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Changes in the Occurrence and Behavior of Mammal-eating Killer Whales in Southern British Columbia and Washington State, 1987–2010

Abstract

The primary prey species of mammal-eating killer whales in the Salish Sea, the inland waters of southern British Columbia and Washington state, have experienced dramatic increases in population abundances in the last 25 years. It is possible that changes in prey abundance over time have resulted in changes in predator spatial use, occurrence and group size. Focused studies of mammal-eating killer whale behavior in the area were undertaken from 1987–1993, and an extensive record of sightings with confirmed identifications was available from 2004–2010. Changes in occurrence across years, months, and subareas of the Salish Sea were examined as well as changes in group size and in the identity of specific matrilines using the area. Occurrence of mammal-eating whales increased significantly from 2004–2010 with different seasonal peaks compared to 1987–1993. Different matrilines occurred in different seasons, time periods, and subareas. Group size was larger in 2004–2010 than in 1987–1993. The whales may be increasing use of the area due to increasing prey abundance or an overall increase in the whale population size. Changes in seasonal patterns of occurrence and the increase in group size between the two periods could be due to increased prey diversity.

Key words: predator-prey interactions, spatial use, occurrence, group size, *Orcinus orca*

Introduction

Top predators are key components of ecosystems around the globe. Their removal, and the consequent loss of ecological interactions they facilitate, may be detrimental to ecosystems (Janzen 1974; reviewed in Estes et al. 2011). The marine environment is particularly vulnerable to the loss of top predators due to human interactions such as fishing, whaling, bycatch, boat collisions, pollution, and destruction of habitat. Previously, research focus has been placed on the consumptive effects of predation on prey populations (Estes and Palmisano 1974, Lima 1998, Ainley et al. 2006, London et al. 2012), although increasing emphasis in examining non-consumptive effects

(e.g., changes in prey behavior due to perceived risk of predation) across multiple systems and taxa has recently developed in ecological studies, with an indication that these effects may be universal throughout ecosystems (Wirsing et al. 2008, Sheriff et al. 2009, Wirsing and Ripple 2010). For example, temporal variation in occurrence of sharks in Shark Bay, Australia, significantly alters the behavior of their prey (Heithaus et al. 2007, Wirsing et al. 2007), likely impacting the seagrass ecosystem as a whole. In Bermuda, where numbers of predatory sharks have decreased, an increase in herbivorous sea turtle populations have coincided with declines in seagrasses vital to the ecosystems of this area (Baum et al. 2003, Murdoch et al. 2007, Heithaus et al. 2007). Losing top predators can lead to ecosystem changes stemming from both consumptive and non-consumptive effects on

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prey populations. An examination of occurrence patterns can provide insights into the potential effects of a loss, or of an increase, of predators.

Predator and prey populations can be tightly linked in marine ecosystems (May et al. 1979, McLaren and Peterson 1994, Whipple et al. 2000). As more prey become available through increased population abundance or increased occurrence in a given area (e.g., changes in distribution), predator abundance and occurrence may also increase according to numerical response theory (Soloman 1949).

Mammal-eating killer whales (*Orcinus orca*) in the Gulf of Alaska have been suggested to influence a variety of prey populations (Estes et al. 1998, Springer et al. 2003), although there is considerable controversy about their precise role in the Gulf of Alaska ecosystem (Demaster et al. 2006, Wade et al. 2007). Mammal-eating killer whales are frequently found in the Salish Sea, the inland waters of Washington state and British Columbia, and are classified as part of the west coast stock of 'transient' killer whales (Bigg et al. 1990, Ford et al. 1998, Allen and Angliss 2011). These killer whales are known to prey upon seals, sea lions, porpoises and occasionally other cetaceans throughout their range (Baird et al. 1992, Baird and Dill 1995, Ford et al. 2006, Dahlheim and White 2010). Several of the most common prey species consumed by mammal-eating killer whales in the Salish Sea have undergone dramatic changes in the last 30 years. Harbor seals (*Phoca vitulina*), resident to the area year-round, tripled in abundance between 1978 and 1999, reaching carrying capacity (Jeffries et al. 2003, Fisheries and Oceans Canada 2010, Carretta *et al.* 2011). California sea lion (*Zalophus californianus*) and Steller sea lion (*Eumetopias jubatus*) numbers in the area vary seasonally, with peak occurrence in April and May (Pat Gearin, NOAA National Marine Mammal Laboratory, personal communication), but both species have increased in abundance within the Salish Sea. The U.S. stock of California sea lions in the North Pacific increased in abundance at an annual rate of 5–6% between 1975 and 2005, suggesting that the population more than tripled throughout the 1987–2010 study period (Lowry and Maravilla-Chavez 2005, Puget Sound Action Team 2007, Carretta et al. 2011). The eastern North Pacific Steller sea lion population (ranging from California to southeast Alaska) has also increased in abundance by an average of about 9% per year between 1987 and 2010, reaching the highest breeding population level in recorded history (Pitcher et al. 2007, Steven Jeffries, Washington Department of Fish and Wildlife, personal communication). This population is therefore four to five times larger in 2010 than it was in 1987. The California breeding stock of northern elephant seals (*Mirounga angustirostris*) has doubled in abundance from 1987 to 2006 and individuals are frequently observed in the Salish Sea year-round (Carretta et al. 2011). The population of harbor porpoise (*Phocoena phocoena*) in the Strait of Juan de Fuca and San Juan Islands has tripled since the early 1990s (M.B. Hanson, unpublished data), with a recolonization of this species to Puget Sound (Carretta et al. 2011). There is no trend information available on Dall's porpoise (*Phocoenoides dalli*) abundance, which also are found year-round in the Salish Sea. Although most of these prey species of mammal-eating killer whales have increased in abundance and occurrence, the potential effects on their predator are undocumented.

Current ecosystem-based models in the Salish Sea attempt to incorporate marine mammals as predators, but do not include mammal-eating killer whales due to a lack of current information on spatial use and occurrence (Harvey et al. 2010). The purpose of this study was to determine if there have been changes in mammal-eating killer whale occurrence, spatial use, and/or group size over the period 1987–2010. We hypothesized that there is a change in mammal-eating killer whale occurrence and group size over the 1987–2010 time period. The potential change could be due to an increase in prey abundance and occurrence in the Salish Sea from 1987–2010, or an overall increase in the size of the mammal-eating killer whale population (Ford et al. 2007, Towers et al. 2012). However, a causal relationship between increased prey and changes in killer whale occurrence and behavior cannot be identified from the sighting data. Our findings will inform ecosystem models and ecological studies of predator-prey

dynamics in the Salish Sea. This study will also provide insights for other ecosystems where large-bodied predators have the capacity to alter their movement and behavior on a large scale to take advantage of seasonally or locally abundant prey.

Methods

Using existing long-term catalogs, individual killer whales were identified by unique markings (Bigg et al. 1987, Ford and Ellis 1999, Towers et al. 2012). Mammal-eating killer whales travel in matrilineal groups with dispersal occurring for some adult males and for females that have offspring of their own (Bigg et al. 1987, Ford and Ellis 1999, Baird and Whitehead 2000). For this study, a matriline was defined as a female killer whale and any offspring not known to have dispersed from the maternal group. Between 1987 and 1993, focused studies of mammal-eating killer whale behavior were undertaken in the Salish Sea from a small research vessel (Baird and Dill 1995, 1996). The objectives of the previous study were to document mammal-eating killer whale occurrence, seasonality, group size, and foraging behavior, and the identity of all whales present in each encounter was documented (Baird and Dill 1995, 1996). Documenting whale presence in that effort involved extensive small-boat surveys as well as responding to sightings reported by whale-watch operators, the general public, and other researchers working in the area. Effort from 1987–1993 was highest in the months of May to September (Baird and Dill 1995). From 2004–2010, killer whale sighting networks (i.e. organizations that collect and record sightings of killer whales from multiple sources, including whale-watching boats) created an extensive sighting record of identifications in the area, with attempts to document all occurrences in the area. Orca Network was the largest resource of identification data in the 2004–2010 dataset (Orca Network 2011). Within the 2004–2010 period, the number of commercial whale-watching boats was relatively constant (Giles and Koski 2012). With commercial whale-watching trends as a proxy for sighting effort of whales in the Salish Sea, effort is estimated to have been consistent from 2004–2010.

Prior to 2004, whale-watching effort and sighting network activity were inconsistent. Therefore the years 2004–2010 were chosen as a comparable number of years to the 1987–1993 dataset (Baird and Dill 1995, 1996). The spatial distribution of effort between the two time periods likely varied substantially, but this potential limitation was addressed in the data analysis.

The 2004–2010 sightings were collected mostly through citizen science and therefore reliability of the data may be variable. As a caveat of citizen science, it is possible that misidentifications may have occurred due to similar markings on different individuals. It is also possible that there was a failure to identify individuals or matrilines actually present within aggregations or that group composition may have been based on one or two well-marked individuals. However, only confirmed identifications of mammal-eating killer whales were used in analyses. Identifications were confirmed if either a known, reputable source recorded the sighting (i.e., a researcher or whale-watch operator with several years of experience) or if multiple sources independently recorded the sighting. There are occasionally sightings reported to the sighting network with questionable identifications (e.g., "maybe T101"). Any such identification was not included in this study. Despite the limitations of citizen science, a previous study evaluated the reliability of sightings reported largely by commercial whale-watch operators in the same region (Hauser et al. 2006). It was determined that sighting data can be effective in determining the location and identification of killer whales in the Salish Sea in order to evaluate patterns of spatial use (Hauser et al. 2006, Hauser et al. 2007). The findings from this very similar dataset have validated the use of sighting data for our analyses, as long as the limitations of the method are acknowledged (e.g. only including identifications from experienced observers).

With increased effort from 2004–2010, there were often multiple sightings of the same group when it was encountered in the Salish Sea. To minimize repeated detections of the same group of killer whales when they were in the area, and reduce the bias associated with increased effort

TABLE 1. The number of concurrent days any matriline was encountered in the Salish Sea, restricted to matrilines seen on more than 20 occasions. There were no cases in which one of these matrilines was encountered more than 6 days concurrently.

Number of concurrent days encountered	Frequency
1 [a]	280
2	40
3	15
4	4
5	0
6	1

[a] No concurrent days after the first day of encounter

in the 2004–2010 period, encounters from both periods were reduced to a measure of occurrences. We accomplished this by examining the number of concurrent days that groups of whales were encountered in the Salish Sea (Table 1). From this analysis, we were able to determine that if a group was not encountered again within six days, it had likely left the Salish Sea and any encounters greater than six days before or after the original encounter should be treated as a separate occurrence of that group. Therefore, an occurrence was defined as an encounter of a unique group of mammal-eating killer whales when there was not an encounter of that group in the Salish Sea within six days before or after the encounter.

For geographic analyses the study area was split into five subareas: 1) central Strait of Juan de Fuca; 2) Gulf Islands and southern Strait of Georgia; 3) San Juan Islands (including eastern Strait of Juan de Fuca); 4) Puget Sound; and 5) Hood Canal (Figure 1). Hood Canal was separated from Puget Sound analyses due to an anomalous event of an extended stay by mammal-eating killer whales in 2005 (London et al. 2012). Research effort from 1987–1993 was concentrated in the central Strait of Juan de Fuca, San Juan Islands, and Gulf Islands and Strait of Georgia, with no effort in Puget Sound or Hood Canal. Any comparisons of area use and occurrence between the 1987–1993 and 2004–2010 time periods therefore did not include any occurrences in Puget Sound and Hood Canal.

Cumulative occurrence of mammal-eating killer whale encounters was determined by month, year, and subarea to examine patterns of seasonal/annual occurrence and spatial use. Nonparametric Kruskal Wallis tests in the R programming environment (R Core Team 2013) were used to test for differences in the number of occurrences as a function of month, year, and subarea within each period. Minimum group size was determined from sighting records based on the total number of whales with confirmed identifications. The Wilcoxon rank-sum test was used to compare mean and modal group sizes between the two time periods.

Matrilineal groups were classified based on identifications (Towers et al. 2012) in order to examine differences in the groups of whales most commonly occurring in the Salish Sea. There were 28 matrilines identified and defined for this study that were documented more than once in the Salish Sea in the two periods (Appendix 1). For the 1987–1993 period, the most commonly encountered matrilines were classified as nearshore foragers (n = 3) or as non-nearshore foragers (n = 3), with patterns in seasonal occurrence being one of the differences between the two classifications (Baird and Dill 1995). Changes in seasonal occurrence for these six specific matrilines were compared between the two periods. The patterns of behavior of nearshore versus non-nearshore foragers may be specific to the Salish Sea region, but as this study is a fine-scale analysis of the region the classifications are relevant. For the purposes of our analyses, different matrilines occurring in a given area can be considered analogous to different species present in a community, thus analytical techniques appropriate to community ecology were used in multivariate analyses of matrilineal patterns. The cumulative number of occurrences of each matriline was determined for each season, period, and subarea. Seasons were broken into ecologically relevant periods: August–September (harbor seal pupping–weaning season), October–March, April–May (peak sea lion occurrence season), and June–July. Time periods were broken into 4 sections: 1987–1990, 1991–1993, 2004–2007, and 2008–2010. Season, time period, and subarea were the categorical explanatory variables. Therefore, the multivariate
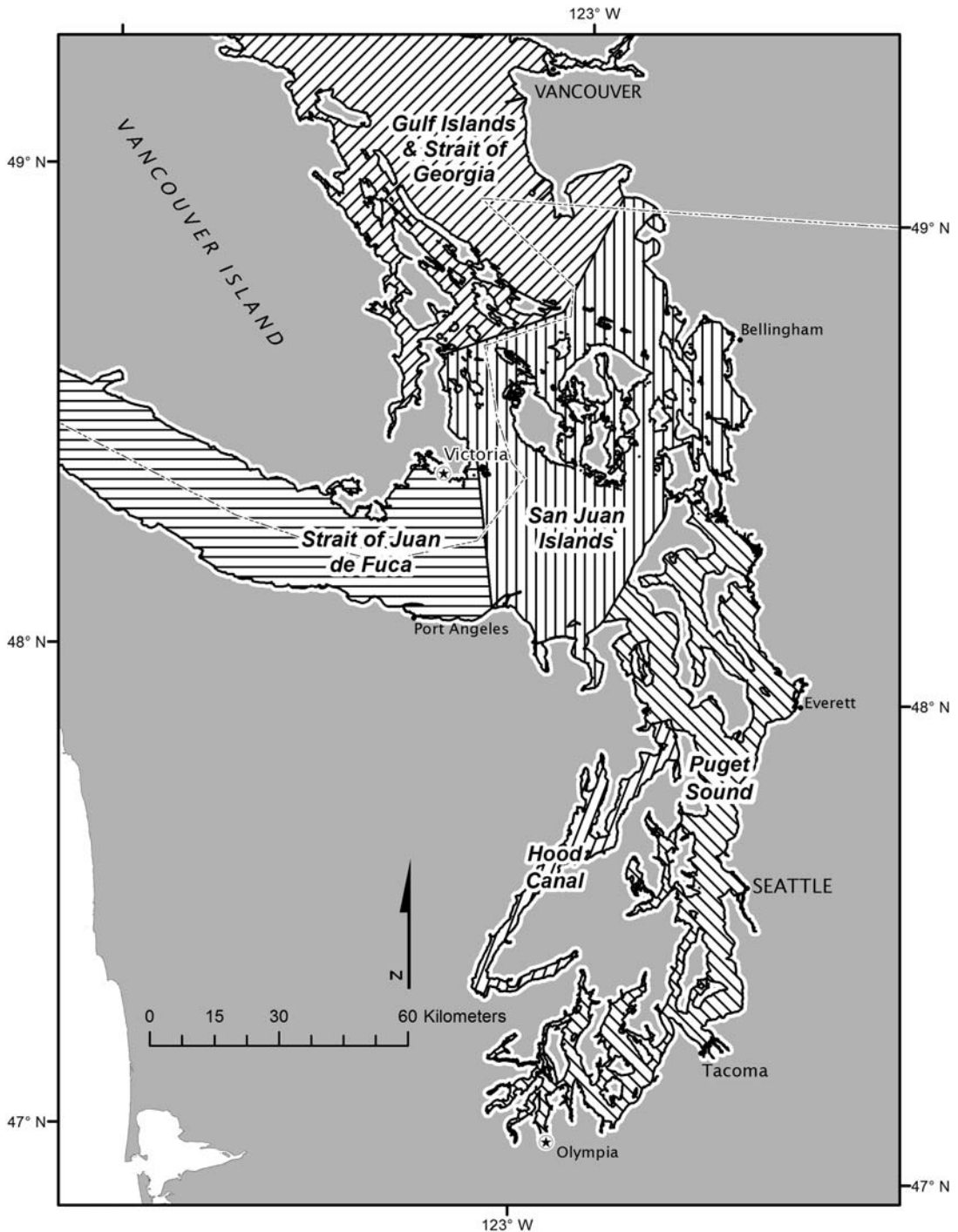
Figure 1. Subareas of the Salish Sea used for analyses of spatial use. The international boundary is shown. The northernmost area of the Gulf Islands and Strait of Georgia and the westernmost area of the Strait of Juan de Fuca had less small boat and sighting effort, thus were excluded from our analyses.

data set included 28 response variables (number of occurrences for each matriline) within each unique combination of season, time period, and subarea (28 x 48 matrix).

A permutational multivariate analysis of variance test (PERMANOVA) was conducted to examine temporal and spatial patterns in matriline occurrence (Anderson 2001). This test was chosen because it does not have distributional assumptions as does a multivariate analysis of variance test. PERMANOVA is a powerful permutation test that can be used to analyze the effect of categorical explanatory variables on multivariate data. The matriline occurrence distance matrix (based on Bray-Curtis distance measures as is appropriate for zero-inflated data; Bray and Curtis 1957, Faith et al. 1987) was compared to the explanatory variables using PERMANOVA to test for a significant effect of season, time and subarea on the occurrence of the most abundant matrilines. Two-way interactions between each explanatory variable were also examined because all were ecologically plausible (e.g., season may have an effect on matrilineal patterns of occurrence in the older period but may not in the more recent period). PERMANOVA was conducted using the adonis function in the vegan (Oksanen et al. 2008) package of R with 10,000 permutations. Statistical significance of an environmental factor (e.g. subarea) would indicate that the matrilines most commonly occurring across different levels of the factor (e.g. the three subareas) were significantly different. The PERMANOVA addresses potential spatial and temporal heterogeneity in the dataset as subareas and time (both seasonally and longitudinally) are explanatory variables in which variability is partitioned. Specifically, this accounts for variable survey and spatial effort between the two time periods for the multivariate analyses.

Results

Mammal-eating killer whales were encountered more frequently in the 2004–2010 period (339 occurrences, excluding Puget Sound and Hood Canal) than in the 1987–1993 period (97 occurrences; Table 2). Between 1987 and 1993, unique groups of mammal-eating killer whales occurred between 9 and 19 times per year (Figure 2). The number of occurrences did not change by year between 1987 and 1993 (Kruskal Wallis χ^2 = 2.504, df = 6, P = 0.868). Between 2004 and 2010, unique groups of mammal-eating killer whales occurred in the Salish Sea between 26 and 79 times per year (excluding Puget Sound and Hood Canal), with an increasing number of occurrences in later years (Figure 2). The total number of occurrences in the Salish Sea significantly differed by year between 2004 and 2010 (Kruskal Wallis χ^2 = 18.996, df = 6, P = 0.004).

The number of occurrences of mammal-eating killer whales was significantly different by subarea for both periods; 1987–1993 (excluding Puget Sound and Hood Canal; Kruskal Wallis χ^2 = 13.632, df = 4, P = 0.001) and 2004–2010 (including Puget Sound and Hood Canal; Kruskal Wallis χ^2 = 24.693, df = 4, P < 0.001). Mammal-eating killer whales were more frequently observed in the Strait of Juan de Fuca than in any other subarea of the Salish Sea throughout this study. Other subareas of the Salish Sea (e.g., Puget Sound) had a slight increasing trend in annual occurrence of mammal-eating killer whales from 2004 to 2010 (Figure 2).

Occurrence of mammal-eating killer whales differed significantly by month in 1987–1993 (Kruskal Wallis χ^2 = 42.671, df = 11, P < 0.001) and in 2004–2010 (Kruskal Wallis χ^2 = 23.795, df = 11, P = 0.014). From 1987–1993, whales occurred most frequently in August–September (Figure 3). From 2004–2010, whales also occurred most frequently in August–September, but there was also a strong second peak in April–May (Figure 3).

The most commonly observed group size increased between the 1987–1993 (mode = 3; see Figure 3 in Baird and Dill 1996) and 2004–2010 periods (mode = 4, Figure 4), although the difference was not statistically significant (W = 18885.5, P = 0.231). The mean group size in the 2004–2010 period (mean ± SD: 5.17 ± 4.36, range: 1 to 36) was greater than the mean group size in the 1987–1993 period (mean ± SD: 4.40 ± 2.82, range: 1 to 15).

TABLE 2. Number of occurrences of mammal-eating killer whales in the San Juan Islands, Gulf Islands and Strait of Georgia, and Strait of Juan de Fuca subareas by year and by month from 1987–2010. Number of occurrences in the Puget Sound and Hood Canal subareas are noted in parentheses.

Month	Year 1987	1988	1989	1990	1991	1992	1993	2004	2005	2006	2007	2008	2009	2010	Total
January	0	1	0	0	0	0	0	0	2 (2)	1	0	1 (1)	2	5	12 (3)
February	1	0	0	0	0	3	0	2	1 (1)	7	0	0	4	3 (1)	21 (2)
March	0	1	1	0	1	0	1	1	2 (1)	1	3 (1)	3	8	5 (2)	27 (4)
April	0	0	1	1	3	3	0	1	5 (1)	1	5	7	9	8 (2)	44 (3)
May	0	0	4	1	0	0	1	2 (2)	4 (2)	0	3	7 (1)	11 (1)	15 (2)	48 (8)
June	0	0	1	0	0	3	0	1	4 (1)	2 (1)	1	3	2	3 (1)	20 (3)
July	0	0	0	0	0	1	0	1	0	0	1	5	2	2 (1)	12 (1)
August	4	2	7	7	3	4	5	7	1	3	10	14	15	9 (1)	91 (1)
September	6	4	3	2	2	3	2	10 (1)	2	11	4	18	12 (2)	2 (2)	81 (5)
October	3	0	2	0	1	1	4	3	2	1	3	7	4	8	39
November	1	0	0	1	0	0	1	7	2	2	1	1	4 (1)	4	24 (1)
December	0	1	0	0	0	0	0	2 (1)	1	2	0	1	6 (1)	4	17 (2)
Total	15	9	19	12	10	18	14	37 (4)	26 (8)	31 (1)	31 (1)	67 (2)	79 (5)	68 (12)	339 (33)

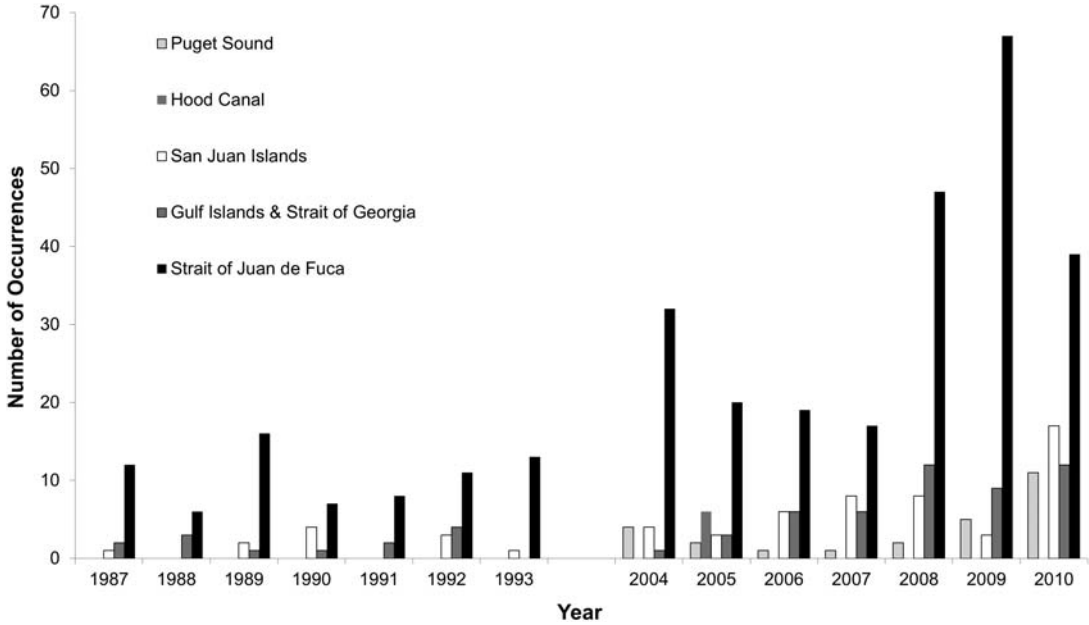Total Occurrence 1987–1993: 97   Total Occurrence 2004–2010: 339 (33)

Figure 2. Cumulative annual occurrence of mammal-eating killer whales in the Salish Sea by subarea from 1987–1993 and 2004–2010.
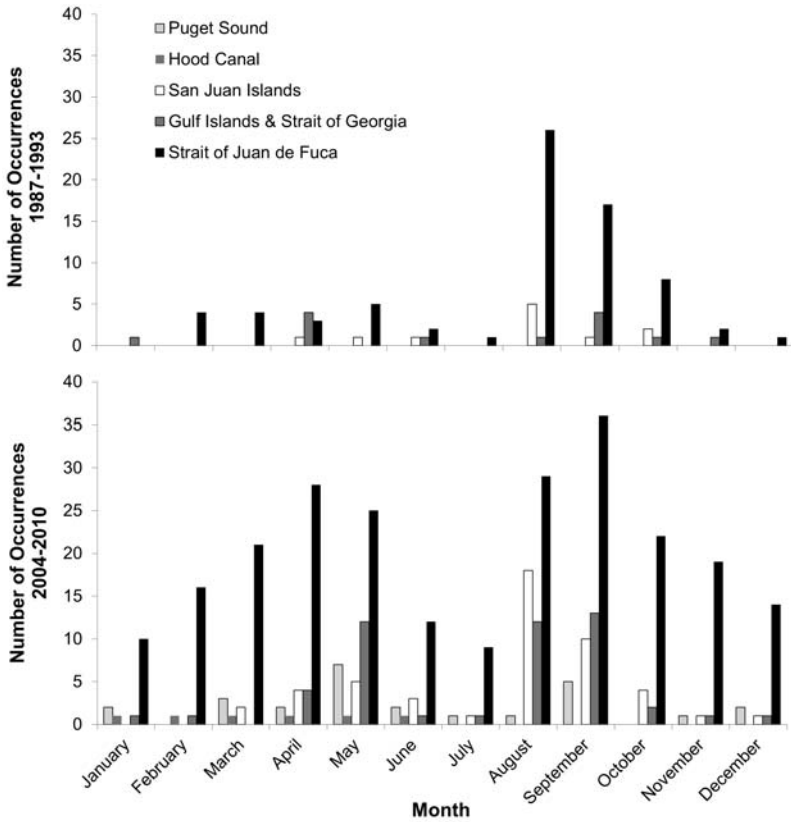

Figure 3. Cumulative monthly occurrence of mammal-eating killer whales in the Salish Sea by subarea from 1987–1993 and 2004–2010.
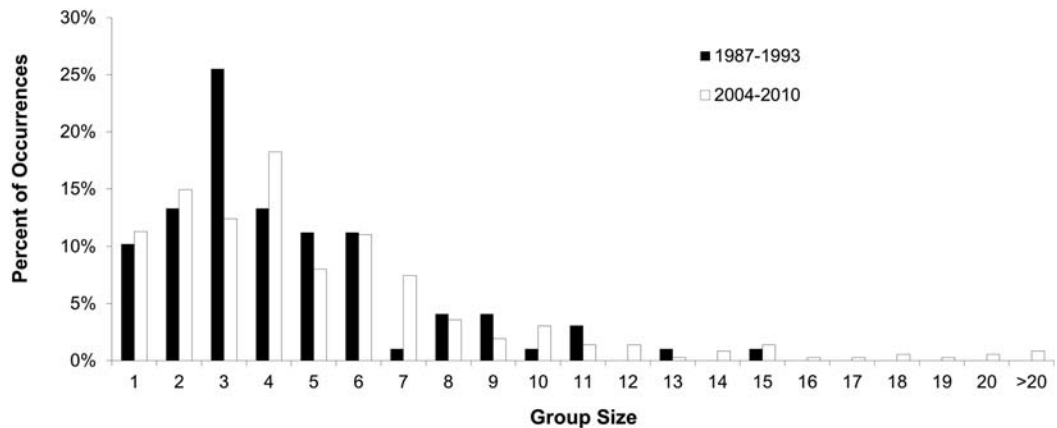
Figure 4. Percent of occurrences for each observed minimum group size of mammal-eating killer whales in the Salish Sea from 1987–1993 and 2004–2010. From 1987–1993, modal group size was 3 whales (mean ± SD: 4.40 ± 2.82). From 2004–2010, modal group size was 4 whales (5.17 ± 4.36).

The most commonly occurring matrilines from the 1987–1993 period also occurred more frequently in the 2004–2010 period (Table 3). However, there were several other matrilines that were not documented in the study in 1987–1993 that were common from 2004–2010 (Table 3). Differences in seasonal occurrence between matrilines existed in both periods. For the 1987–1993 period, the three matrilines classified as nearshore foragers had a more pronounced August–September peak, while the three matrilines classified as non-nearshore foragers were encountered relatively consistently throughout the year (Figure 5; see Baird and Dill 1995). For the 2004–2010 period, the same matrilines of nearshore foragers still had a peak in occurrence from August–September, but the matrilines of non-nearshore foragers had peaks in occurrence in April–May and August–September (Figure 5). The non-nearshore foragers increased in overall occurrence between the two time periods to a greater extent than the nearshore foragers increased.

The matrilines occurring in each season ($F = 2.300$, $df_1 = 3$, $df_2 = 18$, $P < 0.001$), time period ($F = 4.281$, $df_1 = 3$, $df_2 = 18$, $P < 0.001$), and subarea of the Salish Sea ($F = 2.796$, $df_1 = 2$, $df_2 = 18$, $P = 0.002$) differed significantly (PERMANOVA $R^2 = 0.74$). Matrilineal occurrence in each area differed across time periods with marginal significance ($F = 1.336$, $df_1 = 6$, $df_2 = 18$, $P = 0.089$). However, the matrilines that commonly occurred in each season did not differ across time periods or across areas.

Discussion

Some of the increase in mammal-eating killer whales' use of the Salish Sea between 1987 and 2010 is likely due to an increase in sighting effort between the two periods. However, we attempted to control for differences in effort by looking at occurrences of groups in the Salish Sea (i.e., taking into account repeated sightings over six days). We also only included the three subareas that had sighting effort in both time periods when comparing 1987–1993 to 2004–2010. The number of occurrences of mammal-eating killer whales also increased significantly within the 2004–2010 period itself, when sighting effort was relatively consistent. It is relevant to note that the measure of occurrences may affect spatial analyses by underrepresenting certain subareas (e.g., those that are utilized after arrival in the Salish Sea via one of the straits). Although mammal-eating killer whales most commonly occurred in the Strait of Juan de Fuca, they also increased in occurrence in other subareas (e.g., Puget Sound) in recent years. We suggest this apparent increase in occurrence over time in the Salish Sea is due to an increase in the abundance of mammal-eating killer whale primary prey, as seals, sea lions, and porpoises have increased substantially in abundance and

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TABLE 3. Number of occurrences of at least one member of each matriline in each period (see Appendix 1 for matriline designation codes). The total number of occurrences does not include occurrence in the Puget Sound or Hood Canal (noted separately in 2004–2010 column). Six of the commonly occurring matrilines in 1987–1993 were classified as either nearshore foragers or non-nearshore foragers by Baird and Dill (1995).

Matriline	1987–1993 # of Occurrences	2004–2010 # of Occurrences (Puget Sound and Hood Canal Occurrences)	Total # of Occurrences	Classification (Baird and Dill 1995)
T21	17	47 (3)	64	Non-nearshore forager
T13	14	40	54	Non-nearshore forager
T41	16	27	43	Nearshore forager
T100	0	43 (1)	43	
T2	19	20 (1)	39	Non-nearshore forager
T88	3	34 (6)	37	
T124	0	35 (3)	35	
T10	15	20	35	Nearshore forager
T32	24	10	34	Nearshore forager
T30	0	33 (2)	33	
T101	0	31 (6)	31	
T19	0	24 (2)	24	
T49	0	22	22	
T46	0	22 (1)	22	
T11	12	8	20	
T109	12	5	17	
T104	0	16	16	
T36	0	12 (2)	12	
T12	10	2	12	
T65	0	11 (2)	11	
T123	0	6	6	
T124A	0	5 (6)	5	
T99	0	5	5	
T7	2	3	5	
T75	4	1	5	
T137	0	4 (3)	4	
T71	0	3 (6)	3	
T185	0	3	3	

occurrence in the area (Jeffries et al. 2003, Lowry and Maravilla-Chavez 2005, Pitcher et al. 2007, Fisheries and Oceans Canada 2010, Carretta et al. 2011). The increased local occurrence in the Salish Sea could also be due to an increase in abundance of the greater population of west coast 'transient' killer whales throughout the study period (Ford et al. 2007, Towers et al. 2012). These causative links are not mutually exclusive, and it is likely that both prey abundance and overall population growth have contributed to the changes in occurrence documented in the Salish Sea.

Seasonal patterns of occurrence differed between the two periods with a single peak in occurrence of mammal-eating killer whales in August–September from 1987–1993 and two
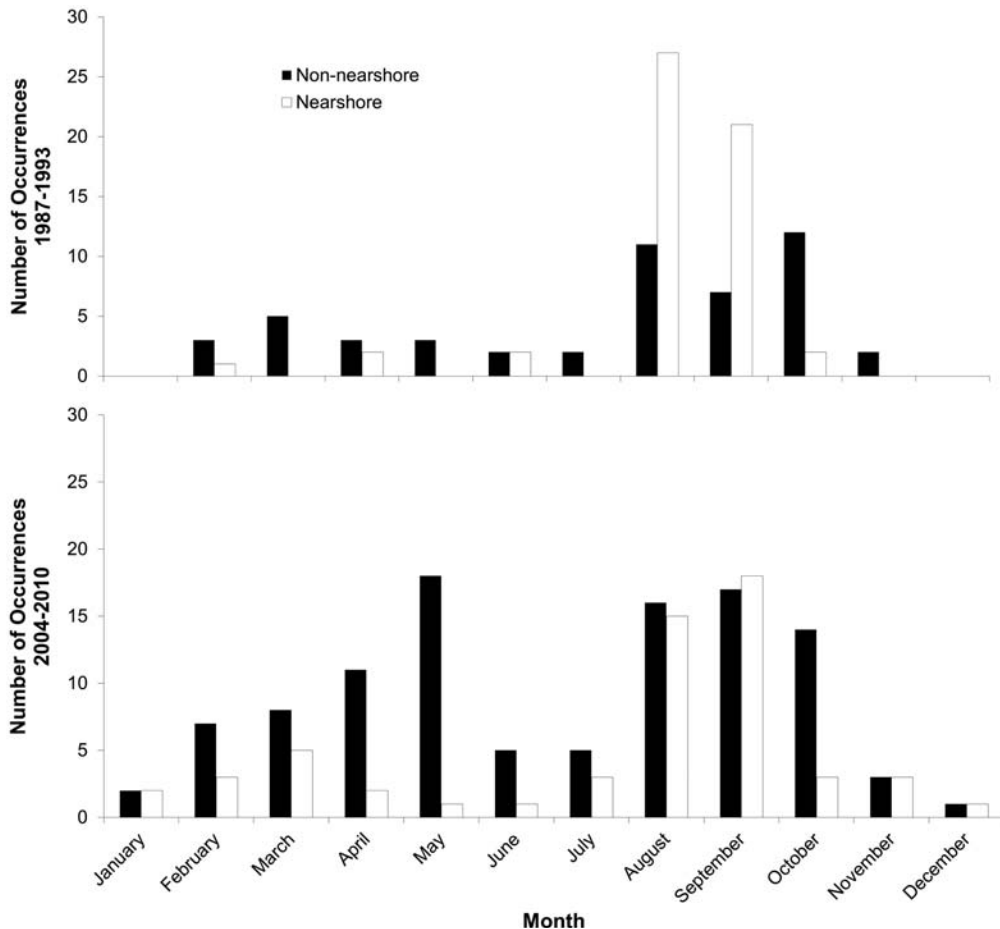
Figure 5. Cumulative monthly occurrence of non-nearshore and nearshore foragers from 1987–1993 and 2004–2010.

peaks in 2004–2010, one in April–May and one in August–September. We suspect these changes in seasonal occurrence could be a consequence of increased prey diversity. From 1987–1993, half of the most commonly observed mammal-eating killer whale matrilines were found to be nearshore foragers, specializing on harbor seal prey near haul-out sites during the pupping-weaning season in inland waters (Bigg 1969, Temte et al. 1991, Baird and Dill 1995). It is likely that the increased use of the Salish Sea was by non-nearshore foragers that did not focus hunting effort near harbor seal pupping and haul-out sites, but still foraged on harbor seals throughout the year. Other prey species, including porpoises, elephant seals, and sea lions, are all found in areas away from harbor seal haul

outs. Although sea lions and occasionally elephant seals also utilize haul out sites, killer whales seem less likely to attack sea lions at haul outs, as attacks are often prolonged and sea lions may be able to reach refuge sites in shallow water or on shore if attacked nearshore (Baird and Dill 1995). The second peak in mammal-eating killer whale occurrence in April–May during 2004–2010 corresponds with the increased occurrence of California sea lions and Steller sea lions in inland waters in those months, suggesting the whales may be taking advantage of the increased occurrence of these pinnipeds. The lower occurrence of mammal-eating killer whales in the Salish Sea in June–July may be associated with seasonal fluctuations in California sea lions and Steller sea lions as many of these pinnipeds migrate to

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the outer coast to return to natal rookeries at that time. Peaks in occurrence in cetacean prey species (Dahlheim et al. 2009) and differences in timing of the peak harbor seal pupping period (Temte et al. 1991) elsewhere throughout the range of mammal-eating killer whales likely also influence killer whale movements to areas outside of the Salish Sea in winter and in the months June–July.

The most commonly occurring group size of mammal-eating killer whales in the Salish Sea had an increasing trend from 1987 to 2010, but this was not statistically significant. This pattern could be due to increased prey diversity as optimum foraging group size changes by prey species, depending in part on the difficulty of capture, risk of injury, and the energetic value of the prey (Baird and Dill 1996). When feeding primarily on harbor seals, the optimum foraging group size was three individuals, the most frequently observed group size in the 1987–1993 period (Baird and Dill 1996). Although we have not been able to quantify it, there is anecdotal evidence of increased predation on faster and more difficult to catch prey species, such as harbor porpoise, and larger prey species, such as sea lions, in our study area in recent years; from observations both in southeast Alaska and in our study area faster and larger prey species are targeted by larger groups of mammal-eating killer whales (Baird and Dill 1995, Dahlheim and White 2010). Mammal-eating killer whales are cooperative hunters with the cost of prey capture varying with group size. Higher encounter rates with increasingly abundant sea lions and porpoises in the Salish Sea facilitate the larger groups recently observed (Baird 2002). Increased prey abundance in the Salish Sea could relax the need to forage in the optimum group size as efficiency becomes less important when there are more foraging opportunities available. Increased prey abundance also likely leads to increased consumption, growth, and reproduction by mammal-eating killer whales. Increased reproduction in this population is consistent with the observation of several commonly occurring matrilines having many young, undispersed offspring in recent years (Towers et al. 2012; e.g., T100, T101, and T124 matrilines; Table 3). Therefore, increased reproductive output due to increased

prey abundance could also lead to the larger group sizes recently observed in the Salish Sea.

Matrilineal differences in annual occurrence contributed to the pattern of increasing use of the Salish Sea over time. Many of the commonly observed matrilines from 1987–1993 increased their use of the area in 2004–2010, and several matrilines previously not encountered in the Salish Sea were also observed frequently between 2004 and 2010. Our results suggest that the changes in annual occurrence are explained by different matrilines utilizing the area in recent years compared to those that were common in 1987–1993. The matrilines that occurred commonly in 2004–2010 but were not encountered in 1987–1993 may have increased their use of the Salish Sea where prey abundance has increased, in addition to utilizing prey resources elsewhere. Several of these matrilines were encountered in southeast Alaska frequently within the 1987–1993 period (Dahlheim and White 2010). In the inland waters of southeast Alaska, harbor porpoise populations have declined significantly from 1991 to 2011 (Marilyn Dahlheim, NOAA National Marine Mammal Laboratory, personal communication) and one of several stocks of harbor seals has also declined from 1992 to 2008 (Womble et al. 2010). The recent changes in mammal-eating killer whale occurrence in the Salish Sea may indicate that these whales are utilizing a broader range of their distribution to take advantage of areas exhibiting increased prey abundance.

Matrilineal differences can explain the changes in seasonal occurrence between the two time periods. Non-nearshore foragers, which did not focus foraging effort on harbor seal pupping and haul-out sites in 1987–1993, increased in overall occurrence to a greater extent than did nearshore foragers. The divergent pattern between the two foraging types contributed to the greater seasonal occurrence of killer whales in times of the year that do not coincide with harbor seal pupping–weaning time. The PERMANOVA results indicated that seasonal differences in occurrence could be attributed to the occurrence of different matrilines. It is possible that the more recently common matrilines in the Salish Sea in 2004–2010 exhibit the same seasonal patterns as non-nearshore foragers, contributing to

the changes in seasonal occurrence between 1987 and 2010. However, the classification of nearshore and non-nearshore foragers may be specific to the Salish Sea region and may differ from broad-scale patterns of occurrence and behavior.

These new findings update our previous understanding of mammal-eating killer whale spatial use, occurrence and group size in the Salish Sea. Mammal-eating killer whales are more common at different times of the year and have also increased in their occurrence and group size. Current information on top predator geospatial ecology will better inform ecosystem-based models in the Salish Sea, and provide insights for marine populations in other systems. Increasing knowledge of predator-prey relationships in the Salish Sea allows for a greater understanding of the role of mammal-eating killer whales in this ecosystem. Findings from this study provide an example of how predators might be altering their spatial use and seasonal occurrence in order to take advantage of increasing prey abundance and occurrence. Other studies have shown that an increase in prey abundance alters the diet and abundance of marine predators (Womble and Sigler 2006), but none have examined changes in aspects of behavior such as occurrence and group size. It is likely that mammal-eating killer whales are also having non-consumptive effects on their prey populations due to the changes in whale behavior and increased use of the Salish Sea in recent years. For example, prey populations could increase predator vigilance in months where mammal-eating killer whales are increasing seasonal use, which would increase the total effect of the predator in this system. Intraspecific variation in occurrence and spatial use by different matrilines is also a unique aspect of this study and will be important to consider in future studies in order to determine how individuals or matrilines may differ in other behavioral traits or patterns.

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Appendix 1

List of matriline codes and matriline membership used in this study

T2	T2 (female), T1, T2A, T2B, T2C
T7	T7 (female), T7A, T7B
T10	T10 (female), T10A, T10B, T10C
T11	T11 (female), T11A
T12	T12 (female), T12A, T12B, T12C
T13	T13 (female), T14
T19	T19 (female), T19B, T19C
T21	T21 (female), T20, T22
T30	T30 (female), T30A, T30B, T30C
T32	T32 (female), T31
T36	T36 (female), T36A, T36B, T36C
T41	T41 (female), T41A, T44
T46	T46 (female), T46A, T46B, T46C, T46D, T46E
T49	T49 (female), T49A, T49B
T65	T65 (female), T63, T65A, T65B
T71	T71 (female), T71A, T71B, T71C
T75	T75 (female), T77, T78, T75A, T75B, T75C
T88	T88 (female), T87, T90
T99	T99 (female), T99A, T99B
T100	T100 (female), T100A, T100B, T100C, T100D
T101	T101 (female), T101A, T101B, T102
T104	T104 (female), T103
T109	T109 (female), T109A, T109B, T109C, T109D
T123	T123 (female), T123A
T124	T124 (female), T124C, T124D, T124E
T124A	T124A (female), T124A1, T124A2, T124A3
T137	T137 (female), T137A, T137B
T185	T185 (female), T186, T187, T185A