

SPATIAL DISTRIBUTION OF NEARSHORE FORAGING SEABIRDS IN RELATION TO A COASTAL MARINE RESERVE

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SUMMARY

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The Vandenberg State Marine Reserve (VSMR) was established in 1994 with the primary goal of protecting fishes and invertebrates targeted by fisheries. However, studies of other reserves have shown that effects cascade and benefit species at several trophic levels. We tested the hypothesis that the VSMR would provide benefits to nearshore foraging seabirds. We measured the foraging rates (mean number of individuals observed per hour) of seabirds at four plots (two inside and two outside the VSMR) over six years to test the hypothesis that foraging rates are greater inside the reserve than outside. The VSMR spans a coastal promontory, and we controlled for promontory effects by selecting plots at windward and leeward sites. All species showed either no difference or higher rates outside the reserve than inside. The consistency of our results over the six-year period illustrates predictable foraging behavior in these species. Piscivorous species foraged more in leeward plots than windward plots, while the benthic invertebrate specialist foraged more in windward plots. Our results reflect reported differences in community structure around coastal promontories; namely, windward habitats enhance biomass of suspension-feeding invertebrates while leeward habitats provide refuge for fish recruitment. Our results suggest that the VSMR is not protecting significant foraging habitat for nearshore foraging seabirds and that coastal geography should be considered when designing marine reserves to protect these species.

Key words: coastal promontory, marine reserve, nearshore foraging, seabird foraging, Brandt's Cormorant, Pelagic Cormorant, Pacific Loon, Surf Scoter

INTRODUCTION

Although seabirds are not directly targeted by fisheries, they can benefit from fisheries management. Tasker *et al.* (2000) describe fisheries impacts on seabirds as direct or indirect. Direct impacts include bycatch and disturbance to breeding colonies (especially where fishing is close to shore), whereas indirect impacts include competition for food resources. Marine reserves offer a means to address both direct and indirect fisheries impacts. Here we focus on the indirect impacts.

There is growing evidence that “no take” reserves can protect ecosystem diversity and even alter the community structure of fished areas, especially when developed within the context of other management schemes (Allison *et al.* 1998). Intense fishing practices have cascading effects on community structure, altering predator–prey relationships and even removing entire trophic groups (Sumaila *et al.* 2000). “No take” reserves offer a potential way to reverse such effects because they protect all ecosystem components (Bohnsack 2000). In theory, a well-designed marine reserve should protect not only commercially valuable species, but their predators as well. Here we evaluate the hypothesis that upper-trophic-level predators can benefit from the protection provided by a marine reserve established in central California, USA. Alternatively, if the benefits of reserve protection are overshadowed by regional physical processes (e.g. interannual variability in coastal upwelling), then foraging distribution should reflect the geography and oceanography influencing prey distribution.

The reserve we studied is located along a large coastal promontory. There is therefore a potential for prey abundance to differ between the windward and leeward sides of this promontory. Recent research has shown that coastal promontories influence the flow of nearshore currents, especially during upwelling events (e.g. Mace *et al.* 2006). In the California Current System (CCS), alongshore winds create Ekman transport that drives coastal upwelling. The net flow of this transport is offshore, carrying the planktonic larvae of fishes and invertebrates away from nearshore habitats (Cury & Roy 1989). However, circulating structures, termed “upwelling shadows,” are formed in the lee of coastal promontories, providing refuge for planktonic larvae against offshore transport (Wing *et al.* 1995, 1998). This, in turn, increases the probability that larvae settle into habitats adjacent to the upwelling shadow. Additionally, upwelling shadows retain nutrients and phytoplankton for long periods of time (Graham & Largier 1997), thereby enhancing primary productivity and potentially attracting nektonic organisms such as schooling fishes and squid. It is therefore important to study both sides of the promontory when addressing questions about this marine reserve.

Based on a six-year dataset on two resident and two migrant seabird species, collected during spring and summer, we investigated whether the presence of a marine reserve and coastal promontory influenced the distribution of foraging seabirds; whether reserve effects were consistent for leeward and windward sites; whether promontory (and associated upwelling shadow) effects were consistent within and outside the reserve; and whether observed effects were consistent across years.

STUDY AREA

The Vandenberg State Marine Reserve (VSMR) is located along the Point Arguello Promontory (34°34'38"N, 120°39'03"W) in central California, USA (Fig. 1). During the upwelling season, near-surface currents over the continental shelf flow equatorward and offshore (Dever 2004, Ohashi & Wang 2004, Dong & Oey 2005). Trainer *et al.* (2000) and Robinette *et al.* (2007) provided evidence of a small, nearshore upwelling shadow created in the lee of Point Arguello during upwelling events. This shadow has since been confirmed (J. Largier pers. comm.).

The VSMR was established in 1994 under the California Marine Resources Protection Act of 1990. It is a "no take" reserve, protecting waters adjacent to Vandenberg Air Force Base, and is enforced by Air Force game wardens. The VSMR extends 8.4 km along the coastal boundary of the promontory and offshore to the 18 m isobath (Fig. 1). It has an average offshore width of 1.0 km and total area of 6.2 km². Bottom habitat in and around the reserve is primarily sand with scattered rocks and small rocky reefs. Data obtained from the California Fisheries Information System (CFIS) show 785 tonnes of fishes and invertebrates were taken from ~85 km² of nearshore habitat around the reserve over our six-year study period.

METHODS

Study species

We analyzed the foraging distributions of the four seabirds observed most frequently during surveys (Table 1); other species were not observed consistently enough to be included. Brandt's Cormorants *Phalacrocorax penicillatus* and Pelagic Cormorants *Phalacrocorax pelagicus* are year-round residents and breed at Point Arguello and Rocky Point (Fig. 1). Brandt's Cormorants forage on schooling, mid-water and demersal fishes in multiple bottom habitats, ranging from rock to sand, at depths from 10 m to 120 m (Wallace & Wallace 1998). Pelagic Cormorants forage predominantly on bottom fishes

within the same bottom habitats as Brandt's Cormorants, but in waters from intertidal to 36 m in depth (Hobson 1997). Pacific Loons *Gavia pacifica* and Surf Scoters *Melanitta perspicillata* are spring migrants that pass through the area on their way to northern breeding grounds. Pacific Loons typically forage on nearshore schooling fishes in aggregations of mixed seabird species (Russell 2002). However, all of our observations were of non-aggregated foraging individuals, likely taking mid-water species such as the surfperch (Embiotocidae) reported by Palmer (1962). Surf Scoters forage on sessile invertebrates in waters less than 9 m deep (Savard *et al.* 1998).

Data collection

We collected data using a paired design, selecting two sites within the VSMR and two sites just outside the northern or southern boundaries. One pair of sites was located on the windward side of the promontory and the other pair on the leeward side (Fig. 1). At each site, we defined a rectangular area of observation (approximately 0.17 km²) based on easily recognizable coastal landmarks. We made observations within this area using binoculars and a 20–60× spotting scope. We conducted weekly surveys from April through July (breeding season for seabirds and marine mammals) in 2000–2005. We surveyed each site once a week during one of the following time periods: 06h00–09h00, 09h00–12h00, 12h00–15h00, or 15h00–18h00 PDT, rotating sites among the four time periods per week. Because it was not possible to follow each individual bird within a study site for three hours, we divided the observation period into 15 min blocks. We recorded the maximum number of foraging individuals for a given species during each time block. We considered a bird to be foraging if it was observed actively diving for prey. Birds rafting on the water or in transit through the area were not recorded.

Data analysis

We averaged counts for 15 min blocks over each 3 h period for each species at each site. Data for a given 15 min block were not analyzed if the entire site was not visible during the observation period, usually due to fog or rain. The dependent variable in each analysis was the number of individuals recorded per 15 min block.

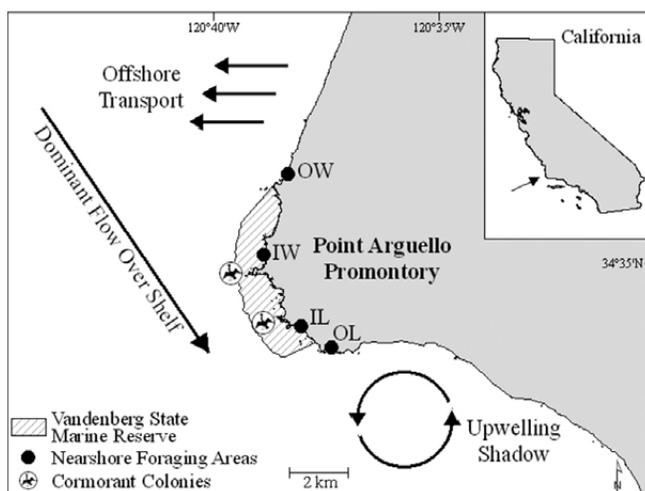


Fig. 1. Map of the Point Arguello Promontory showing the location of the Vandenberg State Marine Reserve and the four observation sites (OW = outside, windward; IW = inside, windward; IL = inside, leeward; OL = outside, leeward). Also shown are the locations of Brandt's and Pelagic Cormorant nesting areas and dominant nearshore currents during the upwelling season.

TABLE 1
Local diet and seasonal occurrence
of the four seabirds selected for this study

| Species | Diet | Seasonal occurrence |
|--------------------|--|--|
| Brandt's Cormorant | Opportunistic on bottom, mid-water and pelagic fishes ^a | Resident Breeds Apr-Aug ^a |
| Pelagic Cormorant | Predominantly bottom fishes ^b | Resident Breeds Mar-Aug ^b |
| Pacific Loon | Predominantly pelagic fishes and squid, but also mid-water fishes ^c | Spring migrant Peak numbers Apr-May ^c |
| Surf Scoter | Benthic invertebrates, predominantly bivalves ^d | Spring migrant Peak numbers Apr-Jun ^d |

^a Wallace and Wallace (1998)

^b Hobson (1997)

^c Russell (2002)

^d Savard *et al.* (1998)

We analyzed data using negative binomial regression (nbreg), an especially appropriate analytic method for count data (Hilbe 2007). Nbreg is an example of a generalized linear model with log link and over-dispersed Poisson residuals. We used a hierarchical approach for the analysis, first determining the within-season trend to the data by analyzing “week” as a quantitative variable, distinguishing among linear, quadratic and cubic trends. Quadratic models included linear and quadratic terms; cubic models included lower-order terms as well, where “week” varied from one to 16. We selected the model corresponding to the highest-order term that was significant at $P < 0.05$. We also used Akaike’s information criterion (AIC) to select models with the best fit. All statistical tests used the likelihood-ratio statistic.

We then examined the effects of reserve (inside or outside) and of promontory (windward vs. leeward), as well as the interaction of reserve and promontory, while controlling for “week” as determined above. We examined the interaction of year, treated as a categorical variable, with reserve (in/out) and with promontory (windward/leeward) to determine whether reserve and/or promontory effects were consistent over the six years. Significance was set at $P < 0.05$. STATA 8.2 statistical software was used for all analyses (STATA Corp. 2005).

Controlling for abiotic influences

Wind speed and wave height during an observation period can affect foraging behavior, independent of the underlying prey distribution. Furthermore, wind and wave effects should differ between windward and leeward sides of the promontory. To disentangle the effects of prey distribution from those of wind and wave effects, we conducted the reserve and promontory analyses with and without controlling for wind speed and wave height. A change in the apparent effect of reserve or promontory as a result of controlling for wind speed and wave height would indicate that physical conditions are influencing foraging behavior directly, in addition to possible influences of the underlying prey distribution. Tidal height can also affect foraging behavior, but the effects should not differ between windward

and leeward sides of the promontory. Thus, confounding was not expected between reserve or promontory and tidal height; tidal height was therefore controlled for in all analyses.

Hourly wind speeds (m/s) and wave heights (m) were downloaded from the National Oceanic and Atmospheric Administration’s (NOAA) weather buoy station 46023 moored at 34°42'50"N, 120°58'00"W, approximately 17 nm northwest of Point Arguello (NOAA 2007). Tidal heights for Point Arguello were obtained using the online tide predictor program XTide (2007). Tidal height was calculated in meters and averaged over each observation hour.

RESULTS

Within-season trends in predator abundance

All species except Brandt’s Cormorants showed a significant within-season trend in abundance (Table 2). Pelagic Cormorants showed a slight linear decrease in abundance with date (Fig. 2), consistent with their post-breeding dispersal from colony sites. The two spring migrants also showed a decrease in abundance with date, as would be expected for birds that breed outside our study area. Pacific Loons showed a cubic trend, with peak abundance between the first and 10th week of our study period, whereas Surf Scoters showed a linear trend.

Effects of marine reserve and promontory on foraging patterns

There were significant reserve effects for all seabirds except Surf Scoters and significant promontory effects for all seabirds except Pacific Loons (Table 3). The promontory effect was marginally significant for Pacific Loons ($P = 0.093$). Results were similar whether or not we controlled for wind and wave height, suggesting that wind and wave height were not confounded by promontory location or inside vs. outside the reserve. Thus, spatial patterns of foraging seabirds were more likely driven by prey distribution than by environmental conditions during our observations. We therefore report our results without controlling for wind and wave height.

TABLE 2
Comparison of within-season models for each species, derived by negative binomial regression analysis

| Species | Model ^a | | | | Best fit ^b |
|--------------------|-----------------------|---|--|--|-----------------------|
| | Constant | Linear | Quadratic | Cubic | |
| Brandt’s Cormorant | (882.61) ^c | (883.95) LRS = 0.65 $P = 0.419$ | (885.87) LRS = 0.08 $P = 0.774$ | (887.60) LRS = 0.27 $P = 0.605$ | Constant |
| Pelagic Cormorant | (668.37) | (663.54) LRS = 10.77 $P = 0.001$ | (669.27) LRS = 0.21 $P = 0.643$ | (674.76) LRS = 0.45 $P = 0.502$ | Linear |
| Pacific Loon | (439.76) | (419.46) LRS = 22.29 $P < 0.001$ | (417.09) LRS = 4.38 $P = 0.036$ | (405.74) LRS = 13.35 $P < 0.001$ | Cubic |
| Surf Scoter | (1183.19) | (1118.38) LRS = 66.81 $P < 0.001$ | (1120.26) LRS = 0.12 $P = 0.729$ | (1121.00) LRS = 1.26 $P = 0.261$ | Linear |

^a Each model is being compared with the model to its left

^b Results of likelihood ratio statistics comparing all four models (constant, linear, quadratic, cubic; six pairwise comparisons)

^c Akaike’s information criterion (AIC) is shown in parentheses for each model

Brandt's Cormorants, Pelagic Cormorants and Pacific Loons foraged mostly outside the reserve at leeward sites (Fig. 3). Surf Scoters foraged mostly at windward sites. There was a marginally significant interaction between reserve and promontory for Brandt's Cormorants ($P = 0.095$), with a larger difference between inside and outside of the reserve at leeward sites than at the windward sites. The majority of Brandt's Cormorant foraging occurred at the leeward site outside the reserve. There were no significant interactions between reserve and promontory for any other species.

With the exception of Surf Scoters, there were no reserve \times year or promontory \times year interactions for any of species, indicating that foraging patterns were consistent for the duration of our study (Table 4). Surf Scoters showed both reserve \times year and promontory \times year interactions, although the latter was due mostly to variable use of windward plots and persistent non-use of leeward plots (Fig. 4). The interaction between year and reserve for this species illustrates alternating use of plots inside and outside the reserve on the windward side.

DISCUSSION

In this study, seabirds did not forage inside the VSMR more than in adjacent areas, as would be expected if their prey were more abundant or available inside the protected area. In fact, the three piscivorous species (Brandt's Cormorant, Pelagic Cormorant and Pacific Loon) foraged more outside the reserve than inside. Also, the foraging distributions of these three species were consistent over our six-year study period. Thus, these species were not responding to stochastic events, but rather cuing into a static resource. Our evidence suggests that potential reserve effects are overshadowed by geographic and oceanographic factors influencing prey distribution.

The three piscivorous predators in our study preferred foraging in leeward areas over windward. Robinette *et al.* (2007) showed differences in diet between leeward-foraging and windward-foraging Pigeon Guillemots (*Cepphus columba*) at Point Arguello. The leeward diet was less variable among years and had a higher incidence of the dominant prey, sanddabs (*Citharychthys* sp.), suggesting that sanddabs were more available in leeward waters and more stable overall than in windward waters. Such increased availability of demersal fishes likely attracts their predators to leeward waters. Furthermore, Trainer *et al.* (2000) documented an algal bloom in the lee of Point Arguello that lasted more than three weeks. Such prolonged primary productivity of an upwelling

TABLE 3
Effects of reserve, promontory, and reserve \times promontory interaction on the foraging behavior of each species, evaluated by negative binomial regression

| Species | Variable (model with all variables compared with model lacking variable) | | |
|--------------------|--|-----------------------------|-----------------------------|
| | Reserve | Promontory | Reserve \times promontory |
| Brandt's Cormorant | LRS = 42.05 $P < 0.001$ | LRS = 141.73 $P < 0.001$ | LRS = 2.78 $P = 0.095$ |
| Pelagic Cormorant | LRS = 9.66 $P = 0.002$ | LRS = 33.23 $P < 0.001$ | LRS = 2.34 $P = 0.126$ |
| Pacific Loon | LRS = 8.55 $P = 0.004$ | LRS = 2.83 $P = 0.093$ | LRS = 0.54 $P = 0.463$ |
| Surf Scoter | LRS = 2.56 $P = 0.110$ | LRS = 186.31 $P < 0.001$ | LRS = 0.09 $P = 0.766$ |

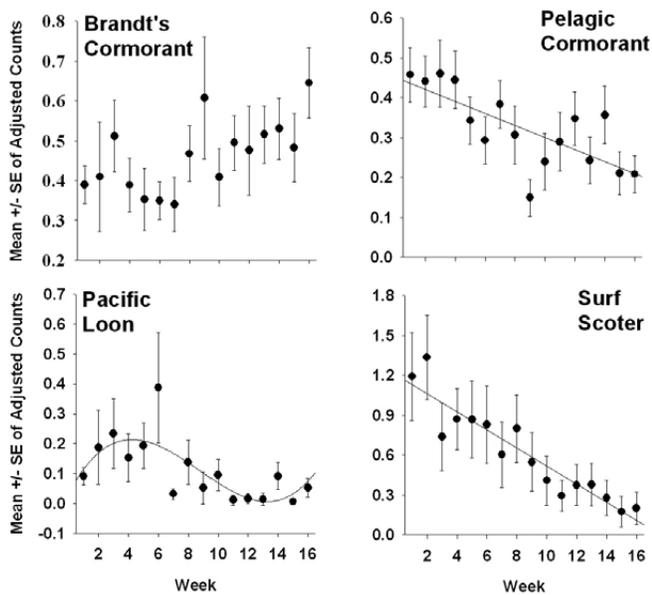


Fig. 2. Within-season trends in the weekly abundances of foraging seabirds using all data from 2000–2005. Values plotted are the means \pm SE of adjusted counts, controlling for tide and observation site.

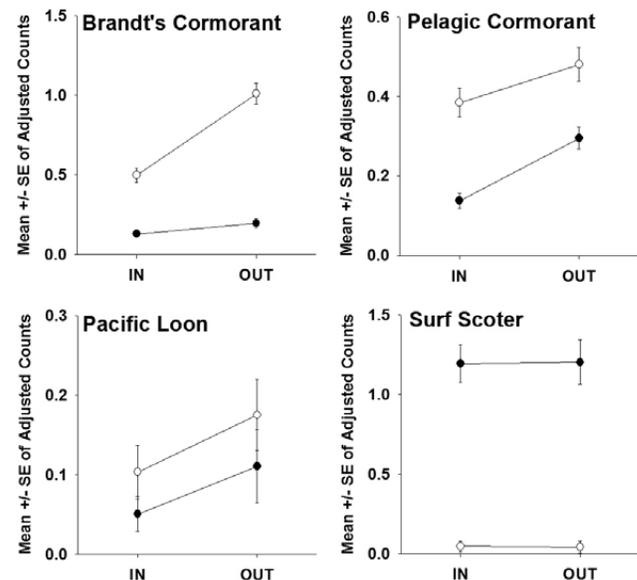


Fig. 3. Reserve \times Promontory interaction plots showing the mean abundance of seabirds foraging in each observation site. Values plotted are the means \pm SE of adjusted counts incorporating the within-season models shown in Fig. 2 and controlling for tide. Means were calculated for observation sites inside (IN) and outside (OUT) the marine reserve over the duration of our study, 2000–2005. Open circles represent leeward sites and filled circles windward sites.

shadow would attract planktivorous organisms and their predators to leeward waters.

An alternative interpretation of these results is that the reserve is protecting large fishes that compete with seabirds for their prey. Brandt's Cormorants typically take fishes <20 cm in length (Wallace & Wallace 1998), and Pelagic Cormorants take fishes <10 cm in length (Hobson 1997). Four of the fisheries adjacent to the VSMR (representing 26% of groundfish catch for the area) have minimum size restrictions that range from 25 cm to 61 cm total fish length (California Code of Regulation 14 CA ADC §28.15, §28.27, §28.28; California Fish and Game Code 8588). For these species, the smallest individuals are being protected both inside and outside the reserve, whereas the largest individuals are protected only within the reserve. The abundance of small fishes might be higher outside the reserve, where they are protected by legal size limits and provided a refuge from the larger fishes taken by fishers. Such shifts in community structure have been documented in other areas where fishing pressure has changed (Scheffer *et al.* 2005, Mumby *et al.* 2006). However, the large fishes, likely benefitting from the VSMR, have movement ranges that span the reserve's boundaries. Movement patterns of the fish groups mentioned above can range from 0.8 km to 20 km, with larger individuals typically moving farther than smaller individuals (Lowe & Bray 2006). The VSMR would need to be much larger in order to protect large fish and produce the hypothesized shift in

community structure. We therefore feel this alternative argument is not compelling and that the VSMR is not protecting important foraging habitat for piscivorous seabirds.

Surf Scoters were the only predator showing no difference between inside and outside sites. Surf Scoters foraged more at the two windward sites. At both sites, they foraged in the surf zone over the low intertidal (during high tide) and shallow subtidal habitats. Inside the reserve, scoters foraged in both rocky and sandy habitats, but outside the reserve, they were limited mostly to sandy habitat. Scoters in our study were likely taking infaunal invertebrates such as small clams and polychaete worms from sandy habitats as well as mussels (likely *Mytilus californianus*) from rocky habitats, as found in diet studies of scoters foraging in these habitats (Stott & Olson 1973, Savard *et al.* 1998).

The distribution of foraging Surf Scoters likely reflects differences in invertebrate community structure. Invertebrate communities are markedly different between windward and leeward habitats, with windward habitats generally being dominated by competitively dominant, wave-resistant species such as mussels (Lubchenco & Menge 1978). Growth rates and overall biomass of filter feeders such as mussels, clams and polychaetes are greater at exposed habitats because waves quickly replenish the planktonic prey as they are filtered from the water (McQuaid & Branch 1985, McQuaid & Lindsay 2000). Our observations on Surf Scoter foraging distributions are consistent with observations that filter-feeding invertebrate biomass is greater at exposed habitats. Furthermore, the alternating use of inside and outside windward sites by Surf Scoters is consistent with the high among-year variability in prey distribution typically observed in windward habitats (McQuaid & Lindsay 2000).

To our knowledge, this is the first study to test the efficacy of a coastal marine reserve in protecting the foraging habitat of nearshore foraging seabirds. Although it is reasonable to expect that "no take" reserves would benefit upper-trophic-level predators, it is important to consider size and location, especially in relation to physical features that may concentrate prey, when designing reserves to protect all trophic levels of a community. Although the predators in our study did not appear to respond to the boundaries of the marine reserve, consistency in their foraging distributions over six years suggests the reserve could provide benefits if the boundaries were redrawn to protect more foraging habitat. Our results suggest the VSMR would be more effective at protecting foraging habitat if it were 1) increased in overall size and 2) expanded to protect more leeward habitat.

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TABLE 4
Reserve × year and promontory × year interactions,
evaluated by negative binomial regression analysis

| Species | Reserve × year | Promontory × year |
|--------------------|--------------------------|--------------------------|
| Brandt's Cormorant | LRS = 6.81 P = 0.235 | LRS = 2.68 P = 0.749 |
| Pelagic Cormorant | LRS = 5.53 P = 0.354 | LRS = 1.33 P = 0.932 |
| Pacific Loon | LRS = 2.85 P = 0.724 | LRS = 4.20 P = 0.521 |
| Surf Scoter | LRS = 55.27 P < 0.001 | LRS = 17.60 P = 0.004 |

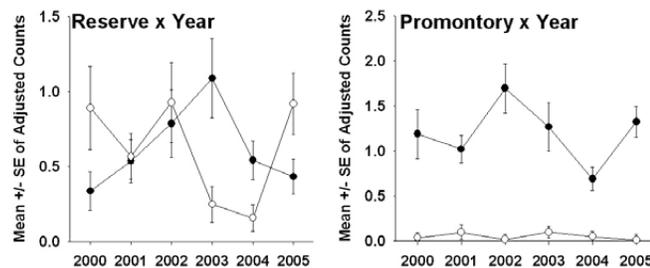


Fig. 4. Reserve × year and promontory × year interaction plots for Surf Scoters, the only species in this study to show significant year interactions (see Table 4). Values plotted are the means +/- SE of adjusted counts incorporating the within-season models shown in Fig. 2 and controlling for tide. Means were calculated over each year for each site category (inside vs. outside for reserve or windward vs. leeward for promontory). Filled circles represent inside or windward sites and open circles represent outside or leeward sites.

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