

Abstract—Six years of bottom-trawl survey data, including over 6000 trawls covering over 200 km² of bottom area throughout Alaska's subarctic marine waters, were analyzed for patterns in species richness, diversity, density, and distribution of skates. The Bering Sea continental shelf and slope, Aleutian Islands, and Gulf of Alaska regions were stratified by geographic subregion and depth. Species richness and relative density of skates increased with depth to the shelf break in all regions. The Bering Sea shelf was dominated by the Alaska skate (*Bathyraja parmifera*), but species richness and diversity were low. On the Bering Sea slope, richness and diversity were higher in the shallow stratum, and relative density appeared higher in subregions dominated by canyons. In the Aleutian Islands and Gulf of Alaska, species richness and relative density were generally highest in the deepest depth strata. The data and distribution maps presented here are based on species-level data collected throughout the marine waters of Alaska, and this article represents the most comprehensive summary of the skate fauna of the region published to date.

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Emerging patterns of species richness, diversity, population density, and distribution in the skates (*Rajidae*) of Alaska

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Patterns of species richness, diversity, density, and distribution for the species of skates inhabiting the North Pacific Ocean and Bering Sea are still largely unknown. Earlier studies have been limited because of problems with identification of skates in the field and, to some degree, in the laboratory. Summarizing trawl survey data for commonly encountered species, Allen and Smith (1988) reported serious problems in the fisheries and survey data reported for even the most common skates throughout Alaska and the eastern North Pacific Ocean because of widespread problems with field identification of skates. Similarly, in the only previously published analyses of skate abundance and distribution data for Alaska, Teshima and Wilderbuer (1990) and Raschi et al. (1994) treated their data in the aggregate at the family level because of difficulty with identification of species. In contrast, Japanese and Russian authors have published several studies including general species-level information on the skate fauna of the western North Pacific Ocean and Sea of Okhotsk (Dudnik and Dolganov, 1992; Nakaya and Shirai, 1992; Dolganov, 1999, 2001).

Skates present difficulties for identification because they are a morphologically conservative group of

fishes, and although they represent a large proportion of the diversity of elasmobranchs worldwide, external morphological differences among species (or even genera) are often subtle. Moreover, the extent of morphological variation in many species is poorly known despite earlier taxonomic work (Ishiyama and Ishihara, 1977; Ishihara and Ishiyama, 1985, 1986), and although molecular methods have shown promise for species identification in the laboratory (Tinti et al., 2003; Bremer et al., 2005; Spies et al., 2006), skates are often difficult to identify in the field. In Alaska waters, namely the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska, this has been particularly true as Allen and Smith (1988), Teshima and Wilderbuer (1990), and Raschi et al. (1994) have noted. More recently, Mecklenburg et al. (2002) stated that the poorly understood taxonomic relationships of the skates in this region complicate the determination of species distributions. These challenges are compounded by the fact that skates are generally large fishes and are, thus, difficult to collect, preserve, and curate. Therefore, they are poorly represented in museum collections and difficult to study in the laboratory.

Because of identification difficulties and a relative lack of commercial im-

portance, species-specific data on skate populations are often not available, and catch statistics are commonly recorded only at the aggregate (genus or family) level. This lack of data is a concern in that skates may be particularly vulnerable to fishing pressure, even if they are only encountered as bycatch, because of their large size, relatively long life expectancy, and low fecundity, and are considered highly vulnerable to extinction or extirpation due to overfishing or habitat disturbances (Casey and Myers, 1998; Stevens et al., 2000; Dulvy and Reynolds, 2002). Moreover, apparent stability or increases in aggregate skate catches may mask declines in some components of those species aggregates, particularly among larger species (Dulvy et al., 2000). Therefore, species-level management, which can only be achieved through accurate identification, reporting, and monitoring, is essential for maintaining viable skate populations (Stevens et al., 2000).

Although skate populations in the eastern North Pacific Ocean and Bering Sea have been inadequately studied and inaccurately represented because of questionable field identifications, recent research efforts are improving the resolution and consistency with which skates can be identified by field survey personnel. The taxonomic works of Ishihara and Ishiyama (1985, 1986), Dolganov (1985), and Stevenson et al. (2004) have helped to clarify the taxonomy of North Pacific skates. In addition, range extensions of species previously unknown from Alaskan waters (Stevenson and Orr, 2005), the ongoing development of a comprehensive field guide to the skates of the region (Stevenson et al., 2007), and the establishment of a voucher collection process that allows for laboratory verification or reidentification of significant specimens, have greatly improved field identifications on Alaska Fisheries Science Center (AFSC) resource assessment surveys.

Because of advances in the knowledge of the skates of the North Pacific Ocean and Bering Sea, species-level skate identifications made by AFSC personnel beginning with the 1999 survey year are reliable and consistent. The purpose of this article is to describe species richness, diversity, relative density, and distribution of skates throughout Alaskan waters, based on data from six years of groundfish bottom-trawl surveys in the Bering Sea, Aleutian Islands, and Gulf of Alaska from 1999 through 2004.

Materials and methods

Specimens were collected aboard a variety of commercial fishing vessels chartered by the AFSC Resource Assessment and Conservation Engineering (RACE) Division from May through August in the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska, between 1999 and 2004 (Fig. 1). Survey gear and methods differed substantially among the four resource assessment surveys (Bering Sea shelf, Bering Sea slope, Aleutian Islands, and Gulf of Alaska), and bottom habitat types differ among regions, resulting in differences in the catch-

ability of skates. The effects of these differences on estimates of skate species richness, diversity, density, and distribution remain largely unknown; therefore the eastern Bering Sea shelf, Bering Sea slope, Aleutian Islands, and Gulf of Alaska were treated separately in this study.

The eastern Bering Sea shelf survey has been conducted annually in approximately its present form since 1982, and data from survey hauls during the years 1999–2004 were used in this study. This survey covered the eastern Bering Sea shelf from the Alaska Peninsula north beyond St. Matthew Island to approximately 62°40'N, from 20 m to 200 m depth, and was conducted with an 83-112 Eastern otter trawl. Hauls were made at previously established survey stations on a 20×20 nautical mile grid, and bottom time for each haul was approximately 30 minutes. For the purposes of this study, the region was divided into three subregions of approximately equal survey effort, each including three depth ranges (<50 m, 51–100 m, and 101–200 m). Subregion 1 comprised the southeastern part of the eastern Bering Sea shelf, extending from the Alaska Peninsula to the southeastern rim of Pribilof Canyon; subregion 2 comprised the central part of the eastern Bering Sea shelf, from the northwestern boundary of subregion 1 to the southeastern rim of Zhemchug Canyon; and subregion 3 comprised the northernmost portion of the survey area, bounded on the northwest by the U.S.-Russian border, with the northernmost hauls at approximately 62°40'N (Fig. 2A). For more information on the design and methods of this survey, see Stauffer (2004) and Lauth and Acuna (2007).

The eastern Bering Sea slope survey was conducted in 2000, 2002, and 2004. It covered the eastern Bering Sea upper continental slope (200 m to >1200 m depth) from just north of Unalaska Island north to the U.S.-Russian border, and was conducted with a Poly Nor'eastern bottom trawl equipped with mud-sweep roller gear on the footrope. Haul locations were chosen according to a stratified random sampling design, with the region divided into six subregions and five depth strata, and bottom time for each haul was approximately 30 minutes. For the purposes of this study the same six sub-regions were used. Subregions 1 and 6 consisted of a broad, low-angle slope, and form the southeastern and northwestern edges of the survey area; subregions 2 and 4 consisted of Pribilof and Zhemchug Canyons, respectively; and subregions 3 and 5 were intercanion faces characterized by a steep-angle slope (Fig. 2A). For this study, depth strata were combined into two depth ranges, representing the upper slope (200–600 m) and the lower slope (>600 m). For more information on the design and methods of this survey, see Hoff and Britt (2005).

The Aleutian Islands survey was conducted in 2000, 2002, and 2004. These surveys covered the continental shelf and upper slope (to 500 m) of the entire Aleutian Archipelago from Unimak Pass (165°W) to Stalemate Bank (170°30'E), and were conducted with a Poly Nor'eastern bottom trawl equipped with rubber bobbin

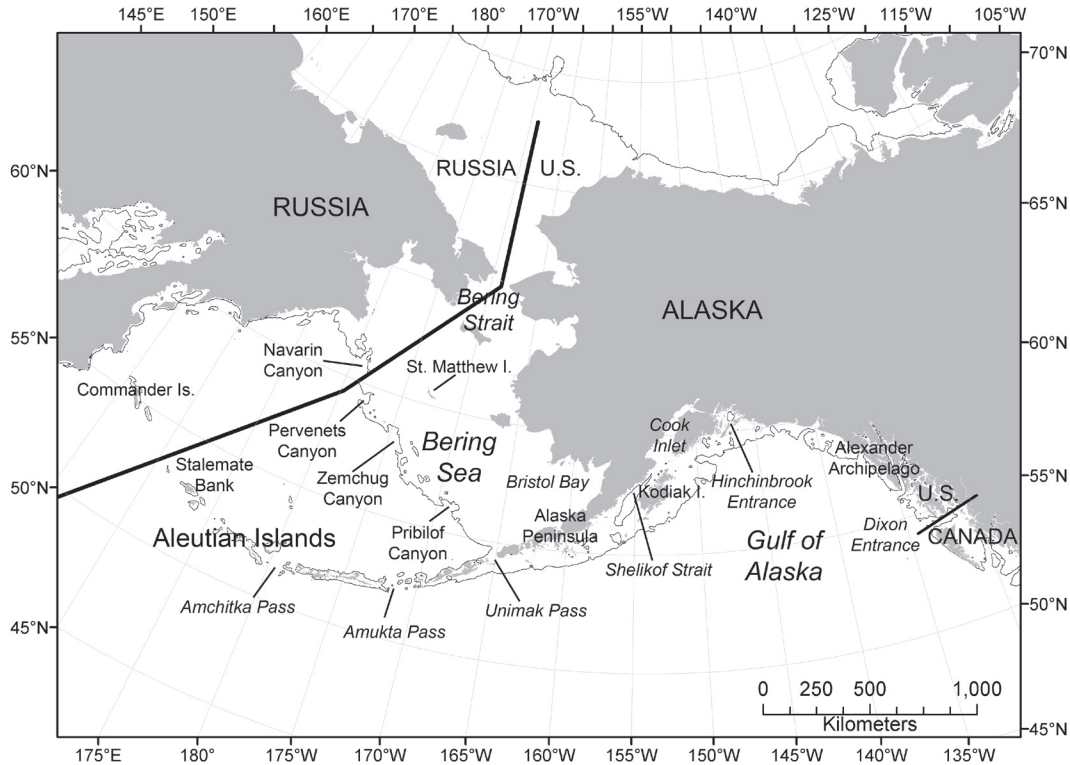


Figure 1

Map of the area covered in bottom-trawl surveys conducted by the Resource Assessment and Conservation Engineering Division of the Alaska Fisheries Science Center between 1999 and 2004. Surveys of the Bering Sea extended from the Alaska Peninsula to the U.S.-Russian border northwest of St. Matthew Island, surveys of the Aleutian Islands extended from Unimak Pass west to Stalemate Bank, and surveys of the Gulf of Alaska extended from Unimak Pass east to the U.S.-Canada border at Dixon Entrance. Black lines (west and east) denote U.S.-Russian and U.S.-Canadian border. Depth contour = 200 m.

roller gear on the footrope. The southern part of the eastern Archipelago from the Islands of Four Mountains to Unimak Pass has been assessed as part of the Gulf of Alaska survey but because zoogeographically it is part of the Aleutian Islands and because survey methods are the same (Britt and Martin, 2000), it was included in our regional study of the Aleutian Islands. Haul locations were chosen on the basis of a stratified random sampling design, and bottom time for each haul was approximately 15 minutes. For the purposes of this study the region was divided into four subregions, numbered from west to east, bounded by the major deep-water passes and gaps bisecting the archipelago. Subregion 1 comprised Stalemate Bank and the Near Islands, extending to approximately 174°30'E; subregion 2 extended east to Amchitka Pass, at the 180° line; subregion 3 extended from Amchitka Pass to Amukta Pass (approximately 171°30'W); and subregion 4 extended from Amukta Pass to Unimak Pass (Fig. 2B). For this study, depth strata were combined into three depth ranges (<100 m, 101–200 m, and >200 m). For more information on the design and methodology of this survey, see Zenger (2004).

The Gulf of Alaska survey was conducted in 1999, 2001, and 2003. It covered the continental shelf and upper slope (to 500 m in 2001, 700 m in 2003, and 1000 m in 1999) of the Gulf of Alaska from the southern part of the eastern Aleutian Islands beginning at the Islands of Four Mountains (included for this study in the Aleutian Islands region) to the U.S.-Canada border at Dixon Entrance, except in 2001 when the survey ended to the east at Hinchinbrook Entrance. Survey design, methods, and gear were the same as those of the Aleutian Islands survey (see Britt and Martin, 2000). For the purposes of the present study the region was divided into five subregions, numbered from west to east, corresponding approximately with National Marine Fisheries Service (NMFS) management areas. Subregion 1 extended from the tip of the Alaska Peninsula west to 159°W; subregion 2 extended from 159°W to the west side of Kodiak Island; subregion 3 extended from the west side of Kodiak Island to Hinchinbrook Entrance (147°W); subregion 4 extended from Hinchinbrook Entrance to Cross Sound at the northern tip of the Alexander Archipelago; and subregion 5 included the Alexander Archipelago, extending to the U.S.-Canada border (Fig. 2C). As in the Aleutian Islands region,

depth strata were combined into three depth ranges (<100 m, 101–200 m, and >200 m).

In all surveys, skate specimens were either examined and discarded at sea or fixed onboard in 10% seawater-buffered formalin or frozen for later study. Many of the specimens were photographed at sea, and the majority of fixed specimens were transferred to 70% ethanol and archived at the University of Washington (UW) fish collection. In compiling a list of skates for Alaska, we followed the comprehensive guide of Mecklenburg et al. (2002), with the following updates. We included *Bathyraja mariposa* (butterfly skate), described in Stevenson et al. (2004), and *Amblyraja badia* (rough-shoulder skate), recently documented in the Bering Sea (Stevenson and Orr, 2005).

Species richness was defined as the number of skate species encountered and identified in each haul. Mean species richness values were calculated for each depth-and-subregion stratum as a simple average of the number of skate species encountered in all hauls performed in that stratum, including zero values for hauls in which no skates were encountered. Because mean species richness figures were heavily influenced by zero values in some regions, and because simple species richness gives no indication of evenness, we also calculated a single Shannon's diversity index (H') for each depth-and-subregion stratum. This index was calculated as

$$H' = \sum_{i=1}^S [(n_i / n) \ln(n_i / n)],$$

where n_i = the number of individuals belonging to the i th of S species in the depth-and-subregion stratum; and

n = the total number of individuals captured in the depth-and-sub-region stratum (Ludwig and Reynolds, 1988).

Bottom area swept was calculated for each haul by multiplying the distance fished by the mean net spread. Density was calculated as the number of individuals per km² of bottom area swept. Means are presented \pm standard error (SE). Because the distributions of both species richness and density values were heavily skewed, and had a large proportion of zero values, tests for significant differences among means were not performed. Species distributions represent a summary of all recorded encounters of each species during standard survey operations in successful survey hauls.

Results

The total amount of effort represented in this data set consisted of 6096 successful bottom trawls covering over 201 km² of bottom area (Table 1). The Bering Sea shelf accounts for significantly more trawling effort than any of the other regions, because of differences in survey frequency (annual [Bering Sea shelf] vs. biennial [other regions]) and standard tow duration (30 minutes [Bering

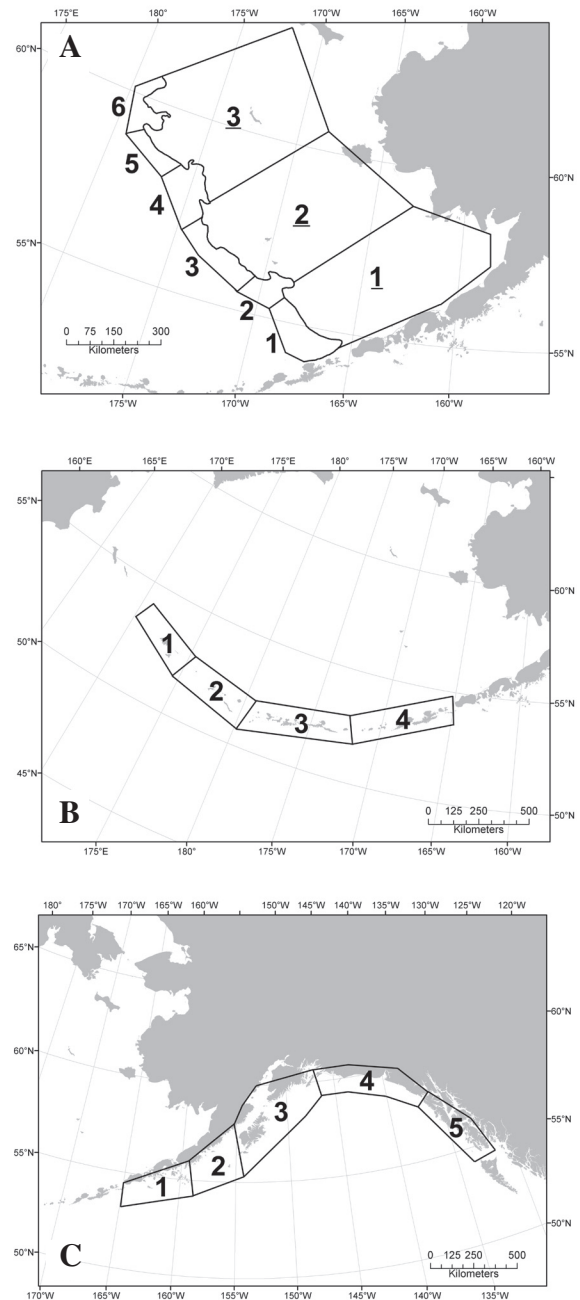


Figure 2

Boundaries of sampled subregions covered in bottom-trawl surveys from 1999 through 2004 in (A) the eastern Bering Sea shelf (underlined numbers) and slope (numbers not underlined), (B) the Aleutian Islands, and (C) the Gulf of Alaska.

Sea shelf and slope] vs. 15 minutes [Aleutian Islands and Gulf of Alaska]). Thirteen of the 14 described species of skates known from Alaskan waters (all but *Bathyraja violacea*) were encountered in bottom-trawl surveys from 1999 through 2004. Survey trawls collected 0–7 species per haul (mean = 0.93 ± 0.01), and at least one species of skate was collected in 62.8% of hauls. The number of

Table 1

Total number of hauls (n) and bottom area swept (km^2) by subregion and depth range for bottom-trawl surveys conducted in the eastern Bering Sea (shelf and slope), Aleutian Islands, and Gulf of Alaska from 1999 through 2004 (see text for subregion boundaries).

Depth range (m)	Subregion												Total	
	1		2		3		4		5		6			
	n	km^2	n	km^2	n	km^2	n	km^2	n	km^2	n	km^2	n	km^2
Bering Sea shelf														
<50	182	7.68	245	10.90	18	0.81							445	19.39
51–100	386	17.86	361	17.18	302	15.03							1049	50.07
101–200	141	7.33	147	7.11	328	16.51							616	30.95
Total	709	32.87	753	35.19	648	32.35							2110	100.40
Bering Sea slope														
201–600	112	4.38	31	1.09	32	1.10	32	1.08	15	0.55	53	1.94	275	10.14
601+	57	2.30	32	1.12	33	1.23	30	1.12	23	0.87	33	1.15	208	7.78
Total	169	6.68	63	2.21	65	2.33	62	2.20	38	1.42	86	3.09	483	17.92
Aleutian Islands														
<100	34	0.78	83	1.83	67	1.54	171	3.90					355	8.05
101–200	103	2.37	154	3.37	164	3.73	103	2.37					524	11.84
201+	70	1.63	134	3.05	170	3.99	156	3.72					530	12.38
Total	207	4.78	371	8.25	401	9.26	430	9.99					1409	32.27
Gulf of Alaska														
<100	247	5.74	174	4.02	280	6.60	50	1.19	15	0.33			766	17.87
101–200	121	2.87	188	4.52	365	8.90	104	2.51	58	1.33			836	20.12
201+	30	0.72	128	3.17	138	3.64	119	3.68	77	1.79			492	13.00
Total	398	9.33	490	11.71	783	19.14	273	7.38	150	3.45			2094	50.99

individual skates captured in a single haul ranged from 0 to 833, yielding aggregate density (all species combined) estimates for individual survey hauls ranging from 0 to 22,005 individuals per km^2 (mean=160.55 \pm 5.39). For individual species, maximum density figures ranged over several orders of magnitude, from 26.42 individuals/ km^2 for the rare and deepwater *B. abyssicola* to over 19,759 individuals/ km^2 for an extraordinarily large haul of *B. parmifera* on the northern Bering Sea slope.

Bering Sea shelf

The Bering Sea shelf received as much trawling effort as the other three regions combined and skates were common, but skate species richness and diversity were low. Approximately half of the effort was expended in the 51–100 m depth range, and the other half of the effort was almost equally distributed between the other two depth strata (Table 1). The southern, central, and northern subregions were sampled approximately evenly, and the depth distribution of the effort was similar in subregions 1 and 2. However, the depth distribution of the effort was significantly different in subregion 3, where the deepest depth stratum (100–200 m) was most heavily sampled, and very little sampling was conducted in the shallow stratum. Skates were encountered

throughout the entire geographic and bathymetric range of the survey area in over 87% (1830 of 2110) of the hauls conducted in this region. Skate species richness was highest in subregion 3 and lowest in subregion 1 (1.21 vs. 0.94), increasing with depth in all three subregions (Table 2). In all three subregions, species richness was highest in the deepest strata, and the lowest species richness was encountered in the shallow stratum of subregion 1. For all subregions combined, species richness increased significantly ($P < 0.0001$) with depth (Fig. 3). Diversity indices were near zero in all three subregions in the shallow and middle depth strata, but were slightly higher in the deepest depth zone (Table 3).

Skates were often encountered at moderate to high densities on the Bering Sea shelf. Aggregate skate density on the eastern Bering Sea shelf ranged from 0 to 5103 individuals/ km^2 , and an overall mean of 229.49 \pm 5.97. The largest mean density values were encountered in the middle depth stratum (51–100 m) of subregion 2 and the shallow and deep strata of subregion 3, although the variability associated with the mean in the shallow stratum of subregion 3 was extremely high. The smallest mean density was encountered in the shallow stratum of subregion 1 (Table 4). Overall mean density for the entire region was considerably lower in the shallow depth stratum than in either of the two

Table 2

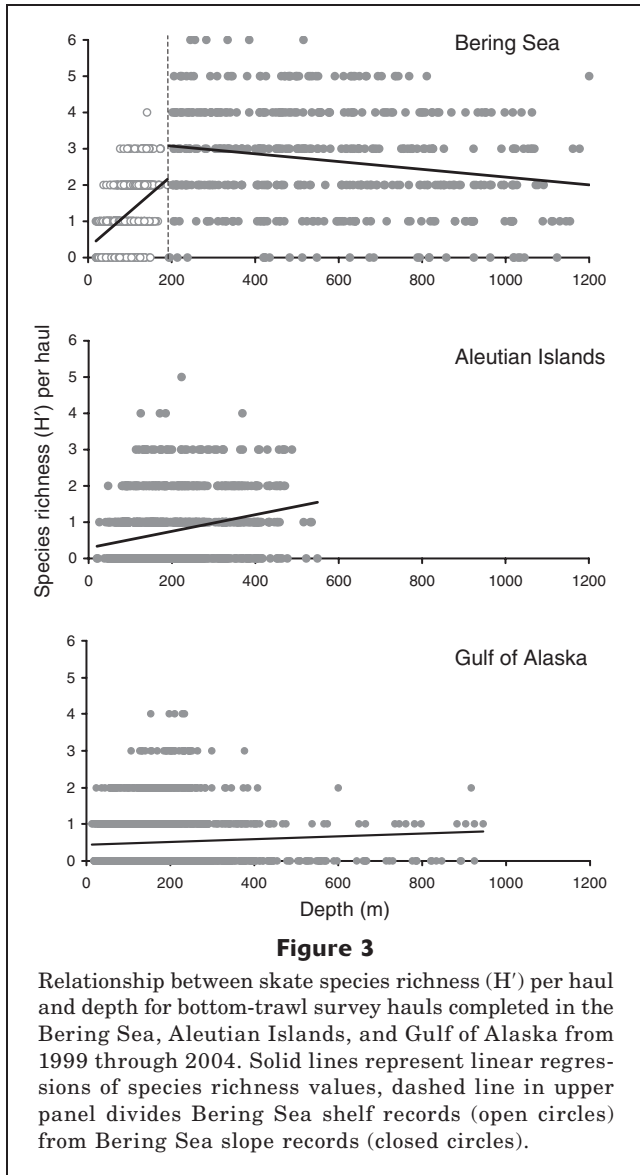
Mean skate species richness (no. of species/haul, with standard error in parentheses) by subregion and depth range for bottom-trawl surveys conducted in the eastern Bering Sea (shelf and slope), Aleutian Islands, and Gulf of Alaska from 1999 through 2004.

Depth range (m)	Subregion						Total
	1	2	3	4	5	6	
Bering Sea shelf							
<50	0.51 (0.04)	0.79 (0.03)	0.72 (0.11)				0.67 (0.02)
51–100	0.93 (0.03)	1.06 (0.02)	0.96 (0.02)				0.98 (0.01)
101–200	1.52 (0.06)	1.58 (0.06)	1.47 (0.04)				1.51 (0.03)
Total	0.94 (0.03)	1.07 (0.02)	1.21 (0.02)				1.07 (0.01)
Bering Sea slope							
201–600	2.43 (0.11)	3.16 (0.32)	2.22 (0.22)	3.59 (0.18)	2.87 (0.40)	3.81 (0.16)	2.91 (0.08)
601+	1.91 (0.16)	3.19 (0.24)	2.94 (0.18)	2.63 (0.28)	1.52 (0.20)	2.27 (0.24)	2.39 (0.09)
Total	2.25 (0.09)	3.17 (0.20)	2.58 (0.15)	3.13 (0.17)	2.05 (0.22)	3.22 (0.16)	2.69 (0.06)
Aleutian Islands							
<100	0.59 (0.10)	0.52 (0.06)	0.51 (0.08)	0.38 (0.04)			0.46 (0.03)
101–200	0.89 (0.11)	0.59 (0.07)	0.77 (0.06)	0.50 (0.07)			0.69 (0.04)
201+	0.69 (0.12)	0.93 (0.08)	1.04 (0.07)	0.90 (0.07)			0.92 (0.04)
Total	0.77 (0.07)	0.70 (0.04)	0.84 (0.04)	0.60 (0.04)			0.72 (0.02)
Gulf of Alaska							
<100	0.25 (0.03)	0.39 (0.04)	0.39 (0.04)	0.44 (0.09)	0.27 (0.12)		0.34 (0.02)
101–200	0.27 (0.05)	0.70 (0.06)	0.74 (0.04)	0.46 (0.06)	0.26 (0.07)		0.60 (0.03)
201+	0.30 (0.10)	1.02 (0.10)	0.65 (0.07)	0.47 (0.07)	0.40 (0.08)		0.64 (0.04)
Total	0.26 (0.02)	0.67 (0.04)	0.60 (0.03)	0.46 (0.04)	0.33 (0.05)		0.51 (0.02)

Table 3

Shannon's diversity index (H') by subregion and depth range for bottom-trawl surveys conducted in the eastern Bering Sea (shelf and slope), Aleutian Islands, and Gulf of Alaska from 1999 through 2004.

Depth range (m)	Subregion						Total
	1	2	3	4	5	6	
Bering Sea shelf							
<50	0.02	0.01	0.00				0.01
51–100	0.15	0.06	0.03				0.09
101–200	0.57	0.62	0.34				0.46
Total	0.28	0.20	0.25				0.24
Bering Sea slope							
201–600	1.48	1.44	1.33	1.42	1.67	1.70	1.71
601+	1.47	1.33	1.30	1.07	1.10	0.99	1.46
Total	1.65	1.42	1.57	1.38	1.85	1.85	1.82
Aleutian Islands							
<100	0.72	0.46	0.70	1.65			1.27
101–200	0.80	1.20	1.04	1.52			1.13
201+	1.31	1.22	0.97	0.93			1.10
Total	0.94	1.32	1.18	1.33			1.33
Gulf of Alaska							
<100	1.01	0.87	0.93	0.52	0.17		0.91
101–200	1.43	1.53	1.32	0.90	0.90		1.42
201+	0.79	1.51	1.35	0.68	1.56		1.44
Total	1.33	1.64	1.46	1.00	1.44		1.53



deeper strata, yielding a significant trend ($P < 0.0001$) of increasing density with increasing depth for combined subregions (Fig. 4). Subregions 2 and 3 exhibited a higher overall mean density than subregion 1. *Bathyrja parmifera* (Alaska skate) was by far the most common species in this region, appearing in over 86% of hauls and with a mean density an order of magnitude larger than the next most common species, *B. interrupta* (Bering skate) (Table 5). A total of seven skate species were encountered in this region, two of which (*B. maculata* and *R. rhina*) were encountered in only one or two hauls over the entire six-year period.

Bering Sea slope

The Bering Sea slope received comparatively little trawling effort, but skates were common and species richness and diversity were high. Slightly more effort was

expended on the upper slope (201–600 m depth) than on the lower slope (>601 m). Subregion 1, in the southern part of the eastern Bering Sea, received the most effort and the remaining five subregions were sampled approximately evenly (Table 1). Skates were encountered throughout the entire geographic and bathymetric range of the survey region, occurring in 95% (460 of 483) of hauls conducted. Species richness was approximately 50% higher in subregions 2, 4, and 6 (canyons and northern gentle slope habitats) than in subregions 1, 3, and 5 (intercanyons and southern gentle slope habitats). In four of the six subregions, mean species richness was higher on the upper slope than on the lower slope (Table 2), and the overall trend was for richness to decrease significantly ($P < 0.0001$) with increasing depth (Fig. 3). Mean species richness was highest on the upper slope in subregion 6 and lowest on the lower slope in subregion 5. Diversity indices for the three southern subregions were similar on the upper and lower slope, whereas in the three northern subregions the diversity index was notably higher on the upper slope (Table 3).

Skates were encountered at high densities on the Bering Sea slope. Aggregate skate density ranged from 0 to 22,005 individuals/km², and had an overall mean of 545.81 ± 53.48 . These figures are heavily influenced by one particularly large haul of *B. parmifera* during the 2002 survey. With this haul removed, the density range and overall mean became 0 to 5350 individuals/km² and 501.29 ± 29.69 individuals, respectively. The largest mean density was encountered on the upper slope in the northernmost subregion (subregion 6), although this mean was also influenced by the large haul of *B. parmifera*. With the aberrant haul removed from the data set, the largest mean was that of the lower slope in subregion 2 (Table 4). The smallest mean density was encountered on the lower slope in subregion 5. Subregions 2, 4, and 6 exhibited considerably higher overall mean density values than those of subregions 1, 3, and 5—a pattern similar to that of species richness in this region. Overall mean density was similar for the two depth ranges, but slightly higher on the lower slope and increasing nonsignificantly ($P = 0.128$) with increasing depth (Fig. 4). Although *B. parmifera* exhibited the highest maximum density, *B. aleutica* produced the highest mean density value in this region, followed by *B. lindbergi* and *B. interrupta* (Table 5). A total of ten skate species were encountered in this region, although two of these (*A. badia* and *B. abyssicola*) were encountered in only two hauls.

Aleutian Islands

The Aleutian Islands received moderate trawling effort, and skates were inconsistently encountered. Trawling effort in this region was distributed approximately evenly between the two deeper depth strata, whereas the shallow stratum received slightly less effort (Table 1). The easternmost subregion (subregion 4) was most heavily sampled, but effort progressively decreased in the more western subregions. Skates were encountered

Table 4

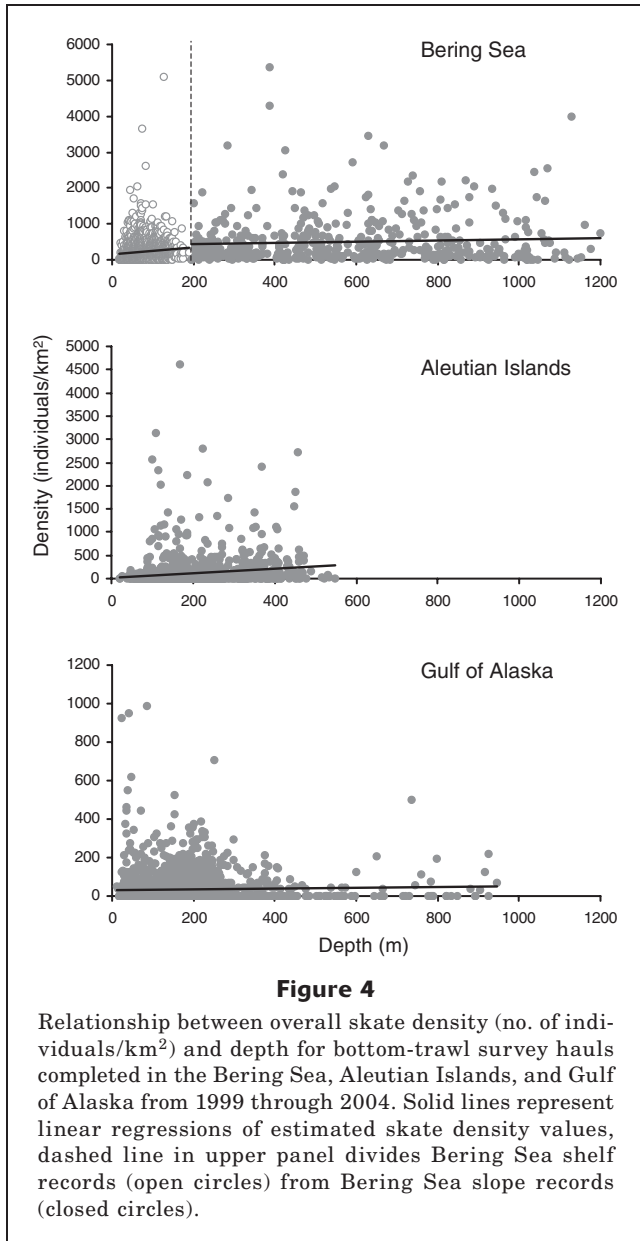
Mean aggregate density (no. of individuals/km², with standard error in parentheses) of all skates combined by subregion and depth range for bottom-trawl surveys conducted in the eastern Bering Sea (shelf and slope), Aleutian Islands, and Gulf of Alaska from 1999 through 2004. * = calculations for this area of the Bering Sea slope did not include the particularly large catch of *B. parmifera* on 29 June 2002 (see text for details).

Depth range (m)	Subregion						Total
	1	2	3	4	5	6	
Bering Sea shelf							
<50	86.20 (10.09)	191.85 (14.24)	340.92 (119.05)				154.67 (10.46)
51–100	220.24 (16.53)	330.91 (15.70)	175.03 (9.74)				245.31 (8.83)
101–200	216.34 (38.33)	215.94 (14.67)	292.13 (11.16)				256.60 (11.24)
Total	185.06 (12.25)	263.22 (9.58)	238.91 (8.27)				229.49 (5.97)
Bering Sea slope							
201–600	311.32 (43.28)	492.60 (83.61)	328.23 (64.99)	670.47 (121.44)	277.00 (57.20)	797.53 (134.44)*	466.14 (38.02)*
601+	255.91 (48.04)	1046.67 (171.08)	467.24 (80.55)	735.72 (145.61)	105.51 (18.05)	784.85 (111.65)	547.59 (47.09)
Total	292.63 (32.92)	774.03 (101.66)	398.81 (52.25)	702.04 (93.61)	173.20 (28.21)	792.61 (92.51)*	501.29 (29.69)*
Aleutian Islands							
<100	135.65 (77.68)	44.54 (7.89)	55.32 (15.28)	21.51 (2.80)			44.21 (8.38)
101–200	279.19 (55.00)	50.33 (7.95)	110.12 (29.89)	45.39 (8.73)			113.06 (15.03)
201+	69.72 (30.45)	99.90 (14.49)	219.66 (32.47)	151.07 (22.86)			149.39 (13.72)
Total	184.78 (32.47)	66.94 (6.55)	147.4 (18.83)	74.24 (9.06)			109.38 (7.96)
Gulf of Alaska							
<100	12.21 (1.68)	35.60 (6.11)	31.92 (4.10)	67.41 (26.64)	76.97 (65.26)		29.60 (3.04)
101–200	12.52 (2.36)	43.31 (4.96)	48.66 (3.61)	30.45 (5.15)	13.96 (4.43)		37.56 (2.14)
201+	18.08 (7.61)	66.67 (7.29)	50.14 (8.04)	41.87 (7.17)	22.25 (4.84)		46.10 (3.59)
Total	12.75 (1.38)	46.67 (3.5)	42.94 (2.66)	42.16 (6.13)	24.52 (7.16)		36.65 (1.64)

Table 5

Mean and maximum density (no. of individuals/km²) by species for skates collected in bottom-trawl survey hauls performed in the eastern Bering Sea (shelf and slope), Aleutian Islands, and Gulf of Alaska from 1999 through 2004. * = not collected in this region, *n* = total number of hauls performed within each region.

Species	Bering Sea shelf (<i>n</i> =2110)		Bering Sea slope (<i>n</i> =483)		Aleutian Islands (<i>n</i> =1409)		Gulf of Alaska (<i>n</i> =2094)		All regions (<i>n</i> =6096)	
	Mean	Max	Mean	Max	Mean	Max	Mean	Max	Mean	Max
<i>Bathyraja parmifera</i>	217.09	5103.83	55.00	19759.77	18.36	1012.26	1.64	201.97	84.30	19759.77
<i>B. aleutica</i>	0.99	575.15	214.16	3981.10	8.52	639.17	5.07	207.53	21.02	3981.10
<i>B. maculata</i>	0.01	19.47	43.07	2350.51	52.37	4414.28	0.12	88.94	15.56	4414.28
<i>B. interrupta</i>	10.95	565.55	60.59	1057.54	1.01	340.40	5.60	238.45	10.75	1057.54
<i>B. taranetzi</i>	0.13	41.67	31.48	1117.97	27.31	1781.36	0.02	40.11	8.86	1781.36
<i>B. lindbergi</i>	*	*	78.02	1953.68	0.09	46.22	0.04	82.24	6.22	1953.68
<i>B. minispinosa</i>	*	*	36.26	1094.62	0.11	66.08	0.02	36.02	2.90	1094.62
<i>B. trachura</i>	*	*	26.79	468.10	0.08	83.66	0.69	502.86	2.38	502.86
<i>B. mariposa</i>	*	*	*	*	0.34	103.78	*	*	0.08	103.78
<i>B. abyssicola</i>	*	*	0.10	26.42	*	*	*	*	0.01	26.42
<i>Raja rhina</i>	0.01	44.67	*	*	0.10	50.81	13.83	592.97	4.78	592.97
<i>R. binoculata</i>	0.25	197.37	*	*	1.08	178.52	9.61	986.51	3.64	986.51
<i>Amblyraja badia</i>	*	*	0.25	80.00	*	*	*	*	0.02	80.00
All skates	229.43	5103.83	545.81	22,005.20	109.38	4609.02	36.65	986.51	160.52	22,005.20



throughout the survey area, but in only 51% (718 of 1409) of the hauls conducted in this region. Species richness was similar among the four subregions of the Aleutian Islands (Table 2) and increased with depth in all but subregion 1, the westernmost subregion. For all subregions combined, species richness increased significantly ($P < 0.0001$) with increasing depth (Fig. 3). Maximum species richness was encountered in the deepest strata of subregions 2, 3, and 4 and the intermediate depth of subregion 1, whereas the minimum species richness was encountered in the shallow stratum of subregion 4. More species of skates were encountered in the Aleutian Islands (11) than in any of the other regions (vs. 10 in the Gulf of Alaska, 9 on the Bering Sea slope, and 7 on the Bering Sea shelf). Diversity indices were lowest in the shallow strata in all but subregion 4, where the shallow

stratum exhibited the highest diversity and the deepest stratum exhibited the lowest (Table 3).

Skate population densities were variable in the Aleutian Islands. Aggregate skate density ranged from 0 to 4609 individuals/km², and had an overall mean of 109.38 ± 7.96 . The spatial pattern of mean density was similar to that of mean species richness and diversity, increasing with depth in all but one subregion (Table 4), although in this case it was the easternmost subregion (subregion 1) that contrasted with the other subregions. The minimum mean density was encountered in the shallow stratum of subregion 4. The maximum mean density was encountered in the middle depth stratum of subregion 1 and in the deep stratum of subregion 3, and mean density was not as uniform as mean species richness across the four subregions. Subregions 1 and 3 yielded overall mean density values considerably higher than those of subregions 2 and 4. For all subregions combined, density increased significantly ($P < 0.0001$) with increasing depth (Fig. 4). The three most common skate species in the Aleutian Islands were *B. maculata*, *B. taranetzi*, and *B. parmifera* (Table 5). *Bathyraja aleutica* was also moderately common.

Gulf of Alaska

The Gulf of Alaska received moderate trawling effort, which was concentrated in the western and central subregions, and skates were comparatively rare in this region. Effort was similar for the shallow and middle depth strata, but the deep stratum was not as heavily sampled (Table 1), and central subregion 3 received the most effort whereas southeastern subregion 5 received by far the least. Although skates were encountered throughout the survey area, they occurred in less than 40% (828 of 2094) of the hauls conducted in the region. Mean species richness was generally higher in the central Gulf of Alaska (subregions 2, 3, and 4) than in either the western (subregion 1) or southeastern subregions (subregion 5) (Table 2). Although the overall trend in this region was for species richness to be higher at deeper depth strata, and the relationship between richness and depth for all subregions combined was significant ($P = 0.0047$) (Fig. 3), this pattern was clearly evident only in subregion 2. Maximum species richness was encountered in the deep stratum of subregion 2, whereas the minimum species richness was encountered across all strata of subregion 1 and the two shallow strata of subregion 5. Diversity indices were not as clearly related to subregion, and only subregion 5 showed a strong trend toward increasing diversity with increasing depth (Table 3).

Skate densities were generally low in the Gulf of Alaska. Aggregate skate density ranged from 0 to 986 individuals/km², and had an overall mean of 36.65 ± 1.64 . The highest mean density was encountered in the shallow depth stratum of subregion 5, but the variability associated with this mean was extremely high. The lowest mean density was encountered in the shallow stratum of subregion 1 (Table 4). Overall mean density generally increased with depth (Fig. 4), although the

Table 6

Depth range (m) for skate species encountered in bottom-trawl survey hauls performed in the eastern Bering Sea (shelf and slope), Aleutian Islands, and Gulf of Alaska from 1999 through 2004. * = not collected in this region.

Species	Bering Sea shelf	Bering Sea slope	Aleutian Islands	Gulf of Alaska	Overall
<i>Bathyraja parmifera</i>	19–190	202–392	47–283	62–375	19–392
<i>B. aleutica</i>	77–173	202–1200	47–535	29–882	29–1200
<i>B. maculata</i>	174	206–1200	91–488	185–208	91–1200
<i>B. interrupta</i>	53–190	202–1017	64–369	37–566	37–1017
<i>B. taranetzi</i>	77–153	202–1063	82–488	64	64–1054
<i>B. lindbergi</i>	*	342–1200	342–458	917	342–1200
<i>B. minispinosa</i>	*	206–1200	223–368	666	206–1200
<i>B. trachura</i>	*	221–1200	369–407	345–946	221–1200
<i>B. mariposa</i>	*	*	95–457	*	95–457
<i>B. abyssicola</i>	*	951–1400	*	*	951–1400
<i>Raja rhina</i>	70–139	*	87–133	24–601	24–601
<i>R. binoculata</i>	37–135	*	26–192	16–376	16–376
<i>Amblyraja badia</i>	*	1508–1556	*	*	1508–1556

relationship was not significant ($P=0.117$). Subregions 4 and 5 seemed to contradict this trend, with considerably higher mean density values in the shallow stratum, but the standard errors of these means indicated that catches in these subregions were highly variable. Like species richness, mean density was higher in the central subregions and lower in the western and southeastern subregions. The two Alaskan species of the genus *Raja* (*R. binoculata* and *R. rhina*) were the most common skates in this region (Table 5). The only two species of *Bathyraja* that were relatively common in the Gulf of Alaska were *B. interrupta* and *B. aleutica*. A total of ten skate species were encountered in this region, but four of these were recorded in five or fewer hauls.

Species distributions

Of the 14 species of skates currently known from Alaska, 13 were encountered on the surveys included in this study, and 5 of these species were found in all four regions. Two species (*B. abyssicola* and *Amblyraja badia*) were encountered only on the Bering Sea slope, and one (*B. mariposa*) was encountered only in the Aleutian Islands. *Bathyraja violacea*, although known from Alaskan waters, was not encountered in these surveys.

Some species of the genus *Bathyraja* were commonly and widely encountered in all survey regions (Table 6). *Bathyraja parmifera*, the most common species of skate in Alaskan waters, was found throughout all the survey regions (Fig. 5A). *Bathyraja aleutica* (Fig. 5B) and *B. interrupta* (Fig. 5C) were also widespread, both geographically and bathymetrically. Although much more rarely encountered than the aforementioned species, *B. trachura* (Fig. 5D) was also found throughout all survey regions in deep hauls.

Other species were common in some survey regions, but rarely (if ever) encountered in others. *Bathyraja*

maculata (Fig. 6A) and *B. taranetzi* (Fig. 6B) were commonly encountered on the Bering Sea slope and in the Aleutian Islands at broad depth ranges (Table 6), but *B. maculata* was recorded only a few times in the Gulf of Alaska, and *B. taranetzi* was not recorded east of Unimak Pass. *Bathyraja lindbergi* (Fig. 6C) and *B. minispinosa* (Fig. 6D) were common only on the Bering Sea slope, but rarely encountered elsewhere. *Raja binoculata* (Fig. 7A) and *R. rhina* (Fig. 7B) were common only in the Gulf of Alaska, although *R. binoculata* was also encountered several times in the Bering Sea and eastern Aleutian Islands.

Three skate species were encountered in only a few hauls throughout the 1999–2004 survey period (Fig. 8). *Bathyraja abyssicola* and *A. badia* were encountered only in a few deep hauls on the Bering Sea slope at depths greater than 950 m, and *Bathyraja mariposa* was encountered only in the central Aleutian Islands.

Discussion

Recent NMFS bottom-trawl surveys provide a wealth of reliable species-specific data on the geographic and bathymetric distributions of the skates of Alaska, as well as insight into relative population densities and regional species assemblages. Although most of the skate species of Alaska have relatively widespread distributions, each geographic and bathymetric region of Alaska has its own characteristic skate fauna and demographic characteristics.

The eastern Bering Sea shelf supports large populations of fishes and invertebrates and serves as an important commercial fishing area. Among skates, *B. parmifera* is by far the most common species, accounting for over 90% of the skate catch of this region. Therefore, even though skates are encountered in the

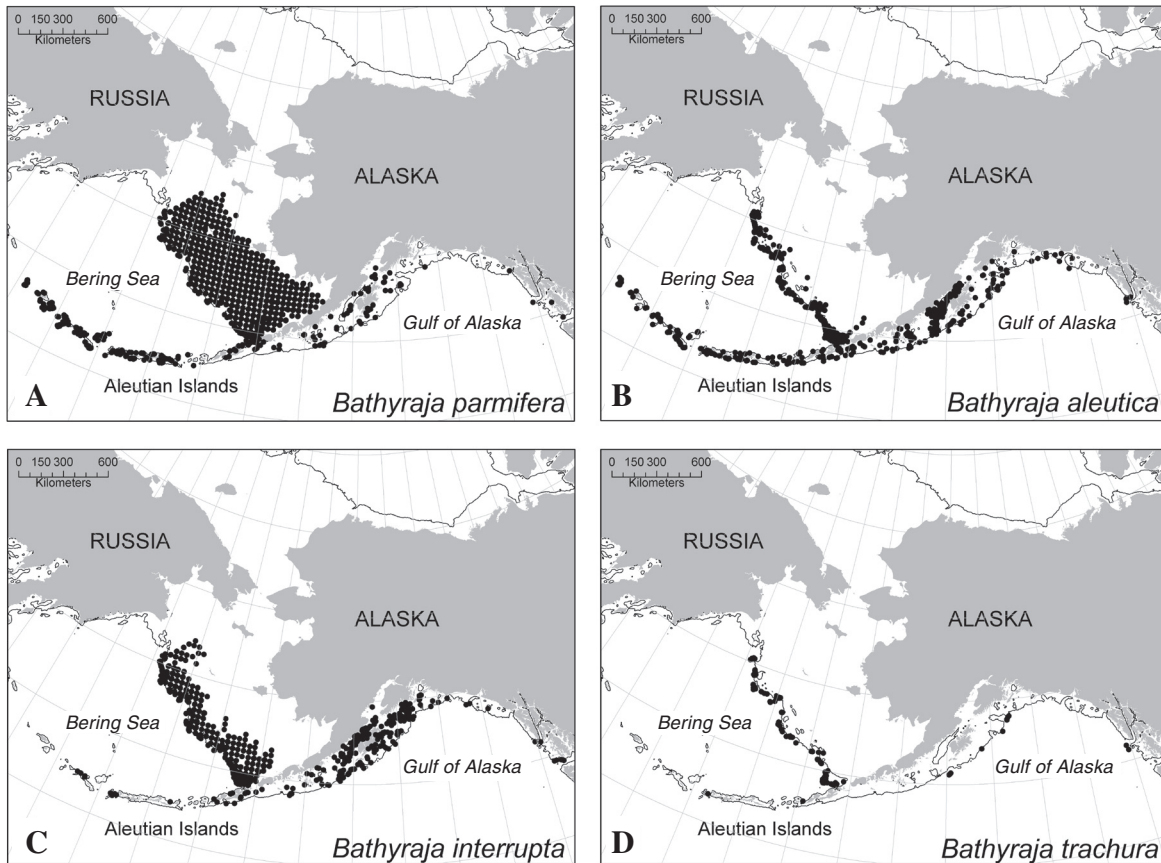


Figure 5

Distribution of (A) *Bathyraja parmifera* (Alaska skate), (B) *B. aleutica* (Aleutian skate), (C) *B. interrupta* (Bering skate), and (D) *B. trachura* (rougtail skate) based on data from bottom-trawl surveys conducted in the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska from 1999 through 2004. Black circles indicate the presence of the species in one or more survey hauls. Depth contour = 200 m.

large majority of the hauls, and overall skate numbers have been increasing over the past 20 years (Hoff, 2006), the mean species richness and skate diversity are quite low in this region. In the deeper waters near the shelf-slope break, the skate fauna is more diverse, and *B. aleutica* and *B. interrupta*, two of the most geographically and bathymetrically widespread species in Alaska, are encountered with greater frequency. In addition to widespread distributions in Alaskan waters, both of these species are also found farther south along the North American west coast and have been collected at depths of 20 to over 1000 m. *Bathyraja taranetzi* and *B. maculata* also begin to appear near the shelf break in the eastern Bering Sea, although they are much more common on the continental slope. The presence of these species near the shelf break accounts for the high mean species richness values in the deep depth strata in this region. In the southeastern corner of the Bering Sea shelf, near the eastern Aleutian Islands, the two Alaskan species of *Raja* are occasionally encountered, and their effect on the mean species richness values in subregion 1 are offset by the fact that this area

includes the extensive shallow waters of Bristol Bay, where skates are less frequently encountered.

There were no clear bathymetric or geographic trends in skate population density on the eastern Bering Sea shelf. Although overall mean density generally increased with increasing depth, the middle and deep depth strata yielded similar overall means. The low overall mean density values for both the shallow depth stratum and the southern subregion (subregion 1) appeared to be heavily influenced by the relatively low skate densities in the shallow waters of Bristol Bay. The mean density for the shallow stratum of subregion 3 was probably not meaningful because of the relatively low sample size and high variability in density data for this stratum.

The continental slope of the eastern Bering Sea is a region of high skate species richness and diversity, and skates are encountered in nearly every haul. Several species, including *B. aleutica*, *B. interrupta*, *B. taranetzi*, and *B. maculata*, are encountered from the shelf break down to well over 1000 m depth. Another group of species, characterized by a dark ventral surface—*B. lindbergi*, *B. minispinosa*, and *B. trachura*—begin to

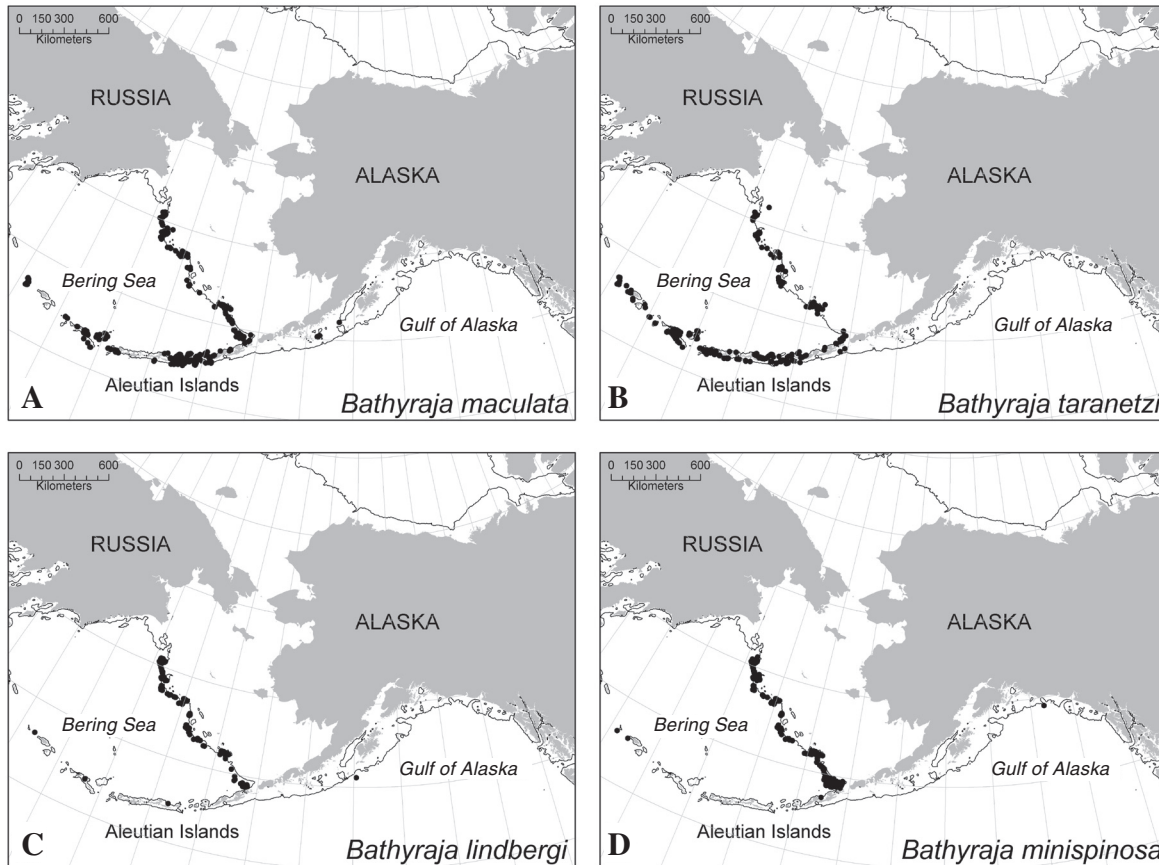


Figure 6

Distribution of (A) *Bathyrāja maculata* (whiteblotched skate), (B) *B. taranetzi* (mud skate), (C) *B. lindbergi* (Commander skate), and (D) *B. minispinosa* (whitebrow skate) based on data from bottom-trawl surveys conducted in the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska from 1999 through 2004. Black circles indicate the presence of the species in one or more survey hauls. Depth contour = 200 m.

appear at depths of 300–400 m and are more common in deeper waters. Thus, there is a degree of assemblage separation; one suite of species is found on the lower slope and another suite is found on the upper slope but overall species richness remains relatively consistent throughout the depth range of the survey. A similar skate fauna has been reported from the northern Kuril Islands and southern Kamchatka (Orlov, 2005; Orlov et al., 2007), although trends in species richness in that region are unclear. Two additional species, *A. badia* and *B. abyssicola*, have been only rarely encountered in the deep waters of the eastern Bering Sea slope, although these species are widely distributed and have been recorded from both sides of the North Pacific Ocean (Zorzi and Anderson, 1990; Stevenson and Orr, 2005). Species richness and density both show a clear geographic pattern in this region; subregions 2, 4, and 6 exhibit higher species richness and density than the other three subregions, although this effect is less pronounced in the diversity indices. These areas of high species richness and density are generally associated with canyon features on the Bering Sea slope; this association may

indicate that skates aggregate near these features. Alternatively, it may simply indicate that the skates in these areas cluster in the same habitats that are most suitable for bottom trawling.

In the eastern Bering Sea, skate density increased with depth from shallow areas to the shelf break, and remained relatively uniform on the upper continental slope. A similar density pattern has also been observed along the Oregon coast (Pearcy et al., 1982) and in northwestern Australia (Williams et al., 2001). In the subregion encompassing Pribilof Canyon the pattern was slightly different; skate density was highest at greater depths on the lower slope, in the same general deeper depth range (700+ m) as noted by Gordon and Duncan (1985) and Merrett et al. (1991) in the northeast Atlantic. Although several distributional studies published for the western Pacific region have included basic distribution, depth range, and relative abundance information for some of the same species of skates reported here (Dudnik and Dolganov, 1992; Nakaya and Shirai, 1992; Dolganov, 1998, 1999; Orlov, 1998, 2003; Orlov et al., 2007), none of these studies have provided

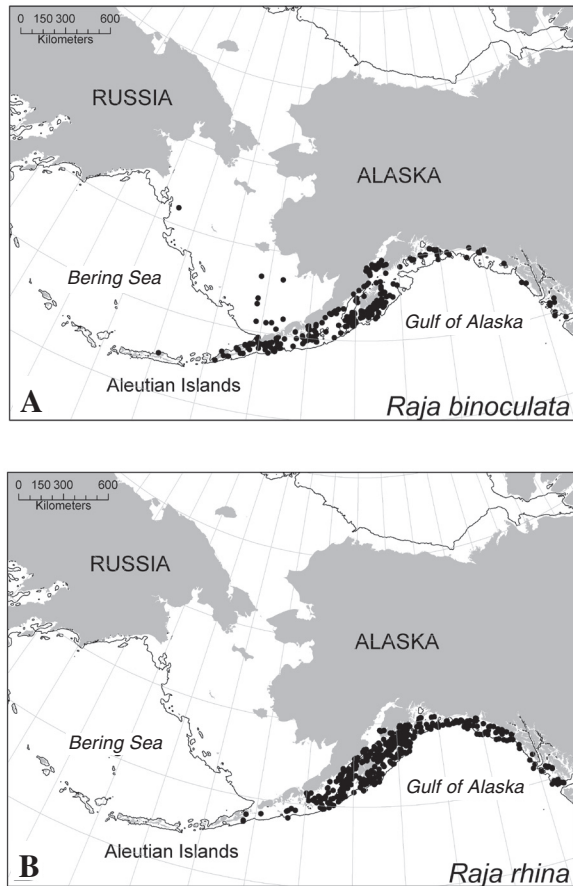


Figure 7

Distribution of (A) *Raja binoculata* (big skate) and (B) *R. rhina* (longnose skate) based on data from bottom-trawl surveys conducted in the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska from 1999 through 2004. Black circles indicate the presence of the species in one or more survey hauls. Depth contour = 200 m.

data on overall skate density in enough detail for direct comparison with the present work. Similarly, limited sampling effort on the continental slope of the Aleutian Islands and Gulf of Alaska have precluded us from demonstrating a similar pattern in other regions of the eastern North Pacific.

More species of skates have been recorded from the Aleutian Islands than from any other survey region, and yet the mean species richness figures are relatively low for this region. This finding is a result of the low encounter rate, because skates were present in only about half of the survey hauls completed in the Aleutian Islands. In areas where skates were encountered in the Aleutian Islands, Shannon's diversity indices were relatively high, which may indicate that many species have similar habitat preferences. The most commonly encountered species of skates in the Aleutian Islands were *B. maculata*, *B. taranetzi*, and *B. parmifera*. *Bathyrāja aleutica* was also relatively common throughout



Figure 8

Distribution of *Amblyraja badia* (roughshoulder skate: squares), *Bathyrāja abyssicola* (deepsea skate: triangles), and *B. mariposa* (butterfly skate: circles) based on data from bottom-trawl surveys conducted in the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska from 1999 through 2004. Black circles indicate the presence of the species in one or more survey hauls. Depth contour = 200 m.

the archipelago. Although the Aleutians Islands survey did not explore depths greater than 500 m, some of the species commonly found on the Bering Sea slope, such as *B. lindbergi*, *B. minispinosa*, and *B. trachura*, have occasionally been collected in the archipelago, and therefore the skate fauna on the continental slope of the Aleutian Islands is probably similar to that of the eastern Bering Sea slope. The fact that these species were only encountered in the deepest hauls in the Aleutian Islands survey explains why mean species richness increases with increasing depth in this region.

The skate fauna of the Aleutians also displayed some regional variation. *Bathyrāja interrupta* was relatively common in the eastern Aleutians but only rarely encountered in the central and western Aleutians, and *Raja binoculata* was not collected west of Unalaska Island. *Bathyrāja mariposa* appeared to be endemic to the central Aleutian Islands. In the western Aleutians *B. parmifera* is apparently replaced by a similar undescribed species (Stevenson et al., 2007), treated here as *B. parmifera*, and the western Pacific species *B. violacea* is known from one specimen collected by a groundfish fisheries observer near Buldir Island in the western Aleutians. According to Orlov (2005) and Orlov et al. (2007), *B. maculata*, *B. aleutica*, and *B. violacea* are the most abundant skate species farther west in the northern Kuril Islands and along the southern Kamchatka Peninsula. At least two of the skate species found in the Aleutian Islands, *B. parmifera* and *B. taranetzi*, exhibit very different coloration in the Aleutian Islands than in other regions where they are known. In the eastern Bering Sea, both of these species are a relatively uniform brown, often with dark brown or black blotches and occasionally pale yellow markings.

However, specimens of both species collected from the Aleutian Islands are much more colorful, usually with vivid yellow or olive-green markings on the disc. Additional investigation of these regional differences may lead to the recognition of more undescribed species. The deepwater species *A. badia* and *B. abyssicola* have not been encountered in the Aleutian Islands in recent trawl surveys, although this may be due to the lack of deep trawling effort in the region because both species are known to inhabit the North Pacific and the eastern Bering Sea (see Stevenson and Orr, 2005), and *B. abyssicola* has been recorded from the Aleutian Islands (Zorzi and Anderson, 1990).

Unlike the eastern Bering Sea and Aleutian Islands, the skate fauna of the Gulf of Alaska is dominated by the two Alaskan species of the genus *Raja*. Moreover, the encounter rate of skates in the Gulf of Alaska is even lower than that of the Aleutians. These two factors combine to produce very low mean species richness values. The depth distributions of the two species of *Raja* appear to be somewhat complementary, in that *R. binoculata* generally inhabits shallower waters than *R. rhina*, but neither species is found frequently below 400 m. Like these two species of *Raja*, *Bathyraja interrupta* and *B. aleutica* are both found throughout the Gulf of Alaska, and the ranges of both species extend well south of the Alaska border. *Bathyraja parmifera* is also found throughout the Gulf of Alaska, but is rare west of Kodiak (i.e., in subregions 3, 4, and 5). Like species richness values for the Aleutian Islands, species richness values are low in the Gulf of Alaska, but Shannon's diversity indices are not particularly low. Some of the species common in the slope waters of the Bering Sea and Aleutian Islands, such as *B. lindbergi* (2005 survey data) and *B. minispinosa* (Love et al., 2005), have recently been recorded in the Gulf of Alaska, as well. *Bathyraja trachura*, a species relatively abundant off the U.S. west coast from Washington to California (Lauth, 2000) as well as on the eastern Bering Sea slope, is also probably common throughout the deeper waters of the Gulf of Alaska, and it seems probable that the deepwater species *B. abyssicola* and *A. badia* (both known from around the Pacific Rim; Zorzi and Anderson, 1990; Stevenson and Orr, 2005) would be found in the Gulf of Alaska if additional deep sampling efforts were initiated.

Interpretations of these data should be viewed within the context of the sampling limitations. Groundfish assessment surveys conducted in Alaska have been primarily restricted to the shelf and the shallowest portion of the continental slope. Although recent surveys on the eastern Bering Sea slope have improved our understanding of the distribution of skates and other deeper dwelling fishes, the lack of deeper samples from the Gulf of Alaska and Aleutian Islands is problematic because without these samples we are unable to make meaningful comparisons among regions. Another limitation of this data set concerns the gear used for AFSC bottom-trawl surveys. All surveys included in this study were performed with otter trawls. However,

the sea floor substrate and topographic features differ markedly among the regions surveyed. Because of differences in the suitability of the sea bottom for trawling, many areas within Alaskan waters (particularly in the Aleutians and Gulf of Alaska) have been considered "untrawlable," and therefore remain unsampled. Moreover, the relatively rough trawling conditions typically encountered in some regions necessitate the use of different types of trawl gear. The effects that these differences may have on the catchability of skates, and how these catchability differences may affect comparisons among surveys, are unknown (Kotwicki and Weinberg, 2005). Finally, information on any seasonal changes that may affect skate distributions (Dolganov, 1998, 1999) in Alaska is very limited. Virtually all NMFS groundfish assessment surveys in Alaska have been conducted during summer months, and we know little about the distributions of these species during the rest of the year.

This study represents a major advance in our knowledge of the species richness, diversity, population density, and distribution of the skate fauna of Alaska. It provides a reference strategy for the reliable assessment and monitoring of skate diversity and abundance with data from resource assessment surveys. It also provides an example of how advances in taxonomy and field identification tools can enable more detailed and robust assessments of species diversity than were previously possible. These considerations are particularly critical for the skates of this region because of their high species diversity and their vulnerability to fishing pressure and habitat disturbance. We hope this study will serve for comparison with similar studies of other regions or other groups of fishes, as well as provide a baseline for monitoring future changes in the skate fauna of Alaska.

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