Spatial and seasonal relationships between Pacific harbor seals (*Phoca vitulina richardii*) and their prey, at multiple scales

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Abstract—Knowing where pinnipeds forage is vital to managing and protecting their populations, and for assessing potential interactions with fisheries. We assessed the spatial relationship between the seasonal distribution of Pacific harbor seals (*Phoca vitulina richardii*) outfitted with satellite transmitters and the seasonal distributions of potential harbor seal prey species in San Francisco Bay, California. Pearson's correlation coefficients were calculated between the number of harbor seal locations in an area of the San Francisco Bay and the abundance of specific prey species in the same area. The influence of scale on the analyses was assessed by varying the scale of analysis from 1 to 10 km. There was consistency in the prey species targeted by harbor seals year-round, although there were seasonal differences between the most important prey species. The highest correlations between harbor seals and their prey were found for seasonally abundant benthic species, located within about 10 km of the primary haul-out site. Probable foraging habitat for harbor seals was identified, based on areas with high abundances of prey species that were strongly correlated with harbor seal distribution. With comparable local data inputs, this approach has potential application to pinniped management in other areas, and to decisions about the location of marine reserves designed to protect these species.

Manuscript submitted 30 May 2008.
Manuscript accepted 21 April 2009.
Fish. Bull. 107:359–372 (2009).

Identification of foraging habitat is essential to understanding the ecology of marine predators. This information is vital to managing and protecting populations, as well as assessing the potential effects of commercial and recreational fisheries on both the marine predator and the fisheries. We determined the spatial overlap of one marine predator, the Pacific harbor seal (*Phoca vitulina richardii*) and its prey in the San Francisco Bay estuary (SFB), California, in order to identify foraging areas and seasonal patterns of resource use by this coastal pinniped.

The Pacific harbor seal (hereafter referred to as the harbor seal) is a small phocid seal common to waters along the west coast of North America. Harbor seals are opportunistic predators, feeding primarily on benthic species and small, epibenthic, schooling fishes, and occasionally foraging on pelagic species (Harkonen, 1987). A relatively small number of species tend to dominate the diet of harbor seals, but seasonal shifts in diet are seen in many areas, associated with seasonal fluctuations in prey availability (Brown and Mate, 1983; Tollit et al., 1998). Fecal samples collected in SFB indicate that harbor seals in this region 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*) (Torok, 1994). Young harbor seals have a reduced diving capability, and eat benthic crustaceans—primarily shrimp (e.g., *Crangon* spp.) (Bigg, 1973). Based on VHF (very high frequency) radiotelemetry tracking, the foraging range of harbor seals in SFB is mainly within 1–5 km of a haul-out site (Torok, 1994; Nickel, 2003), indicating that harbor seals in SFB feed on local prey. Abundance of prey and distance from the primary haul-out site are the strongest predictors of harbor seal use of an area in SFB (Grigg, 2008).

Given information on what harbor seals in the region were eating, our primary goal was to identify where these harbor seals were foraging within the study area. Identifying the preferred foraging habitat of pinnipeds can be difficult because of the logistical challenges associated with locating and tracking these large, highly mobile animals while they are at sea. Harbor seals are considered "central place foragers" (Orians and Pearson 1979) in that they return to a central place (the haul-out site) after foraging trips, they repeatedly visit specific foraging areas, and they tend to focus their foraging effort in areas near the haul-out site (Thompson et al., 1998). Radiotracking, both conventional VHF and satellite-linked (hereafter referred to as satellite tracking), is used to identify areas used by tagged animals, and to measure the frequency with which animals return to these areas. For central-place foragers who feed primarily on a limited number of prey species and exhibit site fidelity to specific foraging areas, telemetry can be used in conjunction with information on prey distribution to identify foraging habitat (North and Reynolds, 1996; Robinson et al., 2007). The harbor seal was therefore an excellent subject with which to assess the usefulness of telemetry in identifying foraging habitat of pinnipeds.

A second goal of this study was to assess the influence of spatial scale on our analysis. A number of investigators have assessed the spatial overlap between distributions of marine predators and their prey (e.g., Rose and Leggett, 1990; Fauchald et al., 2000; Davoren et al., 2003). These investigators noted that the results of such analyses vary depending on scale (Rose and Leggett, 1990; Fauchald et al., 2000). As a result, studies encompassing multiple scales are recommended for addressing questions related to habitat selection (Olivier and Wotherspoon, 2005).

Although harbor seals in SFB appear to forage within the bay, harbor seals do periodically make trips to the outer coast (Grigg, 2008). A third goal of this study was to attempt to identify environmental factors associated with harbor seals leaving SFB to forage. Harbor seals could forage outside of SFB to exploit changes in availability of prey associated with coastal upwelling. Upwelling of cooler, nutrient-rich water is associated with increased productivity along the California coast and can influence the distribution of marine predators (Becker and Beissinger, 2003). Alternatively, harbor seals could forage outside of SFB when high numbers of harbor seals using haul-out sites within SFB result in intraspecific competition for food resources in SFB.

We examined the associations between harbor seals and potential prey species, using satellite tracking to identify patterns of harbor seal distribution in SFB and a database available from the California Department of Fish and Game (CDFG) on abundance and distribution of potential prey species in the area. The objectives of this study were 1) to identify spatial and seasonal patterns of association between harbor seals and their prey in an urbanized estuary; 2) to examine the influence of scale of analysis on the spatial relationship between predator and prey; 3) to relate shifts in prey abundance or environmental factors to seasonal differences in the use of waters inside and outside SFB; and 4) to assess the usefulness of satellite telemetry in identifying foraging areas of harbor seals.

Materials and methods

Study area

San Francisco Bay is a turbid estuary with mean depths ranging from 3–11 m, and is the largest coastal embayment on the Pacific coast of the United States (Conomos et al., 1985) (Fig. 1). Harbor seals use SFB year-round for foraging, pupping, and resting on terrestrial haul-out sites (Allen et al., 1993; Grigg et al., 2004).

Harbor seal telemetry

Between January 2001 and January 2005, harbor seals were captured at a primary haul-out site in SFB (Castro Rocks; Fig. 1). At high tide, "tangle nets" 20–40 m long and 5 m deep were set, and harbor seals were caught as they approached the site. Harbor seals were fitted with dorsal- or head-mounted satellite-linked Platform Terminal Transmitters (PTTs; model ST-18, Telonics, Mesa, AZ; models SDR-T16 and SPOT3, Wildlife Computers, Redmond, WA; depending on model, tag power ranged from 0.4 to 0.5 watt, repetition rate ranged from 45 to 48 sec). Only harbor seals deemed large enough (≥40 kg) to support the PTTs were tagged. The PTTs were glued to the harbor seal's pelage with a quick-setting marine epoxy, and were shed by harbor seals before or during their annual molt.

Service Argos (CLS America, Inc., Largo, MD) was the processing center for the satellite telemetry data and provided the geographical coordinates of the tagged harbor seals. When a harbor seal is at the surface, PTTs send periodic radio transmissions which are detected by polar-orbiting satellites. These satellites relay the signals to processing centers, where animal location estimates are calculated on the basis of the Doppler effect. Based on the number of received transmissions and other factors, all locations are grouped into location accuracy "classes," ranging from zero to three, and two additional classes (A and B) for locations that could not be assigned an accuracy estimate (Table 1). Marine mammals are considered to be good study animals for satellite tracking because they surface to breathe and this allows sufficient time for a position to be determined by the satellites. In addition, the elevation of the tag does not change while the tag is on the animal; changes in tag elevation have been cited as a primary cause of spatial inaccuracy (Keating et al., 1991). Recent studies have assessed the usefulness of PTTs for studying movements and habitat use of marine animals (e.g., Vincent et al., 2002; White and Sjoberg, 2002). Location classes with lesser accuracy are customarily removed from the data set, and filtering methods are used to remove improbable locations and improve the mean accuracy of the remaining locations. Vincent et al. (2002) and Hays et al. (2001) found that locations in classes B and 0 were inaccurate, but class A locations were more accurate and comparable to class 1 locations (Table 1). We therefore removed location estimates in classes B and 0 from the record of each harbor seal's movements, but did not automatically remove locations in class A. All points that fell on land were removed, and then the remaining locations were filtered according to the speed necessary for a harbor seal to move between two successive locations, calculated in a geographic information system (GIS). Any location that would have required a travel speed greater than 10 km/hr, or 2.78 m/s (Lowry et al., 2001),was flagged for inspection. These questionable harbor seal locations were assessed by their spatial and temporal relationship to the prior or subsequent location with a greater accuracy rating, and unlikely locations were 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, were also eliminated (see Keating, 1994). Locations within 1 km of a haul-out site were removed in order to eliminate locations associated with haul-out site use or underwater movements unrelated to foraging (Thompson and Miller, 1990). Finally, for these analyses, we analyzed spatial overlap between harbor seal locations and abundance of potential prey species around SFB, rather than analyzing sequential tracks of movement by individual harbor seals. To improve independence of point location estimates for the correlation analyses, locations recorded within one hour of another location for the same harbor seal were removed from the data set.

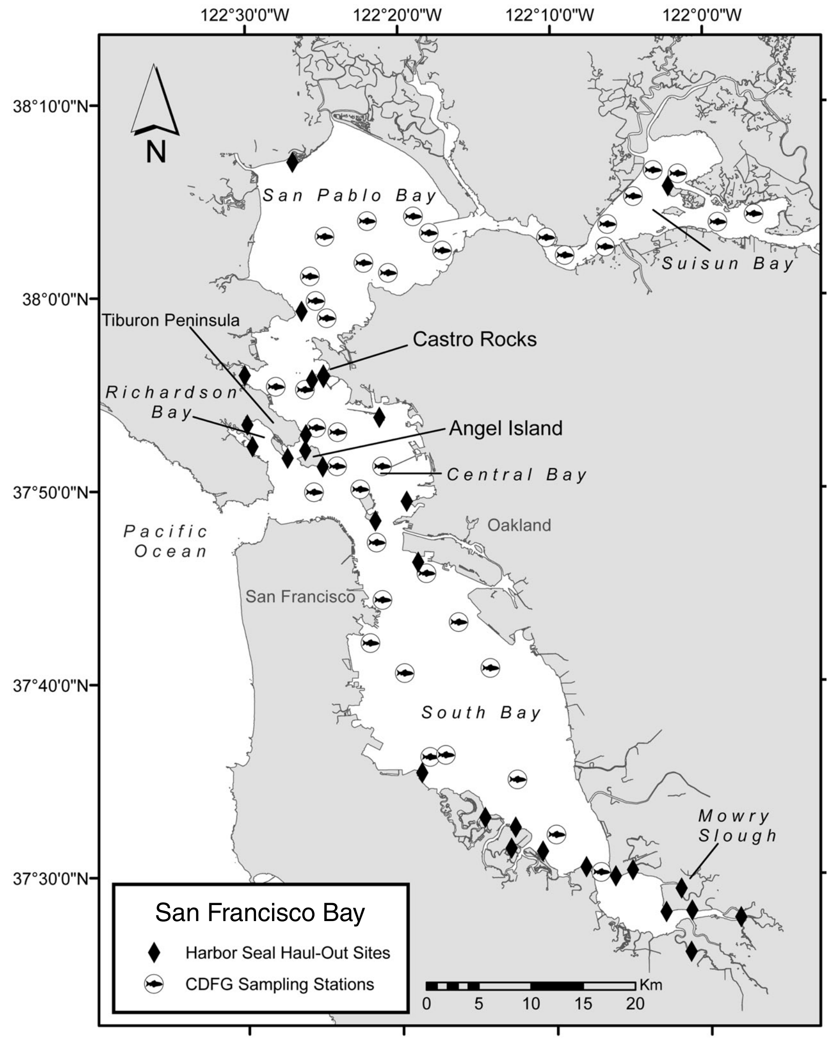

Figure 1

The San Francisco Bay, CA, study area, showing Castro Rocks and other primary harbor seal (*Phoca vitulina richardii*) haul-out sites, and 39 fish sampling stations around the bay sampled by the California Department of Fish and Game(CDFG). Catch-per-unit-of-effort data from the CDFG sampling stations were used to build seasonal harbor seal prey distribution maps for San Francisco Bay. Coastline data layer created by NOAA/NOS/ORR/CPRD (available online).

Correlation analyses

Records of prey distribution and abundance during the study period were obtained from the Interagency Ecological Program for the San Francisco Estuary and from the San Francisco Bay Study, California Dep. Fish and Game. Monthly samples of fish, crab, and shrimp species were collected by CDFG at 39 sampling stations located around SFB (Fig. 1), using two sampling methods: an otter trawl (OT) and a midwater trawl (MWT). The OT was used to sample bottom-dwelling fish, shrimp, and crab, the MWT was used to sample mid-water fish, and both trawls yielded quantitative data on fish abundance. For this study, we focused on eight species of fish known to be prey of harbor seals in SFB, combined crab species (primarily Dungeness crab, *Cancer magister*), and combined shrimp species (primarily *Crangon* spp.). Given concerns about harbor seals foraging on salmonids, CDFG data on the abundance and distribution of Chinook salmon (*Oncorhynchus tshawytscha*) in SFB were included in the analysis. Catch per unit of effort (CPUE) was calculated as follows for each station, month, and species, by using gear-specific formulas from CDFG:

$$OT\ \text{CPUE} = (\textit{number caught}/\textit{tow area}) \times 10{,}000, \quad (1)$$

Table 1

Location-accuracy classes for marine mammal location estimates obtained with satellite telemetry and assigned by Service Argos, and reported in other studies. Also included are the proportions of the final, filtered harbor seal *(Phoca vitulina richardii)* location data set from the present study that fell into each location class. Vincent et al.(2002) calculated accuracy for tags deployed on captive grey seals (*Halichoerus grypus*) in France and calculated accuracy separately for the latitude and longitude of position estimates. Hays et al. (2001) calculated accuracy using tags located in fixed positions in Brazil and on Ascension Island, as mean deviation from true tag location.

Location accuracy class	Proportion of total locations used in this study	Service Argos accuracy estimate (m)	Vincent et al. 2002 (unfiltered; lat./long.) (m)	Hays et al. 2001 (mean deviation from true) (m)
3	0.20	<150	157/295	270
2	0.25	<350	259/485	540
1	0.21	<1000	494/1021	1330
0	0	>1000	2271/3308	10,100
A	0.34	None assigned	762/1244	990
B	0	None assigned	4596/7214	7000

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

$$MWT\ \text{CPUE} = (number\ caught/tow\ volume) \times 10{,}000, \quad (2)$$

where *tow volume* = number of flowmeter revolutions × 0.0269 m/rev × net mouth area (10.7 m^2 in this case).

$$Crab/shrimp\ \text{CPUE} = \text{number caught per 5 minute tow}, \quad (3)$$

CPUE from the 39 sampling stations was used to create maps of the relative abundance of harbor seal prey species in SFB, by using the inverse distance weighting interpolation method (Geostatistical Analyst extension to ArcGIS 9.2, ESRI, Redlands, CA). Inverse distance weighting is a deterministic interpolation method and makes no assumptions about the input data; this was important given the patchy nature of fish distributions in SFB. Given seasonal differences in prey species' abundance and distribution, and in harbor seal behavior related to breeding and molting, we created four maps for each prey species, one for each harbor seal "season" (spring: March–May; summer: June–August; fall: September–November; winter: December–February). In SFB, harbor seals pup during the spring and molt during the summer. Only records for those months and years when we had tagged harbor seals active in SFB waters were included in the analyses.

Using the Hawth's analysis tools extension (available online at http://www.spatialecology.com/htools) for ArcGIS 9.2 (ESRI, Redlands, CA), a 1-km grid was laid over a map of the entire study area, consisting of all waters from the mouth of SFB, to the eastern edge of Suisun Bay (Fig. 1). All harbor seal locations and environmental data sets in the GIS were reprojected to Universal Transverse Mercator (UTM) coordinates, using the North American Datum of 1927 (NAD 27), zone 10N, and resampled to an initial grid resolution of 1-km. For each season, an average CPUE of each prey species was assigned to each 1-km grid cell, by using the area-weighted mean of the values falling within that grid cell. In addition, we counted the number of harbor seal locations falling within each grid cell; because the number of tagged animals was limited, data from individual harbor seals were pooled for this analysis (see Erickson et al., 2001). The minimum scale of analysis was 1 km^2, well within the estimated average accuracy of the filtered harbor seal location data (Table 1; see also Bekkby et al., 2002).

To vary the scale of analysis, data from the 1-km grid cells were combined into progressively larger grid cell sizes, ranging from 2 to 10 km. Given the size of SFB (and the fact that the sample size decreased with each successively larger grouping), we did not consider scales larger than 10 km. Because of the irregular shoreline of SFB, some grid cells overlapped land; therefore, we removed grid cells that represented primarily land from the analyses. For all remaining grid cells, we calculated the number of harbor seal locations per km^2.

For each spatial scale (1 to 10 km) and each season, we calculated the Pearson's correlation coefficient between the number of harbor seal locations per grid cell and the CPUE for each potential prey species in that cell. We plotted correlation coefficients versus scale for each season to assess the effects of scale on the strength of the spatial relationships between harbor seals and potential prey.

To estimate the availability of foraging habitat during each season, we used regression tree analyses (Breiman et al., 1984) to identify threshold values of prey CPUEs that would most strongly differentiate between grid cells with greater use by harbor seals and cells with lesser use by harbor seals, for each season. In other words, this threshold value indicated the minimum CPUE for prey in the grid cells representing areas that were fre-

Table 2

Harbor seals (*Phoca vitulina richardii*) captured in San Francisco Bay, CA (2001–05) and tagged with satellite telemetry tags, with sample size information. Ages are abbreviated as A (adult), SA (subadult), and Y (yearling). Dates and duration (in days) of telemetry tag attachment are shown. Numbers of both raw seal location estimates and filtered location estimates are shown. Accuracy filtering methods were based on location quality rankings provided by Service Argos, and a spatial filtering mechanism to reduce improbable locations. Location filtering consisted of the removal of points that fell within 1 km of a haul-out site, or outside of the study area.

Harbor seal ID	Age	Sex	Dates of tag attachment	Days tagged	Number of raw location estimates	Final sample size after accuracy and location filtering
15345	A	M	1/2001–6/2001	153	307	141, 21
15440	SA	F	7/2001–8/2001	34	106	65, 33
15436	SA	F	7/2001–8/2001	31	69	42, 24
19580	A	F	7/2001–3/2002	233	947	547, 365
19582	A	M	7/2001–8/2001	22	157	81, 3
15439	A	F	1/2001–9/2001	69	204	97, 27
15437	A	M	1/2002–5/2002	126	616	188, 26
10024	A	F	8/2002–1/2003	158	561	206, 87
10278	A	M	8/2002–11/2002	85	45	22, 8
10279	A	M	8/2002–11/2002	97	353	133, 63
10280	A	M	8/2002–3/2003	229	1013	451, 218
10297	SA	M	8/2002–3/2003	215	1156	480, 250
10863	SA	F	8/2002–2/2003	190	1269	588, 336
42526	SA	F	8/2003–1/2004	141	896	308, 111
42527	A	F	8/2003–3/2004	204	1369	485, 274
42529	Y	F	8/2003–12/2003	107	986	397, 270
42530	Y	F	8/2003–12/2003	123	1012	372, 202
21454	A	F	1/2005–6/2005	144	577	236, 53
42528	SA	M	1/2005–6/2005	135	524	179, 49

quently visited by harbor seals; lower abundances were found in cells repesenting areas less frequently visited by harbor seals. Grid cells with CPUE values above the threshold values identified in the regression tree were designated as potential harbor seal foraging habitat. Harbor seal habitat was mapped by using only the prey species with the highest correlations with harbor seal distribution (correlation coefficient >0.7) at the 10-km scale, because this coarser scale may be more appropriate for assessing behavior which influences lifetime fitness (Rettie and McLoughlin, 1999). The area (in km^2) of potential foraging habitat was then calculated, both for SFB as a whole, and within 10 km of the primary haul-out site, Castro Rocks.

To examine potential reasons why some harbor seals were leaving the bay, correlation coefficients were calculated between the proportion of harbor seal locations located outside of SFB, for each season, and the following three variables: 1) prey CPUE inside SFB; 2) number of harbor seals inside SFB and at Castro Rocks; and 3) indices of upwelling measured along the adjacent outer coast. The number of harbor seals in SFB fluctuates seasonally (Fancher, 1979; Grigg et al., 2004; Grigg, 2008), and we hypothesized that an increased number of excursions outside SFB would be positively correlated with the increased number of harbor seals in SFB. To ascertain the numbers of harbor seals in SFB and at Castro Rocks, harbor seals were counted at the three largest haul-out sites in SFB and the numbers were averaged by season across years. For information on the strength of upwelling along the California coast, we used monthly upwelling indices compiled by the National Oceanographic and Atmospheric Administration Environmental Research Division. Statistical significance for all correlations was assessed with $\alpha=0.05$.

Results

Harbor seal telemetry

Nineteen harbor seals were captured between January 2001 and January 2005 (Table 2). Data filtering for accuracy reduced the number of location estimates for individual harbor seals by 39–69%, and additional location estimates were removed when within 1 km of a haul-out site, or outside of SFB. The mean number of locations per harbor seal after all filtering was 120 ±27 (standard error of the mean; SEM). The number of locations per season ranged from 134 during the spring season, to 1139 during the fall. Locations were evenly dispersed between day and night (47% during the day, 6 a.m. to 6 p.m., and 53% during the night, 6 p.m. to 6 a.m.).

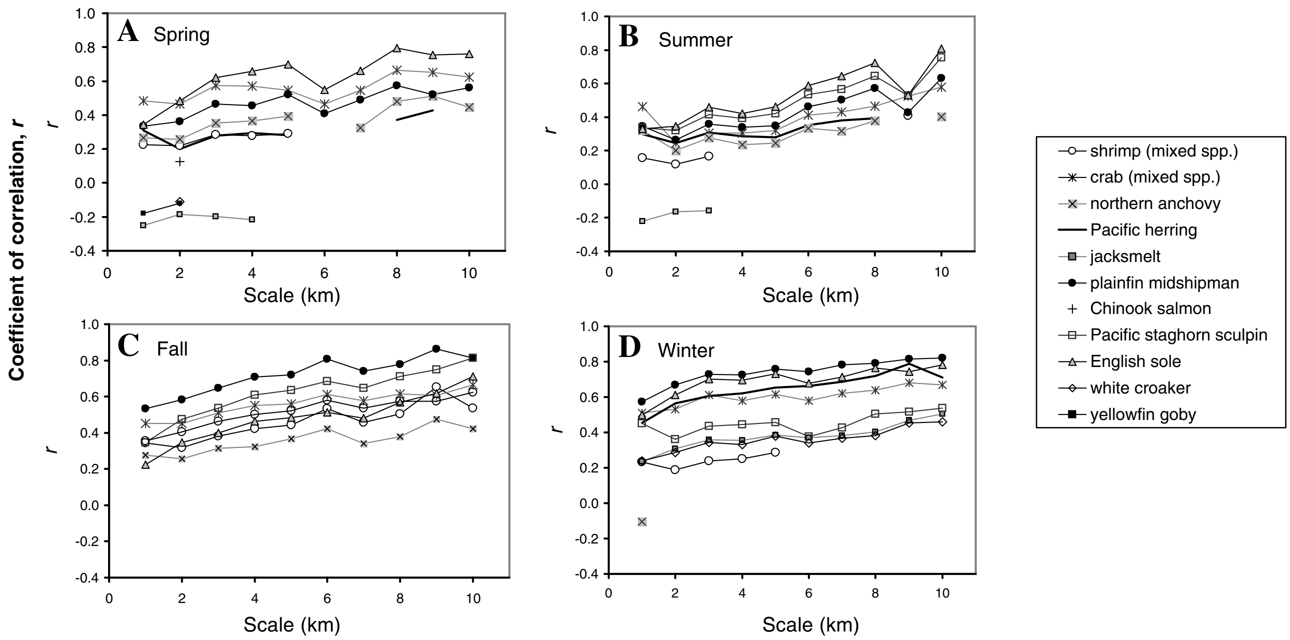

Figure 2

The effects of scale on the analyses of spatial overlap between distribution of Pacific harbor seals (*Phoca vitulina richardii*) and their prey species in San Francisco Bay, CA, 2001–05. Potential prey species included 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*), English sole (*Pleuronectes vetulus*), Chinook salmon (*Oncorhynchus tshawytscha*), shrimp (mixed species, primarily *Crangon* spp.), and crab (mixed species, primarily Dungeness crab, *Cancer magister*). Graphs show the change in strength of Pearson's correlations (r) between seal and prey locations with changes in analysis scale from 1 km to 10 km, for each season. Only statistically significant ($P<0.05$) correlations are shown.

Correlation analyses

According to our analyses, three benthic species—plainfin midshipman, English sole, and Pacific staghorn sculpin—are important prey of harbor seals in SFB (Fig. 2). Spatial overlap between distribution of harbor seals and abundance of primary harbor seal prey species was greatest in central SFB, and in waters around Castro Rocks (Fig. 3). Although harbor seals used areas in the north and south SFB in all seasons, waters of central SFB and surrounding the primary haul-out site, Castro Rocks, were used most frequently. Correlations revealed both year-round consistency in the identity of harbor seal prey species and seasonal differences between primary prey species.

Spring (March–May): During the spring pupping season, harbor seal locations were most highly correlated with English sole and crab (Figs. 2A and 3A). In all seasons, there were strong correlations between the distribution of crab and harbor seals (Fig. 4). In contrast to the fall and summer, there was no significant correlation between harbor seal locations and abundance of Pacific staghorn sculpin during the spring.

Summer (June–August): During the summer molting season, harbor seal locations were most highly correlated with English sole and Pacific staghorn sculpin (Figs. 2B and 3B). Harbor seals in SFB frequently visited areas where high numbers of Pacific staghorn sculpin were found in the 2001–05 CDFG trawls, most notably in the waters around the Castro Rocks haul-out site.

Fall (September–November): During the fall, harbor seal locations were most highly correlated with plainfin midshipman, white croaker, and Pacific staghorn sculpin (Figs. 2C and 3C). Across spatial scales, correlations with plainfin midshipman were particularly strong (often ≥ 0.8) during the fall.

Winter (December–February): During the winter, harbor seal locations were most highly correlated with plainfin midshipman, English sole, and Pacific herring (Figs. 2D and 3D). Harbor seals foraged in Pacific herring spawning areas, and correlations between Pacific herring and harbor seals were greatest during this season. No significant correlation was found between the distribution of harbor seals and Chinook salmon. There was little correlation between the frequency of use of an area by harbor seals and the distribution of yellowfin goby, a non-native species that was found to be an important prey species in an earlier study of the diet of SFB harbor seals (Torok, 1994).

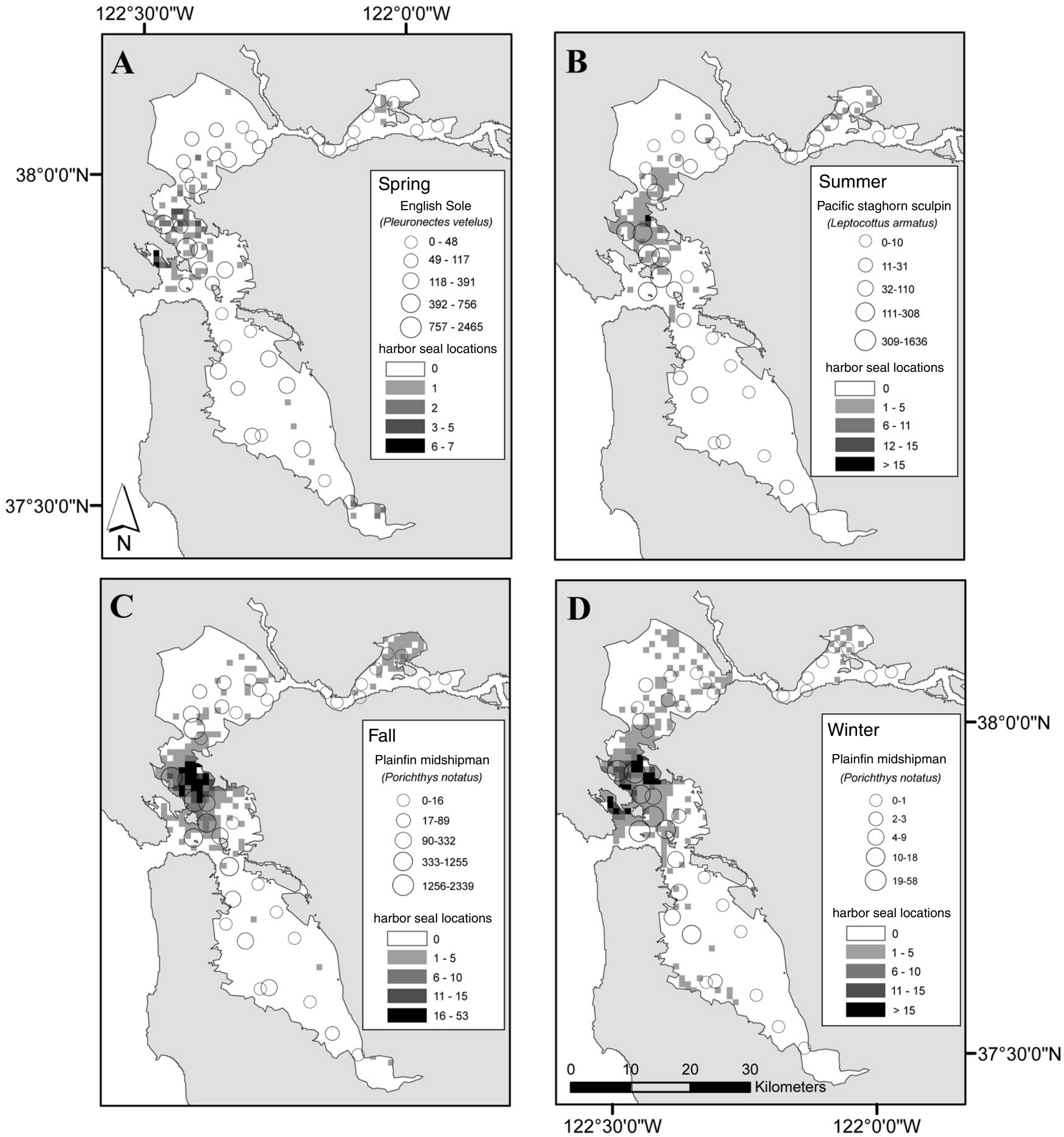

Figure 3

Spatial overlap of Pacific harbor seals (*Phoca vitulina richardii*) and important harbor seal prey species in San Francisco Bay, CA, for four seasons, 2001–05. Density of seal locations is indicated by shading of the 1-km grid, with darker shading indicating more frequent use by seals. Relative abundance of specific harbor seal prey species (as noted in the map legends) caught at each fish sampling station is indicated by size of the circle marking station location, and larger circles indicate greater catch per unit of effort of prey at that location, in number of individuals per hectare (1 hectare=0.01 km^2). Fish species shown are representative of harbor seal prey species found to have the greatest correlation with seal location for that season: **A**) Spring—English sole (*Pleuronectes vetulus*), **B**) Summer—Pacific staghorn sculpin (*Leptocottus armatus*), **C**) Fall—plainfin midshipman (*Porichthys notatus*), and **D**) Winter—plainfin midshipman (*P. notatus*).

At the 1-km scale, most correlations were positive (i.e., greater co-occurrence of harbor seal locations with greater prey CPUE), but not strong (correlation coefficients <0.6). The correlation coefficients for plainfin midshipman were greatest among most spatial scales during the fall and winter. The coefficients for English sole were greatest among most spatial scales during the spring and summer. The coefficients for Pacific staghorn sculpin were second greatest during summer and fall.

In general, correlations increased with scale (Fig. 2). At the largest scale (10-km), correlations between distribution of harbor seals and primary prey CPUEs were often ≥0.8. The prey species with high correlations (>0.7) at the 10-km scale included plainfin midshipman (fall and winter), Pacific staghorn sculpin (summer and fall), English sole (all seasons), and Pacific herring (winter) (Fig. 2). During spring, only English sole had a correlation of >0.7. For the foraging habitat map for spring, therefore, we included crab, which most closely approached the 0.7 threshold value. Based on the threshold prey abundances identified in the regression tree analysis, potential foraging habitat available in SFB ranged from 147 km^2 in spring to 238 km^2 in fall (Table 3, Fig. 5). Foraging habitat available within 10 km of Castro Rocks ranged from 101 km^2 in spring to 144 km^2 in fall.

When assessing seasonal differences in harbor seals' use of waters inside vs. outside SFB, the proportion of harbor seal locations on the outer coast was greater during the summer (0.33) and spring (0.21) than during the fall (0.01) or winter (0.08). Use of areas outside of SFB was not correlated with prey CPUE in SFB, number of harbor seals in SFB or at Castro Rocks, or upwelling indices. In general, the proportion of harbor seal locations recorded outside of SFB decreased with greater levels of prey availability in SFB, increased with greater numbers of harbor seals in SFB as a whole, and increased with greater upwelling indices. In contrast, when the proportion of locations on the outer coast was compared with the average maximum count at Castro Rocks, the proportion on the outer coast tended to be lesser when numbers of harbor seals at Castro Rocks were greater.

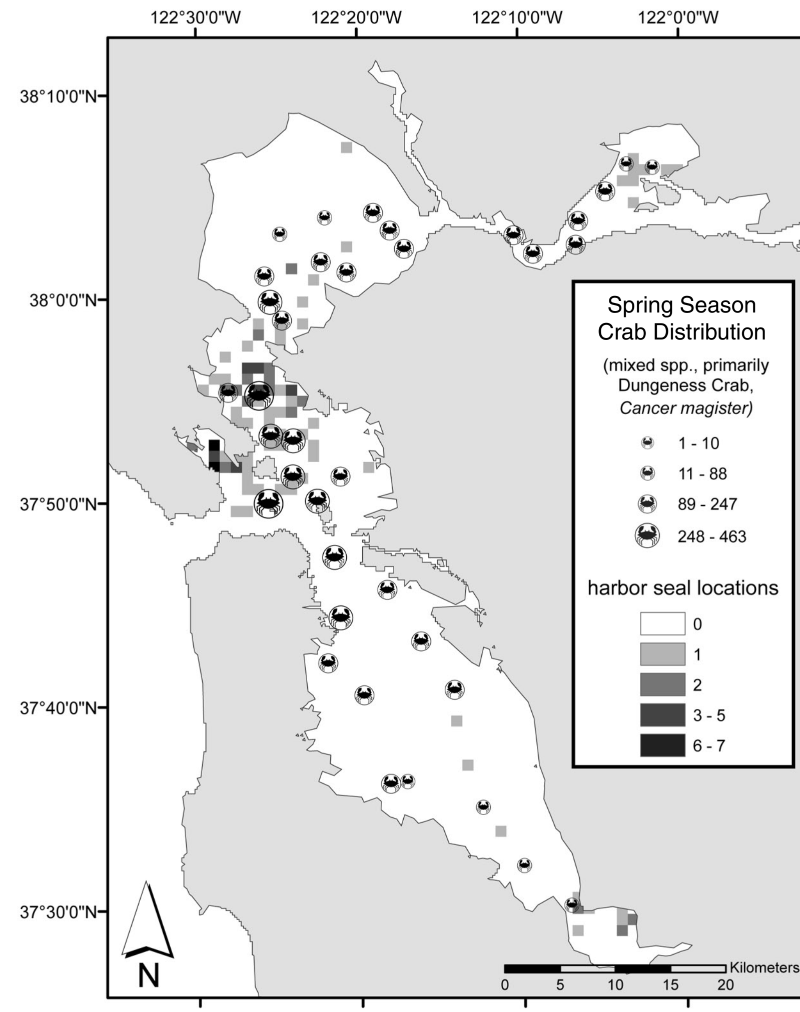

Figure 4

Spatial overlap of Pacific harbor seal (*Phoca vitulina richardii*) distribution with abundance of crab species (mixed species; primarily Dungeness crab, *Cancer magister*) in San Francisco Bay, CA, during the spring seal pupping seasons, 2001–05.

Discussion

We used a simple approach for identifying harbor seal foraging areas, using satellite tracking, available information on harbor seal diets from previous studies, and a data set on prey distribution obtained from a local management agency. In many cases, the abundance and distribution of prey is the most important factor influencing the spatial distribution of predators (Davoren et al., 2003). The primary motivation for a predator to move is to locate prey patches which offer a sufficient energetic "reward" (Charnov, 1976), i.e., provide sufficient energy gained from ingestion of prey, once the energetic costs of capture have been deducted. Not surprisingly, both terrestrial and marine mammals have been found to choose habitats that provide resources necessary for survival and reproduction, and for this reason, use of an area is often assumed to reflect quality or abundance of resources available in that area (Boyce and McDonald, 1999; Davoren et al., 2003).

Despite some controversy about possible biases in fecal analyses used to estimate diets (Harvey, 1989; Tollit et al., 1998), analysis of fecal samples remains an important method of identifying prey species of pinnipeds. However, it is often difficult to identify where harbor seals are foraging, even when fecal analyses are supplemented by VHF telemetry tracking (Torok, 1994). This problem has led some researchers to use techniques such as fatty acid signatures (Iverson et al., 1997) to identify harbor seal foraging areas. Our study presents an alternate approach to identifying these areas.

Table 3

Area (km^2) of Pacific harbor seal (*Phoca vitulina richardii*) foraging habitat in San Francisco Bay, CA, based on areas where abundance of harbor seal prey species was above the threshold value calculated in the regression tree analyses. Area of foraging habitat throughout SFB is given, as well as area of foraging habitat within 10 km of Castro Rocks, the primary haul-out site used by harbor seals in this study.

Season	Prey species used in estimation of foraging habitat	Area of foraging habitat (km^2)	Area of foraging habitat within 10 km of Castro Rocks (km^2)
Spring	English sole (*Pleuronectes vetulus*) Crab (mixed spp.; primarily Dungeness crab, *Cancer magister*)	146.8	100.7
Summer	Pacific staghorn sculpin (*Leptocottus armatus*) English sole	222.9	140.2
Fall	Plainfin midshipman (*Porichthys notatus*) Pacific staghorn sculpin English sole	238.4	144.1
Winter	Pacific herring (*Clupea pallasii*) Plainfin midshipman English sole	220.6	130.8

We assume that the spatial overlap between harbor seals and prey species reflects the tendency of harbor seals to frequent areas where the density of prey is greatest. Seasonal correlations between harbor seal locations and prey density revealed the following patterns.

Spring prey species

The spatial correlation between harbor seals and English sole during spring could reflect harbor seals' use of shallower waters associated with breeding behavior because four of nine of the harbor seals tagged during this season were females of reproductive age, two of which were confirmed breeders (as determined from resightings with a pup). Harbor seal females wean their pups after four weeks and do not fast during the nursing period. Castro Rocks is submerged during high tides, requiring cows and pups to leave the site together. Pups have reduced diving capabilities (Bigg, 1973), which may predispose the females with pups to forage in shallower waters. English sole are abundant in the waters of central SFB and San Pablo Bay during spring, mostly in shoal waters of San Pablo Bay.

The consistent correlations between the distribution of harbor seal locations and crab may be due more to the foraging habits of harbor seal prey than to the harbor seals foraging directly on crab. Harbor seals consume crabs in California (Harvey et al., 1995), but whether crabs are important prey among harbor seals in SFB remains unclear. Pacific staghorn sculpin and English sole are major consumers of juvenile Dungeness crabs, and the vast majority of Dungeness crabs in SFB are juveniles (Reilly, 1983). In addition, crab numbers tend to be greatest in waters around Castro Rocks (particularly during spring), and therefore, the overlap of harbor seals and crab may also be related to proximity to Castro Rocks.

During spring, greatest concentrations of Pacific staghorn sculpin were found in the extreme south bay, indicating that the abundance of this prey species was greater near a large south SFB pupping site, Mowry Slough. These south SFB aggregations of Pacific staghorn sculpin were apparently not used by Castro Rocks harbor seals during spring, and the lack of correlation between harbor seals and sculpin during this season likely reflects the tendency of harbor seals to remain closer to their primary haul-out site during pupping.

Summer prey species

English sole appear to be an important food source for SFB harbor seals. English sole use the SFB as a nursery area and remain in the bay for 6–18 months (Budd, 1940). Although there was a significant correlation between harbor seal locations and English sole abundances in all seasons (see also spring prey species, above), abundance of age-1+ sole was less in the summer, when the correlation between harbor seals and English sole was greatest. Because harbor seals are opportunistic foragers, they may exploit the abundant young English sole found near their haul-out site during the molting season. Large mature English sole (> 250 mm) were rarely caught by CDFG surveys, and Torok (1994) suggested that any foraging on flatfish by south SFB harbor seals took place outside of SFB; however, harbor seals were occasionally observed feeding on large flatfish near the Castro Rocks site. In addition, harbor seals often visited areas where Pacific staghorn sculpin were numerous, particularly in waters around the Castro Rocks haul-out site. Harbor seals spend a greater proportion of their time hauled out during the molting season (Thompson et al., 1989), and harbor seals in this

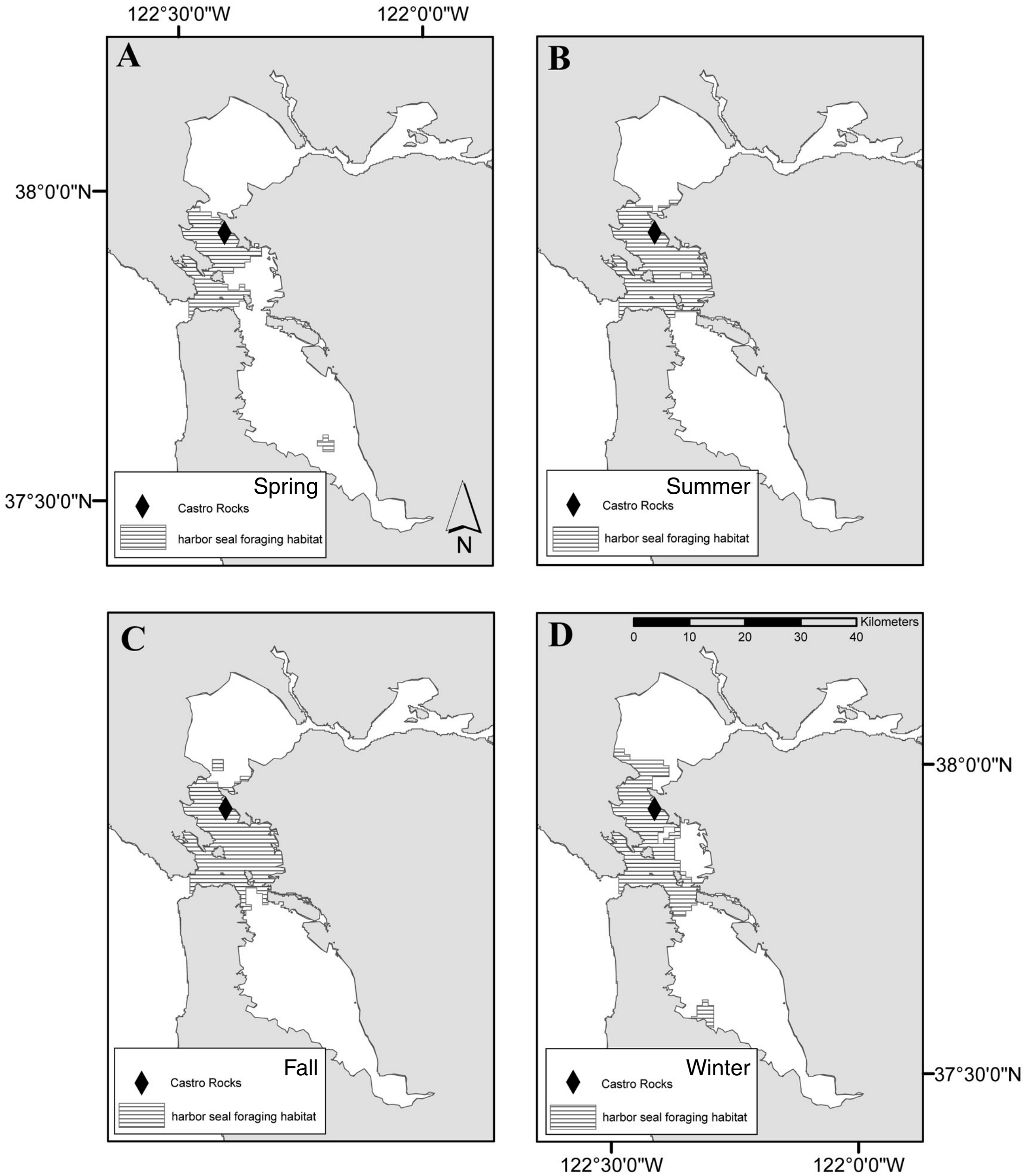

Figure 5

Pacific harbor seal (*Phoca vitulina richardii*) foraging habitat in San Francisco Bay, CA, by season: **A**) Spring; **B**) Summer; **C**) Fall; D) Winter. Areas were designated harbor seal habitat if they contained abundances of primary seasonal prey species which met or exceeded the thresholds identified in the regression tree analyses. Primary seasonal prey species were identified based on strength of correlation in the GIS overlay analysis between harbor seal telemetry locations and abundance of individual prey species.

study were likely foraging on these species because of their close proximity to the harbor seals' primary haul-out site during the annual molt. Longer-range foraging trips by harbor seals tend to occur outside of the molting and pupping seasons (Thompson et al., 1989).

Fall prey species

Harbor seals in SFB frequently visit areas where benthic fish species common in SFB are found in greatest abundance. Adult plainfin midshipman tend to burrow into the sand during the day, emerging at night to feed (Fitch and Lavenberg, 1971). Harbor seals in SFB forage both during the night and day (Torok, 1994; Nickel, 2003), so harbor seals may be feeding on adult plainfin midshipman at night, in the same areas where greater numbers of juveniles were recorded during the day by CDFG trawls; spatial distribution of adult and juvenile plainfin midshipman is similar in SFB. Numbers of plainfin midshipman are greatest in central SFB during the fall. In addition, white croaker are abundant in SFB; age-1+ white croaker move into central SFB in the fall before migrating out of SFB in the late fall and winter. During fall, harbor seals occurred where there were greatest numbers of this species in central SFB and around Castro Rocks. The Pacific staghorn sculpin is one of the most abundant demersal fish in SFB, and is common in central SFB and San Pablo Bay. Numbers of adults are greatest during October through April. Harbor seals are more frequently located in areas with greatest abundance of this species, in both the fall and summer.

Winter prey species

The waters to the northeast of the Tiburon Peninsula and near the southeastern edge of Angel Island appear to represent important foraging areas for SFB harbor seals, particularly those using the Castro Rocks haul-out site. These areas were frequently visited by harbor seals year-round, and use of these areas has been noted in earlier studies of harbor seals in SFB (Torok, 1994, Nickel, 2003). During winter, abundance of plainfin midshipman was greatest in central SFB, most notably in waters to the northeast of the Tiburon Peninsula and the southeastern edge of Angel Island. Similarly, maximum numbers of English sole were found in the central bay, around Tiburon Peninsula and Angel Island.

Pacific herring is believed to be a preferred prey of harbor seals in SFB, and seasonal distribution of harbor seals in SFB reflects seasonal increases in abundance of Pacific herring, which spawn in SFB during the winter (Grigg, 2008). Correlations between the distributions of Pacific herring and harbor seals were greatest during winter, and harbor seals often were seen in SFB covered with herring eggs. Well-known Pacific herring spawning areas, such as Richardson Bay, around the Tiburon Peninsula, and along the eastern shoreline of SFB from Castro Rocks southward, were visited frequently by harbor seals during this season.

Harbor seals do not appear to focus much foraging effort on Chinook salmon while they move through SFB. This part of the analysis may have been limited by the very small numbers of salmon caught by CDFG trawls. However, salmon were not reported in earlier studies of harbor seal diet in SFB based on fecal sample analyses (Torok, 1994).

Overall, our findings agree with previously reported harbor seal diets based on fecal sample analyses in SFB (Torok, 1994), with the notable exception of yellowfin goby. Torok (1994) found that yellowfin goby was the most numerous species in harbor seal fecal samples, although his samples were primarily collected from harbor seals captured in the south SFB, whereas the tagged harbor seals used in this study were captured at a central SFB haul-out site. Yellowfin gobies are seasonally abundant in San Pablo Bay and Suisun Bay. Although both areas were visited by harbor seals in our study, these harbor seals may have foraged on gobies opportunistically, because they did not appear to frequently visit areas with abundant yellowfin goby. This may reflect partitioning of foraging habitat between harbor seals using primarily south SFB haul-out sites and using central and north SFB haul-out sites; separation of harbor seals in northern and southern areas of SFB has been noted before (Allen et al., 1993; Grigg, 2008). Use of haul-out specific foraging areas has been noted in other harbor seal populations (Iverson et al., 1997; Thompson et al., 1998).

The accuracy of our methods for identifying foraging habitat for harbor seals in this region is supported by the fact that our findings agree with earlier studies, which demonstrate the tendency of harbor seals to forage on seasonally abundant, primarily benthic prey found near their primary haul-out site (e.g., Harkonen, 1987; Thompson et al., 1998). Spatial overlap between harbor seals and the prey species surveyed in this study was greatest in waters within approximately 10 km of Castro Rocks and declined in waters beyond this range. This is consistent with central place foraging theory, where site use is expected to decline with distance from the central place (e.g., haul-out site; Orians and Pearson, 1979). There may also be a tendency for harbor seals to feed in areas with more predictable prey, e.g., the waters of central SFB, where abundance of fish caught in CDFG trawls tends to be high year-round. Greater correlations between predator and prey can be expected in these areas where prey is predictably present, and lesser correlations in other less predictable, "ephemeral" prey areas (Davoren et al., 2003), e.g., other parts of SFB. Similarly, harbor seals may select a larger-scale region (e.g., central SFB) where prey are found in greater abundance, a trend that is reflected in the greater correlations at larger scales in our study and in other studies of marine predators and their prey (Rose and Leggett, 1990; Mehlum et al., 1999; Fauchald et al., 2000). Harbor seals' tendency to return repeatedly to the same foraging areas indicates that they can track regions with predictably abundant prey over long time scales (e.g., seasonally), despite the likelihood that locations of individual prey patches may vary over much shorter time scales. In other systems and at smaller scales, prey patches are more variable in location, and correlations between predators and prey at smaller scales likely will be weaker (Mehlum et al., 1999). Harbor seals tend to choose haul-out sites located near abundant prey resources (Loughlin, 1978), and the selection of the Castro Rocks location as a haul-out site almost certainly reflects availability and abundance of prey resources nearby.

We did not attempt to identify average patch size of harbor seal prey in our study, choosing instead to demonstrate overlap with areas of abundant prey resources. As Dungan et al. (2002) noted, patches that are smaller than the size of the sampling unit cannot be detected. Average size of prey patches in SFB may be smaller than our minimum study scale of 1 km. Nickel (2003) suggested that the average maximum prey patch for harbor seals foraging in SFB was 200 m, based on fractal analyses of harbor seal positions obtained by VHF radiotracking. If true, our grid cells could potentially have contained no prey patches or more than one prey patch, and could illustrate relative quality of foraging areas rather than locations or sizes of individual prey patches. On the other hand, we would expect positive correlations between harbor seal locations and prey densities only at scales greater than the dimensions of aggregations of predator or prey. At scales less than the smallest aggregation of predator or prey, we would be more likely to see negative correlations, because of factors such as predator avoidance by prey (Rose and Leggett, 1990). The greater correlations seen at larger scales in our study may also reflect the tendency of large scales to reduce or average out the effects of stochastic processes affecting where prey patches are located (Corsi et al., 2001). Small but significant negative correlations were found only at smaller scales (1 to 4 km) in our study, primarily involving two species: jacksmelt (spring and summer) and yellowfin goby (spring). Jacksmelt are often found in large schools in SFB, and negative correlation of the jacksmelt and harbor seal distributions at smaller scales could be due to avoidance of foraging harbor seals by jacksmelt schools. Catch per unit of effort of yellowfin goby is usually greatest in San Pablo Bay and Suisun Bay, and least in central SFB, which could explain the negative correlation with this species.

Based on observations of foraging locations of individual SFB harbor seals seen in past studies (Fancher, 1979; Torok, 1994), the amount of harbor seal habitat estimated by our methods may be conservative. Our estimates were based on only the species with the strongest correlations between harbor seal locations and prey abundance data during our study period. Had additional species' distributions been included in the potential habitat maps, a greater proportion of SFB may have been designated as foraging habitat for harbor seals. In addition, our estimates were based on strong correlations between predator and prey for harbor seals captured at (and presumably using) a haul-out site in central SFB. Had harbor seals used in this study been captured at a site in the extreme southern or northern SFB, the relative strength of correlations between harbor seals and individual prey species may have been different, if harbor seals that use these other sites focus on different prey species. However, both an earlier radiotracking study using harbor seals captured in southern SFB (Torok, 1994) and a 2000–2001 radiotracking study conducted using harbor seals captured at Castro Rocks (Nickel, 2003) identified large foraging areas in central SFB, a number of which fell within the same areas indicated by our habitat maps. In addition, as harbor seals will shift prey species with seasonal and annual changes in local prey abundance (Tollit and Thompson, 1996), significant changes in the abundance or distribution of prey species in SFB could cause harbor seals to switch to foraging areas not identified in our maps. With new information on prey distribution, locations of potential foraging habitat could easily be updated in the GIS.

Identifying factors that govern when harbor seals leave SFB to forage will require larger sample sizes, information on seasonal patterns of prey availability on the outer coast, and possibly more fine-grained data on individual harbor seal movements and behavior while at sea. In many areas, including SFB, harbor seals exhibit two foraging strategies (Thompson et al., 1998; Grigg, 2008). In one strategy, harbor seals make shorter, daily trips to and from foraging areas near the haul-out site; in the alternative strategy, harbor seals make longer foraging trips to more distant foraging areas, often lasting for a number of days and followed by extended haul-out periods. Harbor seals often move to protected estuarine haul-out sites to breed and molt, and numbers of harbor seals at some haul-out sites in SFB are greatest during these seasons (Grigg et al., 2004). The proportion of harbor seal locations on the outer coast in our study was greater during the spring (pupping) and summer (molting) seasons and may reflect the need for some individual harbor seals to forage in coastal waters when the density of harbor seals was high in SFB, in order to minimize intraspecific competition for prey (and therefore, animals would forage in coastal waters but return to SFB haul-out sites to rest between trips). Alternatively, this behavior could reflect the movement by some harbor seals to pupping or molting haul-out sites located outside of SFB, and use of coastal foraging areas closer to these haul-out sites. Inspection of individual harbor seal movements (not shown) indicated that both patterns were probably occurring during our study period (Grigg, 2008).

Satellite telemetry enabled us to identify correlations between harbor seal distribution and the distribution of prey species known to be present in the diet of local harbor seals. Using the harbor seal locations and GIS overlay analyses, we identified species of fish likely to be important seasonal prey species of harbor seals in SFB, and areas likely to be important foraging areas (particularly for harbor seals using the Castro Rocks haul-out site). Use of Service Argos positions required substantial elimination of inaccurate positions, with resultant loss of sample size and resolution of harbor seal movements, and limited the scale at which the analyses could be conducted. Nonetheless, we feel that satellite telemetry provided a useful way to assess harbor seal distribution in our coastal study area, allowing continual collection of information on harbor seal locations that would have been difficult using currently available VHF radiotelemetry tags, and eliminating the potential disturbance of an observer's presence on foraging harbor seals.

Finally, this spatially explicit approach to the identification of foraging areas has applications to management of pinnipeds in other areas, and other marine predators that can be tracked with satellite telemetry. With local data inputs comparable to those used in this study, this approach could be applied to management of marine predators in other areas. Knowledge of the location of foraging areas is important to such management concerns as the potential effects of future shifts in the spatiotemporal distribution of prey (due to climate change, etc.), the link between local resource availability and local population trends, prediction of possible interactions of marine predators with fisheries, or identification of appropriate locations for marine protected areas.

Acknowledgments

We would like to thank the following individuals: C. Morton and his colleagues at the California Department of Transportation (Caltrans); J. Harvey and his students; F. Gulland; D. Greig; J. Neale; T. Garfield; R. Larson; K. Hieb; D. Kopec; S. Oates; and J. Grigg. We would particularly like to thank the students and staff at San Francisco State University (SFSU) who helped with this study. This project was supported by Caltrans, SFSU, and a University of California Grant to E.K.G. The research was conducted in accordance with Incidental Harassment Authorizations fr23de97-52 and fr14ja00-38 issued by the National Marine Fisheries Service (NMFS) to Caltrans, NMFS scientific research permit no. 373-1575, and SFSU Animal Care and Use Committee permit no. #99-534.

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