Polar Biol (2012) 35:1035–1045
DOI 10.1007/s00300-011-1151-6

ORIGINAL PAPER

Identifying gray whale (*Eschrichtius robustus*) foraging grounds along the Chukotka Peninsula, Russia, using satellite telemetry

M. P. Heide-Jørgensen · K. L. Laidre · D. Litovka · M. Villum Jensen · J. M. Grebmeier · B. I. Sirenko

Received: 19 September 2011 / Revised: 14 December 2011 / Accepted: 19 December 2011 / Published online: 11 January 2012

Abstract The purpose of this study was to evaluate summer and fall residency and habitat selection by gray whales, *Eschrichtius robustus*, together with the biomass of benthic amphipod prey on the coastal feeding grounds along the Chukotka Peninsula. Thirteen gray whales were instrumented with satellite transmitters in September 2006 near the Chukotka Peninsula, Russia. Nine transmitters provided positions from whales for up to 81 days. The whales travelled within 5 km of the Chukotka coast for most of the period they were tracked with only occasional movements offshore. The average daily travel speeds were 23 km day^{-1} (range 9–53 km day^{-1}). Four of the whales had daily average travel speeds <1 km day^{-1} suggesting strong fidelity to the study area. The area containing 95% of the locations for individual whales during biweekly periods was on average 13,027 km^2 (range 7,097–15,896 km^2). More than 65% of all locations were in water <30 m, and between 45 and 70% of biweekly kernel home ranges were located in depths between 31 and 50 m. Benthic density of amphipods within the Bering Strait at depths <50 m was on average ~54 g wet wt m^{-2} in 2006. It is likely that the abundant benthic biomass is more than sufficient forage to support the current gray whale population. The use of satellite telemetry in this study quantifies space use and movement patterns of gray whales along the Chukotka coast and identifies key feeding areas.

Keywords Gray whale · Chukotka · Satellite tracking · Feeding grounds

M. P. Heide-Jørgensen (✉)
Greenland Institute of Natural Resources, Box 570,
3900 Nuuk, Greenland
e-mail: mhj@ghsdk.dk

K. L. Laidre
Polar Science Center, Applied Physics Laboratory,
University of Washington, 1013 NE 40th Street,
Box 355640, Seattle, WA 98105-6698, USA

D. Litovka
Marine Mammals Laboratory, ChukotTINRO,
Box 29, Str. Otke, 56, Anadyr, Chukotka 689000, Russia

M. Villum Jensen
Mikkels Vaerksted, Gislingevej 2, 4571 Grevinge, Denmark

J. M. Grebmeier
Chesapeake Biological Laboratory, University of Maryland
Center for Environmental Science, 1 Williams St.,
PO Box 38, Solomons, MD, USA

B. I. Sirenko
Laboratory of Marine Research, Zoological Institute Russian
Academy of Sciences, Universitetskaya nab. 1.,
St. Petersburg 199034, Russia

Introduction

Eastern Pacific gray whales (*Eschrictius robustus)* are highly migratory baleen whales that visit tropical lagoons in Mexico (south of 28°N) in winter and migrate north to the northern Bering Sea, the Bering Strait, and the Chukchi Sea (north of 65°N) in summer. The summering areas off Alaska and Russia are believed to be the primary feeding areas. There is evidence that some whales do not make the full migration and instead spend the summer off the Pacific Northwest coast of the USA or Vancouver Island, Canada, while others may feed *en route* to the Bering Strait (Nerini 1984; Darling et al. 1998; Moore et al. 2007).

Gray whales are predominantly benthic foragers that feed in shallow water over continental shelves. Although over 100 different prey species have been found in gray whale stomachs, infaunal amphipods constitute a major part of the diet on the Bering Strait summer feeding grounds (Rice and Wolman 1971; Zimushko and Ivashin 1980; Blokhin 1984). An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984) and access to abundant benthic food resources during summer is likely critical for survival and reproduction. Dietary intake on the southern wintering grounds and during their northward migration is presumably of limited importance (Rice and Wolman 1971); however, this has not been extensively investigated.

Beginning in the mid-1970s, large-scale ecosystem changes occurred in the northern Bering Sea that were likely related to climate warming in the Pacific sector of the Arctic (Grebmeier et al. 2006). Specifically, a decline in the benthic prey base for gray whales was reported in the northern Bering Sea at the Chirikov Basin (Coyle et al. 2007). Examination of the distribution of whales from a time series of aerial surveys suggested that the abundance of gray whales at the summer feeding areas in the Chirikov Basin declined over a 20-year period (Moore et al. 2003). There was also speculation that an unusual stranding mortality of gray whales was caused by a downturn in productivity in the Northern Bering Sea (LeBoeuf et al. 2000), although this hypothesis has not been widely accepted because of the flexibility gray whales display regarding prey selection and foraging range (Moore et al. 2001, 2003). Although gray whales may be affected by ecosystem changes in the Northern Bering Sea, there are other large areas of the Bering Strait and Chukchi Sea used for gray whale feeding where ecosystem changes have not yet been identified or studied.

This study examined the movements and area use of foraging gray whales in the coastal waters of the Chukotka Peninsula using satellite telemetry. The purpose was to identify the degree of late summer and fall fidelity to the coast of Chukotka and examine whether gray whales tagged in this sector of the Bering Sea utilized the central feeding grounds in Chirikov Basin, to the east of Chukotka. We estimated the available foraging habitat for gray whales around the Chukotka Peninsula and the affinity for available depths and sections of the coast. This information, used together with synoptic estimates of benthic amphipod prey biomass, was used to evaluate current and potential gray whale carrying capacity for the region and for the entire Bering Sea.

Materials and methods

Satellite transmitters and deployment system

Three different implantable satellite transmitter types and attachment systems were deployed on gray whales in this study (Table 1). Two of the tags had different cylinder lengths (with one or two AA lithium batteries) but both had spear tips with two sets of barbs along the body of the spear and were equipped with stop plates that prevented penetration deeper than 13 and 18 cm, respectively, for short and long tags. The stop plates were secured with a magnesium bolt that allowed the plate to corrode after a couple of days in salt water. The third tag model was designed as a long flat box-shaped tag (one M1 lithium cell) with a harpoon head tip and two barbs along the body of the transmitter (flat box). It had a stop plate that prevented penetration deeper than 10 cm and was delivered with a release cup that slid backward after it hit the whale. All three transmitter models were programmed to make 300 transmissions per day between 0600 and 2300 local time. The long cylinders were duty cycled with one daily position, the short cylinders transmitted every other day, and the flat boxes transmitted every third day. The deployment system used for attaching the tags to whales was the Air Rocket Transmitter System (ARTS, see Heide-Jørgensen et al. 2001a; Mate et al. 2007).

Field work

Field work was conducted at Nuniamo in the outer part of Laurentia Bay, Chukotka (Fig. 1). A reconnaissance field trip conducted in September 2005 demonstrated that gray whales were difficult to locate and approach using a single boat, and therefore, three boats were used for searching for whales in 2006, two of which were equipped for tagging.

When undisturbed, the whales surfaced repeatedly (up to 8 times in a sequence) following a long dive. The footprints (whirls of water at the surface from tail movements underwater) on the surface of the water were typically detected along a straight line identifying the course of the whale. The first footprint was often associated with mud from recent feeding at the bottom. Whales were pursued with three boats from a distance. Boats spread out in three directions to maximize the possibility that at least one boat was close to the whale when it surfaced. After ~30 min, whales would frequently make enough consecutive surfacing events on a straight line course near one of the boats that tags could be deployed. All fieldwork was conducted under permits from Russia.

Data analysis

Data on voltage of the transmitters, number of transmissions used, and geographic positions from the satellite transmitters, also referred to here as ‘tags’, were collected via the ARGOS system (Service Argos 1989; Harris et al. 1990). Location qualities were provided by Service Argos and coded based on predicted accuracy. Location codes

Table 1 Gray whales instrumented with satellite transmitters at Chukotka in September 2006 ($N = 13$)

Tag ID	Instrument type	Date Sept.	Latitude	Longitude	Estimated body length (cm)	Placement	Distance to whale (m)	Chase time (min)	Last day of positions (contact)	Number of days with positions (contact)	Uplinks	Argos location codes					
												3	2	1	0	A	B
7934	Short cylinder	2	65.560	170.632	12	RMM	15	15	(6/11)	0 (65)	8,192						
60007	Flatbox	2	65.560	170.632	10	LML	10	5	na	0	0						
21793	Short cylinder	2	65.561	170.817	13	CMH	10	20	18/11 (18/11)	77 (77)	1,4336	25	73	88	26	100	175
7927	Short cylinder	2	65.562	170.838	10	LMH	15	30	23/9 (25/9)	21 (23)	4,608					1	4
37277	Short cylinder	2	65.593	170.711	8	LBH	5	Na	22/11 (25/12)	81 (114)	1,9456	9	11	16	4	112	494
21803	Short cylinder	2	65.605	170.704	10	CMH	8	Na	na	0	0						
37286	Long cylinder	10	65.604	171.279	13	LHB	7	60	18/9 (19/9)	8 (9)	2,816		1	2	1	17	43
26715	Flatbox	10	65.511	170.765	10	RHB	5	90	22/9 (25/9)	12 (15)	4,096	1		4	8	10	34
37232	Long cylinder	11	65.569	170.876	12	CMH	10	60	na	0	0						
20693[a]	Short cylinder	12	65.608	170.491	13	LMH	2	45	4/11 (8/11)	53 (57)	8,192	1	2	1	1	15	50
20692[a]	Short cylinder	12	65.610	170.378	12	RBH	8	90	17/10 (9/11)	35 (58)	7,424	7	25	37	30	66	96
37233	Long cylinder	12	65.569	170.754	9	LHM	4	30	15/10 (15/10)	33 (33)	14336	26	73	85	64	149	161
20160	Short cylinder	12	65.560	170.782	11	RHM	5	20	13/10 (31/10)	31 (49)	4,864				1	1	12

All deployments were made with an airgun (pressure around 10 bars). Placement is described by: side of the whale; *R* Right, *C* Centreline or *L* Left, Lengthwise; *F* Front, *M* Mid or *B* Back and Height; *H* High, *M* Middle or *L* Low

[a] Group of 2 or 4 whales

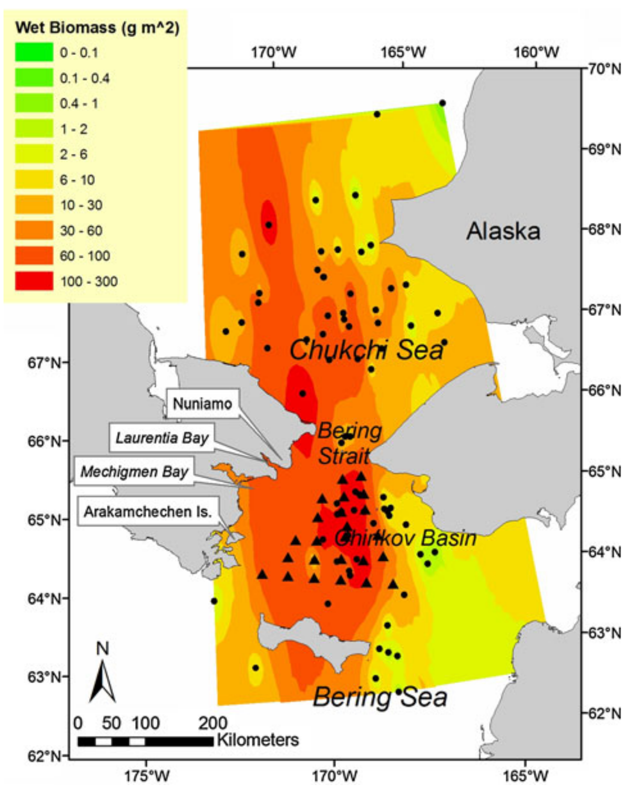

Fig. 1 Map of locations of benthic sampling stations in the Bering Strait (with all samples 1984–2006); 2006 is shown as *black triangles*. The interpolated wet weight biomass of ampeliscid amphipods is shown on a *colored scale* from *green* (low density) to *red* (high density)

(LC) were B, A, and 0–3 in order of increasing accuracy, where Service Argos predicts that 68% of classes 1, 2, and 3 are within 1.0, 0.35, and 0.15 km, respectively, of the actual location (Service Argos 1989). Satellite tracking of pinnipeds has shown that error may be 3.8 km (SD 2.6 km) for class 0 positions, 18.8 km (SD 42.6 km) for class A positions, and 22.8 km (SD 43.9 km) for class B positions (Boyd et al. 1998). Location filtering was conducted by calculating an average daily position for each whale over the entire tracking period. This minimized autocorrelation bias and allowed for the calculation of distance (km) and speed (km day^{-1}) between each average daily location. This averaging is appropriate given the focus on weekly and biweekly general movements rather than fine-scale area use or habitat selection. The distance and minimum speed estimates were averaged for biweekly periods. Track lines of the whales' paths were created for each individual by connecting consecutive average daily locations.

Digital bathymetric data were obtained from USGS (1:2,500,000 and 1:1,000,000) (http://alaska.usgs.gov/science/biology/walrus/bering/bathy/index.html) as developed from the National Ocean Service (NOS). Average daily locations were linked to a mean depth value in ArcINFO.

Area use on the summering ground was estimated as the 95, 75, and 50% fixed-kernel range estimates using the Animal Movement and Spatial Analyst extensions in ArcView (Hoodge and Eichenlaub 1997). The fraction of the range estimates covered by depth categories in 10 m increments was estimated for each 50, 75, and 95% kernel polygon using the Arc9 ArcINFO INTERSECT function. The total area within each depth category was calculated in square kilometers (Polar Stereographic Projection) across the biweekly time series. The total area of the shelf <30 m depths around the Chukotka Peninsula (km^2) was considered primary habitat for gray whales based on several sources: (1) distribution of catches along Chukotka (Votrogov and Bogoslovskaya 1980; Blokhin 1984; Miller et al. 1985), (2) extensive aerial surveys of gray whales in the Bering Strait and Chukchi Sea (Moore et al. 2000), and (3) ship-based sightings of gray whales in the Chukchi Sea (Miller et al. 1986; Clarke and Moore 2002; Bluhm et al. 2007).

Benthic prey availability

Information on benthic biomass and abundance of amphipods from the central Bering Sea were compiled from a ship-based sampling effort in May–June 2006, the same year the whales were satellite tagged. Benthic samples were collected to investigate benthic population structure following standard protocols outlined in Grebmeier et al. (1989). Sediments were collected at each station using a weighted 0.1 m^2 van Veen grab. Four van Veen grabs were used to collect replicate quantitative samples for benthic population studies. Prior studies have shown that 4 van Veen grabs account for 95% of the variance at a single station (Grebmeier unpubl. data). Use of a standard van Veen grab allows quantitative comparisons with historical benthic population studies in this area. For faunal analyses, sediment was sieved through 1-mm screens, and retained animals were preserved in 10% buffered (hexamethylenetetramine) formalin for analysis (Chesapeake Biological Laboratory in Solomons, Maryland, USA). Of 118 stations sampled using benthic van Veen grabs, 24 were within gray whale feeding habitat. Wet weight biomass of ampeliscan amphipods and total biomass of benthic fauna were determined at these stations. These data were used to determine the average biomass of prey available to gray whales in the study region and within the area deemed to be primary habitat.

Results

Performance of tags

Thirteen gray whales ranging in estimated body length from 8 to 13 m (mean 11 m) were instrumented with satellite transmitters over a period of 10 days in 2006 (Table 1). The period between when the whale was sighted and when a tag was deployed ranged widely, from 5 min to 90 min, with a mean of 45 min (Table 1). Whales were, on average, 8 m from the boats when instrumented.

Four of the thirteen transmitters gave no geographic locations. Of these, three gave neither signals nor locations, while the fourth transmitter gave signals for 65 days but no locations (Table 1). Reasons for complete failure might include a poor deployment position on the whale (#7934) or poor implantation (#21803, #37232, #60007). The remaining 9 tags provided, on average, 39 days with positions (range 12–81 days), or 46 days of transmissions of signals. The short cylinder tags had a better longevity than the long cylinder tag (43 vs. 21 days) and the flat boxes provided only 12 days with positions. The long cylinder tag type gave a larger average number of high quality (>0) positions ($n = 94$) than the other models ($n = 59$ for short cylinders and $n = 5$ for flat boxes).

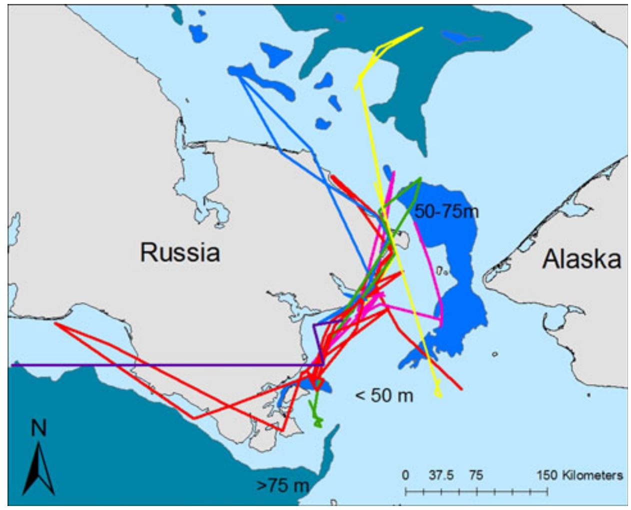

Fig. 2 Tracklines of gray whales based on daily average positions, each individual tracked around Chukotka shown as a different color ($n = 9$). The *light blue* area indicates water depth <50 m

Movements of whales

All of the whales remained in the western part of the Bering Strait along the Chukotka coast throughout the study period. Whales had a strong affinity for specific coastal sites along the peninsula (Fig. 2) and primarily travelled or stayed close to the Chukotka coast for the period they were tracked. If offshore movement occurred, the whale frequently returned to the coastal areas from which it departed, usually within few days. The mean daily distance travelled ranged between 9 and 53 km day^{-1}; however, four of the whales moved infrequently and had daily speeds <1 km day^{-1} (Table 2). The overall average daily distance travelled per day of the nine whales was 23 km day^{-1} for the entire tracking period.

Space use patterns

The kernel home range probability regions (50% probability) for the first 6 weeks following tagging were centered on one site just outside the Laurentia Bay (Fig. 3). In October and November, gray whales shifted their area use south to include an area around Mechigmen Bay. The 95% kernel

Table 2 Daily velocities and travel distances of individual gray whales instrumented with satellite tags

Tag ID	Period with contact	Average speed (km day^{-2})	Range (km day^{-2})	Distance (km)
21793	2/9–18/11	12.7	0.4–84.9	458
7927	2/9–23/9	37.3	4–72.4	116
37277	2/9–22/11	10.1	0.2–86.3	669
37286	10/9–18/9	52.7	8.2–100.7	422
26715	10/9–22/9	32.1	2.5–104.5	128.4
20693	12/9–4/11	16.1	1.3–66.7	193
20692	12/9–17/10	9.2	0.8–32.1	166
37233	12/9–15/10	22.5	0.7–108	742
20160	12/9–13/10	39.2	6.1–15.1	39

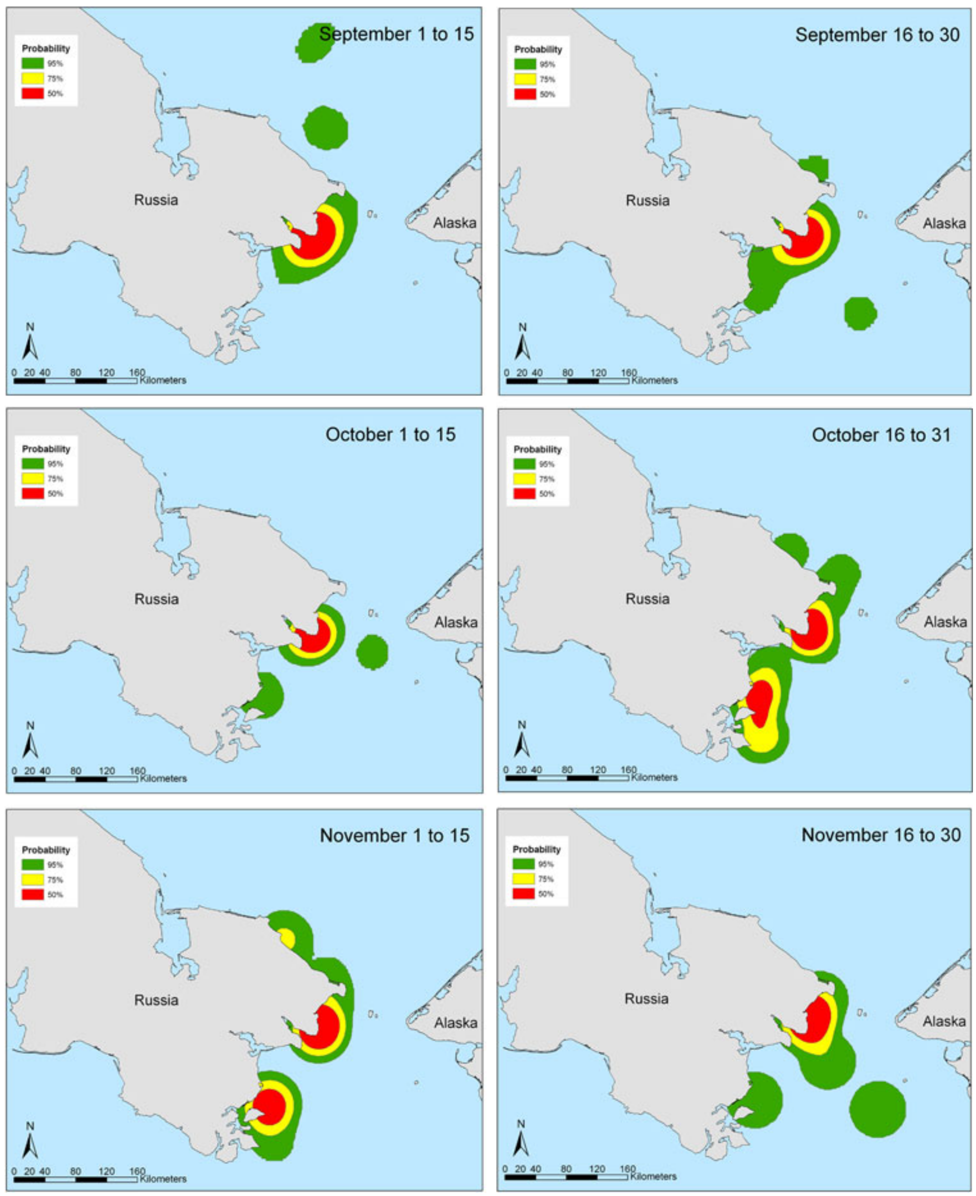

Fig. 3 Kernel home ranges for nine gray whales tracked between 1 September and November 2006. The 95, 75, and 50% kernel probabilities are shown for each bi-weekly period and sample sizes are given in Table 3

Table 3 Estimated area used (km^2) by gray whales in biweekly periods using kernel density estimates

Period	*n*	95%	75%	50%
1–15 Sept.	7	13,354	3,628	1,953
16–30 Sept.	9	10,437	3,045	1,602
1–15 Oct.	6	7,097	2,016	1,083
16–31 Oct.	4	16,508	7,121	3,023
1–15 Nov.	3	14,872	6,462	3,242
16–30 Nov.	2	15,896	3,096	1,617
Mean		13,027	4,228	2,087

Overlapping land was removed from the analysis. *n* is the number of whales in the analysis in each period

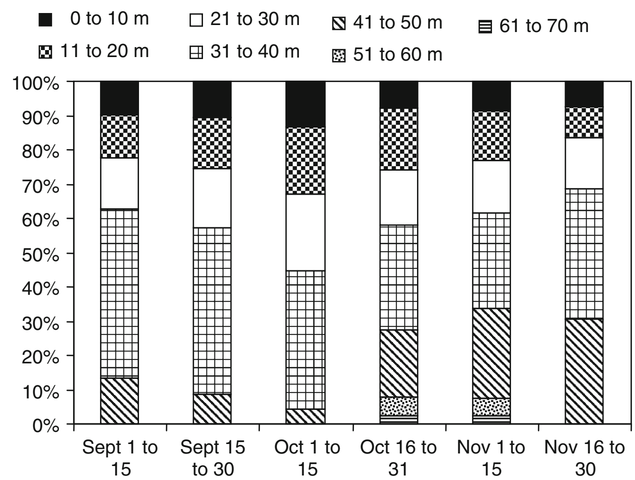

Fig. 4 Depth fractions comprised by the 50% kernel home range for biweekly periods between September 1 and November 20. Sample sizes are given in Table 3

probability regions identified additional focal sites including an area on the northern coast of Chukotka (Fig. 1). In November, there was also some affinity displayed for offshore areas.

The range estimates were relatively constant for each biweekly period. The area with 95% of the locations fluctuated between ~7,000 and ~17,000 km^2 with a mean of ~13,000 km^2 (Table 3). These localized areas were likely used for intensive feeding by the whales given their coastal shallow water locations.

Average daily locations linked to nearest depth values (meters) revealed that over 65% of positions collected from all whales were in depths <30 m. Furthermore, over 30% of the locations were in depths <20 m, demonstrating a particular affinity by the tagged whales for shallow water. Late in the season, whales shifted south along the shore and focused their area use around a small pocket of deeper water (~70 m) just north of Arakamchechen Island. Despite this, few locations (<6%) were in waters deeper than 50 m. It was not possible to determine whether whales were diving into this deep pocket.

Similar results were obtained when range areas were stratified by depth (Fig. 4). In all biweekly periods, the largest percentage of area covered by the kernel ranges was depths between 31 and 50 m (ranging from 45 to 70% of the total kernel) and no difference was detected in this pattern between the 50, 75, and 95% kernel polygons, (i.e., only a minor fraction of the kernel areas included water depths >50 m). The ranges covered slightly deeper depths later in the season (after Oct. 15, >0.2 of the area was deeper than 40 m), similar to the patterns suggested from the bathymetry associated with mean daily locations.

Benthic data

We defined the primary feeding area in the Chukchi Sea as the region with ≤50 m water. Eighteen benthic stations sampled between 1984 and 1988 in waters areas around Chukotka and 20 benthic stations sampled in central Bering Strait in 2006 provided estimates of the density of benthic prey available to gray whales in water ≤50 m deep (Table 4; Fig. 1). Only ampeliscid amphipods were considered to be potential prey for gray whales given they are a dominant prey item for gray whales in the Bering Strait. The total benthic infaunal biomass varied between 35 and 1,459 g m^{-2} across the 20 stations in 2006 in the central Bering Sea, north of Saint Lawrence Island, with an average of 420 g m^{-2} (Fig. 1). The average biomass of ampeliscan amphipods in 2006 ranged from 0 to 214 g m^{-2} indicating a gross mean amphipod biomass of about 54 g m^{-2} at depths ≤50 m (SD = 75, Table 4) or about 13% of the total benthic biomass. Sampling during 1984–1988 was more scattered but an average biomass of ~141 g m^{-2} (SD = 82, Table 4) suggests that the biomass of ampeliscan amphipods at <50 m depth is at least as high in both the central Bering Strait and adjacent areas as that documented in 2006.

Discussion

Performance of tags

Gray whales are difficult to track for long periods using satellite telemetry because of their habit of foraging on sea beds where instruments are rubbed off or damaged during physical contact with the bottom. None of the tags showed any signs of battery exhaustion below 3 V. The cause of the tag failures was rejection by the whale, inter-whale contact, or bottom contact during feeding dives. Diving whales were frequently observed surfacing with large billows of sediment behind them which are likely artifacts of bottom feeding events.

Table 4 Biomass of amphipods in the Bering and Chukchi seas from Russian sampling (2004 and 2005), samples collected by Grebmeier et al. (1989) in 1984–1986 and 1988 (Grebmeier 1992), and from recent sampling in 2006

Station	Dates	Latitude	Longitude	Depth (m)	Number of samples	Abundance (spec./m^{-2})	Biomass Ampeliscid amphipods (g m^{-2})	Biomass total amphipods (g m^{-2})
45	8/9/1988	67.758	172.808	50	4	2,003	275.8	–
61	8/11/1988	67.333	169.750	45	4	4,193	34.9	–
72	8/11/1988	66.533	170.017	49	4	12,560	268.3	–
89	8/20/1988	65.239	169.356	45	4	12,348	165.2	–
100	8/22/1988	64.381	169.192	38	4	9,455	200.7	–
104	8/23/1988	63.853	170.211	30	4	17,693	35.4	–
11	8/12/2004	66.933	170.983	42	3	1,550	–	164.3
13	8/23/2005	66.933	170.983	43	3	1,356	–	138.0
120	7/4/1984	64.992	169.133	47	4	7,383	267.6	284.8
121	7/5/1984	65.184	168.540	50	4	2,865	127.2	133.1
123	7/7/1984	64.992	168.750	49	4	5,548	156.6	186.8
11	7/26/1985	64.967	169.202	45	4	5,845	147.9	165.0
18	7/27/1985	64.967	169.267	42	4	7,628	187.0	209.6
24	7/29/1985	64.966	168.459	44	4	6,398	148.7	164.5
27	7/30/1985	64.800	168.215	40	4	8,605	106.3	136.4
75	8/3/1985	64.683	169.010	43	4	8,908	222.7	261.2
80	8/3/1985	64.408	170.067	40	4	1,668	0.7	2.7
81	8/4/1985	64.666	169.766	42	4	3,245	162.2	165.5
104	8/8/1985	64.175	169.074	34	4	14,365	201.4	226.3
122	8/11/1985	64.367	169.416	40	4	5,555	116.47	126.5
2	8/29/1985	65.867	168.919	49	4	1,080	0.1	7.4
10	8/30/1985	67.501	168.919	48	4	9,188	114.4	133.2
90	7/22/1986	68.000	168.916	54	4	12,115	84.5	142.7
43	5/20/2006	64.285	171.611	50	4	1,108	0	2.0
44	5/20/2006	64.234	170.864	35	4	410	0	0.7
45	5/20/2006	64.189	170.116	39	4	0	0	0
46	5/20/2006	64.134	169.354	38	4	650	0	0.3
47	5/21/2006	64.064	168.615	35	4	2,048	13.9	15.6
48	5/21/2006	64.010	167.860	37	4	1,438	0.1	0.4
49	5/21/2006	64.368	168.042	37	4	9,698	22.0	27.1
50	5/21/2006	64.351	168.629	40	4	5,253	42.1	43.6
51	5/21/2006	64.394	169.279	41	4	935	0	0.2
52	5/22/2006	64.421	170.057	43	4	2,473	0	0.4
53	5/22/2006	64.474	170.831	43	4	1,693	0.1	0.4
54	5/22/2006	64.685	170.566	49	4	3,618	0	0.2
55	5/22/2006	64.658	169.934	46	4	1,925	0	0.7
56	5/22/2006	64.675	169.086	45	4	5,383	202.8	205.2
57	5/23/2006	64.645	168.127	35	4	12,605	17.9	21.8
58	5/23/2006	64.803	169.007	47	4	5,950	214.2	216.6
59	5/23/2006	64.953	169.855	47	4	2,075	70.8	71.0
60	5/23/2006	65.189	169.664	46	4	8,570	163.3	165.7
61	5/23/2006	64.997	169.134	48	4	6,515	164.7	166.6
62	5/24/2006	65.186	169.007	54	4	8,128	117.2	126.2
63	5/24/2006	64.989	168.411	47	4	6,460	109.6	112.1
64	5/24/2006	65.191	168.391	48	4	3,123	64.6	65.1
65	5/24/2006	65.424	168.422	59	4	4,055	2.1	2.6
76	5/25/2006	65.409	168.989	55	4	10,608	136.2	140.0

Movements and focal area usage

Whales were tracked as late as November 22 in this study, and there were no movements that suggested the whales were initiating a southbound migration. Gray whales have been seen in the northern Bering Sea as late as mid-December (Kibal'chich et al. 1986) and some may remain in the Beaufort Sea year round (Stafford et al. 2007).

The daily velocities for individuals tagged in this study were low (in some cases <1 km day^{-1}). Gray whales tracked in and around San Ignacio Lagoon, Mexico, travelled 6–123 km daily (Mate et al. 2003), and one whale traveling northward along the California coast moved at a speed of 134 km day^{-1} (Mate and Urban-Ramirez 2003). The low velocities reported here likely reflect the fact that Chukotka is a foraging area and whales concentrate on feeding in the region without the need to make long or rapid movements to new areas.

The behavior of the tagged whales, with focused movements in a relatively small area over 3 months, distinguishes the foraging tactics of gray whales from other large baleen whales. In comparison, humpback whales (*Megaptera novaeangliae*) make trips that exceed 100 km day^{-1} or even as high as 200 km day^{-1} on their North Atlantic feeding grounds (Heide-Jørgensen and Laidre 2007). Similar large movements are reported for humpback whales in the Antarctic (Zerbini et al. 2006, Dalla Rosa et al. 2008) and for minke (*Balaenoptera acutorostrata*), blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) in the north Atlantic (Heide-Jørgensen et al. 2001a, b, 2003). The exception to this is the bowhead whale (*Balaena mysticetus*), a species that also shows strong site fidelity to restricted feeding grounds and relatively small daily movements until the spring migration begins (Laidre et al. 2007). Benthic or epibenthic feeding baleen whales (gray and bowhead whales) likely encounter more predictable, yet spatially restricted prey concentrations (Laidre et al. 2007) than other baleen whale species that feed on pelagic fish or krill resources (Laidre et al. 2010).

Melnikov and Zagrebin (2005) reported that two-thirds of approximately 100 reported killer whale attacks on marine mammals along Chukotka over a 10-year period were on gray whales in the exact areas where the whales tracked in this study spent their time. The focused occurrence of gray whales at specific coastal sites off Chukotka makes them easy and predictable prey for killer whales. However, given this documented predation risk, the area along the coast of Chukotka is clearly of extreme importance for feeding and the energetic benefits of the productive area appear to outweigh the predation risk.

Examination of stomachs from gray whales harvested along Chukotka between August and September 1984 demonstrated that 85% of stomachs ($n = 91$) were half-full or completely full and that whales primarily fed on amphipods (Blokhin 1986). This is also in agreement with incidental observations of one harvested whale that had a full stomach in September 2005 (MPHJ unpublished data) and consistent with numerous observations of mud plumes from gray whales in the Bay of Laurentia in September 2005 and 2006.

The coast of Chukotka has long been known as a feeding ground for gray whales (Berzin 1984). Gray whale harvests have occurred in this area for centuries, if not millennia (cf. Krupnik 1987), and bone remains in aboriginal ruins are still present along the coast. The abundance of gray whales feeding along Chukotka is unknown, but is likely to be large given that a relatively large and stable harvest of about 125 whales has occurred annually in the area since 1985 (http://www.iwcoffice.org/conservation/table_aboriginal.htm). Past Soviet surveys along Chukotka did not provide sufficient information for deriving abundance estimates; however, they do show a continuous occurrence of gray whales close to the coast of the Chukotka Peninsula with few sightings beyond 35–50 km offshore (Berzin 1984, Yablokov and Bogoslovskaya 1984). Catch positions also indicate a continuum of gray whales around Chukotka (Blokhin 1984, Yablokov and Bogoslovskaya 1984).

It is possible that there is some age class segregation in the region, where relatively young whales and females are found closer to the coast and are more likely taken in the harvest. The estimated length of the whales tagged in this study was on average 11 m, the same as the length estimate for whales taken in the local harvest (Zimushko and Ivashin 1980; Blokhin 1986). Gray whales are assumed to reach sexual maturity at a length of ~11 m, they attain a maximum length of 15 m (Jones and Swartz 2002), so those whales found along the Chukotka Peninsula appear to be relatively small and could potentially represent the immature segment of the Eastern Pacific gray whale population (cf. Blokhin 1984).

Implications for carrying capacity for gray whales

The coastal zone along the Chukotka coast appears to be a very important feeding ground for gray whales in summer and early fall. This is supported by long-term whaling records in the area and other observations consistent with the tracking data reported in the present study. The gray whales tagged in this study were instrumented in a relatively small area around the eastern part of Chukotka (at 170°W), and they showed remarkable affinity for water depths <50 m. The average 95% area use was ~13,000 km^2 on the Chukotka coast, of which 34% or about 4,415 km^2, was in water depths <30 m.

It is well documented that almost 100% of the gray whale diet along Chukotka consists of amphipods

(Bogoslovskaya et al. 1981, 1982; Blokhin 1982) and that the whales feed intensively in this area (Blokhin 1986). Nerini (1984) estimated that an individual gray whale consumes about 409 kg day^{-1} of benthic prey per day, or ~61 tons during the five-month feeding period along Chukotka. The benthic biomass data presented here suggests a biomass of ampeliscid amphipods of ~54 g m^{-2} in the Bering Sea and nothing suggests that the biomass is lower in the area near the Chukotka coast. Unpublished data from Russian sampling of benthos along Chukotka in 1988 suggest an amphipod biomass 2–3 times that observed in this study (Sirenko, unpublished data). If it assumed that the potential prey density in the areas used by gray whales tagged in this study is 54 g m^{-2}, then these areas (13,000 km^2) alone can sustain predation by a gray whale population of >11,000 whales consuming 61 tons of amphipods annually per whale, assuming production/biomass (P/B) turnover ratio close to or exceeding 1 (Highsmith and Coyle 1990). The amphipod base around Chukotka occurs in waters <50 m and potentially covers an area >100,000 km^2. Even with a low P/B ratio in some parts of the area, there should still be sufficient benthic prey to sustain an eastern gray whale population at least the size of the currently (1998) accepted population estimate of 26,300 (http://www.iwcoffice.org/conservation/estimate.htm#table).

The Chirikov Basin subarea of the Bering Sea is also used seasonally for intensive feeding by gray whales (~12,000 km^2). The standing stock of ampiliscid amphipods in the Chirikov Basin was previously estimated to be 53.3 gm^{-2} in 1986, 40.1 gm^{-2} in 1987, and 42.3 gm^{-2} in 1988 (Highsmith and Coyle 1992). These values are similar to the average estimates from 2006 for the larger area in this study. The caloric density of amphipods in the Chirikov Basin was estimated to be 222 kcal m^{-2} in 1986 with an annual production in the same order of magnitude (Highsmith and Coyle 1990). Highsmith and Coyle (1992) estimated that if a gray whale population (projected through 2000) utilized an area of 37,500 km^{-2}, then the annual energetic requirement from feeding specifically in the Chirikov Basin would be 28 kcal m^2, or above what can be sustained assuming a trophic energy transfer of 10%. This study demonstrates that the potential feeding area used by gray whales is considerably larger than the Chirikov Basin. Whales tracked in this study did not visit the Chirikov Basin but instead foraged along much of the Chukotka coast. The data presented here support the idea that both the standing biomass and the annual production of amphipods in the northern Bering and southern Chukchi seas are sufficient to sustain a gray whale population at least the current size.

Gray whales also feed in areas beyond those indicated in Fig. 1. The species occurs as far north as 71°N in the Chukchi Sea and as far east as 161°E on the northern Chukotka coast (Miller et al. 1985; Bobkov 1994, Kochnev 1998; Belikov and Boltunov 2002). Gray whales also feed on summering grounds in Alaska, Oregon, and Washington states in the USA (Nerini 1984; Dunham and Duffus 2001, 2002; Moore et al. 2007).

Considering the abundance of benthic prey available in the Bering and Chukchi seas together with opportunities for feeding in other areas, it is likely that there is more than sufficient forage to support the current gray whale population if prey availability is considered to be the primary factor for controlling population size. It is unlikely that a single factor limits the growth of the population, and environmental changes are likely going to impact available prey densities or distribution in the future. Nevertheless, abundant forage on Arctic feeding grounds has a significant impact on the distribution and densities of migratory baleen whales that fast seasonally for several months and use productive Arctic waters to feed intensively in summer and fall (Rice and Wolman 1971; Laidre et al. 2007; Heide-Jørgensen and Laidre 2007; Laidre et al. 2010).

Acknowledgments We thank the personnel at LGL Limited, Sidney, BC, for their enthusiasm and generous support during the preparation of this field effort. We are especially indebted to Stephen Johnson, Sonya Meier, and Sergei Yazvenko who all put an enormous effort into facilitating this project. A permit to deal with endangered species was issued by Ministry of Natural Resources of Russian Federation (Moscow) after ratifications by the Chukotka Department of Natural Resources, the VNIIpriroda (Moscow)—scientific consulting institute for all endangered species, at the Ichtyological Commission Meeting in Moscow. The permits to use radio frequencies were issued by State Radio Frequency Center (Moscow) after review by the State Frequency Commission (Moscow). The permit to use tags on gray whales was issued by Ministry of Defence (Moscow). Permits to bring tags to Russia and lift custom fees were issued by Russian Customs. Bruce Mate kindly loaned us air guns for the field work. The permit for foreign field participants to come to Chukotka was issued by the military border guard. Benthic samples were collected through grants to J.M. Grebmeier from the US National Science Foundation (e.g., OPP-ARC-045454), National Oceanic and Atmospheric Administration, and U.S. Fish and Wildlife Service. This study was funded by Exxon Mobil and Sakhalin Energy Investment Ltd. through a grant to LGL Limited.

References

Belikov SE, Boltunov AN (2002) Distribution and migrations of cetaceans in the Russian Arctic according to observations from aerial ice reconnaissance. NAMMCO Sci Publ 4:69–86

Berzin AA (1984) Soviet studies on the distribution and numbers of the gray whale in the Bering and Chukchi Seas from 1968 to 1982. In: Jones ML, Swartz SL, Leatherwood S (eds) The gray whale. Academic Press, Massachusetts, pp 409–419

Blokhin SA (1982) Investigations of gray whales taken off Chukotka in 1984. Rep Int Whal Commn 32:375–380

Blokhin A (1984) Investigations of gray whales taken in the Chukchi coastal waters, USSR. In: Jones ML, Swartz SL, Leatherwood S (eds) The gray whale. Academic Press, Massachusetts, pp 487–509

Blokhin SA (1986) Investigations of gray whales taken off Chukotka in 1984. Rep Int Whal Commn 36:287–290

Bluhm BA, Coyle KO, Konar B, Highsmith R (2007) High gray whale relative abundances associated with an oceanographic front in the south-central Chukchi Sea. Deep-Sea Res II 54:2919–2933

Bobkov AV (1994) The summer distribution of marine mammals in the coastal Chukchi and East Siberian Seas//Vladivostok. Biol Moria J 20(5):365–373 (in Russian)

Bogoslovskaya LS, Votorogov LM, Semenova TN (1981) Feeding habits of the gray whales off the Chukotka Peninsula. Rep Int Whal Commn 31:507–510

Bogoslovskaya LS, Votorogov LM, Semenova TN (1982) Distribution and feeding of gray whales off Chukotka in the summer and autumn of 1980. Rep Int Whal Commn 32:385–389

Boyd IL, McCafferty DJ, Reid K, Taylor R, Walker TR (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). Can J Fish Aquat Sci 55:845–852

Clarke JT, Moore SE (2002) A note on observations of gray whales in the southern Chukchi Sea and northern Bering Seas, August-November, 1980–1989. J Cetacea Res Manag 4(3):283–288

Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC (2007) Amphipod prey of gray whales in the Northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002–2003. Deep-Sea Res II 54:2906–2918

Dalla Rosa L, Secchi ER, Maia YG, Zerbini AN, Heide-Jørgensen MP (2008) Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic peninsula. Polar Biol. doi:10.1007/s00300-008-0415-2

Darling JD, Keough KE, Steeves TE (1998) Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island BC. Mar Mammal Sci 14:692–720

Dunham JS, Duffus DA (2001) Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Mar Ecol Prog Ser 223:299–310

Dunham JS, Duffus DA (2002) Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. Mar Mammal Sci 18:419–437

Grebmeier JM (1992) Studies of pelagic-benthic coupling extended onto the Soviet continental shelf in the Bering and Chukchi Seas. Cont Shelf Res 13:653–668

Grebmeier JM, Feder HM, McRoy CP (1989) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II Benthic community structure. Mar Ecol Prog Ser 51:253–268

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461–1464

Harris RB, Fancy SG, Douglas DC, Garner GW, Amstrup SC, McCabe TR, Pank LF (1990) Tracking wildlife by satellite: current systems and performance. United States Department of the Interior, Fish and Wildlife Service. Fish Wildlife Tech Rep 30:52

Heide-Jørgensen MP, Laidre KL (2007) Autumn space-use patterns of humpback whales (*Megaptera novaeangliae*) in West Greenland. J Cetacea Res Manage 9(2):121–126

Heide-Jørgensen MP, Kleivane L, Øien N, Laidre KL, Jensen MV (2001a) A new technique for deploying satellite transmitters on baleen whales: tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. Mar Mammal Sci 17:949–954

Heide-Jørgensen MP, Nordøy ES, Øien N, Folkow LP, Kleivane L, Blix AS, Jensen MV (2001b) Satellite tracking of minke whales (*Balaenoptera acutorostrata*) off the north Norwegian coast. J Cetacea Res Manage 3(2):175–178

Heide-Jørgensen MP, Witting L, Jensen MV (2003) Inshore-offshore movements of two satellite-tagged fin whales (*Balaenoptera physalus*) off West Greenland. J Cetacea Res Manage 5(3):241–245

Highsmith RC, Coyle KO (1990) High productivity of northern Bering Sea benthic amphipods. Nature 344:862–864

Highsmith RC, Coyle KO (1992) Productivity of Arctic amphipods relative to gray whale energy requirements. Mar Ecol Prog Ser 83:141–150

Hoodge PN, Eichenlaub B (1997) Animal movement extension to Arcview, ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage

Jones ML, Swartz SL (2002) Gray whale *Eschrichtius robustus*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, Massachusetts, pp 525–536

Kibal'chich AA, Dzhamanov GA, Ivashin MV (1986) Records of Greenland right and gray whales in early winter in the Bering Sea. Rep Int Whal Commis 36:291–292

Kochnev AA (1998) The death of cetaceans in Chukchi Sea and Northeast passage (the straight between Wrangel Island and mainland): species structure, distribution and causes of death. Russ Zool J 77(5):601–605

Krupnik II (1987) The bowhead versus the gray whale in Chukotkan aboriginal whaling. Arctic 40(1):16–32

Laidre KL, Heide-Jørgensen MP, Nielsen TG (2007) Role of bowhead whale as a predator in West Greenland. Mar Ecol Prog Ser 346:285–297

Laidre KL, Heide-Jørgensen MP, Heagerty P, Cossio A, Bergstrom B, Simon M (2010) Spatial associations between large baleen whales and their prey in West Greenland. Mar Ecol Prog Ser 402:269–284

Leboeuf BJ, Perez-Cortes MH, Urban RJ, Mate BR, Ollervides UF (2000) High gray whale mortality and low recruitment in 1999: potential causes and implications. J Cetacea Res Manage 2:85–99

Mate BR, Urban-Ramirez J (2003) A note on the route and speed of a gray whale on its northern migration from Mexico to central California, tracked by satellite-monitored radio tag. J Cetacea Res Manage 5(2):155–157

Mate BR, Lagerquist BA, Urban-Ramirez J (2003) A note on using satellite telemetry to document the use of San Ignacio Lagoon by gray whales (*Eschrichtius robustus*) during their reproductive season. J Cetacea Res Manage 5(2):149–154

Mate B, Mesecar R, Lagerquist B (2007) The evolution of satellite-monitored radio tags for large whales: one laboratory's experience. Deep Sea Res II 54:224–247

Melnikov VV, Zagrebin IA (2005) Killer whale predation in coastal waters of the Chukotka Peninsula. Mar Mammal Sci 21(3):550–556

Miller RV, Johnson JH, Doroshenko NV (1985) Gray whales (*Eschrichtius robustus*) in the western Chukchi and East Siberian Seas. Arctic 38(1):58–60

Miller RV, Rugh DJ, Johnson JH (1986) The distribution of bowhead whales, *Balaena mysticetus*, in the Chukchi Sea. Mar Mammal Sci 2(3):214–222

Moore SE, DeMaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. Arctic 53:432–447

Moore SE, Urban RJ, Perryman WL, Gulland F, Perez-Cortes MH, Wade PR, Rojas Brachos L, Rowles T (2001) Are gray whales hitting 'K' hard ? Mar Mammal Sci 17:954–958

Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Can J Zool 81(4):734–742

Moore SE, Wynne KM, Kinney JC, Grebmeier JM (2007) Gray whale occurrence and forage southeast of Kodiak Island, Alaska. Mar Mammal Sci 23(2):419–428

Nerini M (1984) A review of gray whale feeding ecology. In: Jones ML, Swartz SL, Leatherwood S (eds) The gray whale. Academic Press, Massachusetts, pp 423–450

Rice D, Wolman AA (1971) Life history and ecology of the gray whale (*Eschrichtius robustus*). American Society of Mammalogy, Special Publications no. 3

Service Argos (1989) Service Argos Inc. Guide to ARGOS system, September 1989. CLS ARGOS, Toulouse

Stafford KM, Moore SE, Spillane M, Wiggins S (2007) Gray whale calls recorded near Barrow, Alaska, throughout the winter of 2003–04. Arctic 60:167–172

Votrogov LM, Bogoslovskaya LS (1980) Gray whales off the Chukotka Peninsula. Rep Int Whal Commn 30:435–437

Yablokov AV, Bogoslovskaya LS (1984) A review of Russian research on the biology and commercial whaling of the gray whale. In: Jones ML, Swartz SL, Leatherwood S (eds) The gray whale. Academic Press, Massachusetts, pp 465–509

Zerbini A, Andriolo A, Heide-Jørgensen MP, Pizzorno JL, Maia YG, van Blaricom GR, De Master DP, Simoes-Lopes P, Moreira S, Bethlem C (2006) Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. Mar Ecol Prog Ser 313:295–304

Zimushko VV, Ivashin MV (1980) Some results of soviet investigations and whaling of gray whales (*Eschrichtius robustus*, Lilljeborg, 1961). Rep Int Whal Commn 30:237–246