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ARTICLE

Site fidelity and movement of humpback whales (*Megaptera novaeangliae*) in the western Gulf of Alaska as revealed by photo-identification

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Abstract: We describe feeding-site fidelity in terms of the rate of annual return by individual humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) to Kodiak Archipelago and Shumagin Islands feeding areas and the rate of exchange between these Gulf of Alaska feeding aggregations. Individual whales were photo-identified in both regions between 1999 and 2015 during vessel surveys, either throughout the feeding season (Kodiak region) or in brief 7- to 10-day windows (Shumagin Islands). Feeding-site fidelity was assessed in terms of individuals' annual return rate, sighting interval, total number of years sighted, and movement between feeding areas. We found similarly high degrees of site fidelity in both regions and limited movement of individuals between them, suggesting that the Shumagin Islands and Kodiak Archipelago represent distinct feeding aggregations. Results did not appear affected by temporal differences in sampling strategy in these study areas.

Key words: Megaptera novaeangliae, Gulf of Alaska, photo-identification, site fidelity, annual return, humpback whale.

Résumé : Nous décrivons la fidélité au site d'alimentation en termes du taux de retour annuel de baleines à bosses (*Megaptera novaeangliae* (Borowski, 1781)) dans des aires d'alimentation de l'archipel de Kodiak et des îles Shumagin et du taux d'échange entre ces regroupements à des fins d'alimentation dans le golfe d'Alaska. Des baleines ont été photoidentifiées dans les deux régions entre 1999 et 2015 durant des campagnes d'évaluation en navire, soit durant toute la saison d'alimentation (région de Kodiak) ou durant de courtes fenêtres de 7 à 10 jours (îles Shumagin). La fidélité au site d'alimentation a été évaluée en termes du taux de retour annuel des individus, de l'intervalle entre les observations de ces derniers, du nombre total d'années où ils ont été observés et de leurs déplacements entre les aires d'alimentation. Nous avons constaté des degrés tout aussi élevés de fidélité au site dans les deux régions et des déplacements limités d'individus entre ces dernières, ce qui donne à penser que les regroupements à des fins d'alimentation des îles Shumagin et de l'archipel de Kodiak sont des regroupements distincts. Les variations dans le temps des stratégies d'échantillonnage dans les régions étudiées ne semblent pas avoir d'incidence sur les résultats. [Traduit par la Rédaction]

Mots-clés : Megaptera novaeangliae, golfe d'Alaska, photoidentification, fidélité au site, retour annuel, baleine à bosse.

Introduction

Humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) are medium-sized baleen whales found in all major ocean basins (Clapham and Mead 1999). Like many baleen whales, they execute a seasonal migration between high-latitude feeding grounds and low-latitude breeding grounds (Chittleborough 1958). The unique black and white pigment patterns and trailing edges of humpback whale flukes allow for individual whales to be identified (Katona et al. 1979). As a result, photo-identification of these animals has allowed researchers to use mark–recapture methods to study individuals, movements, and population dynamics of humpback whales throughout their range (Clapham et al. 2003; Mizroch et al. 2004; Calambokidis et al. 2008; Straley et al. 2009; Mizroch et al. 2011). Results of photo-identification research have revealed that humpback whales exhibit site fidelity to both their feeding and breeding grounds. Site fidelity is assessed by documenting the rate at which individuals are resighted in an area between years and may be affected by differences in population size (Calambokidis et al. 2001), behavioral heterogeneity, or differences in survey effort.

The natural history of humpback whales in the North Pacific has been documented on a broad scale (Calambokidis et al. 2008; Barlow et al. 2011; Baker et al. 2013); however, few studies have focused on population dynamics of specific feeding aggregations, including those in the western Gulf of Alaska, Aleutians Islands, and Bering Sea. Feeding aggregations near the Kodiak Archipelago and Shumagin Islands represent two of an unknown number of distinct feeding aggregations in the Gulf of Alaska (Figs. 1*a*, 1*b*). Both regions are included in the Central North Pacific Stock and have documented migration and genetic linkages to breeding grounds in Hawai'i, Mexico, and Asia (Witteveen et al. 2004; Calambokidis et al. 2008; Baker et al. 2013; Allen and Angliss 2015).

Between 1999 and 2015, we conducted dedicated photo-identification research in these two regions using different sampling protocols. In the Kodiak region, sampling was conducted using a more traditional approach, while logistical limitations in the Shumagin Islands forced an abbreviated effort there. Although consistent, long-term, within-season sampling effort may be assumed to yield more reliable population parameter estimates, the impact of shorter survey periods on such estimates has not been documented.

The purpose of this study was to enhance fine-scale understanding of the composition and dynamics of two relatively under-described feeding aggregations in the Gulf of Alaska. We analyzed sighting records of individually identified humpback whales obtained during

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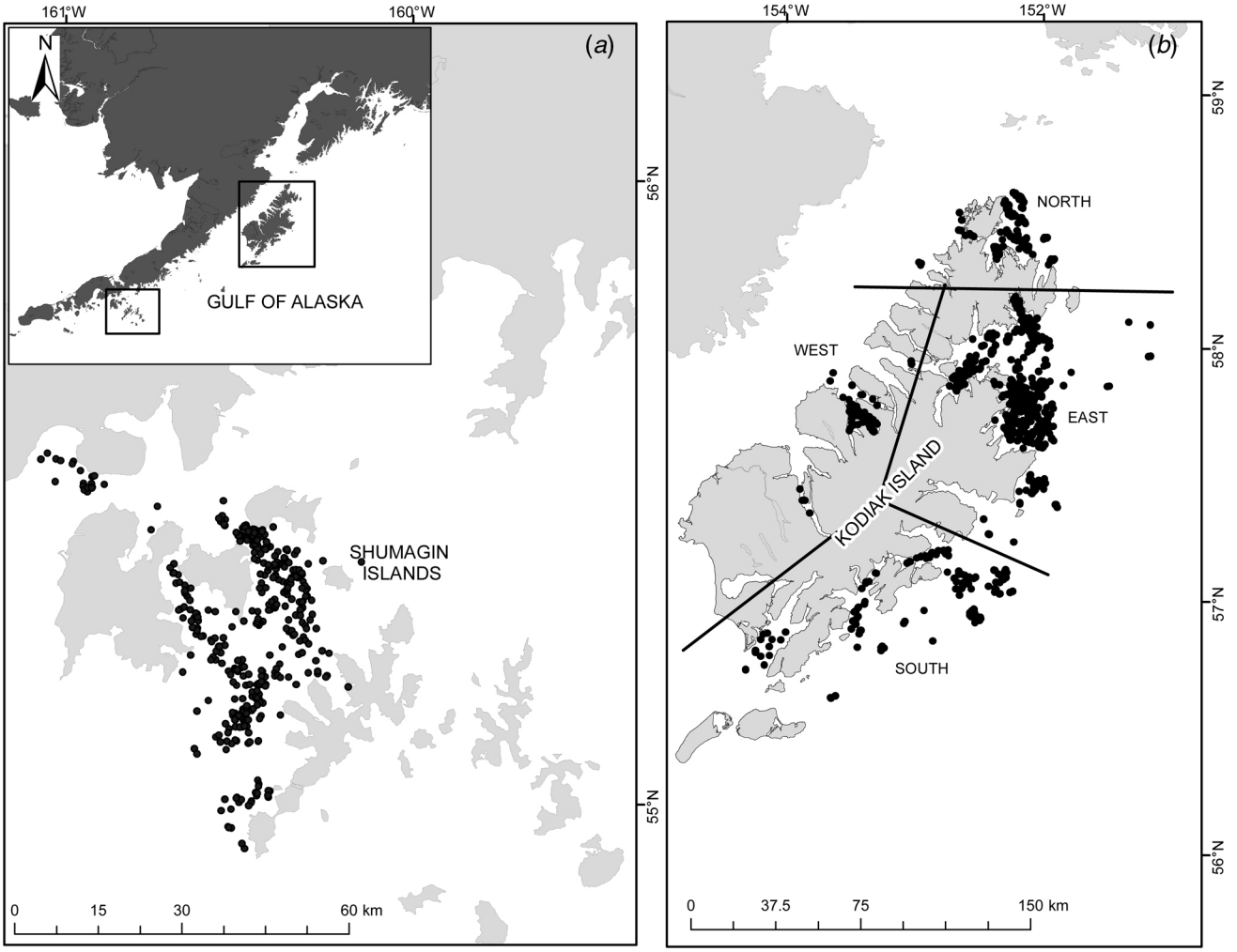
Fig. 1. Location of (*a*) the Shumagin Islands and Kodiak Archipelago study areas within the Gulf of Alaska and (*b*) the subarea designations within the Kodiak study area.



vessel-based surveys within two regions, Kodiak and Shumagin Islands, to describe their fidelity to each site. Interchange between the two regions was also calculated to verify the distinction of these as feeding aggregations. Because our sampling regime differed temporally between areas, we also sought to assess the impact of differing survey strategies on photo-identification study results.

Materials and methods

Individual whales were identified using photographs of the ventral surface of their flukes taken during vessel surveys conducted in the Kodiak Archipelago and Shumagin Islands from 1999 to 2015 (Table 1). Survey effort differed between the study sites due to substantial logistical differences. Our year-round residence on Kodiak Island allowed us to conduct vessel surveys as frequently as conditions permitted, whereas Shumagin Islands vessel surveys were conducted only during brief periods when transient personnel were present in the study area. As a result, survey effort in Kodiak totaled more hours across more days and months than the Shumagin Islands (Table 1).

Fluke photographs were ranked for quality (poor, fair, good, and excellent) based on features that include focus, proportion visible, and vertical and horizontal angles (e.g., Calambokidis et al. 2008; Barlow et al. 2011). Photographs ranked as poor in one or more categories or fair in two or more categories were removed from the data set. For most analyses, only animals that were sighted on more than one occasion (two or more sightings within or between years) were considered. The full data set, including animals with only one documented sighting, was used to determine the total number of animals sighted in each year and region, as well as to generate discovery curves illustrating cumulative totals of identified whales in each region.

In this study, site fidelity was assessed by documenting the repeated presence of individual whales in a feeding area over time. On a population level, site fidelity is reflected in an annual return rate, calculated as the number of animals sighted in the current year that had been identified in a previous year divided by the total number of animals sighted in that year. Sighting intervals of individuals were calculated as the time, in years, between first and next (i.e., subsequent) sighting, as well as the first and last sighting. Intervals such as these can also be used as measures of long-term site fidelity (Baker et al. 1986; Craig and Herman 1997; Wedekin et al. 2010). The degree of interchange of individuals (i.e., documented movement between two locations) is another means of assessing site fidelity. Within- and between-year resightings of whales in both Kodiak and Shumagin Islands were used to document interchange of individuals between these known feeding areas. Additionally, the Kodiak region was divided into four subareas (north, south, east, and west) based on geography, effort, and a priori knowledge of humpback whale distribution (Fig. 1*b*) to assess fine-scale patterns of interchange among subareas within and between years.

Table 1. Summary of vessel-based humpback whale (*Megaptera novaeangliae*) survey effort for two western Gulf of Alaska study areas between 1999 and 2015.

	Kodiak			Shumagin Islands		
Year	Effort days	Effort hours	Sampling period	Effort days	Effort hours	Sampling period
1999	2	*	10–11 Aug.	11	25.2	13 June – 5 Sept.
2000	7	*	1 July – 11 Oct.	18	42.6	21 June – 2 Sept.
2001	20	73.5	13 June – 1 Sept.	5	24.3	5–10 Aug.
2002	46	220.8	2 June – 17 Sept.	4	29.2	29 July – 1 Aug.
2003	45	33.1	21 May – 14 Sept.	NA	NA	NA
2004	22	194.8	28 June – 31 Aug.	4	31.1	21–26 July
2005	18	121.2	17 June – 13 Aug.	4	36.4	19–23 July
2006	15	77.7	21 June – 8 Aug.	NA	NA	NA
2007	46	222.8	13 June – 13 Sept., 28 Nov. – 30 Dec.	5	36.2	2–7 Aug.
2008	31	105.2	2–30 Jan., 12 June – 29 Aug.	5	32.2	4–8 Aug.
2009	18	94.9	12 June – 30 Aug.	2	14.6	7–8 Aug.
2010	18	123.5	18 June – 24 Aug.	4	37.6	24–28 July
2011	14	70.3	30 June – 23 Aug.	3	18.5	14–16 July
2012	19	79.6	5 May – 13 Sept.	6	24.4	1–6 Aug.
2013	15	51.1	26 June – 25 Aug.	5	19.5	7–11 Aug.
2014	12	66.8	2 July – 19 Sept.	NA	NA	NA
2015	8	34.7	16 June – 3 Nov.	2	8.1	8–10 Aug.
Totals	356	1569.9		78	379.6	
Mean	20.9	104.7		5.6	27.1	

Note: The sampling period indicates the first and last days that surveys were conducted within each calendar year. NA, not available.
*Survey hours were not documented in Kodiak in 1999 and 2000.

Results

Kodiak

In Kodiak, vessel-based surveys were conducted from 1999 to 2015, with minimal effort in 1999 and 2000. Annual survey effort averaged just under 21 days; timing was dictated primarily by weather. Survey effort focused on the traditional summer feeding period (May through September), with a single winter survey conducted in 2007–2008 (Table 1).

Across 17 years of data collection, 2173 sightings were made of 1187 individually identified humpback whales in the Kodiak region. The number of individuals seen during a single year ranged from a low of 5 individuals in 1999 to a high of 293 individuals in 2007 (Table 2*a*, Fig. 2*a*). The mean rate of annual return was 34% (SD = 15.2%; Fig. 2*b*). The highest percentage of resighted animals occurred in 2009 (57%), with the lowest in 2002 (7%). A discovery curve for Kodiak showed a strong linear increase in the number of whales identified throughout the study period (Fig. 3).

Most humpback whales sighted in Kodiak were seen within a single year (n = 864), but sightings in up to 10 different years were documented (Table 3). Resightings (n = 323) most often occurred in sequential years, but separation of sightings by 2–6 years was not uncommon.

Subsequent sightings of individuals, whether within or between years in the Kodiak study area, occurred within the same subarea 65% of the time. Interchange among Kodiak subareas was documented for 163 individuals, with 152 being sighted in two subareas and 11 being sighted in three subareas. No individuals were sighted in all four subareas during the study period. Most documented movement between two subareas occurred between the east and the south subareas with movement between the north and the south being the least frequent (Table 4).

Shumagin Islands

Vessel-based survey effort in the Shumagin Islands was limited by logistical restrictions, with a mean of 5.6 survey days per year (Table 1). With the exception of 1999 and 2000, survey effort here was confined to narrow 7- to 10-day windows in July or August (Table 1). No surveys were conducted in this study area in 2003, 2006, or 2014.

In the Shumagin Islands, 654 individual whales were sighted across 14 sampling periods and 1437 total sightings. The highest number of individual whales sighted in a single year was 169 individuals in 2012 and the lowest was 6 individuals in 2015 (Table 2*b*). The rate of annual return was slightly higher, though not significantly different (ANOVA, $F_{[1,27]} = 0.02$, $p = 0.89$) for the Shumagin Islands than for Kodiak, averaging 37% (SD = 11.8%) across the period (Fig. 2*b*). This rate ranged from a low of 10% in 2000 to a high of 57% in 2009. The discovery curve for the Shumagin Islands showed a continuous increase in the number of identified whales, but it was not as steep as for Kodiak (Fig. 3). The curve also showed some indication of slowing rate of discovery (Fig. 3).

Individual humpbacks in the Shumagin Islands were most likely to be seen in two different years rather than in a single year, with one animal being sighted in nine different years. Shumagin Island animals were also more likely to be seen two years after their first sighting rather than one year, but this value may be skewed due to breaks in effort (Table 1).

Interchange between regions

Interchange between Kodiak and the Shumagin Islands was minimal. A total of 31 (1.7%) animals first sighted in Kodiak had a future sighting in the Shumagin Islands, whereas 27 animals showed movement in the opposite direction (1.5%). Sightings were separated by 3.1 years (1137 days), on average. On four occasions, individual whales were sighted in both areas within the same year. Bidirectional movement was documented for seven animals, with four animals moving from Kodiak to the Shumagin Islands and back and three animals following the opposite route. Bidirectional movement was never documented in a single year.

Movement between the Shumagin Islands and specific Kodiak subareas was much higher for the east and south, regardless of the direction of movement (Table 5). Only eight individuals were documented to move between the Shumagin Islands and Kodiak's north (n = 1) and west (n = 7) subareas, whereas 50 movements were documented between the Shumagin Islands and either the east (n = 25) or south (n = 25) Kodiak subareas (Table 5).

Table 2. Total number of unique humpback whales (*Megaptera novaeangliae*) identified by year and the number of animals resighted in each subsequent year of effort for Kodiak (*a*) and the Shumagin Islands (*b*).

(*a*) Kodiak.

Year	Unique IDs	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1999	5	**0**	2	1	1	2	2	2	2	3	2	1	0	0	0	2	0	0
2000	6		**2**	3	2	1	2	3	2	3	2	1	1	0	0	1	0	0
2001	29			**9**	7	3	4	9	4	12	5	2	1	0	4	1	0	2
2002	120				**15**	7	21	17	13	33	6	5	4	4	7	7	4	6
2003	53					**2**	11	7	4	6	3	3	5	1	5	4	1	2
2004	267						**34**	21	13	34	6	11	10	0	5	5	4	7
2005	172							**39**	10	32	8	5	9	7	11	5	5	2
2006	99								**25**	19	9	4	7	1	4	5	0	0
2007	293									**116**	17	16	17	19	18	13	8	8
2008	38										**18**	7	2	1	6	9	4	1
2009	51											**11**	10	9	6	10	6	2
2010	132												**7**	10	6	8	8	5
2011	93													**28**	12	13	10	4
2012	127														**12**	14	9	2
2013	87															**15**	8	2
2014	66																**16**	4
2015	62																	**1**

(*b*) Shumagin Islands.

Year	Unique IDs	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1999	15	**0**	6	6	2	0	4	8	0	2	3	1	7	1	4	2		0
2000	60		**32**	17	9	0	10	16	0	9	8	6	12	1	14	1		1
2001	76			**24**	5	0	5	17	0	10	10	4	11	1	16	4		1
2002	35				**5**	0	7	12	0	11	9	9	6	0	8	1		0
2003																		
2004	56						**9**	13	0	9	6	8	11	1	9	0		0
2005	89							**49**	0	16	18	11	21	6	19	1		1
2006																		
2007	123									**30**	16	19	18	4	25	4		2
2008	116										**36**	17	17	4	20	2		1
2009	69											**13**	16	3	23	1		0
2010	141												**46**	8	37	5		1
2011	39													**5**	11	1		0
2012	169														**69**	7		1
2013	40															**3**		0
2014																		
2015	6																	**0**

Note: Numbers in boldface type along the diagonal represent the total number of within-year resights, meaning an individual was seen on more than one occasion in that year.

Discussion

The limited amount of movement of identified humpback whales between Kodiak and the Shumagin Islands provides evidence that these two regions are discrete feeding aggregations. However, it should be noted that the lack of documented movement between these two areas may also be a function of a multitude of factors, including the timing of effort. Arguably more insightful is the lack of sightings of individual whales in more than one Kodiak subarea. This result may suggest that site fidelity is very specific or that the Kodiak region has more than one distinct feeding aggregation. The specificity and degree of site fidelity within and between regions and subareas may have significant implications in the management of these whales within the North Pacific.

Site fidelity of humpback whales is generally much higher on feeding grounds than breeding grounds, but has been shown to be "strong" for both habitats in the North Pacific (Calambokidis et al. 1996). However, although annual return is a widely used description of site fidelity, defining what these rates mean has remained nebulous with studies citing "high", "very strong", and "moderate" levels of site fidelity for feeding aggregations in the North Pacific (Baker et al. 1986; Calambokidis et al. 2001; Riley 2010). Rates estimated here fall in the middle of rates reported for other feeding areas in Alaska, such as the 23% reported for the eastern Aleutian Islands (Riley 2010) and 47.2% for southeastern Alaska (Baker et al. 1986). Broadly, reported rates of annual return have ranged from 1% on breeding grounds in Brazil (Baracho-Neto et al. 2012) to 73.2% for feeding animals in the Gulf of Maine (Clapham et al. 1993). Annual return rates can be biased by a number of factors, including survey effort, population size, and heterogeneity in fluking behavior (Clapham et al. 1993; Wedekin et al. 2010). Additionally, Zerbini et al. (2006) estimated an annual growth rate for humpback whales in the shelf waters of the Gulf of Alaska of 6.6%, indicating that there are a reasonably high number of animals entering these aggregations each year, as is evident by the lack of plateau in the discovery curves for each area. Annual rates of return may be higher across longer time series and if rates of population increase slowly. Therefore, meaningful comparison of return rates within ocean basins will require establishment of universal definitions or parameters. Comparing rates of annual return between years within regions or neighboring regions, as is the case here, may be more insightful.

Humpback whales from both Kodiak and the Shumagin Islands showed evidence of site fidelity. Long-term site fidelity was supported in both regions by the majority of resights occurring within 1–3 years. The mean rates of annual return were not statistically different between the two regions, although the rate was higher and less variable in the Shumagin Islands. This suggests that site fidelity to the Shumagin Islands may be stronger or that

Fig. 2. The number of new and resighted humpback whales (*Megaptera novaeangliae*) (*a*), as well as calculated rate of annual return (*b*), by year for Kodiak and the Shumagin Islands.

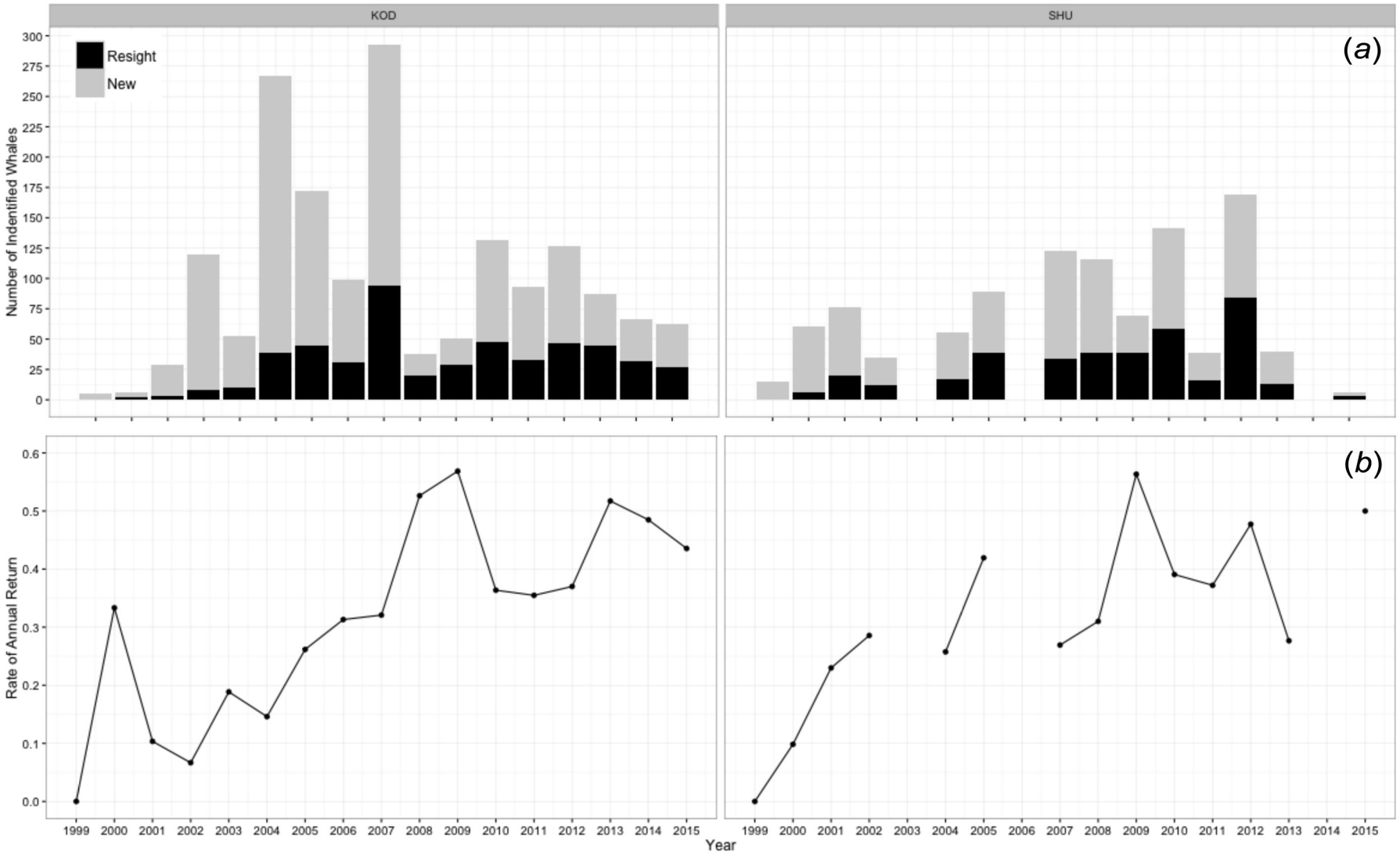


Fig. 3. Cumulative number of newly identified individual humpback whale (*Megaptera novaeangliae*) versus the cumulative total of identified humpback whales in the Kodiak Archipelago (circles) and Shumagin Islands (triangles).

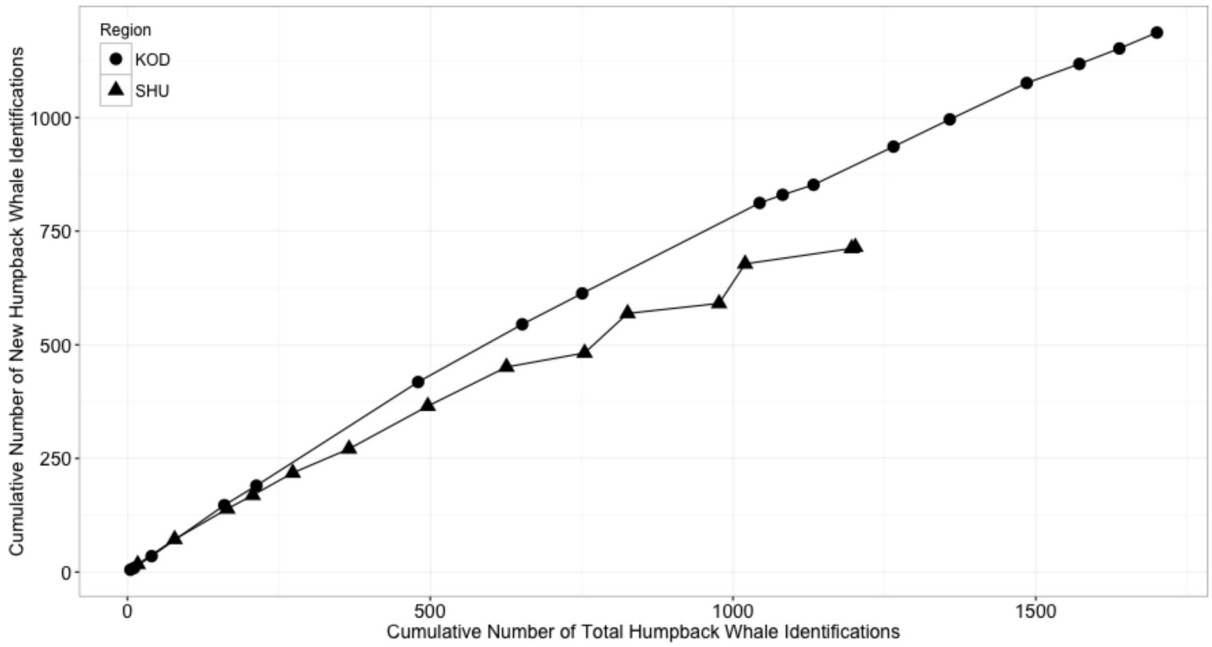


Table 3. Total number of humpback whales (*Megaptera novaeangliae*) sighted in each study region, including totals for animals sighted in one (1) or more (1+) years, on one (1) or more (1+) occasions, and in one (1) or more (1+) areas (for Kodiak only).

	No. of humpback whales	
	Kodiak	Shumagin Islands
Total	1187	654
Years		
1*	864	439
1+	323	215
Sightings		
1	718	309
1+	469	345
Area†		
1	160	NA
1+	163	NA

Note: NA, not available.

*Includes individuals that may have been sighted on more than one occasion within a single year.

†Includes only individuals that were seen on more than one occasion.

Table 4. Movement of humpback whales (*Megaptera novaeangliae*) (n = 152) between two subareas in the Kodiak study area.

	Second subarea			
First subarea	East	North	South	West
East		23 (15%)	39 (26%)	12 (8%)
North	13 (9%)		1 (1%)	3 (2%)
South	48 (32%)	0		3 (2%)
West	4 (3%)	6 (4%)	0	

Note: The column represents the subarea in which the animal was first sighted, whereas the rows represent the subareas of the subsequent sighting. An additional 11 animals were sighted in three areas; these animals are not represented here.

Table 5. Movement of humpback whales (*Megaptera novaeangliae*) between the Shumagin Islands and the Kodiak subareas.

	Kodiak subarea			
	East	North	South	West
From Shumagin Islands	11 (19%)	1 (2%)	11 (19%)	4 (7%)
To Shumagin Islands	14 (24%)	0 (0%)	14 (24%)	3 (5%)

the aggregation may be smaller. The Kodiak aggregation clearly had a higher number of total individual whales identified and the discovery curve showed a steeper and more linear trend. These results also suggest that the Kodiak aggregation is larger than that in the Shumagin Islands.

Despite both temporal and spatial differences in survey effort, rates of annual return and sighting intervals were comparable between the two regions, despite the larger survey area and longer season surveyed in Kodiak. This combination is confounding because protracted survey windows would allow for more resighting opportunities while the spatial breadth reduces animal density. In contrast, survey effort in the Shumagin Islands was concentrated around two major straits and within a narrow time window, which may confound opportunities for resights in the opposite way as in Kodiak. In other words, the narrow time frame reduced resighting opportunities, but the smaller area allowed for more efficient searching and higher animal densities. In addition, the animals in the Shumagin Islands were more often seen on multiple years and had a wider range in the number of years between successive sightings. These results suggest that even brief survey windows in logistically challenging regions can yield results that are comparable in accuracy and consistency to those obtained during more protracted seasonal survey efforts.

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