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Foraging distribution of Pacific harbor seals (*Phoca vitulina richardii*) in a highly impacted estuary

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Assessing the relative importance of environmental and anthropogenic influences on the distribution of wild populations is an important step in designing spatially explicit plans for their management and protection. We examined environmental variables correlated with the spatial distribution of eastern Pacific harbor seals (*Phoca vitulina richardii*), a marine mammal common to coastal waters, in a large, highly urbanized estuary. We assessed the relationship between prey abundance, depth, bottom relief, proximity to terrestrial haul-out sites and 3 potential sources of anthropogenic influence, and the in-water spatial distribution of seals. We identified locations of seals using satellite-linked telemetry, and used partial Mantel tests to assess which environmental variables were most strongly linked to seal foraging distribution, given spatial autocorrelation within variables. Mann–Whitney tests were used to compare environmental characteristics of locations of seals with a random distribution of locations. Because harbor seals are central-place foragers, we incorporated spatial distribution of seals relative to the central place into our analyses. High prey abundance and proximity to the haul-out site were strongly associated with the spatial distribution of seals. Harbor seals also tended to use deeper waters and areas of high bottom relief within the estuary. There was no consistent spatial relationship between the 3 anthropogenic factors and the distribution of seals, although seals tended to be found closer than expected to sites of high human activity. In highly impacted coastal areas where limited alternate suitable habitat exists, foraging seals may need to rely on disturbed (suboptimal) areas, and as a result may habituate to human presence in areas rich in food resources.

Key words: central-place forager, disturbance, geographic information system, habitat use, harbor seal, *Phoca vitulina*, satellite telemetry, spatial distribution

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Essential to understanding the ecology of any species is an awareness of the environmental factors that determine its distribution, including sensitivity of the species to anthropogenic influences. Studying the influences on the in-water spatial distribution of marine predators such as marine mammals is particularly challenging, given the difficulty of tracking these large, wide-ranging animals and the opaque nature of the marine environment. However, satellite-linked telemetry tracking has provided improved means of tracking marine mammals (e.g., Austin et al. 2006; McConnell et al. 1992; Priede and French 1991; Stewart et al. 1989; Vincent et al. 2002), and advances in geographic information systems and remote sensing have facilitated the production of large bodies of descriptive information on marine habitat variables. Increasingly, ecologists are using statistical tools that incorporate the spatial structure of natural systems, and that account for the spatial autocorrelation that is common among data from field studies (Fortin and Gurevitch 2001; Legendre and Fortin 1989). Through the integration of animal location data, spatial statistics, and new and preexisting data sets on marine habitats, we can gain insight into environmental variables influencing spatial distribution of these large marine predators.

This knowledge of environmental variables associated with habitat use by marine mammals is an important prerequisite for their protection, management and conservation, particularly given the coastal distribution of many marine mammal species. Marine mammals that live near shore are potentially at risk from a diversity of anthropogenic processes, and threats to marine mammal populations are expected to increase in severity over the next 100 years (Geraci et al. 1999; Harwood 2001). The degree to which anthropogenic sources influence the in-water distribution of marine mammals is often ambiguous, although other studies have demonstrated the apparent effects of such sources as boats (Allen and Read 2000), aquaculture operations (Markowitz et al. 2004), and oil rig platforms (Schick and Urban 2000). Anthropogenic disturbance, if perceived by marine mammals as predation risk, could play an analogous functional role in habitat selection and use (Heithaus and Dill 2002; Nordstrom 2002).

The eastern Pacific harbor seal (*Phoca vitulina richardii*) is a small phocid seal common in coastal waters of the west coast of North America. The general diet, foraging behavior, and movement patterns are mostly known for this species and can vary by site (Allen 1988; Bigg 1981; Bjorge et al. 1995; Harkonen 1987; Scheffer and Sperry 1931; Thompson 1993). Harbor seals inhabit nearshore areas (sometimes close to dense human development), are bioaccumulators of contaminants present in prey, and are sensitive to human disturbance in many parts of their range (O'Shea et al. 1999). Harbor seals are central-place foragers (Orians and Pearson 1979), tend to exhibit strong site fidelity within season and across years, generally forage close to haul-out sites, and may repeatedly visit specific foraging areas (Suryan and Harvey 1998; Thompson et al. 1998). Given this information, we were able to identify environmental variables important for inclusion in our analyses. We developed a conceptual model of which environmental variables were most likely to influence spatial distribution of seals in our study area, a large coastal estuary subject to high levels of human use. Our hypothesis was that habitat use by seals would be higher in areas near haul-out sites, in areas of high prey abundance, and in areas of greater depth and higher bottom relief (where prey may be concentrated); and lower in areas of the estuary close to consistent sources of anthropogenic disturbance (i.e., areas with predictably high levels of human or boat activity), except commercial or recreational fishing areas, because these latter activities target areas of high fish abundance, or outfall locations, which could increase biomass of surrounding waters via moderate nutrient enrichment (Bishop et al. 2006).

The primary objective of this study was to investigate the in-water distribution of a coastal marine mammal, the harbor seal, in a system subject to high levels of anthropogenic disturbance. Our analysis incorporated biotic variables such as prey distribution, with probable direct effects on predator distribution, and abiotic variables such as depth and bottom topography, with probable indirect effects on distribution via influences on distribution of seal prey. We included information on locations of high human activity in our spatial analyses, to investigate whether these were associated with the in-water distribution of harbor seals. Our specific goals were therefore to identify environmental factors associated with in-water spatial distribution of harbor seals in an urbanized estuary, and to assess the relative influence of anthropogenic factors on in-water habitat use by harbor seals.

Materials and Methods

Study area.—The study was conducted in the San Francisco Estuary, California (more commonly called the San Francisco Bay [SFB]; Fig. 1). SFB is the largest coastal embayment on the Pacific Coast of the United States, a turbid estuary composed of a series of subembayments, with mean depths ranging from 3 to 11 m (Conomos et al. 1985; Jassby et al. 1993). Overall, SFB consists of broad shallows cut by narrow channels, typically 10–20 m deep (Conomos et al. 1985; Kimmerer 2004).

San Francisco Bay is a highly modified, heavily utilized environment (Nichols et al. 1986). Intense fishing (Skinner 1962; Wild and Tasto 1983), land reclamation (Kockelman et al. 1982), water development projects (Kahrl 1978; Nichols et al. 1986), water pollution (Kopec and Harvey 1995; Neale et al. 2005; Risebrough et al. 1977), and invasive species (Cohen and Carlton 1998) have resulted in declines

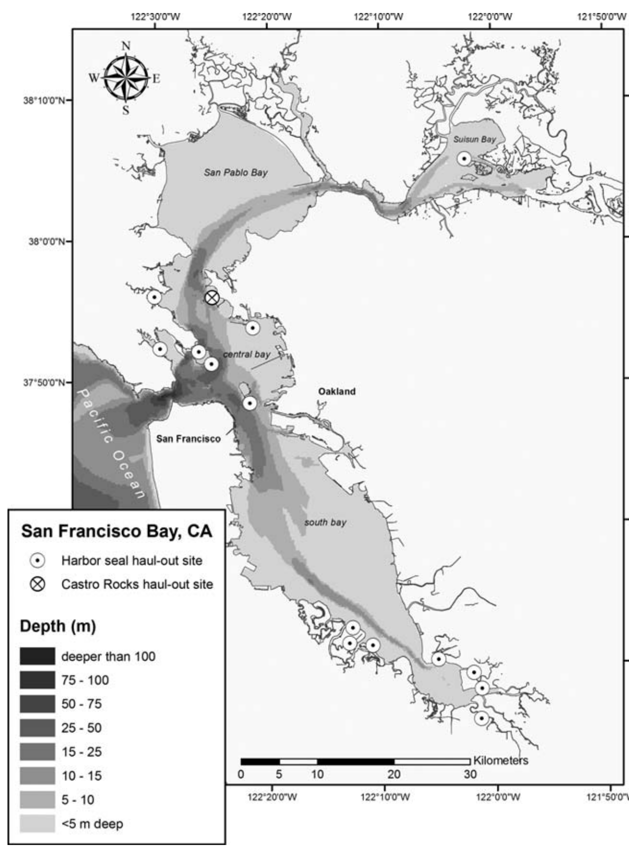

Fig. 1.—Map of the study area, San Francisco Bay, California, showing major haul-out site locations of Pacific harbor seals (*Phoca vitulina richardii*) and bathymetry of the area.

of a number of SFB fisheries and populations of benthic organisms such as native shellfish (Bennett and Moyle 1996; Smith and Kato 1979). Nonetheless, SFB continues to support thousands of species of fish, invertebrates, birds, plants, and other life, although many of these species are nonnative (San Francisco Estuary Project 1992).

Archaeological evidence reveals that harbor seals have used SFB for thousands of years (Nelson 1909), and seals still use SFB year-round for foraging, pupping, and resting on terrestrial haul-out sites (Allen 1991; Grigg et al. 2004; Kopec and Harvey 1995). Until legal protection in 1972, populations of harbor seals in California suffered severe population declines due to anthropogenic hunting pressure (Bonnot 1928; Scammon 1874). Although populations of harbor seals along the coast of California have increased markedly since 1972 (Allen et al. 1989; Sydeman and Allen 1999), numbers of seals in SFB have exhibited a mixed response to protection, based on haul-out site counts (Grigg et al. 2004). Reasons for the lack of a strong population increase in urban SFB are not known, but may include habitat alteration, visual and acoustic disturbance due to boating and other human activities, pollution, prey resource limitations, emigration by seals to outer coastal areas, or a combination of these factors (Allen et al. 1989; Grigg et al. 2004; Kopec and Harvey 1995). As central-place foragers, harbor seals often return to the same SFB haul-out sites throughout the year, although long-distance movements do occur in response to shifts in food resource distribution, or reproductive behavior (Thompson et al. 1998; Torok 1994). In estuarine areas such as SFB, seals often forage in shallow waters <50 m deep, over soft or sandy seabed bottom sediments (Harkonen 1987, 1988; Tollit et al. 1998). In SFB, they have been reported to feed on Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), plainfin midshipman (*Porichthys notatus*), Pacific staghorn sculpin (*Leptocottus armatus*), white croaker (*Genyonemus lineatus*), yellowfin goby (*Acanthogobius flavimanus*), jacksmelt (*Atherinopsis californiensis*), and English sole (*Pleuronectes vetulus*—S. Oates, California Department of Fish and Game, pers. comm., 2005; Torok 1994). Based on earlier very-high-frequency radiotelemetry studies, harbor seals in SFB forage mainly within 1–5 km of a haul-out site (Nickel 2003; Torok 1994), suggesting that these seals rely heavily on local prey resources.

Satellite telemetry.—Between January 2001 and January 2005, we captured harbor seals at Castro Rocks, a primary harbor seal haul-out site in SFB (Fig. 1). We fitted satellite-linked platform terminal transmitters (model ST-18; Telonics, Mesa, Arizona; models SDR-T16 and SPOT3; Wildlife Computers, Redmond, Washington) to the head or back of captured seals. The platform terminal transmitters were glued to the seal's pelage using a quick-setting marine epoxy, and were shed by seals during their annual molt. This work was conducted in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011) and with the requirements of the San Francisco State University Institutional Animal Care and Use Committee (IACUC 99-534).

Geographical coordinates of the tagged seals were processed by Argos (CLS America, Inc., Largo, Maryland). Published accuracy ratings for unfiltered location estimates for marine mammals range from <150 m for highest-rated locations (location class = 3), to >7,000 m for lowest-rated locations (location class = B; Argos—Hays et al. 2001; Vincent et al. 2002). A number of recent studies have utilized satellite telemetry to study movements and habitat use of marine mammals (Thompson et al. 2003; Vincent et al. 2002; White and Sjoberg 2002). We followed the findings of Hays et al. (2001) and Vincent et al. (2002) when filtering inaccurate points using location-class ratings, and we removed all points that fell on land, and all points that fell on water but outside of SFB. We then filtered the remaining locations based on the speed necessary for a seal to move between 2 successive locations, calculated in the geographic information system. Any location that would have required a travel speed greater than 10 km/h, or 2.78 m/s (Lowry et al. 2001), from the previous location was removed. We also removed points that would have required an isolated movement away from and immediately returning to the same area, necessitating a narrow V-shaped movement track (similar to the filtering mechanism proposed by Keating [1994]). In order to limit our analyses to in-water habitat use (versus haul-out site use), we removed locations within 1 km of a haul-out site. Given the accuracy estimates for our location data set, lower-quality locations within 1 km of a haul-out site may have represented times when the seal was actually hauled out. Finally, to improve independence of location estimates for each seal without sacrificing too much of our data set, we removed location estimates within 1 h of another location estimate for the same seal.

Habitat description and analysis.—We assessed the relationship between locations of seals and the following environmental variables: distance from the haul-out site, prey distribution and abundance, depth and bottom relief, and human activity. Given that harbor seals are central-place foragers, and other studies have noted that most foraging is done near the haul-out site, we calculated the distance of all areas of SFB from Castro Rocks, and from any haul-out site in SFB. We used the cost–distance function in ArcGIS 9.2 (ESRI, Redlands, California) to calculate the across-water distance rather than the straight-line distance from the haul-out sites, so that distances would take into account the irregular shoreline of SFB and better reflect the distance a seal would actually need to travel to and from a haul-out site.

Data on prey distribution during the study period were obtained from the Interagency Ecological Program for the San Francisco Estuary and the California Department of Fish and Game's San Francisco Bay Study (K. Heib, California Department of Fish and Game, pers. comm., 2007; Orsi 1999). Monthly samples of fish species were collected at 39 sampling stations located around SFB, using 2 sampling methods: an otter trawl to sample bottom-dwelling fish, and a midwater trawl. All fishes captured in the otter trawl and midwater trawl were identified to species. We used a subsample consisting of only those species identified as harbor seal prey species in

SFB (see above; Grigg et al. 2009). We analyzed catch data from the otter trawl and the midwater trawl separately. We calculated catch per unit effort (CPUE) for each station and each month using gear-specific formulas used by the California Department of Fish and Game:

$$\text{otter trawl}: \ \text{CPUE} = (\text{number caught}/\text{tow area}) \times 10{,}000,$$

where tow area = distance towed in meters × 3.42 m (door spread); and

$$\text{midwater trawl}:$$
$$\text{CPUE} = (\text{number caught}/\text{tow volume}) \times 10{,}000,$$

where tow volume = number of flowmeter revolutions × 0.0269 m/revolution × 10.7 m^2 (net mouth area).

We used the catch per unit effort data from the 39 sampling stations to create continuous distribution maps of abundance (in number of individuals/ha) of harbor seal prey species for SFB, using the inverse distance weighting interpolation method in the geographic information system (Geostatistical Analyst extension to ArcGIS 9.2; ESRI). Inverse distance weighting is a deterministic interpolation method and estimates values for unmeasured locations based on values of nearby measured locations, with influence decreasing with distance from the measured location. Prey species collected with the otter trawl reflect benthic prey abundance; prey abundances collected by the midwater trawl reflect midwater prey abundance. Because we assumed fish distribution would change with season, we created 4 maps for abundance of each prey type (benthic and midwater) and 1 for each harbor seal ''season'' (pupping: March–May; molting: June–August; autumn: September–November; and winter: December–February). We included only catch records for those months and years that we had tagged seals active in SFB waters. In this way, individual location estimates for seals could be matched with a seasonally appropriate value of fish distribution, based on the date of the location estimate.

Bathymetry for SFB was obtained from the California Department of Fish and Game's bathymetry development project. We generated a surface ratio grid for SFB (Jenness Enterprises, Flagstaff, Arizona; ArcView extension available online at www.jennessent.com) by dividing the surface area of a given grid cell by the planimetric area of the same cell. The resulting grid provides a useful index of topographic roughness of the substrate. Previous work on harbor seal foraging behavior in SFB has indicated that seals may be targeting areas near specific submerged features (such as bridge supports) and areas with higher topographic roughness, because physical characteristics of these areas may indirectly promote prey aggregation (Fancher 1979; Nickel 2003).

We calculated the distance from all areas of SFB to locations of persistent human activity (including commercial and recreational fishing areas, marinas and boat ramps, shoreline and beach access points, airports, United States Coast Guard facilities, ferry terminals, and other human-use sites). Given the possibility that recreational or commercial fishing could have an opposite effect on seal spatial distribution than other types of human activity, we divided the locations into 2 subsets: ''fishing'' (commercial and recreational fishing areas) and ''other'' (other sites of human activity such as marinas, airports, and ferry terminals). These records of human activity were compiled as a part of the National Ocean Service's Environmental Sensitivity Index assessment for SFB, by the National Oceanic and Atmospheric Administration and the California Department of Fish and Game. In addition, we calculated the distance between all areas of SFB and the locations of major outfalls and wastewater treatment dischargers in and around SFB. Sewage input has been linked with higher primary productivity in some estuarine areas (Surge and Lohmann 2002), and although large nutrient inputs have been linked with mortality of invertebrates and fish, smaller inputs may enhance biomass of all trophic levels (Bishop et al. 2006). Data on the outfall locations came from the United States Environmental Protection Agency's National Pollution Discharge Elimination System permitting program, with each location representing the discharge point of a discrete conveyance such as a pipe or man-made ditch (National Pollution Discharge Elimination System 2001). Data for the analysis of anthropogenic factors were provided by the National Oceanic and Atmospheric Administration's SFB Watershed Database and Mapping Project (release 2.1, August 2004; available online at http://response.restoration.noaa.gov/cpr/cpr.html).

Spatial data processing.—All environmental variables in the geographic information system were reprojected and resampled to a grid resolution of 2 km. Although many of the sets of environmental measurements were available at higher resolutions, the 2-km grid size was chosen to buffer any estimation errors for locations of harbor seals, given the estimated average accuracy of our filtered seal telemetry data (see location filtering methods above [also see Bekkby et al. 2002]). As a rule, habitat analyses should be conducted at the scale at which the study organism selects habitat (Garshelis 2000). Given the dynamic nature of the marine environment and the highly mobile nature of harbor seals, very fine-scale habitat analyses may be problematic, because location error could obscure actual habitat use at these scales.

Using the Hawth's Analysis Tools extension to ArcGIS 9.2 (Spatial Ecology, LLC, Glasgow, United Kingdom; available online at www.SpatialEcology.com), we overlaid a 2-km grid over the entire study area, consisting of all water areas from the mouth of SFB at the Golden Gate, to the eastern edge of Suisun Bay (Fig. 1). Individual tagged seals had been observed to move the length and breadth of SFB (Grigg 2008), so it was feasible that seals could access the entire bay in their search for food. We assigned a value for each environmental variable (including seasonal fish distributions) to each 2-km grid cell, using the area-weighted mean of the values falling within that grid cell. Finally, we used Hawth's Analysis Tools to tally the number of locations of seals that fell within each 2-km grid cell.

Statistical analyses.—We assessed spatial autocorrelation among telemetry locations of seals, and within each of the environmental variables, in the geographic information system using global Moran's *I* (Moran 1950). Because harbor seals are central-place foragers, it was necessary to incorporate distance from the central place (i.e., the haul-out site) into our analyses. This was done in order to be sure that relationships between environmental variables and locations of seals were real, and not just an artifact of the spatial distribution of foraging harbor seals with respect to their primary haul-out site. The partial Mantel test (Mantel 1967; Smouse et al. 1986) is useful for analyzing relationships among 3 distance (dissimilarity) matrices when spatial autocorrelation is present and when intercorrelation between variables may be present (Oden and Sokol 1992; Schick and Urban 2000). A significant partial Mantel coefficient, $r_{(AB.C)}$, indicates that the relationship between variables A and B is not related to C, the common spatial structure (Legendre and Fortin 1989). A larger *r*-value indicates a stronger relationship between variables, although *r* does not have to be large to be significant (Schick and Urban 2000). We used partial Mantel tests to assess the strength of the relationship $r_{(AB.C)}$ between use of a grid cell by seals and each of the environmental variables, while keeping effects of distance from haul-out site constant. We then used partial Mantel tests to reassess the strength of the relationship $r_{(AB.S)}$ between use by seals and each of the environmental variables, and between use of an area by seals and the distance of that area from the primary haul-out site, this time taking into account the spatial autocorrelation between locations of seals.

In addition, we compared values of associated environmental variables for locations of seals versus an equal number of randomly distributed points, in order to test whether the distribution of seals differed from the null model with regard to each variable, using Mann–Whitney tests. Our null model for this comparison took into account the fact that seals would more likely be found closer to the central place, that is, the haul-out site, by using a form of stratified sampling for the selection of the random points. The proportion of the random points placed within a set distance (10 km—Grigg et al. 2009) of the primary haul-out and capture site was based on the observed proportion of actual locations of seals that fell within this distance. For both the partial Mantel and Mann–Whitney tests, an error rate of $\alpha = 0.05$ was used, with a Bonferroni correction for multiple comparisons (Abdi 2007).

Euclidian distance matrices for the partial Mantel tests were calculated using PopTools (Australian Commonwealth Scientific and Research Organization, CSIRO, Clayton South, Victoria, Australia; available online at www.cse.csiro.au/poptools/), an add-in for Microsoft Excel (Microsoft Corp., Redmond, Washington). All statistical analyses were performed in Minitab 13.32 (Minitab, Inc., State College, Pennsylvania), ArcGIS 9.2 (ESRI), or using XLSTAT 2011 (Addinsoft USA, New York, New York), an add-in for Microsoft Excel.

Results

Satellite telemetry.—We tagged 19 harbor seals between January 2001 and January 2005 (Appendix I). Although we targeted adult seals for tagging, logistical challenges associated with capturing seals in SFB meant that our study animals were of both sexes and all age classes, except pups. Location data filtering for accuracy reduced sample sizes for individual seals by 39–69%, and additional location estimates were removed due to location within 1 km of a haul-out site, or outside of the study area. Locations used were evenly dispersed between day and night, with 47% during the day (0600–1800 h) and 53% during the night (1800–0600 h).

Environmental and anthropogenic correlates with the distribution of seals.—The following environmental variables were significantly correlated with use of an area by seals, in order of relationship strength and while accounting for the effect of distance from the primary haul-out site: benthic prey abundance >> bottom relief > midwater prey abundance > depth > human use (fishing activity) >> human use (other activity; Table 1). No relationship was found between outflow locations and spatial distribution of seals. All environmental variables tested revealed spatial autocorrelation; locations of seals also were spatially autocorrelated (Table 2). The partial Mantel tests that directly incorporated spatial autocorrelation (distance between locations of seals held constant) confirmed that these relationships persist despite this spatial structure, with 1 exception: human use (fishing activity) was no longer significantly correlated with locations of seals, after Bonfer-

Table 1.—Environmental and anthropogenic correlates of the distribution of Pacific harbor seals (*Phoca vitulina richardii*). Results of the partial Mantel tests on locations of seals (number of locations per grid cell) and the listed environmental variables, with A) distance from the primary haul-out site (central place) held constant, and B) distance between locations of harbor seals (spatial autocorrelation) held constant. Statistically significant results are shown in boldface type; significance level was set at 0.007 for A and 0.006 for B (e.g., for A: overall $\alpha = 0.05$, with 7 comparisons, so $0.05/7 = 0.007$).

	A (central place)		B (space)	
	$r_{(AB.C)}$	*P*	$r_{(AB.S)}$	*P*
Depth (m)	**0.200**	**<0.0001**	**0.197**	**<0.0001**
Bottom relief index[a]	**0.289**	**<0.0001**	**0.269**	**<0.0001**
Harbor seal prey—benthic species (individuals/ha)	**0.630**	**<0.0001**	**0.647**	**<0.0001**
Harbor seal prey—midwater species (individuals/ha)	**0.229**	**<0.0001**	**0.252**	**<0.0001**
Human use (fishing activity)	**−0.186**	**<0.0001**	−0.034	0.015
Human use (other activity)	**0.046**	**0.001**	**0.047**	**0.001**
Outflow locations	0.001	0.923	0.001	0.950
Distance from the primary haul-out site (m)	—	—	**0.294**	**<0.0001**

[a] Index = surface area/planimetric area.

TABLE 2.—Spatial autocorrelation of anthropogenic and environmental variables, and locations of Pacific harbor seals (*Phoca vitulina richardii*). All *I*-values were statistically significant; *P*-values are shown.

	Moran's *I*-value (*P*)
Depth (m)	0.489 (<0.001)
Bottom relief index[a]	0.342 (<0.001)
Harbor seal prey—benthic species (individuals/ha)[b]	0.765 (<0.001)
Harbor seal prey—midwater species (individuals/ha)[b]	0.549 (<0.001)
Human use (fishing activity)	0.378 (<0.001)
Human use (other activity)	0.676 (<0.001)
Outflow locations	0.745 (<0.001)
Locations of harbor seals	0.626 (<0.001)

[a] Index = surface area/planimetric area.
[b] Spatial autocorrelation is expected, based on interpolated sampling station data.

roni correction of the α-value. There was a significant relationship between use of an area by seals and the distance of that area from the primary haul-out site, even when spatial autocorrelation was incorporated into the analysis (Table 1; Fig. 2).

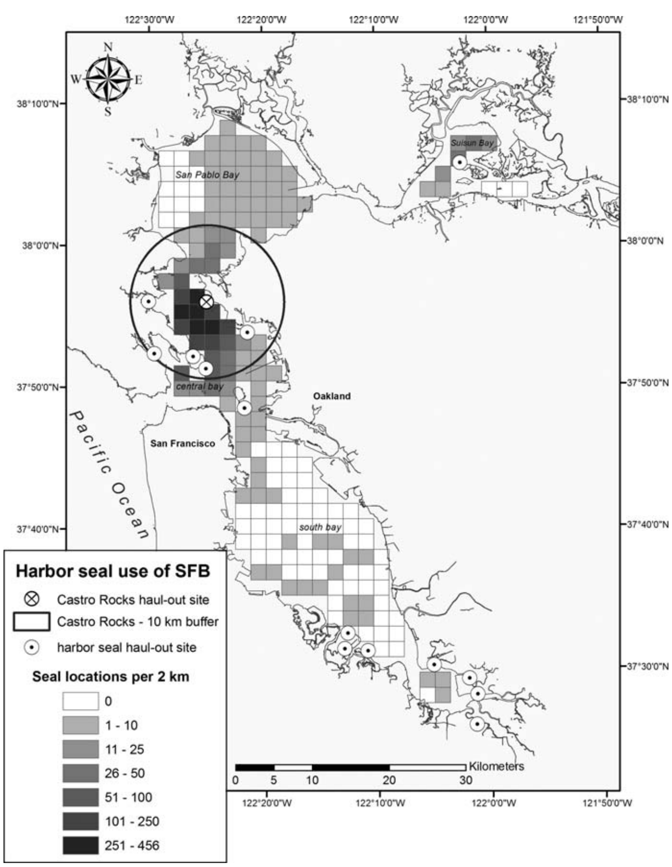

FIG. 2.—Use of San Francisco Bay (SFB), California, by Pacific harbor seals (*Phoca vitulina richardii*). Numbers of locations of seals, 2001–2005, in each of the 2-km grid cells are shown, in relation to the primary haul-out site, Castro Rocks. Also indicated is the area of highest use by seals, the 10-km buffer around this haul-out site.

The proportion of actual locations of seals that fell within 10 km of the primary haul-out and capture site was 0.86 (Fig. 2); therefore, we assigned that proportion of random points to within this distance of Castro Rocks. There was a significant difference between depth of locations of seals and random locations ($W = 254{,}037$, $n_1 = n_2 = 483$, $P < 0.001$), with seals found in deeper water (Table 3). In addition, there was a significant difference in bottom relief of locations of seals versus random locations ($W = 210{,}049$, $P < 0.001$), with seals tending to use areas with higher bottom relief. Seals were found in areas with higher abundances of benthic prey ($W = 212{,}913$, $P < 0.001$), and closer to outflow locations ($W = 251{,}559$, $P < 0.001$), than would be expected based on our stratified random model. Seals were found closer to the primary haul-out site ($W = 265{,}695$, $P < 0.001$), and closer to any haul-out site in SFB ($W = 266{,}968$, $P < 0.001$), than would be expected (Table 3; Fig. 2). However, there was no difference in proximity to human activity (either fishing activity or other types of activity), or abundance of midwater prey species, between locations of seals and randomly selected locations (Table 3). In light of these findings, we revised our conceptual model of influences on the distribution of seals in this highly disturbed estuary (Fig. 3).

DISCUSSION

Based on our analyses, the observed spatial distribution of harbor seals in SFB reflects the trade-offs faced by a central-place forager between habitat quality and distance from the central place when selecting optimal foraging habitat (Orians and Pearson 1979). For the environmental variables, our analyses supported our initial hypotheses. High abundance of benthic prey species, deeper depths (in an otherwise shallow estuarine ecosystem), higher bottom relief, and proximity to the haul-out site all were associated with increased use of an area by seals. The relationships with environmental predictors (depth, bottom relief, and prey abundance) hold, even when distance from the central place is accounted for; and when the existing spatial autocorrelation between the environmental variables and between locations of seals is taken into consideration. Given existing knowledge about behavior of harbor seals, these ecological relationships were not a surprise. For example, the finding that SFB seals forage near their primary haul-out site agrees with other studies reporting similar findings for this central-place forager, both for SFB (Grigg et al. 2009; Kopec and Harvey 1995; Torok 1994) and other areas (Iverson et al. 1997; Lowry et al. 2001). The relatively strong relationship between abundance of benthic prey species and use of an area by seals supports benthic feeding by seals in SFB, as has been reported in other areas (Harkonen 1987; Olesiuk 1993). Our analyses, however, have the added benefit of explicitly incorporating spatial structure of the data (both spatial autocorrelation, and distance from the central place) into the analyses. Habitat selection of wild populations is often inferred from patterns of observed use of disparate environments, with the assumption that disproportionate use results

TABLE 3.—Comparison of environmental characteristics of Pacific harbor seal (*Phoca vitulina richardii*) locations versus random locations around San Francisco Bay, California, based on Mann–Whitney tests with Bonferroni corrections for multiple comparisons. Selection of random locations took into account expected distribution of this central-place forager. Also shown are median values for locations of harbor seals, and for the random locations. Statistically significant results are shown in boldface type; $n_1 = n_2 = 483$ for all comparisons.

	Harbor seals (median)	Random (median)	*W* (*P*)
Depth (m)	**−7**	**−2**	**254,037 (<0.001)**
Bottom relief index[a]	**1.000144**	**1.0000094**	**210,049 (<0.001)**
Harbor seal prey—benthic species (individuals/ha)	**515.2**	**270.1**	**212,913 (<0.001)**
Harbor seal prey—midwater species (individuals/ha)	260.5	251.7	238,176 (0.28)
Distance from human use—fishing activity (m)	2,034	1,996	240,064 (0.13)
Distance from human use—other activity (m)	2,032	2,271	242,231 (0.04)
Distance from outflow locations (m)	**2,587**	**3,300**	**251,559 (<0.001)**
Distance from Castro Rocks (m)	**4,580**	**7,326**	**265,694 (<0.001)**
Distance from any haul-out site (m)	**1,931**	**3,014**	**266,967 (<0.001)**

[a] Index = surface area/planimetric area.

from selection (Garshelis 2000; Rosenberg and McKelvey 1999). Given the strong relationship between benthic prey abundance and in-water distribution of harbor seals in SFB, we infer that the observed spatial distribution reflects foraging behavior.

Our results did not support the hypothesis that presence of seals would be lower in areas of SFB close to consistent sources of anthropogenic disturbance (Figs. 3 and 4). Influence of anthropogenic factors on the spatial distribution of harbor seals proved difficult to resolve using the distance from human use and outfall point locations. The partial Mantel tests incorporating distance from the primary haul-out site revealed a weak negative relationship between human fishing activity and use of an area by seals, and a weak positive relationship between other sources of human activity and use by seals. This could reflect the lack of an influence of these types of activity on in-water distribution of harbor seals, because seals habituate to human presence in their foraging areas. Alternately, it could reflect variable influences of human activity on seal behavior, in light of other local environmental characteristics that more strongly influence the distribution of seals, such as availability of prey (Gill et al. 2001). Numerous studies of wild populations have documented avoidance of areas where humans are present (Reijnen et al. 1995; Stalmaster and Newman 1978), although

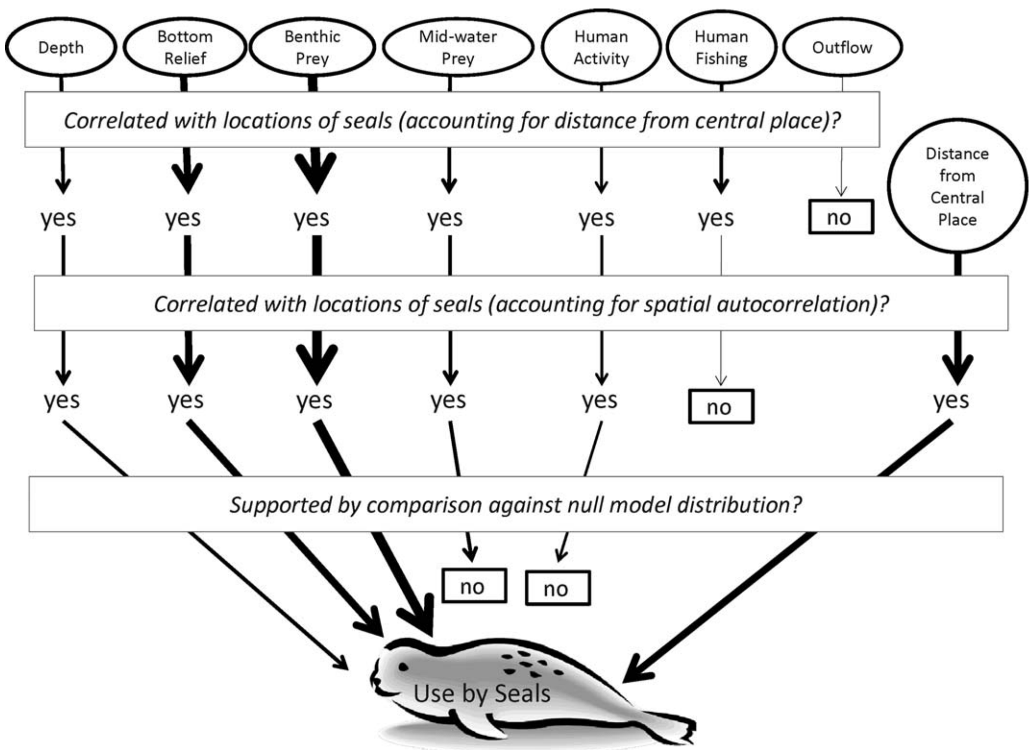

FIG. 3.—Final conceptual model of influences on the in-water spatial distribution of foraging Pacific harbor seals (*Phoca vitulina richardii*) in San Francisco Bay, California, incorporating results of the partial Mantel tests on use of an area by seals and the environmental predictor variables, and the Mann–Whitney comparisons between characteristics of random locations versus locations of seals. Strength of the relationship is indicated by line thickness.

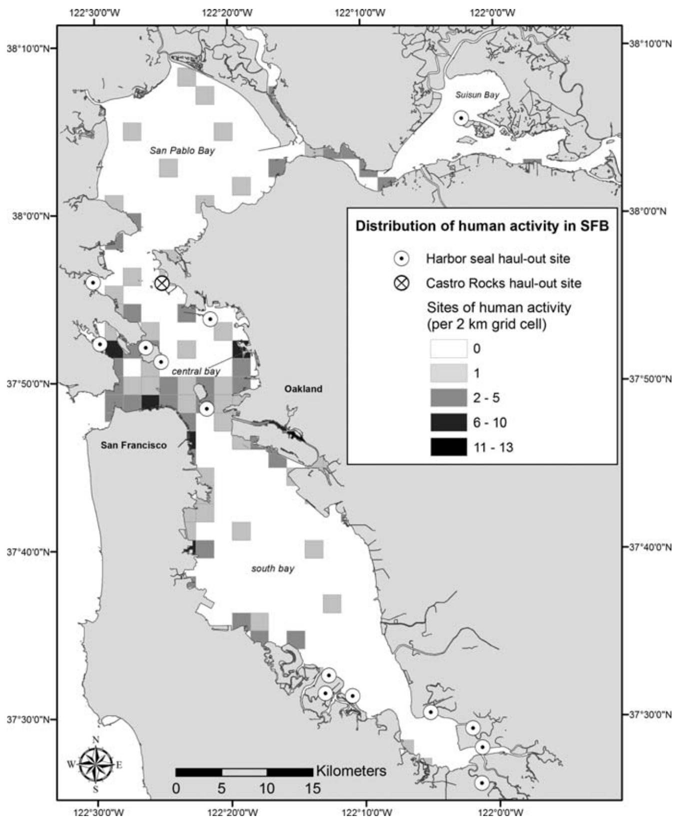

FIG. 4.—Spatial distribution of persistent human activity (boat launches, ferry terminals, commercial and recreational fishing areas, etc.) in San Francisco Bay, California, represented by number of such sites per 2-km grid cell.

others note continued use of valuable habitat areas despite high levels of human disturbance (Rugh et al. 2010). In our study area, there were no significant differences between in-water harbor locations of seals and the randomly selected locations for distance from human activity (fishing activity, or other types of human activity such as marinas, boat launches, shoreline access points, etc.).

We had originally predicted that presence of seals would increase with proximity to fishing areas, which fit with our hypothesis that seals would be attracted to these areas for the same reasons that human fishers were. However, the partial Mantel coefficient between distance from a fishing area and intensity of use of an area by seals was negative, indicating that the more similar the values of one variable, the less similar the values of the other variable (Smouse et al. 1986). Given the spatial variability in use by seals surrounding human fishing areas, these locations were not a reliable predictor of use by seals. This is supported by the fact that there was no significant difference between distances of seal versus randomly selected locations from fishing areas. Seals were found closer to outflow sources than would be expected based on a random distribution (Table 3). The increased use by seals in areas near outfalls seen may be related to increased biomass associated with the introduction of nutrients in these areas, but additional sampling would be needed to confirm this possibility. The relationship seen in the Mann–Whitney test may be due to spatial autocorrelation among the data, given that the relationship was lost once the spatial relationships were accounted for. Other studies have noted that assessing anthropogenic impacts on marine mammals is difficult given the highly mobile nature of these large marine predators, and the large amount of information on the level and type of disturbances involved that would be necessary to accurately model these impacts (Goetz et al. 2007). Human activities are often dynamic rather than fixed, making consistent effects on the spatial distribution of seals difficult to resolve.

Harbor seals are both sensitive to and habituate to disturbance. In some areas, seals will reduce overall use of, switch to nocturnal use of, or abandon haul-out sites subject to high levels of diurnal human disturbance (Allen 1991; Becker et al. 2009, 2011; Grigg et al. 2002; Newby 1973). In other areas, however, harbor seals appear to tolerate relatively high levels of disturbance while hauled out; both tolerance and sensitivity to disturbance have been reported for haul-out sites in SFB (Grigg et al. 2002, 2004) and in other study areas (e.g., Suryan and Harvey 1999). In highly impacted coastal waters where disturbance levels are consistently high and limited alternate habitat exists, the best strategy for harbor seals may involve habituation to predictable disturbance levels and continued use of disturbed (but profitable) foraging habitat close to the central place. Previous work in this area revealed that central SFB (Fig. 1), the busiest portion of the bay (Fig. 4), also supports high densities of many harbor seal prey species and includes valuable foraging areas for harbor seals (Grigg 2008; Grigg et al. 2009; Nickel 2003; Torok 1994). Pacific herring (*C. pallasii*) is a preferred prey of harbor seals in SFB, and the marked increase in numbers of harbor seals in central SFB during the winter most likely reflects seasonal increases in abundance of spawning Pacific herring in this area (Grigg et al. 2009). As noted above, SFB is shallow overall, with mean depth of 4.6 m (Jassby et al. 1993; Kimmerer 2004), but some of SFB's deepest waters are located in central SFB; our findings reveal that seals tend to use deeper parts of SFB. Nearly one-half (7 of 15) of the harbor seal haul-out sites in SFB are located in the central SFB (Fig. 1). Given the tendency of harbor seals to select haul-out sites near seasonally abundant prey resources (Harkonen 1987; Thompson et al. 1998), this spatial distribution of haul-out sites supports the concept that seals continue to use foraging habitat in central SFB despite high levels of human disturbance in these areas.

Our results did not support avoidance by harbor seals of foraging areas subject to high anthropogenic impacts. Given the lack of a strong increase in harbor seal population in SFB, this spatial overlap should not be assumed to mean that human disturbance has no impact on harbor seal populations in SFB. Physiological costs due to stress (such as increased heart rate and overall energetic costs) are analogous to nonlethal predator impacts (Frid and Dill 2002; Gill et al. 2001), and have been associated with human disturbance of wild populations (Ellenberg et al. 2006; MacArthur et al. 1982; Moen et al. 1982). In this way, unavoidable human disturbance may be contributing to the lack of a strong increase in the harbor seal population in SFB and low productivity compared to more-remote coastal areas (Grigg et al. 2004). Future research that compares body condition, survival, and reproductive success of harbor seals in highly disturbed areas such as SFB versus more-remote areas would help to reveal any such population-level impacts of human disturbance, should they exist.

One potential weakness of our approach is that, due to logistical and budgetary constraints on the number of study animals we could deploy with satellite-linked telemetry tags, small sample size required us to pool data from individual seals for these analyses. However, habitat selection analysis techniques using pooled data, such as the Neu method (Neu et al. 1974), are commonly used to assess habitat selection. McClean et al. (1998) compared various methods of assessing habitat selection, using a species with known habitat requirements, and found the Neu method superior to other methods that did not pool data. The high degree of agreement between our findings and other studies concerning the environmental influences on habitat use by harbor seals provides support for the effectiveness of our methods. However, given probable differences between individual seals based on sex, age class, or breeding status, or a combination of these (e.g., females with a pup versus alone), future studies might focus on identifying these differences, particularly with regard to sensitivity to human disturbance. In addition, similar tagging studies done in other parts of SFB may help to increase our understanding of in-water distribution of harbor seals in this highly impacted estuary.

In summary, we used a geographic information system, satellite-linked telemetry, spatial analyses, and available environmental data to provide a data-driven summary of environmental influences on in-water distribution of harbor seals in a busy coastal habitat. From a management perspective, our findings reflect the importance of maintaining a local prey base for harbor seals and of protecting harbor seal haul-out sites, because both local prey availability and distance from a suitable haul-out site are strongly associated with the distribution of foraging harbor seals.

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Appendix I

Pacific harbor seals (*Phoca vitulina richardii*) captured in San Francisco Bay, 2001–2005, and tagged with satellite-linked telemetry tags, with sample size information.

Seal	Age[a]	Sex[b]	Dates of tag attachment	Final (filtered) no. location estimates[c]
1	A	M	January 2001–June 2001	121
2	SA	F	July 2001–August 2001	33
3	SA	F	July 2001–August 2001	24
4	A	F	July 2001–March 2002	365
5	A	M	July 2001–August 2001	3
6	A	F	January 2001–September 2001	27
7	A	M	January 2002–May 2002	26
8	A	F	August 2002–January 2003	87
9	A	M	August 2002–November 2002	8
10	A	M	August 2002–November 2002	63
11	A	M	August 2002–March 2003	218
12	SA	M	August 2002–March 2003	250
13	SA	F	August 2002–February 2003	336
14	SA	F	August 2003–January 2004	111
15	A	F	August 2003–March 2004	274
16	Y	F	August 2003–December 2003	270
17	Y	F	August 2003–December 2003	202
18	A	F	January 2005–June 2005	53
19	SA	M	January 2005–June 2005	49

[a] Ages: A = adult, SA = subadult, Y = yearling.
[b] M = male, F = female.
[c] Location estimate filtering methods are described in the text.