Evidence for long-term spatial displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades[†]

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ABSTRACT

1. Shellfish mariculture is increasing worldwide and often occurs adjacent to marine mammal breeding and feeding habitat. To better understand breeding pinniped vulnerability to potential shellfish mariculture disturbance and displacement effects in a US National Park, potential mechanisms were explored that may affect the proportion of harbour seals (*Phoca vitulina*) selecting high quality haul-out sites near shellfish aquaculture within a large colony, and overall seal utilization of that colony in relation to other regional colonies.

2. Seal haul-out sites isolated from the mainland (no predator access) had higher pup:adult ratios, indicating they are generally more important for pupping. Short-term human disturbance did not have a significant effect on spatial use, but rather spatial use was pre-determined by general sandbar isolation. Using multiple competing hypothesis and an information-theoretic approach, it was found that within the estuary, after removing effects of El Niño, the proportion of seals (total seals and pups only) hauled out near mariculture sites was $8 \pm 2\%$ lower during years of higher oyster harvest. Annual oyster harvest was used as a measure of aquaculture activity that could result in direct disturbance or indirect displacement of harbour seals.

3. At the regional scale, oyster harvest, seal counts at a nearby colony, and loss of a major haul-out site within the estuary, best explained pup and total seal use compared with the region. Regional population size, short-term human disturbance rate, and other factors were not important. Concurrent with higher oyster harvest, the proportion of regional seals using the estuary declined by $7 \pm 2\%$ for seal pups (-65 ± 18 total pups), and $5 \pm 2\%$ for total counts (-192 ± 58 total seals). These findings (both within the estuary and at the regional scale) were essentially identical whether modelling oyster harvest as either a continuous or categorical (low/high) variable and when using either frequentist or Bayesian statistical analyses.

4. Marine reserves set aside for wildlife may be less effective when the highest quality breeding and pupping sites are adjacent to regular aquaculture activities. These effects may not be detectable until additional natural variation lowers the quality of nearby habitats.
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INTRODUCTION

A variety of factors may influence habitat availability for breeding, moulting, and resting 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 (Freitas *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 human disturbances by increasing heart rates and energetic costs (Bisson *et al.*, 2009). Thus, seals are expected to move away from, or remain vigilant to, disturbance sources rather than habituate as some smaller, quickly reproducing species do (Bisson *et al.*, 2009). This might be particularly evident for females with pups, which should be more risk averse than adult males. Furthermore, 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 14

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bird and mammal studies they reviewed. In marine mammals, bottlenose dolphin (*Tursiops* sp.) declined in relative abundance owing 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).

Shellfish aquaculture and aquaculture in general is increasing worldwide (FAO, 2006). Würsig and Gailey (2002) concluded that there is a 'need to consider potential loss of (i.e. marine mammal) 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 in habitat use by bottlenose dolphins (Watson-Capps and Mann, 2005) and dusky dolphins (Markowitz *et al.*, 2004). A recent review by the US National Research Council (NRC, 2009) concluded that oyster harvest activities may have 'potential negative interactions' with harbour seal use (*Phoca vitulina*) of haul-out sites near mariculture operations in an ∼800 ha estuary in California known as Drakes Estero. They stated that 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, 2009: p. 49) and noted that seal counts near oyster operations were over-dispersed (higher than expected variation) during a high oyster harvest year when compared with a low oyster harvest year, which may be indicative of undetected disturbance events. These conclusions were based on expert opinion, reviews of other studies (Allen and Huber, 1984a; Montgomery *et al.*, 2007), and a limited analysis of seal monitoring data (Becker *et al.*, 2009). In this work a more thorough investigation of these factors is made and the following questions are posed: (1) are these potential negative interactions still apparent with additional years of monitoring data and at different scales? (2) Are females with pups sensitive to negative interactions? (3) Is there a difference in the impact of typically short-term national park visitor (generally hikers) disturbance at sites that are already suboptimal for pupping since they are attached to the mainland (and therefore can easily be accessed by predators), versus potentially longer-term activities, such as from aquaculture operations that use motorboats and place and service aquaculture structures on and adjacent to the isolated (predator and hiker free) sandbars where seals haul out? (4) Could any negative spatial effects on seal use caused by human disturbance or aquaculture activities cascade up from the haul-out subsites near the oyster operations to throughout the entire estuary's breeding and pupping season population and to surrounding regional colonies? If seals simply moved to other areas within the estuary, the proportion of the population using the estuary compared with the region would not change. Conversely, if there was 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 resulting in some seals not using the estuary (Gill, 2007).

Here, seal use is investigated within Drakes Estero in response to mariculture by testing multiple factors at three spatial scales that may be related to seal use (for total seals and pups). The scales range from (a) *subsite* level seal counts and pup:adult ratios, to (b) *colony* level for distribution of seals within all of Drakes Estero, to (c) the *regional* level comparing seal counts in Drakes Estero with those in the other regional colonies (Figure 1). This last regional effect would be somewhat surprising, since aquaculture chiefly occurs in only about 50% of the estuary in the upper sandbars of Drakes Estero (see Figure 1). 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 estuary, and increased migration to other less disturbed colonies. 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; Becker *et al.*, 2009). Several predictions were made that scaled from *subsite* to *intra-colony* to *regional* scales (Figure 1).

Subsite scale – We predicted that (1) isolated island sandbars, 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 individual haul-out sites, 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; Figure 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 those by mariculture activities (Becker *et al.*, 2009).

Regional scale – We predicted that (1) the effects of El Niño–Southern Oscillation (ENSO) on seal use of the estuary as a whole, would be the same as for other colonies in the region; (2) regional population size expansion would affect the proportion of regional seals using the estuary only if it had more good habitat than other colonies; (3) overall estuary 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 the estuary compared with 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 the estuary), and (c) mariculture activity that would partially explain overall use of the estuary 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 owing to factors (a) and (b).
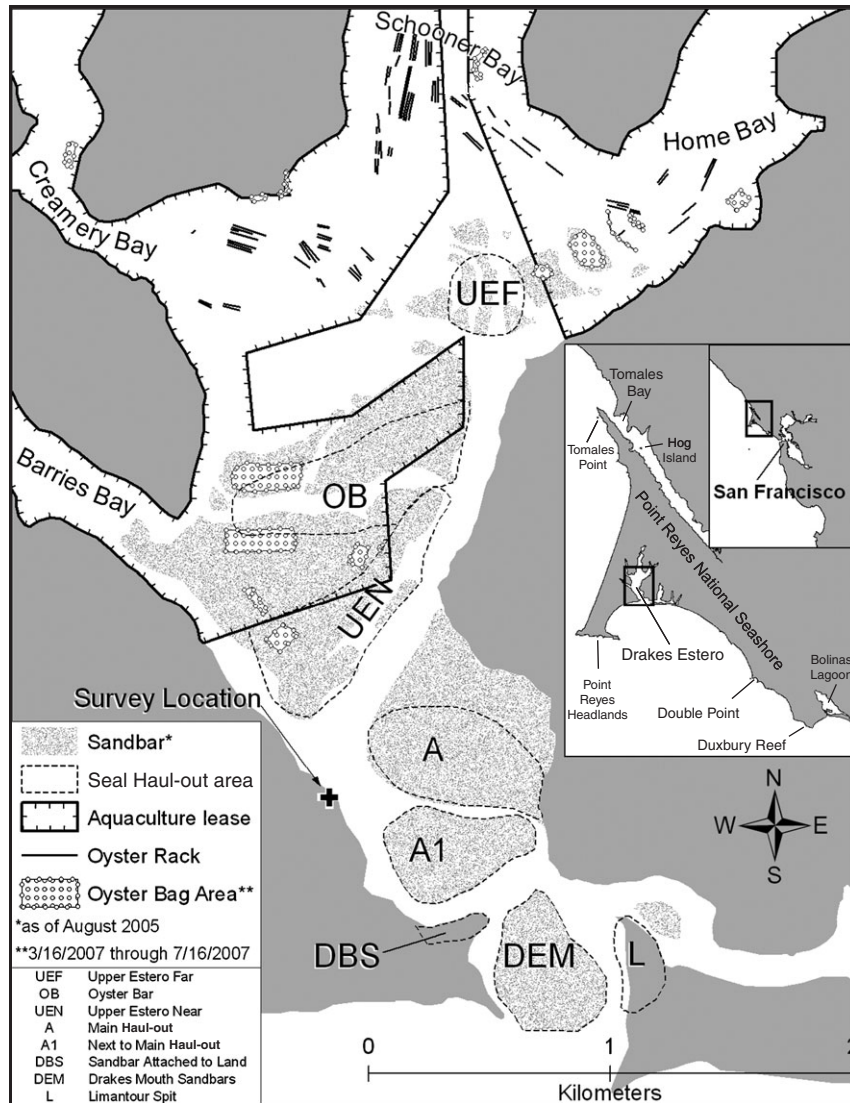
Figure 1. Drakes Estero and the eight labelled seal haul-out subsites. Subsites UEF, OB, and UEN are considered 'near' mariculture, while A, A1, DBS, DEM, and L are considered 'away' from mariculture. Inset shows all the Point Reyes area colonies: Tomales Bay, Tomales Point, Point Reyes Headlands, Drakes Estero, Double Point, Duxbury Reef, and Bolinas Lagoon. Figure modified from Becker et al. (2009).

METHODS

Study area

The Point Reyes peninsula is on the north-central California Coast (38°30′N to 37°30′N) and is located within Point Reyes National Seashore, a unit of the US National Park Service (NPS). The topographic diversity of the peninsula provides a broad range of substrates for harbour 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 is typically a collection of haul-out sites within a limited geographic area. Drakes Estero is an estuary that contains a complex of eight sandbar sites where seals haul out, here which are referred to as 'subsites' (Figure 1). Drakes Estero is typically the largest of several harbour seal colonies along the Point Reyes peninsula. Seals use the subsites at

various times of the year depending on their reproductive status, moulting condition, and the level of disturbance encountered (Allen Miller, 1988). Within a day, seals can shift to adjacent sandbars when crowding occurs or when the tide rises limiting the amount of haul-out space (Cunningham et al., 2009). At rising tides, seals also float over submerged sandbars until the sand bars reemerge with receding tides.

All eight subsites in Drakes Estero are used during the breeding and moult seasons, and some are used regularly year-round. Females with pups disproportionately use 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 (L) at the south of the estuary is mostly used by non-breeding seals during the breeding season (Allen Miller, 1988). Subsites in the lower estero, which are generally attached to the mainland, have historically suffered higher annual human disturbance rates during the breeding season when compared with the isolated island sandbars of the upper estero (Becker et al., 2009).

Human access to the seal haul-out sites within Drakes Estero is limited because it is part of a US National Park and managed as a congressionally designated wilderness area. No motorized boats are allowed within the estuary except for those from a commercial shellfish operation which currently makes approximately 1500 motorboat trips per year into the estuary[1] (but not all trips are near seal haul-out sites). Other than at the oyster processing facility, there is nowhere in the estuary to launch a trailered motorboat. The nearest port available to launch a small boat is over 29 km away over open ocean, and the harbour seal monitoring programme (described below) which conducts surveys at the mouth of the estuary has not observed any motor boats entering or leaving via the mouth of the estuary during more than 400 surveys over 21 years. With special permission and regulation, research and rescue boats may enter the estuary in rare instances (generally less than three times per year). Non-motorized boats, primarily kayaks, were allowed year-round access until 1994, but thereafter were excluded from 1 March–1 July to avoid seal disturbance during the breeding and moult seasons. Nonetheless, violations do occasionally occur.

Three of the subsites where seals haul out are proximate to the commercial shellfish aquaculture operation (OB, UEN, and UEF) (Figure 1). Subsite OB is within the aquaculture lease area but was not used much for oyster culture in the recent past ($\sim$2000–2004), portions of subsite UEN are within or adjacent to the lease area, and subsite UEF is in a navigational channel that bisects a gap in the mariculture lease where aquaculture boats traversed Drakes Estero (Figure 1). The aquaculture operation primarily raises oysters (and occasionally small amounts of manila clams). The California Department of Fish and Game (CDFG) produces an annual report on the mass of oyster harvest production.

Datasets

Disturbance data

Harbour seal survey methods are described in Becker *et al.* (2009) and Adams *et al.* (2009). Disturbance rate was derived from the number of human related disturbances (park visitors, kayaks, airplanes, aquaculture activity, etc.) that resulted in a head alert, a flush (seals move but do not enter the water), or a flush of seals into the water during the breeding period (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 ($\sim$2 h), except for three longer surveys (5–9 h) during 1982–1983. Using Spearman tests, daily and hourly disturbance rates were compared for the years 1982–2009 (15 years surveyed) to ensure that variation in survey length during 1982–1983 did not affect realized disturbance rate. Motorboat sighting rate was derived from this dataset. However, the surveys were not designed to systematically record motorboats, so there may be some error associated with motorboat sighting rate (NRC, 2009).

Intra-colony data

When assessing *intra-colony* variation in use, the daily counts (converted to binomial proportions when modelled) at each subsite for all surveys during the peak breeding season (April 15–May 15 of each year) were used for a total of 21 years between 1982 and 2009. NPS seal count data from 1997–2009 were used and QA/QC was identical to that used in Becker *et al.* (2009). This was augmented with additional subsite seal count data from (1) the years 1982–1983, 1986–1987, 1989, and 1991–1993 derived from field notes of one of the co-authors (SGA), and (2) annual maximum breeding season pup and adult colony counts (Allen and Huber, 1984a, b). Oyster harvest data were obtained from the California Department of Fish and Game (1982–2009).

Regional data

The maximum counts of pups and adults from the maximum total count of the day were used 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) (Figure 1 inset).

Analyses

Boat sightings, oyster harvest and the spatial extent of mariculture equipment

A Pearson correlation test was used to assess the relationship between the daily rate of all motorboats sighted in the estero during March–May of each year, and annual oyster harvest activity from 1996–2009. The annual oyster production was related to the acreage of oyster equipment either on sandbars OB, UEF, and UEN, including equipment within $\sim$300 m ($\sim$1000 ft) of UEF. The NRC (2009) concluded that harbour seals within 500 m of aquaculture equipment could be expected to suffer from short-term disturbance by oyster workers. Subsequently, this somewhat conservative 300 m boundary was chosen since this eliminates equipment in the upper arms of the estero, but includes areas near subsite UEF (Figure 1). Acreage was calculated from available aerial photos or site visits with a GPS during nine years between 1993 and 2009. Density of oyster planting, planting methods (stake vs bags), and time of year were not taken into account. However, images and data were generally collected in the spring/summer except the 2009 image, which was from November. At the 2009 harvest level, there were approximately 1500 oyster boat trips per year into the estuary, and some unknown percentage of these trips must attend to oyster equipment near seal haul-outs. While it has not been determined if the number of motorboat trips varies with annual harvest, if the spatial extent of the equipment changes with harvest level, then workers should need to travel over larger or smaller areas to tend oysters, and presumably vary the duration and/or number of workers on site.

We also related spring (seal pupping season: March–May) oyster harvest to annual oyster harvest for 27 years between

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[1]K. Lunny, Drakes Bay Oyster Company, Marine Mammal Commission Meeting, June 7, 2010.

1982 and 2009 to ensure that any within-year variation in seasonal harvest would not affect use of annual oyster harvest as a covariate in the modelling section of this paper. Simple Spearman and Kendall non-parametric correlations were used to test for a significant relationship between the two variables (spring harvest vs annual harvest and area vs annual harvest).

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 (March–May) anthropogenic disturbance rate (explanatory variable) was related to annual maximum seal counts, maximum pup counts, and pup:adult ratios (response variables) within subsites and across all subsites between 1997 and 2009. Some upper estero subsites (OB, UEN, UEF) were occasionally pooled in the 1982–1993 field note data, so those years were not used for this within subsite analysis. The counts were modelled 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/number of surveys) in either the upper or lower estero (Figure 1), or the pooled maximum annual seal counts of all other Point Reyes area colonies (regional population size). A two-step process was used for modelling. Using the 15 year dataset, generalized linear mixed models (GLMMs) were used to assess effects on seal distribution between the near (upper) and far (lower) from 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). Models for the full time series (all 21 years) without regional counts and disturbance covariates were then tested using generalized estimating equations (GEEs). GEEs are similar to GLMMs, but allow for more flexible autocorrelation and distribution assumptions (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. 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 modelled 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 size differently at different breeding colonies. Year was considered a random effect.

'Years since ENSO' were modelled as log (years since ENSO+1) because both observational and theoretical evidence suggest that any demographic ENSO effects should taper off and not be linear. Annual changes in the spatial extent of sandbars in Drakes Estero and other regional colonies are not available and were therefore not modelled. However, dramatic changes in the size and isolation of subsite A (Figure 1) were documented and that process was explicitly modelled in the 'regional scale' analysis (below). Tests were made (post-hoc) for a potential effect of a 1992 agreement by the oyster company to restrict operations near seal haul-out sites, and yearly count data were weighted by the number of annual surveys to account for any potential reduced precision due to fewer annual harbour seal surveys during the 1980s and early 1990s.

GEEs were run in R using 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 (15 April–15 May) in each year and counts closer together should have higher correlation since seal counts generally rise, peak, and decline during this time (Allen and Huber, 1984b; Hayward et al., 2005). Nested models (e.g. ENSO+oyster harvest vs ENSO only) were tested for differences with likelihood ratio tests with the simplest adequate (difference not less than $P < 0.05$) model retained. The final model logit coefficients were then back transformed (Crawley, 2007) to calculate the proportional change in seals using the three subsites near mariculture model, and the proportion was multiplied 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 owing to any significant factors.

Regional scale: Drakes Estero compared with surrounding colonies

Regional anthropogenic and natural effects during the breeding season were examined by comparing maximum seal counts (pups and total) in Drakes Estero with the sum of all other regional Point Reyes colonies (Tomales Bay, Tomales Point, Point Reyes Headlands, Double Point, Bolinas Lagoon, and Duxbury Reef) (Figure 1). Several variables were examined, as well as a null model, in relation to the annual maximum proportion of seals (total seals and pups only) using Drakes Estero compared with the proportion using the other six regional colonies. 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 became 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 between Double Point and Drakes Estero (Allen Miller, 1988; Grigg et al., 2009), and in 2003 an aggressive elephant seal probably displaced numerous harbour 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 motorboats. Kayaks have been prohibited from the estero during the breeding season since 1994.

- *Years since the last major ENSO* (1982–1983 and 1997–1998). Strong ENSO events depress reproduction and thus may influence habitat use.
- *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 of equal quality.
- *Annual oyster harvest* (Appendix A) as a measure of shellfish mariculture activity and/or equipment placement in the estero.
- *Five- and six-year periods of lowest oyster harvest* (2000–2004 and 1999–2004) (Appendix A) as a measure of the simple presence/absence of oyster activity and equipment. Aerial images confirm that oyster bags were present on top of and adjacent to seal haul-out sites in 1993, 1994, 2005, and 2007–2009. Personal observations (DTP), and aerial images indicate that there were few or no bags on the upper seal islands from 2001–2004. We infer from the oyster harvest records that there were few or no bags in 2000 since the harvest was lower than 2002–2004, and conversely that there probably was infrastructure from 1997–1998 when harvest was higher. The year 1999 is difficult to categorize based on the available data. Thus, the oyster harvest covariate for 1999 was modelled as both a high and low oyster harvest year.

Modelling the pups and the total seals (adults+pups) 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 and Huber, 1984a; Allen Miller, 1988; Nordstrom, 2002). Covariates were not combined in a single model if the variance inflation factors (VIFs) were above 3 (Zuur *et al.*, 2009). Tests were made for interannual autocorrelation in the proportion of pups and total seals in Drakes Estero using detrended time series and by inspecting autocorrelation and partial autocorrelation plots.

Binomial generalized linear models (GLM) were used to model the probability that any random seal was found in Drakes Estero (success) versus somewhere else in Point Reyes (failure). To account for overdispersion (variance larger than expected for binomially distributed data a quasi-binomial family was used to assess *P* values and overdispersion, and a 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). The best-ranking models were bootstrapped (the model was refitted with data from each year sampled at random with replacement) 2000 times to gain unbiased standard errors for the oyster harvest variable (Crawley, 2007). Bootstrapping should also uncover any highly leveraged effects from 1 or 2 years of data. Models and QAICc values are reported for *both* the continuous oyster harvest value and the low/high oyster models, but only the 2000–2004 low/high variable is considered 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 four 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 (R Development Core Team, 2009).

To further assess the robustness of the GLM results, a Bayesian analysis was performed on a subset of the best-performing regional scale models for harbour seal pups. This analysis was conducted in WinBUGS 1.4 (Lunn *et al.*, 2000; Zuur *et al.*, 2009; Kéry, 2010) using the R package R2WinBUGS for combinations of oyster harvest (continuous data), pup counts at Double Point, and regional pup counts. Similar to the GLM models, a binomial distribution was used both with and without overdispersion, and models were ranked using the Deviance Information Criterion (DIC), the Bayesian equivalent of AIC. The analyses used non-informative priors for all coefficients (including overdispersion), initial values of zero for all parameters (slopes, intercept, precision, and overdispersion), ran 100,000 iterations (after a 100,000 iteration burn in to remove effects of initial values), thinned the data by every 25th iteration to remove autocorrelation, and ran three model chains.

RESULTS

During 1982–2009, the mean number of breeding season harbour seals hauled out in Drakes Estero was 775 ± 269 total seals and 180 ± 94 pups (Figure 2). 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; proportion using Drakes Estero shown in Figure 3(A)). Daily maximum Drakes Estero seal breeding season counts varied throughout the study period, with upper estero seals showing a peak during 2002–2004. Annual maximum counts of harbour 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
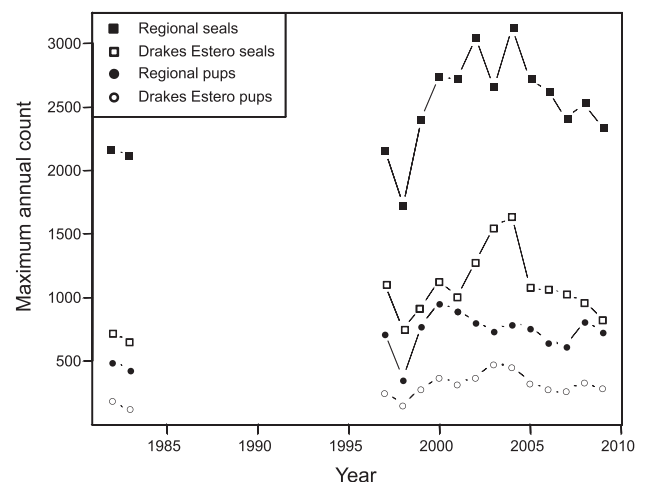
Figure 2. Annual maximum counts of harbour seals in Drakes Estero and the Point Reyes region (less Drakes Estero) during the peak pupping period (15 April–15 May) from 1982–2009. Regional surveys were not conducted between 1984 and 1996.

(Figure 2). Pup counts in Drakes Estero climbed from 2000–2004, while those in the rest of the region slowly declined. Excluding the period from 2000–2004, the pup counts between Drakes Estero and the region appeared to have similar trends.

Oyster harvest and the spatial extent of mariculture equipment

Oyster harvest experienced a low period from ∼2000–2004 (Appendix A, Figure 3(B)). During years of higher oyster harvest, there were more motor boats observed in the estero during March–May of each year ($r_p = 0.67$, $P < 0.01$). Spearman rank correlation tests had similar results ($r_s = 0.53$, $P < 0.06$). Spring (March–May) oyster harvest and annual (January–December) oyster harvest were highly correlated ($r_p = 0.97$, $P < 0.001$, $n = 27$). The spatial extent of mariculture equipment within 300 m of seal haul-out sites was also highly correlated with annual (and subsequently Spring) oyster harvest ($r_s = 0.91$, $P < 0.01$, $n = 9$; Figure 4).

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: Figure 5). 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 counted each year.

Annual human disturbance rate during spring (March–May) of each year (1982–1983 and 1997–2009) had a similar pattern whether using daily or hourly rate ($r_s = 0.99$, $n = 15$) and so daily rate was used in all subsequent models and calculations. There were 153 spring human disturbance events during this time, the majority of which were non-motorboat related and at lower estero haul-outs. The daily disturbance rate averaged 0.71 ± 0.41 for each year, with 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 human disturbance rates. 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). 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 these results. We conclude that there is not a robust, detectable
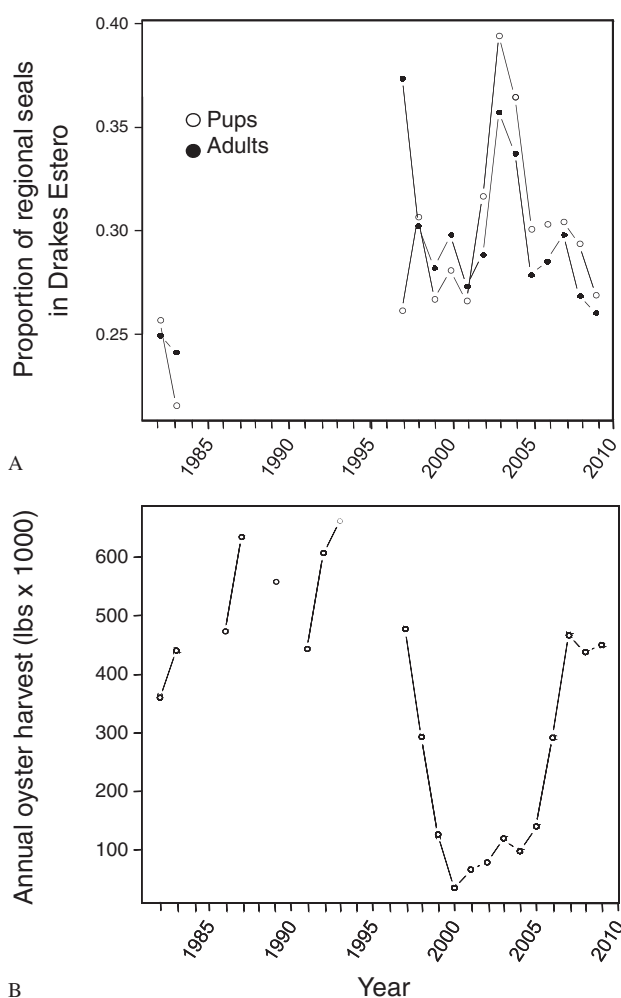

Figure 3. 1982–2009 time series of (A) proportion of Point Reyes region pup and adult harbour seals in Drakes Estero during the breeding/pupping season and (B) oyster harvest in Drakes Estero. Oyster harvest is shown for years with colony and regional scale analyses.
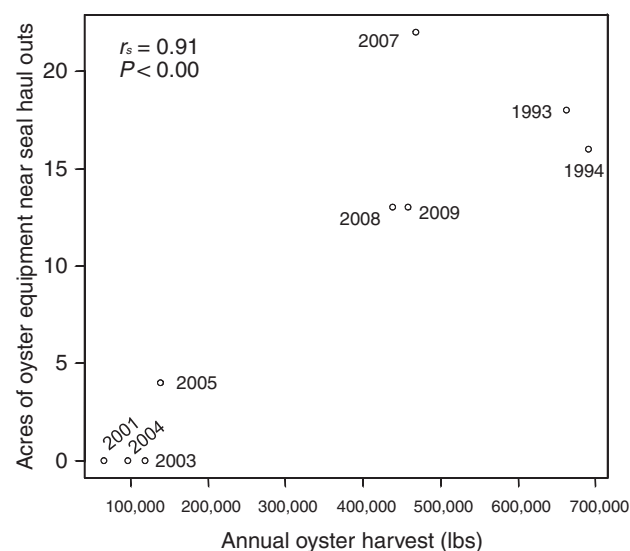
Figure 4. Relationship between annual oyster harvest and the acreage of oyster equipment near (<300 m) or adjacent to seal haul-out sites.
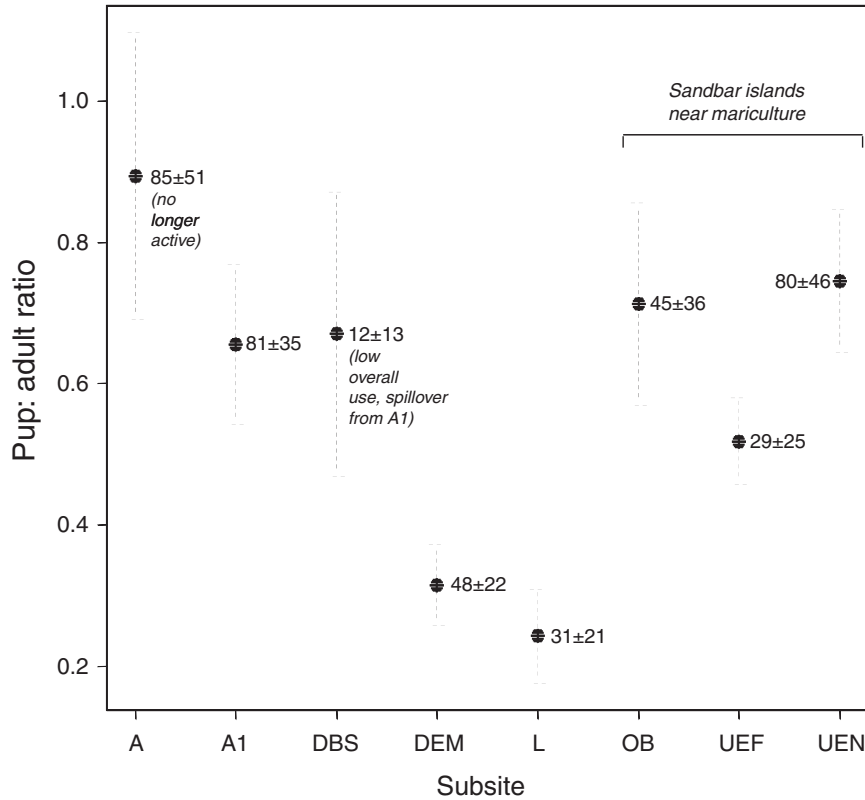
Figure 5. Mean ($\pm$SE) of maximum annual pup:adult ratios by subsite in Drakes Estero, 1997–2009. Numbers next to points represent the mean ($\pm$SD) of the maximum annual pup counts at that subsite from 1997–2009. The ratios at the estero mouth (DEM and L) are lower than the other six subsites and UEF is lower than A. DBS is adjacent to A1 and has very low seal and pup counts ($\sim 12\,\mathrm{y}^{-1}$), indicating it is a minor site that appears to catch spillover seals when A1 gets crowded. Since 2004, seals have abandoned subsite A due to attachment to the mainland and subsequent predator and human access.

relationship between spring human disturbance rate and pup:adult ratios at individual or subsites or overall in Drakes Estero. Further, individual subsite based binomial GLMs for the years 1997–2009 indicated that subsite pup:adult ratio trends with disturbance rate were not significant.

Colony scale: Drakes Estero subsite models

Oyster harvest and ENSO best explained the proportion of seals (pups and total) using the upper estero (Table 1). Both the 'lmer' and 'glmmML' functions in R reported similar results, as did quasibinomial and binomial distributions. Upper estero disturbance rate was 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 1982–1983 and 1997–2009 models, GEEs were used to analyse 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

Table 1. 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 in bold

Model	ΔAIC	
	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).

sites closest to mariculture activity (Table 2). 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 that 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 human 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 2).

Post-hoc GEE models (overdispersion corrected) only testing annual seasonal survey sample size, oyster harvest, ENSO, and the pre/post 1992 restrictions, showed that there was no detectable effect of the 1992 seal area restrictions on the total proportion of seals using the upper versus lower estuary ($P > 0.66$). However, contrary to expectations, it appears that fewer seal pups used the upper estuary after the agreement ($P < 0.05$), possibly since oyster harvest rate was still relatively high. Weighting the data by the annual number of surveys had no affect on the model results shown in Table 2.

Regional scale: Drakes Estero compared with 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 (Figure 3(A)). Because 1997 was an outlier for the adult and/or pup proportion of seals in Drakes Estero, the total seal count data for 1997 was weighted by the ratio of the proportion of pups to adults in that year ($\sim$ 0.3) (Venables and Ripley, 2002). This is reasonable (and preferable to omitting the data) since there was an anomalous harbour 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. and NPS unpubl. data), although the sampling from that study was not random.

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 because of an aggressive elephant seal (Mortensen and Follis, 1997; Hayward, 2003; pers. comm. F. Gulland, The Marine Mammal Center), 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. Variance inflation factors (VIF) also found no evidence of collinearity as long as year or ENSO were not modelled with subsite A. 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 ($\varphi = 4.5$) and somewhat more over-dispersed for the total seal count global model ($\varphi = 8.6$). These values were used 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; Figure 6, Table 3). Similarly, using direct (continuous) oyster harvest rather than the low/high classification also appeared in all the top ranking models. 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 it was not included 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 3). 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 3 and the oyster harvest standard errors were smaller than those reported by model fitting alone, indicating robust and conservative estimates from the GLM (Table 4). 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 4) during high oyster harvest years.

The Bayesian analysis reported nearly identical results to the GLM, but suggested that oyster harvest alone (without other covariates) best explained seal pup use of Drakes Estero (Table 5), although other models were closely ranked. The model converged within the first 100 000 iterations. Thinning the results to one out of 25 iterations removed all serial dependence in the chains. Logit model coefficients for annual oyster harvest and Double Point pup counts were nearly identical to the GLM results (Table 4). Models that did not

Table 2. 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

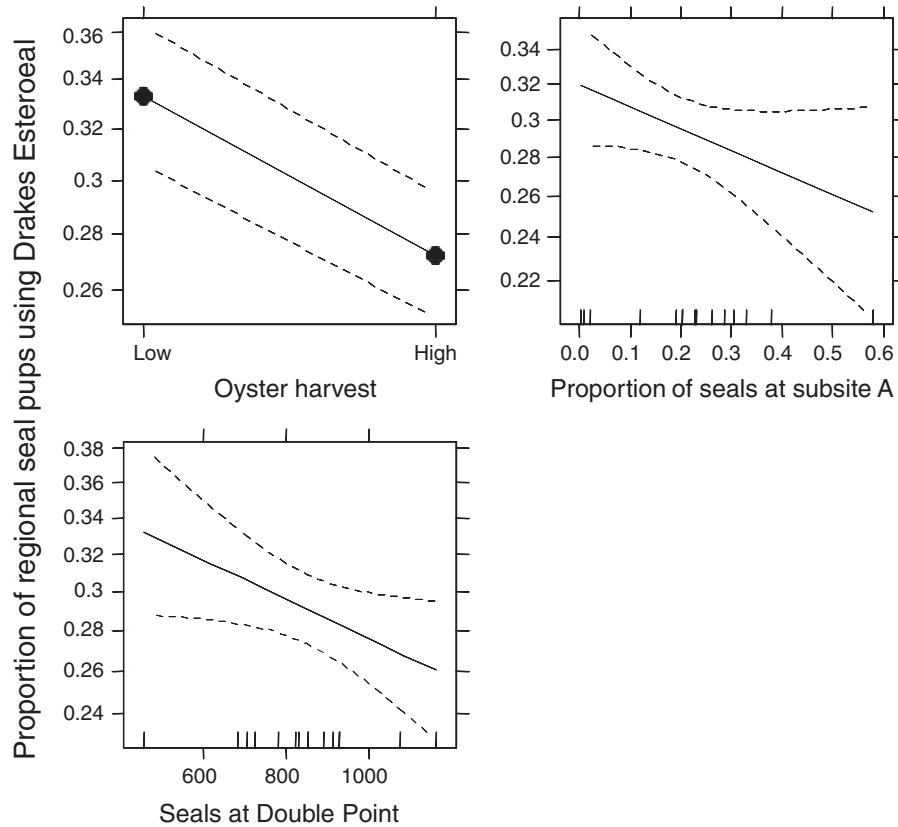| Model	Pups				Total seals			
	Coefficient	Proportion	Effect size	P	Coefficient	Proportion	Effect size	P
Intercept	-1.39 ± 0.34			<0.001	-1.50 ± 0.25			<0.001
Log(ENSO+1)	0.65 ± 0.20			<0.001	0.52 ± 0.14			<0.001
Oyster high/low	-0.41 ± 0.19	-0.08 ± 0.03	-14 ± 4	<0.03	-0.44 ± 0.14	-0.08 ± 0.02	-59 ±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

Figure 6. Model effects plots with standard errors estimating the proportion of regional seal *pups* using Drakes Estero. Plots derived from the best model containing all three terms (oyster harvest, subsite A, and Double Point). Plots from multi-model averages and Bayesian analyses are similar, but not identical. Plots for total seals (not shown) are essentially identical.

account for over-dispersion had a much poorer fit (higher DIC) and were therefore not considered.

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 (Ellenberg *et al.*, 2006; Bisson *et al.*, 2009). Harbour seals have both a long lifespan ($\sim$20–25 years), and give birth to a single pup per year, which suggests 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.*, 2009). Present findings agree with those of Frid and Dill (2002), who reported that chronic, long-term disturbance stimuli result in habitat shifts and reduced access to resources. In this present study, aquaculture activity is related to a habitat shift and subsequent reduced access to high quality haul-out sites. Conversely, shorter term disturbance stimuli (primarily hiking park visitors at lower quality haul-out sites) were not related to reduced pup:adult ratios at subsites in the estuary, or strongly to detectable patterns in intra-estuary (upper versus lower) or inter-colony proportional use by seals. Rather, pup:adult ratios at haul-out sites appear to be strongly

driven by their physical isolation from the mainland (Nordstrom, 2002) and when disturbed, seals shift to alternative sandbars away from disturbance sources (Allen *et al.*, 1984). However, this relationship may be complex. For example, 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.

There are some inherent difficulties in the use of disturbance rates to infer effects on seals (Frid and Dill, 2002; Hayward *et al.*, 2005; NRC, 2009). For example, many disturbances related to mariculture probably go undetected (NRC, 2009), especially since about 50% of harbour seal surveys are on weekends and more visitors are out on weekends, while the oyster harvest work occurs primarily during weekdays, and less frequently on weekends (NRC, 2009). Surveys may also miss any disturbances on the ebb tide that might prevent seals from hauling out (NRC, 2009) or due to simple lack of detection owing to distance from observers.

Oyster harvest and ENSO were the primary variables associated with temporal variation in spatial use by seals in Drakes Estero at these remote, isolated sand bars. 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 regional colonies. Instead, oyster harvest, internal subsite, and nearby colony dynamics were consistently important.

Table 3. 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. Models ranking within the lowest 4 QAICc units (in bold) 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. Rankings are similar if using continuous oyster harvest rather than *categorical*

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

It is logical that ENSO is important for the within-estuary dynamics, but not the regional dynamics. Within the estuary, the upper sandbars are important pupping sites. Seals pup less during ENSO events, so mothers with pups which predominantly use the upper estero, should be less represented. Conversely, all regional colonies produce pups, so lower pup counts during strong ENSO events should be ubiquitous across all colonies.

We suggest 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 QAICc units), that the pattern appears quite robust to both statistical methodology and length of the time series.

Results do not indicate that the seals are lost from the regional 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 regional colonies (for the regional analysis). This seems reasonable since 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).

Table 4. Multimodel weighted coefficients of all models within 4 QAICc of the best model for pups and total seals in Drakes Estero (see Table 3). Models represent an Akaike weight (wi) of 0.87 for both pups and total seals. 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

Variable	Logit coefficients		Proportional change		Effect size	
	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.

Table 5. Results of Bayesian analysis for the proportion of harbor seal pups using Drakes Estero. Deviance information criteria (DIC) ranks, model coefficients (±SE) and model ranks are similar to the frequentist GLM approach in Tables 3 and 4. Oyst: continuous annual oyster harvest; DP: Double Point pup counts; Pup: annual regional pup counts (less Drakes Estero)

Model	DIC	ΔDIC	Logit coefficients			
			Intercept	Oyst	DP	Regional pups
Oyst	135.3	0	−0.75±0.10	−0.05±0.04	–	–
Oyst+DP	135.4	0.1	−0.10±0.33	−0.08±0.03	−0.07±0.03	–
Oyst+DP+Pup	135.6	0.3	−0.20±0.41	−0.07±0.04	−0.08±0.04	−0.02±0.04
DP	136.0	0.7	−0.58±0.32	–	−0.04±0.04	–
Pup	136.0	0.7	−1.09±0.26	–	–	−0.03±0.04
Oyst+DP*	182.9	47.6	−0.09±0.10	−0.08±0.01	−0.07±0.01	–
Oyst*	220.6	85.3	−0.75±0.03	−0.05±0.01	–	–
DP*	224.2	88.9	−0.50±0.09	–	−0.04±0.01	–

*Overdispersion not accounted for in model.

The proportional reduction in seal use was generally larger for the upper estero (−0.08 pups and −0.08 total counts) 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, suggest 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, the findings are consistent with a scenario where subsite A lost habitat in 2003–2004, 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, before 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 in which seal resilience in the ecosystem is a function of both natural and human 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 1997–1998 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 owing 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 (i.e. attached to mainland). The estuary contains a dynamic system of sandbars near the mouth 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 harbour seal colonies in San Francisco Bay (Bartholomew, 1949; Allen, 1991). Similarly, Hog Island in Tomales Bay (Figure 1) was mostly abandoned by harbour seals in the early 1990s coincident with increasing numbers of boaters landing on the island (Allen and King, 1992). Prohibition of boat landings and camping coincided with a gradual resumption of use by seals (Allen *et al.*, 2010). 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 increase greatly, and then the counts (and proportion of seals using the subsites) rapidly declined again with increased mariculture beginning in 2005. The a priori modelling 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 harvest increased, similar to the seal response patterns at Hog Island.

Additional processes occurring at other colonies in the San Francisco Bay Area could also affect the patterns observed. This might include excessive disturbance, as well as immigration to or emigration from the entire study area. However, the fact that the best-fitting covariates (oyster harvest, Double Point, and subsite A) explain much of the intra- and inter-colony patterns observed over a long time series, suggests that these are probably not spurious relationships.

These 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.' The current data and analyses are consistent with natural and anthropogenically (aquaculture) driven seal colony dynamics both within Drakes Estero and between Drakes Estero and other colonies in the Point Reyes region. Encroachment by aquaculture or other chronic activities on or near 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. This cumulative process, which appears to have occurred in Drakes Estero, may diminish the effectiveness of this marine protected area for harbour seals. When identifying MPAs, planning would benefit from a review of potential cumulative effects that may reduce the resiliency of special status populations, such as marine mammals (Thompson *et al.*, 2001).

presented here are the work of the authors and do not represent a policy of US National Park Service.

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APPENDIX A

Sources and inferences for level of oyster harvest activity on or near subsites OB, UEF, and/or UEN. Data from CDFG and NRC (2009). In mid-2010, CDFG updated the annual oyster harvest records (K. Ramey, CDFG.), but the correlation between the original and the revised harvest values was very high ($r^2 > 0.94$), suggesting no significant changes in overall temporal patterns. 'Analysis scale' summarizes the years where complete seal count or disturbance data were 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.

Table A1.

Year	Oyster harvest (lbs)	Inferred level of mariculture use of sandbars near seals	Source(s) of inference	Analysis scale			
				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, oblique 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	aerial image of bags		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	modelled 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	aerial image of absence of bags	x	x	x	NPS
2002	78,064	low	DTP, pers. obs, harvest data	x	x	x	NPS
2003	118,643	low	aerial image of absence of bags	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 harvest	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	458,000	high	aerial image of bags	x	x	x	NPS