Distribution and relative abundance of seven species of skates (Pisces: Rajidae) which occur between Nova Scotia and Cape Hatteras

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DISTRIBUTION AND RELATIVE ABUNDANCE OF SEVEN SPECIES OF SKATES (PISCES: RAJIDAE) WHICH OCCUR BETWEEN NOVA SCOTIA AND CAPE HATTERAS[1]

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ABSTRACT

Data collected during eight groundfish surveys of the area from Nova Scotia to Cape Hatteras, North Carolina, and during five seasonal surveys of Chesapeake Bight were used to define the distribution and relative abundance of *Raja eglanteria, R. garmani, R. laevis, R. erinacea, R. ocellata, R. senta,* and *R. radiata.* Ancillary distributional data for the area from the Straits of Florida to Cape Hatteras and the areas off northern Nova Scotia and the Gulf of St. Lawrence were used qualitatively to extend the distributional study.

Raja eglanteria is a Carolinian species abundant north of Cape Hatteras only during the warmer months. *Raja garmani*, a skate of the outer continental shelf and upper slope, consists of two populations which have different temperature preferences. *Raja laevis* is the most widespread species studied and does not appear to be as abundant as the other skates in any region of the study. *Raja erinacea*, a Virginian to boreal species, occurs from southern Nova Scotia to Cape Hatteras in shallow water but is present at depths down to 384 m. *Raja ocellata* is a Virginian to boreal species distributed similarly to *R. erinacea* except that the former is widespread in the Gulf of St. Lawrence and off northern Nova Scotia. *Raja senta*, a boreal species, frequently occurs on the northern offshore banks of Nova Scotia and at temperatures as low as −1.3°C. *Raja radiata* is a boreal to arctic species.

Raja erinacea and *R. ocellata* are sympatric over the greater part of their ranges as are *R. senta* and *R. radiata.* The two pairs of species have complementary distributions. *Raja ocellata* has slightly lower temperature preferences than *R. erinacea*, and *R. radiata* is more widespread and has wider temperature tolerances than *R. senta.*

The genus *Raja* is represented by *R. eglanteria, R. garmani, R. laevis, R. erinacea, R. ocellata, R. senta* and *R. radiata* along the continental shelf of North America between Nova Scotia and Cape Hatteras, NC. Notes on the occurrence and distribution of these species have been summarized by Bigelow and Schroeder (1953, 1954), Leim and Scott (1966), and McEachran (1973); however, most of this information is based on scattered regional studies. The present study presents data gathered during comprehensive groundfish surveys of the area from Nova Scotia to Cape Hatteras and defines the distribution and relative abundance of each species, as well as cooccurrence among species.

MATERIALS AND METHODS

Data used in this study were divided into two categories: 1) quantitative data used to determine relative abundance of the skates, and 2) qualitative data used only to determine the temperature, depth, and geographical ranges of the skates.

Data supplied by National Marine Fisheries Service (NMFS) Biological Laboratory at Woods Hole, Mass. (now Northeast Fisheries Center) and by the Virginia Institute of Marine Science (VIMS) at Gloucester Point, Va. were used to determine relative abundance. The former data consisted of eight groundfish surveys of the continental shelf (27-366 m) from LaHave Bank, off southeastern Nova Scotia, and the Gulf of Maine to Cape Hatteras. A total of 2,247 stations were made during the winters of 1968-70, the summer of 1969, and the autumns of 1967-70 (Table 1) by the RV *Albatross IV*, except that part of 70-06 was conducted by the RV *Delaware II*. The survey area was divided into 58 strata according to depth and geographical area, and three or more stations were randomly selected within each stratum per cruise (Figure 1) (Grosslein 1969). A No. 36 Yankee trawl equipped with a cod end liner of 0.25-inch bar mesh and

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TABLE 1.—Groundfish surveys conducted by the Biological Laboratory of the National Marine Fisheries Service at Woods Hole, Mass (now Northeast Fisheries Center).

Cruise	Dates	Season	No. of stations
67-21	17 Oct.- 9 Dec. 1967	Autumn	271
68-03	4 Mar.- 16 May 1968	Winter	262
68-17	10 Oct.- 26 Nov. 1968	Autumn	275
69-02	5 Mar.- 10 Apr. 1969	Winter	266
69-08	14 July- 18 Aug. 1969	Summer	267
69-11	8 Oct.- 23 Nov. 1969	Autumn	276
70-03	12 Mar.- 29 Apr. 1970	Winter	289
70-01	15 Oct.- 20 Nov. 1970	Autumn	341
Total			2,247

18 inch rollers on the ground rope was towed at 3.5 knots for 0.5 h at each station. Distance of tow averaged 1.75 miles.

Prior to data analysis, the 58 sampling strata were grouped into five ecological subareas according to hydrography and substratum. Schopf and Colton (1966) stated that the southern Nova Scotian shelf, Gulf of Maine, and Georges Bank have different bottom temperatures and faunal assemblages. Although Georges Bank and Nantucket shoals (northern section of the mid-Atlantic Bight) have similar bottom temperatures and faunal assemblages (Schopf and Colton 1966), the area extending from Georges Bank to Cape Hatteras was subdivided because of its great size. The southern section of the mid-Atlantic Bight consisted of strata 61 to 76; the northern mid-Atlantic Bight was composed of strata 1 to 12 and 25; Georges Bank was made up of strata 13 to 23; the Gulf of Maine included strata 24, 26 to 30, and 36 to 40; and the Nova Scotian shelf consisted of strata 31 to 35, 41, and 42. All four depth zones (27-55, 56-110, 111-183, 184-366 m) were sampled in the first three subareas; the three deeper zones were surveyed in the Gulf of Maine; and only two zones, 56-110 and 111-183 m, were sampled on the Nova Scotian shelf.

Preliminary examination of the skate data indicated contagion as Taylor (1953) and Roessler (1965) had demonstrated for trawl catch data in general. A logarithmic transformation tends to normalize contagious distributions (Pereyra et al. 1967), so skate counts were transformed to log $(X + 1)$. Transformed values were used to determine the geometric mean numbers (indices of abundance) of skates per stratum per cruise. The indices of abundance were weighted by dividing them by the area of the strata to correct

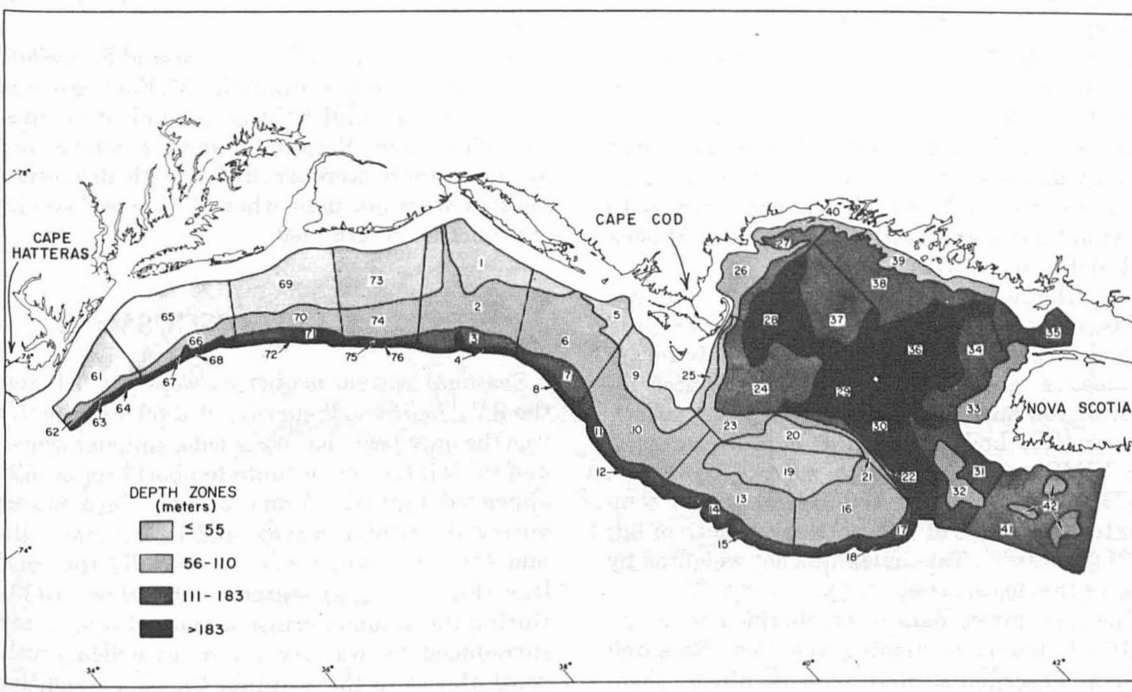

FIGURE 1.—Strata sampled by the RV *Albatross IV* and *Delaware II*, 1967-70. Strata numbers 43-60 were not included in the surveys.

for areal differences between strata. Area of the strata are listed in Table 2.

Indices of abundance for all stations, within temperature intervals of 1°C for each of the five ecological subareas, were calculated for each species. Indices were not weighted. Length frequencies were calculated for strata sets corresponding to each of the four depth intervals (27-55, 56-110, 111-183, 184-366 m) within each of the subareas. This analysis gave the percentages that each 3-cm length increment contributed to the total catch of a species within each of the strata sets of the subareas.

Hurlbert's (1969) index of association was used to determine the level of cooccurrence based on presence and absence of two species at the same stations. Species pairs with a significant positive index were compared by the product moment correlation (simple correlation coefficient) to determine if the two species were positively or negatively related by numbers. The correlation indices were computed from transformed abundance values [log $(X + 1)$] at stations where the two species cooccurred. According to Hurlbert (1969), a negative correlation, showing an inverse relationship in numbers of individuals between the species, may indicate that the two species compete for the same resources.

The VIMS data included five seasonal groundfish surveys of the Chesapeake Bight (lat. 38° 43′N to 35°13′N) in 9 to 274 m during the four seasons of 1967 and winter of 1968. This area was divided into grids of lat. 15′ by long. 12.5′. A 1-h tow was made in each grid per survey with an Atlantic western trawl without rollers (Musick and McEachran 1972).

The Chesapeake Bight was divided into two areas, one north and one south of the Virginia Capes (lat. 37°N) for data analysis. Index of abundance (geometric mean) was computed for each of the species (*R. eglanteria, R. garmani, R. erinacea,* and *R. ocellata*) captured during the VIMS survey, by depth zone (0-18, 19-37, 38-73, 74-110, 111-165, 166-274 m) and by temperature intervals of 1°C, north and south of lat. 37°N separately. This index was not weighted by area of the depth zone.

The qualitative data were obtained from the NMFS Exploratory Fishing and Gear Research Base at Pascagoula, Miss. (now Southeast Fisheries Center, Pascagoula Laboratory) for the area from the Straits of Florida to Cape Hatteras, and from the Fisheries Research Board of Canada Biological Station at St. Andrews, New Brunswick for the area off northeastern Nova Scotia, including Banquereau, Sable Island Bank, Western Bank, and the Gulf of St. Lawrence. Distributional data from south of Cape Hatteras were collected from 1961 to 1968, and data from northeastern Nova Scotia and the Gulf of St. Lawrence were collected from 1960 to 1970. Several vessels and different types of trawling gear were used.

Small specimens of *R. erinacea* and *R. ocellata* are difficult to distinguish (McEachran and Musick 1973), and field personnel often misidentified them. Records of species not verified by the authors were evaluated with discretion. Records were not used when the correct species could not be determined.

TABLE 2.—Area of sampling strata.

Stratum number	Area (mi²)	Stratum number	Area (mi²)	Stratum number	Area (mi²)
1	2,516	21	424	40	578
2	2,078	22	454	41	3,752
3	566	23	1,016	42	589
4	188	24	2,569	61	1,318
5	1,475	25	390	62	243
6	2,554	26	1,014	63	86
7	514	27	720	64	60
8	230	28	2,249	65	2,832
9	1,522	29	3,245	66	555
10	2,722	30	619	67	86
11	622	31	2,185	68	52
12	176	32	712	69	2,433
13	2,374	33	816	70	1,024
14	656	34	1,766	71	281
15	230	35	1,097	72	105
16	2,980	36	4,069	73	2,145
17	360	37	2,108	74	1,273
18	172	38	2,560	75	139
19	2,454	39	730	76	60
20	1,221				

RESULTS AND DISCUSSION

Seasonal bottom isotherms were plotted from the RV *Albatross IV* surveys of 1969 because this was the only year that included a summer cruise, and the winter and autumn temperature profiles appeared typical. Temperatures were lowest during the winter survey, and isotherms in the mid-Atlantic Bight tended to parallel the coast line (Figure 2), as stated by Bigelow (1933). During the summer cruise a mass of cold water, surrounded by warmer water, extended southward almost to the Virginia Capes, a condition previously described by Bigelow (1933). Temperatures were warmest during the autumn survey.

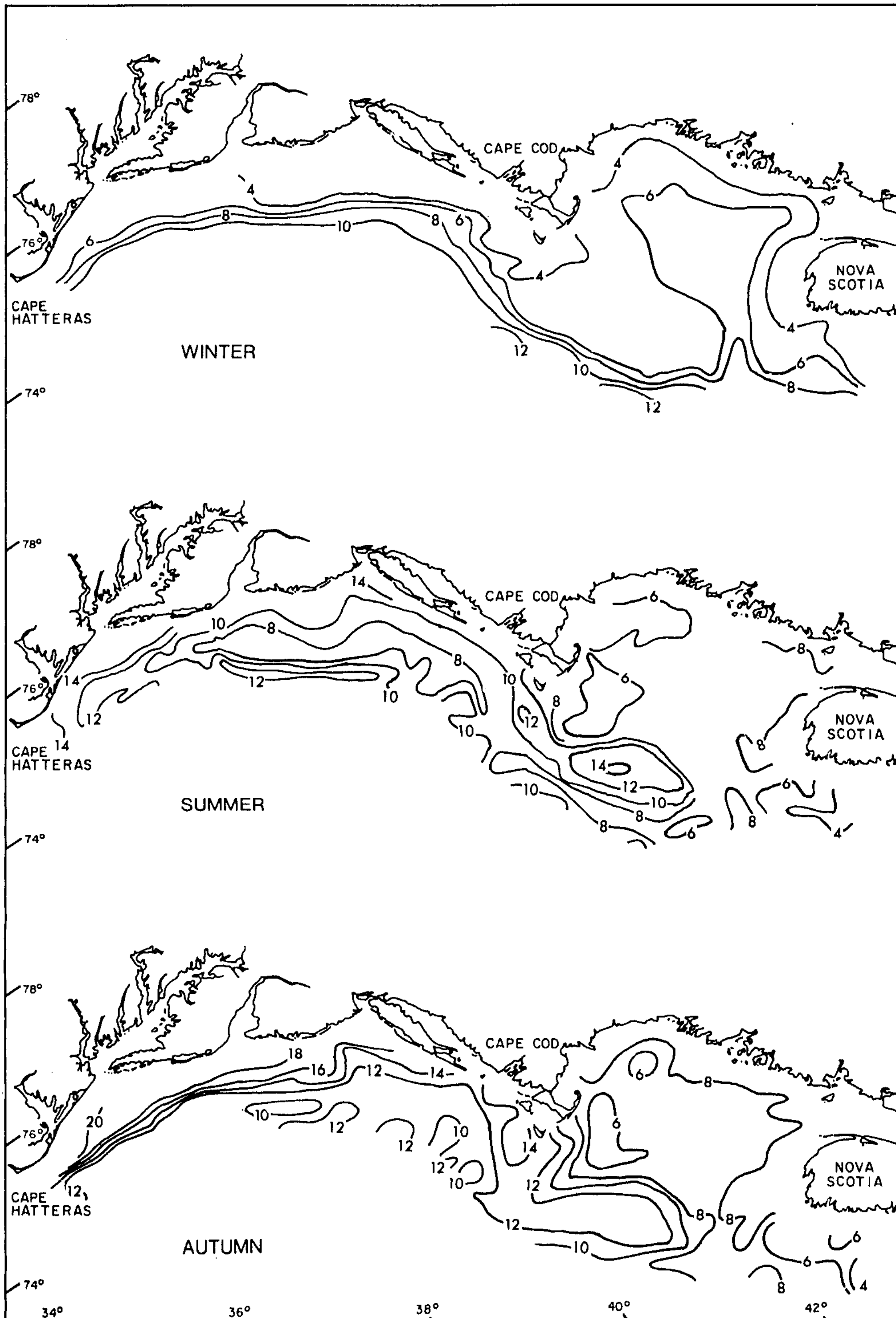

FIGURE 2.—Bottom isotherms plotted from measurements taken during winter, summer, and autumn 1969 surveys of the RV *Albatross IV*. Temperatures are in degrees Celsius.

The summer survey was conducted during July and August, and the autumn survey during October and November (Table 1). Waters of intermediate depths of both the mid-Atlantic Bight and Georges Bank reach their maximum temperatures in October (Bigelow 1927, 1933; Schopf and Colton 1966).

Length frequencies by strata sets revealed that small to large specimens of each species were found together and all length sizes were pooled for the distributional analyses of each species. Small specimens of *R. erinacea* and *R. ocellata* were seldom captured. The young of these two species may lie outside the sampling region or may be less vulnerable to the gear used. Richards et al. (1963) also noted the absence of young *R. erinacea* on the fishing grounds of Block Island and Long Island sounds where the larger individuals were abundant.

Charts showing the distribution by strata, and histograms showing the distribution by temperature were illustrated for the *Albatross IV* cruises of 1969. Only the four most abundant species (*R. erinacea, R. ocellata, R. senta,* and *R. radiata*) were included. Distribution by temperature and depth zones was illustrated for two species (*R. eglanteria* and *R. garmani*) captured during the VIMS survey of the Chesapeake Bight.

Raja eglanteria

Raja eglanteria was captured from the southern section of the mid-Atlantic Bight to about midway along the eastern coast of Florida. A few individuals were taken in the southern section of the mid-Atlantic Bight on all *Albatross IV* cruises, except for summer 1969 and winter 1970. During the VIMS survey of the Chesapeake Bight *R. eglanteria* was more abundant in shoal water during the spring and summer than during the autumn and winter (Figure 3) and was more abundant in the Chesapeake Bight during the summer and autumn than in the winter and spring. It was captured between 5° and 26°C in the Chesapeake Bight and was most abundant between 9° and 20°C (Figure 4). South of Cape Hatteras it was taken from 9° to 27°C. Over its entire range, it was most abundant at depths less than 111 m. *Raja eglanteria* was captured only at 9 of the 676 stations which were in water deeper than 110 m. It was taken at 5 of the 43 deeper stations during the VIMS survey but at only 4 of the 633 deeper stations south of Cape Hatteras, thus it has a greater tendency to inhabit deeper water in the northern part of its range.

Raja eglanteria, a Carolinian species in the sense of Johnson (1934) and Hedgpeth (1957), occurs north of Cape Hatteras all year but is abundant there only during the warmer months. Bigelow and Schroeder (1953) stated that it is most abundant from the sublitoral zone to about 55 m. However, Edwards et al. (1962) captured it in 280 and 329 m off Cape May, N.J. during the winter. In autumn, *R. eglanteria* leaves the embayments and shallow areas of the mid-Atlantic Bight (Bigelow and Schroeder 1953; Schwartz 1961; Massman 1962; Fitz and Daiber 1963; Schaefer 1967) and moves offshore and southward. *Raja eglanteria* was not captured in the mid-Atlantic Bight during the summer *Albatross IV* cruise probably because the species is concentrated then at depths less than 27 m. Apparently many individuals that summer in the southern part of the Chesapeake Bight move around Cape Hatteras during the autumn or early winter. The individuals south of Cape Hatteras inhabit slightly warmer water as suggested by Bigelow and Schroeder (1953) and do not appear to move into deeper water during the winter. Dahlberg and Odum (1970) reported that this species is resident year-round in Georgia estuaries.

Raja garmani

Raja garmani was captured in deep water from Nantucket Shoals to the Straits of Florida. Between Nantucket Shoals and Cape Hatteras it was most abundant in the southern section of Chesapeake Bight. Over the Chesapeake Bight it was found between 33 and 196 m and generally deeper than 73 m (Figure 5), and appeared to move shoreward in the summer. In the Chesapeake Bight *R. garmani* was captured at temperatures of 6° to 17°C and was most abundant bewteen 9° and 13°C (Figure 6). Between Cape Hatteras and Georgia it was found in 66 to 123 m at 17°C; off Georgia and northern Florida it was captured in 77 to 155 m at 11° to 19°C. From northern Florida to the Straits of Florida it occurred in 99 to 366 m at 17°C, and all but one of the captures were in 183 to 366 m.

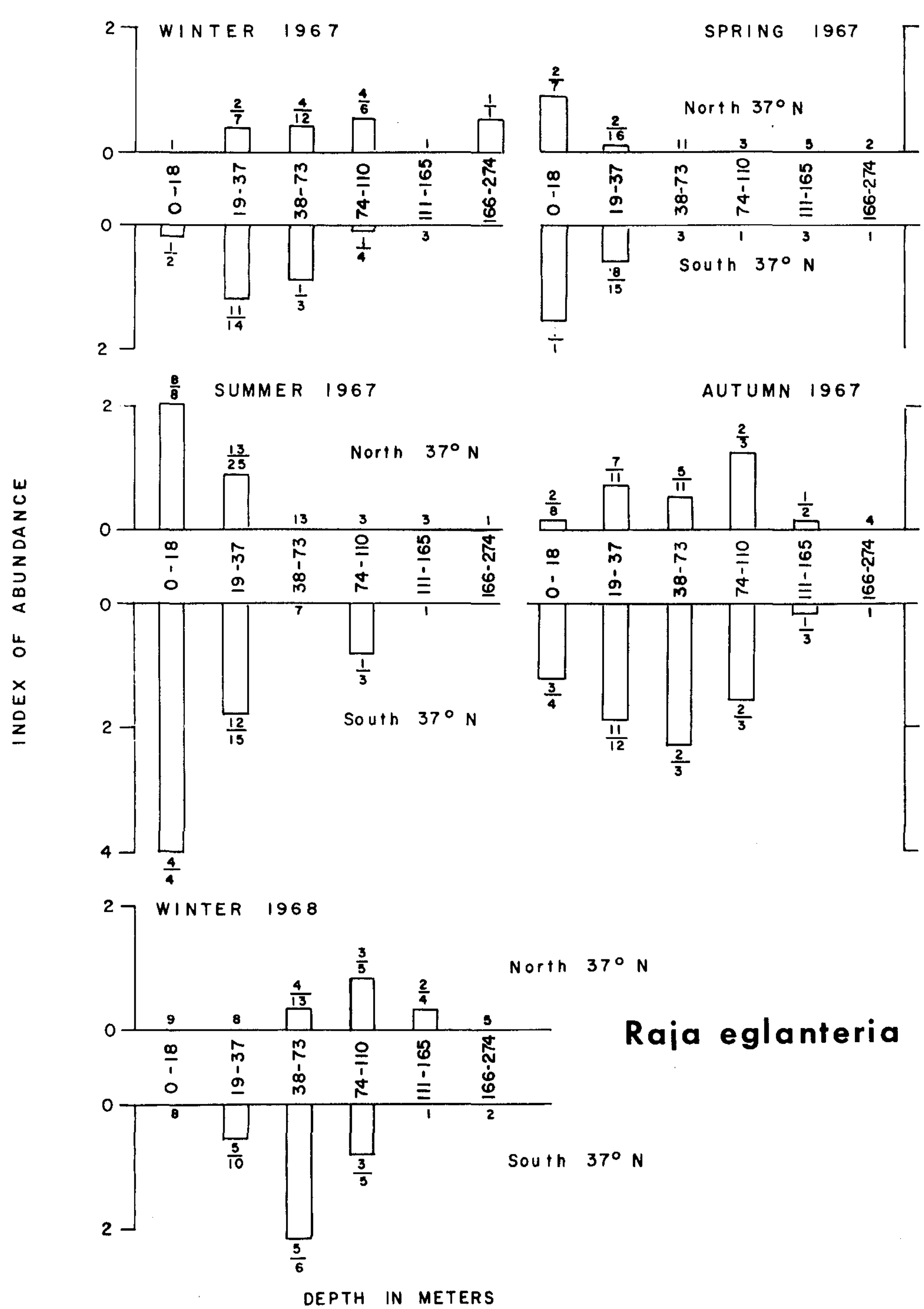

FIGURE 3.—Index of abundance (geometric mean) of *Raja eglanteria* captured in Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of lat. 37°N were analyzed separately. The fraction over each bar is the ratio of the number of stations at which the species was captured to the total number of stations in each stratum. Whole numbers represent the number of stations in the strata in which no specimens were captured.

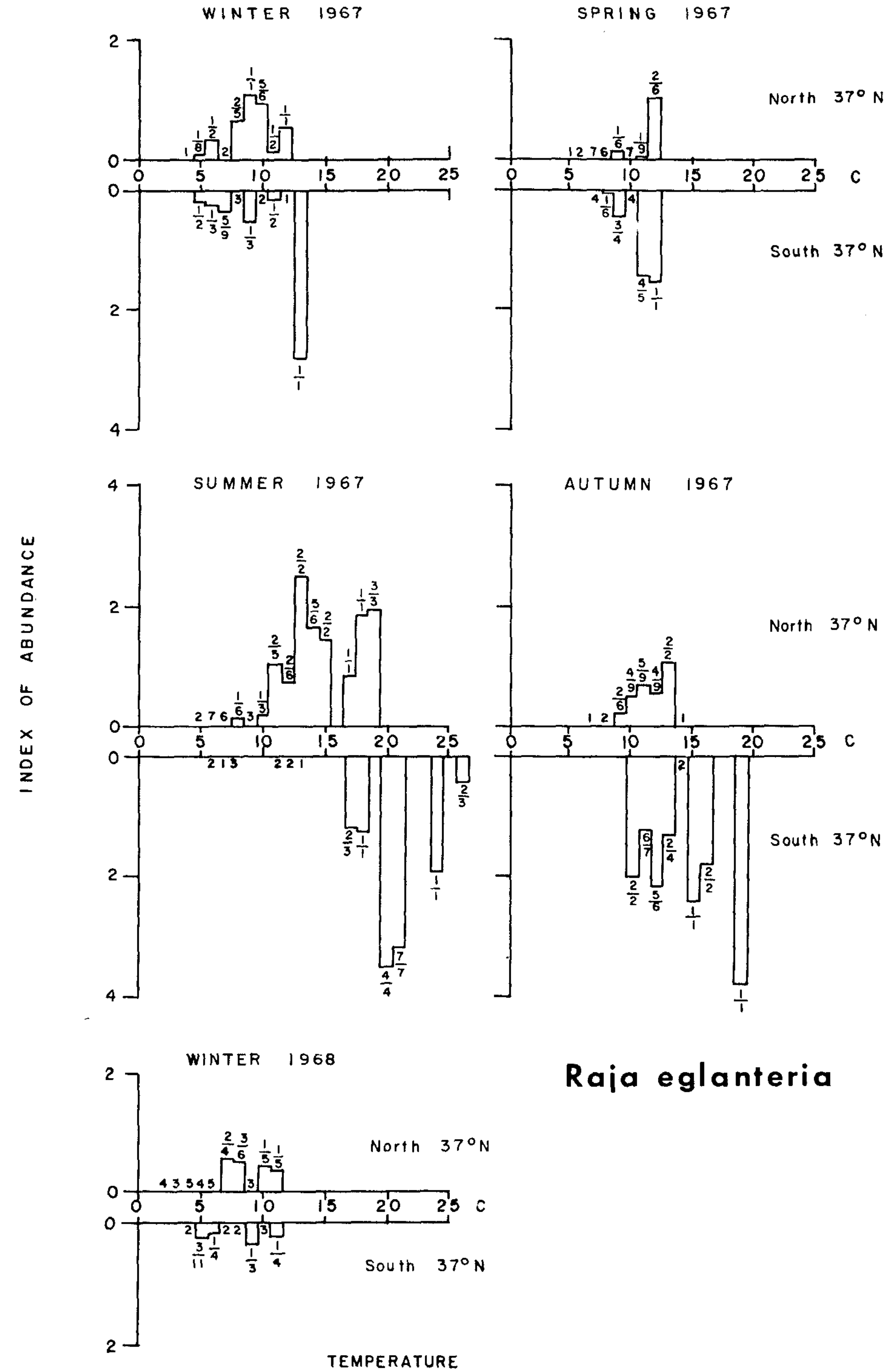

FIGURE 4.—Index of abundance (geometric mean) of *Raja eglanteria* captured in the Chesapeake Bight during each cruise within temperature intervals of 1°C. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for explanation of fractions and whole numbers.

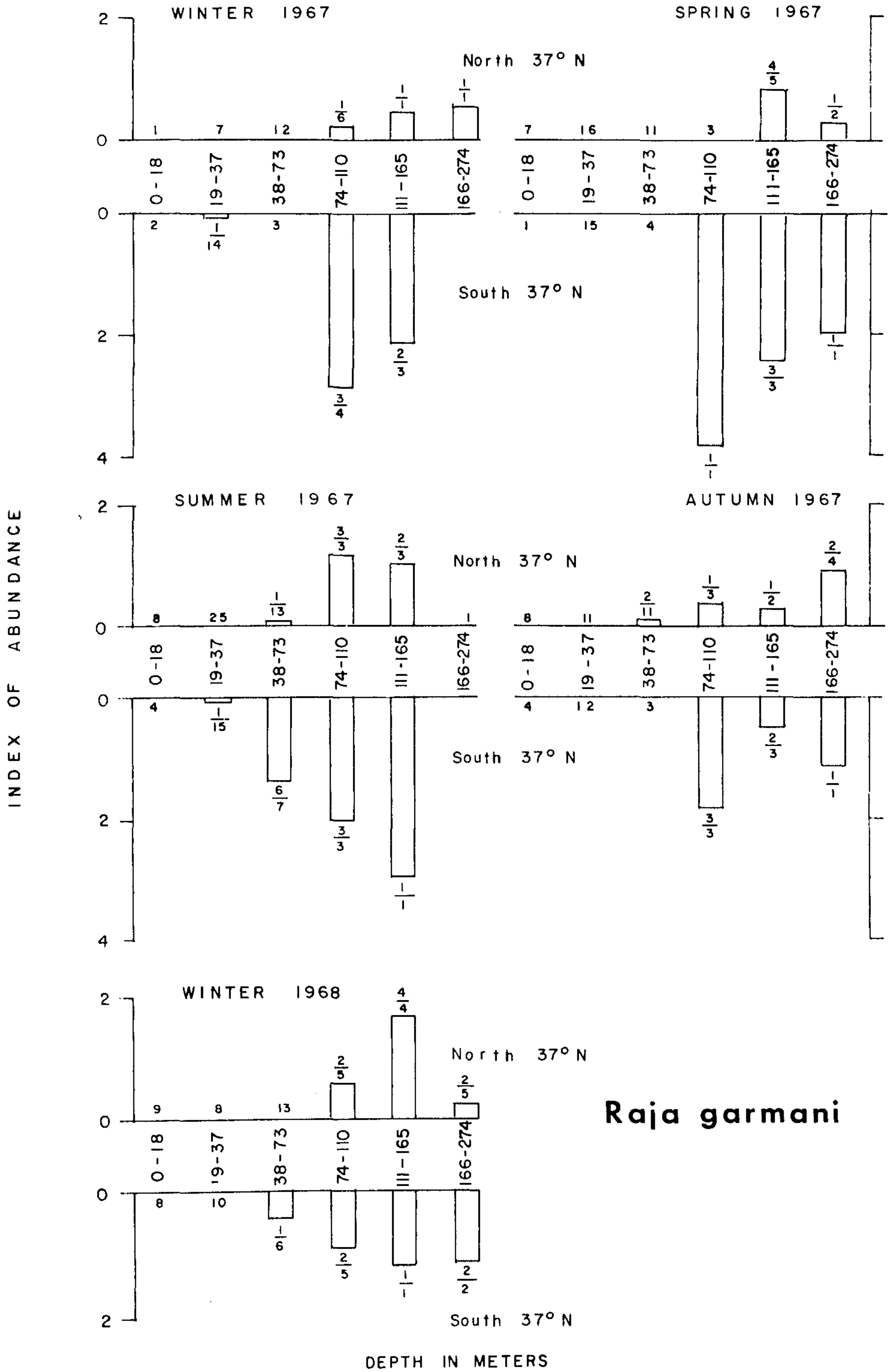

FIGURE 5.—Index of abundance (geometric mean) of *Raja garmani* captured in the Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for an explanation of fractions and whole numbers.

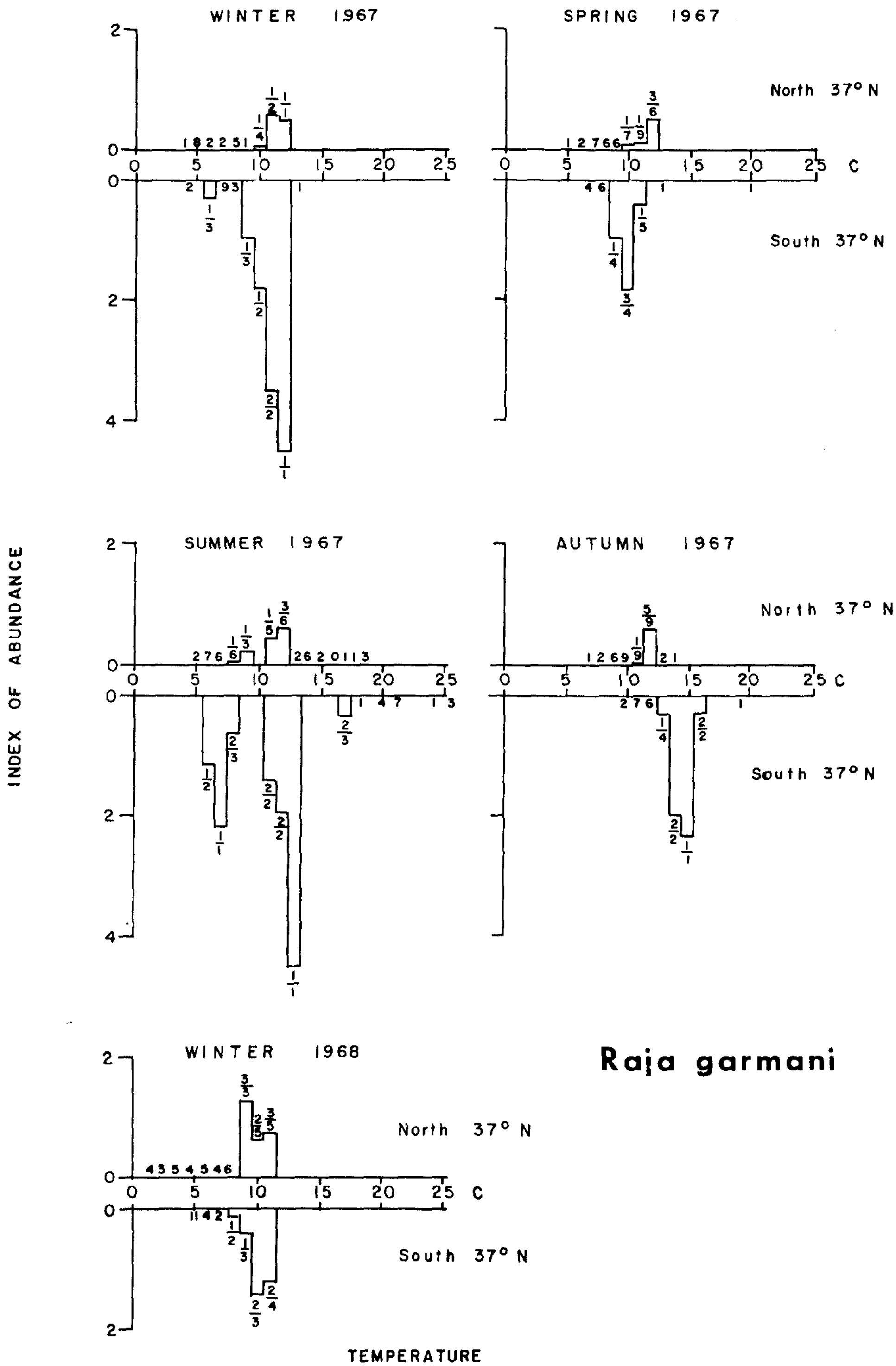

FIGURE 6.—Index of abundance (geometric mean) of *Raja garmani* captured in the Chesapeake Bight during each cruise within temperature intervals of 1°C. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for explanation of fractions and whole numbers.

Raja garmani probably does not occur regularly on the eastern slope of Georges Bank, contrary to Schroeder (1955), because no specimens were captured there during the *Albatross IV* cruises. The depth and temperature ranges of 51 to 494 m and 5.3° to 15°C given by Bigelow and Schroeder (1953) are close to those for the area north of Cape Hatteras in the present study. It has more limited depth range and is found in warmer water in the southern part of its range than in the northern part as stated by Bigelow and Schroeder (1953). Staiger (1970) stated that it is found between the 119- and 366-m isobaths on Pourtales Terrace, and north of Pourtales Terrace it occurs in 183 m up the coast of Florida. This species appears to have separate populations, one north and the other south of Cape Hatteras. North of Cape Hatteras mature specimens are 335 mm TL (McEachran 1970) to 439 mm TL and south of Cape Hatteras they are mature between 250 and 314 mm TL. The differences in temperature ranges north and south of Cape Hatteras may be due to differences in physiological requirements of the two populations.

Raja laevis

Raja laevis was captured from the Gulf of St. Lawrence, along the northeastern coast and offshore banks of Nova Scotia, to the northeastern coast of Florida. During the *Albatross IV* cruises it was taken from the Nova Scotian shelf to the southern section of the mid-Atlantic Bight and was most frequently taken in the northern section of the mid-Atlantic Bight, the eastern part of Georges Bank, eastern Gulf of Maine, and the Nova Scotian shelf. No specimens were obtained from the western Gulf of Maine. Seasonal changes in abundance were not evident. In the Gulf of St. Lawrence, *R. laevis* was found in 315 m at 4.7°C. Off northeastern Nova Scotia it was caught at depths of 24 to 375 m at 1.2° to 10.7°C. Depths and temperatures at capture for the area from southern Nova Scotia to Cape Hatteras ranged from 38 to 351 m and 3° to 20°C. *Raja laevis* was caught in 302 to 368 m off northeastern Florida.

Raja laevis is the most widespread of the species studied, but too few were taken during this study to elaborate on its distribution. Bigelow and Schroeder (1953) stated that this species occurs from the tidemark to about 750 m at 1.2° to 20°C. The southern limit of its range remains in doubt because of the apparent confusion of this species with *R. floridana* which has been captured from Cape Lookout, N.C. to Dry Tortugas, Fla. (Bigelow and Schroeder 1968). *Raja floridana* is very similar to *R. laevis* (Bigelow and Schroeder 1962) and the specimens used to describe *R. floridana* came from some of the same stations at which Bullis and Thompson (1965) listed *R. laevis*. The senior author has examined the specimens identified as *R. laevis* at the United States National Museum and University of Miami School of Marine and Atmospheric Sciences, and all of those from south of Cape Hatteras have proven to be *R. floridana*. Also *R. laevis* does not occur in the species lists of Struhsaker (1969) or Staiger (1970). Thus it is likely that many or all of the records of *R. laevis* from south of Cape Hatteras refer to *R. floridana*.

Raja erinacea

Raja erinacea was recorded from the Gulf of St. Lawrence; off Cape Breton, Nova Scotia; Western Bank; and two specimens were positively identified from Sable Island Bank. It was the most abundant species captured on Georges Bank and in the northern section of the mid-Atlantic Bight. It was rarely taken in the western Gulf of Maine (Figure 7). *Raja erinacea* was most abundant in Chesapeake Bight during the winter and those that remained there during the summer moved into deeper water.

Throughout its range, *R. erinacea* was generally caught at depths less than 111 m, but was occasionally taken at depths greater than 183 m, especially in the northern section of the mid-Atlantic Bight and on Georges Bank where it occurred as deep as 329 m. Edwards et al. (1962) captured *R. erinacea* as deep as 384 m off New Jersey, thus the species is not as restricted to shallow water as stated by Bigelow and Schroeder (1954) who reported that 159 m was the maximum depth of the species. Temperatures at depth of capture ranged from 2° to 19°C with most captures occurring between 2° and 15°C. The recorded temperature range of the species is 1.2°C (Tyler 1971) to 21°C (Bigelow and Schroeder 1953).

Raja erinacea is a Virginian to boreal species whose center of abundance is in the northern section of the mid-Atlantic Bight and on Georges Bank. Only in these areas was it found year-round over almost the entire range of temperatures recorded for the areas (Figures 8-10). In

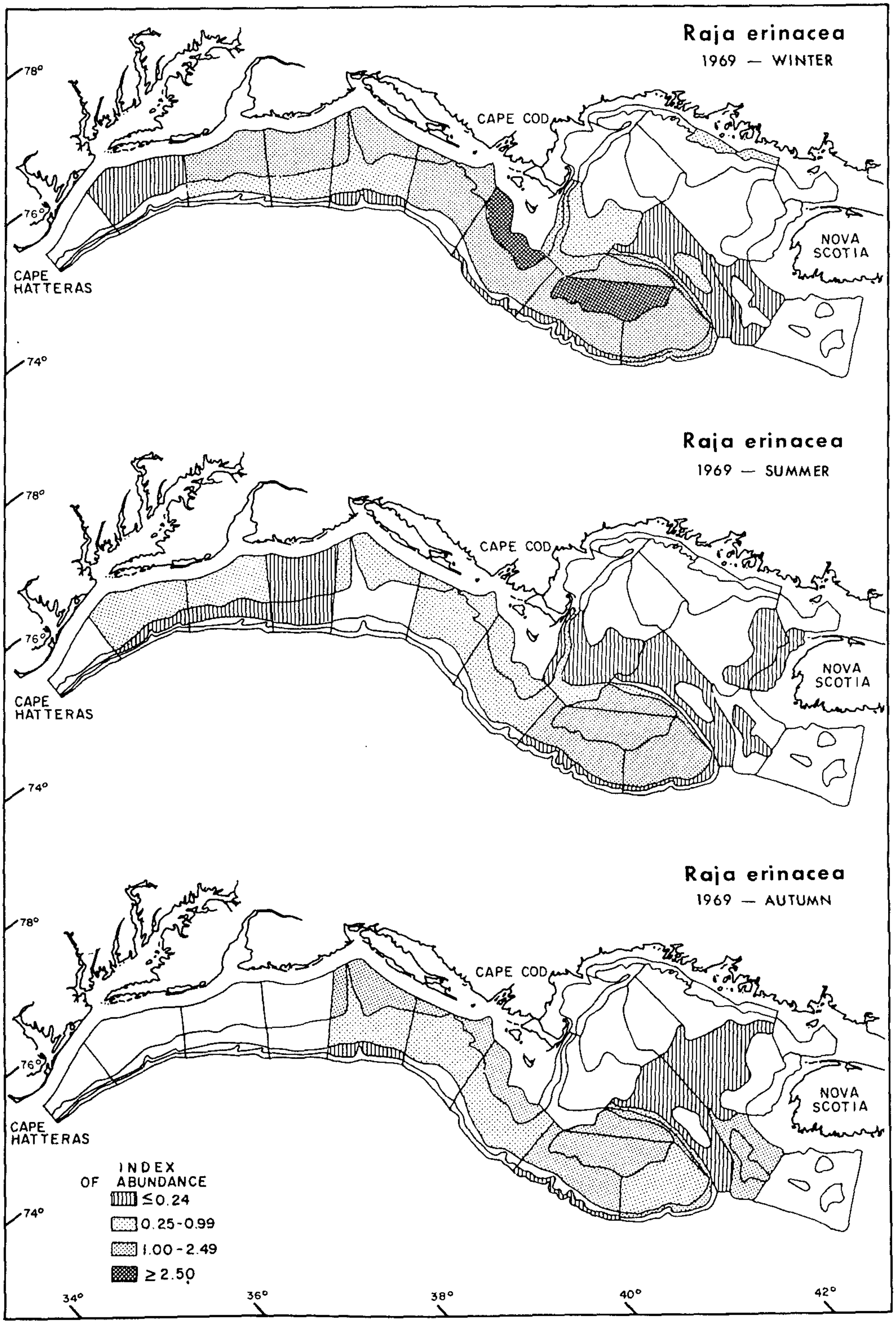

FIGURE 7.—Index of abundance (geometric mean) of *Raja erinacea* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

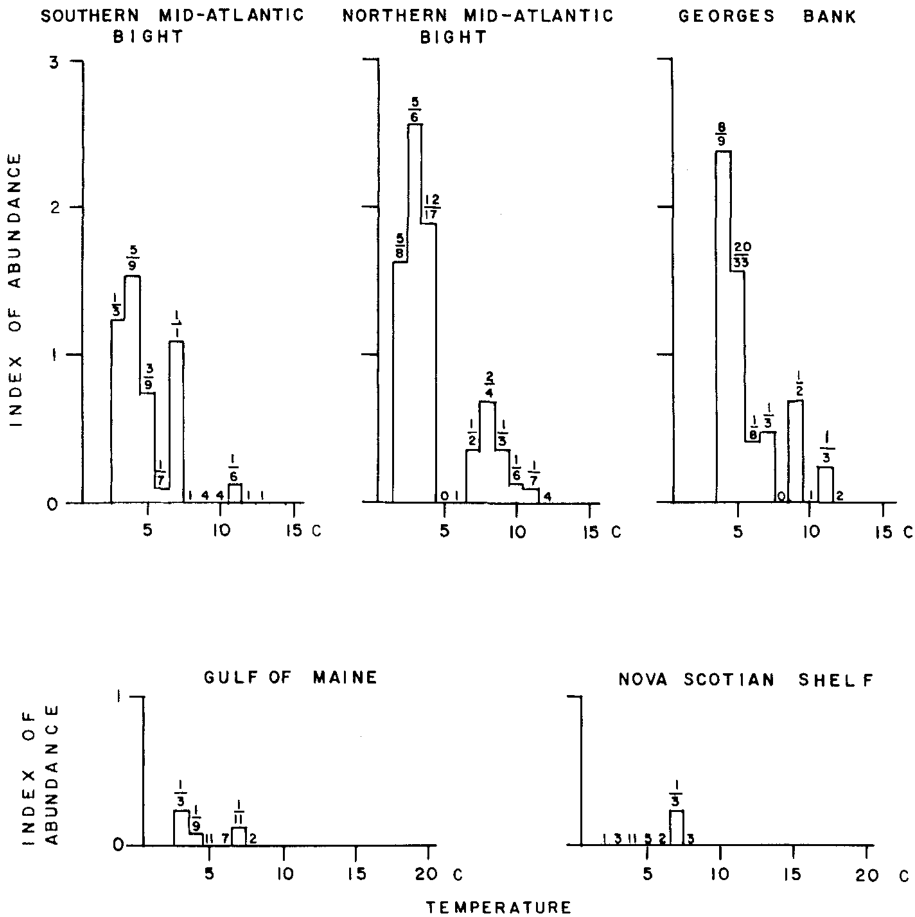

FIGURE 8.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

the southern section of the mid-Atlantic Bight it was usually caught in the lower part of the area's temperature range, and on the Nova Scotian shelf in the upper part of the temperature range.

Along the inshore fringe of its range the species moves onshore and offshore with seasonal temperature changes as stated by Bigelow and Schroeder (1953); Merriman et al. (1953); Fitz and Daiber (1963); Richards (1963); Schaefer (1967); and Tyler (1971, 1972). *Raja erinacea* also moves north and south with seasonal temperature changes along the southern fringe of its range. Contrary to Bigelow and Schroeder (1953) and Leim and Scott (1966), *R. erinacea* probably does not regularly occur off Nova Scotia north of LaHave Bank, and it may be entirely absent in the Gulf of St. Lawrence (McEachran 1973).

Raja ocellata

Raja ocellata was frequently taken in the Gulf of St. Lawrence, off northeastern Nova Scotia, and the offshore banks of Banquereau, Sable Island, and Western Bank. It was second to *R. erinacea* in abundance on Georges Bank and in the northern section of the mid-Atlantic Bight (Figure 11). *Raja ocellata* was much more abundant in the southern section of the mid-Atlantic Bight during the winter than during the remainder of the year. This species was most frequently captured in water shallower than 111 m, but was occasionally caught deeper than the maximum depth of 110 m recorded by Bigelow and Schroeder (1953). In the Gulf of Maine it was taken at 205 m, and in the Gulf of St.

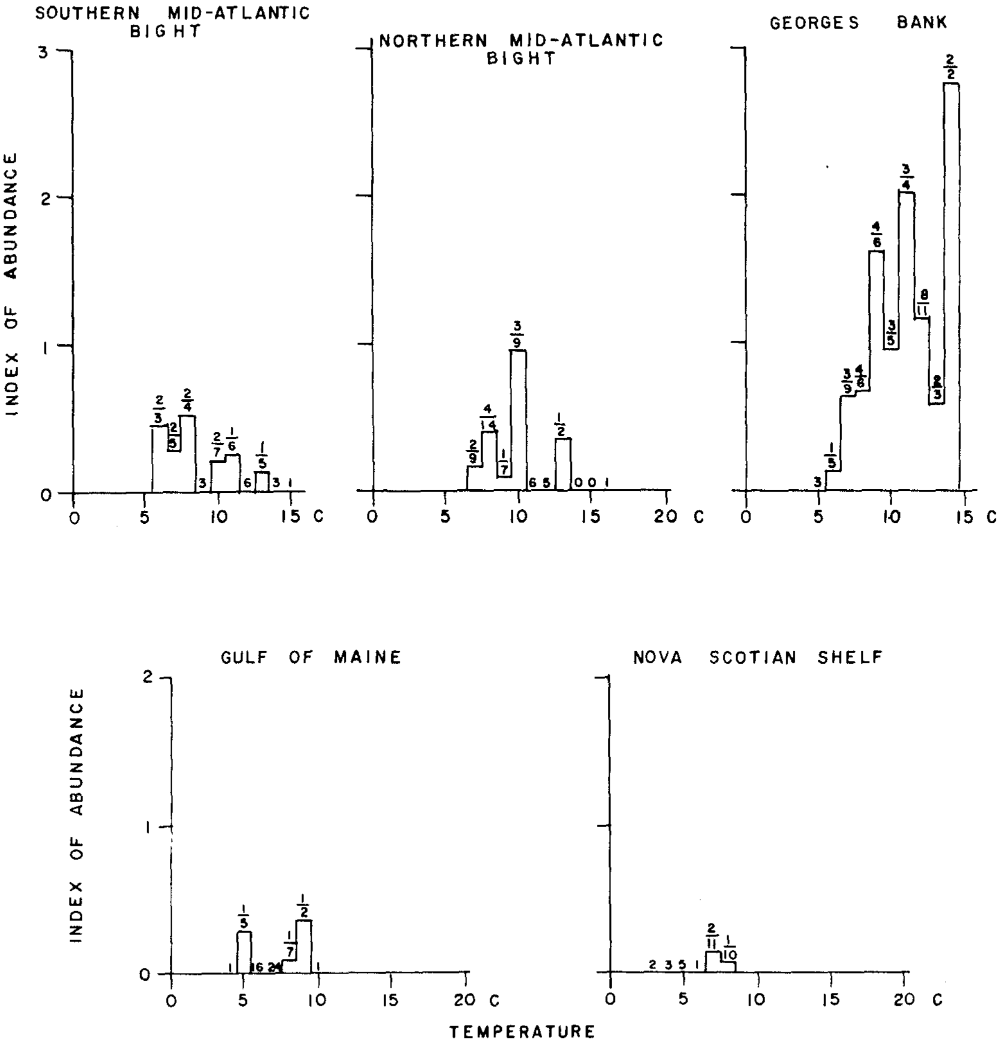

FIGURE 9.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Lawrence as deep as 371 m. Temperatures at depth of capture ranged from −1.2° to 4.8°C in the Gulf of St. Lawrence, 1.1° to 12.7°C off northeastern Nova Scotia, and 2° to 15°C from southern Nova Scotia to Cape Hatteras. Only in the Gulf of St. Lawrence was *R. ocellata* taken at temperatures below its previously recorded temperature range of 1.2°C (Tyler 1971) to 19°C (Bigelow and Schroeder 1953).

Raja ocellata is a Virginian to boreal species whose center of abundance is on Georges Bank and in the northern section of the mid-Atlantic Bight. In both subareas it was found year-round over almost the entire temperature range for the areas (Figures 12-14). It was captured only at the lower part of the temperature range recorded for the southern section of the mid-Atlantic Bight and at higher temperatures recorded for the Nova Scotian shelf.

This species was widespread in the Gulf of St. Lawrence, off northeastern Nova Scotia, and the offshore banks, and it was not as abundant as *R. erinacea* in the southern mid-Atlantic Bight. All reports of *R. erinacea* from the Gulf of St. Lawrence and most records of it from northern Nova Scotia probably refer to *R. ocellata*.

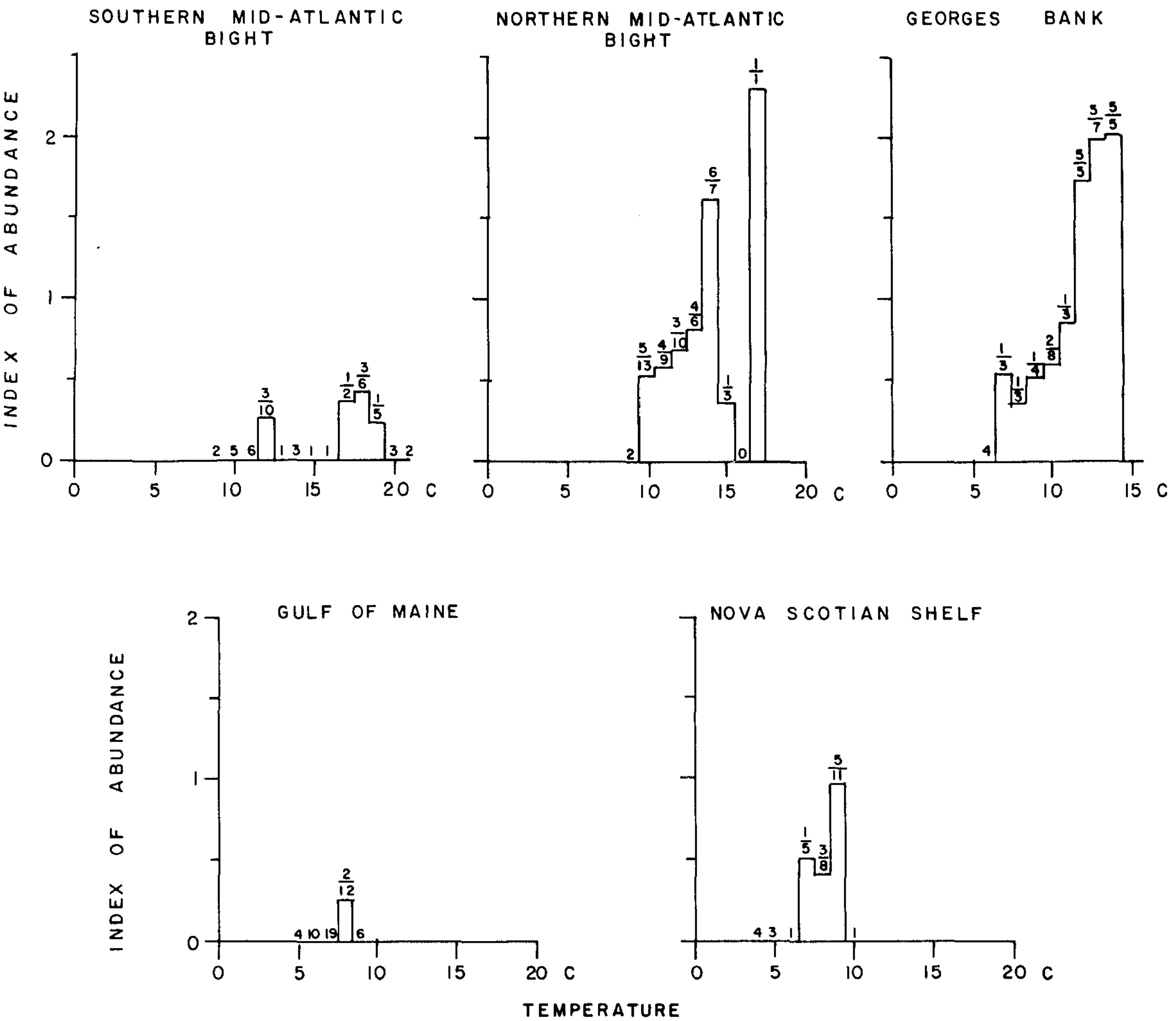

FIGURE 10.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Raja senta

Raja senta was taken in the Gulf of St. Lawrence, along the northeastern coast of Nova Scotia and, contrary to the reports of Bigelow and Schroeder (1953) and Leim and Scott (1966), it was fairly abundant on the offshore banks of Banquereau, Sable Island, and Western. It was found throughout the Gulf of Maine, off southern Nova Scotia, and on Georges Bank (Figure 15). No seasonal trends in abundance were noted. Depth of capture ranged from 31 to 413 m but it was most abundant below 110 m. Bigelow and Schroeder (1953) stated that *R. senta* occurred between 46 and 874 m and was most abundant between 91 and 457 m. This species was found at temperatures from 0.5° to 4.8°C in the Gulf of St. Lawrence, −1.3° to 11.8°C off northeastern Nova Scotia, and 2° to 10°C from southern Nova Scotia to Georges Bank. In the northern part of its range, it was occasionally caught at temperatures less than 2°C, which Bigelow and Schroeder (1953) stated was the minimum temperature for the species.

Raja senta is a boreal species whose center of abundance occurs in the Gulf of Maine, where it is found over the greater part of the range of temperatures (Figures 16-18). It is found only at the lower part of the temperature range on Georges Bank.

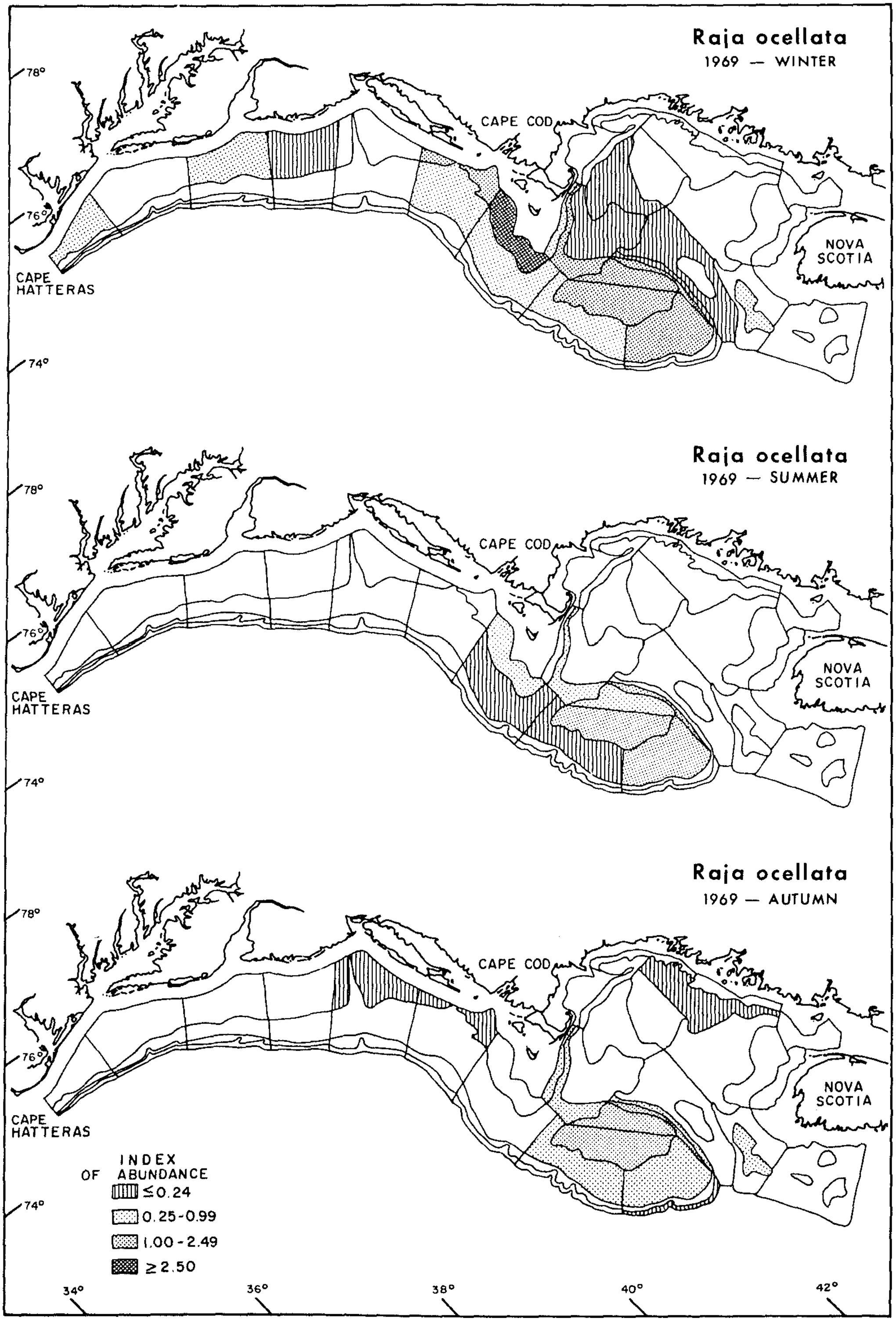

FIGURE 11.—Index of abundance (geometric mean) of *Raja ocellata* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

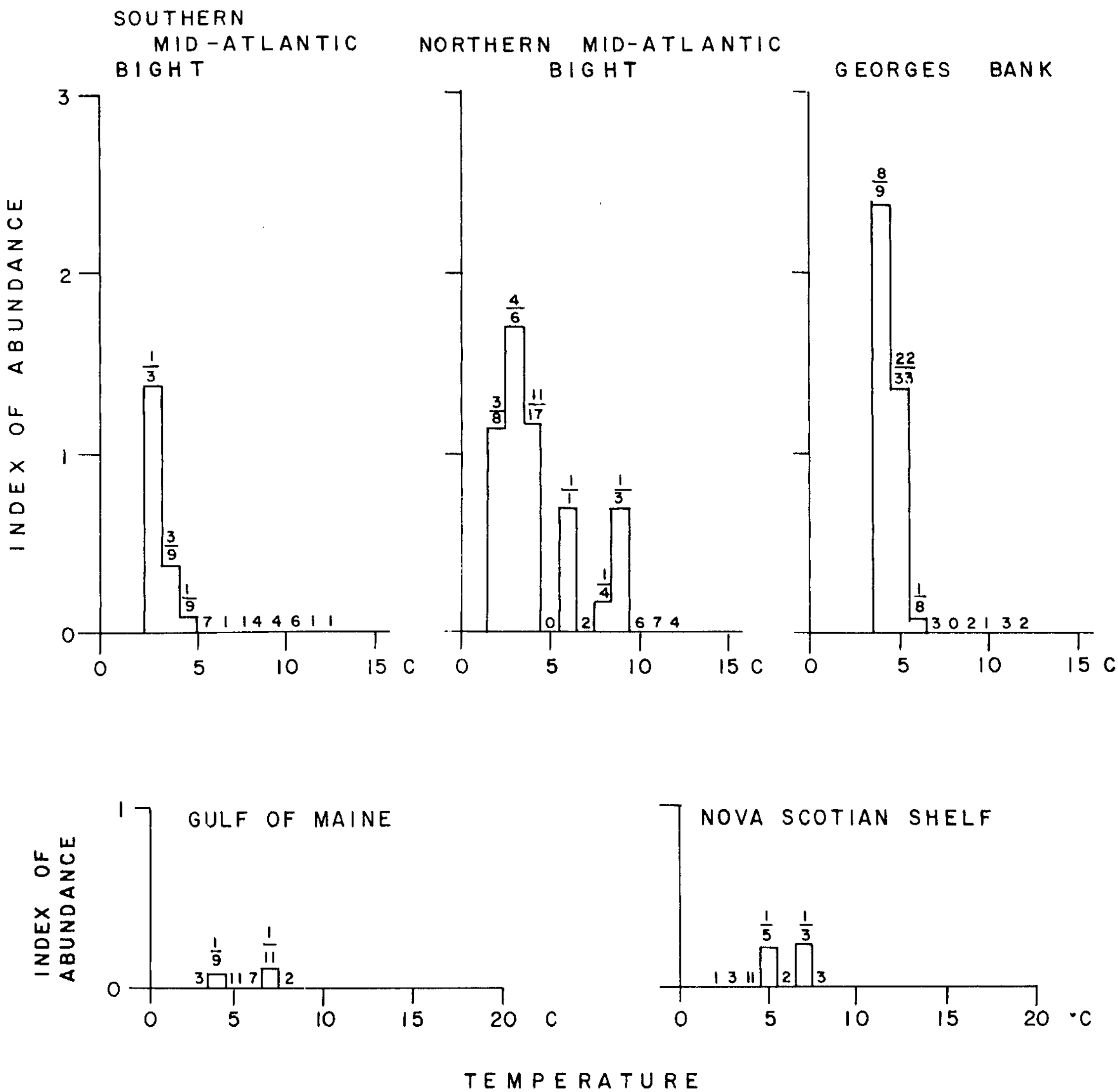

FIGURE 12.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Raja radiata

Raja radiata was the most abundant skate encountered in the Gulf of St. Lawrence, off northeastern and southeastern Nova Scotia, and in the Gulf of Maine. It was widespread along the eastern and northwestern slopes of Georges Bank (Figure 19). *Raja radiata* occurred between 27 and 439 m but was most abundant between 111 and 366 m. Bigelow and Schroeder (1953) listed a depth range of 18 to 896 m for this species in the western Atlantic. Temperatures at which it was captured ranged from −1.3° to 14°C. The previously recorded temperature range was −1.4°C (Backus, 1957) to 10°C (Bigelow and Schroeder 1953).

Raja radiata is a boreal to arctic species whose center of abundance in the western Atlantic extends northward from the Gulf of Maine probably as far as the Gulf of St. Lawrence. It

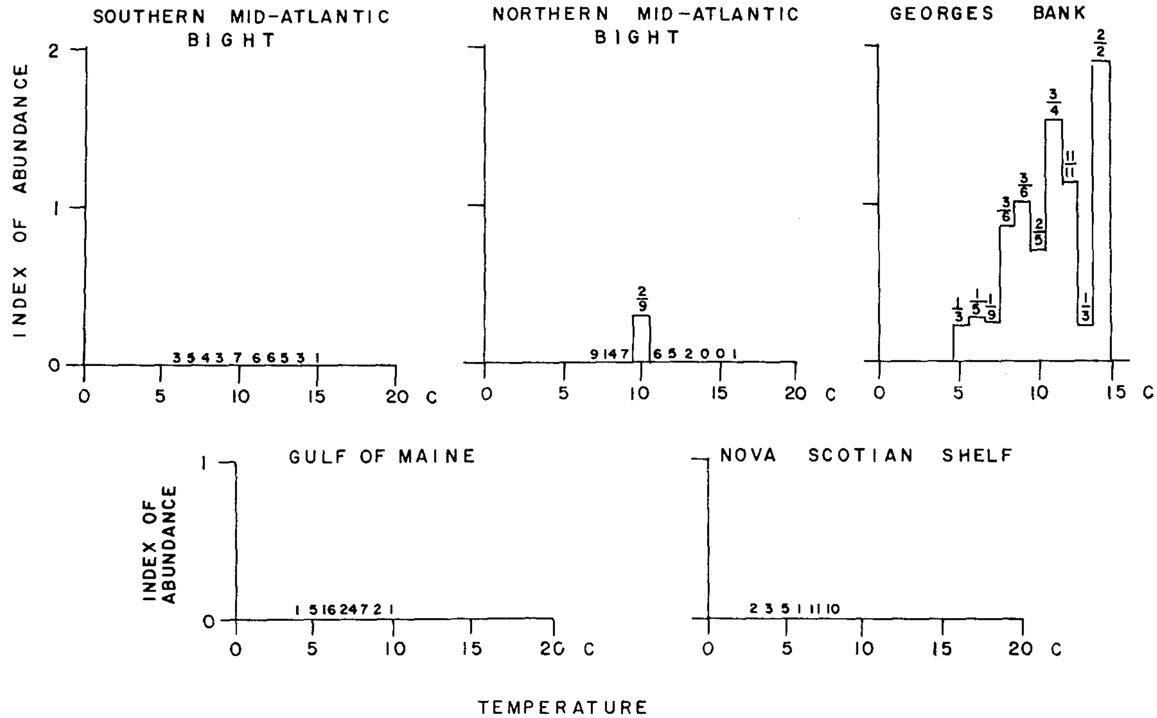

FIGURE 13.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

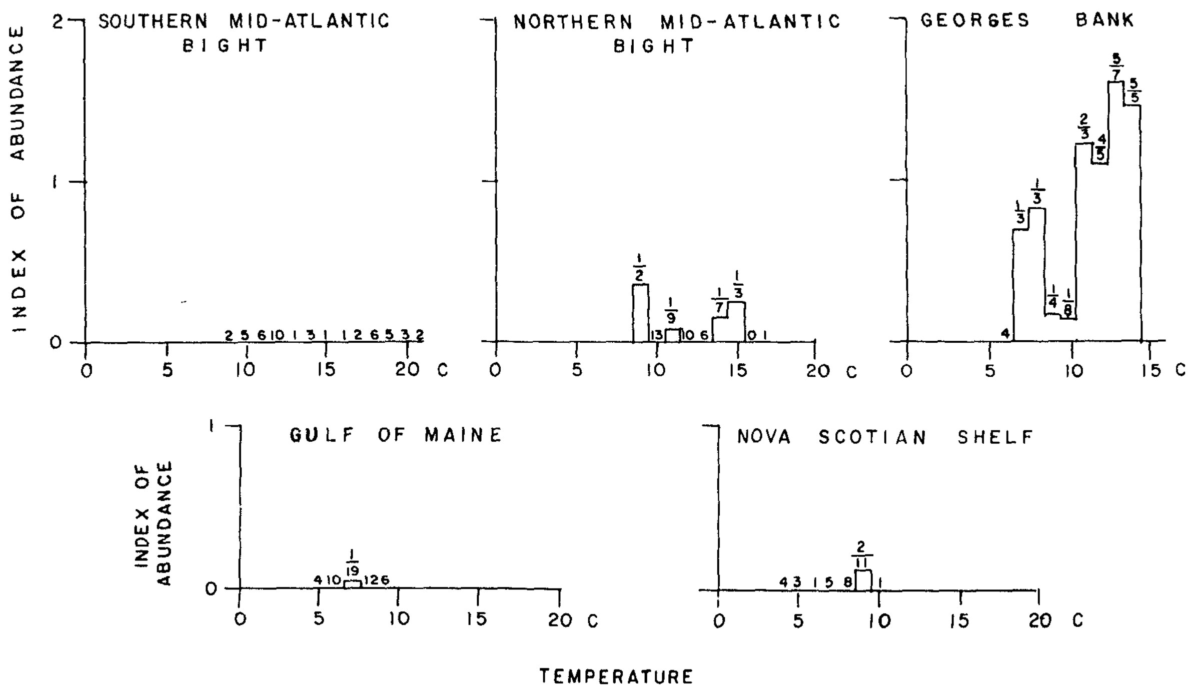

FIGURE 14.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

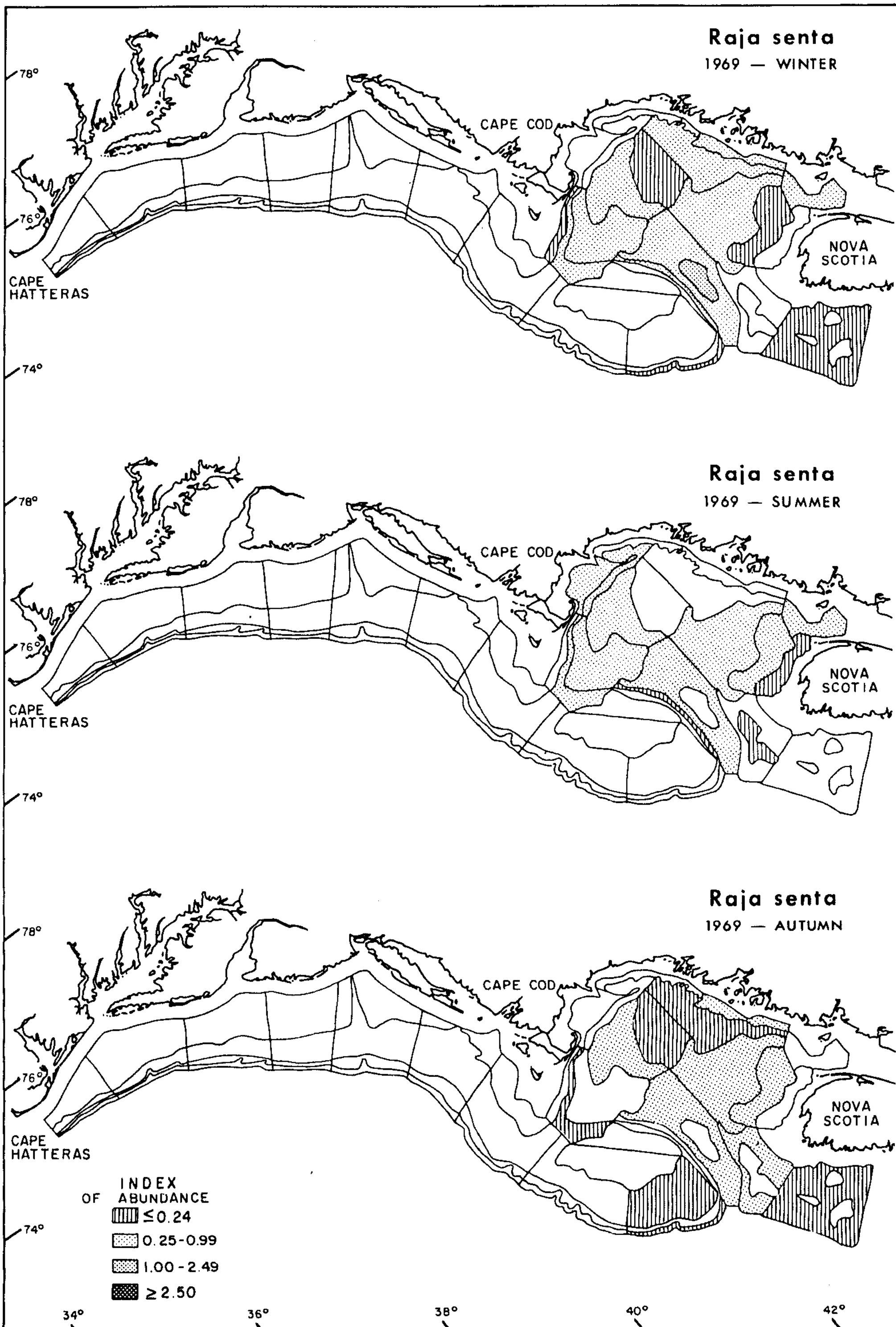

FIGURE 15.—Index of abundance (geometric mean) of *Raja senta* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

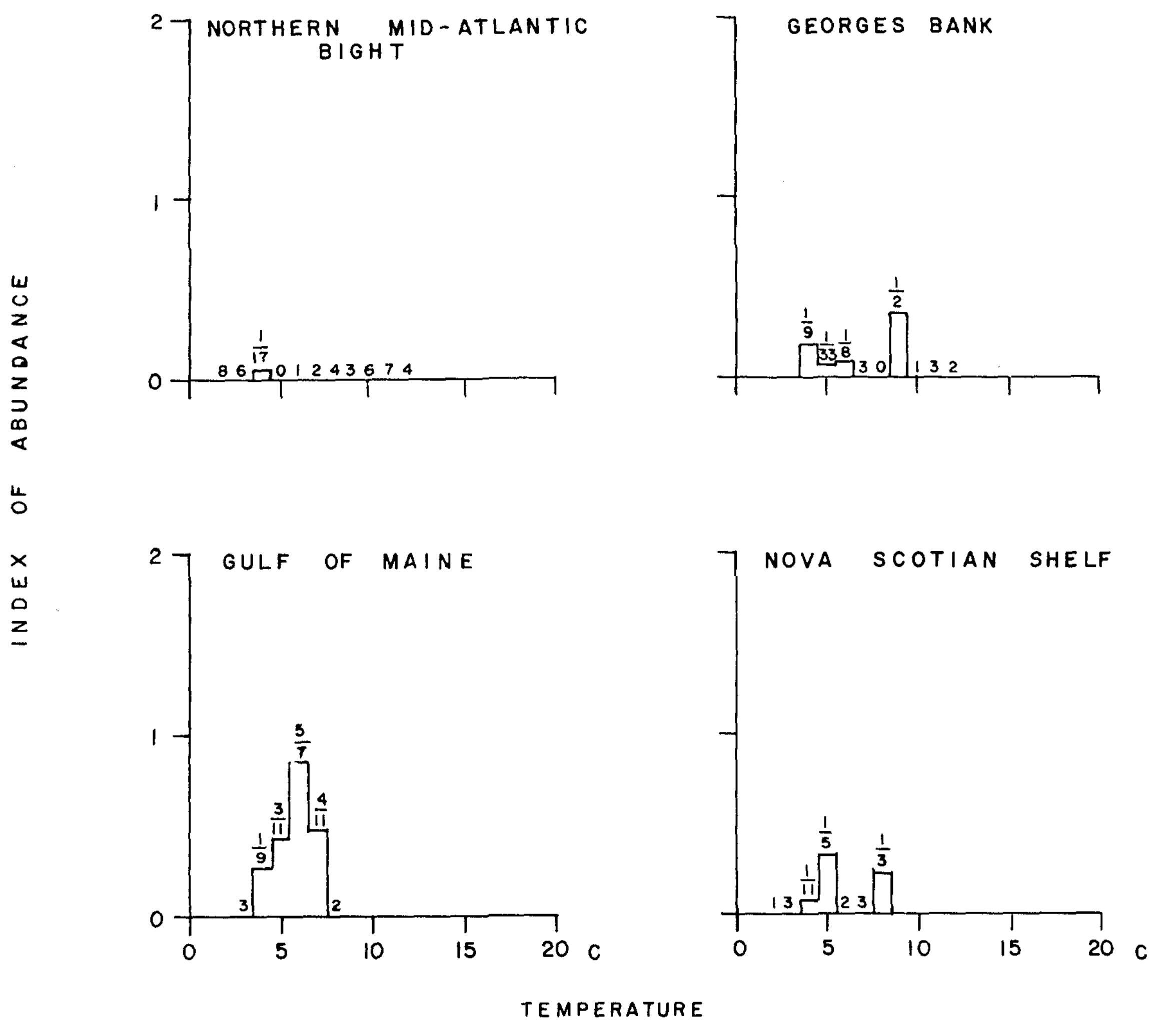

FIGURE 16.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

was found over almost the entire temperature range in the Gulf of Maine and off southeastern Nova Scotia. (Figures 20-22).

INTERSPECIFIC RELATIONSHIPS

Five of the species cooccurred significantly with one or more of the other species (Table 3). *Raja laevis* was associated with both *R. erinacea* and *R. ocellata* for half or more of the *Albatross IV* cruises. *Raja erinacea* and *R. ocellata* cooccurred significantly during all of the survey cruises and were positively associated by abundance. The product moment coefficients for the *Albatross IV* winter, summer, and autumn cruises of 1969 were: $r = 0.656, 0.471$, and 0.640. Percent of the variation in y associated with x was: 43%, 22%, and 41% respectively. The slopes of all three regressions were significant at the 1% probability level. No reason was apparent for the low correlation obtained during the summer cruise. *Raja senta* and *R. radiata* had the highest coefficient of association, and these two species were often negatively associated with *R. erinacea* and *R. ocellata*. *Raja senta* and *R. radiata* were not correlated by numbers; the coefficients for the *Albatross IV* winter, summer, and autumn cruises of 1969 were: 0.310, 0.081, and 0.283. Only a

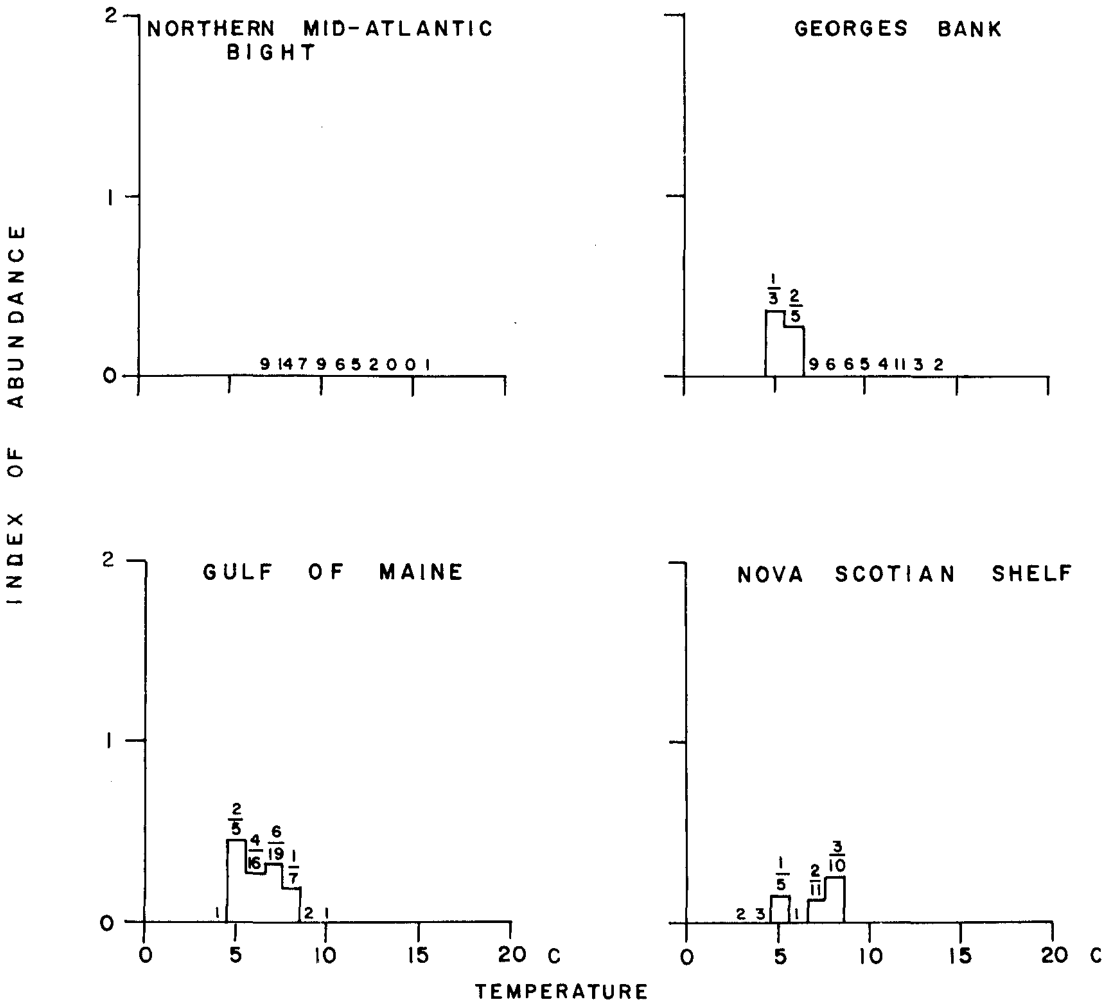

FIGURE 17.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

small part of the variance could be assigned to the correlation, and the slopes were not significant at the 5% probability level.

Raja erinacea and *R. ocellata* are predominantly found at depths less than 111 m in areas which, according to Uchupi (1963) are covered with sand or gravel. They have similar responses to seasonal temperature changes. In the southern periphery of their ranges they move southward during the colder months of the year and offshore and northward during the warmer months of the year. Within their centers of abundance, neither species undergoes a seasonal migration, each being able to tolerate the seasonal temperature extreme. *Raja ocellata* appears to have a slightly lower temperature preference as suggested by the difference in latitudinal distribution of the species. The apparent rareness of the species pair in the Gulf of Maine may be due to insufficient sampling. The shallowest depth zone (27-55 m) was not sampled during the *Albatross IV* cruises. Although the species have similar habitat requirements their positive correlation by numbers suggests that they are not competing for the same resources. Also a study of the food habits of the two species indicates that *R. erinacea* feeds largely on epifaunal organisms, and *R. ocellata* predominately selects infaunal organisms (McEachran 1973).

Raja laevis is found in the same areas as the

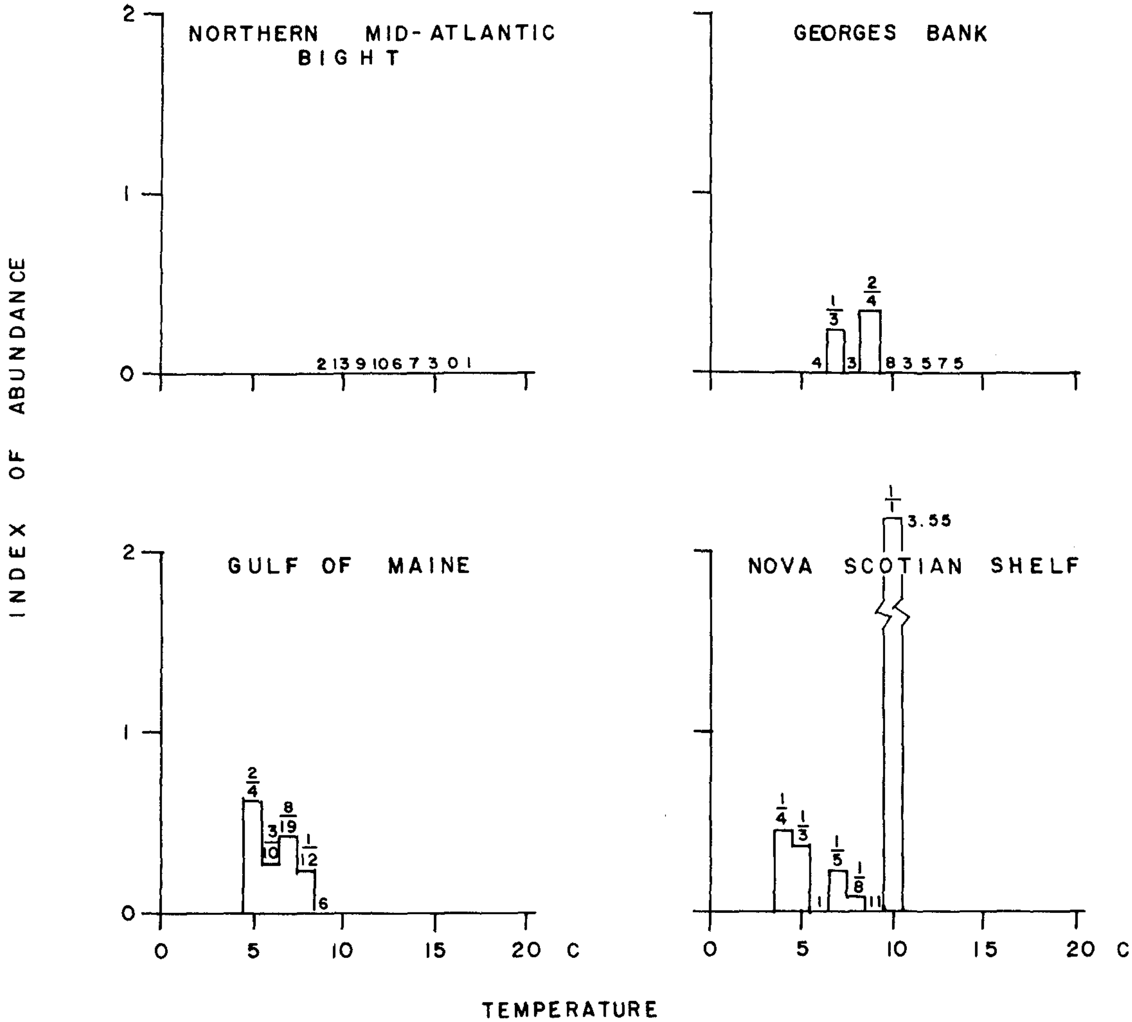

FIGURE 18.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

above species pair but has wider substratum and depth tolerance. Its low abundance may in part be explained by its considerably larger maximum size (Bigelow and Schroeder 1953) which makes it less available to the sampling gear.

The distribution of the *R. senta*-*R. radiata* species pair complements that of the *R. erinacea*-*R. ocellata* species pair. The former is found predominately in areas which, according to Uchupi (1963), were covered with sandy silt to silt and clay. They are taken over a narrower and lower temperature range than *R. erinacea*-*R. ocellata* and generally occur below 110 m. In the southern periphery of their ranges they are limited to a narrow band on the continental slope where the waters are thermally stable (Bigelow, 1933). Neither species appears to make seasonal movements. *Raja radiata* appears to have a wider temperature range and a lower temperature preference, and it is the more abundant of the two. The low abundance of *R. senta* may explain the lack of a positive or negative correlation by numbers between the species.

SUMMARY

Below the geographical, temperature and depth distribution of each species, based on literature

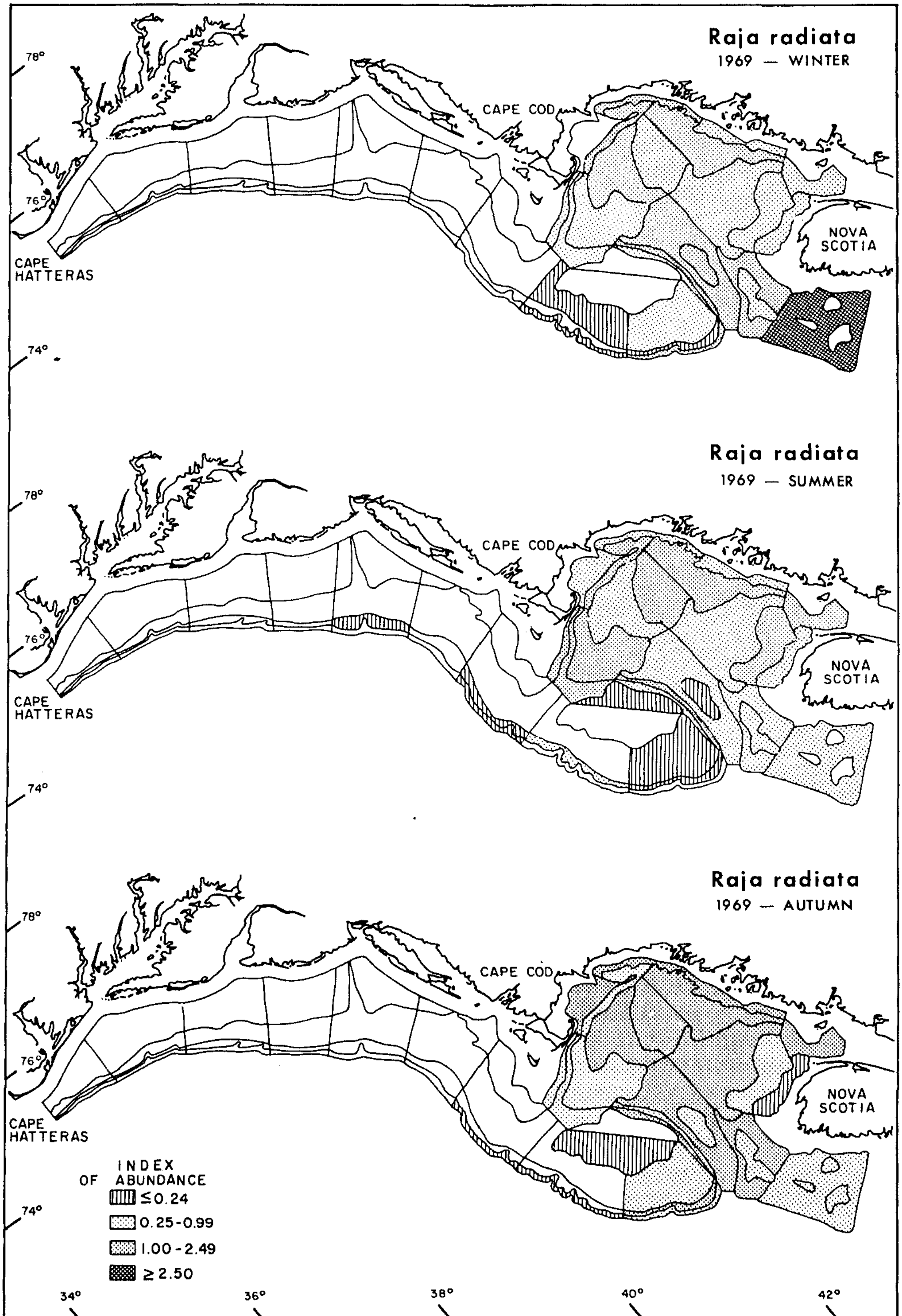

FIGURE 19.—Index of abundance (geometric mean) of *Raja radiata* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

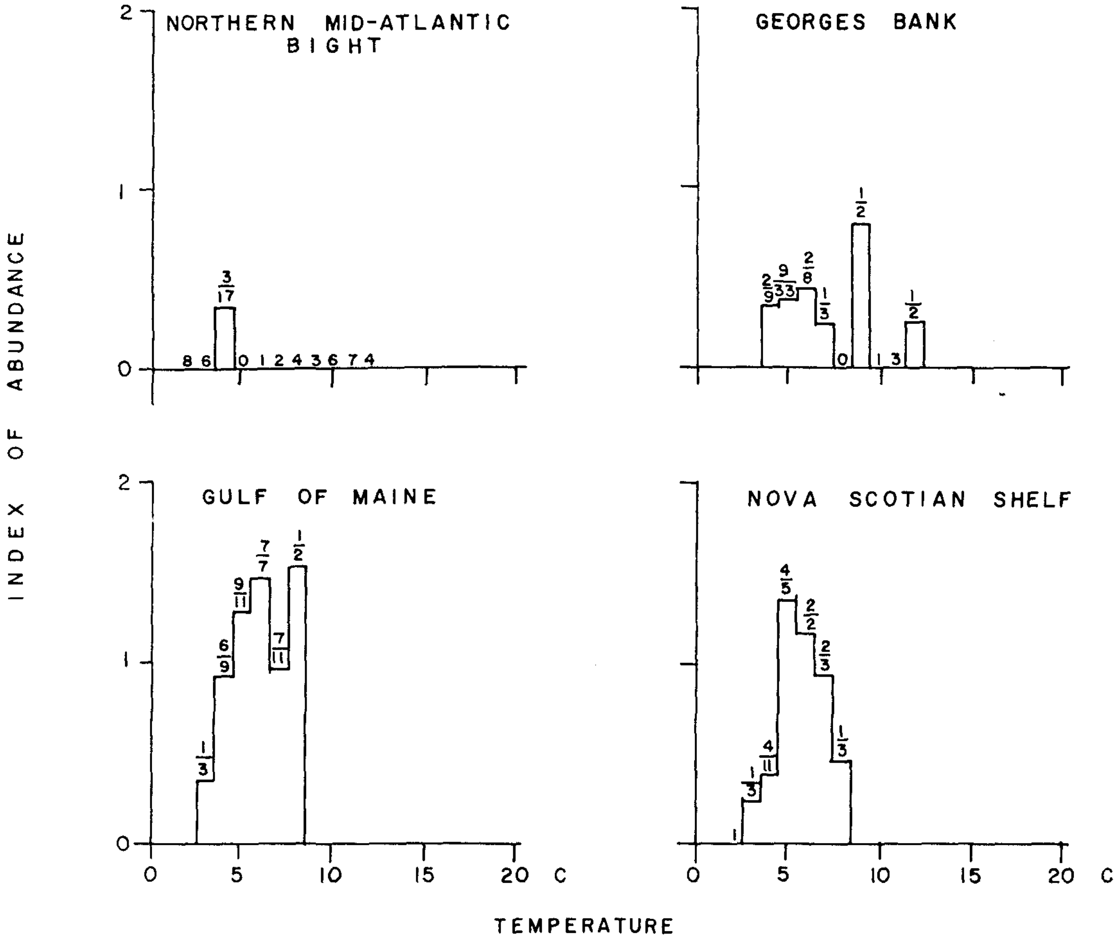

FIGURE 20.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

reports (Bigelow and Schroeder 1953; Leim and Scott 1966; and McEachran 1973) and findings in the present study, are summarized.

Raja eglanteria is found from Long Island to northern Mexico but is rare off southern Florida. It occurs from the shore zone to 329 m at 5° to 27°C, but is most abundant between the shore zone and 111 m at 9° to 20°C.

Raja garmani occurs from the offing of Nantucket Shoals to the Dry Tortugas, Fla. North of Cape Hatteras, N.C., it is found in 37 to 366 m at 6° to 17°C, and south of there it occurs from 66 to 366 m at 11° to 19°C.

Raja laevis extends from the southern Newfoundland banks and the Gulf of St. Lawrence south to North Carolina. It is found from shore to 750 m at 1.2° to 20°C.

Raja erinacea regularly occurs from southern Nova Scotia to Cape Hatteras. It is found between shore and 384 m at 2° to 21°C but is most abundant in water shallower than 111 m at 2° to 15°C.

Raja ocellata is found from the Newfoundland banks and southern Gulf of St. Lawrence to Cape Hatteras. It occurs from shore to 371 m at −1.2° to 19°C but is most abundant in water shallower than 111 m at 2° to 15°C.

Raja senta occurs from the southern Newfoundland banks and the Gulf of St. Lawrence to South Carolina. It occurs from 31 to 974 m at −1.3° to 14°C but is most abundant below 110 m at 2° to 10°C.

Raja radiata extends from Labrador, west Greenland, Hudson Bay, Grand Banks, and Gulf of St. Lawrence to South Carolina. It occurs from

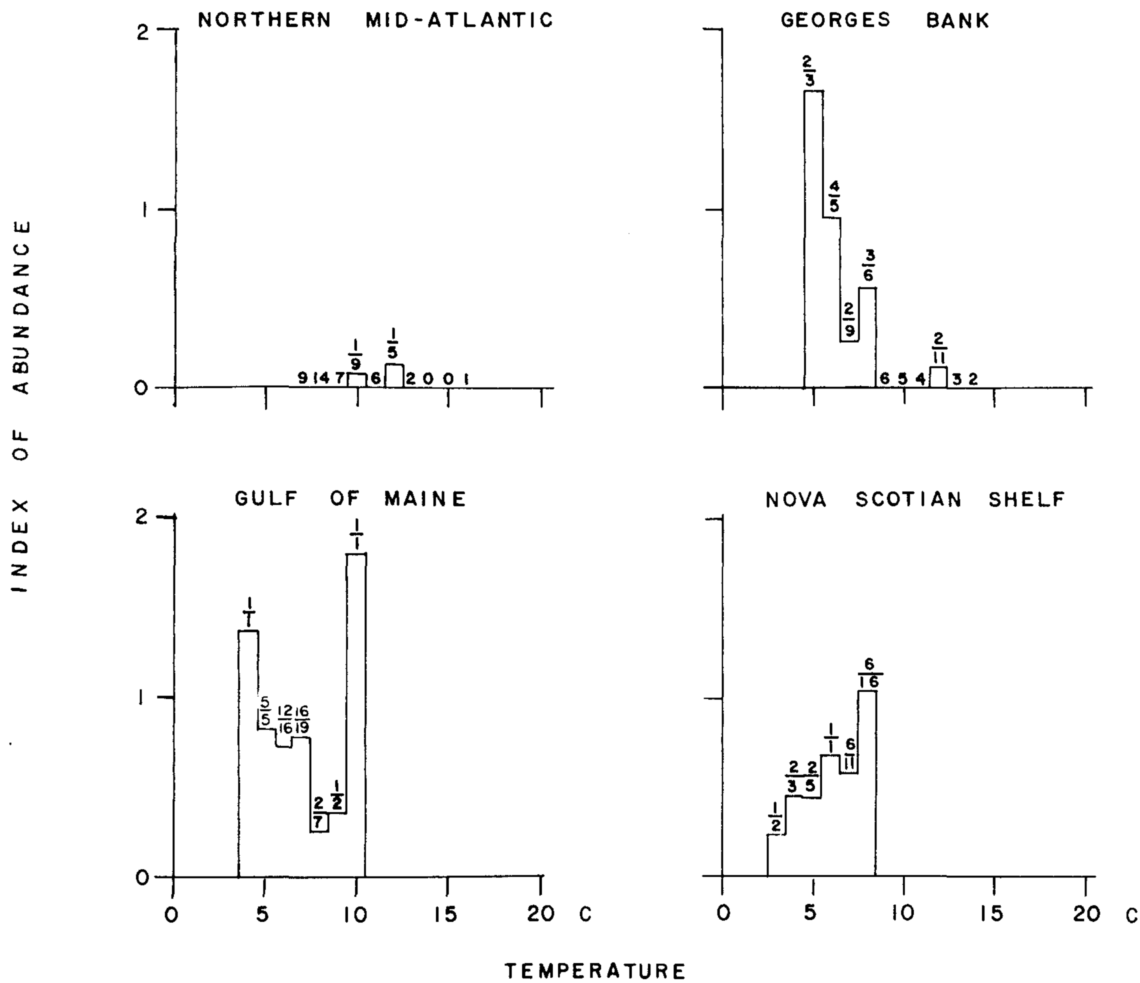

FIGURE 21.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

18 to 996 m at −1.4° to 14°C but is most abundant below 110 m at 2° to 10°C.

Raja erinacea and *R. ocellata* are sympatric species with very similar habitat requirements. *Raja ocellata* has slightly lower temperature preferences than *R. erinacea* and occurs farther to the north than the latter. *Raja senta* and *R. radiata* are sympatric species; *R. radiata* has wider temperature range and is more widespread than *R. senta*.

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The Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA gave access to their computer programs and computer facilities to summarize data. The VIMS survey of Chesapeake Bight was supported in part by the NMFS under P.L. 88-309, Project 3-5-D, Jackson Davis, Principle Investigator.

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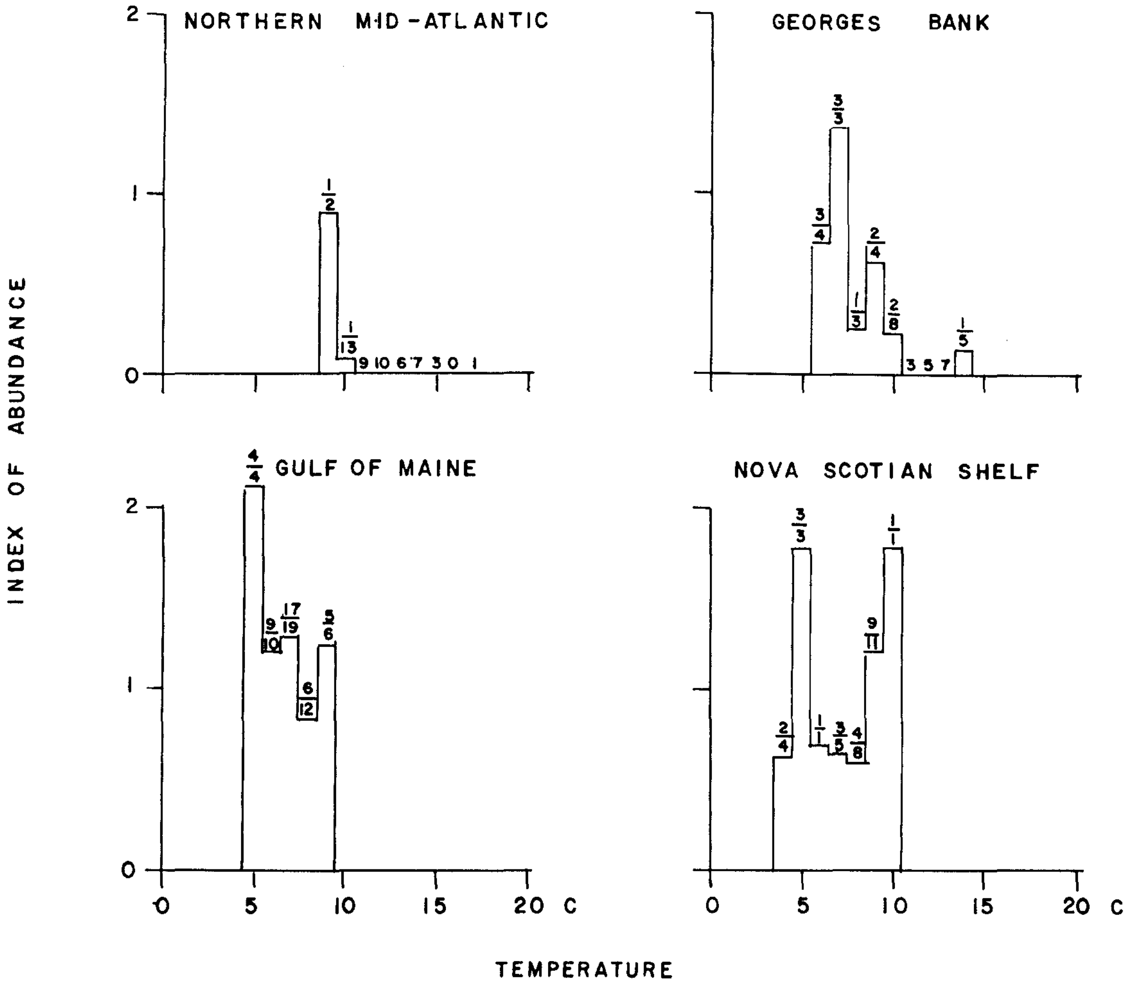

FIGURE 22.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Laboratory, NMFS, NOAA for his cooperation during all phases of this study. John B. Colton, Jr., also of the Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA supervised the construction of the isotherm charts. The following VIMS staff members and students contributed greatly to this study: Mark E. Chittenden and George C. Grant reviewed the manuscript; Russel L. Bradley and Kay Stubblefield did the drafting; Ken Thornberry did the photographic work; and Charles Wenner, Linda Mercer, Ken Able, Doug Markle, and Jim Weaver assisted with data collection.

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TABLE 3.—Coefficients of interspecific association for *Raja ocellata*, *R. erinacea*, *R. senta*, *R. radiata*, and *R. laevis*.

Cruise and species	R. ocellata	R. erinacea	R. senta	R. radiata
Cruise 67-21:				
R. erinacea	0.61**	—	—	—
R. senta	−0.02	−0.71	—	—
R. radiata	−0.28	−0.53**	0.60**	—
R. laevis	−0.02	0.00	0.00	0.00
Cruise 68-03:				
R. erinacea	0.67**	—	—	—
R. senta	0.00	0.00	—	—
R. radiata	−0.04	−0.32	0.84**	—
R. laevis	0.25*	0.53**	0.00	0.27
Cruise 68-17:				
R. erinacea	0.52**	—	—	—
R. senta	0.00	0.00	—	—
R. radiata	−0.85**	−0.54**	0.78**	—
R. laevis	0.14	0.45	0.00	0.00
Cruise 69-02:				
R. erinacea	0.63**	—	—	—
R. senta	−0.35	−0.34	—	—
R. radiata	−0.31	−0.23	0.95**	—
R. laevis	0.54**	0.36	−0.01	−0.03
Cruise 69-08:				
R. erinacea	0.71	—	—	—
R. senta	0.00	−0.62**	—	—
R. radiata	−0.56*	−0.42*	0.75**	—
R. laevis	0.72**	0.84**	−0.09	−0.02
Cruise 69-11:				
R. erinacea	0.57**	—	—	—
R. senta	−0.70	−0.85*	—	—
R. radiata	−0.21	−0.54**	1.00**	—
R. laevis	0.48	0.79**	0.00	0.34
Cruise 70-03:				
R. erinacea	0.53	—	—	—
R. senta	−0.01	−0.42	—	—
R. radiata	−0.12	−0.38	1.00**	—
R. laevis	0.13	0.47*	−0.09	0.01
Cruise 70-06:				
R. erinacea	0.41**	—	—	—
R. senta	−0.82**	−0.84**	—	—
R. radiata	−0.61**	−0.44**	0.80**	—
R. laevis	0.01	0.01	0.00	0.51

*Significant at the 0.05 probability level.
**Significant at the 0.01 probability level.

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