Individual gray whale use of coastal waters off northwest Washington during the feeding season 1984–2011: Implications for management

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ABSTRACT

Gray whales (*Eschrichtius robustus*) in northwest Washington were studied, with the aims to: (1) increase understanding of gray whale use of the study area; (2) document the annual and seasonal fluctuations in the numbers of whales utilising the area; and (3) assess the fidelity of whales to the study area within and between years. Together these goals establish a baseline of gray whale behaviour during summer and autumn in the region of the Makah Tribe's proposed whale hunt. From 1984 to 2011, a total of 225 unique gray whales were observed, with 49% being observed again in a future year. There was significant variability in observation rates of gray whales by month and year. During the feeding season, the observation rate increased to a peak in August in the north research segment in the Pacific Ocean and to a peak in October in research segments in the Strait of Juan de Fuca and in the southern research segment in the Pacific Ocean. Gray whales were most commonly observed at depths of 5–15m over rocky substrates and often near kelp forests, although the locations where they fed were dynamic by both month and year. Some whales habitually returned to northwest Washington, however the average whale in the study area was observed in only 31.6% (SE = 1.6%) of the possible years in which they could have been observed. Gray whales in the study area had an average minimum tenure (residency time) of 24.8 days out of a possible 183 days of the feeding season. A discovery curve analysis did not reach an asymptote over the 27 years of this study showing that there is no population closure to the research area. Based on these findings, it can be concluded that even though northwest Washington is an important feeding area, most Pacific Coast Feeding Group (PCFG) gray whales do not have strong fidelity to this one region within the IWC defined PCFG range. The findings presented in this paper provide a baseline for evaluating the impact of Makah hunting activities on the behaviour of PCFG whales that utilise the Makah's traditional hunting area once hunting activities resume.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; FEEDING GROUND; MOVEMENTS; SITE FIDELITY; NORTHERN HEMISPHERE; SURVEY–VESSEL

INTRODUCTION

Most Eastern North Pacific (ENP) gray whales (*Eschrichtius robustus*) migrate from wintering grounds in Baja California, Mexico, to feeding grounds in the Bering, Chukchi and Beaufort seas. A small subset of the ENP gray whale population does not complete the migration to arctic feeding grounds and instead spends the summer and autumn at feeding grounds along the coast of the Pacific Ocean from California through Southeast Alaska (Calambokidis *et al.*, 2002). This group of whales has been referred to by many names since it was first studied in the 1970s and is currently recognised as the Pacific Coast Feeding Group (PCFG) by the International Whaling Commission (IWC, 2011) and the US Government (Carretta *et al.*, 2013). The IWC defines the PCFG as gray whales seen in more than one year in the months of June to November within the range of northern California to northern British Columbia (41°N–52°N), excluding gray whale sightings in Puget Sound, Washington (IWC, 2012). The range is restricted to 52°N even though PCFG whales are known to frequently occur as far north as Kodiak Island, Alaska (Gosho *et al.*, 2011) and have been observed in the Beaufort Sea (Calambokidis *et al.*, 2014). The IWC-defined range of the PCFG is narrower than previous definitions of this group. This is primarily because most photo-identification surveys have been focused on 41–52°N. Population estimates are therefore more reliable for this range. There are few historic or projected future catches of gray whales north of 52°N and south of the Bering Sea, making the more narrowly defined range more applicable to management (IWC, 2012). The abundance estimate for the PCFG in 2012 was 209 whales (Calambokidis *et al.*, 2014).

Recent genetic studies have found small but statistically significant differences in frequencies of mtDNA haplotypes between samples collected from PCFG whales and other ENP whales in other portions of their range (Frasier *et al.*, 2011; Lang *et al.*, 2014). No statistically significant differences have been found in the frequencies of nuclear DNA (D'Intino *et al.*, 2013; Lang *et al.*, 2014). Despite the significant difference in mtDNA haplotype frequency, PCFG and ENP whales had similar haplotype diversity which suggests that immigration into the PCFG could be occurring (Lang *et al.*, 2014). The results of a genetics simulations study (Lang *et al.*, 2012) and photo-identification work (Calambokidis *et al.*, 2014) were consistent with immigration from other portions of the ENP range into the PCFG having a significant role in the

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population dynamics of the group. Given that there is evidence both for the PCFG having open population dynamics and evidence for matrilineal recruitment, there is currently debate on whether or not the PCFG is a stock. NOAA Fisheries used a panel of experts to evaluate whether the PCFG is a stock; the panel could not agree whether the PCFG is a stock for US domestic purposes but did agree that more research is needed (Weller *et al.*, 2013).

Interest in PCFG whales has been inspired by concern regarding the possible impacts on the PCFG of the Makah Tribe resuming their treaty protected right to hunt whales. In 1855, the Makah Tribe protected its whaling rights in the Treaty of Neah Bay. In the 1920s, the Tribe voluntarily suspended whale hunting due to the impacts of commercial whaling on gray and humpback whale populations (Renker, 2012; Thompson, 2006). In 1994, when the gray whale was removed from the US Endangered Species List, the Makah Tribe informed the US Government of its intentions to resume traditional whale hunting. The US Government has obtained aboriginal whaling catch limits for the harvest of gray whales from the IWC to be used by the Makah Tribe since 1997. However, since that time the Makah Tribe has only landed one gray whale due to domestic court cases and regulatory processes suspending the hunt in 2000. The Tribe has submitted a proposed management plan to the US Government and the IWC for review. The management plan restricts the hunt to the migratory season in the Pacific Ocean portion of the Makah Usual and Accustomed (U&A) fishing grounds to minimise the risk that a hunt takes a PCFG whale. Nonetheless, it is recognised that the hunt may still take PCFG whales, so the management plan also has a provision to limit the number of PCFG whales landed through a conservative calculation based on the abundance of PCFG whales (IWC, 2013). The IWC evaluated the impact of Makah hunting on PCFG population dynamics and found that the Tribe's proposed management plan meets the conservation goals of the IWC of ensuring the PCFG will remain above 60% of its carrying capacity over a 100-year simulation (IWC, 2013).

Past studies have documented the behaviour of PCFG whales throughout their entire range (Calambokidis *et al.*, 2002; 2010; 2012; 2014). This paper reports on the behaviour of gray whales in the coastal waters of northwest Washington during the summer and autumn feeding season. Data were collected from 1984–2011 with the goals of: (1) increasing our understanding of gray whale use of the study area; (2) documenting the annual and seasonal fluctuations in the numbers of whales utilising the area; and (3) assessing the fidelity of whales observed within the study area within and between years. Together these three goals establish a baseline of gray whale behaviour in the region of the Makah Tribe's proposed whale hunt to evaluate (once the hunt is approved) whether the hunt impacts gray whale behaviour in the northwest Washington.

METHODS

Study area

Research effort was conducted along the northwest tip of Washington State, USA (Fig. 1). Northwest Washington is bounded by two bodies of water: the Strait of Juan de Fuca to the north and the Pacific Ocean to the west. The rocky shorelines are interspersed with sandy beaches, and rocky underwater habitats dominated by forests of bull kelp (*Nereocystis luetkeana*) and giant kelp (*Macrocystis spp.*) in waters 5–15m deep. The waters of northwest Washington have high biological productivity due to the confluence of currents from the California Current and the drainage of Puget Sound through the Strait of Juan de Fuca, and seasonal winds causing upwellings (Marchetti *et al.*, 2004). The study area encompasses most of the nearshore habitat of the Makah U&A and the entire area in which the Makah Tribe has proposed for hunting gray whales (Makah Tribal Council, 2011).

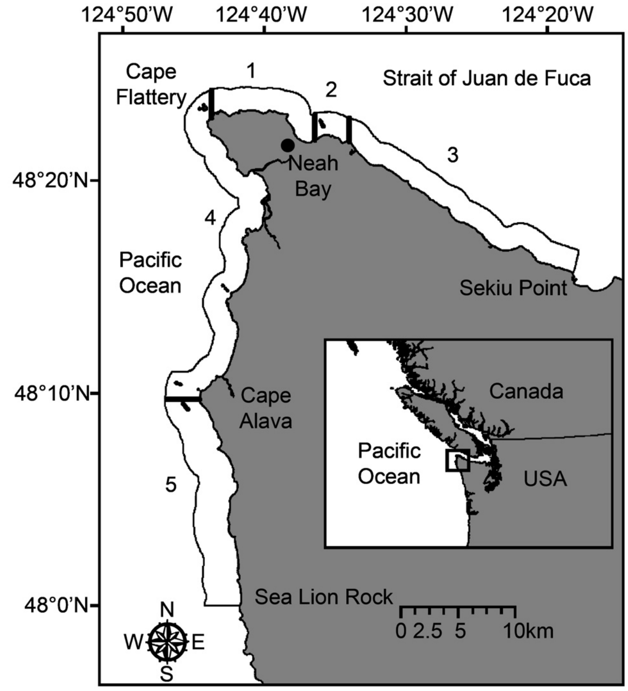

Fig. 1. Map of the gray whale survey region in northwest Washington with the focal survey area shown enclosed with a line. The numbered survey segments are: (1) West Strait; (2) Neah Bay Entrance; (3) East Strait; (4) North Ocean; and (5) South Ocean.

Survey methodology

The northwest Washington survey area is too large to be surveyed effectively in one day. One day of survey effort covered the area to the east of Neah Bay along the shores of the Strait of Juan de Fuca to Sekiu Point, approximately 25km from Neah Bay. The other survey day covered the area west along the shores of the Strait of Juan de Fuca to Cape Flattery and then south following the shoreline of the Pacific Ocean to Sea Lion Rock (47°59.58'N, 124°43.45'W). The total distance covered in the southbound leg is approximately 60km. Surveys for gray whales were generally conducted within 1–2km of shore because gray whales feeding in northwest Washington primarily congregate near shore. Portions of the survey in the Pacific Ocean, particularly south of Cape Alava, were conducted further from shore due to poorly charted submerged rocks.

Survey effort was variable by year. The early years of survey effort in northwest Washington were conducted opportunistically with three years of surveys in the 1980s (1984, 1986 and 1989) by Cascadia Research Collective

(CRC). Starting in 1992 surveys were conducted annually by the National Marine Mammal Laboratory (NMML) and CRC but effort was low and opportunistically conducted during studies of other marine mammal species. After 1996, surveys were standardised and were generally conducted on a bi-weekly basis from June through November as weather and ocean conditions allowed with NMML and the Makah Tribe as the primary research groups. The objective was to collect photo-identification of whales. Thus, if the researchers had good reason to suspect that survey effort in the Strait of Juan de Fuca would result in limited or no photographs of gray whales, then effort was focused on the Pacific Ocean and vice versa. The Pacific Ocean survey area was generally surveyed monthly regardless of anticipated opportunities to photograph gray whales because the surveys were also used for monthly California and Steller sea lion research. All research effort was conducted from small vessels of 6–9m in length.

During surveys, observers periodically recorded time and location and variables that could have influenced the probability of sighting a whale such as cloud cover and Beaufort sea state. When gray whales were sighted, their location, depth and activities were recorded. Observers then attempted to take photographs of the dorsal ridge along both flanks as well as the flukes. Photographs were taken using digital SLR cameras with a 70–300mm lens (35mm film cameras were used prior to 2004). The lens magnification allowed photo-documentation of unique colouration patterns on the lateral sides and flukes of the whales (Darling, 1984). The frame numbers from the photographs were recorded on the field data sheet with the sighting information.

Photo-identification methodology

All gray whale photographs of suitable quality were compared to a catalogue of gray whales previously seen in the PCFG as described in Calambokidis *et al.* (2012) by CRC. If a photographed whale was matched to a catalogued whale then the catalogue number of the whale was recorded. If a match could not be made, and the photograph was of sufficient quality, then the photographed whale was assigned a new catalogue number. All catalogue numbers of sighted gray whales were recorded in a database along with attributes of the sighting such as date, time, water depth, location and whale behaviour.

Data exploration

The three primary goals of this research were: (1) to increase understanding of gray whale use of the study area; (2) to document seasonal and annual fluctuations in the numbers of whales using the study area; and (3) to assess fidelity of whales to the study area. The analyses conducted could be interpreted as achieving one or more of these goals but for the purpose of explaining each method, and why it was conducted, each method is listed by research goal. For all analyses observations of uniquely identified whales were used instead of all gray whale observations to prevent pseudo-replication. Research effort and data collection was not consistent in all years (as described above) and as a result some analyses could not use all collected data whereas others could (Table 1).

To address the goal of increasing understanding of gray whale use of the study area four analyses were conducted. The first analysis was to characterise the depth range and habitat types where gray whales were observed. The second analysis was to document the occurrence of new whales in the study area. The purpose of this analysis was to determine the turnover of individuals in the study area. New whales were simply defined as whales not previously observed in the study area although they may have been observed within the PCFG in the past. For each year the number of new whales observed and the proportion of those that were observed to ‘recruit’ into the study area and be observed again in a subsequent year were determined. The third analysis documented how many calves were observed and calculated an estimate of proportion of newly observed whales that were calves (see Calf Analysis below). The last analysis determined if there is population closure to the study area. Calambokidis *et al.* (2010) concluded that gray whales who utilise northwest Washington have fidelity to a region at least as large as Oregon to Southern Vancouver Island. Despite the findings of Calambokidis *et al.* (2010), domestic processes for evaluating the impact of the proposed Makah whale hunt still question what the local area should be for analysis. To evaluate closure discovery curves were constructed both for all whales observed and for whales that were observed to have some fidelity to the area and were observed in more than one year.

Two analyses were used to document seasonal and annual fluctuations of whales in the study area. In the first analysis

Table 1

Years of data used and justification for each analysis.

Analysis	Years of data used	Justification
Depth	1984–2011	All depths recorded were used for the analysis.
Temporal and spatial distribution of sightings	1996–2011	Data prior to 1996 was not used for analysis because effort was opportunistic in nature and could not be quantified to research segment.
Mapping	2004–2011	We used 2004–11 only because during prior years whale locations were not recorded precisely leading to challenges in interpreting maps.
Fidelity to research area	1984–2011	All data was used.
Minimum tenure	1996–2011	Survey effort was standardised for 1996–2011 in all years but 2004 with effort throughout the summer and fall feeding season.
Occurrence of new whales	1996–2011	All years were used in the analysis. Some of the analysis focused on 1996–2011 to ensure that new whales were not whales that commonly use the study area but had not been ‘discovered’ yet.
Photo analysis of new whales	2004–2011	The analysis was performed at Makah Fisheries and only photographs after 2004 were available for analysis.
Population closure in study area	1984–2011	All data was used.

all sightings were divided into five research segments (Fig. 1). The five research segments were: (1) East Strait (Sekiu Point to Third Beach); (2) Neah Bay Entrance (Third Beach to Waadah Island); (3) West Strait (Waadah Island to Tatoosh Island); (4) North Ocean (Tatoosh Island to Cape Alava); and (5) South Ocean (Cape Alava to Sea Lion Rock). The number of sightings were divided by the number of surveys in the research segment and the length of the research segment in km to standardise the number whales observed per segment for comparison purposes, hereafter this standardised sighting rate will be referred to as 'observation rate'. Observation rates were compared by month and year within each research segment using ANOVA. The second analysis used was mapping and is described in more detail below. The purpose of these analyses was to provide a baseline of habitat use behaviour in the area.

To evaluate gray whale fidelity to the study area, two analyses on different temporal scales were used. Fidelity was evaluated on an annual basis by analysing sighting histories of individual whales to determine the proportion of individuals that were observed in a subsequent year after being first observed. The average percent of years whales were observed in the study area was determined by dividing the number of years each whale was seen in the study area by the number of possible years it could have been observed in the study area. Fidelity was also evaluated within each feeding season by calculating the average 'minimum residency time' for each identified individual by year. For this analysis, minimum residency time was defined as the number of days between the first and last day a whale was seen during the June through November survey time period. The residency time estimate is a minimum because it was possible that a whale was present before the first day (or after the last day) it was sighted during a given year. This estimate may also overestimate residency time because whales could have left the survey area for some unknown length of time between the first and last sighting of the year. Minimum residency time calculations are sensitive to the number of days of survey effort within a year and the temporal distribution of surveys within the survey season. Calambokidis *et al.* (2014) noted that whales observed in the PCFG range during the summer can generally be described as 'transient' whales who are only observed in one year and then not observed in the future and 'PCFG whales' who show some level of fidelity to the IWC defined PCFG range. Fidelity analyses were conducted both for all whales including transients and for whales that have been seen in more than one year. This analysis was conducted to determine a baseline of gray whale fidelity to the area where hunts were planned.

Mapping

To analyse trends in monthly and annual gray whale use of northwest Washington coastal water, the number of photo-identifications made during a whale survey were mapped onto a grid of 1km^2 cells that were aggregated into one of five regions: (1) East Strait; (2) Neah Bay Entrance; (3) West Strait; (4) North Ocean; and (5) South Ocean. Each of these regions extended 2km offshore except the South Ocean which extended 3km, and according to the survey protocol, any survey effort in one of these regions was counted as a full day of effort.

To develop spatial statistics for the survey effort, latitude/longitude coordinates from whale sightings were spatially joined to the 1km^2 grid in ArcGIS 10.1 and exported to MS Excel where total whale counts per 1km^2 grid cell were divided by the survey effort from the same monthly or yearly period to determine sighting density of whales corrected for effort. The sighting densities for each grid cell were re-imported to ArcGIS and plotted as estimates of areal use by gray whales. The grid cells with whale sighting density less than 0.1 were ranked as 'Rare'; cells with sighting density greater than 0.1 but less than 0.3 were ranked as 'Seldom'; cells with sighting densities greater than 0.3 but less than 0.6 were 'Common'; and cells with sighting density greater than 0.6 were ranked as 'Very Common'. This coding was standardised for monthly and annual maps.

The objective of mapping was to document what areas within the larger study area were most important to gray whales and to document how use of those sites changed by month and year.

Calf analysis

During the surveys a whale was recorded as a calf if it was in close association with a much larger individual and appeared to be less than 8m in length. It is possible that calves weaned prior to when they were first observed in the study area as cow-calf pairs in the PCFG have been observed separated as early as the beginning of July (Calambokidis *et al.*, 2012). To make an estimate of what proportion of new whales observed in the study area are calves, photographs were analysed following methods developed by Bradford *et al*. (2011). The analysis was limited to new whales in the study area that were also seen in the PCFG for the first time in that year. Only whales with suitable photo-quality of the

Table 2

Number of gray whale dedicated surveys tallied by year for each segment of research area and total opportunistic surveys by year.

	East Strait	West Strait	North Ocean	South Ocean	Neah Bay entrance	Opportunistic surveys
1984	–	–	–	–	–	3
1986	–	–	–	–	–	10
1989	–	–	–	–	–	2
1992	–	–	–	–	–	2
1993	–	–	–	–	–	5
1994	–	–	–	–	–	7
1995	–	–	–	–	–	5
1996	13	32	23	7	40	5
1997*	22	54	38	14	63	6
1998	28	37	29	13	55	4
1999	14	23	17	15	30	1
2000	13	19	13	8	26	4
2001	12	15	15	10	28	1
2002	10	12	8	6	21	0
2003	15	19	15	8	27	0
2004	4	2	1	1	6	0
2005	11	17	14	6	21	1
2006	15	22	15	9	30	0
2007	13	19	11	8	27	1
2008	25	19	10	5	35	3
2009	23	22	12	7	32	0
2010	18	28	22	14	40	0
2011	11	29	24	18	35	1
Total	**247**	**369**	**267**	**149**	**516**	**81**

*20 surveys were conducted during effort to monitor the Makah setnet fishery. All of these surveys transited the West Strait and into the Northern Ocean research segment.

head and postcranial region were used for the analysis. Whales with evidence of only recently attached barnacles, no old barnacle scars, and white pigmentation mottling the postcranial region were recorded as calves (Bradford *et al.*, 2011). The goal of this analysis was to determine how important northwest Washington was as a site for cow-calf pairs and for recently weaned calves.

RESULTS

Effort to photographically identify gray whales in northwest Washington was conducted between 1984 and 2011. From 1996–2011, surveys were conducted on a more dedicated and rigorous basis resulting in 516 surveys in the research area. Survey effort was greatest from 1996–1998 and 2008–11 (Table 2). By month, effort during dedicated surveys was greatest in the late summer and early autumn (Table 3). The majority of field effort during the autumn was conducted within the Strait of Juan de Fuca due to weather conditions in the Pacific Ocean and the distribution of gray whales. Research effort resulted in the collection of photographs from 225 gray whales that could be identified as unique individuals during the months of June through November from 1984 through 2011.

Gray whales were most often observed in water 5–15m deep, often associated with either kelp forests or emergent offshore rocks (Fig. 2). Sightings of gray whales in waters greater than 20m or less than 5m were rare and were not associated with any obvious habitat type (Fig. 2).

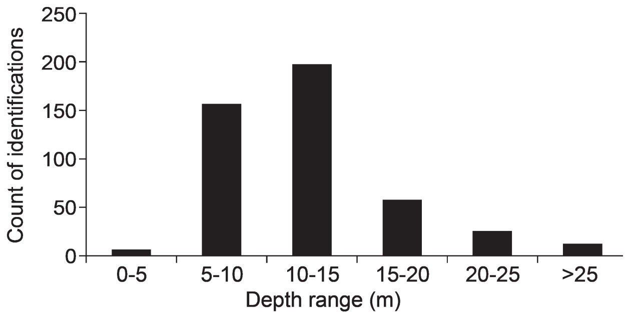

Fig. 2. Histogram of the count of gray whale identifications by depth binned in 5m increments.

Table 3

Number of surveys tallied by month for each segment of research area during gray whale dedicated survey effort from 1996 through 2011.

	East Strait	West Strait	North Ocean	South Ocean	Neah Bay entrance
Jun.	29	50	40	26	64
Jul.	43	78	59	34	99
Aug.	40	98	69	31	120
Sep.	56	79	57	31	114
Oct.	51	41	27	19	78
Nov.	28	23	15	8	41
Total	**247**	**369**	**267**	**149**	**516**

Temporal and spatial distributions of sightings

Gray whale distribution in the Strait of Juan de Fuca (hereafter Strait) varied widely by month and year. Gray whale use of feeding sites in the West Strait and East Strait

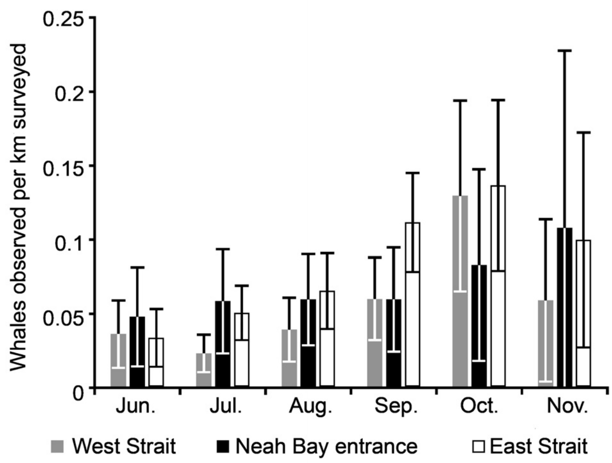

Fig. 3. Average observation rates in the three research segments in the Strait of Juan de Fuca by month for the years 1996 to 2011. Error bars are two times the SE.

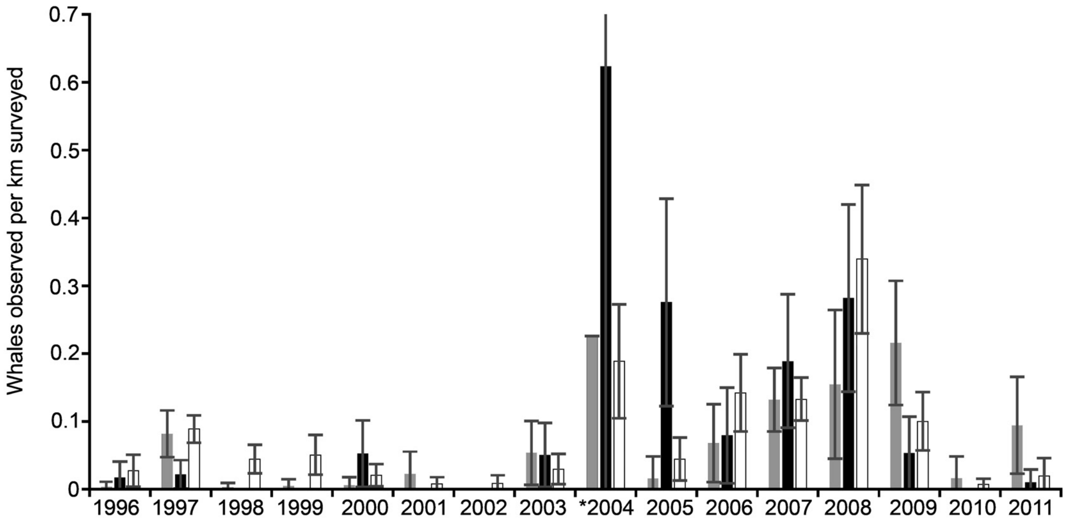

Fig. 4. Average observation rates in the three research segments of the Strait of Juan de Fuca by year with months of the feeding season, June to November, pooled. Error bars are 2 times standard error. * 2004 had much lower effort than other years of the study.

research segments increased through the summer and early autumn until use peaked in October (Fig. 3). The average observation rate varied significantly between months in both the West Strait (ANOVA, df = 368, $p < 0.001$) and the East Strait (ANOVA, df = 246, $p = 0.004$) as the observation rate increased from June to a peak in October. At the entrance to Neah Bay, no significant differences in observation rate by month were detected (ANOVA, df = 515, p = 0.73).

Significant differences in observation rate by year were observed in the Strait of Juan de Fuca in all three research segments (ANOVA: West Strait, df = 325, $p < 0.001$; Neah Bay, df = 514, $p < 0.001$; East Strait, df = 249, $p < 0.001$) (Fig. 4). From 1996 to 2003 (particularly 2000–03) and from 2010 through 2011, there were low observation rates in all three of the research segments (Fig. 4). In contrast, the time period 2004–09 had higher observation rates (Fig. 4).

Gray whale distribution in the Pacific Ocean (hereafter Ocean) also varied by month and year. Within the North Ocean survey area (Cape Flattery to Cape Alava), the observation rate varied significantly by month (ANOVA, df = 266, $p = 0.001$), peaking in August and with lows in June and November (Fig. 5). In the South Ocean research segment (Cape Alava to Sea Lion Rock), there were no significant differences in observation rate by month (ANOVA, df = 148, $p = 0.34$).

Similar to the Strait, significant year to year variability in observation rate was observed in both ocean survey segments (ANOVA: North Ocean, df = 266, $p < 0.001$; South Ocean, df = 148, $p < 0.001$) (Fig. 6). Years of high and low observation rates were not the same years as observed for the Strait (Fig. 4, Fig. 6). Like the Strait survey areas, the Ocean research segments had low observation rates during the early years of the time series from 1996 to 2001. Opposite the Strait, the observation rate increased in 2001

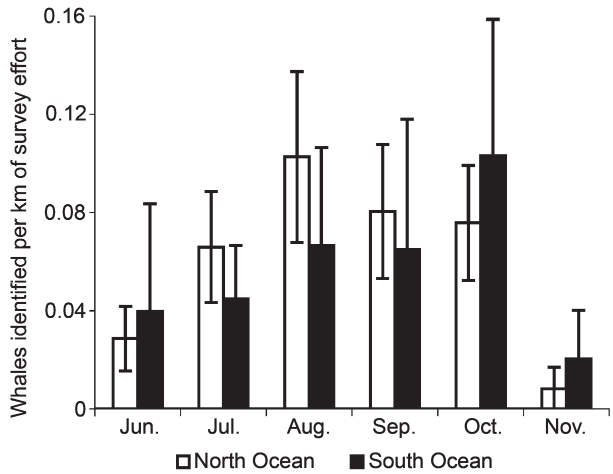

Fig. 5. Average observation rates in the two research segments of the Pacific Ocean by month for the years 1996 to 2011, error bars are two times standard error.

through 2003 and was also high in 2010 and 2011. The years with greatest observation rates were 2005–11. The South Ocean showed more year to year variability than the North Ocean.

Maps were made using the average number of whales identified per km^2 of research area to examine finer scale trends in gray whale distributions in northwest Washington by month and year. Trends observed in whale densities by month reaffirm our findings that the number of gray whales identified per survey increased to greatest densities and greatest spatial coverage in September and October in the Strait and in August and September in the North Ocean (Fig. 7). Some sites were consistently used both in the Strait and in the Ocean each month; whale densities at these sites increased through the summer and into autumn in the Strait

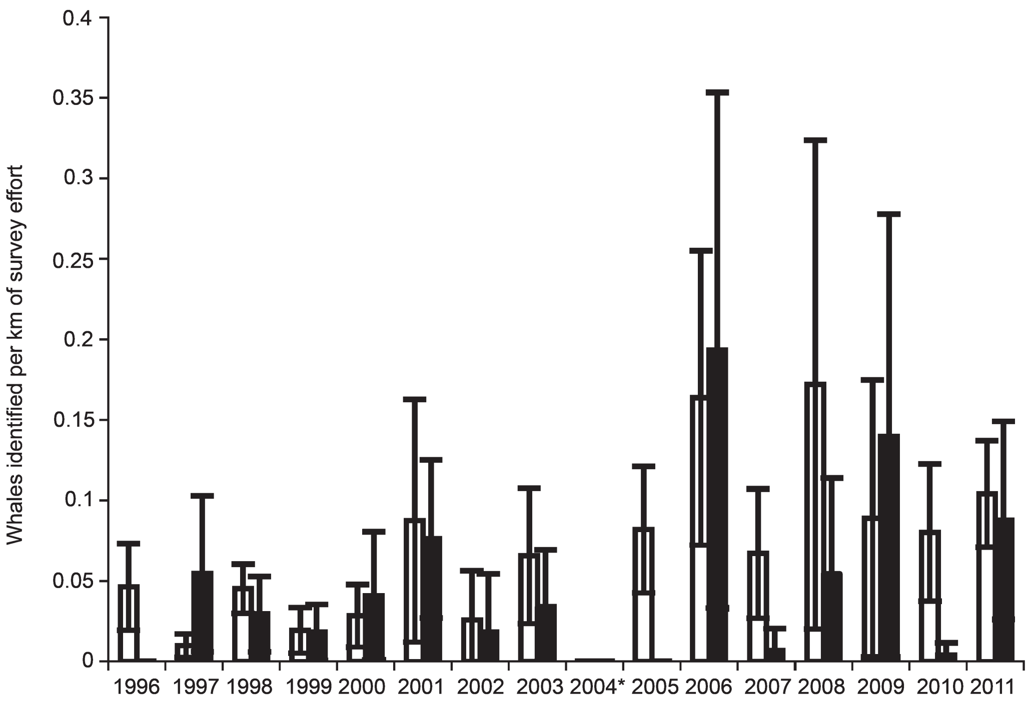

Fig. 6. Average observation rates in the two research segments of the Pacific Ocean by year for the months of the feeding season, June to November. Error bars are two times standard error. *No surveys were conducted in the ocean in 2004.

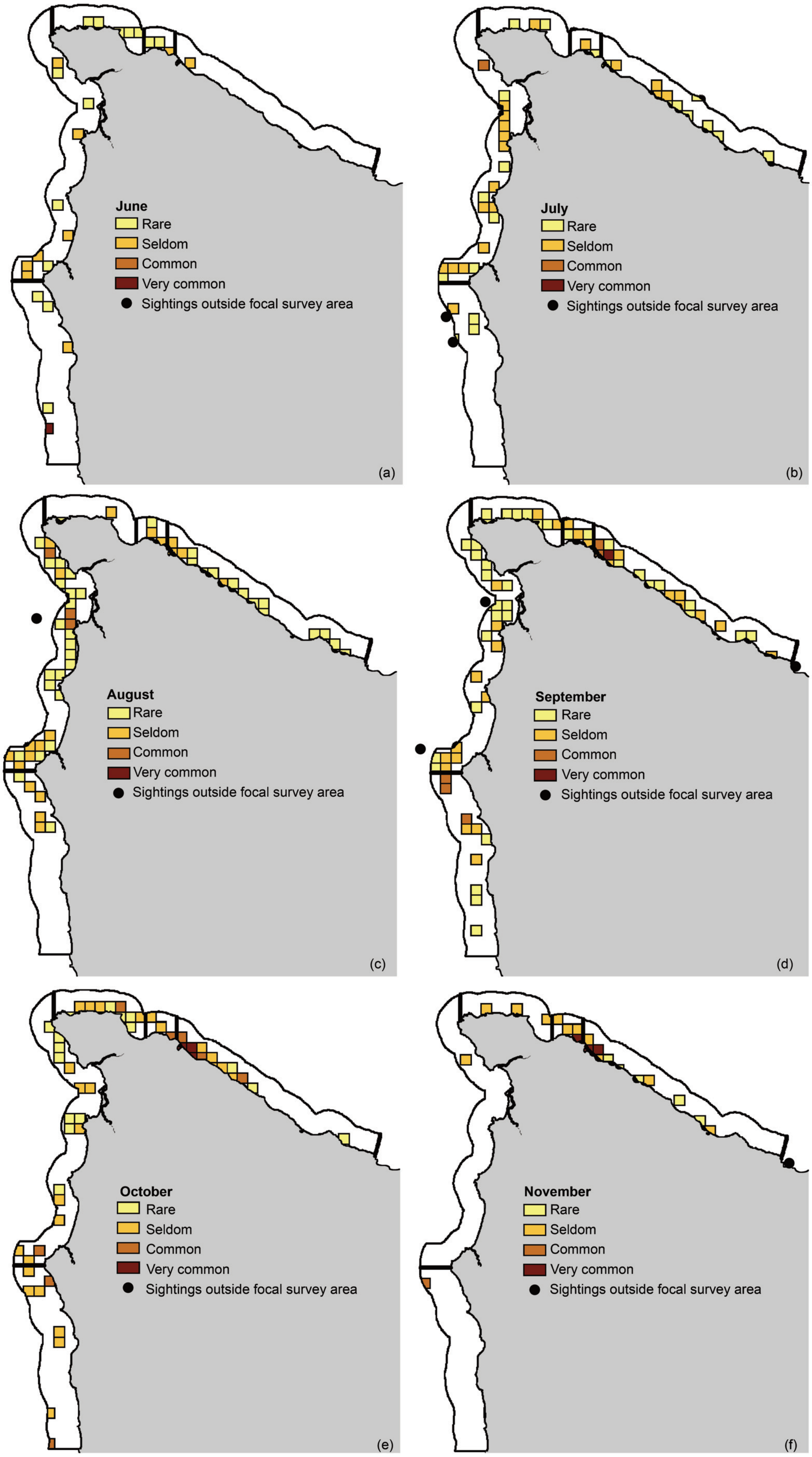

Fig. 7. Sighting density of gray whales identified per km^2 in northwest Washington per day of research effort in 2004 to 2011 by month: (a) June; (b) July; (c) August; (d) September; (e) October; and (f) November. Grid cells with sighting densities of less than 0.1 whales were ranked as 'Rare', cells with sighting density greater than 0.1 and less than 0.3 whales were ranked as 'Seldom', cells with sighting densities greater than 0.3 and less than 0.6 whales were ranked as "Common" and cells with sighting densities greater than 0.6 whales were ranked as 'Very Common'.

and increased until late summer/early autumn in the Ocean (Fig. 7). A review of nautical charts and knowledge of the area show that sites with high use were generally characterised by rocky bottoms and large kelp forests, whereas sites with low use were characterised by sandy bottoms. The maps do show sightings of whales in areas of sandy bottoms, however these sightings were primarily of whales that were presumed to be travelling or resting. The greater distance from shore of gray whale distributions in the ocean as compared to the Strait was likely due to the gradual slope of the bottom in the ocean as compared to the steep drop off in the Strait.

Maps of the yearly distribution of whales display greater variability in gray whale site use, where whales appeared to use some areas frequently for a number of years and then subsequently either abandon those areas or use them intermittently (Fig. 8). This phenomenon can be observed by examining the area just east of the Neah Bay research segment. From 2006 to 2009, high densities of whales were observed in this area and then were not observed using the site at all in 2010 and only rarely in 2011. Other areas appeared to be used intensively for one year and then not used again. This can be seen most easily by looking at the southern border of the South Ocean research segment and noting the changes in gray whale sighting density through the years.

Fidelity to the research area

Fidelity to the research area was examined by comparing the number of individual whales that returned to the northwest Washington research area after the first year observed and estimating how long individual whales used the research area within a given year. Some gray whales were observed to use the waters of northwest Washington consistently after they were first observed. Sixteen percent of whales were observed in six or more years in the study area, although not necessarily in consecutive years. Roughly half (51%) of the whales identified in this study were only observed in the area during one year (Fig. 9). The average whale was observed in 2.48 years (SE = 0.14). Removing the individuals that were only observed in one year, the average whale was seen in 4.01 years (SE = 0.20). Whales first observed in 2010 or earlier were observed in an average of 31.6% (SE = 1.6%) of possible years after they were first observed (number of years observed divided by total number of possible years to be observed for each whale); removing whales only seen in one year increased the average percentage to 38.7% (SE = 1.9%) of possible years. Among the whales that were first identified prior to 2010 and therefore have more than one year in which they could have been resighted, only two whales were seen in all possible years after the first observation; these whales were seen in every year after being first observed in 2004 and 2006, respectively.

The length of time a whale used the study area during the feeding season was estimated by calculating minimum tenure, in this case the minimum number of days an individual whale resided in the research area assumed to be equal to the difference in time between the date of first and last observation. The average minimum tenure calculated for whales observed in the northwest Washington research area

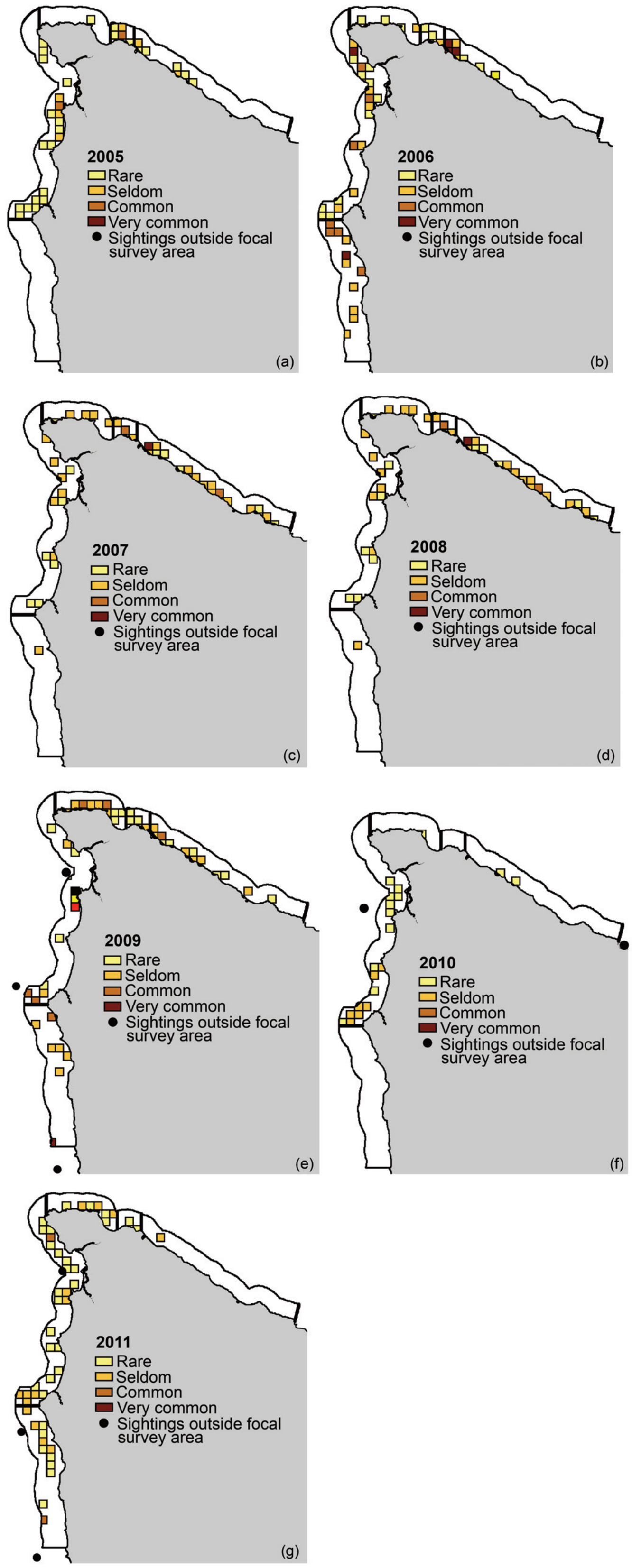

Fig. 8. Sighting density of gray whales identified per km^2 in northwest Washington per day of research effort in the feeding season, June through November by year: (a) 2005; (b) 2006; (c) 2007; (d) 2008; (e) 2009; (f) 2010; and (g) 2011. Grid cells with densities of less than 0.1 whales were ranked as 'Rare', cells with sighting density greater than 0.1 and less than 0.3 whales were ranked as 'Seldom', cells with sighting densities greater than 0.3 and less than 0.6 whales were ranked as 'Common' and cells with sighting densities greater than 0.6 whales were ranked as 'Very Common'. No map was provided for 2004 because data collection lacked spatial and temporal resolution.

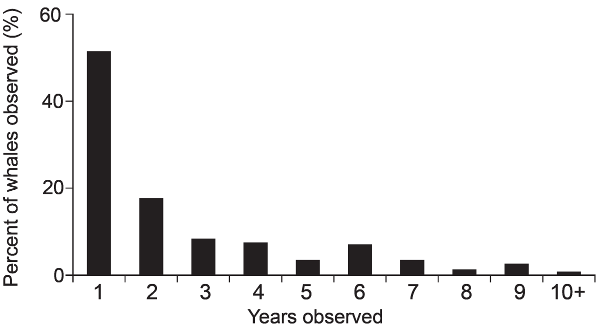

Fig. 9. Count of unique whales observed by the number of years a whale was observed.

was 24.8 days (range 1 to 151 days) out of a possible 183 days in the June to November feeding season. A large degree of variability in minimum tenure by year was observed in the research area (ANOVA, df = 493, $p < 0.01$) (Fig. 10).

No evidence was found that the number of years a whale has been observed in northwest Washington affected average minimum tenure during the study (ANOVA, df = 202, $p = 0.62$) (Fig. 11). However, it was found that average minimum tenure was a good predictor of whether a whale would be seen in the following year. Whales seen in year *Y* and in the following year (*Y*+1) had an average minimum tenure of 28.3 days, which was significantly greater than whales seen in year *Y* but not year *Y*+1 (19 days; Two-sample *t*-test, df = 506, $p = 0.002$).

Occurrence of new whales

From 1996 through to 2011, an average of 10.8 new whales were observed per year (SE = 1.8) in the northwest Washington study area. From 1996 through 2010 (excluding 2011 to allow a year for recruitment), an average of 5.6

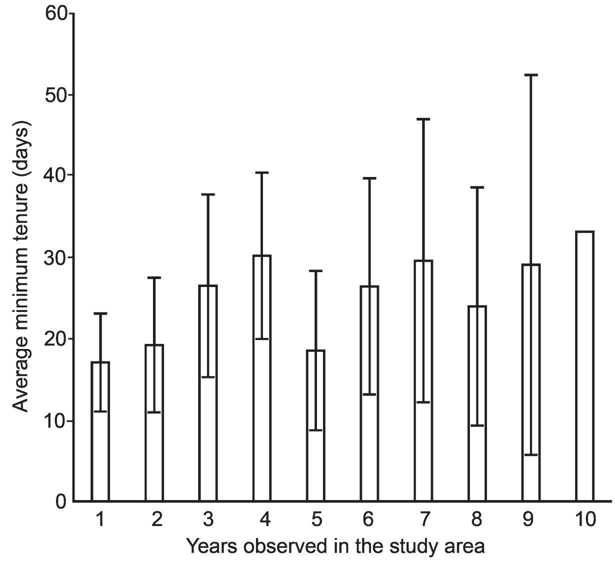

Fig. 11. Average minimum tenure of whales in days compared to the number of years they have been observed in northwest Washington.

new whales per year (SE = 1.1) were observed again in a future year. The number of new whales observed was not consistent between years. High numbers of new whales (> 15) were observed in 1993, 1995, 1998, 2001, 2006 and 2008 (Table 4). It is possible that the high numbers of new whales observed in 1993 and 1995 were not actually new whales to the research area; rather it is likely that some of these whales regularly used the area but had not been seen previously due to low research effort in the early years of the study. In a time series of population estimates, Calambokidis *et al.* (2014) found a large increase in PCFG gray whale abundance in the late 1990s and early 2000s that they postulated was caused, at least in part, by immigration from

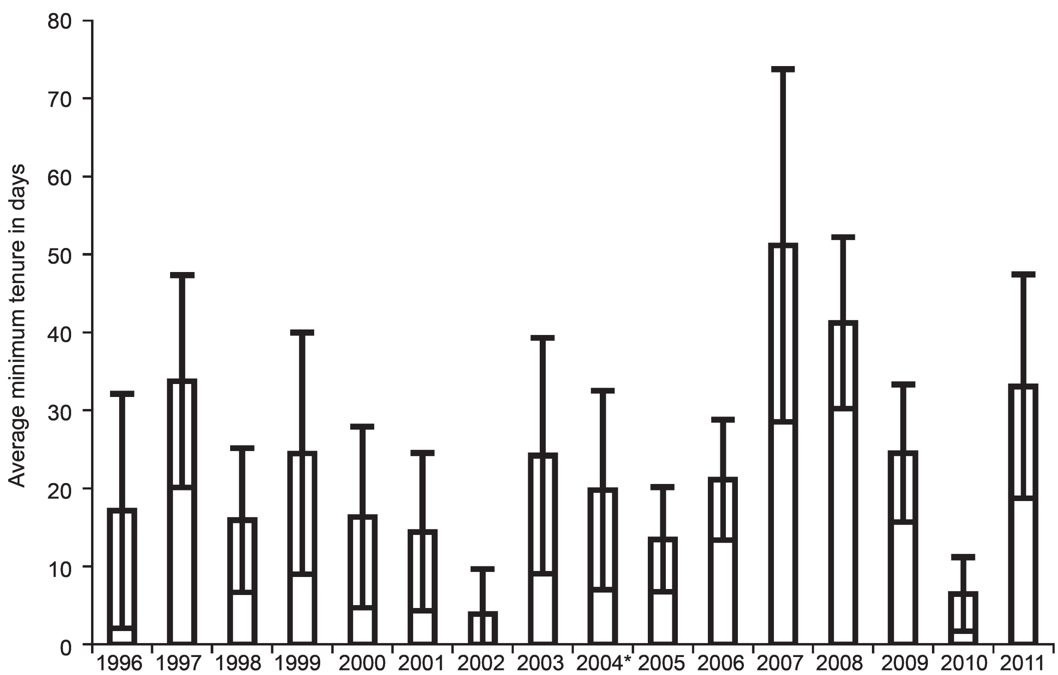

Fig. 10. Average minimum tenure (residency time) computed as the number of days between the first and last sighting of an individual in a given year. *2004 had lower total survey effort and lower temporal coverage of survey effort than other years, and the estimate of minimum tenure is likely underestimated.

Table 4

This table shows the sighting history of whales by the first year they were observed (row). Column totals report the number of uniquely identified whales from each cohort in each feeding season. The first value in each row is the number of new whales observed for that year.

Year	1984	1986	1989	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
1984	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
1989			4	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
1992				2	0	1	1	2	2	0	1	0	0	0	0	1	1	1	0	0	0	0	1
1993					21	4	4	4	4	10	4	1	3	1	3	1	4	4	2	6	5	1	2
1994						5	2	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1	0
1995							15	5	7	2	1	0	2	0	0	0	3	2	2	3	1	0	0
1996								8	4	3	2	1	1	0	1	1	1	4	0	3	4	1	2
1997									8	1	1	0	1	0	1	1	2	1	1	1	1	0	0
1998										17	1	1	1	0	0	0	0	2	1	2	0	1	0
1999											1	0	0	0	0	0	0	0	0	0	0	0	0
2000												11	6	3	2	0	2	5	1	5	3	4	3
2001													16	2	2	1	0	1	0	1	1	0	0
2002														1	1	1	1	1	0	1	1	1	1
2003															11	3	2	3	0	1	1	2	1
2004																12	7	7	3	7	5	3	5
2005																	10	4	2	3	2	1	1
2006																		20	5	10	7	4	6
2007																			2	1	2	0	1
2008																				29	11	3	3
2009																					11	1	1
2010																						4	1
2011																							11
Total	**2**	**4**	**4**	**2**	**21**	**10**	**22**	**19**	**27**	**35**	**11**	**14**	**32**	**8**	**22**	**21**	**33**	**56**	**20**	**74**	**56**	**27**	**39**

northern feeding grounds during the 1999/2000 mortality event (Gulland *et al.*, 2005). Based on the findings of Calambokidis *et al.* (2014) a large increase in the number of new whales observed and of new whales observed in a future year during the time period of 1998–2002 was to be expected. Instead, the average number of new whales observed from 1998–2002 was lower than the 1996–2010 average, with 9.2 new whales (SE = 4.3) of which 4.3 whales (SE = 1.5) were seen in a future year. The percentage on average of new whales observed from 1998–2002 that were seen in a future year (44.3%, SE = 18.4%) was also lower than the 1996–2010 average.

Calf analysis

There were seven mother-calf pairs observed during surveys (Table 5), showing that some of the new whales observed in this study were internally recruited. One mother, CRC 67, was observed with three calves: a suspected calf (CRC 169) in 1995 and a confirmed calf in both 2004 (CRC 819) and 2011 (CRC 1350). Four other females were each observed with one calf (Table 5).

Some new whales were first observed later in the year (i.e. autumn) than when calves become independent of their mothers (Bradford *et al.*, 2011; Calambokidis *et al.*, 2012). To determine the proportion of new whales which are actually calves digital photographs taken between 2004 and 2011 were analysed. Only new whales for which photographs had already been obtained from the first year they were seen in the entire PCFG (i.e. not just the first year seen in northwest Washington) were analysed. Twenty one photographs of new whales for which the first year they were sighted in northwest Washington was also the first year they were sighted in the PCFG were available. Of those, 18 photographs showed the head and post-cranial region clearly in order to be able assess if they were calves. Of the 18 whales evaluated, 4 (22%) were either confirmed calves (CRC 819 and CRC 1350) or were most likely calves (CRC 1047 and CRC 1054) and the other 14, based primarily on observation of old barnacle scars, were not calves of that year. CRC 1047 and CRC 1054 were both first observed in 2008.

The occurrence of calves in northwest Washington shows that the site is used by cow-calf pairs and recently weaned calves. The number of calves observed during the study were low suggesting that the site is not a very important for cow-calf pairs for the PCFG as a whole although it does appear important for CRC 67.

Table 5

All known mother-calf pairs observed in northwest Washington from 1984–2011 with whales only suspected to be calves noted with an asterisk.

Mother	Calf	Dates observed together
105	104	09/07/94
43	107	09/07/94 to 04/08/94
67	169*	19/07/95 to 23/07/95
596	595	26/06/01
216	860*	26/07/03 to 28/07/03
67	819	27/08/04
67	1350	23/06/11 to 01/09/11

Population closure in the study area

If population closure exists within the study area (no immigration or emigration), one would expect that over the 17 years of research effort that all of the whales in the 'population' would have been photographed and identified and the best fit line would approach a horizontal asymptote. To test if there is closure a discovery curve was plotted with the number of new whales observed for 1984 through 2011 and the number of whales observed in more than one year for 1984 through 2010 (Fig. 12). The function best fitting the discovery curve was linear for all new whales ($y = 9.15x$–

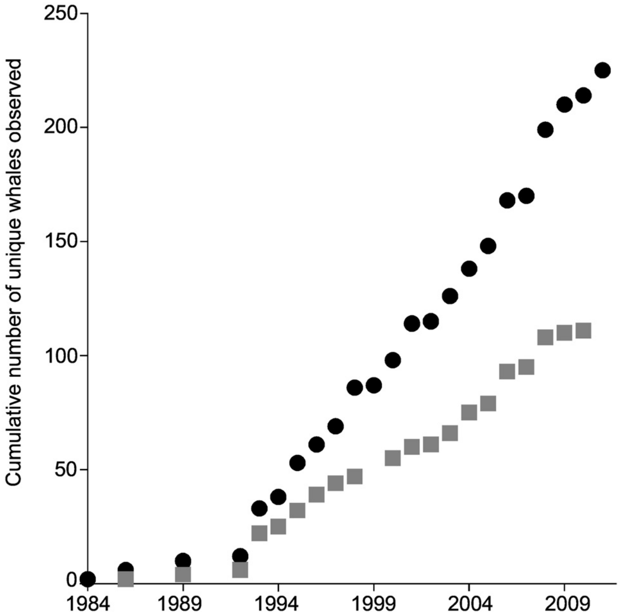

Fig. 12. Plot of the cumulative number of whales observed during the duration of this project for all whales (black dots) and whales observed in greater than one year (grey squares).

18,193, $r^2 = 0.95$) and whales observed in more than one year ($y = 5.07x–10,076$, $r^2 = 0.97$), suggesting that closure is not occurring for the northwest Washington survey area.

DISCUSSION

Temporal and spatial distribution of whales

There was large annual variability in the numbers of whales identified per survey in all research segments and large amounts of inter-year and intra-year variability in where whales were observed. Observation of variability is similar to Darling *et al.* (1998) who concluded that year-to-year variability in timing, prey type and feeding location is the key feature of gray whale observations from the central coast of Vancouver Island. Gray whale researchers of the PCFG have noted that the whales are commonly observed to exhibit benthic feeding behaviours (Avery and Hawkinson, 1992; Darling *et al.*, 1998; Dunham and Duffas, 2001; Kvitek and Oliver, 1986; Oliver *et al.*, 1984). However, in the present study mud plumes were rarely observed, suggesting that benthic feeding is uncommon in the northwest Washington area. Within the dynamic nature of site use it was found that more whales were observed per day of survey effort in the autumn in both the Strait of Juan de Fuca and the South Ocean research segment, whereas in the North Ocean research segment peak use was late summer. Also, the vast majority of gray whales were observed in waters between 5 and 15m of depth. This depth range coincides with the primary depth range of the mysid shrimp (small epibenthic and planktonic crustaceans of the family *mysidae*, suborder *pericarida*) (Nelson *et al.*, 2009). The primary mysid species consumed by gray whales off Vancouver Island were *Holmesimysis sculpta, Acanthomysis pseudomaropsis* and *A. anassa californiensis* (Murrison *et al.*, 1984; Darling *et al.*, 1998; Dunham and Duffus, 2002; Feyrer and Duffas, 2011) and they are also likely to be the primary prey species in northwest Washington. Feyrer and Duffus (2011) found that average mysid density was significantly correlated with the average number of whales in the survey area near Vancouver Island. We hypothesise that shifting mysid density and fluctuations in abundance caused the observed variability in gray whale counts in northwest Washington since most of the gray whale sightings occurred in optimal mysid habitat. Systematically monitoring prey at sites commonly used in northwest Washington would allow testing of this hypotheses on prey preference and specifically the influence of mysid abundance on whale distributions.

A consistent pattern observed through the years was lower observation rates in June compared to later in summer and autumn. This fits with the movements of migrating gray whales which generally reach Arctic feeding grounds from May to June (Swartz *et al.*, 2006). To date, there have been three publications on the movements of six satellite tagged PCFG whales, each of which had active tags between April and June; of these six whales, four were observed to migrate steadily north into southeast Alaska before their transmitters stopped transmitting (Calambokidis *et al.*, 2014; Ford *et al.*, 2013; Mate *et al.*, 2010). Given that 66% (4 out of 6) of the PCFG whales with documented spring movement patterns travelled north of the PCFG area, it is quite possible that other whales that feed in the PCFG also feed further north in the spring and early summer before returning south to the PCFG area later in the summer and autumn. It should be noted that the migratory behaviour of four of the six individuals may not be representative of all PCFG whales, as the three tags applied by Ford *et al.* (2013) targeted whales presumed to be migrating past Vancouver Island and one tag applied to a PCFG whale by Calambokidis *et al.* (2014) targeted a feeding whale.

Occurrence of new whales in northwest Washington

From 1996 to 2011, an average of 10.8 new whales were observed each year, of which 5.6 were observed in a future year. Many of the whales that were new to the northwest Washington study area had been seen previously in another research area of the PCFG. For whales that were photographed in northwest Washington during the first year they were seen in the PCFG, analysis of photographs using techniques described by Bradford *et al.* (2011) found that 22% of the whales were calves. Thus 78% of the new whales observed in our research area and to the PCFG were either born in a previous year in the PCFG and were not observed, or were non-calves who emigrated from another feeding area into the PCFG.

An analysis of the time series of population estimates of PCFG whales shows a large increase in the number of whales in the PCFG from 1998 through 2002 concurrent with the timing of the 1999 gray whale mortality event (Calambokidis *et al.*, 2014). Somewhat surprisingly, a smaller average of new whales (9.2) was observed from 1998 to 2002. The lower number of new whales observed in that time period could have been a result of poorer feeding conditions in Washington compared to later years in the data series. Of the new whales observed during those five years, a smaller portion was observed again in a subsequent year (44.3%) than the average for the whole data series. Based on the calculated population increase of the overall PCFG, we would have expected the average proportion of new whales and new whales seen in more than one year to be much greater from 1998 to 2002 than was observed in this study.

CONCLUSION

Northwest Washington is a small but important region within the summer and autumn feeding range of PCFG gray whales. Individual gray whale use of this region is variable, with some individuals observed regularly whereas most do not show strong site fidelity to this region. This study allowed examination of trends in site use over multiple decades within northwest Washington and it was found that rocky habitat in the 5–15m depth range is very important to gray whales and that gray whale use of these habitats is dynamic by year. The impacts of the Makah gray whale hunt are a debated issue, thus it is hoped that the baseline of gray whale behaviour provided here can be used to help evaluate if there are discernible effects on PCFG whale behaviour in the proposed hunt area when hunting resumes.

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