Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998

JOHN CALAMBOKIDIS[*], JAMES D. DARLING[+], VOLKER DEECKE[#], PATRICK GEARIN[++], MERRILL GOSHO[++], WILLIAM MEGILL[**], CHRISTINA M. TOMBACH[##], DAWN GOLEY[°], CAITLYN TOROPOVA[¥] AND BRIAN GISBORNE[×]

E-mail: Calambokidis@cascadiaresearch.org

ABSTRACT

This study documents the range, abundance and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) in the Pacific northwest. Identification photographs were collected by eight collaborating organisations between March and November 1998. Surveys extended between northern California and southeastern Alaska. Effort was variable by region and was concentrated off the northern Washington coast and Vancouver Island. Of 1,242 occasions when suitable photographs of gray whales were obtained in 1998, 155 unique whales were identified. Each individual was photographed an average of 8.0 times (SD = 8.4, range 1-42) and the average tenure of whales seen multiple times was 56 days (SD = 41, range 1-170). Whales seen longer than three months generally were seen in multiple regions. Movements among regions in 1998 were documented for 57 whales with the most frequent interchange among three adjacent areas from northern Washington to central Vancouver Island. The overall pattern of movements among regions was complex; whales were not always moving in the same direction at the same time of year. Movements within 1998 among more distant locations did occur but were less frequently observed. Total distances between resighting positions for individual whales ranged from < 1 to 526 n.miles. Most whales photographed in 1998 had been identified in previous years when compared to photographs collected by some of the collaborators. At least 86 (55%) of the whales identified had been seen previously. The rate of inter-year resightings was highest for whales identified off northern Washington and three areas off British Columbia (from southern Vancouver Island to north of Vancouver Island). In these areas, from 70-100% of the whales seen in each region had been photographed previously. Mark-recapture abundance estimates based on comparisons to samples in 1996 and 1997 were 181 and 179, respectively. The management implication for these whales has become controversial due to the resumption of whaling by the Makah tribe in northern Washington, an area used by both migrating and feeding whales. This research shows that there are a few hundred gray whales that range in summer months from at least northern California to southeastern Alaska. The mechanism by which these animals are recruited into this group and the degree to which they should be managed as a separate unit from the overall population is not resolved.

KEYWORDS: GRAY WHALE; PHOTO-ID; PACIFIC OCEAN; FEEDING GROUNDS; MOVEMENTS; SITE FIDELITY; MARK-RECAPTURE; ABUNDANCE ESTIMATE; WHALING-ABORIGINAL

INTRODUCTION

Gray whales make one of the longest migrations of any mammal between their winter breeding grounds off Baja California, Mexico, and their feeding grounds in the Bering and Chukchi Seas. Migrations along the Pacific northwest coast occur in December and January when the animals are southbound and again in the spring when the whales are northbound. Outside these migratory time periods, summer feeding aggregations of gray whales have been reported in a number of areas along the coasts of California, Oregon, Washington and British Columbia (Howell and Huey, 1930; Gilmore, 1960; Rice, 1963; Rice and Wolman, 1971; Patten and Samaras, 1977; Flaherty, 1983; Darling, 1984; Murison *et al.*, 1984; Nerini, 1984; Sumich, 1984; Mallonée, 1991; Avery and Hawkinson, 1992; Calambokidis *et al.*, 1992; 1994; Weitkamp *et al.*, 1992). These animals have been referred to as summer or seasonal residents (Pike, 1962; Darling, 1984; Murison *et al.*, 1984; Weitkamp *et al.*, 1992) and more recently as the 'Pacific Coast Feeding Aggregation' whales (National Marine Fisheries Service [NMFS], 2001).

In the early 1970s, photographic identification research demonstrated that many of the gray whales that would remain off Vancouver Island to feed through late spring and summer were the same individuals that returned to the same area each year (Hatler and Darling, 1974; Darling, 1984). Similarly, gray whales photographically identified off Washington State and northern British Columbia from late spring to autumn were also found to return annually (Calambokidis *et al.*, 1994). These whales appear to be part of the overall eastern gray whale population and generally arrive and depart from these feeding grounds concurrently with the migration to and from the wintering grounds. Gray whales in these regions have been observed feeding on a variety of prey including herring eggs/larvae, crab larvae, amphipods, mysids and ghost shrimp (Murison *et al.*, 1984; Nerini, 1984; Oliver *et al.*, 1984; Weitkamp *et al.*, 1992; Duffus, 1996; Darling *et al.*, 1998). Movements over distances of less than 100km and changes in distribution of

[*] *Cascadia Research, 218½ W Fourth Ave., Olympia, WA 98501, USA.*
[+] *West Coast Whale Research Foundation, 2155 W 13th Ave, Vancouver, BC V6K 2S2.*
[#] *University of British Columbia, 6248 BioSciences Rd, Vancouver, BC V6T 1Z4.*
[++] *Alaska Fisheries Science Center, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA.*
[**] *Coastal Ecosystems Research Foundation, Allison Harbour, PO Box 124, Port Hardy, BC V0N 2P0.*
[##] *Whale Research Lab, University of Victoria, PO Box 3050, Victoria, BC V8W 3P5.*
[°] *Humboldt State University, 1 Harpst Street, Arcata, California 95521, USA.*
[×] *Juan de Fuca Express, 427-118 Menzies Street, Victoria, BC V8V 2G5.*

animals in response to shifting prey types have been documented (Darling, 1984; Darling *et al.*, 1998). Darling (1984) suspected gray whales seen along the coast of British Columbia in summer months were part of a larger 'northwest coast' sub-population that numbered at least 100 animals.

Information on the status, range and movements, and abundance of these whales is crucial in the management of gray whales especially due to the resumption of whaling by the Makah Tribe in northwest Washington State. Although the current management plan for hunting of gray whales calls for targeting migratory animals, it may be difficult to avoid taking whales from this seasonal feeding aggregation (Quan, 2000). It is currently unclear whether the feeding aggregation of gray whales in the Pacific northwest should be treated as a separate population. Genetic differences have not been found to date between these animals and the overall population (Steeves *et al.*, 2001).

This paper examines the range of movements and tenure of individual gray whales between spring and autumn 1998 based on photo-identification research conducted collaboratively in many regions between northern California and southeastern Alaska. With data on these whales from previous years, this paper also examines site fidelity, interchange and estimate of abundance.

MATERIALS AND METHODS

Identification photographs of gray whales were collected by eight collaborating organisations between 12 March and 18 November 1998 from northern California to southeastern Alaska (Table 1). Effort by region was variable with most intensive coverage along the southern and western coast of Vancouver Island. Effort and identifications were grouped into 12 regions (Fig. 1) based on bodies of water and operating areas for surveys.

Photographic identification methods

Although a variety of vessels were used in different areas, most of the effort was conducted using small vessels (< 10m) and photo-identification methods were similar. Whales were approached slowly from the side at a distance of 50-100m. Both left and right sides of the dorsal region around the dorsal hump and the flukes of gray whales were photographed if possible. Most groups used 35mm cameras usually equipped with 300mm lenses and high-speed black and white negative film. Markings used to distinguish whales included pigmentation of the skin, mottling and scarring, which varied among individuals and have provided a reliable means of identifying gray whales over periods of

Table 1

Summary of areas of effort, participating organisations, number of identifications and dates of identifications in 1998.

Region	Region code	Description	Organisations	IDs	Unique IDs	Dates of identifications	
						Begin	End
Northern California	CA	Eureka to Oregon border with most identifications from Patricks Pt. and Pt. St George	Humboldt State Univ. (HSU) Cascadia Research Collective (CRC)	27	15	21 Jul. 1998	10 Oct. 1998
Oregon coast	OR	Primarily central coast near Depoe Bay and Newport, OR	Humboldt State Univ. (HSU) Cascadia Research Collective (CRC)	46	18	29 Jul. 1998	4 Oct. 1998
Grays Harbor and S Washington	GH+	Includes waters inside Grays Harbor and coastal waters along the S Washington coast	Cascadia Research Collective (CRC)	59	7	21 Mar. 1998	11 May 1998
N Washington coast	NWA	Northern outer coast waters with most effort from Cape Alava to Cape Flattery	National Marine Mammal Laboratory (NMML) Cascadia Research Collective (CRC)	46	21	6 Jun. 1998	18 Nov. 1998
US Strait of Juan de Fuca	SJF	US waters east of Cape Flattery extending to Admiralty Inlet (entrance to Puget Sound)	National Marine Mammal Laboratory (NMML) Cascadia Research Collective (CRC)	35	15	17 Aug. 1998	11 Nov. 1998
Northern Puget Sound	NPS	Inside waters and embayments from Edmonds to the Canadian border	Cascadia Research Collective (CRC)	27	6	12 Mar. 1998	20 May 1998
Southern Puget Sound	SPS	Central and southern Puget Sound (S of Edmonds) and Hood Canal	Cascadia Research Collective (CRC)	6	4	18 Mar. 1998	17 Nov. 1998
Boundary Bay	BB	Canadian inside waters in and around Boundary Bay, only a single survey	Vancouver Aquarium	3	3	7 Apr. 1998	7 Apr. 1998
S Vancouver I.	SVI	Canadian waters of the Strait of Juan de Fuca along Vancouver I. from Victoria to Barkley Sound, most effort along the West Coast Trail	West Coast Whale Research Foundation (WCWRF) Juan de Fuca Express Univ. of British Columbia (UBC) National Marine Mammal Laboratory (NMML) Cascadia Research Collective (CRC) Dep't of Fisheries and Oceans (DFO)	487	61	4 May 1998	9 Oct. 1998
Central Vancouver I.	CBC	Central portion of the western coast of Vancouver I. with heaviest effort in and around Clayoquot Sound	West Coast Whale Research Foundation (WCWRF) Univ. of Victoria (UVIC)	401	57	13 Jun. 1998	3 Sep. 1998
N of Vancouver I., BC	NBC	British Columbia waters north of Vancouver I., with principal effort around Cape Caution	Coastal Ecosystems Research Foundation (CERF)	100	22	3 Jul. 1998	11 Sep. 1998
SE Alaska	SEAK	Waters of southeastern Alaska with the only effort in the vicinity of Sitka (single survey)	Cascadia Research Collective (CRC)	4	4	8 Nov. 1998	8 Nov. 1998
All areas				1,241	155	12 Mar. 1998	18 Nov. 1998

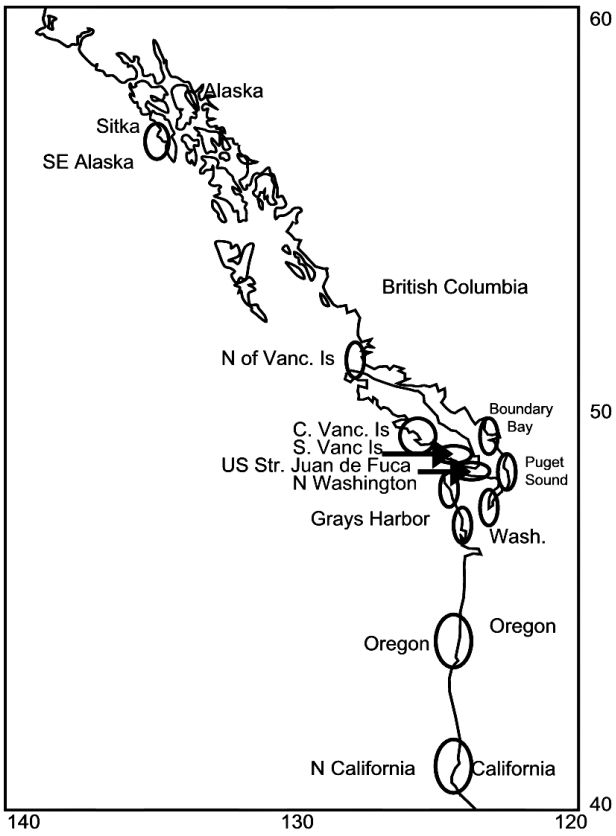

Fig. 1. Study area showing principal areas of effort.

close to 20 years (Darling, 1984; Darling *et al.*, 1998). The relative spacing between the knuckles along the ridge of the back behind the dorsal hump was also used to find photographic matches.

Photographic matching

Comparison of whale photographs to determine matches was made in a series of steps. First, the negatives of gray whales were examined and the best image of the right and left side of each whale (for each sighting) was selected and printed (17.8 × 6.4cm). To determine the number of whales seen during the season, all photographs from 1998 were compared to one another to identify whales seen on multiple days. Finally, a comparison was made between the best photograph in 1998 and Cascadia's catalogue of whales seen in past years (see below). Whale photographs that were deemed of suitable quality but did not match the existing catalogue (compared by two independent matchers) were assigned a new identification number.

Information on sightings from previous years came from two sources. Cascadia's catalogue from past years consisted of 835 records of 171 unique gray whales identified between 1984 and 1997. While most of these identifications were from Washington State, including Puget Sound and inland waters, small samples were also collected off California and southern British Columbia. These photographs were collected by Cascadia Research personnel or other collaborating scientists and naturalists. Additionally, individual research groups participating in the 1998 collaboration provided information on past years' sightings of animals they saw in 1998 (they did not have access to the entire collection of 1998 photographs). Since these groups only compared photographs from their own regions to its past collections, there was not a complete comparison among these collections. The proportions of individuals identified in previous years, therefore, are reported as minimums.

RESULTS

Sighting patterns and movements within 1998

From the 1,241 occasions when suitable photographs of a gray whale were obtained in 1998, 155 were identified as unique whales (Table 1). Each individual was photographed from 1-42 times (mean 8.0, SD = 8.4). The largest number of individuals were identified off the southern coast of Vancouver Island, especially in June and July, and from central Vancouver Island around Clayoquot Sound in July and August (Table 2).

Of the 155 identified whales, 117 (75%) were photographed on more than one day. Time between multiple sightings of individual whales ranged from 1-170 days (average of 56 days, SD = 42). Whales seen with a tenure of over three months generally were seen in multiple regions. The whale (ID# 192) seen over a 170 day period was first seen on 4 May and was resighted 42 times up to 21 October: it was seen from 4 May to 6 July off the West Coast Trail of southern Vancouver Island; 9 to 31 July in the Clayoquot Sound vicinity of central Vancouver Island (with a single resighting off the West Coast Trail on 24 July); 6 to 27 August off the West Coast Trail; and then from 5 September to 21 October, it was seen repeatedly off the northern Washington coast.

Table 2

Number of unique individual gray whales photographed in each region by month in 1998.

	Month									All months
	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	
Northern California					2	1		13	1	15
Oregon coast					4	17		1		18
Grays Harbor and S Washington	4	7	1							7
N. Washington coast				1	12	6	8	5	1	21
US Strait of Juan de Fuca						1	2	9	7	15
Northern Puget Sound	6	4	1							6
Southern Puget Sound	1							1	2	4
Boundary Bay		3								3
S Vancouver I.			8	40	45	15	30	9		61
Central Vancouver I.				17	40	42	7			57
N of Vancouver I., BC					18	14	3			22
SE Alaska									4	4
All areas	11	14	10	54	88	81	43	37	15	155

Movements among regions in 1998 were documented for 57 whales (Table 3): 38 seen in two regions; 18 in three regions; and 1 in four regions. The most frequent interchange was among three adjacent sites from northern Washington to central Vancouver Island (Table 4a). The overall pattern of movements among regions was complex (Fig. 2). Whales were not always moving in the same direction at the same time of year. Despite the wide variations in movement patterns of different individuals, a few patterns could be discerned. A high concentration of whales identified off southern Vancouver Island in June (40 individuals) and July (45) then appeared to disperse somewhat with 19 transits observed from this area north to Clayoquot Sound in July and, to a lesser degree, August. Some animals also moved south from southern Vancouver Island at this same time with 10 transits to the Washington coast and several more toward Oregon and California (arriving in later months). In August, the number of whales in the Clayoquot Sound area (42 individuals) peaked and a high number of transits were observed late in the month and extending into September from this area back to southern Vancouver Island (14 transits) as well as other areas primarily to the south.

Movements within 1998 among distant locations were rare. Only one whale was found to move from northern California to another location: whale ID# 76 was seen multiple times between 12 June and 9 July off southern Vancouver Island and was not observed again until 10 October when it was seen feeding off Point St George in

Table 3

Summary of identifications and resighting rates of gray whales in 1998 by region.

Region	Unique IDs	No. seen more than once in 1998	No. seen in same region in a previous year	No. seen in another region in 1998	No. seen in any region in a previous year	% seen in any region in a previous year
Northern California	15	6	3	1	7	47
Oregon coast	18	14	0	8	8	44
Grays Harbor and S Washington	7	7	3	0	3	43
N Washington coast	21	19	17	17	17	81
US Strait of Juan de Fuca	15	12	2	6	5	33
Northern Puget Sound	6	4	4	0	4	67
Southern Puget Sound	4	2	0	0	0	0
Boundary Bay	3	0	0	0	0	0
S Vancouver I.	61	60	21	49	45	74
Central Vancouver I.	57	55	20	43	41	72
N of Vancouver I., BC	22	18	10	14	22	100
SE Alaska	4	0	0	0	1	25
All areas	155	119		57	86	55

Table 4a

Matrix of matches between region within 1998. **Bold** numbers along the diagonal show number of animals resighted within the same area.

		Region									
Region	*n*	CA	OR	GH+	NWA	SJF	PS/BB	SVI	CBC	NBC	SEAK
Northern California	15	**5**									
Oregon coast	18		11								
Grays Harbor and S Washington	7			**7**							
N Washington coast	21		1		**8**						
US Strait of Juan de Fuca	15				1	11					
Puget Sound/Boundary Bay	13						**6**				
S Vancouver I.	61	1	6		17	6		**54**			
Central Vancouver I.	57		6		8	3		33	**50**		
N of Vancouver I., BC	22				1			7	9	1**6**	
SE Alaska	4										**0**

Table 4b

Matrix of matches for whales sighted in 1998 and other years between regions. Diagonal (**bold**) shows number of whales seen both in 1998 and a previous year in the same region. Columns reflect region seen prior to 1998 and rows show region seen in 1998.

	n for	Region sighted prior to 1998									
Region sighted in 1998	1998	CA	OR	GH+	NWA	SJF	PS/BB	SVI	CBC	NBC	SEAK
Northern California	15	**3**		2	1	2					
Oregon coast	18		**0**	2	6	1		3	2	1	
Grays Harbor and S Washington	7			**3**	1						
N Washington coast	21				**16**	9		10	6	5	
US Strait of Juan de Fuca	16					**2**		4	5	4	
Puget Sound/Boundary Bay	13						**4**	1			
S Vancouver I.	61			1	25	16		**21**	20	20	
Central Vancouver I.	57	1		3	17	8		10	**20**	19	
N of Vancouver I., BC	22				2	1		2	3	**21**	
SE Alaska	4				1	1					**0**

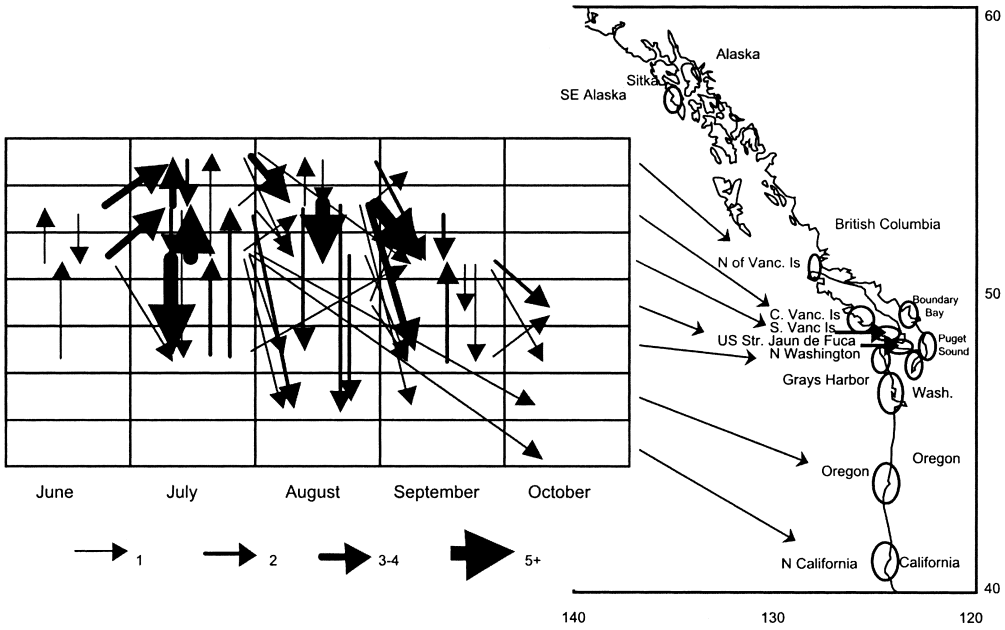

Fig. 2. Movements of gray whales among locations in 1998. Size of arrow indicates number of transits. Movements within a month are shown as vertical lines and movements across months are on diagonals.

northern California. Identifications were primarily made late in the season off Oregon (August) and California (October).

Distance and travel speed were also examined for the 117 whales that were seen on more than one day (Fig. 3). Total distances between resighting positions for individual whales ranged from < 1 to 526 n.miles (great-circle route). The distance a whale was documented travelling through the season averaged 110 n.miles (SD = 137) and was generally directly related to the number of times and span of time over which it was seen. The majority of travel speeds were well under 1 n.mile per hour as would be expected for feeding whales and because the data underestimate the true distance covered (and therefore the speed). Some whales remained in the same area for long periods; for example, ID# 231 was seen 30 times over a 136-day period (23 May to 6 October 1998) off southern Vancouver Island. It accumulated a total distance travelled of only 74 n.miles. The most rapid movement was for an animal (ID# 295) seen seven times from 10-25 August but which moved from central Vancouver Island to Oregon in that period (308 n.miles in less than 10 days). For the eight whales documented moving over 400 n.miles, one transited in one direction from Vancouver Island to California, while the remaining seven made multiple transits in different directions among locations.

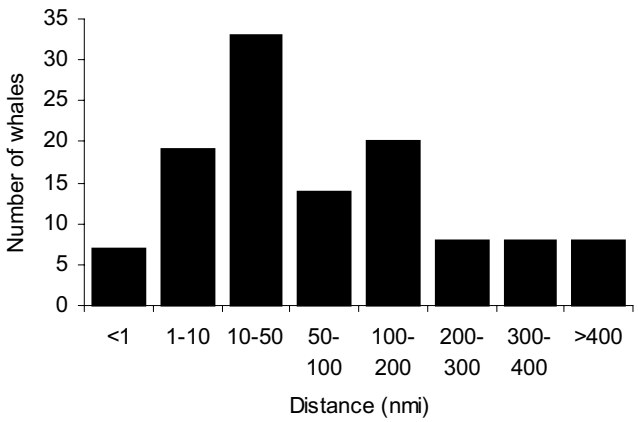

Fig. 3. Distribution of minimum distance whales travelled for 116 gray whales identified multiple times in 1998.

Inter-year resightings

Most of the whales photographed in 1998 had been identified in previous years (Tables 3 and 4b). At least 86 (55%) of the whales identified had been previously identified. This number is a minimum because the matches to past years come from comparison of all 155 of the whales identified in 1998 to the historical catalogue maintained by Cascadia Research of whales primarily seen off Washington. There were also matches to previous years identified by several of the collaborating research groups but these were confined to comparisons of whales identified in the same area (the full 155 whales were not compared to the historical catalogues of the other collaborating research groups). Such a comparison would yield additional documentation of resightings of whales in previous years.

Inter-year resightings were highest for whales identified off northern Washington and the three regions of British Columbia from southern Vancouver Island to north of Vancouver Island. In these areas, from 72-100% of the whales seen in each region had been identified in a previous year. These areas are the regions with the heaviest consistent survey effort in past years.

For some areas, such as Oregon and California, there were few identification photographs available from previous years so inter-year resightings were primarily animals that had been seen in other regions in past years. For Oregon, where no identification photographs were available previously, 8 of 18 (44%) whales identified in 1998 had been seen in six other regions from Grays Harbor to northern British Columbia in the previous years (Table 4b). Whales identified off California in 1998 had been seen previously in the Grays Harbor area, the northern Washington coast and the Strait of Juan de Fuca. Three of the whales identified off California were also seen in the only past sample available: a collection of 13 whales identified in November 1991 in the same location they were photographed in 1998 (off Point St George).

Whales identified in 1998 in southern Puget Sound and Boundary Bay had not been seen in a previous year in any region. This finding from southern Puget Sound is consistent with observations from past years; the presence of gray whales in this area is highly variable each year and whales have not been identified previously (Calambokidis *et al.*, 1994). This is different, however, for whales seen in northern Puget Sound, where four of six whales identified were known from sightings in past years. All four of these whales had been identified multiple times since 1990 or 1991. Whales seen in northern Puget Sound generally have been seen from March through May and then move to other unknown areas.

During 1998, whales that had been identified in previous years were seen more times (mean of 10.6 versus 4.7, $t = 4.73$, $p < 0.001$) over a longer period of time (61 versus 21 days, $t = 6.32$, $p < 0.001$) (starting earlier and extending later) than whales that had not been identified in previous years (Table 5). This was partly a function of the lower proportion of whales known from previous years in areas like California, Oregon and Puget Sound where resightings within 1998 were less common. Even with the elimination of this regional bias, however, this general trend remained within the three best-sampled regions (northern Washington and southern and central Vancouver Island).

Although only four whales were identified in southeastern Alaska in 1998 (and none previously), one of these was seen in past years off Washington. Although it was not seen elsewhere in 1998, it had been sighted 18 times in five of the previous six years off both the Washington outer coast and in the Strait of Juan de Fuca. Despite the small sample size, the movement of this whale suggests either the range of this feeding aggregation extends farther north than the primary effort of this study, or that there are other feeding aggregations with some interchange among them.

Seasonal patterns in resighting rates

Whales were identified from 12 March to 19 November 1998 and whales identified early and late in the season included animals seen over extended periods in 1998 and in previous years. There were, however, seasonal differences in the resighting rates of animals in 1998 (Table 6). Less than 50% of whales identified early (March and April) and late (November) in 1998 were known from previous years compared to 57% to 81% for those seen in previous years for May to October (Table 6). These whales were

Table 5

Summary of sighting rates and parameters for gray whales identified in 1998 for whales identified in previous years and whales not identified in previous years.

	All whales			Seen previous years			Not seen prev. years		
Times seen by region	*n*	Ave	SD	*n*	Ave	SD	*n*	Ave	SD
Northern California	15	1.8	1.3	7	1.9	1.6	8	1.8	1.2
Oregon coast	18	2.6	2.4	8	2.1	2.1	10	3.0	2.6
Grays Harbor and S Washington	7	8.3	3.9	3	6.0	4.0	4	10.0	3.4
N Washington coast	21	2.2	2.5	17	2.3	2.7	4	1.8	1.0
US Strait of Juan de Fuca	15	2.3	1.8	5	1.4	0.5	10	2.8	2.0
Northern Puget Sound	6	4.5	2.8	4	4.8	2.6	2	4.0	4.2
Southern Puget Sound	4	1.5	0.6	0			4	1.5	0.6
Boundary Bay	3	1.0	0.0	0			3	1.0	0.0
S Vancouver I.	61	8.0	7.3	45	8.8	7.3	16	5.6	6.9
Central Vancouver I.	57	7.0	7.0	41	7.4	6.4	16	6.1	8.6
N of Vancouver I., BC	22	4.5	4.6	22	4.5	4.6	0		
SE Alaska	4	1.0	0.0	1	1.0		3	1.0	0.0
All areas	155	8.0	8.3	86	10.6	9.0	69	4.7	6.1
Number of regions seen	155	1.5	0.8	86	1.8	0.8	69	1.2	0.4
First date seen (SD in days)	155	13 Jul.	61.4	86	29 Jun.	47.7	69	30 Jul.	71.7
Last date seen (SD in days)	155	24 Aug.	57.9	86	28 Aug.	49.2	69	19 Aug.	67.3
Tenure (minimum days)	155	42.8	44.0	86	60.6	45.9	69	20.6	29.2

Table 6

Summary of identications and resighting rates of gray whales in 1998 in relation to season.

Season	Unique IDs	No. seen in more than one month/season in 1998	% seen in more than one season in 1998	No. known from a previous year	% known from a previous year
By month					
March	11	8	73	5	45
April	14	9	64	6	43
May	10	9	90	6	60
June	54	54	100	44	81
July	89	80	90	62	70
August	83	69	83	60	72
September	43	41	95	35	81
October	37	21	57	21	57
November	14	5	36	3	21
By season					
Spring (Mar. to May)	25	7	28	13	52
Summer (Jun. to Aug.)	107	45	42	72	67
Fall (Sep. to Nov.)	74	44	59	46	62
All seasons	155	45	29	86	55

disproportionately sampled in Grays Harbor and in Puget Sound so this could partly be the result of regional differences. It also likely reflects the increased probability of sampling migrating whales closer to the time of the migration past the Pacific northwest.

Geographical recruitment

Although it appears that many whales consistently spend most of the feeding season in Pacific northwest waters, it is not known how they are recruited into this group. This is a critical question for evaluating how exploitation would impact this group (Quan, 2000). Some of the sightings in 1998 provide insight into one possible mechanism for the means by which animals adopt this alternate feeding area.

To examine the role that maternally-directed site fidelity plays in whales feeding in the Pacific northwest, some of the sighting history of identified cows and calves was examined. Although females with calves were sighted infrequently, three of the whales sighted in 1997 or 1998 were known reproducing females, plus one was a returning calf. One whale identified off Washington and British Columbia (ID# 43) has been seen in many years since 1984, including every year from 1992-1998. It was documented with a calf in July 1994 (ID# 107) and the calf was seen independently off Washington in three following years, 1995, 1997 and 1998. In the two other cases (ID# 67 and ID# 105), adult females known from multiple years (between 1992 and 1998) had a calf one year (1994 or 1995) that has not been resighted. In at least one of these two cases, the calf photograph was of marginal quality and there is a chance it would not have been recognised even if it had returned.

Estimation of abundance

The sample from 1998 provides a minimum estimate of the total number of whales feeding in summer months from northern California to southeastern Alaska. Although a total of 155 whales were identified, only 137 of these were seen after 1 June, outside the timing of the northern migration (Table 7). Mark-recapture estimates using annual samples from 1998 and either 1996 or 1997 yielded estimates of 181 and 179, respectively (Table 7).

Table 7

Petersen capture-recapture estimates for gray whales identified between June and November 1998 in the Pacific Northwest. See text for explanation of violations of assumptions and biases.

Sample 1		Sample 2				
Year	*n*	Year	*n*	Match	Est.	CV
1997	29	1998	137	22	179	0.09
1996	24	1998	137	18	181	0.10

DISCUSSION

While the presence of gray whales feeding during summer months in the Pacific northwest has been reported, there has been only limited research on the abundance and range of movements of these animals. Darling (1984) reported resightings of whales off Vancouver Island over an eight-year period. He documented movements of animals between different areas of up to 80km in the same season and 150km between seasons and estimated that the Vancouver Island area was occupied by 35-50 whales each summer. There were gaps, however, in the sighting histories of these whales, with some individuals not identified in the study area for several years.

This study shows that these whales inhabit a broad region during the spring, summer and autumn extending from at least northern California to southeastern Alaska. Within this range, gray whales can move widely both within and between years. The use of this broad area by these whales provides one explanation for why many of these individuals would not be seen in specific areas in some years. Even with the broad field effort reported here, only relatively small portions of the potential areas of use by these animals are being searched (Fig. 1). The interval of three months between sightings of one individual during which it moved from northern Vancouver Island to California without being sighted in intermediate areas of British Columbia, Washington and Oregon, demonstrates the limited survey coverage. Animals not seen in a particular year could inhabit neighbouring areas where there was no research coverage.

This sample provides both a minimum estimate of abundance based on the number of identifications and an estimate of total abundance using mark-recapture. The estimates using the Petersen mark-recapture method require several assumptions (e.g. Hammond, 1986) that are not totally satisfied by the current sampling.

1. The population is closed

There would have been some natality and mortality between annual samples, although this should be small. There also may be emigration or immigration of animals with the overall 'population' of gray whales.

2. All animals have an equal probability of capture in at least one of the samples

The 1998 sample is the most complete sample obtained and covers a broad geographic area. Even in 1998, however, effort was not systematic and some areas were covered far more thoroughly than others; there was no effort in some portions of the known range of these animals.

3. The two samples are independent of each other such that animals caught or not caught in one sample both have equal probability of being caught in the other sample

The 1996 and 1997 samples are clearly geographically biased and are based on identifications made in a relatively small area (northern Washington, Strait of Juan de Fuca and southern Vancouver Island). Since there is also some bias in the 1998 sample and animals do not appear to redistribute randomly, this would create heterogeneity of capture probabilities.

4. All matches, if present, are found and there are no false matches

There is little probability of false matches because only matches based on photographs showing multiple markings and verified by a second observer were used. Some matches could have been missed although this was kept to a low number by only including good quality photographs and requiring all comparisons to be made by two matchers.

Violations of assumption No. 1 and the probable violation of No. 4 (missed matches) would both bias the estimate upward while the violations of No. 2 and No. 3 would bias the estimate downward. Since violations of No. 1 and No. 4 are likely small, it is possible that the most significant bias would be a downward one caused by the unequal sampling. This would mean the estimates are likely underestimates. Multiple-year samples that more completely and evenly sample the range of this feeding aggregation are needed to refine the estimate.

The gray whales in this feeding aggregation are a relatively small proportion of the overall gray whale population. The total gray whale population was estimated at 26,365 (95%CI 21,800-32,400) in 1997/98 based on censuses conducted on the southbound migration (Hobbs and Rugh, 1999; IWC, 2000). The few hundred animals identified from photographs and based on mark-recapture estimates would make up less than 1% of this population.

The timing of the arrival and departure of the gray whales described in this study coincided with the timing reported for the overall gray whale migration past the Pacific northwest. Initial sightings of these whales that stayed through the season occurred in March, during the peak of the northward migration past the Pacific northwest as determined by Herzing and Mate (1984). Similarly, resightings of whales identified in the summer were made through late November, when the last field effort ended. This is close to the December/January peak of the southward migration (Herzing and Mate, 1984). Since migratory animals could be present through May (Herzing and Mate, 1984), it is hard to distinguish early in the season which whales are migrating through and which would remain in the region. Given this potential overlap, mark-recapture estimates were made excluding animals identified only before 1 June.

Some species of baleen whales show a high degree of maternally-directed site fidelity to specific feeding areas. This has been examined in detail for humpback whales (*Megaptera novaeangliae*) in both the North Pacific and North Atlantic. In the western North Atlantic, humpback whales breed at one primary wintering ground but during the spring disperse to a number of distinct feeding areas in the North Atlantic; interchange among these North Atlantic feeding grounds is limited (IWC, 2002). There are differences in mtDNA among some of these areas (Palsbøll *et al.*, 1997). Similarly, humpback whales in the North Pacific use a number of distinct feeding areas with little interchange among them (Calambokidis *et al.*, 1996; 2001), although interbreeding among these groups does occur to some degree on the wintering grounds (Darling and McSweeney, 1985; Baker *et al.*, 1986; Calambokidis *et al.*, 2001). As in the North Atlantic, maternally directed site fidelity to specific feeding grounds has resulted in pronounced mtDNA differences between these areas (Baker *et al.*, 1990; 1998).

Only limited genetic studies have been done on gray whales. Steeves *et al.* (2001) compared mtDNA from a sample of 16 summer 'resident' whales from Clayoquot Sound, Vancouver Island and compared them to whales from the overall population. They detected no significant differences in mtDNA patterns between these two groups. The lack of a difference could result from one or more of the following: small sample size, too short time frame for isolation to develop detectable differences, or lack of isolation of this group. The power to detect differences genetically could be limited as exemplified by comparisons between eastern and western North Pacific gray whales. Despite the generally accepted separation of these two populations, differences in the proportion mtDNA haplotypes, while significant, do not allow reliable separation of individual animals from these two populations (LeDuc *et al.*, 2002).

The degree to which the gray whales in this feeding aggregation should be managed as a unit separate from the overall gray whale population is unclear. Treating two sub-populations as one when dispersal between them is less than several percent per year could result in depleting one of these sub-populations (Taylor, 1997). There is some evidence from whaling data to support the existence of sub-populations of baleen whales on a relatively small geographic scale that were depleted and failed to recover (see discussion in IWC, 2001). The gray whales from the Pacific northwest feeding aggregation appear to migrate to Mexico each winter and therefore are part of the larger breeding population of gray whales. Depending on the stability of this group and how they are recruited, they may represent a unit that should be managed separately. While there are some parallels in the site-fidelity to feeding areas between humpback and gray whales there are some clear differences. The low proportion of gray whale calves documented and the possible evidence for a male bias in this group (Steeves *et al.*, 2001) are different from humpback whale feeding aggregations. Additionally, the overall gray whale population migrates past the Pacific northwest *en route* to their main feeding grounds in the Bering and Chukchi Seas. This would provide a mechanism for animals to encounter productive feeding areas on this migration and potentially adopt this alternate feeding area.

The results also indicate that early in the season it could be difficult to determine with certainty which whales were migrating through the region and which were part of the feeding aggregation that remained in the region. This could be an important management concern related to aboriginal takes of whales in the Pacific northwest. During the migration it would be expected that the overwhelming majority of whales in the migratory corridor would be migrating animals based on the large size of the overall gray whale population and the low numbers of whales estimated in the group that stays in the region. However, some of the gray whales identified in this study as early as March (during the gray whale migration) were animals that had been seen in previous years and stayed through the summer and autumn. The most reliable way to select migratory animals would be based on a combination of season (as close as possible to the time of peak migratory passage), location (in the migratory corridor and away from known feeding areas) and behaviour (animals travelling and not milling in an area).

This paper provides new information on the range, movements and abundance of gray whales utilising the waters of California to southeastern Alaska as a feeding area. While this approach does provide valuable new information, a multi-year effort, currently underway, will provide more accurate estimates of inter-year resighting rates and interchange, and abundance estimates.

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