

California and Steller sea lion use of a major winter haulout in the Salish Sea over 45 years

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ABSTRACT: Populations of California sea lions *Zalophus californianus* and Steller sea lions *Eumetopias jubatus* in much of the eastern North Pacific Ocean have experienced significant growth since being protected in the early 1970s (by the US Marine Mammal Protection Act and Canada's Fisheries Act) from commercial harvests and fisheries-related culls. However, there remains substantial and unexplained variance in the annual number of sea lions using a major winter haulout at the entrance to the Salish Sea. We used linear regression on principal components to show maximum annual sea lion counts, adjusted for population growth, varied as a function of herring biomass and not local sea surface temperatures or precipitation. Results suggest that Race Rocks, British Columbia, Canada, is used as a stopover for an increasing number of sea lions approaching southern Vancouver Island to feed during the nonbreeding season. Reports of resource-driven movements of sea lions are not new, but this is the first study to use a multidecade data set to show resource-driven movements can underlie long-term patterns of population growth. Finally, we found an unexplained change in the seasonal use of Race Rocks affecting both species. Arrival at Race Rocks has occurred in late summer since 1965, but up to 1979 departure had occurred the following spring; since as late as 1997, departure has occurred mid winter. This study highlights the complexities of enacting conservation plans for species with latitudinal distributions and undergoing long-term population change.

KEY WORDS: Pacific herring · Race Rocks · Sea surface temperature · Strait of Georgia · Pinniped · Juan de Fuca Strait · Vancouver Island

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INTRODUCTION

A major challenge to marine mammal conservation stems from population ranges extending across latitudinal clines between feeding and breeding seasons. California sea lions *Zalophus californianus* and Steller sea lions *Eumetopias jubatus* are high profile species that redistribute widely between seasons along the Pacific coast of North America from California to Alaska. Their distributions appear to be driven by a complexity of biotic, abiotic and anthropogenic factors.

Such large-scale movements complicate management decisions because environmental factors, which control wildlife movements and ultimately popula-

tion trends, can be confounded across geopolitical boundaries. To understand population trends, therefore, conservation biologists are encouraged to consider large spatial scales. However, to effectively enact conservation strategies (e.g. Fisheries and Oceans Canada 2011), we first need detailed knowledge of localized environmental factors throughout the species' range. We attempted to identify some of the factors affecting sea lion abundance at a major winter (i.e. nonbreeding) haulout and ecological reserve, Race Rocks, off southern Vancouver Island, British Columbia, Canada (Fig. 1). Race Rocks is one of several major winter haulouts for Steller and California sea lions along the Pacific coast of Canada. The site is of special importance to local conservation

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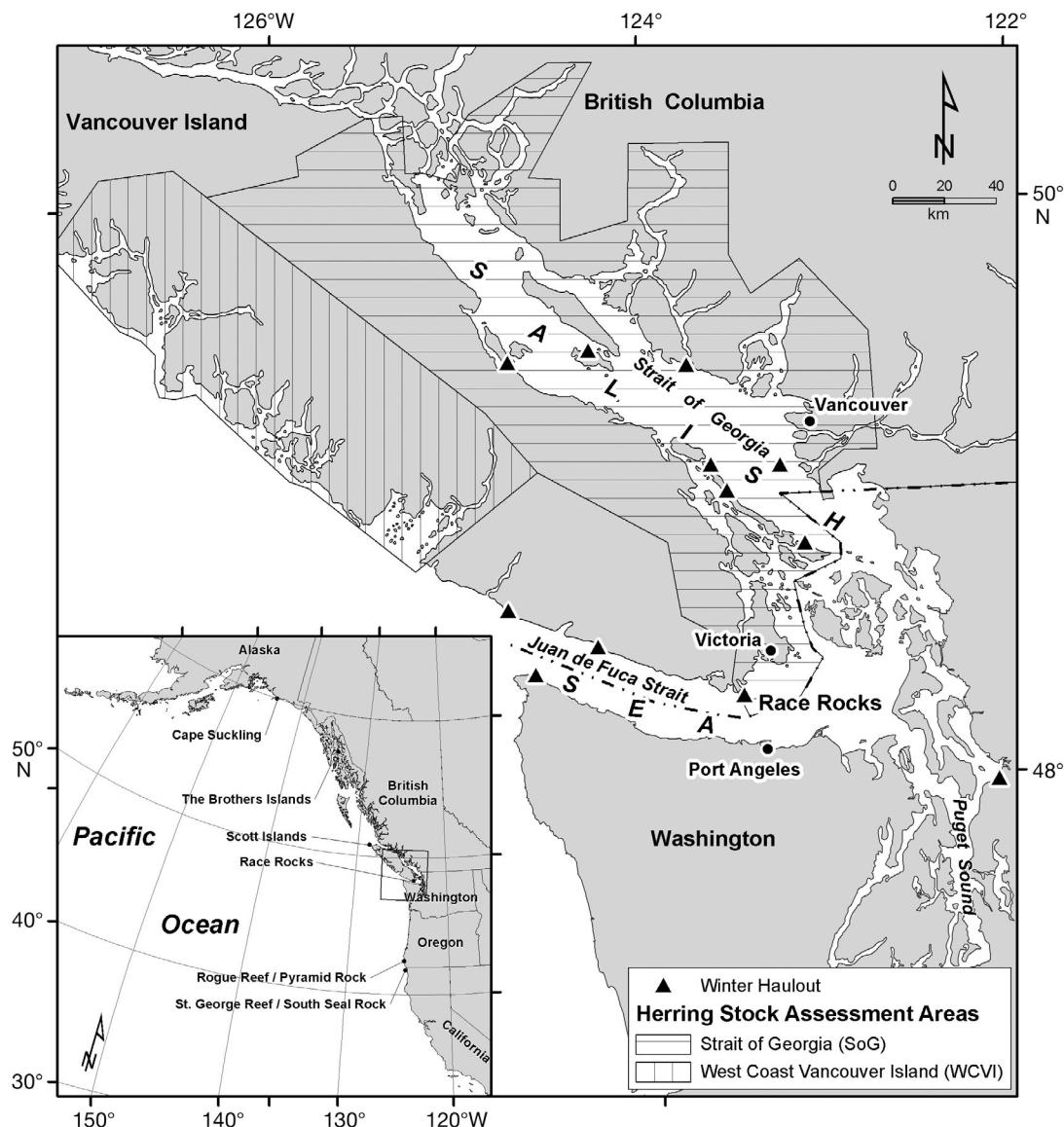


Fig. 1. Location of Race Rocks and other regional winter haulouts of sea lions in the Salish Sea, together with Pacific herring stock assessment areas (hatched)

efforts because its position in Juan de Fuca Strait makes it a gateway for thousands of marine mammals and billions of Pacific herring *Clupea pallasii* and salmon returning to the Salish Sea each year (Bigg 1988a,b, Jeffries et al. 2000; Fig. 1).

Seasonal movement of both species of sea lions is influenced in part by the availability of prey fish, as has been documented in Alaska, Washington and California for salmonids, Pacific herring and eulachon *Thaleichthys pacificus* (Gearin et al. 1986, Lowry et al. 1991, Weise & Harvey 1999, Womble 2005, 2009, Sigler et al. 2009). Scat analyses suggest Pacific herring is one of the most important prey for Steller sea lions in British Columbia, as is Pacific

hake *Merluccius productus* off the coast of Oregon (reviewed in Bredeson et al. 2006). Anomalies in oceanic conditions, such as increased sea surface temperature (SST) or decreased productivity, are shown to correlate with California sea lion distribution and foraging behaviour (Weise et al. 2006, Bargu et al. 2010) and may have played important roles in the decline in the number of Steller sea lions in southern California (Bartholomew & Boobootian 1960). Similarly, although we suspect seasonal sea lion distributions in the Salish Sea are ultimately driven by climatic conditions or prey availability, such patterns lack empirical evidence in this region.

Steller sea lions in the Salish Sea are part of the genetically distinct eastern stock, comprising individuals born at rookeries east and south of Cape Suckling, Alaska at southeastern Alaska, British Columbia, Oregon and California (Bickham et al. 1996, Loughlin 1997). That stock has rookeries in southeastern Alaska, British Columbia, Oregon and California (Bigg 1988a, Loughlin et al. 1992, Raum-Suryan et al. 2002, Fisheries and Oceans Canada 2008). California sea lions do not breed north of California, although adults and subadults regularly disperse into Canadian and increasingly Alaskan waters during the nonbreeding season to exploit food resources (Jeffries et al. 2000, Maniscalco et al. 2004, Carretta et al. 2011). The vast majority of those animals are males.

We used linear regression on principal components to explore the relationship between yearly maxima of sea lions on the Race Rocks haulout (from 1965 to 2009) and select local environmental factors (herring biomass, winter SST, winter precipitation). Precipitation was included because it might reflect the prevalence of low pressure systems and winter storms, which could cause sea lions to avoid haulouts if wave or swell action was too severe or individuals could not bask in the sun. To avoid spurious correlations between multiple parameters undergoing long-term directional changes (e.g. population growth, ocean warming), data were transformed to remove variance predicted by linear trends. Results corroborate population census data for California and Steller sea lions (e.g. Fisheries and Oceans Canada 2008, Allen & Angliss 2010, Carretta et al. 2011) by showing an upward trend in the number of sea lions wintering at Race Rocks between 1965 and 2009. After removing variance attributed to population growth and climate change, the yearly maximum number of sea lions at Race Rocks was best described by principal components 1 and 2 (PC1 and PC2), which loaded heavily on estimates of prefishery herring biomass near southern Vancouver Island. Finally, we discussed a previously undocumented shift in the timing of sea lion departure from Race Rocks; during the period 1965 to 1979, departure occurred in mid spring, and since at least 1997, departure has occurred in mid winter.

MATERIALS AND METHODS

Race Rocks is a rocky archipelago at the southernmost point of Vancouver Island in Juan de Fuca Strait, Salish Sea ($48^{\circ} 17' 55''$ N, $123^{\circ} 31' 54''$ W; Fig. 1). Sea lion count data at Race Rocks were combined from 3

sources: (1) monthly maximum counts for the period 1965 to 1979 were extracted digitally from figures in Bigg (1988a,b) using ImageJ 1.43s software; (2) count data for select dates in the period 2001 to 2009 were taken from the Race Rocks guardian's log, an open access database (www.racerocks.ca/wp/); (3) count data were collected by the authors on 108 days in the periods 1997 to 1998, 2002 to 2003 and 2007 to 2009 using binoculars (Bushnell 10 × 40 mm) and a spotting scope (Bushnell 15–45 × 60 mm) from atop the Race Rocks lighthouse (~30 m above sea level, ~0.65 km to farthest haulout). Prefishery herring biomass estimates for the Strait of Georgia (SoG) and West Coast Vancouver Island (WCVI) were provided by Fisheries and Oceans Canada (J. Schweigert pers. comm.), as described in Fisheries and Oceans Canada (2010). Pacific herring data were used for analyses because this fish is identified as one of the most important prey species for sea lions in British Columbia (Bredeson et al. 2006) and herring fishery records were available from 1965 to the present, which showed good overlap with available sea lion data. Lack of historical records combined with poor overlap with existing sea lion data precluded the use of other fishery data sets in analyses, such as those for sockeye salmon *Oncorhynchus nerka*, coho salmon *O. kisutch*, Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, pink salmon *O. gorbuscha*, steelhead *O. mykiss* and walleye pollock *Theragra chalcogramma*. Data for daily SST at Race Rocks were collected from an open access database hosted by Lester Pearson College (www.racerocks.com); we calculated winter average SST (°C) as the mean value for the period from November to February (inclusive) of each winter haulout year (e.g. the 1997 winter haulout year is the period including July 1997 to June 1998). Data for daily precipitation was combined from 2 adjacent meteorological stations at Race Rocks and William Head (4.6 km apart) to give rainfall data for all winter haulout years (available at www.racerocks.com and from Environment Canada at www.climate.weatheroffice.gc.ca). We calculated winter sum precipitation (mm) as the sum for the period from November to February (inclusive) of each winter haulout year. Before combining data sets from 2 meteorological stations, we first inspected precipitation data for overlapping years (1984 to 1997) to ensure the data were congruent, which they were ($R^2 = 0.94$, mean percent error = 0.086 mm, $n = 129$ mo).

We analyzed 17 winter haulout years from a possible 21 years of available sea lion data. Conditions for including specific years of data were (1) the maximum sea lion count did not occur on the first or last obser-

vation day of that haulout year, and (2) there was a conspicuous trend in sea lion abundances throughout the haulout year, where abundances increased over time to reach a peak value and then decreased afterwards. Herring biomass, SST, and precipitation data were limited to these same 17 years.

To quantify interannual changes in sea lion abundances at Race Rocks beyond the general trend of linear population growth (e.g. Bigg 1988a,b, Fisheries and Oceans Canada 2008), we calculated residual values from the linear relationship between (log) maximum winter sea lion count and year ($n = 17$). Residual values were counted for California and Steller sea lions separately. This data transformation was meant to eliminate spurious correlations between sea lion abundance and any other factor that has increased since 1965 (e.g. SST at Race Rocks). Residual values are hereafter referred to as adjusted sea lion counts. The same procedure was used to remove long-term temporal trends from herring biomasses, winter SST and precipitation data; hence, our analyses are designed to detect potential relationships between parameters in the absence of long-term temporal trends.

Principal component analysis (PCA) scores were calculated from the correlation matrix of adjusted SoG and WCVI prefishery herring biomasses, and winter SST and precipitation at Race Rocks. We then tested for correlations between PCA scores and adjusted sea lion abundances.

RESULTS

For the period 1965 to 2009, we detected trends in sea lion numbers, environmental variables and herring abundance. First, the maximum annual count of Steller sea lions at Race Rocks increased ($R^2 = 0.67$, $p < 0.0001$, $n = 17$; Table 1, Fig. 2). Concurrently, the maximum annual count of California sea lions at Race Rocks appeared to not change ($R^2 = 0.17$, $p = 0.096$, $n = 17$), although this relationship was driven strongly by a single low value in 2007. When that value was removed, a strong upward trend in California sea lion abundance over time was apparent ($R^2 = 0.71$, $p < 0.0001$, $n = 16$; Table 1). Prior to 1980, Steller sea lions began arriving at Race Rocks in August and California sea lions in September to October, and both species tended to remain until departure the following May (Fig. 2). In contrast, records since 1997 show both Steller and California sea lions to begin arriving simultaneously in about August and departing in January or February. Also,

Table 1. *Zalophus californianus* and *Eumetopias jubatus*. Maximum observed count (Max.) of sea lions per haulout year (July to June of following year) and month of the maximum observed count within each haulout year at Race Rocks. Counts from 1965 to 1979 are reproduced from Bigg (1988a,b); counts from 1997 to present are from the LGL Limited database and the Race Rocks website (www.racerocks.com)

Year	Steller sea lion		California sea lion	
	Max.	Month	Max.	Month
1965	7	Dec	13	Jan
1966	13	Jan	8	Dec
1967	7	Jan	7	Nov
1968	19	Dec	30	Feb
1969	18	Nov	34	Dec
1970	72	Apr	33	Jan
1971	71	Feb	43	Mar
1974	119	Feb	93	Apr
1976	128	Apr	96	Nov
1977	257	May	232	Nov
1978	213	May	103	Dec
1997	344	Nov	836	Oct
2002	385	Dec	355	Jan
2003	555	Nov	244	Sep
2007	244	Dec	1	Nov
2008	251	Oct	180	Oct
2009	680	Oct	805	Oct

the average winter SST at Race Rocks ranged between 7.0°C in 1971 and 9.3°C in 1997, and there was a central trend of increasing temperature from 7.7 to 8.4°C from 1965 to 2009 ($R^2 = 0.26$, $p = 0.038$, $n = 17$). The sum of winter precipitation at Race Rocks ranged from 191 mm in 1971 to 27 mm in 2007, and there was a significant downward trend from 135 mm to 72 mm between 1965 and 2009 ($R^2 = 0.30$, $p = 0.023$, $n = 17$). The average prefishery biomass of SoG herring increased from 5775 t in 1967 to >150 000 t in 2002, and there was a significant centralized trend of increasing biomass from ~23 000 to 110 000 t between 1965 and 2009 ($R^2 = 0.58$, $p = 0.0004$, $n = 17$). Finally, the average prefishery biomass of WCVI herring was 6000 t in the late 1960s and lower from 2007 to 2009, and there was a maximum biomass of >130 000 t in 1976, although there was not a consistent trend of growth or decline in this stock from 1965 to 2009 ($R^2 = 0.078$, $p = 0.28$, $n = 17$).

The first 3 principal components (PCs) explained 95.2% of the cumulative variance for environmental parameters (i.e. adjusted values of SoG prefishery herring biomass, WCVI prefishery herring biomass, winter SST at Race Rocks, winter precipitation at Race Rocks). PC1 explained 44.2%, PC2 explained 29.8% and PC3 explained 21.2% (Table 2). PC1 loaded heavily on SoG and WCVI prefishery herring biomasses, and less so on winter SST and winter pre-

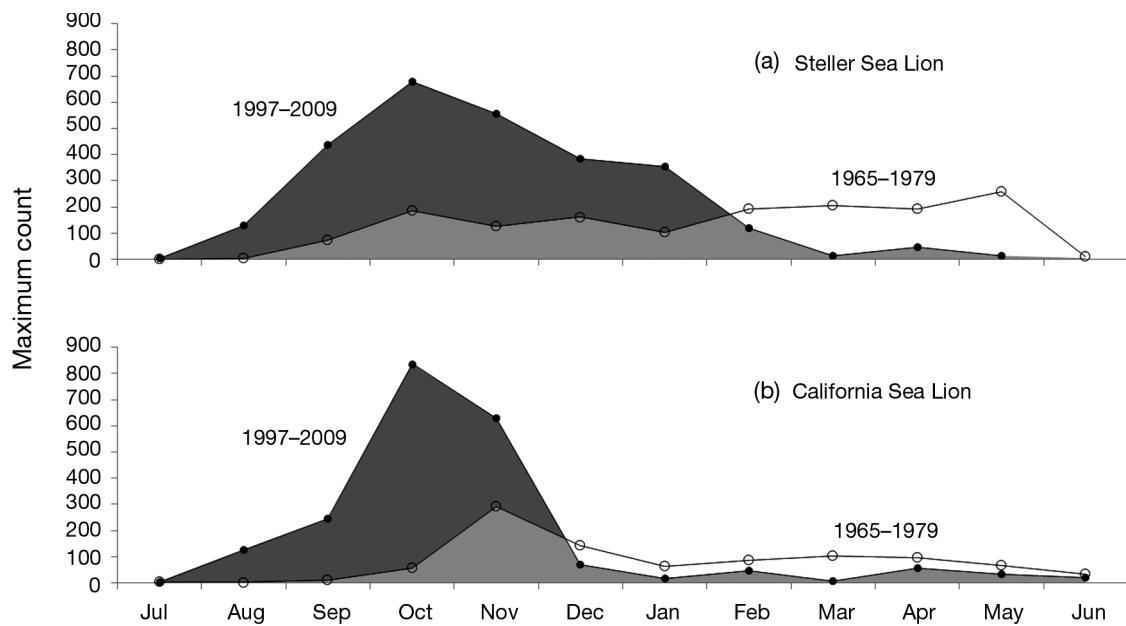


Fig. 2. *Zalophus californianus* and *Eumetopias jubatus*. Historical timing of (a) Steller and (b) California sea lion abundance at Race Rocks. Counts from 1965 to 1979 are reproduced from Bigg (1988a,b); counts from 1997 to present are from the LGL Limited data base and the Race Rocks website (www.racerocks.com)

cipitation; thus, PC1 mainly reflects variance in herring biomass and, to a lesser degree, variance in the physical environment. PC2 loaded most heavily on WCVI herring biomass, winter SST and precipitation only, and SoG herring biomass was not important. PC3 loaded almost entirely on physical factors, winter precipitation and SST, whereas herring biomass from either SoG or WCVI were not important.

The adjusted values for annual peak abundances of Steller sea lions correlated strongly with PC1 and PC2. California sea lion abundance correlated well

with PC1; there was no change in statistical significance when the single outlying value for California sea lions in 2007 was removed (Table 3). The association between adjusted sea lion abundance and herring biomass was confirmed with a positive and significant correlation between adjusted sea lion counts and adjusted herring biomasses for both SoG and WCVI, but no such correlation existed between sea lions and SST or precipitation (Table 3).

DISCUSSION

Our results suggest the number of California and Steller sea lions using Race Rocks during the non-breeding season is driven proximally by food resources and not by climate (Table 3). Although food-driven sea lion movements have been demonstrated in other regions, this study provides the first evidence that resource-driven movements are detectable across a timescale of decades and that such a factor can underlie long-term patterns of population growth. We also provide evidence of substantially later peak abundances in the period 1965 to 1978 relative to 1997 to 2009 (Table 1), and a change in timing of arrival and departure between eras, from residency of late summer to spring over the period 1965 to 1979 to a residency of late summer to mid-

Table 2. *Zalophus californianus* and *Eumetopias jubatus*. Principal component analysis (PCA) of variation in sea lion abundance at Race Rocks; variables include estimates of prefishery Pacific herring biomasses for the Strait of Georgia (SoG) and West Coast Vancouver Island (WCVI), average winter sea surface temperature (SST) at Race Rocks and the sum winter precipitation at Race Rocks

PCA	PC1	PC2	PC3
Eigenvalues	1.77	1.19	0.85
Cumulative variance (%)	44.2	74.0	95.2
Eigenvectors			
SoG prefishery herring biomass	0.712	-0.090	0.019
WCVI prefishery herring biomass	0.458	-0.689	0.047
SST at Race Rocks	0.356	0.539	0.696
Precipitation at Race Rocks	0.394	0.476	-0.717

Table 3. *Zalophus californianus* and *Eumetopias jubatus*. Relationships between annual adjusted sea lion counts and adjusted biophysical parameters ($n = 17$). Analysis for California sea lion was rerun after removing single outlier value ($n = 16$). PC1 m = 0.16, b = 0.10, $R^2 = 0.25$, p = 0.05. PC2 m = -0.15, b = 0.13, $R^2 = 0.17$, p = 0.11. PC3 m = 0.03, b = 0.12, $R^2 = 0.006$, p = 0.78. SoG m = 0.006, b = 0.11, $R^2 = 0.19$, p = 0.09. WCVI m = 0.0065, b = 0.11, $R^2 = 0.43$, p = 0.006. SST m = 0.005, b = 0.12, $R^2 = 0.003$, p = 0.84; Precipitation m = 0.00008, b = 0.12, $R^2 = 0.00005$, p = 0.98. Slope (m), y-intercept (b), for other abbreviations see Table 2 legend

Parameter	Steller sea lion				California sea lion			
	m	b	R^2	p	m	b	R^2	p
PC1	0.17	-1.73×10^{-15}	0.36	0.009	0.27	-2.43×10^{-15}	0.32	0.018
PC2	-0.21	-1.72×10^{-15}	0.38	0.008	-0.10	2.41×10^{-15}	0.03	0.51
PC3	0.11	-1.7×10^{-15}	0.07	0.38	0.039	-2.41×10^{-15}	0.003	0.83
SoG Herring	0.008	-7.51×10^{-16}	0.36	0.012	0.01	-1.03×10^{-15}	0.25	0.039
WCVI herring	0.008	2.11×10^{-15}	0.72	<0.001	0.008	-2.81×10^{-15}	0.26	0.035
Winter SST	-0.18	-1.53×10^{-15}	0.05	0.369	0.28	-2.7×10^{-15}	0.05	0.386
Winter precipitation	0.002	1.66×10^{-15}	0.036	0.468	0.003	-2.31×10^{-15}	0.037	0.458

winter since at least 1997 (Fig. 2). This apparent contraction in residency time at Race Rocks was evident for both California and Steller sea lions. Unfortunately there was insufficient sampling effort at Race Rocks between 1980 and 1996 to pinpoint when this apparent contraction began or whether it happened suddenly or gradually within that period.

Temporal changes in sea lion abundance at Race Rocks

A large volume of research has been conducted on the western stock of Steller sea lions since a significant population decline was first noted in the mid-1970s (Braham et al. 1980, Loughlin et al. 1984, Trites & Larkin 1996, Womble et al. 2005, Guenette et al. 2006, Pitcher et al. 2007, Sigler et al. 2009, Tollit et al. 2009). In contrast, the eastern Steller sea lion stock is relatively understudied, has declined significantly in southern California since the late 1930s, is increasing in numbers throughout southeastern Alaska and British Columbia and is stable or increasing slowly in Oregon through central California (Pitcher et al. 2007, National Marine Fisheries Service 2008, Allen & Angliss 2010). The US California sea lion stock has grown since at least 1975; however, notable declines in pup counts have been observed during El Niño years (Caretta et al. 2011). Our analysis showed annual growth in the abundance of sea lions at Race Rocks from 1965 to 1979 (data reproduced from Bigg 1988a,b) and from 1997 to 2009 (present study), which suggests the use of Race Rocks by both California and Steller sea lions has increased for nearly 5 decades (Fig. 2). These trends are consistent with decades of formal population census records that show Steller sea lion populations in British Columbia

have increased 3-fold in size and 4-fold in pup productivity since 1970 (Fisheries and Oceans Canada 2008, 2011). A similar pattern of population growth is reported for California sea lions from the US stock (Caretta et al. 2011). Population growth of the eastern stock of Steller sea lions and of California sea lions has been attributed to the legislated end of commercial harvests and fisheries-related culls in the early 1970s (Bigg 1988a,b, National Marine Fisheries Service 2008, Fisheries and Oceans Canada 2011).

The increasing abundances of sea lions at Race Rocks appear to reflect the number of individuals approaching southern Vancouver Island and entering the Salish Sea to forage. Both California and Steller sea lions frequent the SoG east of Vancouver Island, but do not reside there year-round, entering mainland inlets and estuaries during the nonbreeding season in pursuit of migratory fishes like salmon and herring (discussed below). Race Rocks is ideally positioned as a staging area for sea lions dispersing from both northern and southern breeding areas because Race Rocks intercepts billions of fish returning to the Salish Sea (see Fig. 1). The only other entrance to the Salish Sea is Johnstone Strait to the north, which is a plausible pathway for Steller sea lions dispersing from northern British Columbia and Alaska, but an unlikely route for California sea lions that invariably disperse northward along the west coast of Washington State (Fig. 1).

We have presented compelling evidence to link the number of sea lions at Race Rocks to food resources around southern Vancouver Island, including the Salish Sea, with the strong correlations between annual maximum sea lion counts and PC1 (both species) and PC2 (Steller sea lions only) but not PC3 (Table 2). PC1 accounts for 44 % of the variance of the 4 environmental factors considered in this study and

loads most heavily on estimates of herring biomass for the SoG and second to herring biomass for WCVI (see Table 2). We show this relationship more directly with the significant, positive relationship between adjusted sea lion abundance and herring biomass for both regions, in contrast to no such relationship between sea lion abundance and adjusted SST or precipitation (Table 3). Whether sea lions have learned to follow shoals of migrating herring (or other prey fish whose abundances covary with herring) as they gather around southeastern Vancouver Island in preparation for spring spawning is unclear; dietary studies (e.g. scat analysis) for sea lions at Race Rocks are lacking. However, studies elsewhere show that sea lions have a varied diet and herring abundance may be positively associated with other sea lion prey species or ocean productivity in general (Lowry et al. 1991, Sigler et al. 2009, Tollit et al. 2009). Moreover, Pacific herring appear to be among the most important prey fish to Steller sea lions in British Columbia (Bredeson et al. 2006).

A summary of scat analyses in the northeast Pacific Ocean suggests the prevalence of herring as prey for Steller sea lions varies widely among regions (from 0.1 to 47%; Bredeson et al. 2006). Forty-seven percent of scats from British Columbia contained evidence of Pacific herring (meta-analysis included walleye pollock, Pacific herring, Pacific cod *Gadus macrocephalus*, north Pacific hake, arrow-tooth flounder *Atheresthes stomias*, Atka mackerel *Pleurogrammus monopterygius* and rockfish *Sebastes* spp. Conversely, sea lions from Oregon showed a strong preference for Pacific hake (84% occurrence in scats), followed by herring (20%). Trites et al. (2007) found herring comprised 31 to 40% occurrence in Steller sea lion scats (depending on season) from southeastern Alaska. Nevertheless, sea lions in other regions are known to aggregate in areas and at times of year when fish densities are high, including areas in Alaska where Pacific herring spawn near shore (Womble et al. 2005). Steller sea lions are also known to aggregate in salmon migration corridors (Womble et al. 2009), making Race Rocks an ideal haulout in late summer and early autumn (the time when sea lions begin arriving at Race Rocks, Fig. 2) for predators wanting to intercept schools of salmon returning to spawn (Groot & Margolis 1991). Diet information for California sea lions outside of California is rare; however, there is general consensus that they hunt opportunistically on schooling fish such as salmon and herring (Lowry et al. 1991, Weise and Harvey 1999). An alternate explanation for the correlation between sea lion abundance at Race Rocks and PC1

and PC2 (i.e. herring biomass) is that sea lions facilitate herring survival by eating herring predators, such as salmon, spiny dogfish *Squalus acanthias* or walleye pollock. Thus, relatively higher sea lion abundance may reduce local predation on herring, thereby conserving herring biomass. Future study should aim to better understand the diet of sea lions in the Salish Sea, either by conventional methods such as scat analysis (e.g. Lowry et al. 1991) or more complex and arguably higher-resolution methods such as the use of PCR techniques to identify prey DNA (e.g. Tollit et al. 2009).

It is plausible that the association between sea lion abundance and herring biomasses is spurious, deriving from a more complex interaction between ocean productivity, sea lion diet and sea lion physiology. For example, concurrent changes in SST and ocean productivity associated with the Pacific Decadal Oscillation may have affected Steller sea lion abundance and distribution in Alaska by causing associated changes in prey availability (Guenette et al. 2006). Small spatial-scale anomalies in SST have also been shown to influence Steller sea lion distribution and foraging activity because prey are often associated with small-scale, oceanographic frontal features (Lander et al. 2010, but see Lander et al. 2011). Furthermore, winter precipitation in itself may not be directly relevant to haulout behavior, considering these 2 species are adapted to cold, wet conditions. Rather, it could be a proxy for other environmental conditions such as storms. At Race Rocks on 25 September 2011, one of us (M.W.D.) observed that a rapidly advancing storm front with winds gusting to ~50 knots and hard rain resulted in all 134 Steller sea lions abandoning the haulout within minutes. Other disturbances, including ecotour boats, recreational boats or explosions on a nearby military training area have also been observed to affect short-term haulout behaviour at Race Rocks (Demarchi et al. 2012). Although such a complex interaction between sea lion abundance, local SST or local precipitation may have been detected by association with PC1 (Table 2), the putative relationship must be relatively weak or not detectable on the scales presented in this study given there was not a detectable relationship when sea lion and SST or precipitation were compared directly (Table 3).

Origins of sea lions at Race Rocks

Since 1997, one of us (M.W.D.) has recorded incidental observations of sea lions with branding marks

at Race Rocks. Steller sea lions at Race Rocks are therefore known to originate from Rogue Reef, Oregon, (two 4 yr olds, a 5 yr old and a 7 yr old) and St. George Reef, California, (three 1 yr olds, two 6 yr olds and a 7 yr old) (L. Fritz pers. comm.; Fig. 1). A 2 yr old male Steller sea lion was from The Brothers Islands in southeast Alaska. The extent to which Steller sea lions from rookeries in British Columbia use Race Rocks is not known because no extensive branding or tagging studies have been conducted in that province. However, considering that the nearest rookeries in Canadian waters (i.e. Scott Islands) are closer than those in the USA we suspect that many of the Steller sea lions are from Canadian rookeries.

All California sea lions at Race Rocks originate from southern rookeries because there are no California breeding colonies north of California. Nearly all branded California sea lions sighted at Race Rocks and at least one Steller sea lion (a 1 yr old) were marked at Shilshole in Puget Sound, Washington, where individuals were marked as part of a study led by NOAA. A few California sea lions were branded on the lower Columbia River near Bonneville, Oregon, and one was from San Miguel Island, California. Incidentally, California sea lions were notably absent from haulouts in San Francisco during the winter of 2009 to 2010, possibly owing to the influences of anomalous marine conditions (e.g. Melin et al. 2010, Carretta et al. 2011). Meanwhile, large numbers of California sea lions were spotted north of California in Oregon, indicating a northward shift in population distribution that could also explain the high number of California sea lions at Race Rocks in that same year (Table 1, Fig. 2). A similar shift in the distribution of Steller sea lions from southerly haulouts would also explain the unusually high numbers of this species at Race Rocks in 2009.

It is clear that both California and Steller sea lions travel great distances during postbreeding dispersal from rookeries, and the limited branding data available to us showed that some individuals travel from rookeries as far away as California and Alaska. Future tagging studies should include individuals from Canadian rookeries to better understand the importance of Race Rocks and the Salish Sea for the eastern stock.

Seasonal shifts in departure timing from Race Rocks: an unexplained trend

A distinct shift in the timing of when the majority of sea lions depart from Race Rocks, from

spring during the period 1965 to 1979 to mid winter during the period 1997 to 2009, is shown in Fig. 2. Moreover, Table 1 shows a general trend of earlier peak abundances since 1997. There were insufficient data available to identify when this change in haulout use occurred within the period 1980 to 1996, or whether it happened gradually or suddenly. That this trend is shared by both California and Steller sea lions, which can originate from rookeries separated by vast geographic distances (e.g. Steller sea lions from California and Alaska were identified at Race Rocks), suggests this departure phenomenon was induced by external factors (e.g. change in the distribution of ocean resources, change in climate) and was not an intrinsic population effect. We were unable to find comparable evidence of such a dramatic change in timing of haulout use for sea lions or other marine mammals in other regions, and so we remain necessarily circumspect about its cause. Increased sea lion abundance in recent years may have caused greater levels of prey exploitation and depletion in the immediate vicinity of Race Rocks. A reduced prey base could account for some or all of the changes in the timing and residency evident in Fig. 2. Additionally, limited information suggests that resident (cf. migratory) populations of Pacific herring in the Salish Sea have been overexploited by commercial fisheries in recent decades (Schweigert & Linekin 1990). Assuming this is correct, it is possible that use of Race Rocks by sea lions has been affected. Finally, this previously undescribed change in the seasonality of haulout use reminds us how little we know about factors controlling sea lion movements and, particularly, what factors have made Race Rocks an important winter haulout for sea lions from California to Alaska.

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