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Cetacean Habitat Selection in the Alaskan Arctic during Summer and Autumn

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ABSTRACT. Ten years (1982–91) of sighting data from aerial surveys offshore of northern Alaska were analyzed to investigate seasonal variability in cetacean habitat selection. Distinct habitats were described for bowhead whales (*Balaena mysticetus*), white whales (*Delphinapterus leucas*), and gray whales (*Eschrichtius robustus*) on the basis of habitat selection ratios calculated for bathymetric and ice cover regimes. In summer, bowheads selected continental slope waters and moderate ice conditions; white whales selected slope and basin waters and moderate to heavy ice conditions; and gray whales selected coastal/shoal waters and open water. In autumn, bowheads selected inner shelf waters and light ice conditions; white whales selected outer shelf and slope waters and moderate to heavy ice; and gray whales selected coastal and shoal/trough habitats in light ice and open water. Habitat differences among species were significant in both seasons (ANOVA $F > 28$, $p < 0.00001$). Interseasonal depth and ice cover habitats were significantly different for bowhead whales ($p < 0.00002$), but not for gray whales ($p > 0.35$). White whale depth habitat was significantly different between seasons ($p < 0.00002$), but ice cover habitat was not ($p < 0.08$).

Key words: Alaska, Arctic, Beaufort Sea, bowhead whale, Chukchi Sea, gray whale, habitat selection, white whale

RÉSUMÉ. Des données d’observation réalisées sur dix années (1982–1991) grâce à des relevés aériens au large de l’Alaska septentrional ont été analysées dans le cadre de recherches sur la variabilité saisonnière dans la sélection de l’habitat des cétacés. On a décrit des habitats distincts pour la baleine boréale (*Balaena mysticetus*), la baleine blanche (*Delphinapterus leucas*) et la baleine grise de Californie (*Eschrichtius robustus*) en se fondant sur les taux de sélection de l’habitat calculés pour le régime bathymétrique et celui de la couverture de glace. En été, la baleine boréale choisissait les eaux de la pente continentale et des conditions de glace modérée; la baleine blanche choisissait les eaux de la pente continentale et du bassin océanique, et des conditions de glace allant de modérée à épaisse; et la baleine grise choisissait des eaux côtières et de hauts-fonds ainsi que l’eau libre. En automne, la baleine boréale choisissait les eaux intérieures du plateau continental, où se trouvait une faible concentration de glace; la baleine blanche choisissait les eaux à l’extérieur du plateau et sur la pente, ainsi qu’une glace allant de modérée à épaisse; et la baleine grise choisissait des habitats côtiers et de hauts-fonds ou des fossés à faible concentration de glace et à eau libre. Les différences d’habitat entre les espèces étaient importantes durant les deux saisons (ANOVA $F > 28$, $p < 0{,}00001$). D’une saison à une autre, les habitats différaient sensiblement quant à la profondeur et à la couverture de glace pour la baleine boréale ($p < 0{,}00002$), mais pas pour la baleine grise ($p > 0{,}35$). La profondeur de l’habitat pour la baleine blanche variait sensiblement d’une saison à une autre ($p < 0{,}00002$), mais pas la couverture de glace ($p < 0{,}08$).

Mots clés: Alaska, Arctique, mer de Beaufort, baleine boréale, mer des Tchouktches, baleine grise de Californie, sélection de l’habitat, baleine blanche

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INTRODUCTION

The Alaskan Arctic is a region of seasonal extremes. The southern extent of sea ice varies by over 1000 km between March and September, and transport through Bering Strait by about 1.0 Sv between March and July (Niebauer and Day, 1989; Roach et al., 1995). Although killer whales (*Orcinus orca*) and harbor porpoise (*Phocoena phocoena*) are regular visitors (Suydam and George, 1992; George and Suydam, 1998), bowhead whales, white whales, and gray whales are the only cetacean species that routinely migrate to and feed in the Alaskan Arctic in conspicuous numbers. These species display distinct differences in preferred prey and foraging dynamics. Bowhead whales filter zooplankton (e.g., copepods and euphausiids) on long (to 4.9 m), finely fringed baleen (Lowry, 1993). White whales (also called beluga, or belukha, whales) catch nekton with monodont teeth (Stewart and Stewart, 1989). Arctic cod (*Boreogadus saida*) are thought to be their primary prey in the Alaskan Beaufort Sea, with cephalopods, shrimps, and other fishes taken occasionally (Frost and Lowry, 1984). Gray whales are unique among

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mysticetes in that they suction sediment and benthic organisms (e.g., amphipods and mysiids) from the sea floor, then filter prey on short (to 25 cm), coarse baleen (Nerini and Oliver, 1983; Nerini, 1984). Of note, foraging gray whales create large excavations (2–20 m^2) that significantly alter benthic community structure (Oliver and Slattery, 1985) and in this way participate in a form of 'niche construction' (Odling-Smee et al., 1996).

Ten years (1982–91) of sighting data for bowhead, white, and gray whales resulted from aerial surveys conducted off the shores of northern Alaska in late summer and autumn. Surveys were funded by the Minerals Management Service (MMS), a branch of the United States Department of the Interior, and their primary goal was to ascertain the timing and character of the autumn bowhead whale migration in relation to oil and gas development offshore of northern Alaska. In addition to permitting a variety of descriptive accounts of cetacean distribution and relative abundance (e.g., Moore and Reeves, 1993), data from these surveys were integrated for the first time to provide a provisional description of cetacean seasonal distribution and habitat associations (Moore and DeMaster, 1997). Here, we refine that description by calculating habitat selection ratios to provide the first-ever quantitative index of cetacean seasonal habitat selection in the Alaskan Arctic.

Alaskan Arctic Oceanography

A brief overview of oceanographic patterns offshore of northern Alaska is provided as background for discussion of cetacean seasonal habitat selection. The northern Bering and Alaskan Chukchi and Beaufort Seas represent distinctly different bathymetric habitats. The Bering Sea, north of St. Lawrence Island, consists of the shallow Chirikov Basin (between Norton Sound and the Gulf of Anadyr) and the narrow Bering Strait (Fig. 1). The Chukchi Sea is broad and shallow. Its topographic features include the Herald and Hanna shoals and the Barrow, Herald, and Hanna Sea submarine canyons. Conversely, the Beaufort Sea's narrower continental shelf is demarcated by a steep slope that drops to abyssal depths within 70–150 km of shore.

Transport of North Pacific water through the Bering Strait defines the character of the Chukchi Sea and strongly influences the hydrography of the Beaufort Sea. There is a marked, wind-driven seasonal cycle, with maximium and minimum northward transport in June and February, respectively (Coachman and Aagaard, 1988; Roach et al., 1995). Overall, summer transport is roughly 50% greater than in winter (Aagaard et al., 1985). Two water masses enter the Chukchi Sea: the saline Bering Sea Water (BSW: 32.2–33.0 psu) and the comparatively fresh Alaskan Coastal Water (ACW: 32.1–32.5 psu). Both are bathymetrically channeled towards Point Hope (ca. 68˚30'N), where they bifurcate (Fig. 2). From there, the BSW flows northwestward to about 70˚N, 175˚W, then turns northward and enters the Arctic Basin through Herald Canyon, while the ACW flows northeastward along the Alaskan coast and enters the Arctic Ocean through Barrow Canyon (Paquette and Bourke, 1981; Bourke, 1983). At Barrow Canyon, the ACW encounters a third major water mass, the Resident Chukchi Water (RCW), consisting of water that has remained on the shelf from the previous winter and incursions of water onto the shelf from the Arctic Basin (Overland and Roach, 1987).

In the Beaufort Sea, BSW and ACW are identifiable on the outer shelf (seaward of the 50 m isobath) as the subsurface, eastward-flowing Beaufort undercurrent (Aagaard, 1984). The warm, relatively fresh ACW mixes with ambient surface waters as it flows eastward and is usually not clearly identifiable east of about Prudhoe Bay (147–148˚W), while the BSW can be traced at least to Barter Island (143˚W). Although the northern extent of the undercurrent is poorly defined, Aagaard (1984) suggests it extends from about the 50 to the 1000–2000 m isobaths, a horizontal distance of 60–70 km. Seaward of the undercurrent is a westward flow, known as the Beaufort Gyre. On the Beaufort Sea inner shelf, current flow is usually westward, driven by the prevailing easterly winds. However, inner shelf circulation responds quickly to wind change, so that under westerly winds, the flow is eastward (Fissel et al., 1987). Significant flow on the inner shelf is primarily a phenomenon of summer and early autumn, when winds drive near-surface currents at about 3% of wind speed.

Sea ice typically covers the Beaufort and Chukchi Seas from December through July, with the furthest retreat of ice cover (between 72˚ and 75˚ N) in September (Niebauer and Schell, 1993). The ice edge, or marginal ice zone (MIZ), a 10–100 km wide dynamic boundary between ice cover and open water, features sharp temperature and salinity fronts and is an area of upwelling and localized productivity (Paquette and Bourke, 1981). Ice edge location is driven primarily by wind stress (Rogers, 1978), although in the Chukchi Sea, the pattern of MIZ deformation is also directly influenced by the intrusion of relatively warm water currents mentioned above (Bourke, 1983). Inter-annual differences in MIZ position can be as great as 400 km, with daily ice drift of 2 to 9 km/day (Muench et al., 1991).

METHODS

Study Area and Aerial Survey Protocol

The study area extended north from 64˚N to 73˚N, between 169˚W and 140˚W; south of 65˚30'N, surveys were occasionally flown to 171˚W. Line transect aerial surveys were flown in blocked subsets of this broad region (Fig. 3). Transects were flown at 150 to 460 m altitude between randomly determined start and end points, maintaining a speed of 220 to 300 km/h (Ljungblad et al., 1986).

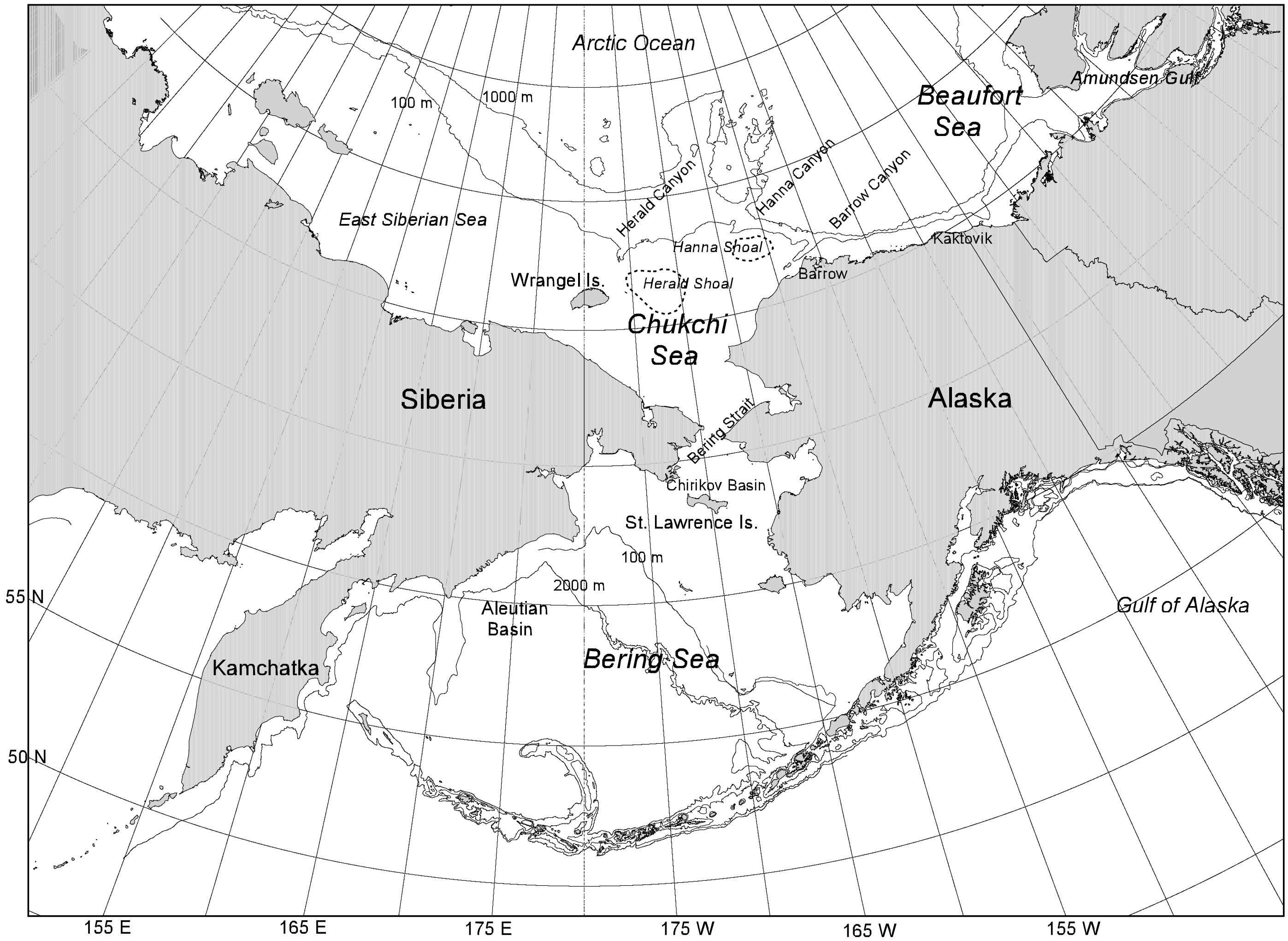


FIG. 1. Bathymetry of the Bering, Chukchi and Beaufort Seas. Isobaths are 100, 200 and 1000 m; modified from Niebauer and Schell (1993). Revised from Moore and DeMaster (1997: Fig 1A).

Two primary observers maintained a continuous watch for marine mammals, one from on each side of the aircraft, while a third observer/recorder entered data for each sighting, whenever survey conditions changed, or every ten minutes. Data routinely logged when cetaceans were seen included time, altitude, position, sea state, ice cover, visibility range, species, inclinometer angle (to determine distance from the trackline), number of whales, initial heading and behavior. Sea state was classified according to the Beaufort scale (Chapman, 1977), and ice cover estimated as a percentage of the sea surface. Additional details of survey protocol are provided elsewhere (e.g., Moore and Clarke, 1992; Moore, 1997).

Available Data and Statistical Approach

Overall survey effort consisted of 634 flights, with 139 flown in summer (July and August) and 495 in autumn (September and October). Summer surveys were not conducted from 1987 to 1990, and there was only one summer flight in 1991, on 31 August. Sightings made during randomly derived transect legs are considered a random sample (Buckland et al., 1993) and are hereafter called transect-sightings (t-SI), each of which represents the location of one or several animals. The number of t-SI, not the total number of whales, was used in all analyses because circling to obtain "best estimates" of group size was seldom conducted. Although surveys were sometimes continued when sea states exceeded Beaufort 04, cetacean detection in seas of Beaufort 05 and higher is severely hampered by whitecaps and considered poor (e.g., Forney et al., 1995). Therefore, survey effort was post-stratified to include only transect-kilometres (t-km) during good (i.e., Beaufort ≤ 04) sea conditions. Post-stratification resulted in 60 728 t-km of survey effort in summer, and 216 026 t-km in autumn (Moore and DeMaster, 1997: Fig. 3). Concomitant cetacean sightings comprised 722 t-SI in summer (79 bowhead whale, 146 white whale, and 497 gray whale) and 1271 t-SI in autumn (475 bowhead whale, 685 white whale, and 111 gray whale).

Water depth and sea ice cover were the only two environmental features recorded on the same temporal and spatial scale as cetacean sightings, restricting habitat selection analyses to these two parameters. Post-survey

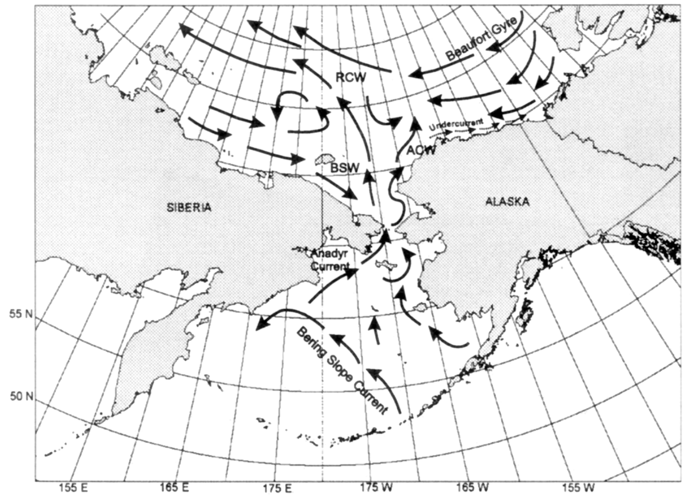


FIG. 2. Surface currents in the Bering, Chukchi, and Beaufort Seas: Bering Sea Water (BSW); Alaska Coastal Water (ACW); and Resident Chukchi Sea Water (RCW). Beaufort undercurrent shown as dashed arrows along Beaufort continental slope; modified from Niebauer and Schell (1993). Revised from Moore and DeMaster (1997: Fig. 1B).

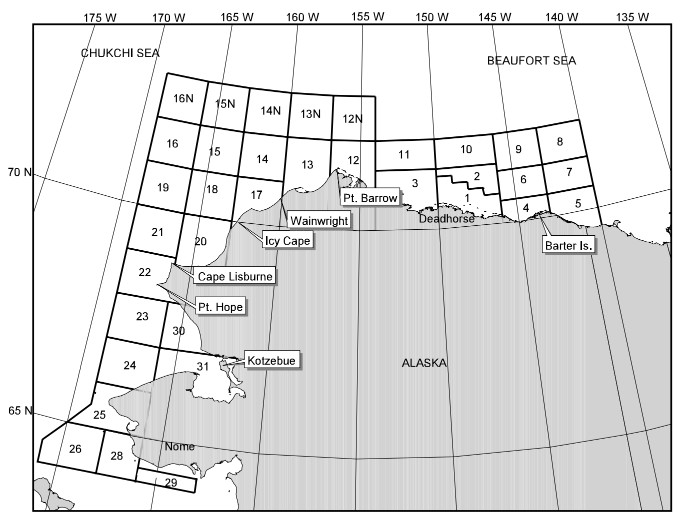


FIG. 3. Aerial survey study area and survey blocks. Revised from Moore and DeMaster (1997: Fig. 2A).

stratification of the study area into bathymetric subregions provided a means to calculate survey effort (t-km) and cetacean sightings (t-SI) by depth regimes that correspond to broad patterns of current flow offshore of Alaska. Referring to NOAA Charts 16003, 16004, and 16005, isobaths of 50 m, 200 m, and 2000 m were used to establish bathymetric-block boundaries in the Beaufort Sea, while 35 m, 50 m, and 200 m isobaths were adopted as boundaries in the Chukchi and northern Bering Seas (Fig. 4). Depth regimes and oceanographic features associated with the bathymetric blocks are summarized in Table 1. Survey effort and t-SI were similarly post-stratified by ice cover class in increments of 10% surface cover.

Habitat selection was tested via chi-square analysis and the calculation of habitat selection ratios (Manly et al., 1993). The chi-square test was used to investigate the null hypothesis that the distribution of cetacean t-SI was proportional to survey effort for each depth and ice cover habitat regime. The Pearson chi-square statistic was calculated as:

$$\chi^2 = \sum (0_i\text{-}E_i)^2/E_i \qquad (1)$$

where 0_i is the observed number of cetacean t-SI by depth regime, or ice cover percentage, E_i is t-SI expected by survey effort if distribution is uniform, and I-1 gives the degrees of freedom where I is the number of habitat categories (Manly et al., 1993:43). A standard condition for the chi-square test to be valid is that expected frequencies should be greater than 5. Results of the test when $E_i < 5$ may still be valid, but should be treated with caution. To address this concern, ice cover was grouped into habitat regimes to provide an evaluation of selection of open water/light (0–10%), light/moderate (11–40%), moderate/heavy (41–70%), and heavy (71–100%) ice cover conditions. Even so, sample sizes sometimes still resulted in cases where $E_i < 5$, and these cases were so noted.

Following the chi-square test, habitat selection ratios (w_i) were calculated as:

$$w_i = o_i/pE_i \qquad (2)$$

where, o_i = proportion of cetacean t-SI observed in habitat *i;* and pE_i = proportion of survey effort (t-km) in habitat *i*. Selection ratios were subsequently standardized (B_i) as:

$$B_i = w_i \,/ \sum_{i=1} w_j \qquad (3)$$

to provide a measure of the estimated probability that a category *i* habitat unit would be the next one selected if it were possible to make all habitat types equally available. Standardized ratios provide indices of habitat selection that are directly comparable among species and between seasons (Manly et al., 1993). In cases where standardized selection ratios indicated habitat preference, but the Pearson chi-square statistic was not significant, a chi-square statistic with one degree of freedom was derived for specific selection ratios, via calculation of the standard error (se) of w_i, as:

$$se(w_i) = \sqrt{[(1 - pE_i)/u_+ pE_i)]} \qquad (4)$$

where, pE_i is the proportion of survey effort in the category tested and u_+ is the total t-SI sample size; then

$$\chi^2 = (w_i\text{-}1)^2/se(w_i)^2 \qquad (5)$$

Testing selection ratios in this manner provided a means to examine specific habitat categories for significance, as recommended in Manly et al. (1993).

Finally, interspecific habitat selection variability was tested via analysis of variance (ANOVA), for differences in mean depth and ice cover between summer and autumn cetacean t-SI. The ANOVA provided an alternative means

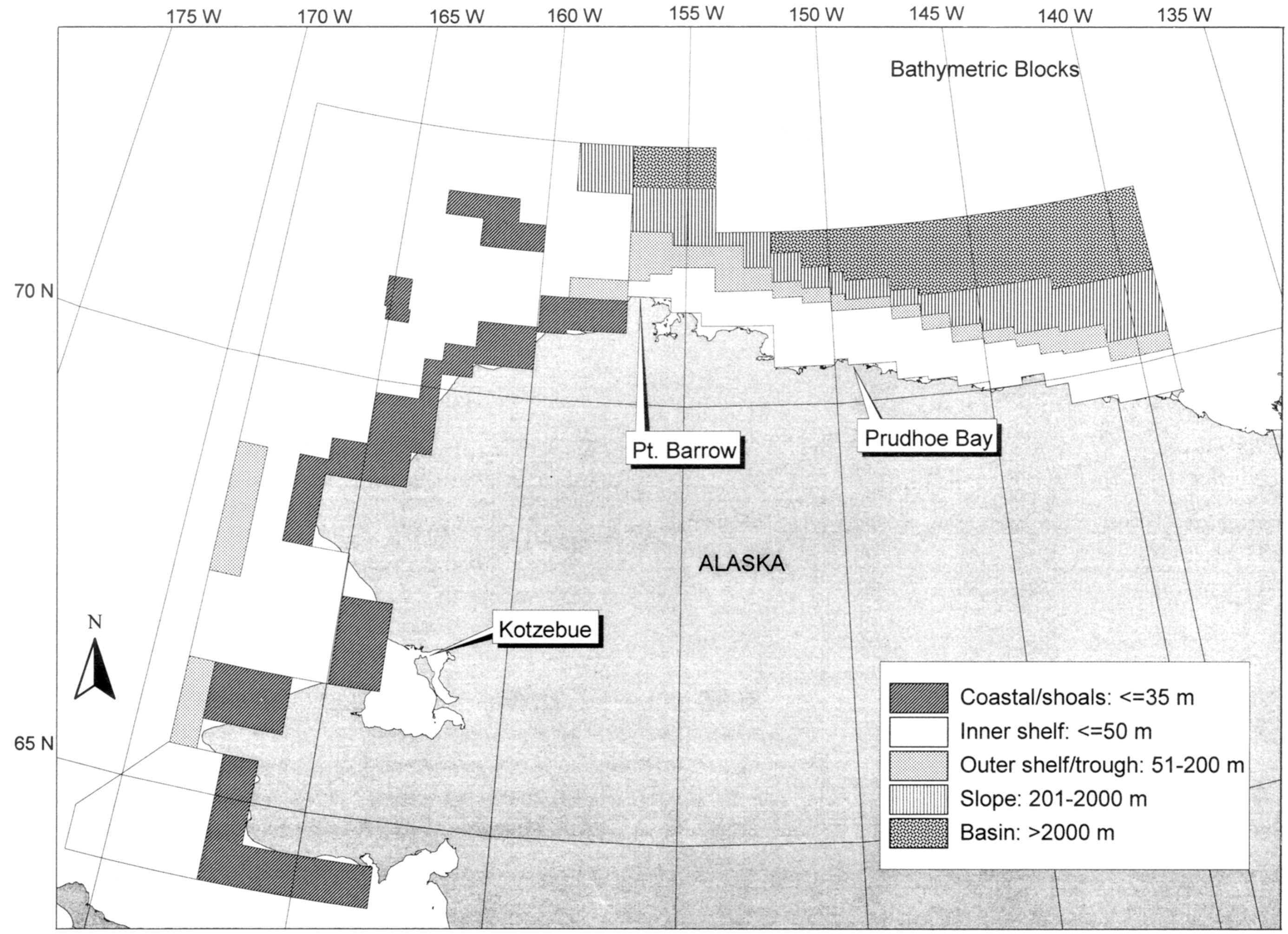


FIG. 4. Bathymetric blocks defined for the study area, based on NOAA depth charts.

to evaluate differences in average depth and ice cover habitats among species and between seasons and was calculated to augment habitat selection ratios. The significance of differences among paired means was tested by the Tukey "honestly significant difference" (HSD) procedure. The ANOVA and Tukey HSD tests were carried out using STATISTICA (StatSoft, 1995).

RESULTS

Summer Habitat Selection

In summer, bowhead and white whales were seen only in the Alaskan Beaufort Sea (Figs. 5 and 6). Distribution was not uniform with respect to depth (Table 2). Both species were observed far more often than expected in continental slope (201–2000 m) habitat, and far less frequently than expected in inner shelf (< 50 m) habitat. For both species, standardized selection ratios were highest for continental slope habitat (Table 3). Bowheads selected slope habitat ($B_2 = 0.48$) four times as often as inner shelf habitat ($B_4 = 0.11$) and five times as often as basin habitat ($B_1 = 0.09$), and they chose outer shelf habitat ($B_3 = 0.32$) nearly three times as often as inner shelf waters. White whales selected basin ($B_1 = 0.33$) nearly as often as slope ($B_2 = 0.38$) habitat, and both of these were five to six times as likely to be selected as inner shelf habitat ($B_4 = 0.06$).

TABLE 1. Depth regime and oceanographic features delimited by bathymetric blocks depicted in Figure 4. Oceanographic features are those shown in Figures 1 and 2.

Bathymetric Block (m)	Oceanographic Features (bathymetry; currents)
Beaufort Sea	
> 2000	Canadian Basin; Beaufort Gyre
201–2000	Continental Slope; Beaufort Undercurrent
51–200	Outer Shelf; Beaufort Undercurrent
≤ 50	Inner Shelf; Wind-driven Surface Currents
Chukchi Sea	
> 200	Continental Slope; Beaufort Gyre
51–200	Shelf/Trough; Bering Strait and Barrow Canyon
36–50	Continental Shelf; BSW/ACW
≤ 35	Coastal/Shoal areas; border BSW/ACW
Northern Bering Sea	
36–50	Shelf/Chirikov Basin; BSW/ACW
≤ 35	Coastal/Norton Sound; ACW

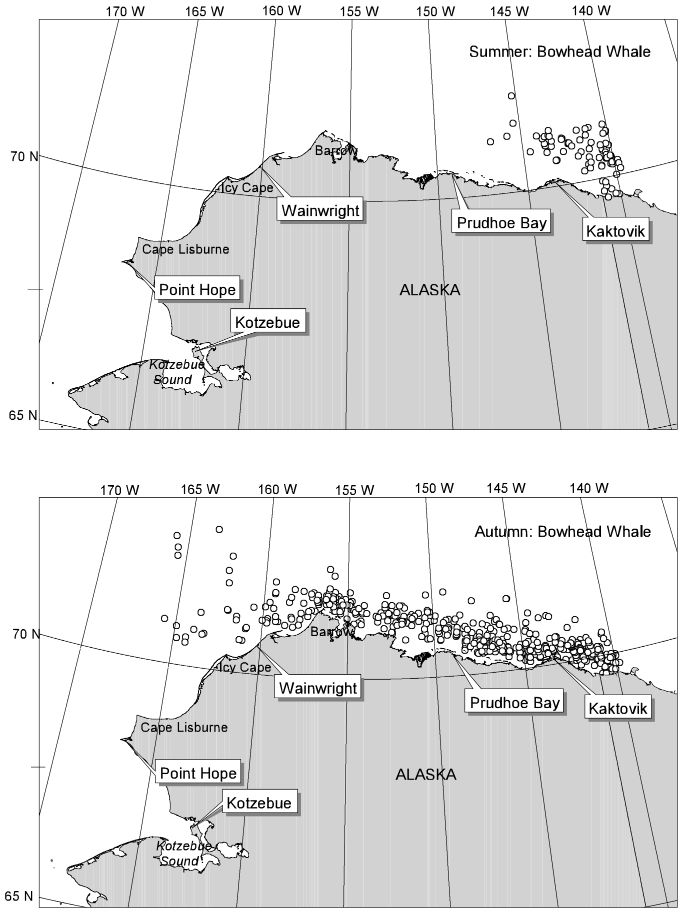


FIG. 5. Bowhead whale seasonal distribution: summer (79 t-SI) and autumn (475 t-SI). Each symbol indicates the location of one or more whales. Revised from Moore and DeMaster (1997: Fig. 4).

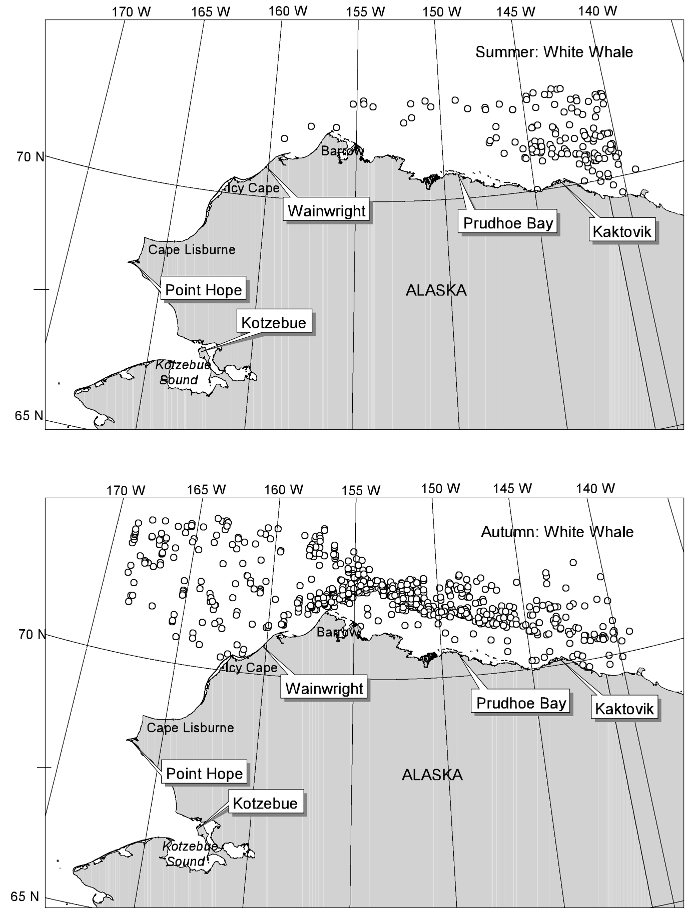


FIG. 6. White whale seasonal distribution: summer (146 t-SI) and autumn (685 t-SI). Each symbol indicates the location of one or more whales. Revised from Moore and DeMaster (1997: Fig. 6).

TABLE 2. Bowhead (BH) and white whale (WW) transect sightings by depth regime in the eastern Alaskan Beaufort Sea, summer 1982–86.

Depth Regime (m)	Effort (t-km)	Observed		Expected	
		BH	WW	BH	WW
> 2000	9022	6	41	18	30
201–2000	12389	47	64	25	41
51–200	6047	15	18	12	20
≤ 50	11985	11	9	24	41
Total	39443	79	132	79	132
			χ^2 =	35	42
			p <	0.001	0.001

TABLE 3. Depth regime selection ratios (w_i) and standardized ratios (B_i) for bowhead and white whales in the eastern Alaskan Beaufort Sea, summer 1982–86.

Depth Regime (m)		Bowhead Whales			White Whales		
	pE_i	o_i	w_i	B_i	o_i	w_i	B_i
> 2000	0.23	0.08	0.348	0.09	0.31	1.348	0.33
201–2000	0.31	0.59	1.903	0.48	0.48	1.548	0.38
51–200	0.15	0.19	1.267	0.32	0.14	0.933	0.23
≤ 50	0.31	0.14	0.452	0.11	0.07	0.226	0.06
Total	1.0	1.0	3.970	1.0	1.0	4.055	1.0

The white whales selected outer shelf habitat nearly four times as often ($B_3 = 0.23$) as inner shelf habitat. Comparison of ratios between species indicates that bowheads selected outer shelf and slope habitat, and white whales selected outer shelf, slope, and basin waters.

While bowhead summer distribution appeared uniform with respect to ice cover, white whales were observed more often than expected in 0–10% and 71–100% ice cover habitat, and far less often than expected in 11–40% ice cover habitat (Table 4). Although not statistically significant, standardized selection ratios indicated bowheads were seen nearly twice as often in 0–10% ice cover ($B_1 = 0.30$) and 41–70% habitat ($B_3 = 0.33$) as in 71–100% ice cover ($B_4 = 0.17$; Table 5). Calculation of a chi-square statistic specifically for the 0–10% ice cover selection ratio (w_i =1.333) supported the contention that selection of this habitat was not significant ($\chi^2 = 2.2$, $p < 0.25$). White whales occurred with nearly equal likelihood in all ice habitats *except* 11–40% ice cover (Table 5). The chi-square statistic for the 11–40% ice cover selection ratio ($w_i = 0.083$) indicated that white whales avoid this habitat ($\chi^2 = 15.0$, $p < 0.001$).

TABLE 4. Bowhead (BH) and white whale (WW) transect sightings by ice cover percentage in the eastern Alaskan Beaufort Sea, summer 1982–86.

Ice Cover (%)	Effort (t-km)	Observed		Expected	
		BH	WW	BH	WW
0–10	8351	22	38	17	28
11–40	4883	9	2	9	16
41–70	5848	17	20	12	20
71–100	20361	31	72	41	68
Total	39443	79	132	79	132
			χ^2 =	6	16
			p <	0.25	0.01

TABLE 5. Ice category selection ratios (w_i) and standardized ratios (B_i) for bowhead and white whales in the eastern Alaskan Beaufort Sea, summer 1982–86.

Ice Category (%)	pE_i	Bowhead Whales			White Whales		
		o_i	w_i	B_i	o_i	w_i	B_i
0–10	0.21	0.28	1.333	0.30	0.29	1.381	0.39
11–40	0.12	0.11	0.917	0.20	0.01	0.083	0.02
41–70	0.15	0.22	1.467	0.33	0.15	1.000	0.29
71–100	0.52	0.39	0.750	0.17	0.55	1.058	0.30
Total	1.0	1.0	4.467	1.0	1.0	3.522	1.0

Gray whale summer distribution was concentrated in the northern Bering Sea, with 93% (462 of 496) of all t-SI in the Chirikov Basin (Fig. 7). In the Chukchi Sea, gray whale sightings were clustered along the shore, mostly between Cape Lisburne and Point Barrow. Reflecting this pattern of distribution, gray whales were strongly associated with shallow (< 35 m) coastal/shoal habitat in the Chukchi Sea and with the somewhat deeper (36–50 m) Chirikov Basin shelf habitat in the northern Bering Sea (Table 6). Standardized selection ratios based on these data further exemplify the very strong association of gray whales with Chirikov Basin habitat ($B_2 = 0.95$), as well as their tenacious adherence to coastal/shoal habitat ($B_3 = 0.67$) in the Chukchi Sea (Table 7).

Gray whales were associated with ice only in the northern Chukchi Sea. During summer surveys, they were seen in ice conditions to 30% surface cover and, more often than expected, in 0–20% ice habitat ($\chi^2 = 12.5$; $p < 0.01$). Standardized habitat selection ratios also indicate the strong association of gray whales with this open water/light-ice habitat ($B_1 = 0.87$).

The summer habitats of the three cetacean species were defined by depth, and somewhat less so by ice cover. In the eastern Alaskan Beaufort Sea, bowhead whales occupied outer continental shelf and slope depth habitats, without regard to ice cover, while white whales selected continental slope and basin habitat and were primarily associated with 1–10% and 71–100% ice cover. Gray whale habitat was delimited by the northern Bering and Chukchi Seas, where depth selection ratios indicated strong association with the Chirikov Basin and coastal/shoal habitats, repectively. Gray whales were associated with ice only in the northern Chukchi Sea, where selection ratios indicated strong preference for 0–20% ice cover.

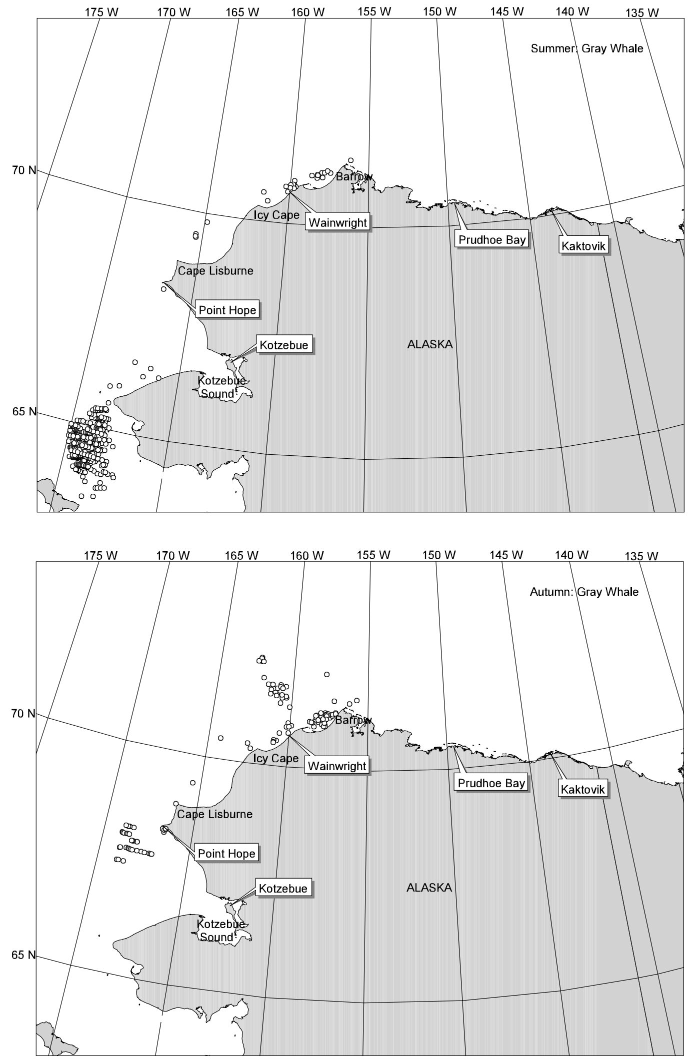


FIG. 7. Gray whale seasonal distribution: summer (497 t-SI) and autumn (111 t-SI). Each symbol indicates the location of one or more whales. Revised from Moore and DeMaster (1997: Fig. 5).

TABLE 6. Gray whale (GW) transect sightings (t-SI) by depth regime in the Chukchi Sea and northern Bering Sea, summer 1982–86.

Depth Regime (m)	Effort (t-km)	Observed GW	Expected GW
Chukchi Sea			
51–200	964	3	3
36–50	6278	4	20
≤ 35	3442	27	11
Total	10684	34	34
		χ^2 =	42
		p <	0.001
Northern Bering Sea			
36–50	3705	460	393
≤ 35	644	2	69
Total	4349	462	462
		χ^2 =	76
		p <	0.001

TABLE 7. Depth regime selection ratios (w_i) and standardized ratios (B_i) for gray whales in the northern and southern Chukchi Sea and northern Bering Sea, summer 1982–86.

Sea	Depth Regime (m)			Total
	51–200	36–50	≤ 35	
Chukchi Sea				
pE_i	0.09	0.59	0.32	1.0
o_i	0.09	0.12	0.79	1.0
w_i	1.000	0.203	2.469	3.672
B_i	0.27	0.06	0.67	1.0
Northern Bering Sea				
pE_i	na	0.85	0.15	1.0
o_i	na	0.99	0.01	1.0
w_i	na	1.165	0.067	1.232
B_i	na	0.95	0.05	1.0

Autumn Habitat Selection

In autumn, bowhead and white whales were distributed across the Alaskan Beaufort and northern Chukchi Seas (Figs. 5 and 6). In the Alaskan Beaufort Sea, neither bowhead nor white whales were distributed uniformly with respect to depth (Table 8). Bowheads were seen more often than expected in inner and outer shelf waters and far less often than expected in slope and basin waters. Conversely, white whales were seen far more often than expected in slope waters, and far less often than expected in inner shelf habitat. In the northern Chukchi Sea, bowheads were distributed uniformly with respect to depth, and white whales were observed more often than expected in slope (> 200 m) and shelf (36–50 m) habitat and less often than expected in coastal/shoal (< 35 m) waters.

Habitat selection ratios reflected differences evident in the chi-square analyses (Table 9). In the Alaskan Beaufort Sea, bowheads were strongly associated with inner continental shelf habitat ($B_4 = 0.48$), and white whales, with continental slope habitat ($B_2 = 0.48$). As in summer, bowheads seemed to avoid basin ($B_1 = 0.03$) and white whales inner shelf ($B_4 = 0.02$) habitats. In the northern Chukchi Sea, habitat selection ratios reflect the range of depth habitats for bowhead sightings. The apparent selection of shelf-trough habitat ($B_2 = 0.46$) was not significant ($\chi^2 = 1.83$, $p < 0.75$) and was possibly an artifact of comparatively low (5%) sampling effort. White whales appeared strongly associated with continental slope habitat ($B_1 = 0.56$; i.e., the same depth habitat selected in the Alaskan Beaufort Sea) and seemed to avoid coastal/shoal ($B_4 = 0.09$) waters.

Neither bowheads nor white whales were distributed uniformly with regard to ice cover (Table 10). In the Alaskan Beaufort Sea, bowheads were observed far more often than expected in 0–10% ice cover, and white whales, in moderate and heavy (i.e., 41–100%) ice cover. Conversely, in the northern Chukchi Sea, bowheads were observed more often than expected in 71–100% ice cover, while white whales appeared more often than expected in

TABLE 8. Bowhead (BH) and white whale (WW) transect sightings (t-SI) by depth regime in the Alaskan Beaufort and northern Chukchi Seas, autumn 1982–91.

Depth Regime (m)	Effort (t-km)	Observed		Expected	
		BH	WW	BH	WW
Alaskan Beaufort Sea					
> 2000	16708	5	88	46	57
201–2000	28549	29	261	80	98
51–200	31407	96	140	89	109
≤ 50	72711	291	28	206	253
Total	149375	421	517	421	517
			χ^2 =	117	453
			p < <	0.001	0.001
Northern Chukchi Sea					
> 200	1897	0	16	2	5
51–200	3037	5	8	3	8
36–50	44352	34	123	37	116
≤ 35	14995	15	21	12	39
Total	64281	54	168	54	168
			χ^2 =	4	33
			p <	0.25	0.001

TABLE 9. Depth regime selection ratios (w_i) and standardized ratios (B_i) for bowhead and white whales in the Alaskan Beaufort and northern Chukchi Seas, autumn 1982–91.

Depth Regime (m)		Bowhead Whales			White Whales		
	pE_i	o_i	w_i	B_i	o_i	w_i	B_i
Alaskan Beaufort Sea							
> 2000	0.11	0.01	0.091	0.03	0.17	1.545	0.27
201–2000	0.19	0.07	0.368	0.12	0.51	2.684	0.48
51–200	0.21	0.23	1.095	0.37	0.27	1.286	0.23
≤ 50	0.49	0.69	1.408	0.48	0.05	0.102	0.02
Total	1.0	1.0	2.962	1.0	1.0	5.617	1.0
Northern Chukchi Sea							
> 200	0.03	0.0	0.0	0.0	0.10	3.333	0.56
51–200	0.05	0.09	1.800	0.46	0.05	1.000	0.17
36–50	0.69	0.63	0.926	0.24	0.73	1.074	0.18
≤ 35	0.23	0.28	1.167	0.30	0.12	0.500	0.09
Total	1.0	1.0	3.893	1.0	1.0	5.907	1.0

all ice cover categories *except* 0–10%. Standardized habitat selection ratios also support these observations (Table 11). Bowheads were strongly associated with open water/light ice cover (0–10%) in the Alaskan Beaufort Sea ($B_1 = 0.58$), and with heavy ice cover (71–100%) in the northern Chukchi Sea ($B_4 = 0.42$). White whale selection ratios were highest for 41–70% ice cover in the Alaskan Beaufort Sea ($B_3 = 0.37$) and for 11–40% cover in the northern Chukchi Sea ($B_2 = 0.35$). Low selection ratios ($B_1 = 0.15$) reflected white whale avoidance of 0–10% ice cover in both the Alaskan Beaufort and northern Chukchi Seas.

In autumn, gray whale distribution in the Chukchi Sea was clustered near shore at Pt. Hope and between Icy Cape and Pt. Barrow, and in offshore waters northwest of Pt. Barrow (Hanna Shoal) and southwest of Pt. Hope (Fig. 7). There were more sightings than expected in shelf/trough

TABLE 10. Bowhead (BH) and white whale (WW) transect sightings (t-SI) by ice cover percentage in the Alaskan Beaufort and northern Chukchi Seas, autumn 1982–91.

Ice Cover (%)	Effort (t-km)	Observed		Expected	
		BH	WW	BH	WW
Alaskan Beaufort Sea					
0–10	65897	323	126	185	227
11–40	14855	16	52	42	52
41–70	19446	27	115	55	67
71–100	49177	55	224	139	171
Total	149375	421	517	421	517
			χ^2 =	184	95
			p <<	0.001	0.001
Northern Chukchi Sea					
0–10	35561	12	72	30	92
11–40	3593	3	8	3	10
41–70	4289	5	19	4	12
71–100	20838	34	59	17	54
Total	64281	54	168	54	168
			χ^2 =	28	15
			p <	0.001	0.005

TABLE 11. Ice category selection ratios (w_i) and standardized ratios (B_i) for bowhead and white whales in the Alaskan Beaufort and northern Chukchi Seas, autumn 1982–91.

Ice Category (%)	pE_i	Bowhead Whales			White Whales		
		o_i	w_i	B_i	o_i	w_i	B_i
Alaskan Beaufort Sea							
0–10	0.44	0.77	1.750	0.58	0.25	0.568	0.12
11–40	0.10	0.04	0.400	0.13	0.10	1.000	0.22
41–70	0.13	0.06	0.462	0.16	0.22	1.692	0.37
71–100	0.33	0.13	0.394	0.13	0.43	1.303	0.29
Total	1.0	1.0	3.006	1.0	1.0	4.563	1.0
Northern Chukchi Sea							
0–10	0.55	0.22	0.400	0.09	0.43	0.782	0.15
11–40	0.06	0.06	1.000	0.21	0.11	1.833	0.35
41–70	0.07	0.09	1.286	0.28	0.11	1.571	0.30
71–100	0.32	0.63	1.969	0.42	0.35	1.094	0.20
Total	1.0	1.0	4.655	1.0	1.0	5.280	1.0

and coastal/shoal depth habitats, and far fewer than expected in shelf waters (Table 12). Standardized habitat selection ratios showed strong gray whale preference for trough habitats (B_2 = 0.77), indicating that these waters may serve as corridors for the southbound migration (Table 13). As in summer, gray whales were observed far more often than expected in open water/light (0–20%) ice cover (χ^2 = 46; p < 0.001). Standardized selection ratios were identical to those calculated for summer distribution, and indicated gray whales were nearly seven times as likely to be seen in 0–20% ice cover (B_1 = 0.87) as in waters where ice cover exceeded 20%.

For all three cetacean species, autumn habitats—like summer habitats—were differentiated by depth selection and less so by ice cover regimes. Bowhead whales occupied continental shelf, white whales continental slope, and gray whales coastal/shoal habitats. Ice cover was somewhat less diagnostic. Bowheads selected open water/light ice cover in the Alaskan Beaufort Sea and heavy ice cover in the northern Chukchi Sea. White whales were associated with moderate to heavy ice cover, and seemed to avoid light ice cover in both seas. As in summer, gray whales selected open water to less than 20% ice cover in the northern Chukchi Sea.

TABLE 12. Gray whale (GW) transect sightings (t-SI) by depth regime in the northern Chukchi Sea, autumn 1982–91.

Depth Regime (m)	Effort (T-Km)	Observed GW	Expected GW
> 200	1897	0	3
51–200	3037	38	6
36–50	44352	27	75
≤ 35	14995	44	25
Total	64281	109	109
			χ^2= 219
			p<< 0.001

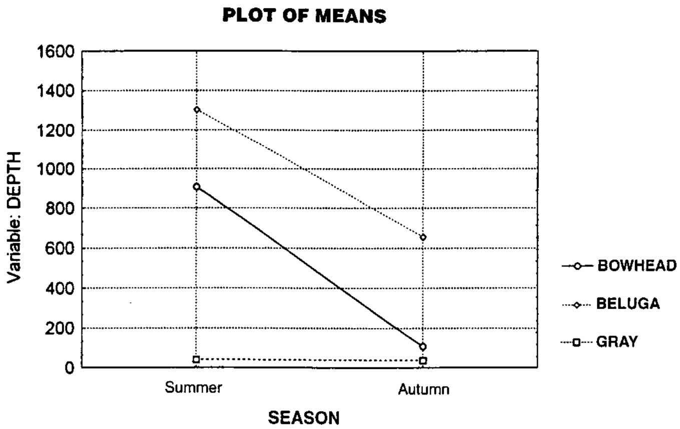
TABLE 13. Depth regime selection ratios (w_i) and standardized ratios (B_i) for gray whales in the northern Chukchi Sea, autumn 1982–91.

Depth Regime (m)	pE_i	Gray Whales		
		o_i	w_i	B_i
> 200	0.03	0.0	0.0	0.0
51–200	0.05	0.35	7.000	0.77
36–50	0.69	0.25	0.362	0.04
≤ 35	0.23	0.40	1.739	0.19
Total	1.0	1.0	9.101	1.0

Bathymetry and Ice Cover as Cetacean Habitat Indices

Results of the ANOVA depict strong significant differences for both mean depth and ice cover variables among t-SI for the three species ($F= 36.13_{depth}$; $F =28.45_{ice}$, p < 0.00001; Table 14). Bowhead whales displayed the sharpest seasonal differences, shifting from deep to shallow depths, and from moderate to open water/light ice cover habitats, between summer and autumn (Fig. 8). White whales also shifted to comparatively shallower water and lighter ice conditions from summer to autumn, although the differences were not as dramatic. Gray whale depth and ice cover habitat remained constant between seasons: shallow and nearly ice-free.

With few exceptions, cetacean depth and ice cover means were significantly different between seasons and among species (Table 14). Tukey HSD paired comparisons of mean depth at t-SI resulted in significant differences in all but gray whale interseasonal comparisons, and gray whale depth in either season compared to bowhead depths in autumn. Similarly, ice cover habitats were significantly different in all cases except interseasonal comparisons of white and gray whales (i.e., white whales were ice-associated and gray whales ice-phobic, in both seasons). White whale ice cover habitat in either season compared to that of bowheads in summer.



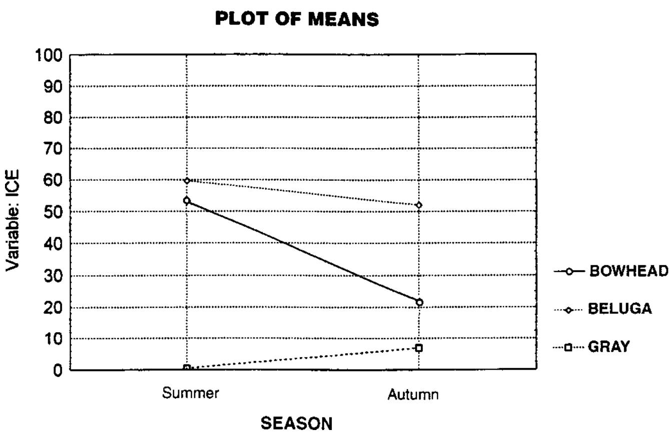


FIG. 8. Seasonal differences in depth and ice cover means among bowhead, beluga, and gray whales (see Table 14 for Tukey HSD comparisons).

The strong seasonal and interspecies differences in depth and ice cover associations shown in the ANOVA and Tukey HSD comparisons suggest bathymetry and sea ice cover are good indices of cetacean habitat partitioning offshore of northern Alaska. These analyses underscore seasonal distinctions in bowhead and white whale habitats, while emphasizing the comparatively static nature of gray whale habitat selection. Intraseasonal comparisons among the three species depict habitats demarcated by depth and by ice cover, except for bowhead and white whale ice cover habitat in summer.

DISCUSSION

Seasonal Habitats

Habitat selection ratios define seasonal differences in cetacean distribution within and among species and between seas in the Alaskan Arctic. In the Alaskan Beaufort Sea, bowhead whales shifted towards shore: from slope and outer shelf habitat in summer to inner/outer shelf waters in autumn. Bowheads were associated with a range of ice cover conditions in summer, but selected open water-light ice cover in autumn. White whale distribution also shifted shoreward from summer to autumn, from slope-basin to slope habitat. White whales selected both light and heavy (and seemed to avoid 11–40%) ice cover in summer, and moderate to heavy ice cover in autumn. In the northern Chukchi Sea, bowheads were associated with a range of bathymetric regimes, but selected heavy ice cover, in autumn. White whales selected slope waters associated with Barrow Canyon, and light to moderate ice cover. Gray whales selected predominantly ice-free habitat in both seasons. Their summer distribution was strongly weighted toward shelf waters of the northern Bering Sea (Chirikov Basin) where there was no ice and toward shallow coastal/shoal habitats in the northern Chukchi Sea. In autumn, grays shifted to shelf-trough habitat in the northern Chukchi Sea.

Seasonal habitat differences demonstrated by depth and ice cover selection ratios were supported by ANOVA results. Among the three species, white whales were consistently associated with the deepest water and heaviest ice cover, and gray whales with the shallowest water and lightest ice cover, while bowhead depth and ice cover habitat were intermediate to the two. While both analyses support the finding of cetacean seasonal habitat partitioning offshore of northern Alaska, only habitat selection ratios incorporate survey effort in their calculation and provide a means to associate distribution with oceanographic regimes.

Both habitat selection ratios and ANOVA results may be biased to some degree with regard to ice cover associations. Specifically, from analyses of detection distance, it appears that ice cover facilitated detection of white whales, but hampered detection of bowhead whales (Moore, 1997). Although correction factors could not be determined for lack of some means to quantify detection bias in various ice cover habitats, the implied bias must be kept in mind when making inferences about ice habitat selection. Gray whale detection distance was also negatively correlated with ice cover, but grays were seen so infrequently near ice that effects on habitat selection indices are likely negligible.

Depth did not affect detection distance for any of the three species (Moore, 1997). The selection of specific bathymetric regimes provides the clearest link to broad-scale oceanographic habitats offshore of northern Alaska. Bathymetry has been linked to cetacean habitat partitioning in other areas. Davis et al. (1995) found that depth was the most significant environmental variable in terms of habitat partitioning among cetaceans in the northern Gulf of Mexico. Baumgartner (1997) further refined this analysis for one species, reporting that Risso's dolphins (*Grampus griseus*) in the Gulf of Mexico are distributed nonuniformly with respect to both depth and depth gradient. Similarly, Hui (1985) reported that distribution of pilot whales (*Globicephala macrorhynchus*) and common dolphins (*Delphinus delphis*) offshore of southern California could be differentiated on the basis of bottom topography and speculated that differences may be related to dissimilar foraging patterns.

TABLE 14. Results of Tukey HSD paired comparisons of mean depth and ice cover at bowhead (BH), white whale (WW), and gray whale, (GW) t-SI in summer and autumn.

General ANOVA	F = 36.13 $p < 0.00001$	Tukey HSD test: variable **DEPTH** Interaction: 1 × 2					
Species	Season	(1) 906.9359	(2) 108.7747	(3) 40.68008	(4) 38.16364	(5) 1303.091	(6) 654.8438
BH	Summer (1)		.000020	.000020	.000020	.000238	.015218
BH	Autumn (2)	.000020		.578932	.909863	.000020	.000020
GW	Summer (3)	.000020	.578932		1.000000	.000020	.000020
GW	Autumn (4)	.000020	.909863	1.000000		.000020	.000020
WW	Summer (5)	.000238	.000020	.000020	.000020		.000020
WW	Autumn (6)	.015218	.000020	.000020	.000020	.000020	

General ANOVA	F = 28.45 $p < 0.00001$	Tukey HSD test: variable **ICE** Interaction: 1 × 2					
Species	Season	(1) 53.05128	(2) 21.96842	(3) .5372233	(4) 6.963636	(5) 59.66434	(6) 52.00438
BH	Summer (1)		.000020	.000020	.000020	.650707	.999754
BH	Autumn (2)	.000020		.000020	.000081	.000020	.000020
GW	Summer (3)	.000020	.000020		.357067	.000020	.000020
GW	Autumn (4)	.000020	.000081	.357067		.000020	.000020
WW	Summer (5)	.650707	.000020	.000020	.000020		.075741
WW	Autumn (6)	.999754	.000020	.000020	.000020	.075741	

Seasonal Habitats and Oceanographic Regimes

Because currents are bathymetrically channeled, cetacean seasonal habitats can be related to oceanographic regimes via selection ratios. For example, summertime selection of continental slope habitat by bowheads and white whales in the Alaskan Beaufort Sea indicates both species were associated with the Beaufort undercurrent, potentially an important conduit of nutrients and prey from the North Pacific (Aagaard, 1984). In autumn, bowheads selected continental shelf waters, where currents are largely wind-driven, while white whales remained in bathymetric habitat associated with the undercurrent. Bowheads did not exhibit bathymetric habitat selection in the northern Chukchi Sea in autumn. Conversely, white whales selected slope depths associated with Barrow Canyon, an extremely dynamic oceanographic feature (Aagaard and Roach, 1990).

The well-established importance of the Chirikov Basin to feeding gray whales (e.g., Nerini, 1984; Highsmith and Coyle, 1990, 1992) was underscored by summer habitat selection ratios presented here. This continental shelf region is a dynamic, highly productive zone where pelagic-benthic coupling maintains high populations of benthic fauna, especially ampelicid amphipods (Walsh et al., 1989; Grebmeier and Barry, 1991). In the northern Chukchi Sea, gray whales selected shoal and coastal areas where secondary productivity is influenced by carbon transport from ACW and BSW (Grebmeier et al., 1989). Gray whale selection of shoal and coastal habitat was strongest in summer. In autumn, gray whales selected trough habitats in the northern Chukchi Sea, a shift possibly coupled with a transition from feeding to migratory behavior.

Selection of ice cover habitat among the three species was less diagnostic than depth selection. It is important to emphasize that ice cover is, in part, influenced by patterns and strength of current flow, and current flow in turn is affected by bathymetry; therefore, these two variables are not completely independent. In summer, bowhead whales were associated with a range of ice cover habitats, but not significantly. In autumn, ice cover habitat selection shifted from light (≤ 10%) in the Alaskan Beaufort Sea to heavy (> 70%) in the northern Chukchi Sea. This result is particularly noteworthy because bowheads are often referred to as "pagophilic" (or ice-loving) at the outset of many scientific articles. Habitat selection ratios show that the association of bowheads with ice is not static. That is, while bowheads are indeed ice-adapted (e.g., George et al., 1989) and are often seen in heavy ice cover, they are not always associated with ice.

White whale association with ice was somewhat more consistent. While the highest ratio in summer indicated 0–10% ice cover was selected most often, white whales were also commonly seen in 41–70% and 71–100% ice cover habitat. Indeed, the significance of summertime ice habitat selection was based largely upon the (seeming) avoidance by white whales of the intermediate 11–40% ice cover regime. This 'ice habitat duality' may be related to behavior. In summer, some white whales commonly enter brackish lagoons and estuaries throughout their range, while others remain offshore (Hazard, 1988; Frost and Lowry, 1990; Frost et al., 1993). White whales seen in open water could be animals swimming to or from feeding or molting lagoon areas, while feeding or migrating whales occupy offshore habitats, where ice cover is heavier. This very behavior was dramatically demonstrated in the tracks of white whales equipped with satellite tags near Kasegaluk Lagoon in summer 1998 (Suydam et al., 1999) and 1999 (Suydam, pers. comm. 1999): some whales remained in the vicinity of the lagoon, while others swam over 2000 km, reaching 80˚N and 133˚W by traveling through 700 km of 90–100% ice cover. In autumn, white whales were associated with ice in both the Alaskan Beaufort and northern Chukchi Seas, though they selected somewhat lighter ice cover in the latter.

Ice cover habitat selection ratios must be interpreted with caution both because of bias in detection distance (Moore, 1997) and because study area boundaries can affect inferences of habitat use in environments where cover types are aggregated, such as sea ice. In model simulations, Porter and Church (1987) found that when habitats are arranged in an aggregated pattern, inferences drawn regarding habitat selection can vary substantially with delineation of the study area. For example, extending the study area north may have resulted in the detection of bowhead or white whales in the heavier ice found there and altered inferences about habitat selection. Porter and Church (1987) suggested that one way researchers can correct for such bias is to let distribution, or an animal's home range, define areas for habitat analysis. Subsequent examination of distribution plots indicated that autumn ice habitat selection indices for white whales were more likely influenced by study area boundaries than were bowhead whale selection indices.

Broad-scale seasonal associations of cetaceans and pinnipeds with sea ice, as described by principal components analysis (PCA; Ray and Hufford, 1989), provide some provisional comparisons to cetacean seasonal habitat selection ratios. As expected, the strongest PCA associations were described for bowhead and white whale winter distribution with broken pack ice in the northern Bering Sea. In summer, bowheads were associated with ice in the Beaufort Sea, but had a weak negative association with ice in the Chukchi Sea—results opposite those reported here. Distribution of the Beaufort Sea white whale population was not subject to PCA in summer, while gray whales were negatively associated with ice in the vicinity of Bering Strait. Discrepancies in results of the two approaches may be related to scale. Ray and Hufford (1989) summarized marine mammal distribution from a variety of sources and relied on remote sensing of sea ice. Conversely, this study provides the first analyses of cetacean habitat associations from data collected on an integrated spatial and temporal scale. In their conclusions, Ray and Hufford (1989) emphasize the need to examine marine mammal distribution and environmental attributes simultaneously, across a range of time and space scales, to arrive at predictive capability. Comparison of results between this study and theirs supports that conclusion.

Seasonal Habitats and Trophic Relationships

Habitat partitioning among bowhead, white, and gray whales likely reflects dissimilar feeding modes and preferred prey. These species forage on distinct prey assemblages (plankton, nekton, and benthos), and all three rely on finding dense prey concentrations. However, oceanographic processes that lead to such concentrations are largely unknown, except those that affect the benthos preyed upon by gray whales (see Grebmeier and Barry, 1991). Various studies have reported the marine distribution of seabirds to be closely related to oceanographic structure over broad spatial scales (e.g., Griffiths et al., 1982; Hunt and Schneider, 1987). Specifically, patterns of seabird distribution and abundance have been linked to water masses and their constituent prey in the northern Bering Sea (Divoky, 1984; Elphick and Hunt, 1993). Although similar relationships have not been directly investigated for cetaceans in the Alaskan Arctic, whale association with depth and ice regimes (i.e., proxy water masses) provides an avenue for speculation.

Planktivorous bowhead whales switch habitats from summer to autumn, from comparatively deep to shallow water. Ice associations are not constant. This indicates that bowhead prey availability may be influenced more by bathymetry, and its concomitant hydrography, than by ice. Bowheads feed primarily on copepods and euphausiids, although epibenthic organisms such as mysids and gammarid amphipods are often eaten (Lowry, 1993). Bowheads rely, at least in part, on oceanic processes to concentrate prey, irrespective of type. For example, in summer, bowheads are often seen near coastal upwelling zones and frontal features that can concentrate zooplankton in the Canadian Beaufort Sea (Bradstreet et al., 1987). Ainley and DeMaster (1990) found that bowhead distribution was directly associated with high copepod prey concentrations at the boundary between the Mackenzie River plume and Arctic marine waters. Opportunistic zooplankton sampling near whales feeding in Camden Bay, Alaska, found bowheads associated with dense surface and subsurface swarms of *T. raschii* or copepods (*Pseudocalanus* spp.) located at distinct frontal boundaries separating turbid nearshore waters from inner shelf waters (Schoenherr and Wartzok, 1991). Near Point Barrow, aggregations of feeding whales were associated with a warm water eddy identifiable from satellite images of surface water temperature (Moore and Clarke, 1992). Lastly, Moore et al. (1995) reported a group of feeding bowheads directly associated with a dense 5 m × 8 km patch of zooplankton that contained the euphausiid *T. raschii*. This patch occurred at a sharp salinity (proxy density) gradient at about 30 m depth offshore of the Chukchi Peninsula in October 1993.

Bowhead summer occupation of depths associated with the Beaufort undercurrent may be related to increased prey availability due to advection, or concentration at frontal boundaries. The undercurrent, a major circulation feature of the outer shelf and slope below 40–50 m depth, provides a direct conduit for nutrients (and possibly prey) from the Bering Sea. Niebauer and Schell (1993) report high densities of zooplankton, especially euphausiids, advected from the northern Bering Sea at least as far north as Point Barrow, and Fissel et al. (1987) identified a BSW component of the undercurrent as far east as Barter Island in September 1986. Furthermore, Conover (1988) reported that *Calanus hyperboreus*, a common bowhead prey species, exhibits a seasonal vertical migration from 500–1000 m depths with C4, C5, and adult copepods available at the surface only after mid-June. Thus, densities of both euphausiids and copepods may be adequate for bowhead foraging along slope habitat in summer.

A shift towards shore and shelf waters in autumn may provide bowheads the best opportunities to encounter copepods fattened from a summer of feeding and euphausiids advected into concentrations along frontal boundaries mediated by local winds. Fissel et al. (1987) described intense frontal features over spatial scales ranging from a few hundred to a few thousand metres, including dynamic, large-scale fronts over the inner and outer continental shelf of the eastern Alaskan Beaufort Sea. One fairly consistent front was identified at the boundary of turbid nearshore waters and colder inner shelf waters, near the site where bowheads were seen feeding in Camden Bay in 1989 (Schoenherr and Wartzok, 1991). Both large- and small-scale fronts were wind-driven and were described as ephemeral, differing considerably between 1985 and 1986, the only two years of the study.

Without zooplankton sampling or hydrographic data, bowhead whale distribution across the Alaskan Beaufort Sea is the only indicator of zones of comparatively high secondary production. This speculation is confirmed in part by the reported association of bowheads with comparatively high zooplankton biomass for coastal waters of the Yukon coast (Bradstreet et al., 1987) and along the northeastern Alaskan coast (Griffiths et al., 1987), and other studies offer further support. For example, the co-occurrence of the right whale (*Eubalaena glacialis*), a congener of the bowhead whale, with dense patches of the copepod *Calanus finmarchicus* was confirmed during a multidisciplinary study in the southwestern Gulf of Maine (Kenney and Wishner, 1995). Concomitant physical oceanographic studies supported the hypothesis that advection and concentration of prey by hydrographic processes was primarily responsible for prey availability, which was possibly augmented by the tendency of *Calanus* to aggregate. Still, while aggregations of planktivorous whales might indicate areas of high secondary productivity, it is likely that many such areas go unsampled by whales and therefore remain undetected during visual-only surveys.

Piscivorous white whales were associated with ice and relatively deep water throughout the summer and autumn, which may reflect their penchant for feeding on ice-associated arctic cod. Although arctic cod distribution in Alaskan waters is poorly described, elsewhere cod appear to be associated with ice and large zooplankters (Lowry and Frost, 1981; Crawford and Jorgenson, 1990). The ice edge is a highly productive zone, primarily because of local oceanic upwelling (Dunbar, 1981; Smith and Nelson 1985), and birds and marine mammals presumably aggregate there to enhance feeding opportunities (Bradstreet and Cross, 1982) whatever the water depth. Results of tagging studies show that white whales can dive to depths of more than1000 m and exhibit behaviors indicative of foraging at depths of several hundred metres (Martin et al., 1993). Conversely, Craig et al. (1982) reported arctic cod abundance increased during late summer in an ice-free lagoon located along Alaska's north-central coast. Selection of ice-free habitat by some white whales in summer may be a response to foraging opportunities in nearshore waters, or habitat desired for skin molting, or both (Frost and Lowry, 1990). Foraging on cod may be a primary motivator in all seasons. For example, in the Canadian High Arctic, hundreds of white whales preyed upon large schools of arctic cod, to the point of driving fish ashore (Welch et al., 1993).

Benthic foraging gray whales occupy virtually the same habitat throughout both summer and autumn. Shallow shoals and coastal areas provide habitat rich in gray whale prey, and there is little reason for whales to abandon it prior to onset of the southbound migration. Gray whale feeding areas offshore of northern Alaska are characterized by low species diversity, high biomass, and the highest secondary production rates reported for any extensive benthic community (Highsmith and Coyle, 1990, 1992). These rich benthic pastures are fed by nutrients carried in the primary currents (Grebmeier et al., 1989). It is notable that consistent patterns of gray whale habitat utilization along the southern west coast of Vancouver Island, British Columbia, have also been described, although primary prey species were far more varied than in subarctic waters, often including planktonic organisms (Darling et al., 1998). Among Arctic cetaceans, gray whales differ markedly from bowhead and white whales in that their foraging excavations appear to structure the benthic community upon which they feed (Oliver and Slattery, 1985). In this way, gray whales participate in a dynamic feedback loop, recently termed "niche construction" (Odling-Smee et al., 1996): that is, their own activities serve to shape their niche through alteration of the benthos.

While the gray whale feeding grounds offshore of northern Alaska are extensive, they are not exhaustive. Feeding areas offshore of the Chukchi Peninsula augment those offshore of Alaska and provide key foraging habitat, especially to juvenile whales (Berzin, 1984). Habitat evaluation may be especially important for gray whales because the eastern Pacific population has only recently recovered from exploitation (Reilly, 1992; Hobbs et al., 1996). In a modeling study, Hobbs and Hanley (1990) note that habitat use ratios change with population density and may bear no relationship to carrying capacity if resource quality and quantity are not interchangeable. It appears that the quality of gray whale prey is far better in the Chirikov Basin, and possibly the southern Chukchi Sea and along the Chukchi Peninsula, than in the northern Chukchi Sea (Stoker, in press). Gray whale feeding habitats in the northern Chukchi Sea appear limited to shoal and coastal waters, in contrast to the usual swath-like depictions of available foraging habitat there (e.g., Stoker, in press). Both the quantity and quality of habitat in this northern periphery of the feeding range may be of particular importance to this population as it approaches its theoretical carrying capacity.

Finally, while classification of seasonal cetacean habitats provides a foundation upon which to interpret variation in distribution, it lacks the predictive power of ordination techniques (e.g., Palmer, 1993). However, ordination of species along environmental gradients requires *simultaneous* collection of environmental and marine mammal data across a range of temporal and spatial scales. Ideally, future investigations of habitat partitioning among the three cetacean species considered here will incorporate means to determine prey availability and associated hydrography to bolster inferential power. Until then, classification analyses like this one could be carried out as a provisional investigation of variability in habitat selection with regard to environmental conditions (Moore, 2000) and anthropogenic factors, such as underwater noise from offshore oil and gas activities.

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REFERENCES

AAGAARD, K. 1984. The Beaufort undercurrent. In: Barnes, P.W., Schell, D.M., and Reimnitz, E., eds. The Alaska Beaufort Sea: Ecosystems and environments. Orlando, Florida: Academic Press Inc. 47–71.

AAGAARD, K., and ROACH, A.T. 1990. Arctic ocean-shelf exchange: Measurements in Barrow Canyon. Journal of Geophysical Research 95(C10):18,163–18,175.

AAGAARD, K., ROACH, A.T., and SCHUMACHER, J.D. 1985. On the wind-driven variability of the flow through Bering Strait. Journal of Geophysical Research 90:7213–7221.

AINLEY, D.G., and DeMASTER, D.P. 1990. The upper trophic levels in polar marine ecosystems. In: Smith, W.O., Jr., ed. Polar oceanography Part B: Chemistry, biology and geology. San Diego, California: Academic Press, Inc. 599–563.

BAUMGARTNER, M.F. 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Marine Mammal Science 13(4): 614–638.

BERZIN, A.A. 1984. Soviet studies of the distribution and numbers of the gray whale in the Bering and Chukchi Seas, from 1968 to 1982. In: Jones, M.L., Swartz, S.L., and Leatherwood, S., eds. The gray whale, *Eschrichtius robustus*. Orlando, Florida: Academic Press, Inc. 409–419.

BOURKE, R.H. 1983. Currents, fronts and fine structure in the marginal ice zone of the Chukchi Sea. Polar Record 21(135): 569–575.

BRADSTREET, M.S.W., and CROSS, W.E. 1982. Trophic relationships at high Arctic ice edges. Arctic 35(1):1–12.

BRADSTREET, M.S.W., THOMSON, D.H., and FISSEL, D.B. 1987. Zooplankton and bowhead whale feeding in the Canadian Beaufort Sea, 1986. Section 2 In: Bowhead whale food availability characteristics in the southern Beaufort Sea: 1985 and 1986. Environmental Studies No. 50. Ottawa: Indian and Northern Affairs Canada.

BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P., and LAAKE, J.L. 1993. Distance sampling. New York: Chapman & Hall.

CHAPMAN, C.F. 1977. Piloting, seamanship and small boat handling. New York: Hearst Books.

COACHMAN, L.K., and AAGAARD, K. 1988. Transports through Bering Strait: Annual and interannual variability. Journal of Geophysical Research 93(C12):15,535–15,539.

CONOVER, R.J. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the Northern Hemisphere. Hydrobiologia 167/168:127–142.

CRAIG, P.C., GRIFFITHS, W.B., HALDORSON, L., and McELDERRY, H. 1982. Ecological studies of arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Canadian Journal of Fishery and Aquatic Science 39: 395–405.

CRAWFORD, R., and JORGENSON, J. 1990. Density distribution of fish in the presence of whales at the Admiralty Inlet landfast ice edge. Arctic 43(3):215–222.

DARLING, J.D., KEOGH, K.E., and STEEVES, T.E. 1998. Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. Marine Mammal Science 14(4): 692–720.

DAVIS, R.W., FARGION, G., MAY, N., HANSEN, L., MULLIN, K., and SCHROEDER, S. 1995. Cetacean habitat partitioning along the continental slope in the northern Gulf of Mexico. Abstract, Eleventh Biennial Conference on the Biology of Marine Mammals. 28.

DIVOKY, G.J. 1984. The pelagic and nearshore birds of the Alaskan Beaufort Sea: Biomass and trophics. In: Barnes, P.W., Schell, D.M., and Reimnitz, E., eds. The Alaska Beaufort Sea: Ecosystems and environments. Orlando, Florida: Academic Press Inc. 417 – 437.

DUNBAR, M. 1981. Physical causes and biological significance of polynyas and other open water in sea ice. In: Stirling, I., and Cleator, H., eds. Polynyas in the Canadian Arctic. Canadian Wildlife Service Occasional Paper 45. 29–43.

ELPHICK, C.S., and HUNT, G.L. 1993. Variations in the distribution of marine birds with water mass in the northern Bering Sea. The Condor 95:33–44.

FISSEL, D.B., MARKO, J.R., BIRCH, J.R., BORSTAD, G.A., TRUAX, D.N., and KERR, R. 1987. Water mass distributions. In: Richardson, W.J., ed. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985-86. OCS Study MMS-87-0037. Final Report to the U.S. Minerals Management Service, Alaska OCS Region. NTIS PB88-150271. 11–133.

FORNEY, K.A., BARLOW, J., and CARRETTA, J.V. 1995. The abundance of cetaceans in California waters. Part II: Aerial surveys in winter and spring of 1991 and 1992. Fishery Bulletin 93:15–26.

FROST, K.J., and LOWRY, L.F. 1984. Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. In: Barnes, P.W., Schell, D.M., and Reimnitz, E., eds. The Alaska Beaufort Sea: Ecosystems and environments. Orlando, Florida: Academic Press Inc. 381–401.

———. 1990. Distribution, abundance and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. Canadian Bulletin of Fishery and Aquatic Science 224:39–57.

FROST, K.J., LOWRY, L.F., and CARROLL, G. 1993. Beluga whale and spotted seal use of a coastal lagoon system in the northeastern Chukchi Sea. Arctic 46(1):8–16.

GEORGE, J.C., and SUYDAM, R. 1998. Observations of killer whale (*Orcinus orca*) predation in the northeastern Chukchi and western Beaufort Seas. Marine Mammal Science 14(2): 330–332.

GEORGE, J.C., CLARK, C., CARROLL, G.M., and ELLISON, W.T. 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. Arctic 42(1):24–30.

GREBMEIER, J.M., and BARRY, J.P. 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: A benthic perspective. Journal of Marine Systems 2: 495–518.

GREBMEIER, J.M., FEDER, H.M., and McROY, C.P. 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. Marine Ecology Progress Series 51:253–268.

GRIFFITHS, A.M., SIEGFRIED, W.R., and ABRAMS, R.W. 1982. Ecological structure of a pelagic seabird community in the southern ocean. Polar Biology 1:39–46.

GRIFFITHS, W.B., THOMSON, D.H., and JOHNSON, G.E. 1987. Zooplankton and hydroacoustics. In: Richardson, W.J., ed. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985–86. OCS Study MMS-87-0037. Final Report to the U.S. Minerals Management Service, Alaska OCS Region. NTIS PB88-150271. 135–256.

HAZARD, K. 1988. Beluga whale, *Delphinapterus leucas*. In: Lentfer, J.W., ed. Selected marine mammals of Alaska. Marine Mammal Commission Report NTIS PB88-178462. 195–235.

HIGHSMITH, R.C., and COYLE, K.O. 1990. High productivity of northern Bering Sea amphipods. Nature 344:8662–8664.

———. 1992. Productivity of arctic amphipods relative to gray whale energy requirements. Marine Ecology Progress Series 83:141–150.

HOBBS, N.T., and HANLEY, T.A. 1990. Habitat evaluation: Do use/availability data reflect carrying capacity? Journal of Wildlife Management 54(4):515–522.

HOBBS, R.C., RUGH, D.J., WAITE, J.M., BREIWICK, J.M., and DeMASTER, D.P. 1996. Preliminary estimate of the abundance of gray whales in the 1995/1996 southbound migration. Report of the International Whaling Commission 46:127–139.

HUI, C.A. 1985. Undersea topography and the comparative distribution of two pelagic cetaceans. Fishery Bulletin 83(3): 472–475.

HUNT, G.L., and SCHNEIDER, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall, J.P., ed. Seabirds: Feeding, ecology and role in marine ecosystems. Cambridge: Cambridge University Press. 7–41.

KENNEY, R.D., and WISHNER, K.F., eds. 1995. The South Channel Ocean Productivity EXperiment: SCOPEX. Continental Shelf Research 15(4/5).

LJUNGBLAD, D.K., MOORE, S.E., and VAN SCHOIK, D.R. 1986. Seasonal patterns of distribution, abundance, migration and behavior of the western Arctic stock of bowhead whales, *Balaena mysticetus*, in Alaskan Seas. Report of the International Whaling Commission, Special Issue 8:177–205.

LOWRY, L.F. 1993. Foods and feeding ecology. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. The Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press Inc. 201–238.

LOWRY, L.F., and FROST, K.J. 1981. Distribution, growth and foods of arctic cod (*Boreogadus saida*) in the Bering, Chukchi, and Beaufort Seas. Canadian Field-Naturalist 95:186–191.

MANLY, B.F.J., McDONALD, L.L., and THOMAS, D.L. 1993. Resource selection by animals: Statistical design and analysis for field studies. New York: Chapman and Hall.

MARTIN, A.R., SMITH, T.G., and COX, O.P. 1993. Studying the behaviour and movements of High Arctic belugas with satellite telemetry. Symposia of the Zoological Society of London 66:195–210.

MOORE, S.E. 1997. Cetacean habitats in the Alaskan Arctic. Ph.D. Dissertation, Scripps Institution of Oceanography, University of California-San Diego. 318 p.

———. 2000. Variability of cetacean distribution and habitat selection in the Alaskan Arctic, autumn 1982–91. Arctic 53(4):448–460.

MOORE, S.E., and CLARKE, J.T. 1992. Patterns of bowhead whale distribution and abundance near Barrow, Alaska, in fall 1982–1989. Marine Mammal Science 8(1):27–36.

MOORE, S.E., and DeMASTER, D.P. 1997. Cetacean habitats in the Alaskan Arctic. Journal of Northwest Atlantic Fishery Science 22:55–69.

MOORE, S.E., and REEVES, R.R. 1993. Distribution and movement. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. The Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press Inc. 313–386.

MOORE, S.E., GEORGE, J.C., COYLE K.O., and WEINGARTNER, T.J. 1995. Bowhead whales along the Chukotka coast in autumn. Arctic 48(2):155–160.

MUENCH, R.D., PEASE, C.H., and SALO, S.A. 1991. Oceanographic and meteorological effects on autumn sea ice distribution in the western Arctic. Annals of Glaciology 15: 231–247.

NERINI, M.K. 1984. A review of gray whale (*Eschrichtius robustus*) feeding ecology. In: Jones, M.L., Swartz, S.L., and Leatherwood, S., eds. The gray whale, *Eschrichtius robustus*. Orlando, Florida: Academic Press, Inc. 423–450.

NERINI, M.K., and OLIVER, J.S. 1983. Gray whales and the structure of the Bering Sea benthos. Oecologia 59:224–225.

NIEBAUER, H.J., and DAY, R.H. 1989. Causes of interannual variability in the sea ice cover of the eastern Bering Sea. GeoJournal 18(1):45–59.

NIEBAUER, H.J., and SCHELL, D.M. 1993. Physical environment of the Bering Sea population. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. The Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press Inc. 23–43.

ODLING-SMEE, F.J., LALAND, K.N., and FELDMAN, M.W. 1996. Niche construction. American Naturalist 147(4): 641–648.

OLIVER, J.S., and SLATTERY, P.N. 1985. Destruction and opportunity on the sea floor: Effects of gray whale feeding. Ecology 66(6):1965–1975.

OVERLAND, J.E., and ROACH, A.T. 1987. Northward flow in the Bering and Chukchi Seas. Journal of Geophysical Research 92:7097–7105.

PALMER, M.W. 1993. Putting things in even better order: The advantages of canonical correspondence analysis. Ecology 74 (8):2215–2230.

PAQUETTE, R.G., and BOURKE, R.H. 1981. Ocean circulation and fronts as related to ice melt-back in the Chukchi Sea. Journal of Geophysical Research 86 (C5):4215–4230.

PORTER, W.F., and CHURCH, K.E. 1987. Effects of environmental pattern on habitat preference analysis. Journal of Wildlife Management 51(3):681–685.

RAY, G.C., and HUFFORD, G.L. 1989. Relationships among Beringian marine mammals and sea ice. Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer 188:225–242.

REILLY, S.B. 1992. Population biology and status of eastern Pacific gray whales: recent developments. In: McCullough, D.R., and Barrett, R.H., eds. Wildlife 2001: Populations. New York: Elsevier Applied Science. 1062–1074.

ROACH, A.T., AAGAARD, K., PEASE, C.H., SALO, S.A., WEINGARTNER, T., PAVLOV, V., and KULAKOV, M. 1995. Direct measurements of transport and water properties through the Bering Strait. Journal of Geophysical Research 100 (C9):18,443–18,457.

ROGERS, J.C. 1978. Meteorological factors affecting interannual variability of summertime ice extent in the Beaufort sea. Monthly Weather Review 106(6):890–897.

SCHOENHERR, J.R., and WARTZOK, D. 1991. Prey distribution of feeding bowheads during the fall migration in the Beaufort Sea. Abstract, Tenth Biennial Meeting of the Biology of Marine Mammals. 43.

SMITH, W.O., Jr., and NELSON, D.M. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: Spatial coherence with the density field. Science 227:163–166.

STATSOFT, Inc. 1995. STATISTICA™ for Windows. Tulsa, Oklahoma: Statsoft, Inc.

STEWART, B.E., and STEWART, R.E.A. 1989. *Delphinapterus leucas*. Mammalian Species No. 336:1–8.

STOKER, S.W. In press. Distribution and carrying capacity of gray whale food resources in the northern Bering and Chukchi Seas. Journal of Cetacean Research and Management, Special Issue 2.

SUYDAM, R.S., and GEORGE, J.C. 1992. Recent sightings of harbor porpoise, *Phocoena phocoena*, near Point Barrow, Alaska. Canadian Field-Naturalist 106(4):489–492.

SUYDAM, R.S., FROST, K.J., LOWRY, L.F., O'CORRY-CROWE, G.M., and PIKOK., D., Jr. 1999. Satellite tracking of eastern Chukchi Sea beluga whales in the Arctic Ocean. SC/51/SM39. Available from the International Whaling Commission, The Red House, 135 Station Road, Histon, Cambridge CB4 9NP, United Kingdom. 7 p.

WALSH, J.J., McROY, C.P., COACHMAN, L.K., GOERING, J.J., NIHOUL, J.J., WHITLEDGE, T.E., BLACKBURN, T.H., PARKER, P.L., WIRICK, C.D., SHUERT, P.G., GREBMEIER, J.M., SPRINGER, A.M., TRIPP, R.D., HANSELL, D., DJENIDI, S., DELEERSNIJDER, E., HENRICKSEN, K., LUND, B.A., ANDERSEN, P., MULLER-KARGER, F.E., and DEAN, K. 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: Source regions for organic matter effecting AOU demands of the Arctic. Ocean. Progress in Oceanography 22:279–361.

WELCH, H.E., CRAWFORD, R.E., and HOP, H. 1993. Occurrence of arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. Arctic 46(4): 331–339.