Spatial use of Drakes Estero, California, by harbor seals correlated to anthropogenic disturbance and natural variation during 1982-2009

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Abstract

Long-lived, slowly reproducing K-selected species maximize their long-term survival and are predicted to respond to anthropogenic disturbances by moving away or remaining vigilant rather than habituating. Thus, spatial buffers in breeding areas may provide some resilience for populations facing disturbance as well as climate change, urbanization, and other anthropogenic and natural impacts. To better understand pinniped 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 large colony (Drakes Estero), and utilization of that colony in relation to other nearby colonies. Isolated sandbars had higher pup:adult ratios, indicating they are generally more important for pupping. There was no detectable relationship between human-related disturbance rate and the number of seals or pup:adult ratios at specific haul-out sites within Drakes Estero, suggesting that short-term human disturbance did not have a significant effect on spatial use, but rather that spatial use is

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determined by general sandbar isolation. However, within Drakes Estero, after removing effects of El Niño, the proportion of seals (total seals and pups only) hauled out near mariculture activities (a longer-term disturbance) was lower during years of higher oyster harvest (-0.08 ± 0.02, ~ 59 seals). Compared to oyster harvest, regional population size did poorly in explaining total seals or pups in the upper estero. Binomial generalized linear models ranked by quasi-AICc indicated that oyster harvest, seal counts at a nearby colony, and loss of a major haul out site within Drakes Estero, best explained pup and total seal use of Drakes Estero. Regional population size, short-term human disturbance rate, and other factors were not important in explaining overall seal use of Drakes Estero. Concurrent with higher oyster harvest and after removing effects of other covariates, the proportion of Point Reyes regional 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). This study, while correlational, supports the prediction that chronic human disturbance (as measured by mariculture activities) coupled with natural processes, affects seal haul out patterns at both the colony and regional scales.

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 coastal development (Seuront and Prinzivalli 2005), human encroachment and disturbance (Yochem et al. 1987, Gerrodette and Gilmartin 1990, Suryan and Harvey 1999, Thompson et al. 2001), predation (Nordstrom 2002), climate change (Freitasa et al. 2008), and natural variation in habitat suitability. Moreover, since longer lived, slowly reproducing K-selected species maximize their long-term survival, they tend to respond to anthropogenic disturbances by increasing heart rates and energetic costs. Thus, we 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 should be more risk averse than adult males. Further, Frid and Dill (2002) found that chronic, long-term disturbance stimuli resulted in habitat shifts and subsequently 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). Similarly, Hawaiian monk seal (*Monachus schauinslandi*) pup survival was lower when seals were displaced to suboptimal habitats (Gerrodette and Gilmartin 1990). In the few disturbance studies where alternative habitat was not available, disturbed animals did not move, but may have sustained higher stress levels and reduced reproductive success (manatees: Buckingham *et al.* 1999, diving ducks: Knapton *et al.* 2000).

Wursig and Gailey (2002) stated 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 also have been found in ranging bottlenose dolphins (Watson-Capps and Mann 2005). Similarly, several questions are generated by recent findings that oyster harvest activities may have "potential negative interactions" with harbor seal use (*Phoca vitulina*) at two sites near mariculture operations in Drakes Estero, California (NRC 2009, Becker et al. 2009) and it is "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). First, are these potential negative interactions detected with additional years of monitoring data? Second, are females and pups sensitive to negative interactions? Third, is there a difference in the impact of typically short-term park visitor disturbance versus potentially longer-term activities that place and service mariculture structures on and adjacent to the sandbars where seals haul out? Last, could any spatial effects on seal use cascade up from the subsites near the oyster operations to throughout the entire estuary's breeding and pupping season population and 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 ten additional years of data for a total of 21 years of survey between 1982 and 2009, 2) improving the statistical methods, and 3) testing multiple factors at three spatial scales that may be related to seal use (for total seals and pups). The scales ranged from a) *subsite* level seal counts and pup:adult ratios (13 years of data: 1997 - 2009), to b) *colony* level for distribution of seals within all of Drakes Estero (21 years of available data during 1982 – 2009), to c) the *regional* level comparing seal counts in Drakes Estero to the other surrounding colonies at the Point Reyes Peninsula (15 years of data during 1982 – 2009) (Fig. 1). This last regional effect would be somewhat surprising, since mariculture chiefly occurs in a limited area in the upper 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 if available. Furthermore, the upper intertidal sandbars that are isolated from the mainland (and therefore from park visitors and predators) have historically had more

females and pups than the sandbars attached to the mainland near the mouth of the estero (Allen Miller 1988). We made several predictions that scaled from *subsite* to *intra-colony* to *regional* scales (Fig. 1).

Subsite scale - We predicted that 1) isolated island sandbars in Drakes Estero which are buffered from predators (Nordstrom 2002) and human disturbance should be more important for pupping (as measured by higher pup:adult ratios); 2) disturbance should reduce use of these island sandbars by females with pups (as measured by the pup:adult ratio); and 3) short-term 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.

Intra-colony scale – We predicted that 1) changes in regional population size should be manifested in increased or decreased use of the upper estero due to density-dependence, and 2) increased mariculture activity (as measured by harvest level) would shift seal use away to other haul-outs. The second prediction is based on the assumption that oyster harvest should explain seal distribution better than overall human disturbance since the former is more likely to consist of long-term and persistent events (placement and tending equipment, long-term presence of equipment (NRC 2009, Fig. 1), while the latter is typically of brief duration by hikers and park visitors. We predicted this despite the fact that documented disturbances by visitors are far more common than by those by mariculture activities (Becker et al. 2009, NPS Data).

Regional scale - We predicted that 1) the effects of El Niño - Southern Oscillation (ENSO) on seal use of Drakes Estero as a whole, would be the same as for other colonies in the region; 2) regional population size expansion would only affect the proportion of regional seals using Drakes Estero if the estero had more good habitat than other colonies; 3) overall Drakes Estero human disturbance rates would not be related to overall seal use because disturbance would increase with population size and human disturbances are typically of short duration; and 4) relative use of Drakes Estero compared to other seal colonies would be influenced by (a) within site sandbar dynamics (e.g., natural loss of a major pupping subsite), (b) nearby colony dynamics (disturbance at a nearby colony that could move more seals to Drakes Estero), and (c) mariculture activity that would partially explain overall use of Drakes Estero in relation to other regional colonies. The latter could occur if seals were displaced locally by mariculture activity, but had reduced options for haul out areas due to factors (a) and (b).

Methods

Study Area

The Point Reyes peninsula is along the north-central California Coast (38º30'N to 37º30'N). The peninsula is located within the Point Reyes National Seashore, a unit of the National Park Service (NPS). The topographic diversity of the peninsula provides a broad range of substrates for harbor seals to haul out of the water. These include tidal mud flats, offshore and onshore rocky tidal ledges, and sandy beaches. A "haul-out site" is defined as a terrestrial location where seals aggregate for periods of rest, birthing, and suckling of

young (Harvey 1987). A colony may be a collection of haul-out sites within a limited geographic area. Drakes Estero and Estero de Limantour encompass a complex of eight subsites where seals haul out (Fig. 1), which are referred to collectively as the Drakes Estero/Limantour colony. Seals used the subsites at various times of the year depending upon their reproductive status, molting condition, and the level of disturbance encountered (Allen Miller 1988). Within a day, seals shifted to adjacent sandbars when crowding occurred or when the tide rose limiting the amount of haul out space. At rising tides, seals also floated over submerged sandbars until the sand bars reemerged with receding tides.

All subsites were used during the breeding and molt seasons, and some were used regularly year-round. Females with pups disproportionately used the sand bars exposed at low tide in the upper and middle portions of the Estero that are isolated from the mainland, and consequently from humans and predators. Limantour Spit was mostly used by non-breeding seals during the breeding season (Allen Miller 1988). Subsites in the lower estero, which are generally closer or attached to the mainland, have historically suffered higher annual human disturbance rates during the breeding season when compared to the isolated island sandbars of the upper estero (Becker et al. 2009).

Human access to the seal haul-out sites within Drakes Estero was limited because it is part of a national park and a congressionally designated wilderness area. During the breeding season (1 March--1 July), no motorized boats were allowed within the Estero except for those from a commercial mariculture operation. Non-motorized boats, primarily Kayaks, were allowed until 1996, but thereafter were excluded during the breeding season to avoid seal disturbance. Research and rescue boats may enter the estero

in rare instances. Three of the subsites where seals haul out are proximate to the commercial mariculture operation (OB, UEN and UEF). Subsite OB was within the mariculture lease but was not used much for culture in the recent past (~1999-2004), portions of subsite UEN were within or adjacent to the lease, and subsite UEF was in a navigational channel that bisects a gap in the mariculture lease where mariculture boats traversed Drakes Estero (Fig. 1). The mariculture operation raised oysters and the California Department of Fish and Game (CDFG) produced an annual report on oyster harvest production. No annual report or data is available on manila clams produced (Kirsten Ramey, CDFG, E-mail: Jan. 14, 2010).

Datasets

Disturbance data - Survey methods are described in Becker et al. (2009). Disturbance rate was derived from the number of human related disturbances (park visitors, kayaks, airplanes, mariculture activity, etc.) 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 three longer surveys (5-9 hrs) during 1982-83. We also compared (with Spearman tests) daily and hourly disturbance rate between the years 1982 – 2009 (15 years surveyed) to ensure that variation in survey length during 1982-83 did not affect realized disturbance rate.

Intra-colony data - When assessing *intra-colony* variation in use (rather than population size), we used the daily counts (converted to binomial proportions when modeled) 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 seal count database with additional subsite data from 1) the years 1982 - 1983, 1986 – 1987, 1989, and 1991 - 1993 derived from field notes of SGA which were reviewed twice before transcribing the data to spreadsheets for analysis, and 2) annual maximum breeding season pup and adult colony counts derived from tables in Allen and Huber (1984a, 1984b), for a total of 21 years between 1982 and 2009. 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.

Regional data - We used the maximum counts of pups and adults from the maximum total count of the day during the peak breeding season. Values for Drakes Estero were compared (again, in a binomial proportion) 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 at this site), Double Point, Bolinas Lagoon, and Duxbury Reef) (Fig. 1).

Analyses

Subsite 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 spring anthropogenic (March – May) disturbance rate (explanatory variable) was

[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).

related to annual maximum seal counts, maximum pup counts, and pup:adult ratios (response variables) within subsites and across all subsites between 1997 - 2009. Some upper estero subsites (OB, UEN, UEF) were occasionally pooled in the 1982-1993 field note data, so we therefore did not use those years for this within subsite analysis. However, this pooling did not affect data when pooling the total upper 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 binomial. Random intercept, random intercept and slope, and null models were compared with AIC and likelihood ratio tests, and were checked to ensure randomly distributed residuals.

Colony scale: shifts in haul-out (subsite) use in Drakes Estero related to mariculture, ENSO, disturbance rate, and regional population size - These models were designed to test if variation in the proportion of seals using the upper (near mariculture) versus lower (away from mariculture) estero were related to ENSO events, oyster harvest level, the spring (March – May) pooled disturbance rate (disturbances / # surveys) in either the upper or lower estero (Fig. 1), or the pooled maximum annual seal counts of all other Point Reyes area colonies (regional population size). We used a two-step process for modeling. Using the 15 year dataset, we used generalized linear mixed models (GLMMs) to asses for effects on seal distribution between the near (upper) and far (lower) mariculture areas of the estero due to *a priori* combinations of ENSO, binary high/low oyster harvest, anthropogenic disturbance rates, and regional counts (pup and total counts). We then tested models for the full time series (all 21 years) without regional

counts and disturbance covariates using generalized estimating equations (GEEs) (Venables and Ripley 2002, Faraway 2006, Zuur et al. 2009).

Binomial and quasibinomial GLMMs were ranked using AIC with the “lmer” and “glmmML” packages in R. Both of these packages report rounded AIC values. GLMMs were used rather than GEEs for this step because GLMMs allow calculation of AIC to compare non-nested models. Since regional population size and oyster harvest were correlated, they could neither be modeled together nor compared via likelihood ratio tests in nested models. Similarly, regional population size was tested *a priori* with disturbance measures, but not with ENSO since there is no reason to believe that ENSO should interact with regional population or size differently at different colonies. Year was considered a random effect.

We expanded and improved the analysis in Becker et al. (2009) in three significant ways. First, the GEEs 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 and GLMMs 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). Third, the aforementioned inclusion of spring (March – May) anthropogenic disturbance rates for the upper and lower estero and regional population size (pups or total seals) were included as covariates for step one of the analysis for 1982 - 1983 and 1997 - 2009.

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. Annual changes in the areal extent of sandbars in Drakes Estero and other regional colonies are not available and were therefore not modeled. However, dramatic changes in the size and access of subsite A were documented and we explicitly modeled that process in the following "*regional scale*" section.

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.

Nested models (e.g., ENSO + oyster vs. ENSO only) were tested for differences with likelihood ratio tests with the simplest adequate (difference not less than $P < 0.05$) model retained. We then transformed the final model 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 due to any significant factors.

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, as well as a null model, in relation to the annual maximum proportion of seals (total seals and pups only) using Drakes Estero compared to the proportion using the other six Point Reyes area colonies (Fig. 4A). These included:

- *Year*, to account for any linear time trends.
- *Proportion of Drakes Estero seals using haul out subsite A*, a major pupping subsite in Drakes Estero that attached to the mainland and exposed to predators around 2004. This should account for variation in the importance of this site through time.
- *Maximum annual count of seals at nearest colony (Double Point)*. Seals are thought to transit easily between Double Point and Drakes Estero, and in 2003 an elephant seal likely displaced numerous harbor seals from Double Point to Drakes Estero.
- *Annual spring (March-May) human related disturbance rate (disturbances/survey) in Drakes Estero*. This includes disturbances by hikers, kayakers, dogs, airplanes, and mariculture. Kayaks have been prohibited from the estero during the breeding season since 1996.
- *Years since the last major ENSO* (1982-83 and 1997-98). Strong ENSO events appear to depress reproductive success and thus may influence habitat choice.

- *Regional annual maximum count (less Drakes Estero).* Density-dependent effects could alter spatial use of Drakes Estero, especially if all haul-out sites are not equally desirable.
- *Annual oyster harvest* (Table 1) as a measure of mariculture activity and equipment placement in the estero.
- *Five-year and six-year periods of lowest oyster harvest* (2000-2004 and 1999-2004) (Table 1). This binary value may be useful for analyses for two reasons. First, the oyster harvest metric might not be linearly related to actual harvest activity near the seal haul-outs, and using a binary measure eliminates assumptions of such a relationship. Second, 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. 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 (NRC 2009). 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. 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 and an apparent break point of around 138,000 lbs of oysters.

Aerial images confirm that oyster bags were present on top of and adjacent to seal haul out sites in 2005 – 2009. Personal observations (DTP) during regular fieldwork indicate that there were few or no bags on the upper 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 conversely that there likely was infrastructure from 1997-1998 when harvest was higher. The year 1999 is difficult to categorize based on the available data. Thus, we modeled the oyster harvest covariate for 1999 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 Miller 1988, Allen and Huber 1984a Nordstrom 2002). 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 also tested for interannual autocorrelation in the proportion of pups and total seals in Drakes Estero using detrended time series and the autocorrelation and partial autocorrelation functions in R.

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 over-dispersion (variance larger than expected for binomially distributed data), we used a quasi-binomial family to assess *P* values and over-dispersion, and the binomial distribution to derive log-likelihoods to rank models using an over-dispersion 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 Point Reyes area seal population during the study period. All analyses were done in R 2.9.2 (R Development Core Team 2009).

Results

During 1982 – 2009, the mean number of breeding season harbor seals hauled out in Drakes Estero was 775 ± 269 total seals and 180 ± 94 pups. The mean of the maximum annual breeding season counts in Drakes Estero were 1052 ± 279 total seals (range: 656-1644) and 302 ± 102 pups (range: 122-486). The other regional colonies had a combined

mean maximum breeding season count of 2499 ± 369 total seals (range: 1728-3125) and 710 ± 167 pups (range: 366-962). Oyster harvest experienced a low period from ~2000-2004 (Table 1, Fig 6B) and manila clam harvest levels are unknown. Daily maximum Drakes Estero seal breeding season counts varied throughout the study period, with upper estero seals showing a peak during 2002 – 2004 (Fig. 4). Annual maximum counts of harbor seals in Drakes Estero also peaked around 2002 – 2004, while the regional population size (less Drakes Estero) peaked from about 2000 – 2005 with two very high years in 2002 and 2004 (Fig. 5). Pup counts in Drakes Estero climbed from 2000-2004, while those in the rest of the region slowly declined (Fig. 5). Excluding the period from 2000 – 2004, the pup counts between Drakes Estero and the region appeared to have similar trends.

Subsite Scale: Seal counts, pup:adult ratios and disturbance rate – During 1997 – 2009, the upper intertidal sandbars (OB, UEN, UEF) generally had higher pup:adult ratios than the sandbars attached to the mainland or near the mouth of the estero (L, DEM, DBS: Fig. 2). Subsite A, while showing a high pup:adult ratio, lost nearly all of its productivity since attaching to the mainland in 2004, but subsite A1 was still the one major subsite away from mariculture that maintained a high pup ratio and high overall pup production each year. Lower estero subsites DBS and L (attached to the mainland), and DEM (at the mouth of the estero in high current), tended to have either low pup:adult ratios *or* relatively low absolute numbers of pups produced each year.

Annual human disturbance rate during spring (March-May) of each year (1982-83 and 1997-2009) had a similar pattern whether using daily or hourly rate (r_s = 0.99, n =

15) and so we used daily rate in all subsequent models and calculations. There were 153 spring anthropogenic disturbance events during this time. The daily disturbance rate averaged about 0.71 ± 0.41 for each year, with about 23% of disturbances being seal head alerts, 10% flushes without entry into the water, and 67% flushes into water. Neither subsite pup counts (P > 0.38) nor total seal subsite counts (P > 0.28) were related to spring anthropogenic disturbance rates in Drakes Estero (Figs 3A & B). When using a random intercepts (fixed slopes) model, spring disturbance rate appeared to be negatively related to reduced pup:adult ratios at seal haul outs within Drakes Estero (n = 104, groups = 8, $P < 0.001$, AIC = 889.3) (Fig. 3C). However, the random intercepts and random slopes model had a lower AIC (882.0), was a better fit in a likelihood ratio test ($X^2 = 9.2$, P < 0.001), and indicated no effect (P > 0.32) of spring disturbance rate on pup:adult ratios. The null model was a much poorer fit than either of the disturbance models (AIC = 910.5). Since "flushes" and "flushes into water" represented the majority of disturbances (~77%), removing the "head alerts" from the analysis should not alter the results. Based on this, we conclude that there is not a robust, detectable relationship between spring anthropogenic disturbance rate and pup:adult ratios. Further, individual subsite based binomial GLMs for the years 1997 – 2009 indicated that subsite pup:adult ratio trends with disturbance rate were not significant (Fig. 3C).

Colony Scale: Drakes Estero subsite models – Binomial GLMMs found that high-low oyster harvest and ENSO best explained the proportion of seals (pups and total) using the upper estero (Table 2a). Both the "lmer" and "glmmML" functions in R reported similar AIC rankings, as did quasibinomial and binomial distributions (for "lmer" only). Upper

estero disturbance rate was somewhat important in explaining pup presence in the upper estero, but this model was not a significantly better fit than the oyster + ENSO model alone (likelihood ratio test: $X^2 = 2.97$, $P < 0.08$). Regional population size was not important in explaining the proportion of seals using upper Drakes Estero with ΔAIC values of 9 (total seals) and 17 (pups) from the top ENSO + Oyster models.

Since disturbance rate and regional population size were not important in these 1982-83 and 1997 – 2009 models. We used GEEs to analyze the full time series including 1986-1987, 1989, and 1991-1993 for the relationship between the proportion of seals using the upper estero and just oyster harvest and ENSO as covariates. ENSO and oyster harvest (high/low) were not collinear ($P > 0.89$). The GEE showed that both ENSO and oyster harvest continue to explain seal use at sites closest to mariculture activity (Table 2b). 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 likelihood ratio test indicated the Oyster + ENSO binomial model was a better fit over the ENSO only binomial model for both pups ($X^2 = 4.6$, $p < 0.03$) and total seals ($X^2 = 9.5$, $P < 0.002$). After accounting for the ENSO effect and not including the non-significant anthropogenic disturbance terms, the best GEE models estimated 14 ± 4 fewer pups and 59 ± 15 fewer total seals in the three "near mariculture" subsites during the higher oyster harvest years (Table 2b).

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. 6A). Because 1997 was an outlier for the adult and/or pup proportion of seals in Drakes Estero, we weighted the total seal count data 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 (and preferable to omitting the data) since there was an anomalous harbor seal die-off of mostly adult females which 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. & NPS 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. 6B). Seal use of subsite A in Drakes Estero was high from 1982 – 2004, and dropped rapidly thereafter when the sandbar connected to the mainland. Seal use of Double Point increased from 1997 – 2002, dropped rapidly in 2003 due to an aggressive elephant seal (see Hayward 2003), 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). The detrended proportion of pups and total seals using Drakes Estero did not exhibit interannual autocorrelation or partial autocorrelation at any lag distance. 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 over-dispersion 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 multimodel 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 of ENSO which 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 ($P < 0.05$) over-dispersion corrected P-value. Bootstrapped estimates of model coefficients were similar to those in Table 4 and the oyster harvest 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 about 65 ± 18 fewer seal pups and 192 ± 58 fewer seals overall using Drakes Estero (Table 5, Figs. 7 & 8) 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 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 support those of Frid and Dill (2002) whereby long-term, chronic disturbance or displacement stimuli (in this case mariculture activity including equipment on haul out sites) is related to a habitat shift and subsequent reduced access to subsites in the estero. Conversely, shorter term disturbance stimuli (primarily park visitors) were not related to reduced pup:adult ratios at subsites in the estero, or strongly to detectable patterns in intra-estero (upper versus lower) or inter-colony proportional use by seals. Rather, pup:adult ratios at subsites appear to be strongly driven by their physical isolation from the mainland (Nordstrom 2002). Oyster harvest and ENSO were the primary variables associated with temporal variation in spatial use by seals in Drakes Estero. Our prediction that regional population size would be an important factor in partially explaining the proportion of Drakes Estero seals using the upper estero was not supported. Regional population size and human disturbance rate were also unimportant in explaining seal use of Drakes Estero in relation to the rest of the colonies. Instead, oyster harvest, internal subsite, and nearby colony dynamics were consistently important.

These analyses address suggestions of the NRC (2009) for research into factors driving seal spatial patterns in Drakes Estero. Although the results are correlational, we propose that the variation in oyster harvest paired with *a priori* multiple competing

mechanistic hypotheses represents a robust "natural" experiment which can be used to draw reasonable inferences. Oyster harvest was a human induced rather than a natural covariate, and so there is no reason to believe that oyster harvest is mechanistically correlated with some other unmeasured, non-anthropogenic parameter that also influences seal distribution. The apparently random correlation between oyster harvest and regional population size warrants some caution when interpreting the *colony scale* results. The fit of the oyster harvest models, though, were so much more parsimonious than those of regional population size (lower by 9-16 AIC units), that the pattern appears quite robust to both statistical methodology and length of the time series. Similarly, in our analysis of the 1997 – 2007 Drakes Estero data (Becker *et al.* 2009), we reported that the 2008 seal counts at one subsite appeared to deviate from the inverse relationship with oyster harvest found for the 1997 – 2007 models. This was based on preliminary information that oyster harvest increased in 2008 along with actual seal counts at one subsite (OB). The 2008 actual oyster production estimate, however, actually *declined* by 12% from 2007 to 2008), and is thus still consistent with the reported model for 1997 - 2007. Further, Becker *et al.* (2009) modeled counts in the estero rather than proportional shifts, so further comparisons are not informative here.

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 within each year both within the estero (for the colony scale analysis) and between the estero and other Point Reyes area colonies (for the regional analysis). The use of regional population size as a covariate should account for any density-dependent effects and seals typically do not move between colonies during the breeding season (Lowry et al. 2005).

We focused on low versus high oyster production, but also report nearly identical results when using the continuous linear covariate of oyster harvest. While the binary oyster harvest 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 is more appropriate if the simple presence of oyster equipment caused seal displacement, rather than the frequency of visits. Additionally, the oyster harvest value does not represent activities that may be due to cultivation of manila clams versus oysters in the estero. Any relationships between clam and oyster harvest are currently unknown to us, so a low/high metric may again avoid over-interpreting the impacts of the specific annual oyster harvest. A final benefit of using the high / low oyster metric is that it virtually 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). Johnson and Acevedo-Gutiérrez (2007) reported 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 in Drakes Estero likely go undetected, especially since about 50% of harbor seal surveys are on weekends and more visitors are out on weekends, while the oyster harvest work occurs primarily daily, but less frequently on Sundays (NRC 2009). Further, surveys may miss any disturbances on the ebb tide that might prevent seals from hauling out (NRC 2009). Nonetheless, we believe that because the survey methodology is standardized, it should represent an index

of annual changes. Similarly, the NRC suggested that additional disturbances by oyster boats during high tide might deter seals from using the upper sandbars when tides receded. However, since we did not partition mariculture and non-mariculture related human disturbance in this paper, these unrecorded and undetected disturbances (of all anthropogenic kinds) would be unlikely to alter our results.

The proportional reduction in seal use was generally larger for the upper estero (-0.08 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 regional population, suggests more individual seals were displaced from the overall estero than those simply displaced from the upper estero alone. It is possible that the combined effects of the loss of subsite A, impacts at Double Point, increased oyster activity in the upper estero and other unknown factors, led to the pronounced reduction in counts for the entire estero. Specifically, our findings are consistent with a scenario where subsite A lost habitat in 2003-4, which could have *increased* the proportion of seals using the upper estero. Increasing mariculture activity during 2005 – 2009, though, may have displaced seals away from the upper estero, and without access to subsite A, the overall proportion of seals using Drakes Estero therefore declined. Similarly, prior to 2000 when oyster harvest was generally high and subsite A was an isolated sandbar, the proportion of seals using the upper estero was also low. The additive processes among subsite A, Double Point, and oyster harvest fits a model where seal resilience in the ecosystem 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 as the loss of subsite A, mariculture equipment on the upper estero subsites, and the generally poor suitability of lower estero sites. 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.

Subsite (or colony) recolonization may take years, while abandonment due to chronic displacement / disturbance may be rapid (Gerrodette and Gilmartin 1990). Such a decline was noted with abandonment of harbor seal colonies in San Francisco Bay (Allen 1991, Bartholomew 1949). Similarly, Hog Island in Tomales Bay (Fig. 1) was mostly abandoned by harbor seals in the early-1990s coincident with increasing numbers of boaters landing on the east side of the island (Allen and King 1993). Prohibition of boat landings coincided with a gradual resumption of use by seals (NPS Compendium; Unpubl. NPS data). The decline at subsites OB, UEF and UEN in the upper 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 upper estero, but perhaps simple time delayed movement into the area is also partially responsible (and also density dependence from the concurrent regional population increase). 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 subsite A attachment to the mainland and exposure to predators.

Additional processes occurring at other colonies in the San Francisco Bay Area could also affect the patterns we observed. This might include excessive disturbance, as well as immigration to 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 and the sensitivity of K-selected species to chronic disturbance or displacement. 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.” Our data and analyses are consistent with natural and anthropogenically (mariculture) driven seal colony dynamics both within Drakes Estero and between Drakes Estero and other colonies in the Point Reyes region. Encroachment of mariculture or other persistent activities on preferred pupping sandbars may displace seals but not

have a detectable effect on the colony or the region until natural fluctuations occur which further limit habitat, and cause additional competition for limited space resources.

While density dependence (in the form of regional population size) is likely an important component, it did not fully explain the spatial patterns observed at the colony and subsite scales. Although pup:adult ratios were higher at isolated sandbars presumably because of lower exposure to short-term disturbances, the apparent lack of spatial redistribution at the subsite, colony and regional scales due to short-term anthropogenic disturbance warrants further study since pinniped disturbances are a common concern. At a scale even larger than the Point Reyes region, seals transit between San Francisco Bay and the Point Reyes region (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. While such a signal would be extremely difficult to detect, this concern may be particularly true for Drakes Estero which supports one of the largest breeding colonies in the state and the largest in the San Francisco Bay region (Lowry et al. 2005).

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Table 1. Sources and inferences for level of oyster harvest activity on or near subsites OB, UEF, and/or UEN. Data from. CDFG and NRC. "Analysis scale" summarizes the years where complete seal count or disturbance data available and subsequently modeled in each of the three scales of analysis presented. Data sources: A&H: Allen and Huber 1984a, 1984b; SGA: Sarah G. Allen field notes; NPS: NPS pinniped database.

				Analysis scale			
Year	**Oyster harvest (lbs)**	**Inferred level of mariculture use of sandbars near seals**	**Source(s) of inference**	**Haul-out site**	**Intra-colony**	**Regional**	**Seal data source**
1982	360,004	high	harvest data		x	x	SGA / A&H
1983	440,139	high	harvest data		x	x	SGA / A&H
1986	437,043	high	harvest data		x		SGA
1987	634,869	high	harvest data, aerial image of bags		x		SGA
1989	549,953	high	harvest data		x		SGA
1991	442,745	high	harvest data		x		SGA
1992	606,484	high	harvest data		x		SGA
1993	662,388	high	harvest data		x		SGA
1997	476,791	high	harvest data	x	x	x	NPS
1998	292,188	high	harvest data, higher than 2005	x	x	x	NPS
1999	125,749	modeled high & low	slightly higher than 2000-2004, declining	x	x	x	NPS
2000	34,094	low	lower than 2002-2004	x	x	x	NPS
2001	65,676	low	lower than 2002-2004	x	x	x	NPS
2002	78,064	low	DTP, pers. obs, harvest data	x	x	x	NPS
2003	118,643	low	DTP, pers. obs, harvest data	x	x	x	NPS
2004	96,754	low	DTP, pers. obs, harvest data	x	x	x	NPS
2005	138,958	high	aerial image of bags, increasing activity	x	x	x	NPS
2006	291,538	high	increasing harvest, bags in '05	x	x	x	NPS
2007	468,000	high	aerial image of bags	x	x	x	NPS
2008	438,000	high	aerial image of bags	x	x	x	NPS
2009	450,000*	high	aerial image of bags	x	x	x	NPS

*Harvest estimate based on 2007-2008. Official data likely available in mid-2010. Only affects inferred mariculture level if harvest was less than ~138,000 lbs.

Table 2a. Direct comparison of rounded delta AIC values from binomial GLMMs explaining the proportion of pups or total seals using the upper estero for the years 1982-83 and 1997-2009. "Oyst": high/low oyster value; "Oyster": continuous oyster value; "ENSO": El Nino; "up dist": spring upper estero disturbance rate; "lo dist": spring lower estero disturbance rate; "Regional pop"; annual maximum regional population size (total or pups respectively, less Drakes Estero). Models less than 4 AIC units from the best model are shaded grey.

	ΔAIC	
Model	**Pups**	**Total**
Oyst+ENSO	1	0
Oyster+ENSO	3	2
Oyst+ENSO+up dist	0*†	4
Oyst+ENSO+up dist+lo dist	1	6
ENSO+up dist	4	6
ENSO+up dist+lo dist	4	6
Regional pop	17	9
Regional pop+up dist	18	11
Regional pop+lo dist	17	11
Regional pop+up dist+lo dist	16	13
Oyst	20	18
Null	14	19
up dist+lo dist	17	19

*Pup model upper estero disturbance coefficient = -0.62 ± 0.35.
†Likelihood ratio test indicates that *Oyst+ENSO+up dist* is not a better fit than *Oyst+ENSO* alone (X^2 = 2.97, P < 0.08).

Table 2b. Coefficients, proportional change, and effect size from binomial generalized estimating equation (GEE) for proportion of Drakes Estero Seals using the upper (OB, EUF + EUN) versus lower estero based on the 21 year time series. 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 775 total and 180 for pups.

	Pups				Total seals			
Model	**Coefficient**	**Proportion**	**Effect size**	**P**	**Coefficient**	**Proportion**	**Effect size**	**P**
Intercept	-1.39 ± 0.34			< 0.001	-1.50 ± 0.25			< 0.001
log(ENSO + 1)	0.65 ± 0.20			< 0.001	0.52 ± 0.14			< 0.001
Oyster high/low	-0.41 ± 0.19	-0.08 ± 0.03	-14 ± 4	< 0.03	-0.44 ± 0.14	-0.08 ± 0.02	-59 ± 15	< 0.003

Table 3a. Spearman rank correlations between independent variables. Significant (P < 0.05) correlations have an asterisk. N = 15. If adjusted for multiple comparisons using Holm's method, only the three oyster values are correlated. Oyster harvest (categorical or continuous) and annual regional population size had an r_s of ~0.78 (P < 0.001), and were also not used in the same model.

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

Table 3b. Variance inflation factors from full models. VIFs of less than 3 represent no functional collinearity within the models (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
ENSO	1.09	1.06
Disturbance rate	1.13	1.14

Table 4. *A priori* models ranked by delta QAICc for the proportion of Point Reyes seal pups and total seals using Drakes Estero. Δi indicates QAICc distance from the best model and wi indicates model weight. Modeling oyster harvest as a continuous variable or low oyster during 1999-2004 gives similar results (see appendix). Models ranking within the lowest 4 QAICc units (in grey) were used for multimodel inference in table 5. Oyst: low oyster harvest from 2000-2004; DP: Double Point Counts; A: proportion of Drakes Estero seals using subsite A; Dist: anthropogenic disturbance rate.

Age class	Model	Δi	wi	r^2
Pup	Oyst + Double Point (DP)	0.0	0.35	0.51
	Oyst + DP + A	1.3	0.18	0.63
	Oyst + A	1.4	0.18	0.46
	Oyst + ENSO	2.6	0.09	0.42
	Oyst	3.3	0.06	0.26
	Year	5.0	0.03	0.20
	Oyst + Dist	5.6	0.02	0.32
	Oyst + DP + Dist + A	6.3	0.01	0.66
	DP + Year	6.4	0.01	0.29
	DP	7.3	0.01	0.12
	Null	7.7	0.01	0.00
	Regional pup count	10.3	0.00	0.02
Pup + Adult	Oyst + Double Point (DP)	0.0	0.55	0.54
	Oyst + DP + A	2.4	0.16	0.61
	Oyst + A	3.9	0.08	0.42
	Oyst	4.3	0.06	0.29
	Oyst + Dist	4.5	0.05	0.41
	Oyst + DP + Dist + A	6.1	0.02	0.67
	Oyst + ENSO	6.3	0.02	0.35
	Regional total count	7.9	0.01	0.19
	Year	8.5	0.01	0.17
	DP + Year	9.6	0.00	0.25
	DP	10.4	0.00	0.11

Table 5. Multimodel weighted coefficients of all models within 4 QAICc of the best model for pups and total 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. Proportional change represents change in use of Drakes Estero. Effect size is based on mean seal counts of all Point Reyes area colonies during the study period.

	Logit Coefficients		Proportional change		Effect Size	
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.

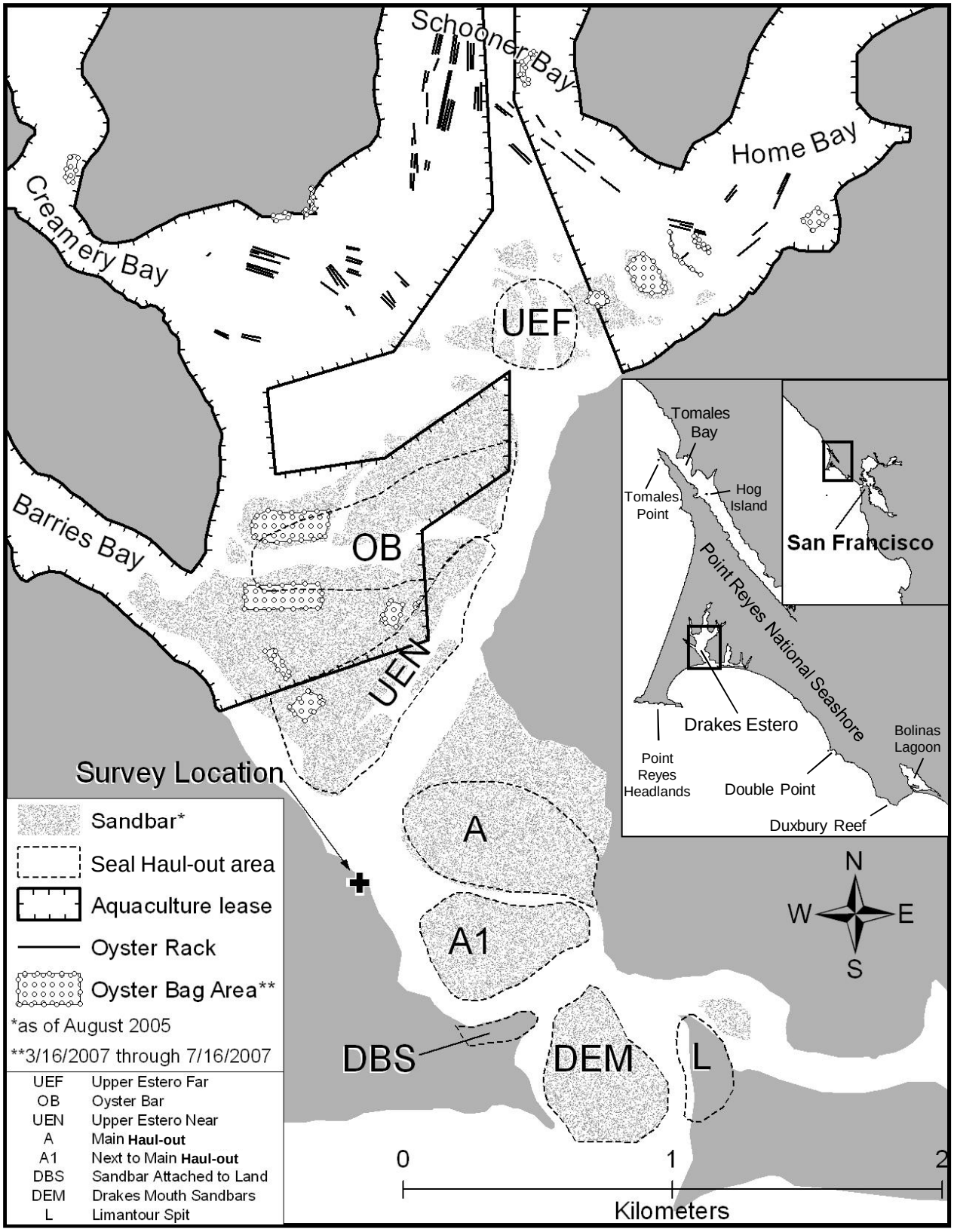

Figure 1. Drakes Estero and the eight labeled seal haul out subsites. Subsites UEF, OB, and UEN are considered "near" mariculture, while A, A1, DBS, DEM, and L are considered "away" from mariculture. Inset shows all the Point Reyes area colonies: Tomales Bay, Tomales Point, Point Reyes Headlands, Drakes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

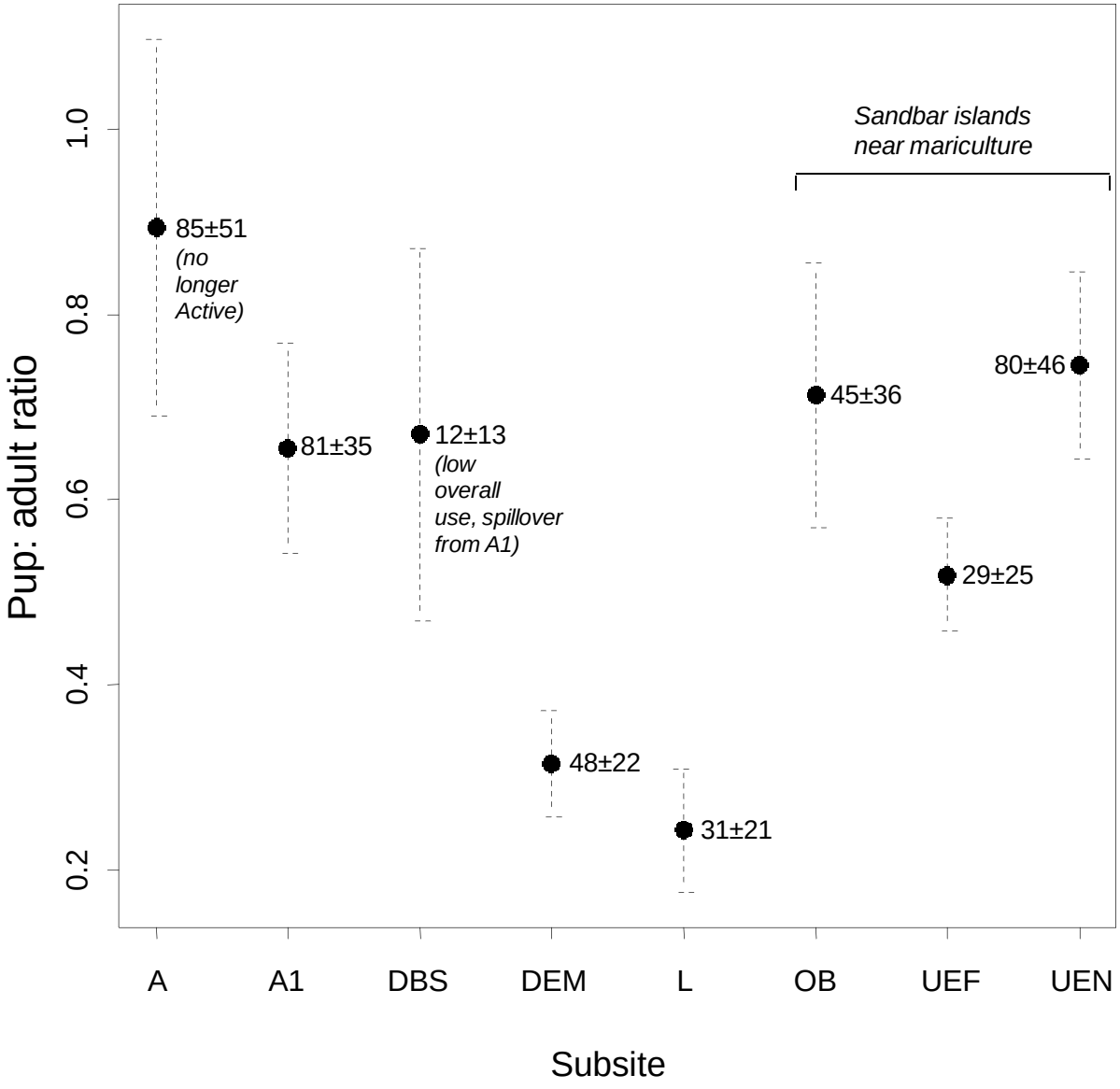

Figure 2. Mean (± SE) of maximum annual pup:adult ratios by subsite in Drakes Estero, 1997 - 2009. Numbers next to points represent the mean (±SD) of the maximum annual pup counts at that subsite from 1997 – 2009. The ratios at the estero mouth (DEM and L) are lower than the other six subsites and UEF is lower than A. DBS is adjacent to A1 has very low seal counts and pup production (~12/yr) indicating it is a minor site that appears to catch spillover seals when A1 gest crowded. Since 2004, seals have abandoned subsite A due to attachment to the mainland and subsequent predator and human access.

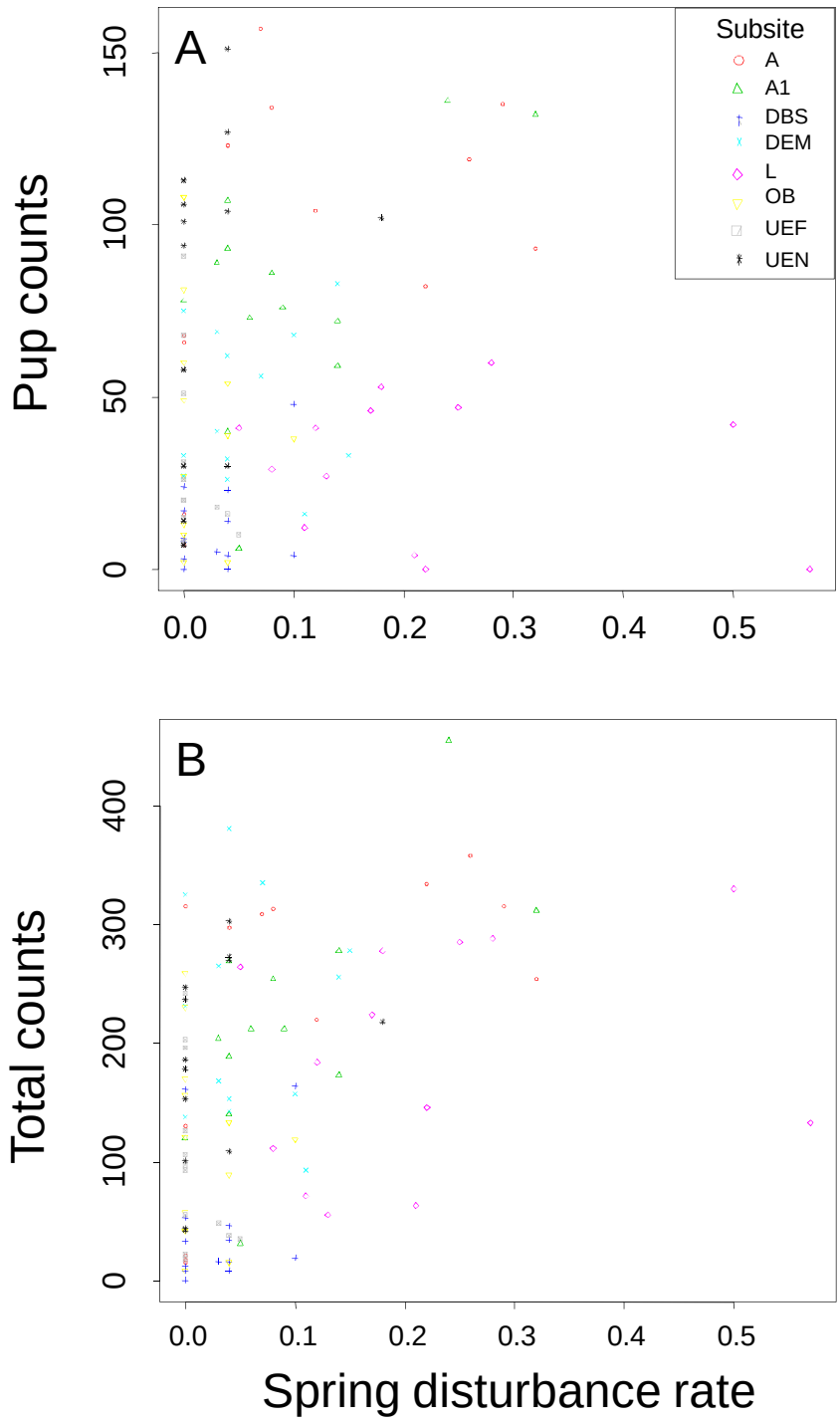

Figure 3 A & B. There is no significant relationship between Spring anthropogenic disturbance rate and (A) maximum annual pup counts at individual Drakes Estero subsites (P > 0.38) or (B) maximum annual total counts at individual Drakes Estero subsites (P > 0.28) for 1997 – 2009. Analyses were done with subsite as a random effect allowing random intercepts.

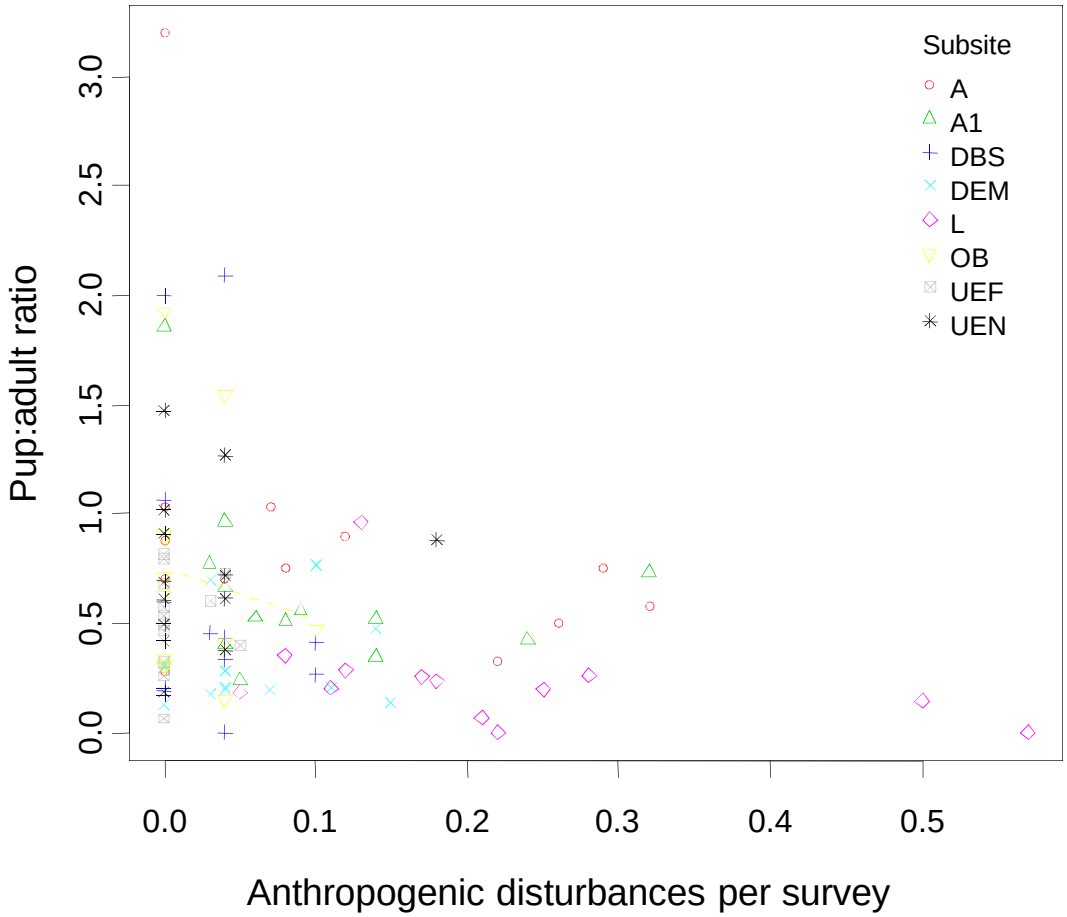

Figure 3C. The pup:adult ratio has no detectable relationship with anthropogenic disturbance rate either at the subsite level or the estero level.

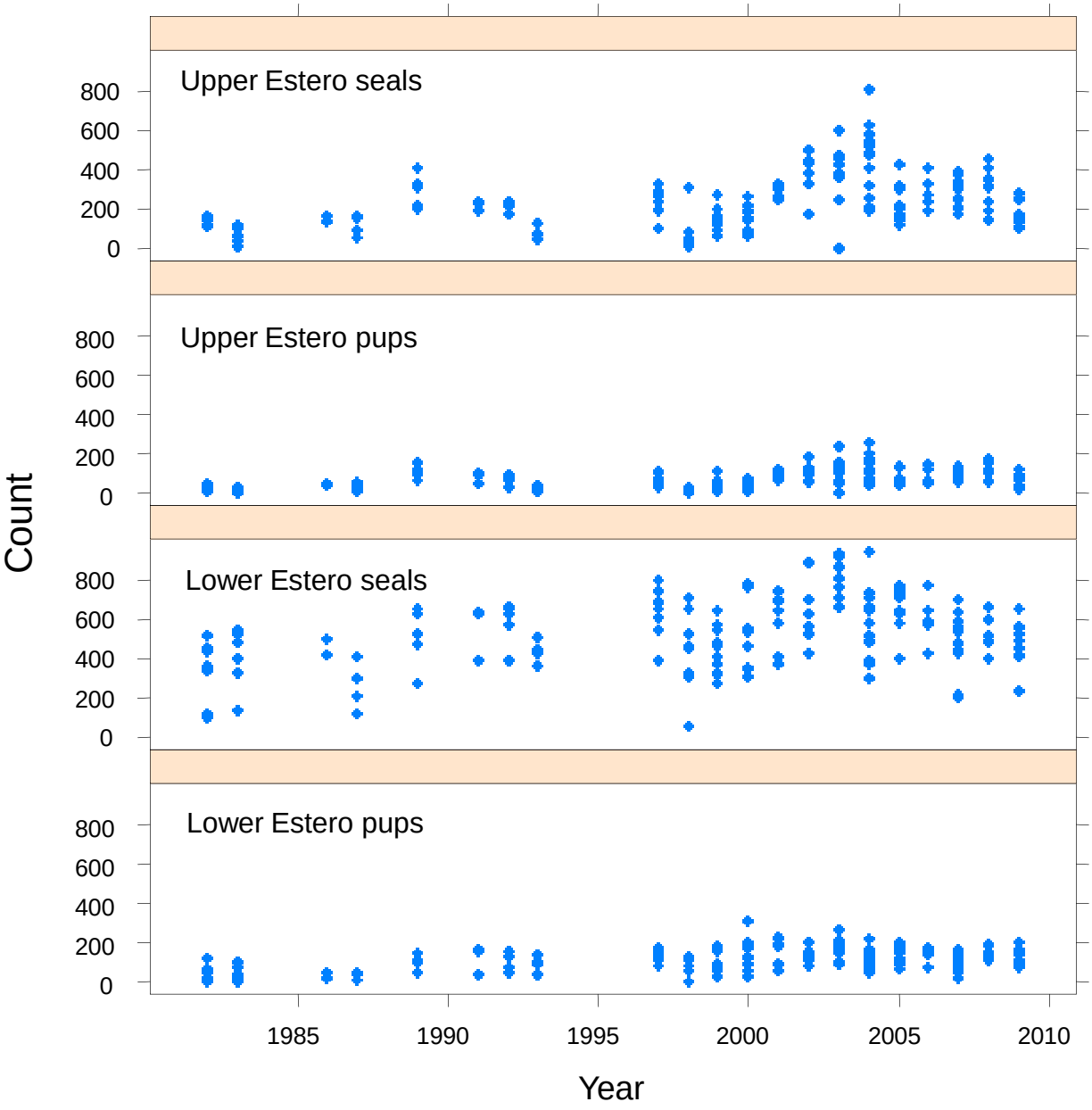

Figure 4. Daily maximum counts of harbor seals in Drakes Estero during April 15 – May 15, between 1982 and 2009.

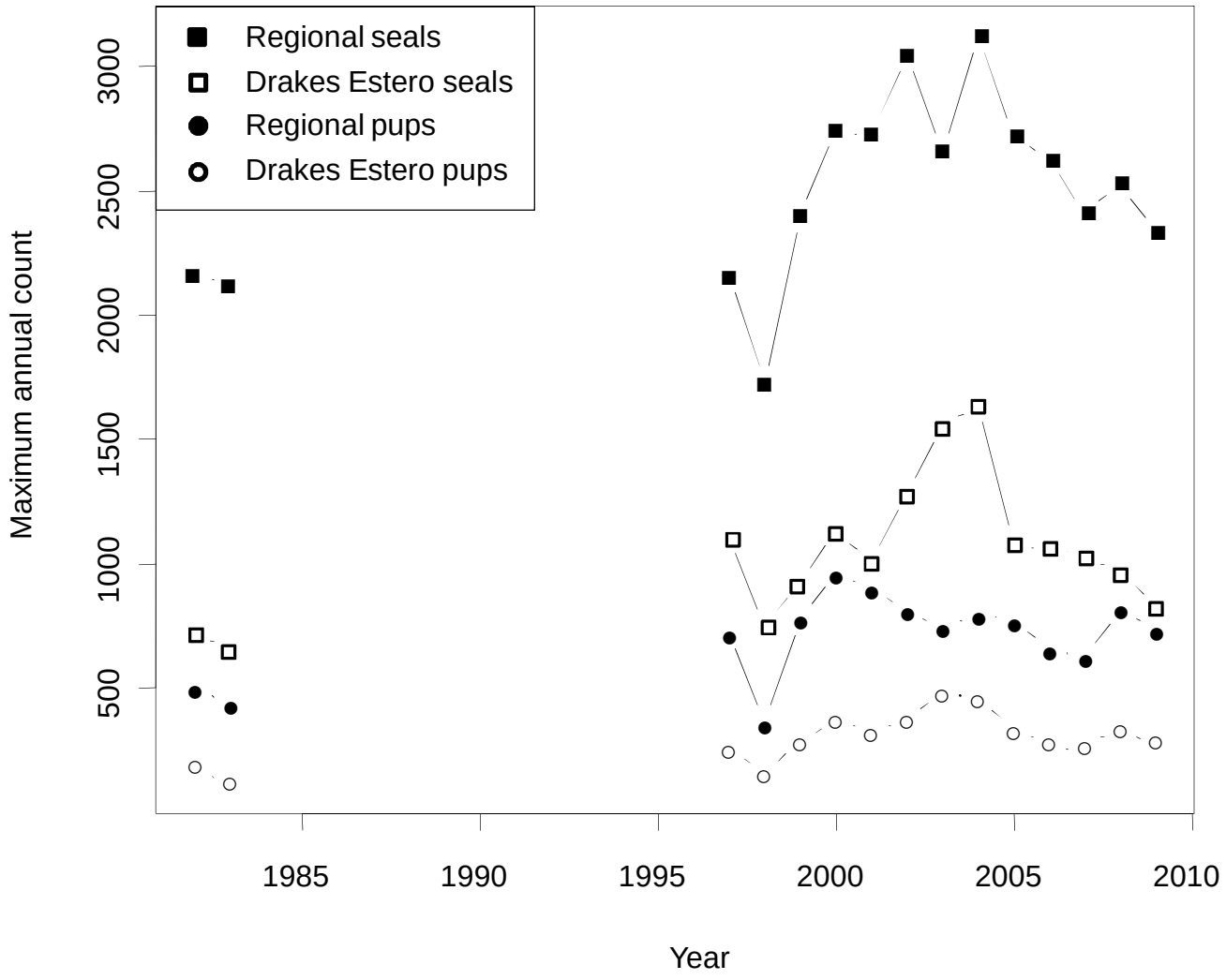

Figure 5. Annual maximum counts of harbor seals in Drakes Estero and the Point Reyes region (less Drakes Estero) during April 15 – May 15, between 1982 and 2009. Regional surveys were not conducted between 1984 and 1996.

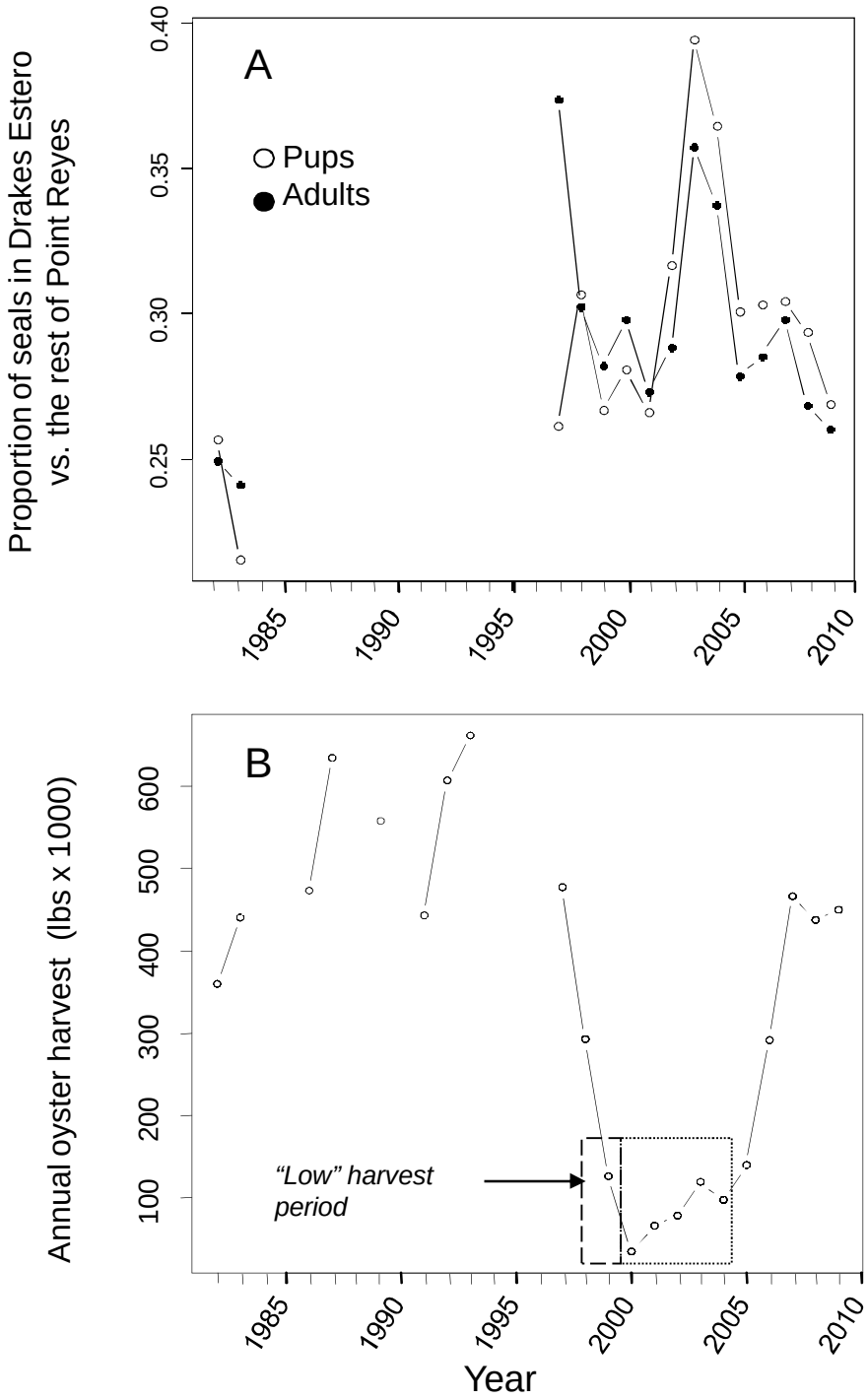

Figure 6. 1982 – 2009 time series of (A) proportion of Point Reyes region pup and adult harbor seals in Drakes Estero during the breeding/pupping season and (B) oyster harvest in Drakes Estero. Due to uncertainty in classification (Table 1), 1999 was modeled as both a "high" and "low" oyster harvest year. The 2009 oyster harvest is estimated based on 2007-2008 harvest.

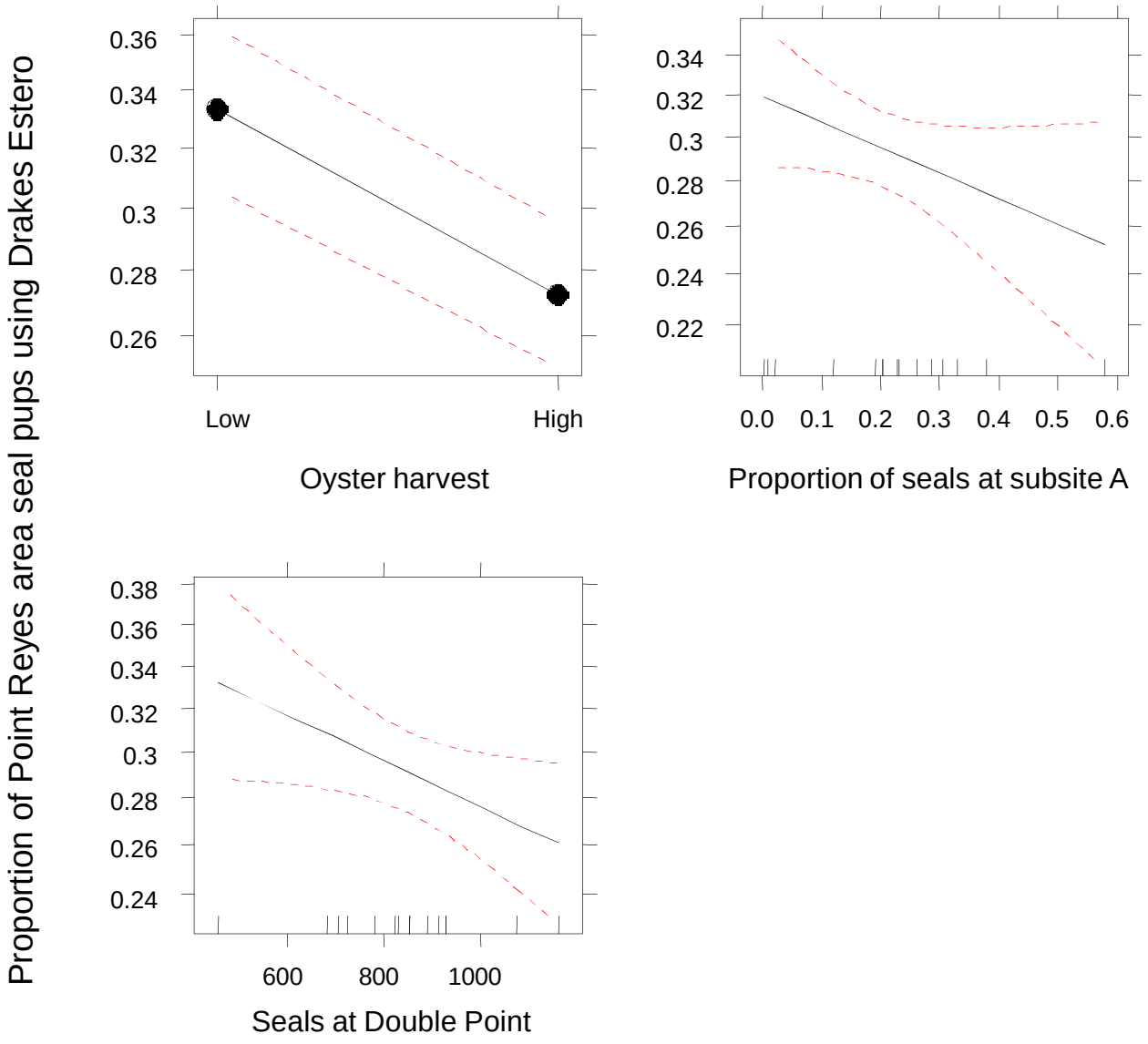

Figure 7. Model effects plots with standard errors for the proportion of Point Reyes area seal *pups* using Drakes Estero. Plots derived from the best model containing all three terms (oyster harvest, subsite A and double point. Multi-model averaged results are similar, but not identical (Table 5).

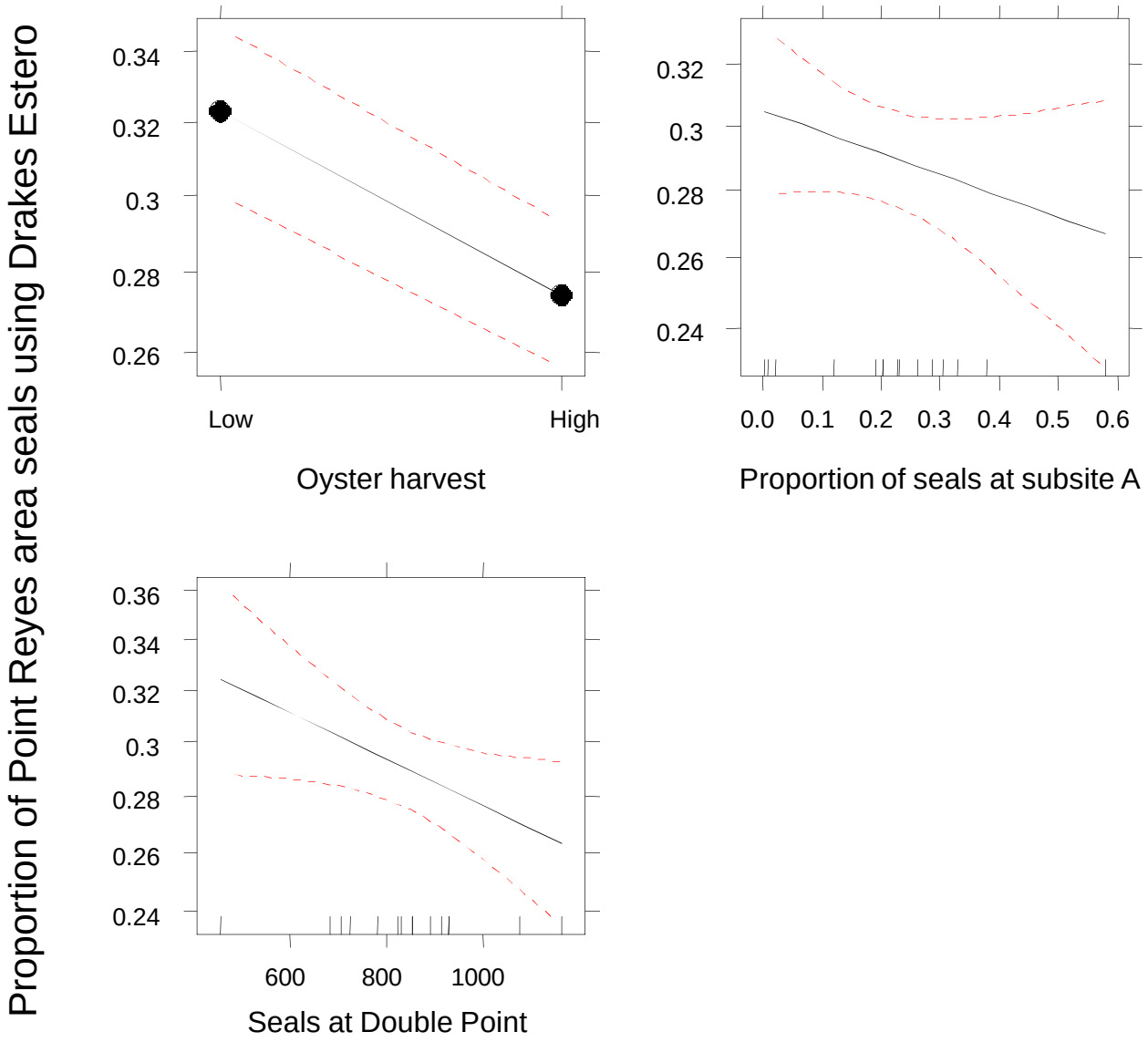

Figure 8. Model effects plots with standard errors for the proportion of Point Reyes area *seals* using Drakes Estero. Plots derived from the best model containing all three terms (oyster harvest, subsite A and Double Point). Multi-model averaged results are similar, but not identical (Table 5).

Supplement to Table 4. This table includes information in Table 4 and additional details of models tested. *A priori* models ranked by QAICc for the proportion of Point Reyes area seals 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			Nearby colonies		Internal colony effects							
Age class	**Model**	**Low oyster 2000-2004**	**Low oyster 1999-2004**	**Oyster harvest**	**Total regional counts**	**Double Point counts**	**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	0.06	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	0.01	0.66
	15					x				x		6.4	0.01	0.29
	16			x								6.5	.	0.15
	17					x						7.3	0.01	0.12
	18										x	7.7	0.01	0.00
	19								x			7.7	0.01	0.11
	20							x				8.2	0.01	0.09
	21					x			x			9.1	0.00	0.19
	22			x			x					9.2	.	0.19
	23					x		x				9.8	0.00	0.17
	24				x							10.3	0.00	0.02
	25						x					10.6	0.00	0.01
	26					x	x					11.0	0.00	0.13
	27				x			x				11.9	0.00	0.10
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	0.09	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							7.9	0.01	0.19
	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			x				10.5	0.00	0.22
	21										x	10.9	0.00	0.00
	22							x				11.7	0.00	0.07
	23						x					12.4	0.00	0.05
	24								x			12.6	0.00	0.05
	25					x		x				13.0	0.00	0.15
	26					x	x					13.2	0.00	0.14
	27					x			x			13.4	0.00	0.14