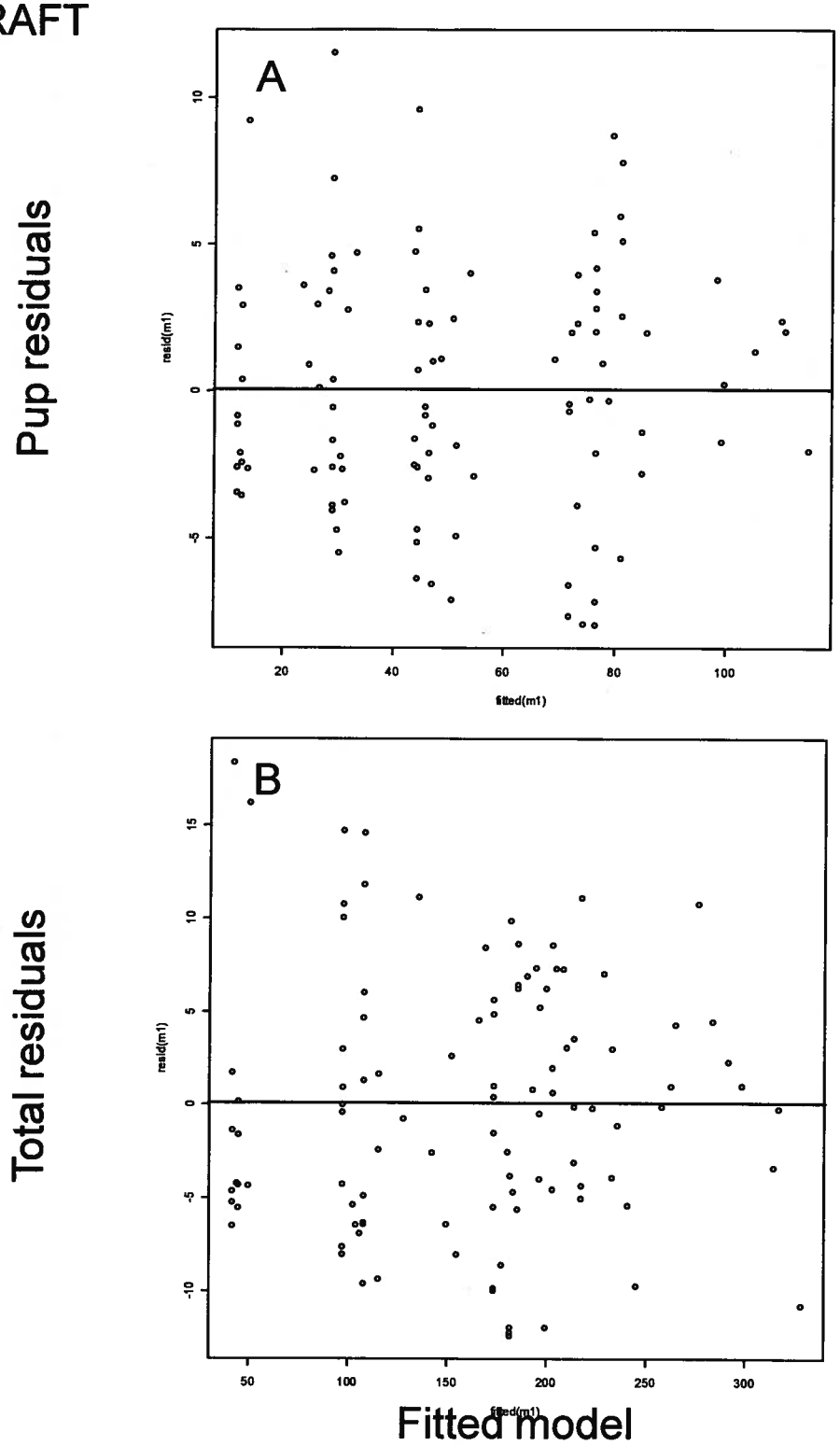

Figure A2. Residuals versus fitted values for poisson linear mixed effects models testing the relationship between between Spring anthropogenic disturbance rate and (A) pup counts at all drakes estero subsites and (B) total counts at all Drakes Estero subsites for 1997 – 2009.

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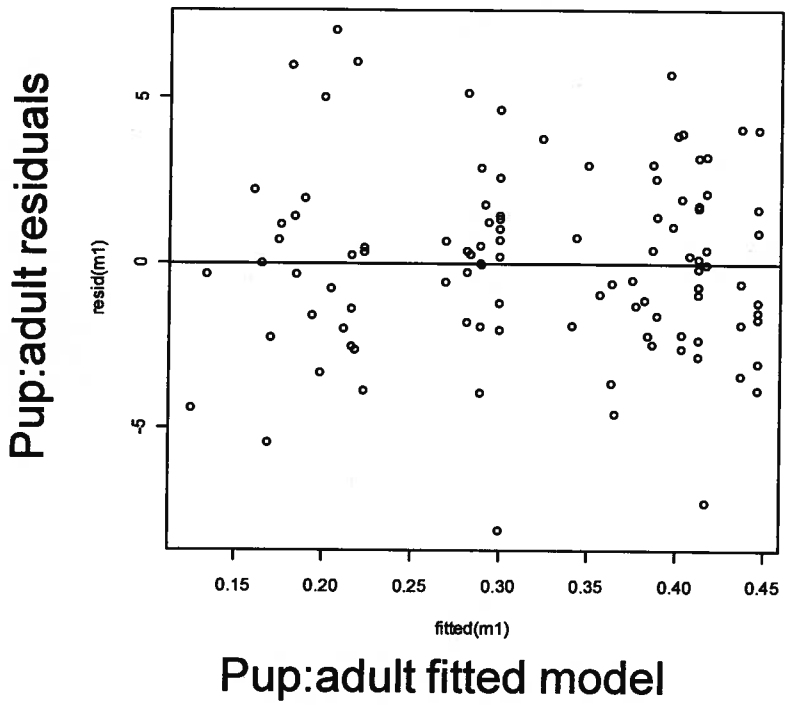

Figure A3. Residuals vs. fitted values for the model assessing the relationship between pup:adult ratios and anthropogenic disturbance rate.

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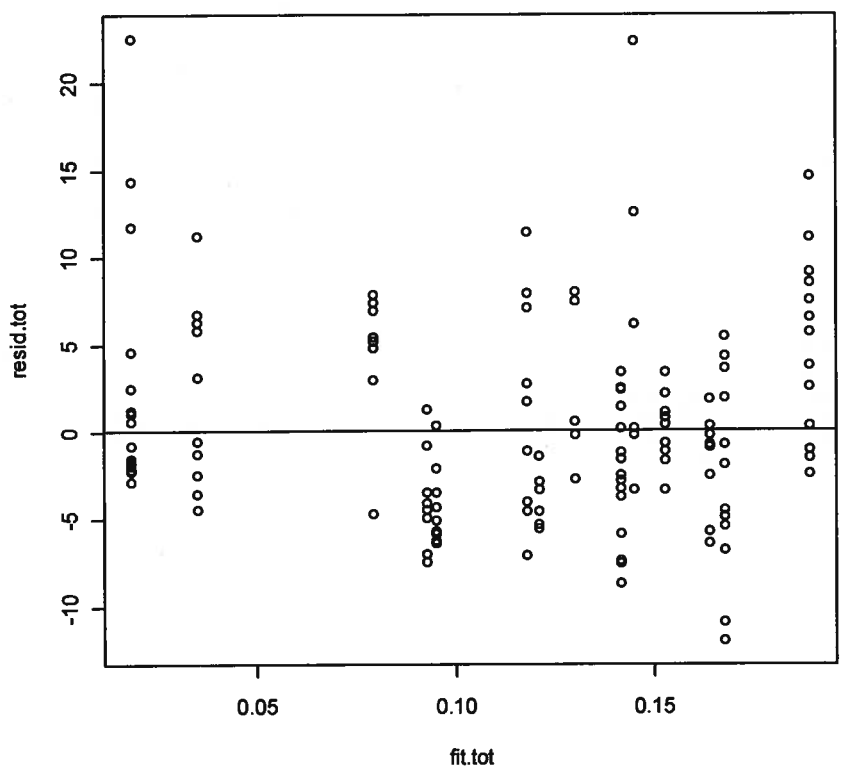

Don't need residual plots

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Figure A4. Residuals versus fitted values for the total seal count models for (A) the GEE subsite model (ENSO + high/low oyster harvest). Pup model residuals were similar.

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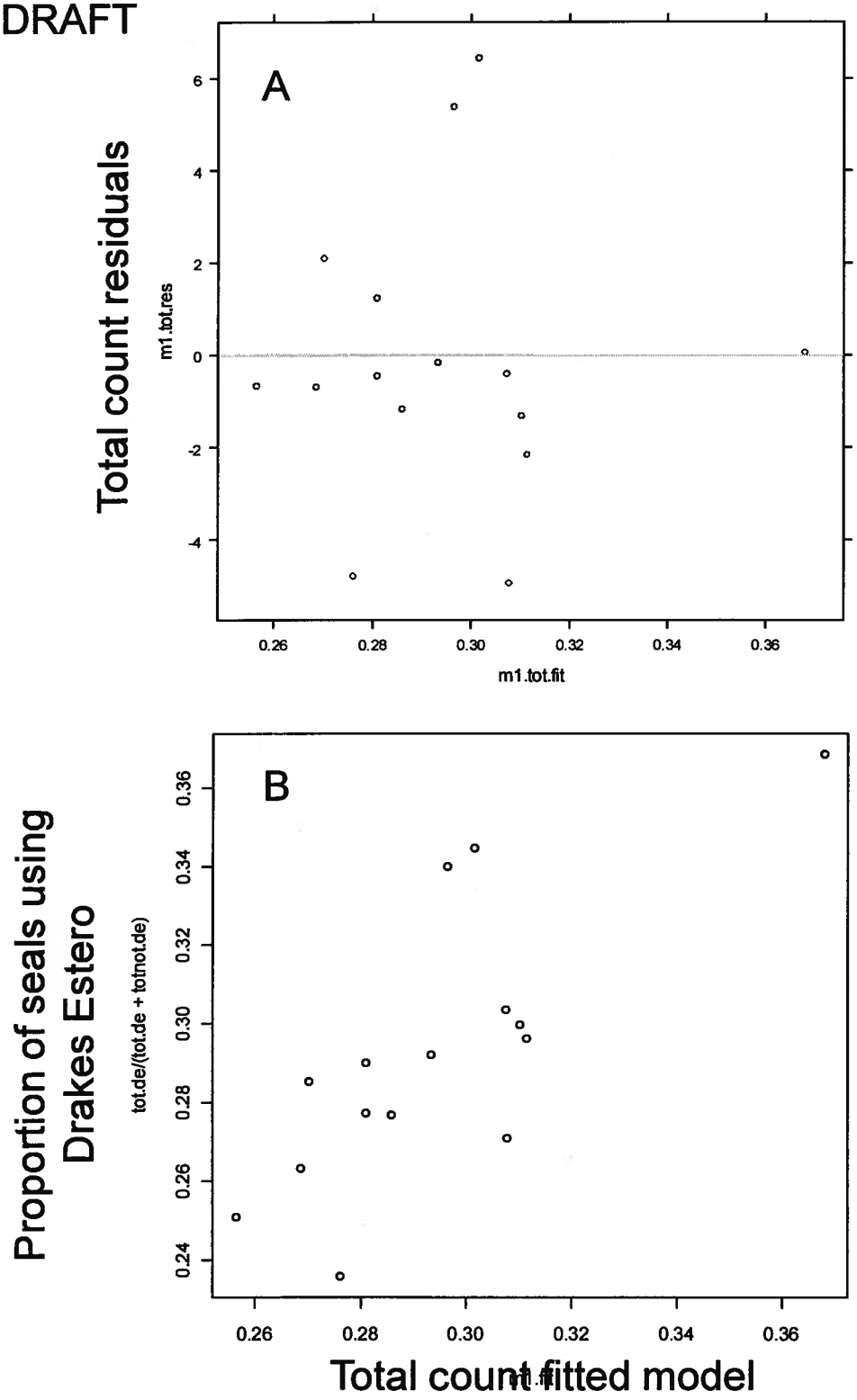

Figure A5. GLM model checking for Drakes Estero versus the rest of Point Reyes area colony models. (A) Residuals versus fitted values, and (B) proportion of seals in Drakes Estero versus fitted values. Model shown is #2 in Table 4 (Double Point + Subsite A + oyster high/low). Pup model residuals and fit are similar.

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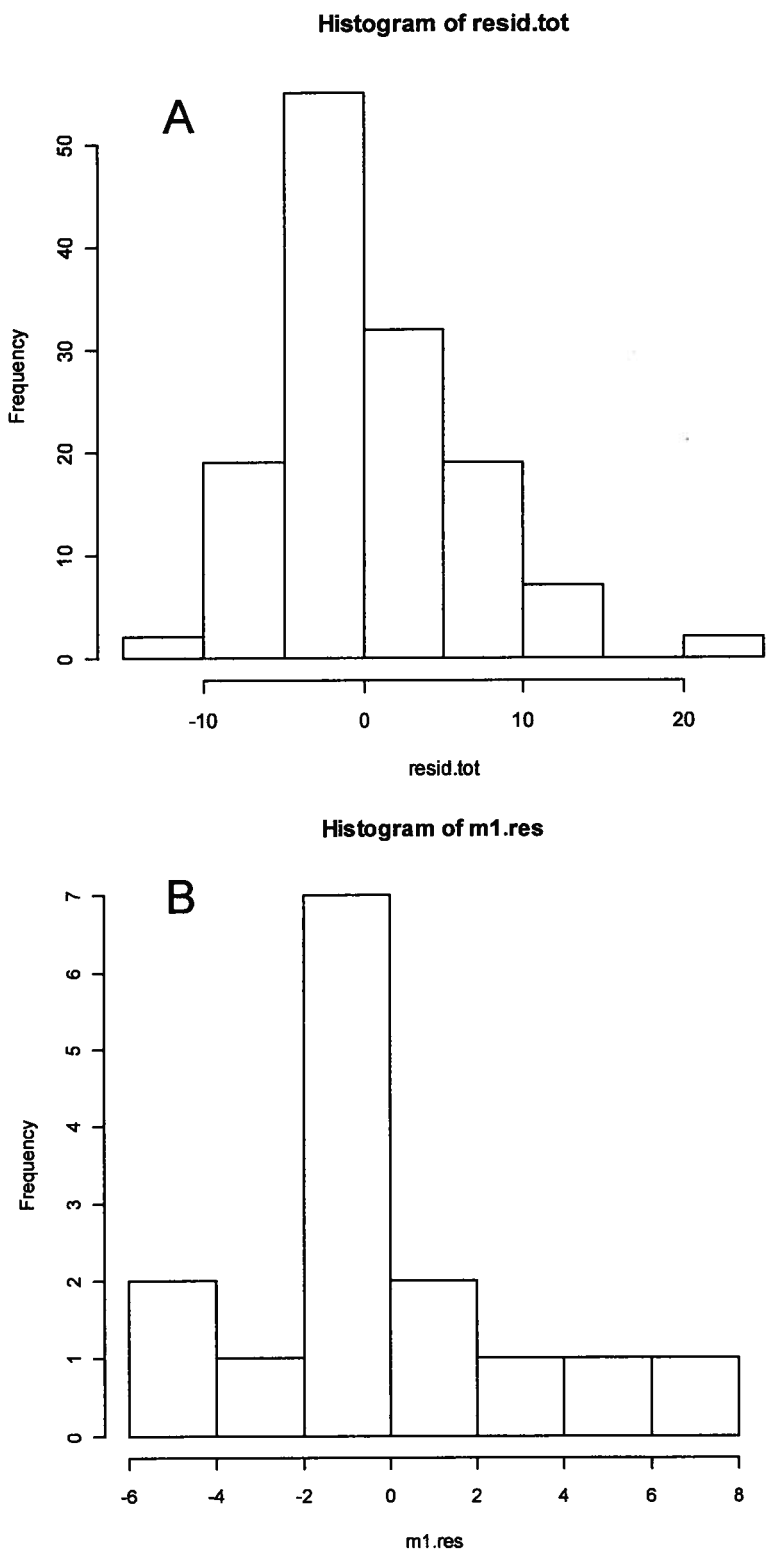

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Figure A6. Histogram of residuals for the GEE subsite model Enso + high/low oyster harvest, and the GLM of proportion of seals using Drakes Estero. Overdispersion in the second model was accounted for by using QAICc and a quasi-binomial model.

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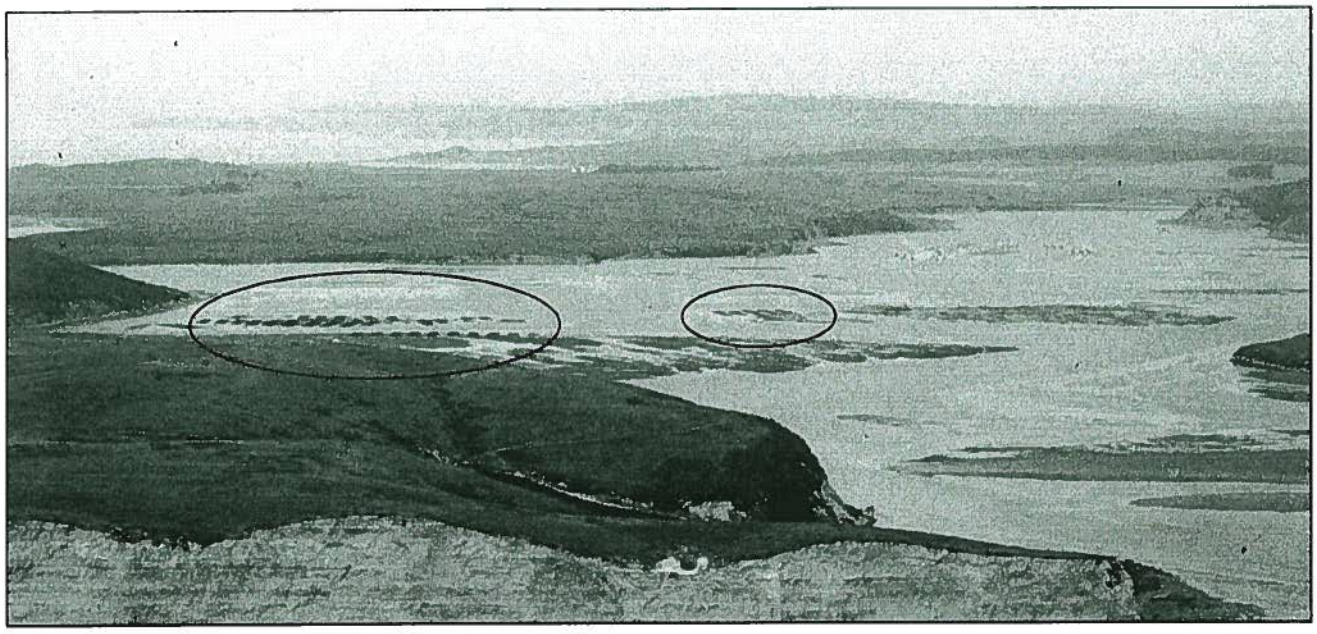

Figure A9. Image of Drakes Estero from June 1987 when annual oyster harvest was 634,869 lbs. Note oyster equipment on western ends of subsites UEN and OB. Image from www.californiacoastline.org.

Supplement.

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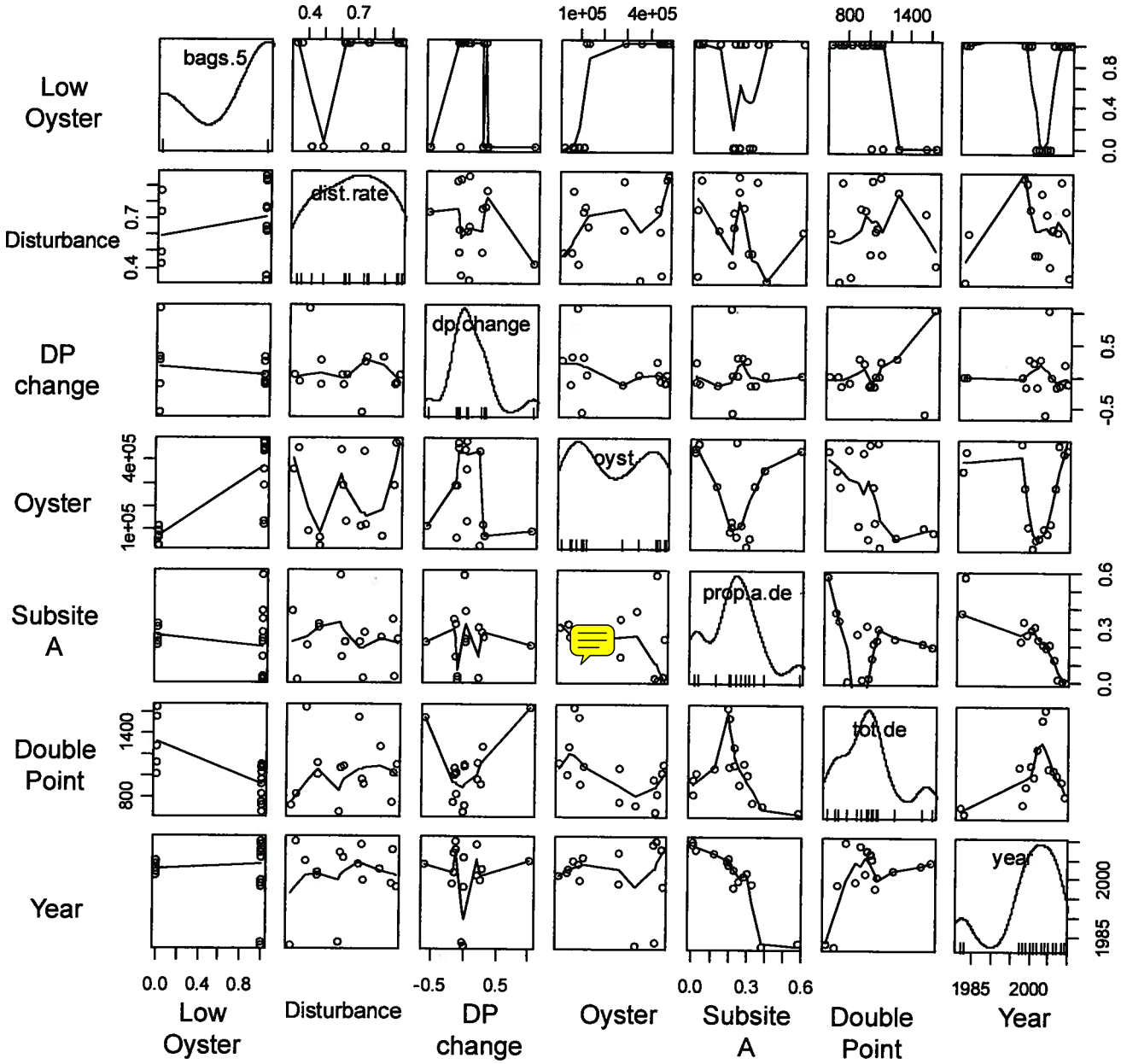
I would not include this figure

To supplement



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~~Figure~~ 5. Scatterplot matrix of variables used in the GLM for seal use of Drakes Estero versus the rest of Point Reyes. Only year and subsite A suggest collinearity and were therefore not used in the same model. Variance inflation factors from the GLMs confirmed that all variables were not collinear except year and subsite A, and the suite of oyster variables: oyster harvest, low oyster (2000-2004), and low oyster (1999-2004), which were not used in the same model. *(Figure to be redone)*

Statistical Review of "Intra- and inter-colony spatial use of Drakes Estero, California, by harbor seals related to anthropogenic disturbance, mariculture activity, and natural variation during 1982-2009," by Benjamin H. Becker, David T. Press, and Sarah G. Allen.

With BECKER RESPONSES INCLUDED 01/20/2010 in *ITALICS*

Reviewed by: (REDACTED) **REVIEWER #4**
Review date: January 14, 2010

REVIEWER SUMMARY: Overall, I thought this manuscript was very interesting and sought the answers to some very important questions regarding the impact of oyster harvest on harbor seals. The manuscript was well-organized, but I did occasionally have to remind myself which analysis was matched with which scale.

BHB response –We agree and have clarified with subheadings for the three scales in the predictions, data, methods, and results.

REVIEWER - The analytical approaches were generally appropriate for the questions asked, and most conclusions reached in the Discussion were appropriate extensions of the Results. I have a few suggestions that I think could improve the statistical analyses in this manuscript. General ideas are given below, and specific comments are included in the attached file.

Subsite scale
REVIEWER - The generalized linear mixed models (GLMM) were used appropriately to examine the effects of disturbance rate on annual maximum pup counts, annual maximum total counts, and annual pup:adult ratios at subsites within Drakes Estero. I recommend determining the best-fit random effects structure for each model (random subsite intercepts, random subsite coefficients, or both) using all fixed effects (disturbance rate, in this case) and fitting the alternative random effects using REML, then choosing the best-fit random effects structure to examine the fixed effects (this procedure is outlined in Zuur et al. (2009)). Despite the small number of models tested for each response variable, I recommend testing the model containing disturbance rate and the best-fit random effects structure to a null model with an intercept and the same random effects structure by fitting the models with ML and using an information criterion or likelihood ratio test to compare them, rather than reporting the p-value of the coefficient. I also recommend reporting the method used to fit the models (ML, REML, other?) and the link functions used.

BHB response –Reviewers recommendations followed and completed - We initially used a random intercept (rather than random intercept and slope) model because, theoretically, while different subsites may have different baseline (intercept) pup:adult ratios, we would expect that the responses (slopes) should be similar. However, the reviewer was correct that the random slopes and intercept model had a lower AIC. Testing using a random effects (NULL) model has AIC = 910.5, subsite with random intercept AIC = 889.3, random intercept and random slope AIC = 882.0. Thus, the final model is best, and likelihood ratio tests also show that last model is much better:

```
## R CODE
> anova(m0,m1,m2)
Data: dist
Models:
m0: pup.ratio ~ 1 + (1 | subsite) ##NULL MODEL
m1: pup.ratio ~ mam.dist.rate + (1 | subsite) ## RANDOM SLOPES
m2: pup.ratio ~ mam.dist.rate+(1+mam.dist.rate|subsite)##RANDOM SLOPE + INT
   Df     AIC     BIC  logLik   Chisq Chi Df Pr(>Chisq)
m0  2  910.46  915.75 -453.23
m1  4  889.26  899.83 -440.63 25.2066      2  3.361e-06 ***
m2  5  882.02  895.24 -436.01  9.2374      1   0.002371 **
```

the coefficients for the random slope and intercept model are:

```
> coef(m2)
$subsite
    (Intercept) mam.dist.rate
A    -0.3907213   -0.60311213
A1   -0.4205638   -1.01218131
DBS  -0.9499936    0.26795298
DEM  -1.3447029    0.69324815
L    -1.1464403   -2.05002167
OB   -0.3435008   -1.65775514
UEF  -0.8543876   -0.07331127
UEN  -0.2548924    0.14165578
```

Indicating that 5 sites show a negative relationship and three have a positive relationship. It also indicates clearly why the random slope and intercept model is best since both the intercepts and slopes are highly variable. Individual binomial regressions show non-significance for all of these subsites. We removed regression lines from the figs since there is no "significance" or low AIC model that indicates a relationship at individual subsites varying though time with varying levels of anthropogenic disturbance. However, the background level of disturbance (both from humans and predators) has already set the use higher at isolated subsites that have background lower disturbance levels. This will impact the discussion in that fluctuations in typical anthropogenic disturbance does not have a detectable impact on pup:adult ratios from year to year (and seal counts at subsites). We consider this "short-term" disturbance while the oyster harvest metric considered in colony and regional scales are considered a "longer-term" disturbance.

Colony Scale –

REVIEWER - Generalized estimating equations (GEE) appear to be a good fit for the analyses at the colony scale, and allow explicit modeling of within-season correlation of counts. The autoregressive correlation structure chosen is intuitive and well-justified. I understand why a binomial model was used for proportions, but I'm not sure that it entirely solves the problem of dealing with density dependence. If density dependence occurs because haul-out space is limiting, the proportion hauling out at each subsite might be a function of the area of sandbars available at each subsite (which likely would vary by year), causing them to be plagued by the same problems as counts (although the binomial model is typically formulated with a total count (in this case, total seal population each year), and might be more appropriate than the unbounded

counts assumed in a Poisson model). My concern is that the binomial parameter *p*, which controls the proportion of seals at each group of sites, might also depend upon the haul-out area available at those sites (instead of, or in addition to, ENSO, oyster harvest, or disturbance). Therefore, if some measure of haul-out area (controlled for tide, so that area of all sites is comparable) is available, it should be included as an explanatory variable in the binomial model. Alternatively, you could model the counts directly, but use haul-out area as an offset in a Poisson rate model (as described in Faraway (2006), and probably elsewhere). The choice of modeling framework depends primarily on whether you view the annual seal population as closed or potentially unbounded (i.e., drawing individuals from a much larger population than those actually hauled out).

BHB Response – There is little annual change in sandbar morphology, but there are long term changes and occasional abrupt changes (like sandbar A). The upper estero sandbars appear to be the most stable. So, while this information is not available, we would not expect it to be an important a factor. Also, while sandbar area could be limiting, it is probably not nearly as important as sandbar isolation (Nordstrom 2002). We have modified the text to address sandbar change and indicate that we explicitly model subsite A (in the regional analysis). Last, all survey data were from the low tide so it should not be necessary to model this as a covariate. Becker et al. 2009 showed that tide level alone was not important for counts since we only use the peak count during low tides. For this study and use of the binomial, we consider the annual seal population closed.

We also have added regional population size (density dependence) as a covariate in our models and discuss the implications. This should alleviate all of the reviewers concerns on this section.

Regional Scale -
REVIEWER - The generalized linear models (GLM) used to model the distribution of seals (pups and total) at the regional scale has some potential difficulties. The use of the quasi-binomial to account for overdispersion, elimination of collinear variables using variance inflation factors, and use of QAICc to compare models were all strengths of the analysis, but I'm not entirely convinced that the data meet the assumptions of the binomial model, even when accounting for overdispersion. If the seals are well-mixed among sites, such that transition probabilities among sites are approximately equal, then the quasi-binomial should perform well. However, if seals are philopatric to sites, or if transition probabilities are spatially structured such that transitions are more likely between neighboring sites than distant sites, then a mixture of probability parameters will exist for the binomial model. Pooling the sites will average over any spatial structure in the transition probabilities, but I'm not sure that it eliminates the problem.

BHB Response – We have previously had several statisticians recommend using the proportional binomial model. Also, because our focus in this analysis is Drakes Estero in relation to the rest of the regional colonies, a multinomial model is not appropriate to the question. Furthermore, as the reviewer points out, ***we pooled the regional sites which averages over spatial structure in the transition probabilities****, so the model should satisfy binomial assumptions since the response variable (seals) is either "in" or "out" of Drakes Estero. As long as the background (due to unmodeled covariates) probability of travelling between the pooled regional sites and Drakes Estero is constant over time, the binomial model should also be valid. We therefore retain the*

binomial model. If we learn of an improved modeling technique or distribution in the future, we will gladly apply it.

REVIEWER - I also think that Table 4 could be greatly simplified by reducing it to a single variable among the correlated variables. For example, you could greatly condense the table by including just one oyster-related variable (low oyster 2000-2004), one major nearby colony variable (Double Point counts), both internal colony effects variables, and the null. By using all the models, you are diluting your evidence among very similar models that use different forms of the same information. Be sure to state that you explored other forms of these variables, but selected the best predictor among correlated potential predictors.

BHB – Response - Regarding reduction/simplification of table 4, we now report a condensed table as suggested and leave this more comprehensive table as an appendix. We have also eliminated the covariate of annual percentage change in double point since it was correlated with double point counts (we did not use them in the same model anyway but merely included it to try to be thorough). We disagree that we watered down our covariates since we only assigned AIC weights to one type of oyster variable for MMI and the additional variables were included only to illustrate that other covariates were not important. However, the reviewer's suggestion is good and we have taken all of his/her advice while leaving the details in the supplementary table for anyone who wants to look into it further.

Intra- and inter-colony spatial use of Drakes Estero, California, by harbor seals related to anthropogenic disturbance, mariculture activity, and natural variation during 1982-2009

Benjamin H. Becker[1], David T. Press, and Sarah G. Allen

Point Reyes National Seashore

Point Reyes Station, CA 94956

Abstract

Spatial buffers in marine mammal breeding areas may provide some resilience for populations facing climate change, urbanization, and other anthropogenic and natural impacts. Longer lived, slowly reproducing species are selected to maximize their long-term survival and should therefore respond to anthropogenic disturbances by moving away or remaining vigilant rather than habituating. To better understand harbor seal vulnerability to anthropogenic disturbance and displacement effects in a National Park, we used data collected between 1982 – 2009 to explore potential mechanisms which may affect the proportion of Point Reyes (California) harbor seals (*Phoca vitulina*) selecting haul-out sites within a major colony (Drakes Estero – 21 years of data), and utilization of that colony in relation to other nearby colonies (15 years of data). There was no detectable relationship between human-related disturbance rate and the number of seals hauled out at specific sites within the estuary. However, pup:adult ratios did decrease with increasing anthropogenic disturbance, suggesting that mothers with pups avoided

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chronically disturbed areas. Within Drakes Estero, after removing effects of El Niño, the proportion of seals hauled out near mariculture activities was lower during years of higher oyster harvest (-61 ± 15 seals). At the regional scale, *a priori* binomial generalized linear models ranked by quasi-AICc indicated that oyster harvest (measured as either binary low/high or continuous harvest level), the counts at a nearby colony, and the gradual loss of a major haul out site in Drakes Estero, best explained pup and total seal use of Drakes Estero. Concurrent with higher oyster harvest, the proportion of Point Reyes area seals using Drakes Estero declined by -0.07 ± 0.02 for seal pups (-65 ± 18 total pups), and -0.05 ± 0.02 for total counts (-192 ± 58 total seals). When considering mass of harvested oysters as a continuous variable with a linear relationship to proportional seal use, there was an estuary-wide decline in seal use of -19 ± 6 pups and -71 ± 25 total seals for every 100,000 lb. increase in oyster harvest. We suggest mechanisms whereby the interplay between naturally fluctuating seal haul out availability may interact with anthropogenically limited habitat (i.e., mariculture activities) to reduce the proportion of Point Reyes area harbor seals (particularly pups) using Drakes Estero.

Key Words

Phoca vitulina, *mariculture, disturbance, harbor seal, resilience, generalized estimating equations.*

Introduction

A variety of factors may influence habitat availability for breeding and molting pinnipeds, including climate change (Freitasa et al. 2008), coastal development (Seuront and Prinzivalli. 2005), human encroachment and disturbance (Yochem et al. 1987, Suryan and Harvey 1999, Thompson et al. 2001), and natural variation in habitat characteristics. Moreover, since longer lived, slowly reproducing species are selected to maximize their long-term survival and therefore tend to respond to anthropogenic disturbances by increasing heart rates and energetic costs, we would expect seals to move away from, or remain vigilant to, disturbance sources rather than habituate as some smaller, quickly reproducing species do (Bisson *et al.* 2008). This might be particularly evident for females with pups which presumably should be more risk averse than adult males. Further, Frid and Dill (2002) found that long-term intense disturbance stimuli resulted in habitat shifts and subsequent reduced access to resources in all of the fourteen bird and mammal studies they reviewed. In marine mammals, bottlenose dolphin (*Tursiops* sp.) declined in relative abundance due to long-term disturbance, primarily from tour boat vessels (Bejder *et al.* 2006). Conversely, in the few disturbance studies where alternative habitat was not available (manatees: Buckingham *et al.* 1999, diving ducks: Knapton *et al.* 2000), the disturbed animals did not move.

Wursig and Gailey (2002) state that there is a "need to consider potential loss of feeding and breeding habitat from shellfish and finfish farms, particularly given predicted increases in these facilities in nearshore environments." Negative impacts of aquaculture have been found on ranging in bottlenose dolphins (Watson-Capps and Mann 2005). Similarly, the recent findings that oyster harvest activities may have "potential negative interactions" with harbor seal ~~use~~ (*Phoca vitulina*) at two sites near the mariculture

operations in Drakes Estero, California (NRC 2009, Becker et al. 2009) and that is ~~it~~ "likely that visits to these areas by oyster farm workers (within 500 m of seals) can be expected to lead to short term disturbance of any seals using these haul-out areas at the time" (NRC, P. 49), leads to several questions. First, are these potential negative interactions still detected with additional years of monitoring data? Second, are females and pups proportionately more affected by negative interactions? Lastly, could any effects on seal use cascade up from the sites near the oyster operations throughout the entire estuary's breeding and pupping season population relative to surrounding areas?

It is likely that proximate impacts of oyster harvest activities (or other disturbances) disturb seals and potentially cause them to move away from the subsites in Drakes Estero and elsewhere (NRC 2009, Becker et al., 2009, Allen and Huber 1984a, Montgomery et al. 2007). This would reduce available habitat for hauled out seals on either short or long time scales, depending on the length and frequency of the disturbance / displacement (Gill 2007). Affected seals might choose to haul out nearby, or leave the Estero for other areas. If the seals simply moved to other areas within the Estero, the proportion of the population using Drakes Estero compared to the rest of Point Reyes would not change. Conversely, if there were some competition for space or reduced use of other naturally or anthropogenically deteriorated haul-outs by females with pups, it could cause crowding on limited sand bar sites, and lead to a cascading population level effect causing some seals to not use the estuary (Gill 2007).

The National Research Council (NRC) reported that the National Park Service (NPS) pinniped monitoring program provides "as yet untapped potential for assessing trends in the abundance of harbor seals in Drakes Estero in relation to wider regional

trends" (NRC 2009, p. 84). Based on the NRC's suggestions, we expanded the Becker et al. (2009) analysis of seal use within Drakes Estero in response to mariculture by 1) adding four additional years of data (1982-1983 and 2008-2009), 2) improving the statistical methods, and 3) testing multiple factors that may be related to seal use (total seals and pups) at three spatial scales. The scales ranged from *subsite* level seal counts and pup:adult ratios (within Drakes Estero), to the *colony* level for distribution of seals within all of Drakes Estero, to the *regional* level comparing seal counts in Drakes Estero to the other surrounding colonies at the Point Reyes Peninsula (Fig. 1). This last regional effect would be somewhat surprising, since mariculture chiefly occurs in a limited area in the upper/middle sandbars of Drakes Estero. However, cascading spatial effects in ecology are possible (Elkin and Possingham 2008) and reduced seal use of individual subsites where breeding/pupping occurs could lead to overall reduced use of the estero, and increased migration to other less disturbed colonies. Furthermore, the upper/middle intertidal sandbars that are isolated from the mainland and have historically had more females and pups than the sandbars attached to the mainland near the mouth of the estero (Allen 1988).

We made several predictions that scaled from *subsite* to *colony* to *region*-wide scales (Fig. 1). At the subsite scale, we predicted that human-induced disturbance would not be related to a reduced number of seals using subsites in Drakes Estero, since more seals could also lead to more opportunity for disturbance. However, disturbance should reduce use of sandbars by females with pups, as measured by the pup:adult ratio. At the estero-wide scale, we predicted that increased mariculture activity (as measured by harvest level) would shift seal use away to other unaffected haul-outs. Lastly, at the

region-wide scale, we predicted that relative use of Drakes Estero compared to other seal colonies would be influenced by (1) within site dynamics (e.g., natural loss of a major pupping subsite), (2) nearby colony dynamics (disturbance at a nearby colony that could send more seals to Drakes Estero), and (3) mariculture activity would partially explain overall use of Drakes Estero in relation to other regional colonies. This could occur if seals were displaced locally by mariculture activity, but had reduced options for haul out areas due to factors 1 and 2. Because disturbance should increase with population size, we predicted that overall Drakes Estero disturbance rates would not be related to overall seal use. Finally, we tested for effects of El Niño – Southern Oscillation (ENSO) on seal use of Drakes Estero as a whole, but had no prediction that ENSO would affect other colonies differently than Drakes Estero.

Methods

Datasets

Survey methods are described in Becker et al. (2009). Disturbance rate was derived from number of human related disturbances that resulted in a head alert, a flush or a flush of seals into the water during March-May of each year, divided by the number of surveys conducted during that time period. Surveys were typically of similar duration throughout the study period (~2 hr), except for a few all-day surveys in 1982-83.

Two types of seal count data were used. When modeling *regional* level effects, we used the maximum counts of pups and adults from the maximum total count day of the breeding season. Values for Drakes Estero were compared with pooled maximum counts (of pups and adults) at the other six colonies in the region (Tomales Bay, Tomales

Point, Point Reyes Headlands (only one count per survey day), Double Point, Bolinas Lagoon, and Duxbury Reef) (Fig. 1). When assessing intra-*colony* variation in use, we used the daily counts at each subsite for all surveys during the peak breeding season (April 15 – May 15 of each year). For data from 1997 – 2009, QA/QC was identical to that used in Becker et al. (2009). We augmented the NPS database with additional subsite data from 1982 - 1983, 1986 - 1988, and 1991 - 1993 derived from field notes of SGA, and annual maximum breeding season pup and adult colony counts derived from the tables in Allen and Huber (1984a, 1984b). Oyster harvest data was obtained from the California Department of Fish and Game (1982 – 2006), the National Research Council (2007 – 2008), and was roughly estimated as 204,000 kg (450,000 lbs) for 2009[2], based on recent harvest values for 2007-2008.

<u>*Analyses*</u>

Haul-out site scale: Subsite counts and pup:adult ratios related to disturbance rate - Linear mixed-effect models (the "lmer" function in R) were used with subsite as a random effect to test if disturbance rate was related to annual maximum seal counts, maximum pup counts, and pup:adult ratios within subsites and across all subsites between 1997 - 2009. Upper/middle estero subsites (OB, UEN, UEF) were occasionally pooled in the 1982-1993 field note data, so we therefore did not use those two years for this within subsite analysis. However, this pooling did not affect data when pooling the total upper/middle estero versus lower estero seals when analyzed at the colony scale (next section). The counts were modeled as quasi-Poisson, and the ratio model as

[2] Actual harvest values are determined from tax records and the 2009 harvest should be available in mid-2010 (Pers. Comm., Tom Moore, Cal. Dept. of Fish & Game).

binomial. Models were checked to ensure randomly distributed residuals. Since there were only two covariates ("disturbance rate" and the grouping factor "subsite"), we did not use model selection techniques (i.e., AIC) and simply report p values and model coefficients.

Colony Scale: shifts in haul-out (subsite) use in Drakes Estero related to mariculture, ENSO, and disturbance rate - These models were designed to test if variation in the proportion of seals using the upper/middle (near mariculture) versus lower (away from mariculture) were related to ENSO events, oyster harvest level, or the spring (March – May) pooled disturbance rate (disturbances / # surveys) in either the upper/middle or lower estero (Fig. 1). We improved the analysis in Becker et al. (2009) in three significant ways. First, we used a form of Generalized Linear Models known as Generalized Estimating Equations (GEE) (Venables and Ripley 2002, Faraway 2006, Zuur et al. 2009) that explicitly model the temporal autocorrelation of multiple harbor seal counts taken during the breeding season within each year. GEEs are therefore a form of mixed-effects (or hierarchical) modeling (Gelman and Hill 2009). The GEEs also allow flexible distributions for the entire dataset and for the within year counts, neither of which were normally distributed. Second, the GEEs were run as binomial models comparing the three subsites near mariculture (OB, UEN, UEF) against the five subsites farther away from mariculture (A, A1, L, DEM, DBS). This removes the need for any density dependence effects since proportions are modeled rather than counts. Last, the aforementioned inclusion of spring (March – May) anthropogenic disturbance rates for the upper/middle and lower estero were included as covariates for 1982 - 1983 and 1997 -

2009. We also compared the proportion of seals at the two (of the three) sites closest to mariculture (OB and UEF) versus the rest of the estuary with a similar binomial GEE.

We modeled "years since ENSO" as *log(years since ENSO+1)* because both observational and theoretical evidence suggest that any ENSO effects should taper off and not be linear. GEEs were run in the software R 2.9.2 using the "geeglm" function in the "geepack" library with year as the grouping variable to account for within year autocorrelation of counts at the same subsite. The correlation structure was set as autoregressive since the counts were during the one month peak pupping period (April 15 – May 15) in each year and counts closer together should have higher correlation since seal counts generally rise, peak, and decline during this time.

Models were tested for combinations of ENSO, binary high/low oyster harvest, and anthropogenic disturbance rates in the near (upper/middle) and far (lower) from mariculture areas of the estero for effects on pup and total (adults + pups) counts. Nested models (e.g., ENSO + oyster vs. ENSO only) were tested for differences with the "anova" model comparison function in R. We then transformed the logit coefficients (Crawley 2007) to calculate the proportional change in seals using the three subsites near mariculture model, and multiplied the proportion by the mean seal count (pups and total) in the estuary during the time series to estimate a change in the number of seals using those subsites.

Regional Scale: Drakes Estero compared to surrounding colonies - We examined regional anthropogenic effects during the breeding season by comparing maximum seal counts (pups and total) in Drakes Estero, and all other Point Reyes colonies combined

(Tomales Bay, Tomales Point, Point Reyes Headlands, Double Point, Bolinas Lagoon, and Duxbury Reef) (Fig. 1). We examined several variables in relation to the proportion of seals (total seals and pups only) using Drakes Estero compared to the sum of those using the other six Point Reyes area colonies (Fig. 4A):

- Year, to search for a time trend.
- Annual oyster harvest. 2009 was estimated to be similar to 2007-2008, but could easily be higher or lower (Tom Moore, pers. comm.).
- Five-year and six-year periods of lowest oyster harvest (2000-2004 and 1999-2004) (Table 1).
- Proportion of Drakes Estero seals using subsite A, a major subsite in Drakes Estero that attached to the mainland ~ 2004.
- Maximum annual count and annual proportional change in seals at nearby Double Point colony.
- Annual spring (March-May) human related disturbance rate (disturbances/surveys) in Drakes Estero.
- Years since the last major ENSO (1982-83 and 1997-98).
- Null model.

As bulleted above, in addition to oyster harvest, we also explored an alternative measure of potential disturbance/displacement: the lowest 5 or 6 years (2000-2004 or 1999 - 2004) of oyster harvest (Fig. 4B). This binary value may be useful for two reasons. First, we do not have an official estimate for 2009 yet; the 2008 estimate departed from the actual harvest by 12%, indicating that some caution is needed when using estimates. Second, while the use of total annual oyster harvest in the estuary was

negatively correlated (when modeled with ENSO) with nearby seal haul out use (Becker et al. 2009, NRC 2009), total oyster harvest is surely not a perfect measure of activity near the seals. The number and distribution of mariculture equipment (bags) on sandbars near seals for extended time periods is another potential measure. Bags need to be tended, potentially causing disturbance, and the simple presence of the bags themselves may cause seal displacement. Thus, the oyster harvest metric might not be linear, and using a binary measure eliminates assumptions of a linear relationship. However, we did have to make a decision as to where the cut point was for high/low and we did this based on the inferences in Table 1 regarding increased presence of oyster equipment at sites near seal haul out sites.

Aerial images confirm that oyster bags were present in proximity to seal haul out sites in 2005 – 2009. Personal observations (DTP) during regular fieldwork indicate that there were few or no bags on the seal islands from 2002-2004. We infer from the oyster harvest records that there were few or no bags in 2000-2001 since the harvest was lower than 2002-2004, and that there likely were bags and infrastructure from 1997-1998. Unfortunately, 1999 is difficult to categorize based on the available data. Thus, we modeled the oyster harvest covariate for 1999 in two ways (as both a high and low oyster harvest year) (Table 1).

Modeling the pups and the total population was done separately because there is potential to have a greater disturbance/displacement effect on females with pups that 1) may be more sensitive to disturbance, or 2) seek out more isolated haul out sites (Allen 1988). We did not combine any covariates in a single model if the variance inflation factors (VIFs) were above 3 (Zuur et al. 2009). VIFs were calculated from models

without the complementary covariate. For example, the VIF for low/high oyster was calculated without "oyster", since these would never be used in the same model.

We used binomial generalized linear models (GLM) which modeled the probability that any random seal is found in Drakes Estero (success) versus somewhere else in Point Reyes (failure). We bound “Drakes Estero” and “non-Drakes Estero” seal maximum counts for each breeding season into a single matrix (pups or total) for use as the dependent variable in this model. Because of overdispersion (variance larger than expected for binomially distributed data), we used a quasi-binomial family to assess *P* values and overdispersion, and the binomial distribution to derive log-likelihoods to rank models using an overdispersion adjusted Akaike’s Information Criteria for small sample sizes (QAICc; Burnham and Anderson 2002). We also bootstrapped (refit the model with data from each year sampled at random with replacement) the best ranking models 2000 times to gain unbiased standard errors for the oyster harvest variable (Crawley 2007). Bootstrapping should also uncover any highly leveraged effects from one or two years of data. We report models and QAICc values for both the oyster harvest and the low/high oyster models, but only consider the 2000-2004 low/high variable when reporting Akaike weights and model averaging. Final model coefficients were calculated from the weighted (by Akaike weights) model coefficients of the best performing models (i.e., lowest 4 QAICc units). These weighted coefficients were then back transformed from binomial logits to proportions and multiplied by the mean number of pups or total seals in the Marin County seal population during the study period. All analyses were done in R 2.9.2 (R Development Core Team 2009).

Results

Subsite Scale: Seal counts, pup:adult ratios and disturbance rate – The upper/middle intertidal sandbars (OB, UEN, UEF) generally had higher pup:adult ratios than the sandbars attached to the mainland or near mouth of the estero (Fig. 2). Subsite A, while showing a high pup:adult ratio, has lost nearly all of its productivity since attaching to the mainland in 2004, but subsite A1 is still the one major subsite away from mariculture that maintains a high pup ratio and high overall pup production each year. Lower estero subsites DBS, DEM, and L tend to have either low pup:adult ratios *or* low absolute numbers of pups produced each year.

Neither subsite pup counts (P > 0.38) nor total seal subsite counts (P > 0.28) were related to spring anthropogenic disturbance rate in Drakes Estero. However, spring disturbance rate was negatively related to a pup:adult ratios at seal haul outs within Drakes Estero (n = 104, groups = 8, $P < 0.001$) (Fig. 3). Residuals for all models were normally distributed and within subsite variance was 0.17. The binomial coefficient for disturbance rate was -0.98 which when compared to the intercept (-0.71) suggests (when the binomial logits were back transformed) that the overall mean pup:adult ratio for 1997 – 2009 was 0.33 and that this value declines on average by 0.16 for every 100% increase in disturbance rate.

Colony Scale: Drakes Estero subsite Models - The more robust GEE modeling methodology using a binomial distribution and the extended time series adding four years of data gave similar results to Becker *et al.* 2009. Both ENSO and oyster harvest best explain seal use at sites closest to mariculture activity (Table 2). Adding the disturbance

rates for the upper/middle and/or lower estero did not improve model fit and the terms were non-significant for both pups and total seal proportions (P = 0.13 – 0.94) when omitting the 1986 – 1993 data, which did not have disturbance rates. The coefficients (although non-significant) suggested that more disturbances may actually occur in the lower estero when there were more seals present. Subsequently, disturbance rate covariates were removed from the final models and we included the full time series 1982 - 2009. ENSO and oyster harvest (high/low) were not correlated (P > 0.89). Residual plots versus model predictions showed no model fitting issues with the GEE model. Within year autocorrelation was moderate (0.45 - 0.60), indicating that GEEs are an appropriate tool for this dataset. A nested ANOVA indicated the Oyster + ENSO binomial model was a better fit over the ENSO only binomial model for both pups (X^2= 6.7, p < 0.005) and total seals (X^2 = 8.1, P < 0.02) ~~seals~~.

After accounting for the ENSO effect and not including the non-significant anthropogenic disturbance terms, the best models estimated 17 ± 4 fewer pups and 62 ± 15 fewer total seals in the three "near mariculture" subsites during the higher oyster harvest years (Table 2). Models for just the two sites closest to mariculture (OB and UEF), reported similar results. If an interaction between ENSO and oyster harvest is included, it is also highly significant (P < 0.002) and oyster harvest alone remains significant (P < 0.04), but we do not report interactions here.

Regional Scale: Drakes Estero compared to surrounding colonies - The proportion of pups and adult seals using Drakes Estero versus the other Point Reyes colonies varied throughout the study period, with a peak from 2003-2004. The pup and adult time series

were generally similar, with the exception of 1997, when relative pup presence in Drakes Estero was low, but adult use was high (Fig. 4A). Because 1997 was an outlier for the adult and/or pup proportion of seals in Drakes Estero, we weighted the total seal count model for 1997 by the ratio of the proportion of pups to adults in that year (~0.3) (Venables and Ripley 2002). We felt this was reasonable since there was an anomalous harbor seal die-off of adults that began during the breeding season in 1997 that did not appear to affect pups, and appears to have affected other colonies (specifically Double Point) more than Drakes Estero (D. Grieg and F. Gulland, The Marine Mammal Center, pers. comm. & unpubl. data), although the sampling from that study was not random.

Oyster harvest was alternately classified as low for both the 2000 – 2004 and 1999 – 2004 periods (Fig. 4B). Seal use of subsite A in Drakes Estero was high from 1997 – 2004, and dropped rapidly thereafter when the island connected to the mainland. Seal use of Double Point increased from 1997 – 2002, dropped rapidly in 2003 due to an aggressive elephant seal, and then rebounded in 2004 – 2005, followed by another smaller decline after 2005.

Spearman rank correlations indicated no issues with collinearity among the variables in the models tested (Table 3a). Variance inflation factors (VIF) also found no evidence of collinearity as long as year or ENSO were not modeled with subsite A (Table 3b). Quasi-binomial GLMs showed that models of the proportion of seals in Drakes Estero were moderately over-dispersed for the seal pup global model (4.5) and somewhat more over-dispersed for the total seal count global model (8.6). We used these values to calculate the QAICc for all the competing models. Binomial models almost always have

some degree of overdispersion with count data because there is no variance parameter in the model (Gelman and Hill 2009).

Among the models tested for pups, the two and three-way combinations of *low oyster* + *Double Point* + *subsite A* (always containing low oyster) models had an Akaike weight of 0.77~~)~~, and the r^2 for the top model had a good fit (r^2 = ~~0.46 – 0.63~~) (Table 4). Annual change at Double Point, disturbance rate, ENSO, and year were poor predictors of seal use of Drakes Estero. ENSO appeared once in model 6, but we did not include it in the model averages since the Akaike weight was only 0.09 and the weighted coefficient would have overlapped with a slope of zero. Similar patterns occurred for the total seal count models, with the exception which ENSO did not appear at all in the top models (Table 4). Low/high oyster harvest alone had an r^2 of 0.26 and 0.29 for pups and total counts, respectively and a significant ($P < 0.05$) quasi-binomial corrected P-value. Bootstrapped estimates of the oyster standard errors were smaller than those reported by model fitting alone, indicating robust and conservative estimates from the GLM (Table 5). After ~~removing~~ the effects of Double Point and subsite A, the best fit weighted coefficients suggest that there were 65 ± 18 fewer seal pups and 192 ± 58 fewer seals overall using Drakes Estero (Table 5, Figs. 5 & 6) during high oyster harvest years.

Discussion

Long-lived, slow reproducing species that invest their energetic resources in long-term survival rather than rapid reproduction tend to have pronounced physiological costs (increased heart rates and overall energetic costs) associated with human induced disturbance (Bisson *et al.* 2008, Ellenberg *et al.* 2006). Harbor seals have both a long lifespan (~20-25 years), and a single pup per year, suggesting that they are a candidate for

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realizing significant stress due to disturbance and might respond defensively (by moving) rather than quickly assimilating and continuing reproduction as is the case with short-lived, rapidly reproducing songbirds (Bisson *et al.* 2008). Our findings also support those of Frid and Dill (2002) whereby long-term disturbance stimuli (in this case mariculture activity) is related to a habitat shift and subsequent reduced access to subsites in the estero. Conversely, while the shorter term disturbance stimuli (park visitors) were related to reduced pup:adult ratios at subsites in the estero, they were not related to detectable patterns in intra-estero or intercolony proportional use by seals.

Our results indicate that during higher oyster harvest years Drakes Estero (1997 – 1999, 2005 – 2009), a smaller proportion of seals (pups and total) used the sandbars closer to mariculture when compared to the lower estero. We estimate that these proportions resulted in about 61 (14 pups) fewer seals in the upper/middle estero. Our previous analysis (Becker et al. 2009) found a similar reduction in seal use in the upper/middle estero related to mariculture and that conclusion was supported here when adding an additional 10 years of data and pooling haul-out sites near and far from mariculture. Somewhat surprisingly, we also found that oyster harvest explained a similar decline in the proportion of seals using Drakes Estero as a whole, even when considering other internal and external colony processes. Disturbance rates did not explain the distributional shifts at the subsite, colony or regional scales, but higher disturbance rates were related to reduced pup:adult ratios at subsites within Drakes Estero.

The results are an important improvement over the methods in Becker *et al.* (2009) because they 1) use mixed-modeling approaches to account for variability within and between years, 2) within year autoregression of counts, 3) a binomial distribution

framework that should eliminate confounding effects of variable overall population size, 4) a flexible distribution structure for the within and between year counts, 5) explicit model~~ing of the~~ overdispersion, and 6) include disturbance rate covariates for both the upper/middle and lower estero. While our results are correlational, we suggest that the increase and decrease in oyster harvest paired with *a priori* multiple competing mechanistic hypotheses represents a robust "natural" experiment which can be used to draw reasonable inferences since oyster harvest was a human induced rather than a natural covariate. Our results do not indicate that the seals are lost from the overall Point Reyes area population (although that is possible), but rather assume a closed population and a proportional shift in seal use both within the estero and between the estero and other Point Reyes area colonies. This closed population assumption is a drawback of using binomial models rather than count based models. However, the alternative of using only counts can lead to difficulties with how much proportional changes are due to overall population changes, rather than simple shifts in use.

Becker et al. (2009) found that oyster harvest and time since the last ENSO were correlated with total seal haul out use near the oyster bag areas. In the present analysis for the entire estero, we focused on low versus high oyster production, but also report nearly identical results when using the continuous linear covariate of oyster harvest. While this binary variable required some inferences (Table 1), it is also somewhat more conservative than the continuous covariate because it does not assume a linear relationship between oyster harvest and seal response. This binary model might be more appropriate if the mere presence of oyster equipment bags caused seal displacement, rather than the frequency of visits. Because of the use of various parts of the Estero by the

oyster growers, the oyster harvest value and activity near the seals need not be linear. Therefore, a simple high-low metric may be more valuable, and fits well in our analysis. We believe, therefore, that the low/high oyster covariate is a more informative covariate than harvest alone. An additional benefit of using the high / low oyster metric is that it eliminates the possibility of model errors if the actual 2009 oyster harvest is dramatically higher or lower than our estimate.

There are some inherent difficulties in the use of disturbance rates to infer effects on seals (Frid and Lawrence 2002, Hayward *et al.* 2005, NRC 2009). While the relationship to reduced pup:adult ratios appears clear, the confounded relationship with disturbance versus counts is expected, but nonetheless fails to help elucidate the ~~affects~~ effects of direct disturbances on counts. Similarly, Johnson and Acevedo-Gutiérrez (2007) found that disturbance rates of seals in Canada were related to frequency of powerboats nearby, but not the number of seals present. The NRC (2009) also noted that many disturbances related to mariculture likely go undetected, especially since many harbor seal surveys are on weekends and more visitors are out on weekends, while the oyster harvest work occurs primarily during weekdays. This should only underestimate the disturbances due to mariculture operations. Similarly, the NRC suggested that additional disturbances by boats during high tide might deter seals from using the upper/middle sandbars. While we do not have data on these phenomena, the NRCs conclusions would logically mean that disturbances in the upper/middle estero related to oyster activities are underestimated by the NPS monitoring program, while disturbances by other sources (park visitors) are less biased. Thus, unrecorded and undetected disturbances would be unlikely to greatly alter our conclusions.

Potential Scenario of Process – We found that the proportional reduction in seal use was larger for the upper/middle estero (-0.09 pups and -0.08 total) versus the estero as a whole (-0.07 pups and -0.05 total counts). However, these proportional values, when scaled up from the Drakes Estero population to the entire Point Reyes population, suggests more individual seals were displaced from the overall estero than those simply displaced from the upper/middle estero alone. It is possible that the combined effects of the loss of subsite A, impacts at Double Point, and increased oyster activity in the upper/middle estero (and other unknown factors) led to the pronounced reduction in counts for the entire estero. Specifically, as subsite A lost habitat during the study period, this could have *increased* the proportion of seals using the upper/middle estero, but then increased mariculture activity during 2005 – 2009 forced seals back away from the upper/middle estero, and without the resilience of subsite A, the overall proportion of seals using Drakes Estero declined. The interaction between subsite A, Double Point, and oyster harvest fits a model where ecosystem resilience is a function of both natural and anthropogenic influences. In a similar scenario, Kent and Crabtree (2008) found that an Australian sea lion (*Neophoca cinerea*) reserve was ineffective because it did not provide suitable habitat. They concluded that "because environmental conditions are variable over time, a fixed sanctuary zone will only aid in reducing impacts when conditions are suitable in that zone." Similarly, Stevens and Boness (2003) reported an ENSO related decline and recovery pattern in southern fur seals (*Arctocephalus australis*) in Peru. After the 1997-98 ENSO induced a decline in fur seals, the seals returning in 1999 avoided haul-out sites with higher human disturbance. In Drakes Estero, suitable conditions for

females with pups may now be more limiting due to variable environmental conditions such the loss of subsite A, mariculture impacts in the upper/middle estero sites, and the generally poor suitability of lower estero sites such as L, DBS, and DEM. The estero contains a dynamic system of sandbars and there will surely be additional changes in the future that both create and remove desirable seal habitat.

It is possible that subsite (or colony) recolonization takes years, while abandonment due to displacement / disturbance is rapid. The decline at subsites OB, UEF and UEN in the upper/middle Drakes Estero follows this pattern, whereby after oyster harvest declined around 1999-2000, it took a few years (until 2002) for the proportion of Drakes Estero seals using the area to greatly increase, and then the counts (and proportion of seals using the subsites) rapidly declined again with increased mariculture in 2005. The *a priori* modeling suggested that an ENSO effect may have explained some of the delayed recolonization in the middle/upper estero, but perhaps simple time delayed movement into the area is also partially responsible. Such a model would then have a lag effect for recolonization as oyster harvest declined, but no lag as it increased, similar to seal response to coyotes at subsite A.

Additionally, there are two local examples of rapid seal abandonment and slow recovery related to anthropogenic impacts. Drakes Estero had a rapid decline in pup counts during increasing kayak use in the early to mid-1990s, and then a slow rebound after kayaking and other human powered vessels were prohibited during the pupping season (SGA, pers. obs.). Similarly, Hog Island in Tomales Bay (Fig. 1) was abandoned by harbor seals in the mid-1990s coincident with increasing numbers of kayakers landing on the east side of the island. Prohibition of kayak landing coincided with a gradual

resumption of use by seals. The seal counts had remained low (< 20) for several years until recently when the island had over 100 seals in the fall of 2009 (SGA, pers. obs.). These examples are anecdotal, but do fit the proposed rapid loss / slow recovery pattern seen in upper/middle Drakes Estero.

Additional processes occurring at other colonies in the San Franscisco Bay Area could also affect the patterns we observed. This might include excessive disturbance, as well as immigration or emigration from the entire study area. However, the fact that our modeled covariates (oyster harvest, double point, and subsite A) explain much of the intra- and inter-colony patterns observed, suggests that these are not likely to be spurious correlations.

Conclusion - Our results highlight the importance of building and preserving resilience in natural systems. Gill (2007) concluded that (in birds), "declines in survival or fecundity will result from density-dependence and not directly through disturbance. Efforts to manage disturbance in order to maintain populations must therefore be based on an understanding of the density-dependent consequences of avoidance of disturbed areas." We have demonstrated natural and anthropogenically (mariculture) driven colony dynamics both within Drakes Estero and between Drakes Estero and other colonies in the Point Reyes area. Human encroachment on sandbars may not have a detectable effect on harbor seals until natural fluctuations occur which further limit habitat, and cause additional competition for limited space resources. At a scale even larger than the Point Reyes area, seals transit between San Francisco Bay and the Point Reyes Area (Kopec and Harvey 1995, Grigg et al. 2009), thus anthropogenic impacts on the Marin Coast may indirectly affect the mobility of seals displaced at other colonies in San Francisco Bay or

elsewhere. This may be particularly true for Drakes Estero which supports one of the largest breeding colonies in the state and the largest in Marin County (Lowry et al. 2005).

This analysis is a first step towards addressing the NRC's recommendation that the NPS pinniped monitoring program be used to test for colony-wide response to natural and anthropogenic factors. Specifically, the NRC suggested that patterns in Drakes Estero be compared to region-wide patterns. Our results show a logical series of steps from disturbance being related to lower pup:adult ratios at the subsite scale, to mariculture being related to an intra-estuarine spatial shift in seal use of subsites, and finally an apparent cascading effect of mariculture and natural disturbance events to lower overall regional population use of Drakes Estero in relation to other local colonies.

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Table 1. Sources and inferences for level of oyster harvest activity on or near OB, UEF, and/or UEN.

Year	Oyster harvest (lbs)	Inferred level of mariculture use of sandbars near seals	Source
1982	360,004	Higher	inferred from harvest data, 1987 image
1983	440,139	Higher	inferred from harvest data, 1987 image
1997	476,791	Higher	inferred from harvest data and disturbance data
1998	292,188	Higher	inferred from harvest data
1999	125,749	Modeled high & low	slightly higher than 2000-2004, declining phase
2000	34,094	Lower	inferred from harvest data lower than 2002-2004
2001	65,676	Lower	inferred from harvest data lower than 2002-2004
2002	78,064	Lower	DTP, pers. obs, harvest data
2003	118,643	Lower	DTP, pers. obs, harvest data
2004	96,754	Lower	DTP, pers. obs, harvest data
2005	138,958	Higher	aerial image of bags, increasing activity
2006	291,538	Higher	increasing harvest, bags in '05
2007	468,000	Higher	aerial image of bags
2008	438,000	Higher	aerial image of bags
2009	450,000*	Higher	aerial image of bags

*Estimate based on 2007-2008. Official data likely available in mid-2010.

Table 2a. Coefficients, proportional change, and effect size from binomial generalized estimating equation (GEE) for proportion of Drakes Estero Seals using the upper (OB, EUF + EUN) vs. lower estero. Effect size is proportion * mean Drakes Estero population size for time series and can be interpreted as the change from the long-term average number of seals. The mean of the maximum seal counts for 1982 - 2009 was 751 total and 180 for pups. Annual disturbance rates in the upper and lower estero did not explain seal redistribution.

	Pups				Total seals			
Model	**Coefficient**	**Proportion**	**Effect size**	**P**	**Coefficient**	**Proportion**	**Effect size**	**P**
Intercept	-1.39 ± 0.34			< 0.001	-1.50 ± 0.26			< 0.001
log(ENSO + 1)	0.65 ± 0.20			< 0.001	0.55 ± 0.15			< 0.001
Oyster high/low	-0.41 ± 0.19	-0.08 ± 0.02	-14 ± 4	< 0.03	-0.46 ± 0.15	-0.08 ± 0.02	-61 ± 15	< 0.003

Table 2b. Binomial generalized estimating equation (GEE) for the proportion of Drakes Estero seals using subsites OB + EUF vs. the rest of the estero.

	Pups				Total seals			
Model	**Coefficient**	**Proportion**	**Effect size**	**P**	**Coefficient**	**Proportion**	**Effect size**	**P**
Intercept	-3.27 ± 0.50			< 0.001	-3.18 ± 0.35			< 0.001
log(ENSO + 1)	1.02 ± 0.28			< 0.001	0.88 ± 0.20			< 0.001
Oyster high/low	-0.75 ± 0.24	-0.06 ± 0.02	-11 ± 4	< 0.003	-0.68 ± 0.23	-0.05 ± 0.02	-38 ± 15	< 0.004

Table 3a. Spearman rank correlations between independent variables. We only used two variables in the same model if their r_s was < 0.51 and not significant. Significant (P < 0.05) correlations are in bold. N = 15. If adjusted for multiple comparisons using Holm's method, only the three oyster vaues are correlated and the Double Point counts with Double Point change.

	Low oyster harvest 2000-2004	Low oyster harvest 1999-2004	Spring Disturbance rate	Annual change at Double Point	Proportion of seals at subsite A	Maximum counts at Double Point
Low oyster 1999-2004	**0.87**					
disturbance rate	0.23	0.13				
Change at Double Point	-0.20	-0.35	-0.09			
Prop. seals at subsite A	-0.11	-0.17	-0.10	0.00		
Counts at Double Point	0.46*	0.50**	-0.21	**0.78**	0.29	
Year	0.00	0.09	-0.02	-0.08	**-0.92**	-0.24

Table 3b. Variance inflation factors from full models.
VIFs of less than 3 represent no collinearity (Zuur et al. 2009)

	Variance inflation factor	
Covariate	**Pups**	**Total**
Oyster harvest	1.39	1.27
Low oyster 2000-2004	1.17	1.12
Prop. seals at subsite A	1.23	1.05
Counts at Double Point	1.21	1.21
Change at Double Point	1.10	1.13
El Nino	1.09	1.06
Disturbance rate	1.13	1.14

Table 4. *A priori* models ranked by QAICc for the proportion of Point Reyes seal pups using Drakes Estero. An "x" indicates the coefficient was selected in the model. Δi indicates QAICc distance from the best model and wi indicates model weight. "Low oyster 1999-2004" and "Oyster harvest" are only included for reference and not included in Akaike weights. Models ranking within the lowest 4 QAICc units are shaded grey and used for multimodel inference in table 5.

		Oyster related			Major nearby colony		Internal colony effects							
Age class	**Model**	**Low oyster 2000-2004**	**Low oyster 1999-2004**	**Oyster harvest**	**Double Point counts**	**Double Point annual change**	**Drakes Estero disturbance rate**	**Seals at A in Drakes Estero**	**ENSO**	**Year**	**Null**	**Δi**	**wi**	r^2
Pup	1	x			x							0.0	0.35	0.51
	2			x	x			x				1.3		0.63
	3	x			x			x				1.3	0.18	0.63
	4	x						x				1.4	0.18	0.46
	5			x	x							1.5		0.46
	6	x							x			2.6	0.09	0.42
	7		x		x							3.3	.	0.40
	8	x										3.3	0.07	0.26
	9			x				x				3.4	.	0.40
	10		x					x				4.2	.	0.36
	11									x		5.0	0.03	0.20
	12	x					x					5.6	0.02	0.32
	13		x									6.3	.	0.16
	14	x			x		x	x				6.3	0.02	0.66
	15				x					x		6.4	0.01	0.29
	16			x								6.5	.	0.15
	17	x				x						7.1	0.01	0.26
	18				x							7.3	0.01	0.12
	19										x	7.7	0.01	0.00
	20								x			7.7	0.01	0.11
	21							x				8.2	0.01	0.09
	22				x				x			9.1	0.00	0.19
	23			x			x					9.2	.	0.19
	24				x			x				9.8	0.00	0.17
	25						x					10.6	0.00	0.01
	26					x						10.8	0.00	0.00
	27				x		x					11.0	0.00	0.13
	28					x		x				11.9	0.00	0.10
	29						x	x				11.9	0.00	0.09
	30					x	x					14.2	0.00	0.02
Pup + Adult	1	x			x							0.0	0.55	0.54
	2	x			x			x				2.4	0.16	0.61
	3			x	x							2.5	.	0.47
	4		x		x							2.5	.	0.47
	5			x	x			x				3.8	0.08	0.57
	6	x						x				3.9	0.08	0.42
	7	x										4.3	0.06	0.29
	8	x					x					4.5	0.05	0.41
	9		x					x				6.0	.	0.36
	10	x			x		x	x				6.1	0.02	0.67
	11	x							x			6.3	0.02	0.35
	12		x									6.8	.	0.22
	13			x				x				7.5	.	0.32
	14	x				x						8.1	0.01	0.30
	15									x		8.5	0.01	0.17
	16			x								8.8	.	0.16
	17				x					x		9.6	0.00	0.25
	18			x			x					9.6	.	0.24
	19				x							10.4	0.00	0.11
	20										x	10.9	0.00	0.00
	21							x				11.7	0.00	0.07
	22						x					12.4	0.00	0.05
	23								x			12.6	0.00	0.05
	24				x			x				13.0	0.00	0.15
	25				x		x					13.2	0.00	0.14
	26				x				x			13.4	0.00	0.14
	27					x						13.9	0.00	0.01
	28						x	x				14.4	0.00	0.11
	29					x		x				15.3	0.00	0.08
	30					x				x		15.5	0.00	0.07

Table 5. Multimodel weighted coefficients of all models within 4 QAICc of the best model or pups and total harbor seals in Drakes Estero (see table 4). Models represent an Akaike weight (wi) of 0.87 for both pups and total. Number in parentheses after the "low oyster" coefficients represent the bootstrapped standard error estimate of 2000 replicates. Effect sizes based on mean seal counts of all Point Reyes area colonies during the study period.

	Logit Coefficients		Proportional change		Effect Sizes	
Variable	**Pups**	**Total**	**Pups**	**Total**	**Pups**	**Total**
Intercept	-0.26 ± 0.19	-0.37 ± 0.16				
Low oyster (low/high)	-0.27 ± 0.08 (0.05)	-0.23 ± 0.07 (0.03)	-0.07 ± 0.02	-0.05 ± 0.02	-65 ± 18	-192 ± 58
Double Point (per 100 seals)	-0.04 ± 0.02	-0.04 ± 0.02	-0.010 ± 0.005	-0.010 ± 0.005	-10 ± 5	-36 ± 18
Subsite A (low to high)	-0.43 ± 0.22	-0.11 ± 0.07	-0.09 ± 0.05	-0.03 ± 0.02	-91 ± 51	-106 ± 71
Oyster (per 100,000 lbs)*	-0.06 ± 0.02	-0.08 ± 0.03	-0.019 ± 0.006	-0.020 ± 0.007	-19 ± 6	-71 ± 25

*not multimodel: from Oyster + Double Point count model.

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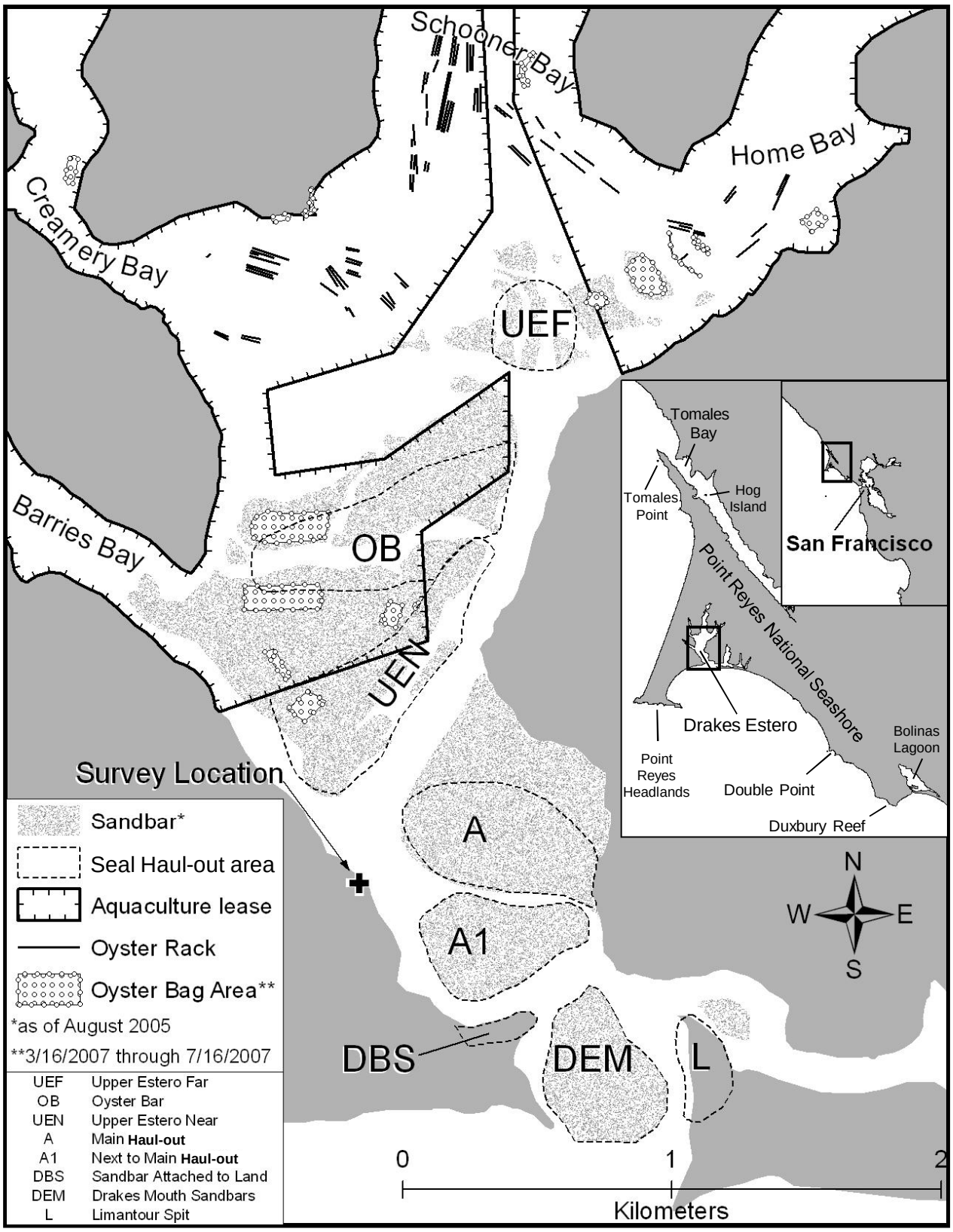

Figure 1. Drakes Estero and the eight labeled seal haul out subsites. Subsites UEF, OB, and UEN are considered "near" mariculture, while A, A1, DBS, DEM, and L are considered "away" from mariculture. Inset shows all the Point Reyes area colonies: Tomales Bay, Tomales Point, Point Reyes Headlands, Drakes Estero, Double Point, Duxbury Reef, and Bolinas Lagoon. Figure modified from Becker et al. (2009).

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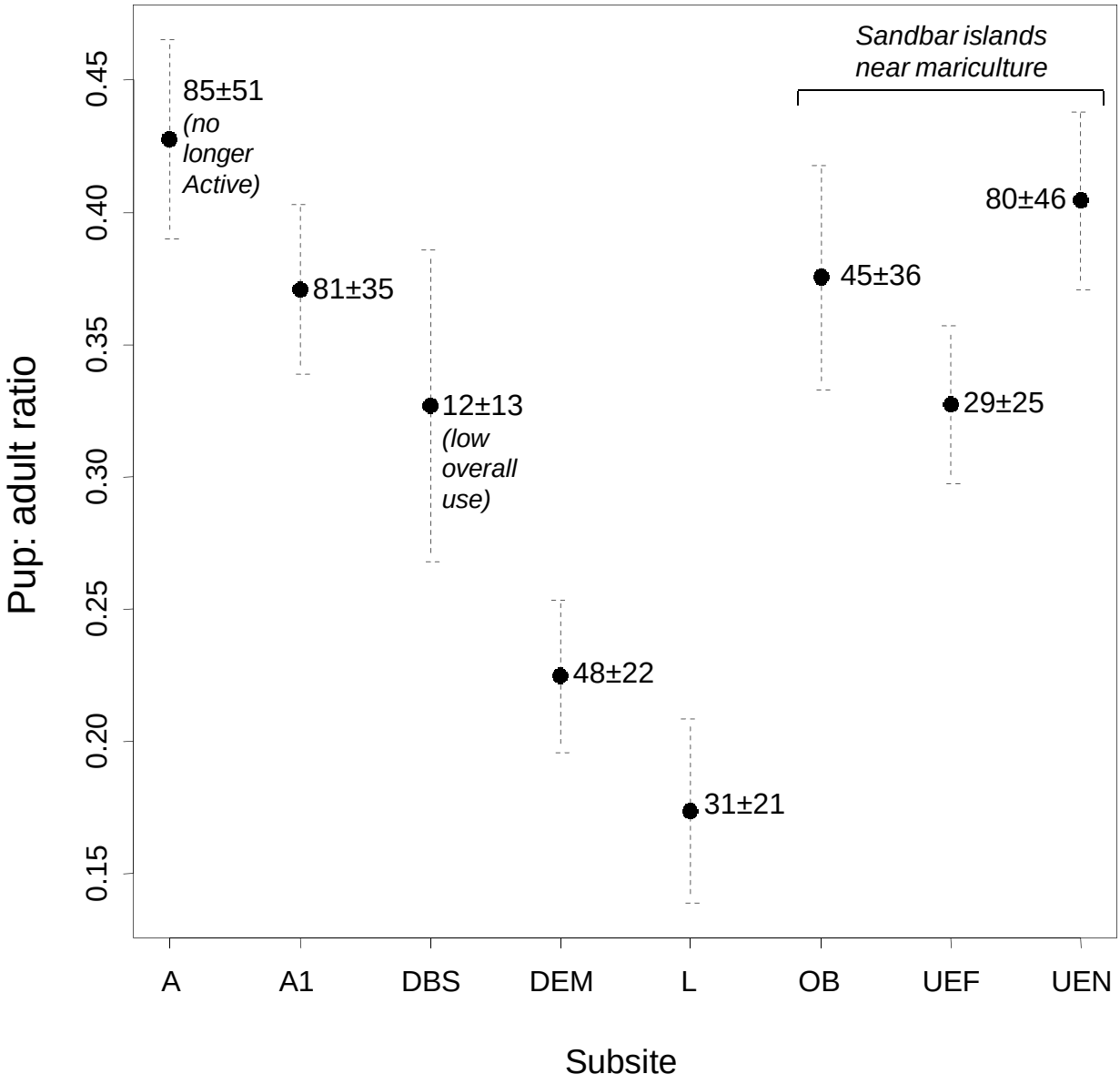

Figure 2. Mean (± SE) pup:adult ratio by subsite in Drakes Estero, 1997 - 2009. *Numbers next to points represent the mean (±SD) of the maximum annual pup counts at that subsite from 1997 – 2009*. The ratios at the estero mouth (DEM and L) are significantly lower than the other six subsites and UEF is lower than A. Furthermore, DBS has very low seal counts and pup production (~12/yr) indicating it is a minor site even though its pup ratio is high. Since 2004, seals have abandoned subsite A due to attachment to the mainland subsequent predator access. This currently leaves site A1 and the three sites near mariculture as the most important (considering pup:adult ratio and pup production) pupping sites in the estero.

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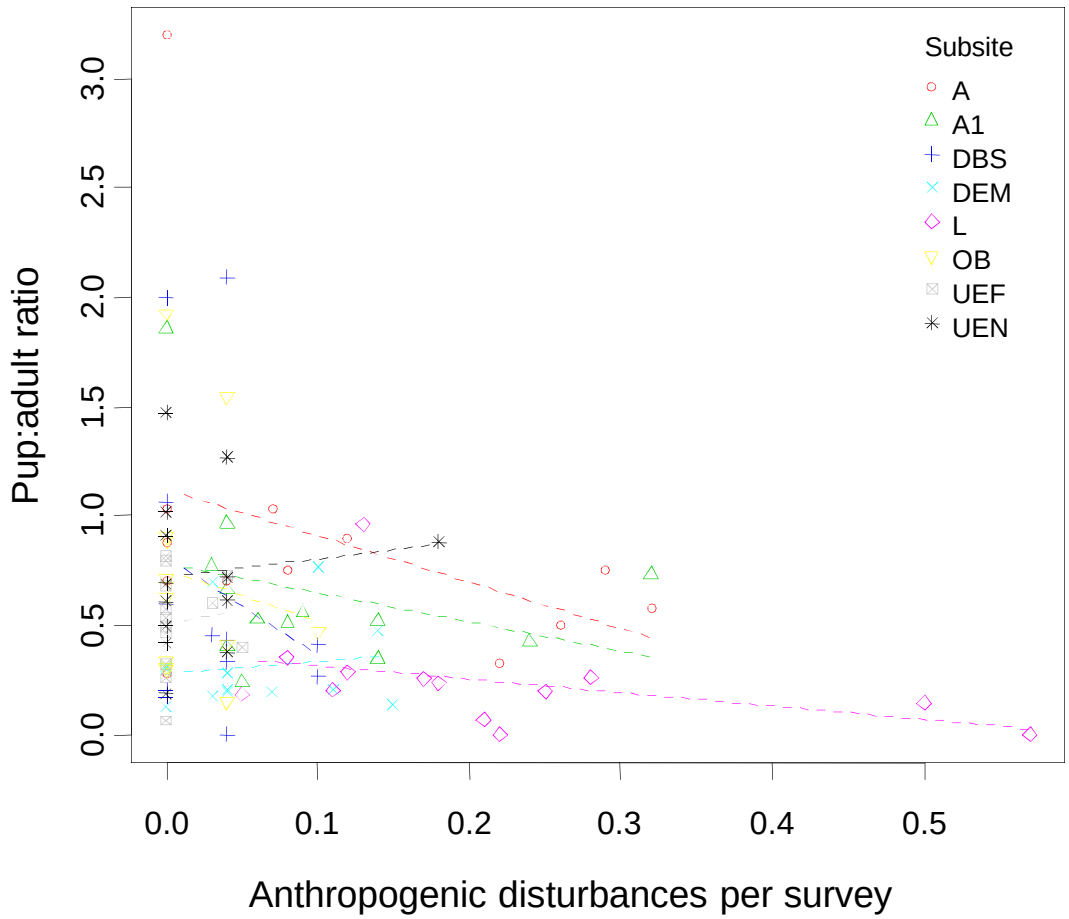

Figure 3. The pup:adult ratio within subsites declines with increasing spring disturbance rate, 1997 - 2009 ($P < 0.001$). Modeled using mixed-effects GLM, but regression lines are simple linear regressions for illustration.

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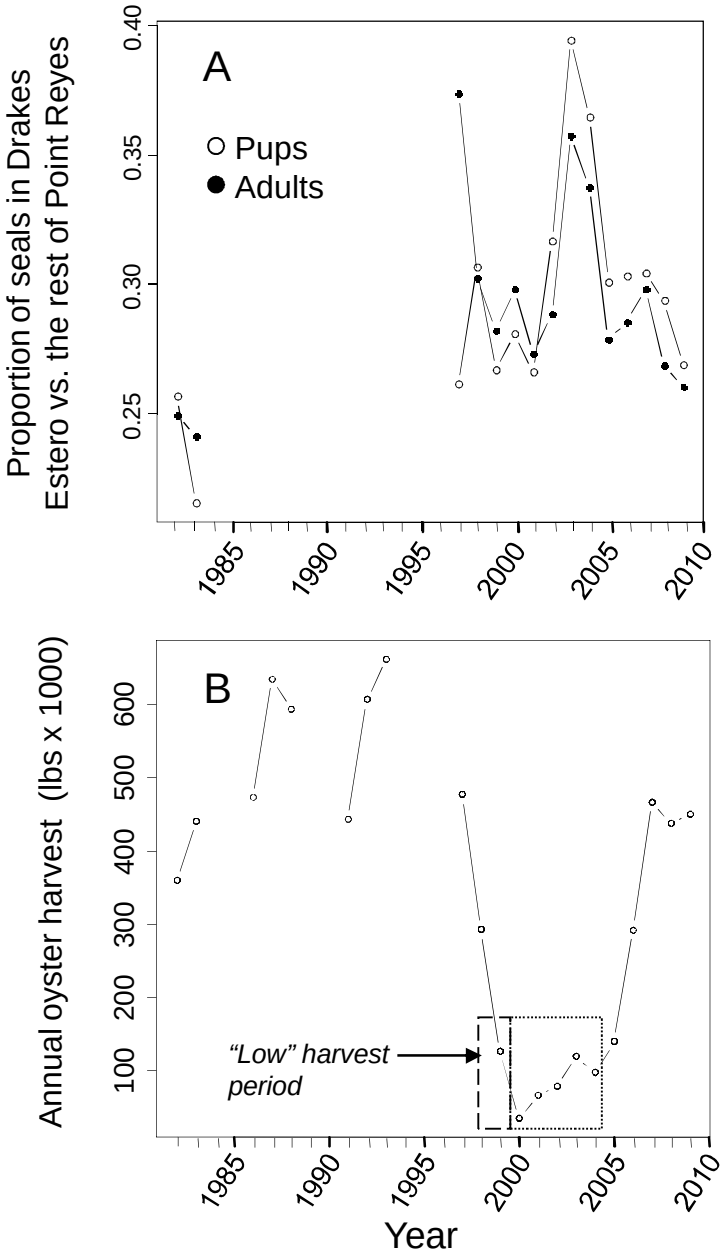

Figure 4. 1982 – 2009 time series of (A) proportion of Point Reyes area pup and adult harbor seals in Drakes Estero during the breeding/pupping season and (B) oyster harvest in Drakes Estero. Due to uncertainty in classification (Table 1), 1999 was modeled as both a "high" and "low" oyster harvest year. The 2009 oyster harvest is estimated. Oyster harvest is shown only for years of within Estero analysis, but is similarly high during the breaks in the 1980s-1990s.

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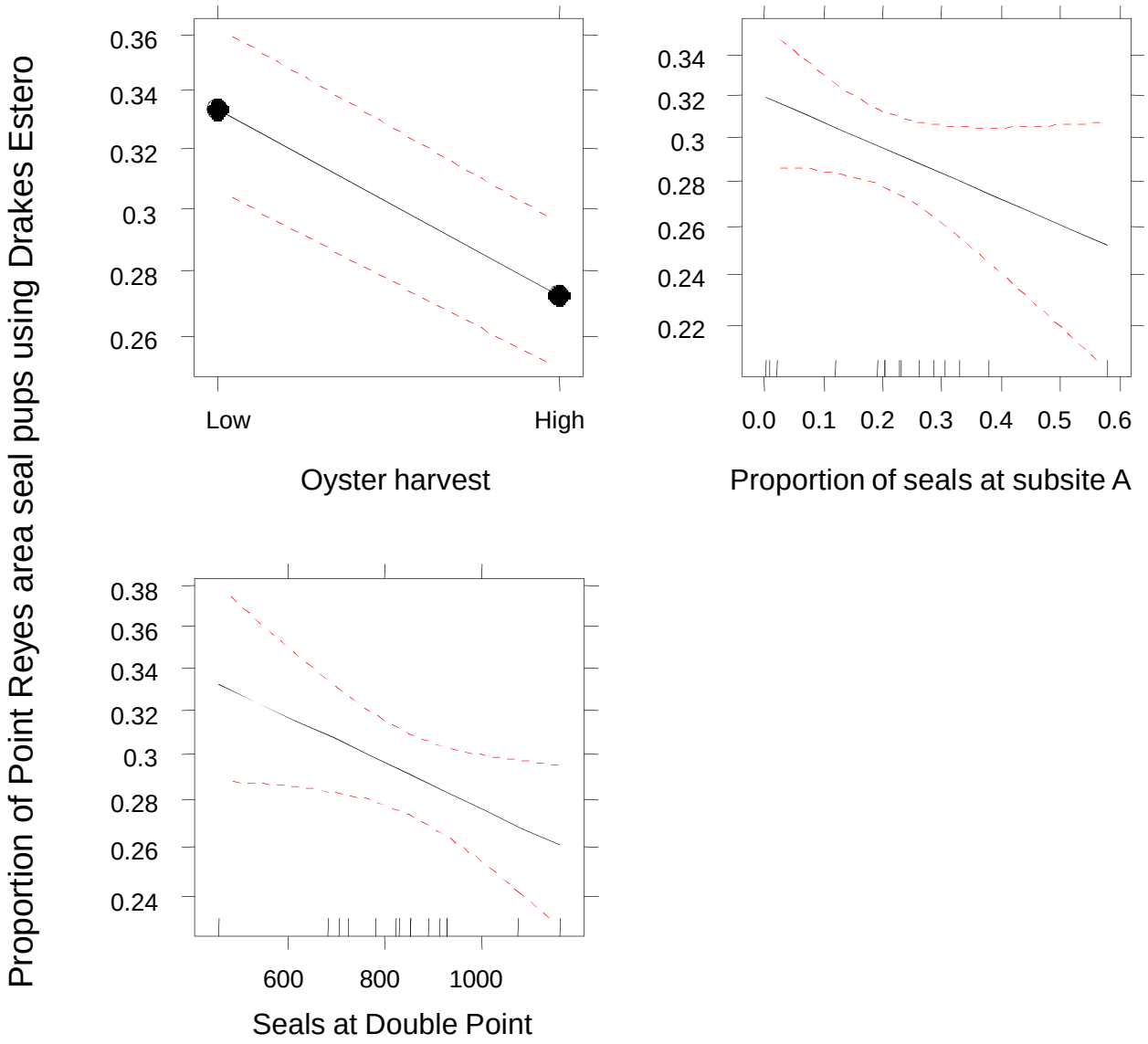

Figure 5. Model effects plots with standard errors for the proportion of Point Reyes area seal *pups* using Drakes Estero. Plots derived from the best model containing all three terms (oyster harvest, subsite A and double point. Multi-model averaged results (Table 5) are similar, but not identical.

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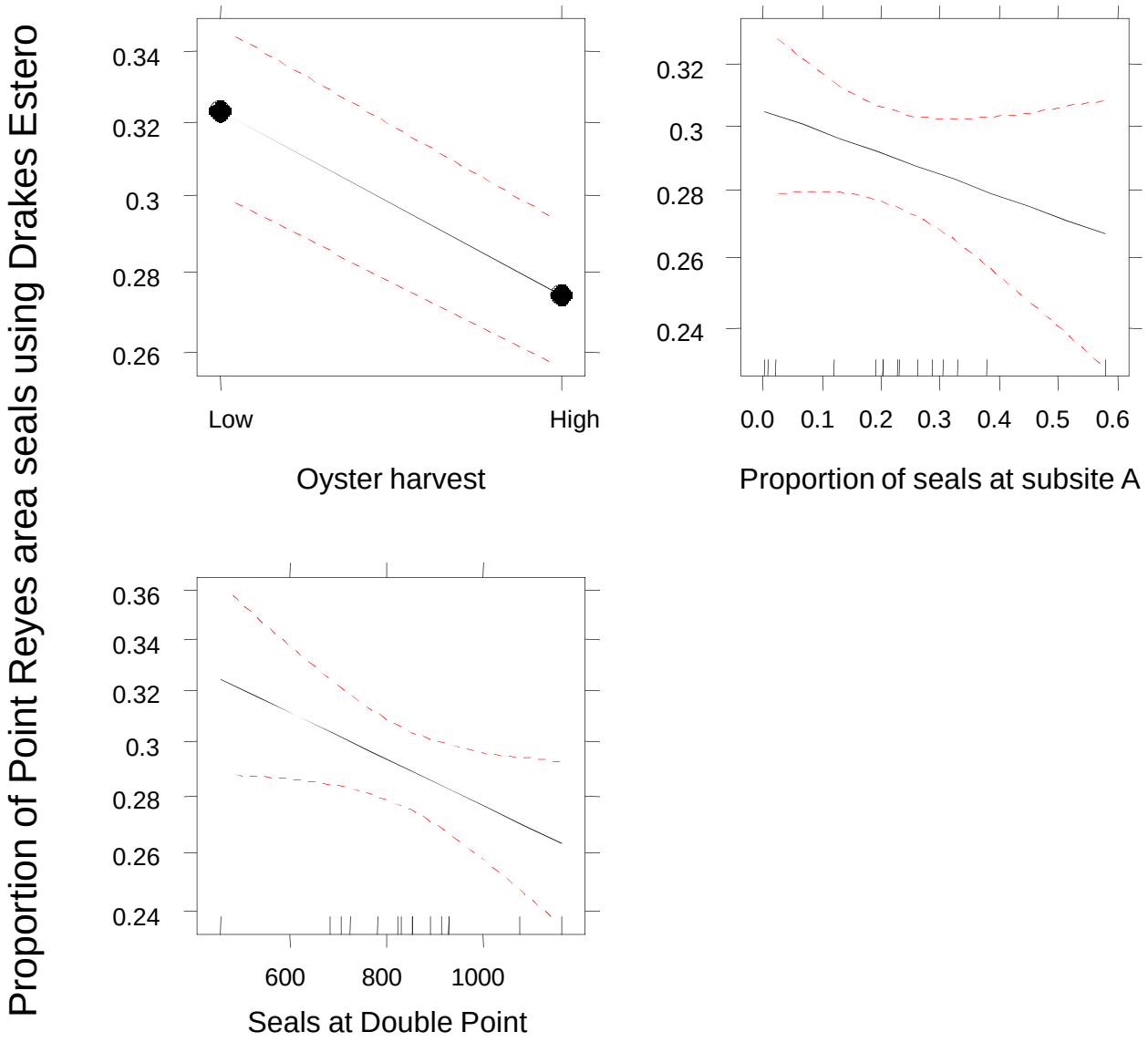

Figure 6. Model effects plots with standard errors for the proportion of Point Reyes area *seals* using Drakes Estero. Plots derived from the best model containing all three terms (oyster harvest, subsite A and Double Point). Multi-model averaged results (Table 5) are similar, but not identical.