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Biology of seven species of skates (pisces: rajidae)

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(PISCES:RAJIDAE).

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BIOLOGY OF SEVEN SPECIES OF SKATES
(PISCES: RAJIDAE)

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

by
John D. McEachran
1973

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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Approved, January 1973

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Dr. E. L. Bousfield and Mrs. D. Laubitz of the National Museum of Canada identified some of the amphipods found in the skate stomachs. Dr. Thomas E. Bowman of the U. S. National Museum identified the species of isopods. Dr. Marian H. Pettibone of the U. S. National Museum identified many of the species of polychaetes. Dr. Charlotte Mangum of the College of William and Mary identified the species of maldanid polychaetes.

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My wife, Judy H. McEachran, encouraged me throughout the study. My Father-in-law, Lewis Hogg gave encouragement and material assistance during the course of the study, for which I am truly grateful.

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ABSTRACT

The number of tooth rows in the upper jaw, the accepted character for separating *R. erinacea* and *R. ocellata* when immature, is a relative rather than an absolute character because neither species achieves a full complement of tooth rows until it grows to about one-half of the size reached at sexual maturity. The ratio of the anterior extension of the pectoral fin rays to the snout length, number of precaudal and predorsal caudal vertebrae and number of pectoral and pelvic fin rays were diagnostic over the entire size range of immature specimens. Width of the tail and shape of the snout distinguished the smallest specimens. Specimens 110-160 mm TL could be separated by the number of tooth rows in the upper jaw and width of the tail. Shape of the mouth and number of tooth rows distinguished forms 161-214 mm TL. Specimens 215-350 mm TL could be separated by the number of tooth rows in the upper jaw, distance between the orbits, and shape of the mouth. Shape of the mouth, development of secondary sexual characters, and number of tooth rows separated individuals from 351-500 mm TL.

The distribution and relative abundance of *Raja eglanteria*, *R. garmani*, *R. laevis*, *R. erinacea*, *R. ocellata*, *R. senta*, and *R. radiata* were determined from data collected during eight ground fish surveys of the area from Nova Scotia to Cape Hatteras and five seasonal surveys of Chesapeake Bight.

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

Raja erinacea and *R. ocellata* fed largely on amphipods, decapods, and polychaetes. However, their food habits were considered distinct because *R. erinacea* consumed relatively more decapods and less polychaetes than *R. ocellata*. *R. ocellata* tended to feed on infauna and *R. erinacea* tended to feed on epifauna. The difference in the shape of the mouth and number of tooth rows may be related to the food habits of the two skates. There does not appear to be a high degree of competitive interaction between *R. erinacea* and *R. ocellata*. They are positively correlated by abundance; and where they are most abundant, they have similar diets and highest diversity of assemblages of prey organisms.

Raja radiata and *R. senta* have similar food habits and many of the prey eaten by *R. senta* are also eaten by *R. radiata*. *R. radiata* has a less specialized diet than *R. senta*. Epifauna and infauna are about equally important to the former whereas the diet of the latter is almost entirely epifauna.

BIOLOGY OF SEVEN SPECIES OF SKATES

(PISCES: RAJIDAE)

INTRODUCTION

The genus *Raja*, with more than 100 nominal species, is the most speciose and widely distributed genus of the order Rajiformes. Between Cape Hatteras, North Carolina and Nova Scotia this genus is represented by *Raja eglanteria*, *R. garmani*, *R. laevis*, *R. erinacea*, *R. ocellata*, *R. senta*, and *R. radiata*. Each is common to very abundant over at least part of the area. Many studies have dealt with the biology of one or more of these species (Smith, 1950; Richards, 1963; Richards, *et al.*, 1963; Fitz and Daiber, 1963; Tyler, 1968, 1971a, 1972), but they were limited to a small section of the total geographical range of the skates and not necessarily the part of the range where they were most abundant. Thus none of these studies clearly defined the ecology of the skates or interrelationships between them.

The purposes of this study are to determine how each of the species is distributed, define its ecological parameters, determine which species are sympatric, and to analyze the amount of interaction between cohabiting species. The first section describes means of distinguishing between two sibling species, the second section defines the distribution and environmental parameters of each species and the level of cohabitation between species, and the third section compares food habits of sympatric species to determine the level of their niche segregation.

PART I

Characters for Distinguishing Between Immature Specimens of the Sibling Species, *Raja erinacea* and *Raja ocellata*

Introduction

Raja erinacea Mitchill and *Raja ocellata* Mitchill are closely related species which are sympatric over the greater part of their respective ranges. *Raja erinacea* has been reported from Newfoundland (Templeman, 1965a) and the southern side of the Gulf of St. Lawrence to North Carolina (Bigelow and Schroeder, 1953) and *R. ocellata* has been recorded from Grand Banks and the southern side of the Gulf of St. Lawrence to North Carolina (Leim and Scott, 1966).

The species have been distinguished by the number of tooth rows in the upper jaw, presence or absence of ocellated spots on upper surface of disc, length at maturity (Bigelow and Schroeder, 1953), and location of pelvic denticles (Templeman, 1965b). *Raja erinacea* has 38-64 tooth rows in the upper jaw whereas *R. ocellata* has 68-100 rows (Bigelow and Schroeder, 1953, Templeman, 1965b). *Raja erinacea* matures at length of 40-54 cm (Richards *et al.*, 1963) and *R. ocellata* matures at a length of 62-66 cm (Templeman, 1965b). Templeman (1965b) demonstrated that ocellated spots are not diagnostic since they occur on both species but that maturing and large immature specimens of the two species could be distinguished by the position of pelvic denticles.

Females of *R. erinacea* developed denticles near the cloaca while both sexes of *R. ocellata* developed denticles more laterally on the pelvic fins.

Only the number of tooth rows in the upper jaw has served to separate immature specimens of the two species (Richards *et al.*, 1963). This paper determines the number of tooth rows which can be used to distinguish between immature specimens of the two species and investigates other meristic and morphometric distinctions.

Materials and Methods

Most of the specimens of *R. erinacea* and *R. ocellata* examined were collected aboard the R/V Albatross IV during five seasonal groundfish surveys of the continental shelf from La Have Bank and the Gulf of Maine to Cape Hatteras, North Carolina during 1969 and 1970. A few specimens were collected during a groundfish survey of Chesapeake Bight (38°43'N to 35°13'N) conducted by the Virginia Institute of Marine Science (VIMS) from February, 1966 through February, 1968. The following specimens were borrowed from the Museum of Comparative Zoology (MCZ) and the United States National Museum (USNM):

R. erinacea: MCZ 35221, male, 97 mm TL, male, 115 mm TL. USNM 25894, female, 95 mm TL. USNM 26011, female, 97 mm TL. USNM 123635, female, 97 mm TL. USNM 278057, male, 94 mm TL. *R. ocellata*: MCZ 918 embryo, 106 mm TL. MCZ 32735, 4 embryos, 75-104 mm TL. MCZ 34400, female, 121 mm TL. MCZ no collection number, embryo, 112 mm TL. USNM 123200, 9 embryos and young, 96-131 mm TL.

Raja erinacea and *R. ocellata* were tentatively separated by their external morphology i.e., shape of the snout, mouth, and disc and width and length of the tail.

Fifty-one specimens of *R. ocellata* (99-643 mm TL) from 38°24'N to 41°05'N and 355 specimens of *R. erinacea* (94-508 mm TL) from 36°11'N to 42°05'N were examined in the meristic and morphometric study. All of the specimens had been preserved in 10% formalin and transferred to either 40% isopropyl or 70% ethyl alcohol. Forty-three specimens were collected aboard the R/V Prince in the Gulf of St. Lawrence in October, 1971. The specimens were examined but were not included in the statistical analyses described below.

Observations of sexual maturity and development of secondary sexual characters were made on 275 *R. ocellata* and 680 *R. erinacea* aboard the R/V Albatross IV during two of the five seasonal cruises. Males with fully developed claspers and testes and females with large ova in ovaries were considered mature according to Richard *et al.*, (1963).

The methods of Hubbs and Ishiyama (1968) were used to take the following measurements and counts on the preserved specimens: total length, disc width, disc length, tail length, preocular length, mouth width, distance between the orbits, distance between the spiracles, distance over the first gill slits, tail width at distal margins of pelvic fins, number of tooth rows in the upper jaw, and number of predorsal median tail spines. In addition, width of the tail at the axil of the pelvic fins was measured and the ratio of the anterior extension of the pectoral fin rays to the snout length was computed. Extension of the pectoral fin rays was measured from the anterior rim of the orbit to the anterior most pectoral fin ray. Snout length was measured from midway along a line connecting the anterior rims of the orbits to the tip of the snout. All measurements except total length, disc width, disc length, and tail length were to the nearest 0.1 mm. The latter measurements were to the nearest millimeter.

These measurements and the number of tooth rows were expressed in relation to disc width. Analyses of covariance were computed between sexes within species to test for sexual dimorphism. All measurements had a linear relationship to disc width. The slope of the regression of the number of tooth rows to disc width changed abruptly at about 100 mm disc width even after a logarithmic transformation of the data. Thus two analyses were computed, one for specimens less than 100 mm disc width and another for those between 100 and 180 mm disc width. Analysis of variance was used to test for sexual differences in number of predorsal median tail spines.

A stepwise discriminant function analysis (Dixon, 1965) was used to determine if the variables were significantly different between the two species and if the variables could be used to assign individuals to species. All of the variables except number of tooth rows and anterior extension of the pectoral fin rays were included in this analysis. Specimens up to 200 mm disc width (*R. erinacea* 94-341 mm TL, *R. ocellata* 99-325 mm TL) were included in the analysis. Separate analyses were made for each sex and for the combined sexes.

Analysis of variance was used to test for differences in the ratio of the anterior extension of the pectoral fin rays to the snout length. Twenty-one specimens of *R. erinacea* were paired with 21 *R. ocellata* of the same sex and about the same length. Prior to the analysis an angular transformation (Quenouille, 1950) was made on the ratios to make the variance independent of the mean.

Differences in number of tooth rows were tested by analysis of convariance on specimens up to 180 mm disc width (*R. erinacea* 94-315 mm TL, *R. ocellata* 99-290 mm TL) because *R. erinacea* attained a full complement of teeth upon reaching a size of about 180 mm disc width.

One female and two male specimens of *R. erinacea* (103-149 mm TL) and two male specimens of *R. ocellata* (140-153 mm TL) were cleared and stained (Taylor, 1967). Six *R. erinacea* (255-318 mm TL) and eight *R. ocellata* (257-325 mm TL) of both sexes were X-rayed. Number of pectoral fin rays (Stehmann, 1970), number of precaudal and predorsal caudal vertebrae (Hubbs and Ishiyama, 1968), and number of pelvic fin rays were determined from the cleared and stained specimens and the radiographs.

Results

Immature specimens of *R. erinacea* and *R. ocellata* were similar in body shape, spine patterns, and coloration; and contrary to Bigelow and Schroeder (1953) and Richards *et al.*, (1963) the two species could not be distinguished by the number of tooth rows in the upper jaw because speciments of neither attained a full complement of tooth rows until they attained about one-half of the size reached at sexual maturity.

Morphometrics and Meristics: *R. ocellata* was sexually dimorphic for one of the measurements and *R. erinacea* was sexually dimorphic for all of the measurements except for mouth width and ratio of the anterior extension of the pectoral rays to the snout length. However, the sexes of each species were lumped for interspecific comparisons because the random dispersions of the regressions for combined sexes were little if any greater than the random dispersions of the regressions for the separate sexes. Sexual dimorphism was thus responsible for only a small portion of the undescribed variance. The difference in degree of sexual dimorphism between the species may be attributable to difference in the sample sizes (analysis of covariance was computed for 181 males and 174 females of *R. erinacea* and for 25 males and 26 females of *R. ocellata*) or *R. erinacea* may become sexually dimorphic at a smaller size than *R. ocellata* because it matures at a much smaller size.

Neither species was sexually dimorphic for the number of tooth rows in the upper jaw ($P > 0.05$) thus the sexes were lumped for the interspecific comparisons.

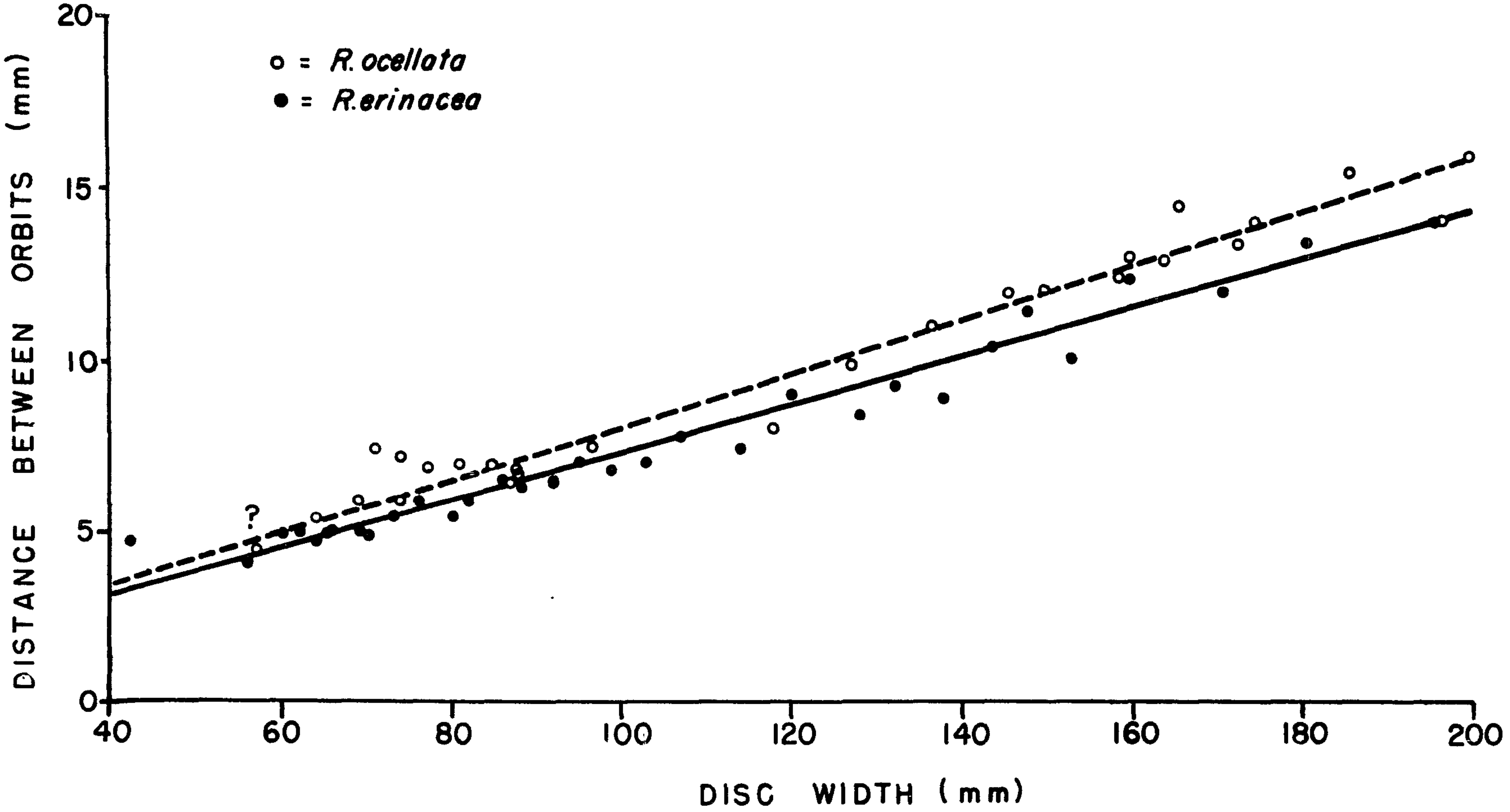
The stepwise discriminant function analysis demonstrated that the 12 variables as a group, were useful in discriminating between the two species and that the same variables were diagnostic for males, females, and combined sexes. Five variables were statistically significant for males, six for females, and seven for the combined sexes at the 0.05 probability level. However, the first variable, number of predorsal median tail spines, accounted for 100% of the dispersion in males and in combined sexes and the first two variables, number of predorsal median tail spines and distance between the orbits, accounted for 100% of the dispersion in females. The derived functions and 12 variables were used to reclassify the individuals that formed the samples. Reclassification correctly reassigned 97.7% of the males, 96.4% of the females, and 97.0% of the combined sexes to their species.

All seven of the significant variables of the analysis for the combined sexes showed some overlap. *Raja erinacea* had a mean of 19.0 and a range of 15-24 predorsal median tail spines and *R. ocellata* had a mean of 21.1 and a range of 17-28 spines. Eighty-five percent of the *R. erinacea* had 20 or fewer spines and 60% of the *R. ocellata* had 21 or more spines.

Raja ocellata had a greater interorbital distance and a shorter and broader tail than *R. erinacea* (Figs. 1, 2, 3). However, none of these three variables, when plotted against disc width, could be used to distinguish between the two species over the entire size range. *Raja ocellata* had a wider mouth, a greater distance between the spiracles, and greater distance over the first gill slits but these differences ($P < 0.05$) when plotted against disc width were too small to be of use in separating the species.

Fig. 1

Relationship of distance between orbits to disc width for *R. erinacea* and *R. ocellata*. Every tenth specimen of *R. erinacea*, when arranged in ascending order of total length, was chosen for the illustration. All specimens were used in deriving the regression line.



○ = R. ocellata
● = R.erinacea
?
DISTANCE BETWEEN ORBITS (mm)
0
5
10
15
20
DISC WIDTH (mm)
40
60
80
100
120
140
160
180
200

Fig. 2

Relationship of tail length to disc width for R. *erinacea* and R. *ocellata*. Every tenth specimen of R. *erinacea*, when arranged in ascending order of total length, was chosen for the illustration. All specimens were used in deriving the regression line.

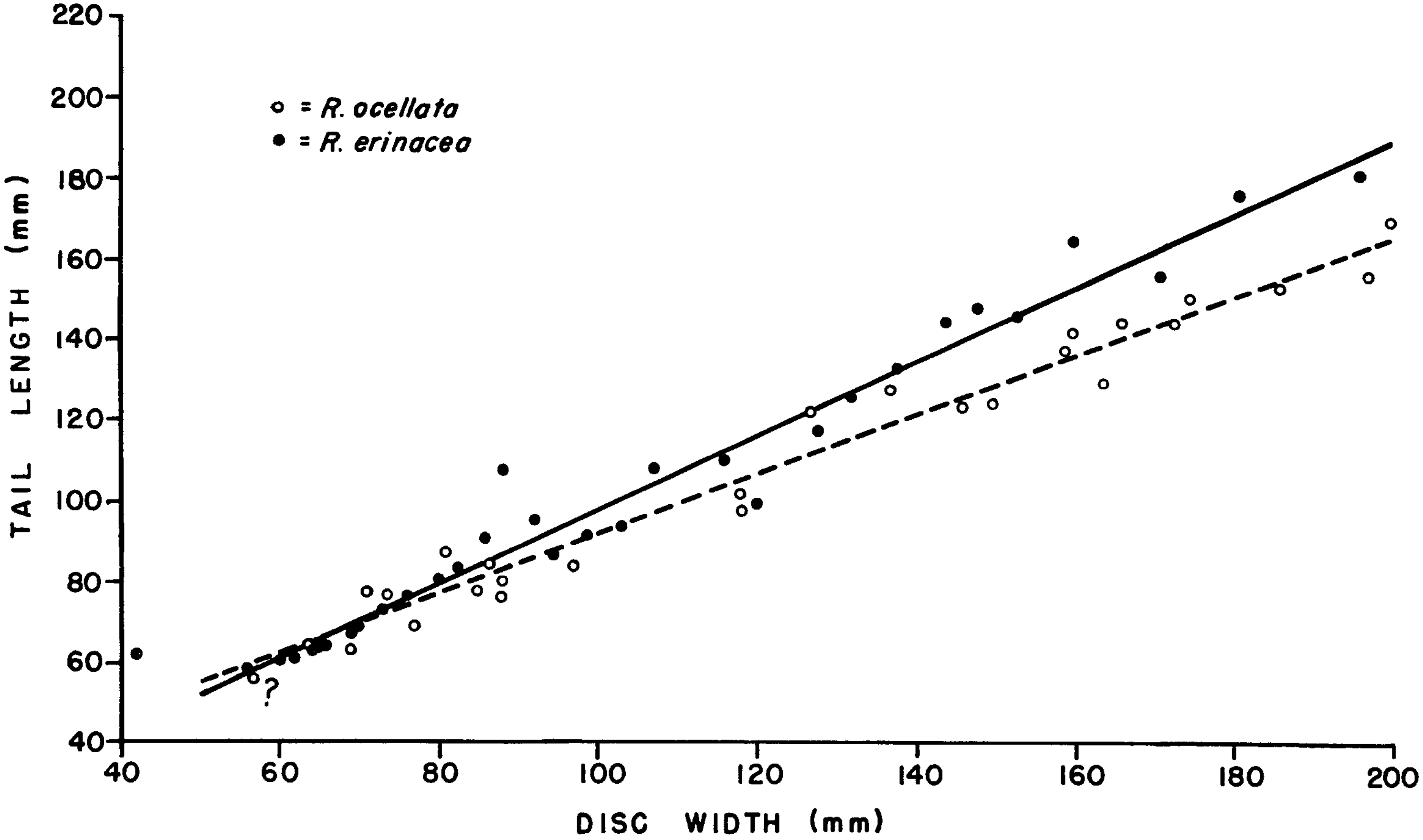
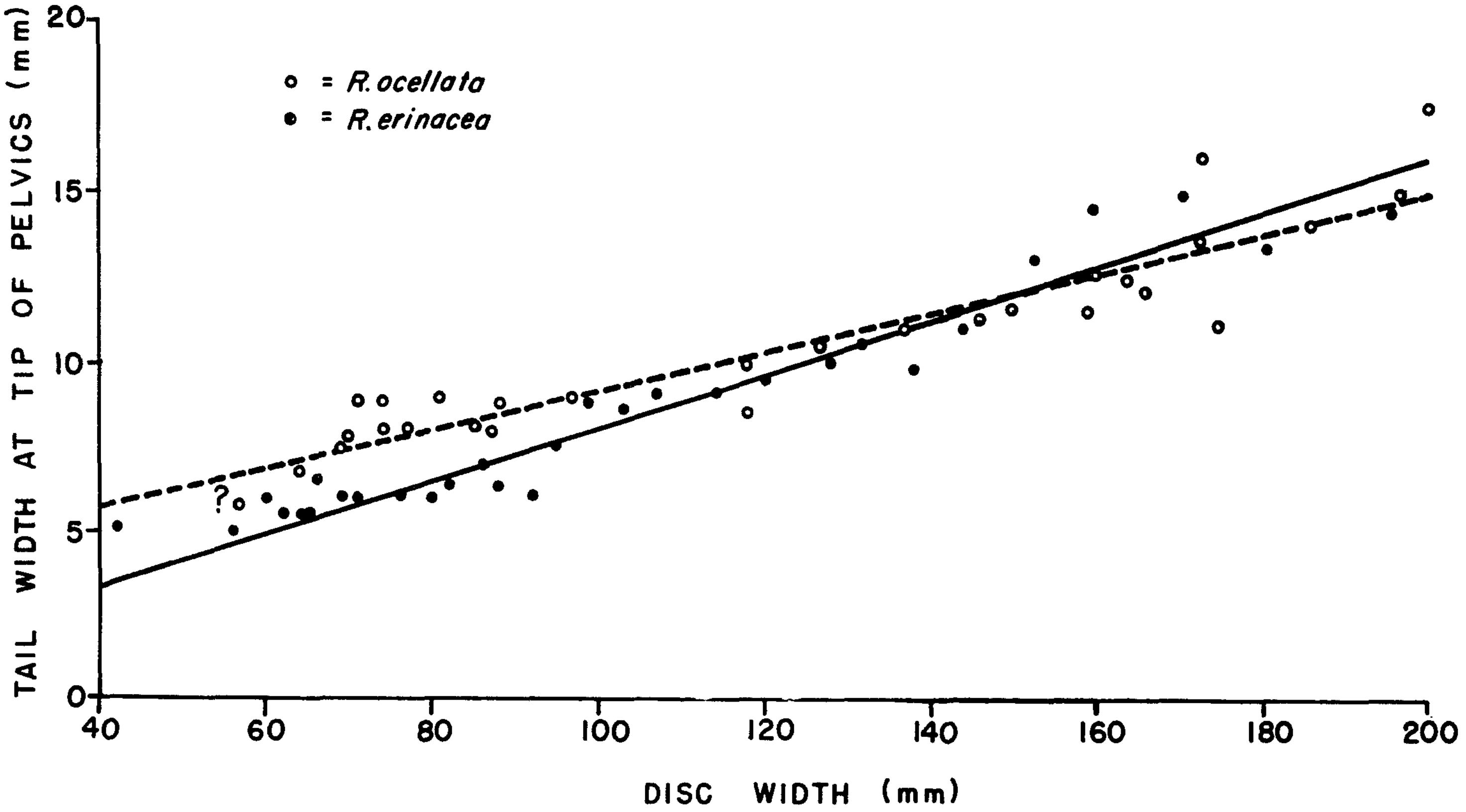

220
200
180
160
140
120
100
80
60
40
TAIL LENGTH (mm)
40
60
80
100
120
140
160
180
200
DISC WIDTH (mm)
○ = *R. ocellata*
● = *R. erinacea*
?

Fig. 3

Relationship of width of tail at tip of pelvic fins to disc width for *R. erinacea* and *R. ocellata*. Every tenth specimen of *R. erinacea*, when arranged in ascending order of total length, was chosen for the illustration. All specimens were used in deriving the regression line.


○ = *R. ocellata*
● = *R. erinacea*
TAIL WIDTH AT TIP OF PELVICS (mm)
DISC WIDTH (mm)
0
5
10
15
20
40
60
80
100
120
140
160
180
200
?

The greatest separation was obtained by plotting the distance between the orbits (greater for *R. ocellata*) against tail length (shorter for *R. ocellata*) and plotting width of tail (greater for *R. ocellata*) against tail length. The former relationship (Fig. 4), in most cases, served to separate each species greater than 120 mm tail length (214 mm TL). The latter relationship (Fig. 5) separated, for the most part, specimens of the two species less than 90 mm tail length (160 mm TL).

The relationship of tooth rows to disc width (Fig. 6) was significantly different ($P < 0.01$) between species for the adjusted mean but not for the slope ($P > 0.05$). *R. ocellata* had an average of about 10 more tooth rows than *R. erinacea* for specimens of 50 to 100 mm disc width, and both species acquired new tooth rows at about the same rate, but between 100 and 180 mm disc width, *R. erinacea* appeared to acquire tooth rows at a slower rate. At 180 mm disc width there was a mean difference between the species of about 20 tooth rows. Number of tooth rows was diagnostic for all but the smallest specimens (50-60 mm disc width or 90-109 mm TL).

The relationship of the anterior extension of the pectoral fin rays to the snout length was significantly different at the 0.01 probability level. The ratio was 0.83-0.97 for *R. ocellata* and 0.77-0.90 for *R. erinacea* but 86% of the former had a ratio of 0.88 or greater and 81% of the *R. erinacea* had a ratio of less than 0.88.

<u>External Morphology</u>: Immature specimens of *R. erinacea* and *R. ocellata* basically agree with the detailed description of *R. erinacea* by

Fig. 4

Relationship of distance between orbits to tail length for R. *erinacea* and R. *ocellata*. Every tenth specimen of R. *erinacea*, when arranged in ascending order of total length, was chosen for the illustration. All specimens were used in deriving the regression line.

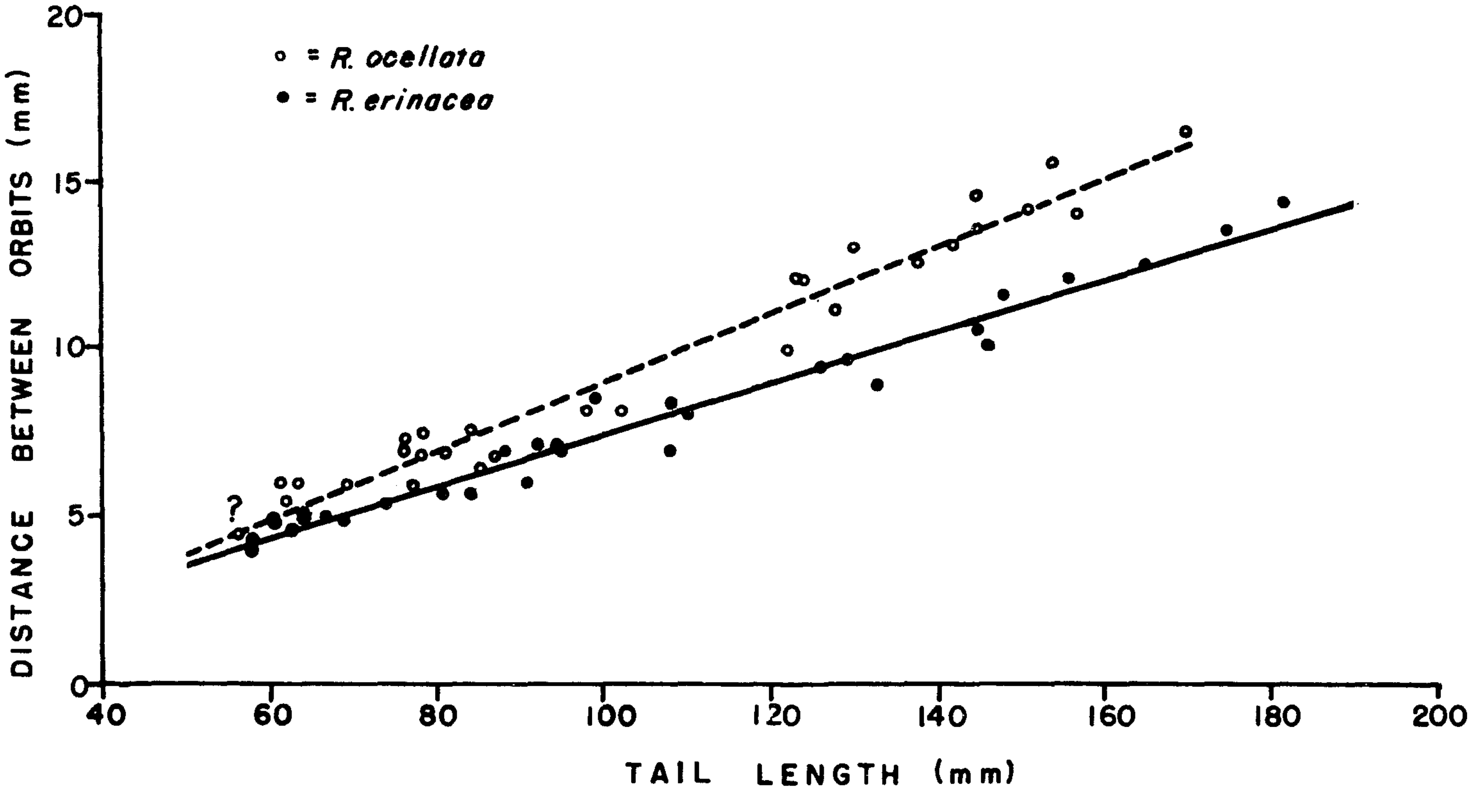

○ = *R. ocellata*
● = *R. erinacea*
?
DISTANCE BETWEEN ORBITS (mm)
0
5
10
15
20
TAIL LENGTH (mm)
40
60
80
100
120
140
160
180
200

Fig. 5

Relationship of width of tail at tip of pelvic fins to tail length for R. *erinacea* and R. *ocellata*. Every tenth specimen of R. *erinacea*, when arranged in ascending order of total length, was chosen for the illustration. All specimens were used in deriving the regression line.

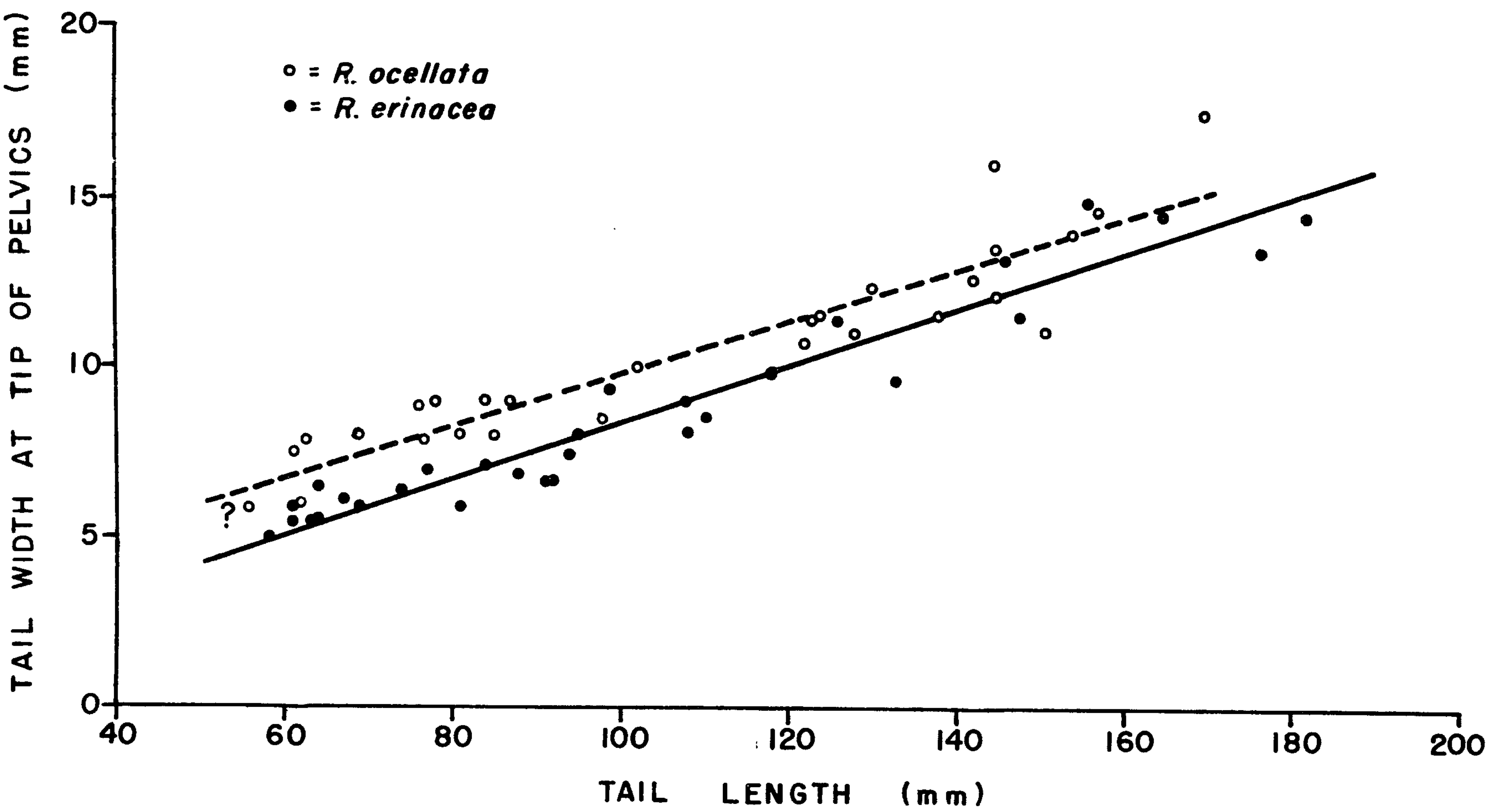
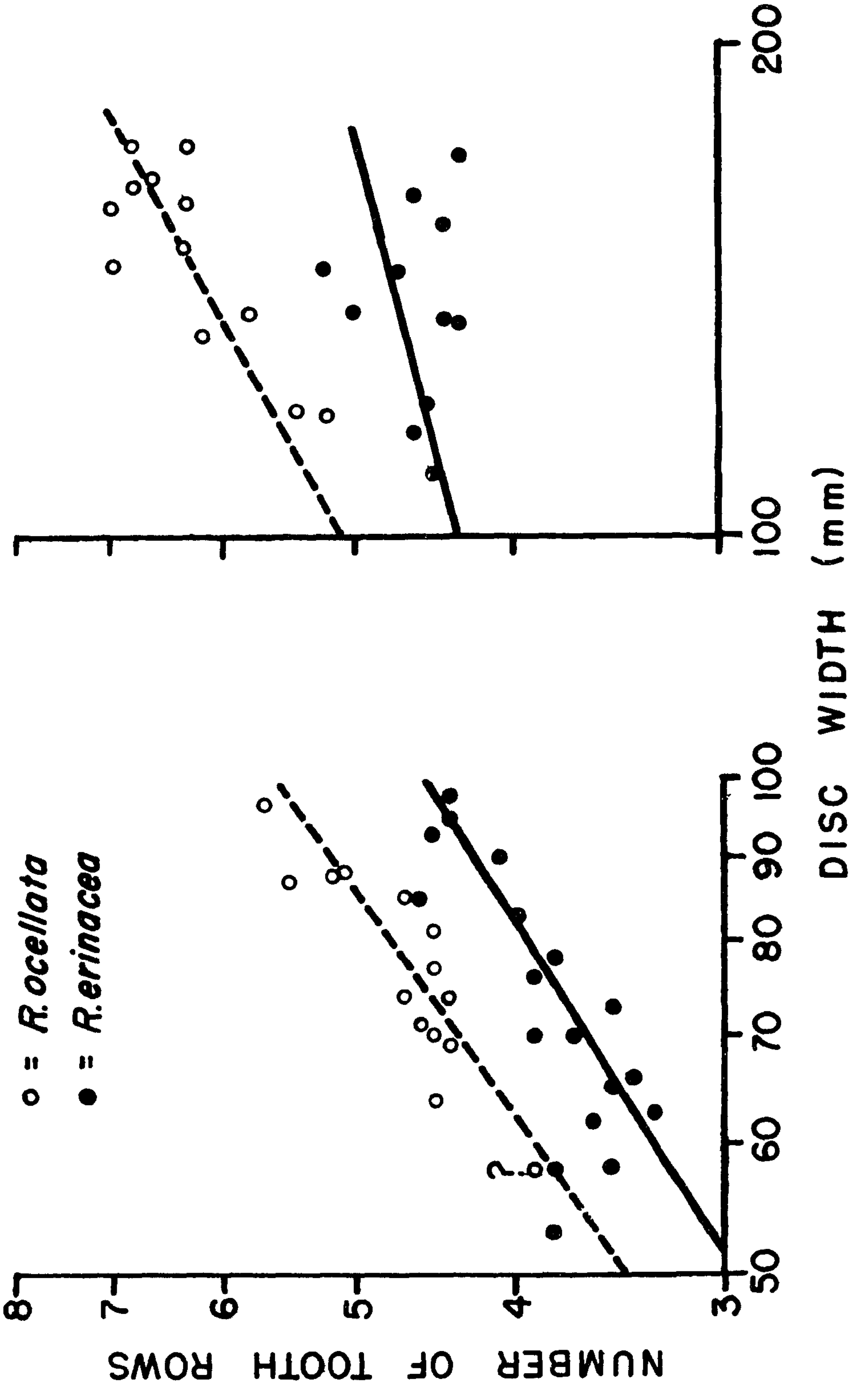

○ = R. ocellata
● = R. erinacea
?
TAIL WIDTH AT TIP OF PELVICS (mm)
0
5
10
15
20
TAIL LENGTH (mm)
40
60
80
100
120
140
160
180
200

Fig. 6

Relationships of number of tooth rows in upper jaw to disc width for R. *erinacea* and R. *ocellata*. Every tenth specimen of R. *erinacea*, when arranged in ascending order by total length, was chosen for the illustration. All specimens were used in deriving the regression line.



○ = R. ocellata
● = R. erinacea
NUMBER OF TOOTH ROWS
3
4
5
6
7
8
50
60
70
80
90
100
200
DISC WIDTH (mm)
?

Bigelow and Schroeder (1953). However, several distinctions are evident.

R. ocellata has a more rounded disc than does *R. erinacea* (Fig. 7) for specimens up to about 160 mm TL. The lateral apices of the pectoral fin of *R. erinacea* are more angular and the snout clearly extends beyond the anterior pectoral rays. The base of the tail of *R. ocellata* is broader than that of *R. erinacea*. The mouth is only slightly arched in *R. ocellata* while in *R. erinacea* it is broadly bowed (Fig. 8). The spine patterns, dorsal fins, nasal curtains, and nasal flaps are similar. The lateral find folds of the tail are narrow and occur from the posterior-most tip of the pelvic fin to the end of the tail in both species. Color patterns of the two species are similar although *R. ocellata* generally has a slightly lighter ground color.

In larger specimens the difference in shape of disc and width of the tail are less evident (Fig. 9). The median series and upper-lateral tail series of spines are more clearly defined in *R. ocellata* than in *R. erinacea*. The tail of *R. erinacea* is longer than that of *R. ocellata*. The mouth of *R. ocellata* rises gently towards the symphysis while that of *R. erinacea* rises abruptly (Fig. 10).

<u>Maturity and Development of Secondary Sexual Characters</u>: The smallest mature *R. erinacea* was a male 41 cm TL. About a third of the specimens between 42-44 cm TL as well as all over 50 cm TL were mature. The smallest mature *R. ocellata* was a female 72 cm TL. All specimens of *R. ocellata* longer than 78 cm TL were mature except for

Fig. 7

Raja ocellata, 135 mm TL ♂♂ (VIMS 1650), left; *R. erinacea*, 134 mm TL ♂♂ (VIMS 1651), right.


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Fig. 8

A. Ventral side of *R. erinacea*, 135 mm TL ♂♂ (VIMS 1652) B. Upper and lower jaw of same. C. Ventral side of *R. ocellata*, 136 mm TL ♂♂ (VIMS 1653). D. Upper and lower jaw of same. *R. erinacea* has about 42 and *R. ocellata* about 47 tooth rows in upper jaw, however, all of the rows are not visible in Fig. 8D.

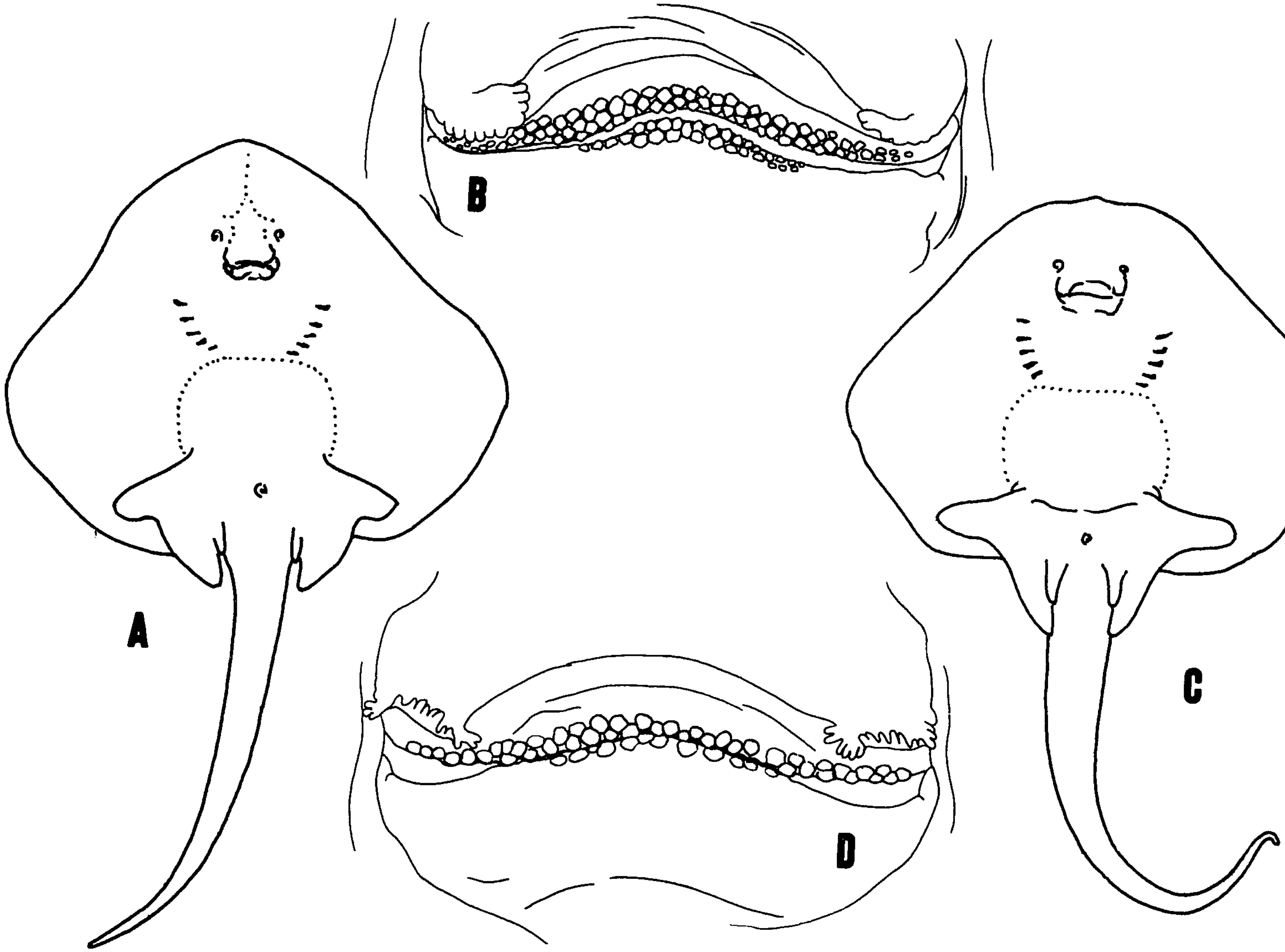
B
A
C
D

Fig. 9

R. ocellata 260 mm TL ♀♀ (VIMS 1654), left. *Raja erinacea* 262 mm TL ♀♀ (VIMS 1655), right.

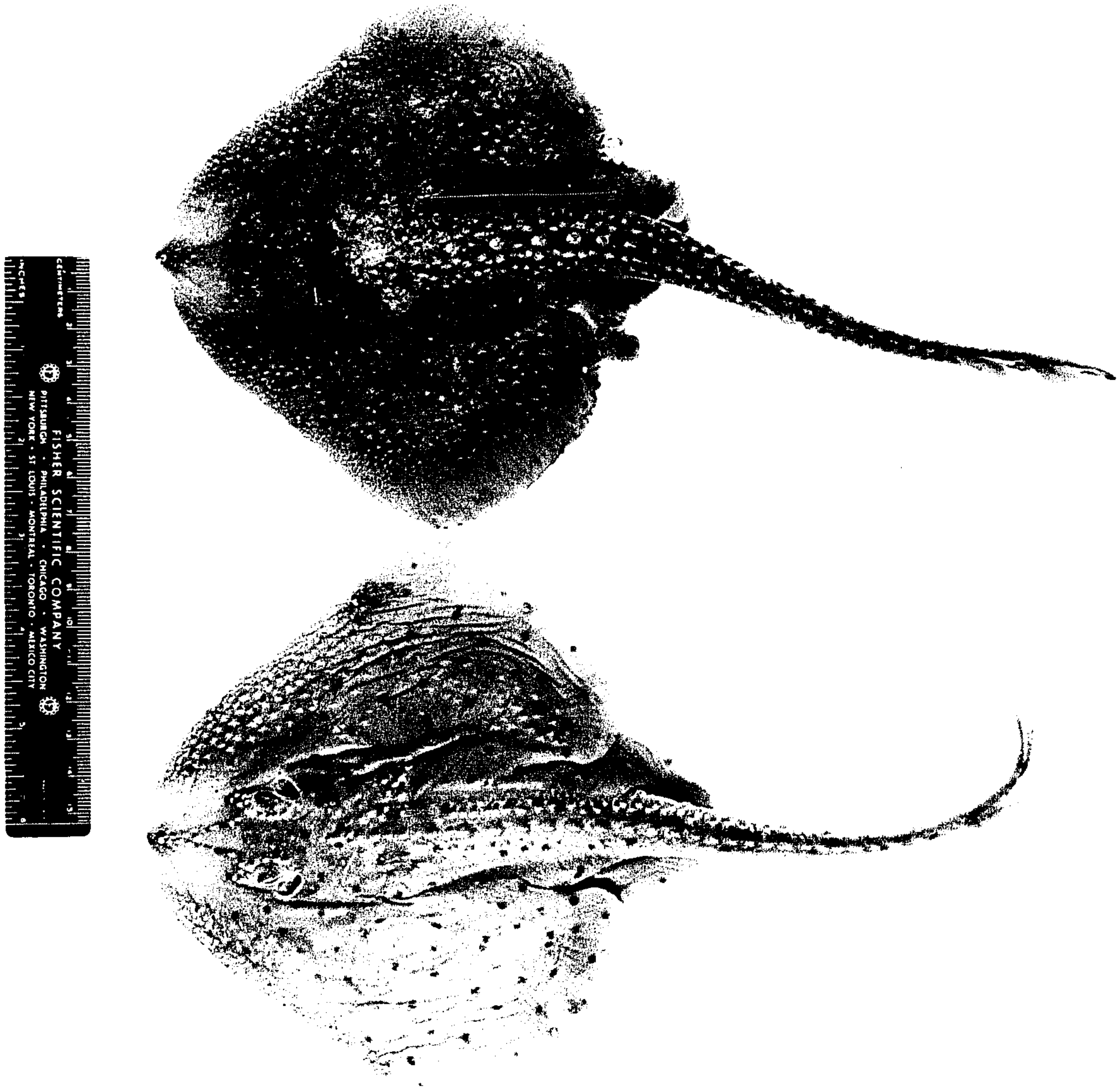
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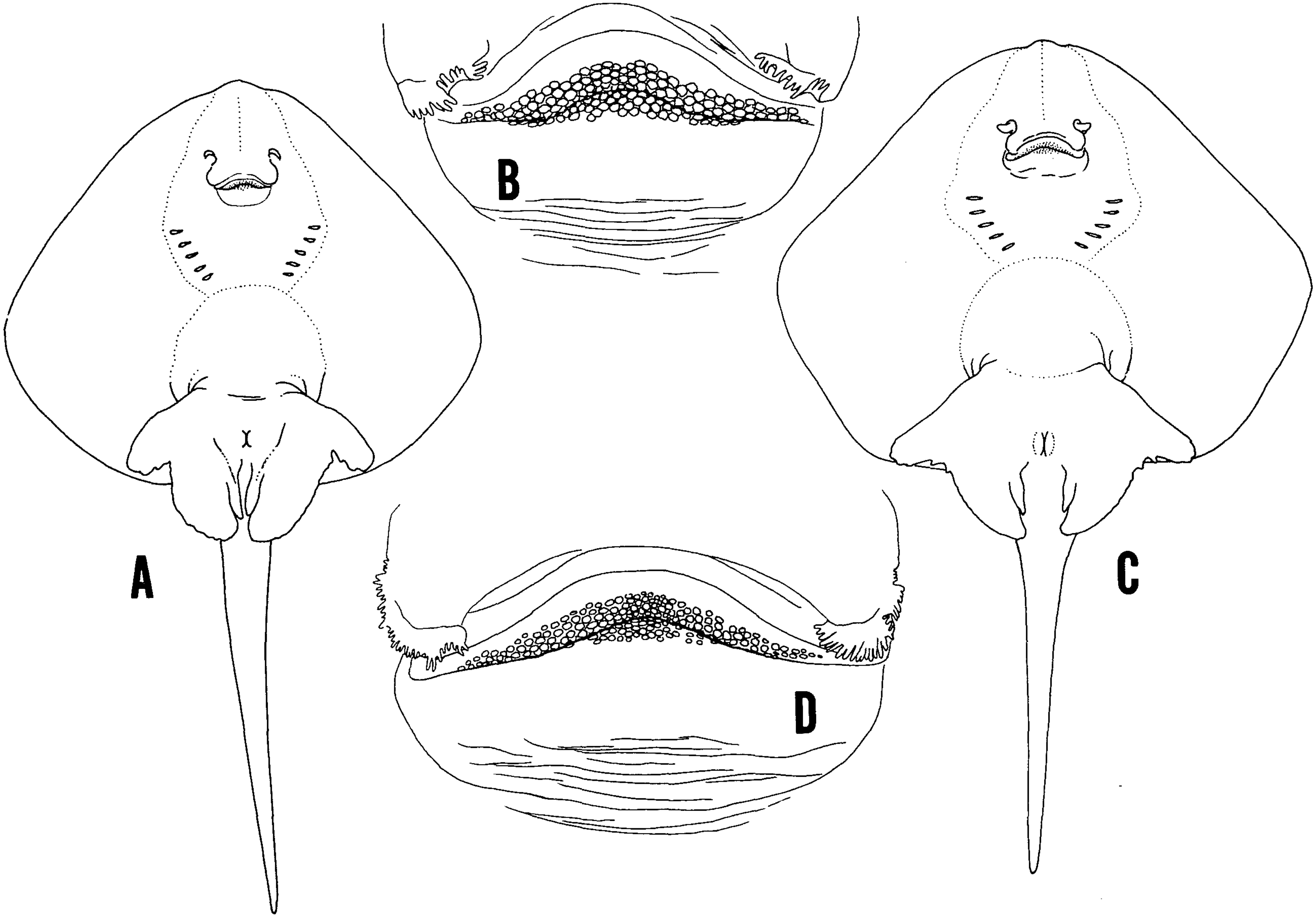
Fig. 10

A. Ventral side of *R. erinacea*, 260 mm TL ♂♂ (VIMS 1656). B. Upper and lower jaws of same. C. Ventral side of *R. ocellata* 260 mm TL ♂♂ (VIMS 1657). Upper and lower jaw of same. *R. erinacea* has about 48 and *R. ocellata* about 70 tooth rows in the upper jaw, however, some of the rows are not visible in Figs. 10B and 10D.


A
B
C
D

a male 88 cm TL.

In addition to maturity, the size at which secondary sexual characters develop could be used to separate the species. Both species lose the median row spines posterior to the scapular spines. Pelvic denticles develop in females of *R. erinacea* and in both sexes of *R. ocellata*. The teeth of the males become pointed, alar spines develop, and the claspers greatly elongate and their internal cartilages calcify. Median row spines start to disappear from specimens of *R. erinacea* between 32-34 cm TL. Spines at the base of the tail are first to disappear. Two of seven specimens between 34-36 cm TL lacked median row spines and all specimens longer than 42 cm TL lacked spines. One of 10 specimens of *R. ocellata* between 45-47 cm TL lacked about one-half of the median row spines. About one-half of the specimens from 57-59 cm TL lacked the spines and spines were absent from all specimens longer than 69 cm TL.

The smallest *R. erinacea* with pelvic denticles was 36 cm TL, three-fourths of the females between 40-42 cm TL had pelvic denticles and all females greater than 44 cm TL had denticles. Pelvic denticles first appeared on *R. ocellata* at 54 cm TL, one-half of the specimens between 62-64 cm TL, and all of the specimens over 72 cm TL had denticles.

Clasper development of *R. erinacea* began at 36 cm TL. Between 40-42 cm all males had claspers which were equal to or longer than the tip of the posterior lobe of the pelvic fins. All males longer than 50 cm TL had fully developed claspers. Clasper development of

R. ocellata did not commence until males attained about 54 cm TL. All males longer than 82 cm TL had fully developed claspers, except for a specimen of 88 cm TL which had incompletely developed claspers.

Alar spines develop on male *R. erinacea* between 40-45 cm TL and on male *R. ocellata* between 55-60 cm TL.

Skeletal Meristics and Morphometrics: Taylor's (1967) clearing and staining technique worked well for immature specimens. Skeletons of both species were calcified except for the tip of the rostral cartilage, rostral appendices, branchial basket, distal parts of pelvic rays, and vertebrae posterior to the second dorsal fin.

There was a significant difference at the 0.01 probability level between the two species in number of precaudal vertebrae, predorsal caudal vertebrae, pelvic, and pectoral fin rays. In *R. ocellata,* the mean and ranges were: precaudal vertebrae 26.7, 25-28; predorsal caudal vertebrae 53.6, 51-59; pectoral fin rays 73.5, 71-78; and pelvic fin rays 24.7, 23-27. In *R. erinacea,* the mean and ranges were: precaudal vertebrae 24.0, 23-25; predorsal caudal vertebrae 59.8, 57-63; pectoral fin rays 64.9, 63-67; and pelvic fin rays 22.3, 21-25. The greater number of predorsal caudal vertebrae of *R. erinacea* corresponded to its relatively longer tail.

The anterior fontanelle of both species was triangular with a rounded, rostrally directed apex. Anterior lateral walls were weakly convex and the posterior lateral walls were strongly convex. The posterior wall was convex.

The posterior fontanelle of *R. erinacea* was broad and constricted midway along the lateral walls. The posterior fontanelle of *R. ocellata* was narrower and the lateral walls were irregular along their entire length but not distinctly constricted.

All of the specimens from the Gulf of St. Lawrence appeared to represent the same species and they were more similar to *R. ocellata* than *R. erinacea* for all of the characters except size at maturity and shape of the mouth. They ranged from 488 to 700 mm TL and the specimens from 514 to 700 mm TL were either mature or approaching maturity. A male 514 mm TL had fully developed claspers and a female 518 mm TL had large ova and enlarged nudemental glands and uteri. A female 653 mm TL had an egg capsule in each uterus. The shape of the mouth was intermediate between the two species; it was more arched than that of *R. ocellata* but not as arched as that of *R. erinacea*. The interorbital distance, length of the tail, number of teeth (62-85), and pelvic denticles were more similar to *R. ocellata*. Also many of the specimens possessed the mid-row spines on the tail.

Discussion

Valid Characters: A combination of the distinctive characters was necessary to separate specimens for a given size range. The anterior extension of the pectoral fin rays, number of precaudal vertebrae, predorsal caudal vertebrae, pectoral, and pelvic fin rays were the only characters which distinguished between immature *R. erinacea* and *R. ocellata* of all sizes. However, there was much overlap in the anterior extension of the pectoral fin rays and detection of the latter four characters required time-consuming preparations. All of the remaining significant characters served to separate the two species over only a limited size range. The smallest specimen identified as *R. ocellata* was 99 mm TL. However, this identification was questionable because all eight of the advanced embryos (those which had absorbed almost all of their yolk sac and had fully developed spines) of *R. ocellata* that were examined ranged from 112-128 mm TL.

Advanced embryos and the smallest juvenile specimens (90-109 mm TL) were separated by width of the tail, shape of the snout, and number of predorsal median tail spines. Number of tooth rows in the upper jaw, width of tail, shape of snout, and number of predorsal median tail spines distinguished between specimens from 110-160 mm TL. Specimens from 161-214 mm TL were identified by the number of tooth rows, shape of mouth and snout, and number of predorsal median tail spines. Number of tooth rows, distance between the orbits, and shape of the mouth identified specimens between 215-350 mm TL. Shape of the mouth, development of secondary sexual characters, and number of tooth rows separated individuals from 351-500 mm TL.

The above character combinations may possibly be applied to specimens from the Nova Scotian Shelf, but probably not to those of the Gulf of St. Lawrence. Templeman (1965b) stated that 13 *R. erinacea* from Canadian waters had a range in tooth count of 44-55/47-54, average 50/50. *Raja ocellata* from the Nova Scotian Shelf and Newfoundland had a tooth count of 68-95/68-104 (Templeman, 1965b). Mature *R. erinacea* ranged from 41-60 cm TL and mature *R. ocellata* ranged from 71-100 cm TL. All female *R. erinacea* (36-55 cm) from Georges Bank and the Nova Scotian Shelf had pelvic denticles. Female *R. ocellata* (56 to 81-90 cm) and one male *R. ocellata* 50 cm and most mature males over 70 cm possessed pelvic denticles. Thus *R. ocellata* and *R. erinacea* from the Nova Scotian Shelf mature at about the same length, and attain pelvic denticles at about the same size, and have about the same number of tooth rows as individuals from the more southern parts of the range. There is no evidence of a cline in numbers of tooth rows as suggested by Richards *et al.* (1963).

Raja erinacea of the Miramichi Estuary, in the Gulf of St. Lawrence, attain a length of 2 ft. (61 cm) and longer and the teeth and alar spines resemble *R. ocellata* (McKenzie, 1959). Four specimens of *R. erinacea* from Miramichi Estuary had 72-76/69-76 tooth rows (Richards *et al.*, 1963). Bigelow and Schroeder (1953) reported that mature specimens (to at least 469 mm TL) of *R. erinacea* from the lower St. Lawrence River had the median row of spines and the relationship of the distance from the center of the cloaca to the tip of the tail to the distance from the center of the cloaca to the snout for three specimens (346-469 mm TL) was closer to that of *R. ocellata* than *R. erinacea*. W. C. Schroeder (pers. comm.) suggested that *R. erinacea* from the Gulf of St. Lawrence may represent a local race or a subspecies.

The specimens described in the above studies agree with those examined in the present study. However, in the present study they were identified as R. *ocellata* rather than R. *erinacea* because the majority of the characters better fit the former than the latter species. The absence of R. *erinacea* from the Gulf of St. Lawrence may contribute to differences from more southerly specimens of R. *ocellata* in size of maturity and shape of mouth. Sympatric distribution of R. *erinacea* and R. *ocellata* in other waters may initiate character divergence. A similar situation occurs in *Urophycis tenuis* and U. *chuss*. *Urophycis tenuis* is allopatric in the Gulf of St. Lawrence and is morphometrically more similar to U. *chuss* than is U. *tenuis* from more southerly parts of its range where it occurs sympatrically with U. *chus* (Musick, 1969). This problem cannot be resolved until specimens from the northern Nova Scotian Shelf and the Grand Banks are examined and claspers from both species from all parts of their range are compared.

Key to Immature *Raja ocellata* and *Raja erinacea*

(Specimens ranging from 90-160 mm TL)

1a. Tail at tips of posterior lobe of pelvic fins, 8-10 times tail length. 44-55 tooth rows in upper jaw. Snout blunt, anterior rays of pectoral fin extend almost to tip of snout (Fig. 11). (60% of specimens with 21 or more spines on median row of tail). . . R. *ocellata*

1b. Tail at tips of posterior lobe of pelvic fin, 10 or more times length of tail. 30-48 tooth rows in upper jaw. Snout less blunt, tip of snout extends clearly beyond anterior rays of pectoral fins (Fig. 11). (85% of specimens with fewer than 21 spines on median row of tail).. R. *erinacea*

(Specimens Ranging from 161-214 mm TL)

1a. Number of tooth rows in upper jaw 50-60. Mouth slightly arched (Fig. 12). Snout blunt, anterior rays of perctoral fins extend almost to tip of snout. (60% of specimens with 21 or more spines on median row of tail) .... *R. ocellata*

1b. Number of tooth rows in upper jaw 36-53. Mouth strongly arched (Fig. 12). Tip of snout extends beyond anterior rays of pectoral fins. (85% of specimens with less than 21 spines on median row of tail) .... *R. erinacea*

(Specimens Ranging from 215-350 mm TL)

1a. 58-70 tooth rows in upper jaw. Distance between orbits less than 12 times tail length. Mouth gently bowed (Fig. 12). (60% of specimens with 21 or more spines on median row of tail) ... *R. ocellata*

1b. 43-52 tooth rows in upper jaw. Distance between orbits greater than 12 times tail length. Mouth sharply bowed (Fig. 12). (85% of specimens with less than 21 spines on median row of tail).. *R. erinacea*

(Specimens Ranging from 350-500 mm TL)

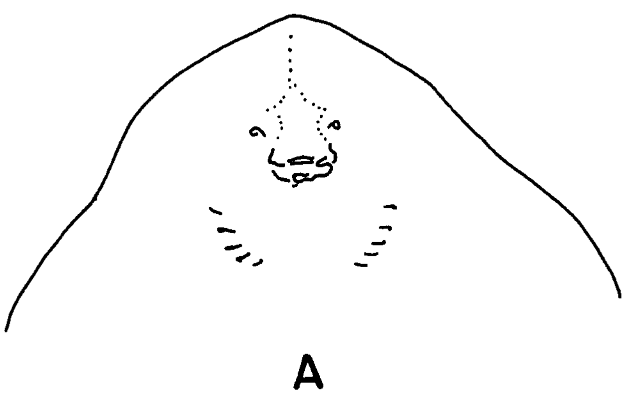
1a. 63 or more tooth rows in upper jaw. Distance between orbits less than 12 times tail length. Mouth gently bowed (Fig. 12). Median row of tail spines usually present. Males lack alar spines and both sexes lack pelvic denticles. Claspers do not extend beyond level of tips of posterior lobe of pelvic fins. All specimens immature .... *R. ocellata*

1b. Less than 64 but usually less than 54 tooth rows in upper jaw. Distance between orbits greater than 12 times tail length. Mouth strongly bowed (Fig. 12). Median row of spines behind scapular spines partially or entirely absent. Males have alar spines and claspers extend beyond level of tips of posterior lobe of pelvic fins. Females have pelvic denticles. Both sexes are maturing or mature .... *R. erinacea*

Phylogeny: Stehmann (1970) stated that *R. ocellata* is closely related to *R. fyllae* and may belong to the same subgenus (*Rajella*). The shape of the disc, spine pattern, and shape of the cranium of *R. ocellata* support Stehmann's opinion. *R. erinacea* also probably should be placed in *Rajella* because of its close relationships with *R. ocellata* and its agreement with Stehmann's definition of the subgenus, even though Leigh-Sharpe (1926) considered that *R. erinacea* and *R. ocellata* differed so sufficiently in the external structure of the clasper to be placed in different pseudo-genera, *Gammaraia* and *Kapparaia* respectively. *Raja erinacea* is more similar to *R. fyllae* in shape of the snout, interorbital distance, length of the tail, number of tooth rows, and size than is *R. ocellata* (Bigelow and Schroeder, 1954). Also, *R. erinacea* and *R. fyllae* are closer in number of abdominal vertebrae and number of pectoral fin rays (Stehmann, 1970). Placement of *R. erinacea* and *R. ocellata* into *Rajella* should be tentative until the external and internal morphology of their claspers is studied.

Fig. 11

Shape of the snout. A. *R. erinacea*,135 mm TL ♂♂.
B. *R. ocellata*, 136 mm TL ♂♂.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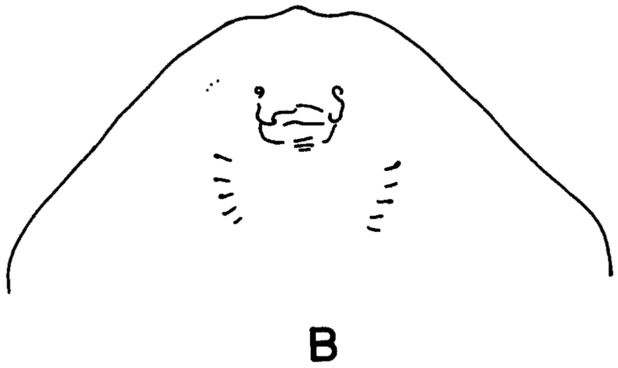
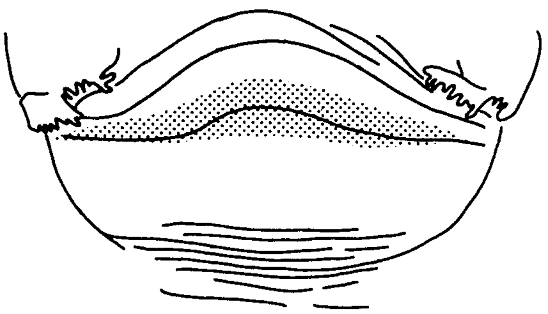

B

Fig. 12

Shape of jaws. A. *R. erinacea*, 250 mm TL ♂♂.
B. *R. ocellata*, 260 mm TL ♂♂.



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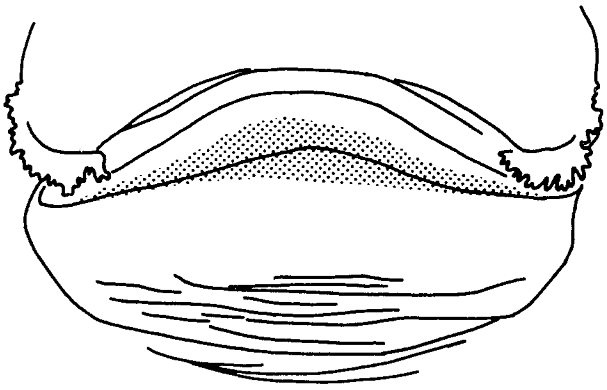


B

PART II

DISTRIBUTION OF SEVEN SPECIES OF SKATES ON THE CONTINENTAL SHELF FROM NOVA SCOTIA TO CAPE HATTERAS

INTRODUCTION

Bigelow and Schroeder (1953, 1954) and Leim and Scott (1966) have summarized the notes on occurrence and distribution of the seven species. The range of each of the species is briefly stated below, and their environmental parameters and distribution from Nova Scotia to Cape Hatteras are reviewed in greater detail.

Raja eglanteria:

Raja eglanteria occurs from Long Island to northern Mexico. A few specimens have been reported from as far north as the northern boundary of Massachusetts Bay. Bigelow and Schroeder (1953) stated that *R. eglanteria* is absent from southern Florida, and Bullis and Thompson (1965) listed only one capture of this species off southern Florida during exploratory fishing surveys of the tropical and subtropical western Atlantic conducted by the National Marine Fisheries Service. The latter authors listed captures of *R. eglanteria* along the norther coast of the Gulf of Mexico west to northern Mexico, and Robinson (1969) reported a specimen taken off the coast of Texas.

Raja eglanteria is most abundant from the sublittoral zone to about 30 fms (55m) (Bigelow and Schroeder, 1953), however, Edwards *et al.* (1962) captured it in 153 fms and 180 fms (280 and 329 m) off

Cape May, New Jersey during the winter. *R. eglanteria* has been taken in waters from 6 to 24 C (Fitz and Daiber, 1963). In the more southern parts of its range it may have slightly higher temperature preferences (Bigelow and Schroeder, 1953). It is more commonly found over sandy bottoms but it has been captured over rocky and gravelly to muddy bottoms (Bullis and Thompson, 1965; Struhsaker, 1969).

In the northern parts of its range *R. eglanteria* moves offshore and southward during the colder months when water temperatures cool to 13 and 16 C (Bigelow and Schroeder, 1953). It appears in the shore waters between Chesapeake and Delaware bays in April, occurs off New Jersey and New York from late April-May to October-November, and is found off southern Massachusetts from July until September (Bigelow and Schroeder, 1953). It was found in Chesapeake Bay from April to December (Massmann, 1962). Schwartz (1961) stated that this species was present in Chinocoteague Bay, Virginia and Sinepuxent Bay, Maryland from May to November. Fitz and Daiber (1963) stated that in Delaware Bay *R. eglanteria* was present when water temperatures were above 9 C (April to November). Schaefer (1967) collected *R. eglanteria* in the surf waters of Long Island, New York from May to November. Dahlberg and Odum (1970) reported that *R. eglanteria* was a year-round resident in Georgia estuaries.

There was a slight decrease in abundance of *R. eglanteria* during the midsummer in Delaware Bay which may have been a response to high water temperatures. (Fitz and Daiber, 1963)

Raja garmani:

Raja garmani occurs along the outer continental shelf and upper slope from the offing of southern New England to southern Florida (Bigelow and Schroeder, 1953). Schroeder (1955) reported that *R. garmani* is fairly abundant from the eastern slope of Georges Bank to Cape Charles, Virginia in less than 200 fms (366m). Bullis and Thompson (1965) listed this species off the Dry Tortugas, Florida. Struhsaker (1969) reported that *R. garmani* was very abundant along the outer continental shelf from Cape Hatteras to Florida. In the Straits of Florida it is found on Pourtates Terrace between the 119 and 366 meter isobaths and north of Pourtates Terrace it occurs at 185 m up the Florida coast (Staiger, 1970).

Raja garmani is found from 28 to 290 fms (49 to 530 m) (Bigelow and Schroeder, 1953; Bullis and Thompson, 1965) between 5.3 and 15 C. Bigelow and Schroeder (1953) stated that it has higher temperature preferences in the southern part of its range than in the northern part. Edwards *et al.* (1962) captured this species off Winter Quarter (37 34'N to 37 50'N Lat.) at 11 to 13 C and off Albemarle Sound, North Carolina at 12 to 14 C. *R. garmani* has been collected over sand to gray mud bottoms (Bullis and Thompson, 1965), smooth mud bottoms (Struhsaker, 1969), mud with echinoid and ophuiroid fragments, and shell and pteropod ooze (Staiger, 1970).

Raja laevis:

Raja laevis is found from southeastern banks of Newfoundland, southern Gulf of St. Lawrence, Bay of Fundy to North Carolina (Bigelow and Schroeder, 1953). It has been reported from the outer coast of Nova Scotia, and in all parts of the Bay of Fundy (Leim and Scott, 1966). Bigelow and Schroeder (1953) doubted its occurrence off Florida, but Bullis and Thompson (1965) listed it from deep water (329 to 412 m) as far south as the Florida Keys.

Raja laevis occurs between the tide mark and 410 fms (750 m) and is most abundant between 5 and 80 fms (9 and 146 m) (Bigelow and Schroeder, 1953, 1954). It has been taken from 1.2 to 20 C (Bigelow and Schroeder, 1953), although they suggest that 17 C may be the upper limit of the optimum range. This species is generally captured over sandy or gravelly bottoms but has been taken over mud bottoms (Bigelow and Schroeder, 1953).

Seasonal migrations are thought to be limited to onshore and offshore movements of the inshore fringe of the population (Bigelow and Schroeder, 1953). Huntsman (1922) stated that *R. laevis* is only found from May to November in Passamaquoddy Bay and slightly longer in the Bay of Fundy. It is most abundant in southern New England during the summer (Merriman and Warfel, 1948) and only occurs in Chesapeake Bay during the spring (Hildebrand and Schroeder, 1928).

Raja erinacea:

Raja erinacea occurs from Nova Scotia and the southern side of the Gulf of St. Lawrence to North Carolina (Bigelow and Schroeder, 1953). One specimen was taken in Conception Bay, Newfoundland at 2 to 4 m (Templeman, 1965a). This species has been reported in the Miramichi Estuary (McKenzie, 1959); along the outer coast of Nova

Scotia, but not the offshore banks of Banquereau, Sable Island, and Western (Leim and Scott, 1966); from the Bay of Fundy, the north and western Gulf of Maine, Georges Bank; and from southern New England wouth to Cape Lookout, North Carolina (Bigelow and Schroeder, 1953).

Raja erinacea is more abundant in water shoaler than 15 to 18 fms (27 to 33 m) than in deeper water (Bigelow and Schroeder, 1953) and 85 to 87 fms (155 to 159 m) is its deepest know occurrence (Bigelow and Schroeder, 1954). Edwards *et al.* (1962) captured specimens during the winter from Nantucket Shoals to Cape May, New Jersey in 31 to 210 fms (57 to 384 m) at 6 to 12 C. *R. erinacea* has a known temperature range of 3 to 21 C and "is usually found on sandy or gravelly bottoms, less often on mud and rarely on submarine rocks or ledges" (Bigelow and Schroeder, 1953).

There are seasonal fluctuations in its abundance but *R. erinacea* does not appear to make extensive seasonal migrations. According to Tyler (1971a) this species is found in the deeper water (37 to 55 m) of Passamaquoddy Bay from November to April with a few remaining until May or June. During the remainder of the year it is found in shallower water (Tyler, 1971b). Merriman *et al.* (1953) noted a seasonal onshore-offshore migration of about three to five miles or more in Block Island Sound. It moved inshore during the spring, offshore in the middle to late summer, inshore in the autumn, and offshore in the midwinter. Richards (1963) noted changes in seasonal abundance of *R. erinacea* at two stations in Long Island Sound. The skates were absent from station 1 (9 m, sand bottom) during the midwinter and midsummer and were absent from station 3a (17 m, mud bottom) during the midsummer. *R. erinacea* was captured in the surf waters of Long Island during the spring and summer with a peak abundance in May and June (Schaefer, 1967). Merriman and Warfel (1948) found *R. erinacea* to be a permanent resident off southern New England in waters between 8 and 25 fms (15 and 46 m) but was most abundant in August. Richards *et al.* (1963), on the basis of tag returns, found no evidence for seasonal migrations of this species off southern New England. Fitz and Daiber (1963) reported that *R. erinacea* occurs in Delaware Bay when temperatures are below 15 C (late October to May). *R. erinacea* has been reported from lower Chesapeake Bay in December (Massmann, 1962) and in March (Hildebrand and Schroeder, 1928).

Raja ocellata

Raja ocellata is found from the Newfoundland banks and the southern side of the Gulf of St. Lawrence to North Carolina (Bigelow and Schroeder, 1953). This species occurs on Banquereau Bank, Sable Island Bank, along the coast of Nova Scotia, Bay of Fundy (Leim and Scott, 1966), the northern and western parts of the Gulf of Maine, Georges Bank, southern New England, and seasonally along the coast to Virginia (Bigelow and Schroeder, 1953).

Raja ocellata ranges from the shore zone to 50 to 60 fms (91 to 110 m) but is most abundant at depths less than 40 fms (73 m) (Bigelow and Schroeder, 1953). It has been reported from 1.2 to 1.6 C (Tyler, 1971a) and 18 to 19 C appears to be the upper limit of the thermal range (Bigelow and Schroeder, 1953). Edwards *et al.* (1962) captured

R. ocellata off the mid-Atlantic states during the winter at depths from 18 to 62 fms (33 to 113 m) at 10 to 12 C. Bigelow and Schroeder (1953) stated that this species is confined to sandy and gravelly bottoms but Tyler (1971a) reported it from mud bottoms in Passamaquoddy Bay.

The section of the population inhaviting depths greater than 10 fms (18 m) appears to be resident year-round, but the coastwise fringe of the population moves shoreward in autumn and offshore in summer (Bigelow and Schroeder, 1953). Tyler (1971a) reported that *R. ocellata* is present in Passamaquoddy Bay from December to March while Huntsman (1922) stated that this species was abundant from May to November. This discrepancy may be due to a difference in the areas sampled by the above authors. Tyler sampled the deeper waters of the bay and Huntsman did not specify the depths that were sampled. In the surf waters of Long Island *R. ocellata* is present during May, June, October, and November (Schaefer, 1967). Merriman and Warfel (1948) stated that this species is a permanent resident off southern New England between 8 and 25 fms (15 and 46 m) although there are seasonal fluctuations in abundance. *R. ocellata* has been reported from Chesapeake Bay during January and April (Hildebrand and Schroeder, 1928).

Raja senta:

Raja senta is found from the Gulf of St. Lawrence, the southern Newfoundland banks, and the Nova Scotian banks to South Carolina (Bigelow and Schroeder, 1953). It is reported from LaHave, Emerald, and Browns banks but from none of the more northern Nova Scotian banks.

R. senta occurs throughout the western side of the Gulf of Maine, on Georges Bank and along the upper slope of southern New England, New York, and New Jersey. (Bigelow and Schroeder, 1953). Isolated specimens have been captured off northern Virginia, off Chesapeake Bay (190 m), and off Charleston, South Carolina (874 m) (Bigelow and Schroeder, 1953).

This species has been reported from 25 to 478 fms (46 to 874 m) and is abundant between 50 and 250 fms (91 and 457 m) (Bigelow and Schroeder, 1953). It occurs in waters of 2 to 11 C and is most frequently taken at temperatures from 6 to 10 C (Bigelow and Schroeder, 1953). It is not known whether or not it makes seasonal migrations.

Raja radiata:

Raja radiata is found on both sides of the Atlantic. In the eastern Atlantic it occurs from the White and Barents seas to Portugal (Clark, 1929) and has been recently reported from Capetown, South Africa (Hulley, 1970). In the western Atlantic it occurs from Laborador, West Greenland, Hudson Bay, Grand Banks, and Gulf of St. Lawrence to South Carolina (Bigelow and Schroeder, 1953). *R. radiata* has been reported from along the outer coast of Nova Scotia, Banquereau, and Sable Island Bank (Leim and Scott, 1966), throughout the Gulf of Maine, Bay of Fundy, Georges Bank, and occurs between 150 and 300 fms (274 and 549 m) from Cape Cod to the Hudson Trough (Bigelow and Schroeder, 1953). Isolated specimens have been reported from off Long Island (59 m) and off Charleston, South Carolina (135 m) (Bigelow and Schroeder, 1953).

Raja radiata is generally found between 10 and 100 fms (18 and 183 m) (Bigelow and Schroeder, 1953) but it has been reported from as deep as 460 fms (841 m) off Greenland (Jensen, 1948), 459 fms (839 m) off Spitzbergen, and from 430 to 490 fms (786 to 896 m) off New York (Bigelow and Schroeder, 1953). Bigelow and Schroeder (1953) reported a temperature range of 1.4 to 10 C but Backus (1957) took a single specimen at -1.4 C off Laborador. *R. radiata* has been captured over sand, gravel, pebble, brokenshell, and mud bottoms (Bigelow and Schroeder, 1953). There are no data to suggest seasonal migrations and in Passamaquoddy Bay it is a year-round resident in 20 to 30 fms (37 to 55 m) at 1.2 to 10.2 C (Tyler, 1971a).

Much of the above information was obtained from scattered regional inshore observations and studies of off-shore cruises of limited scope because there have been no comprehensive survey reports for the area from Nova Scotia to Cape Hatteras. The purpose of the present study was to use the data gathered during comprehensive groundfish surveys of this area to define distribution and relative abundance of each species and to determine the level of co-occurrence among the species.

MATERIALS AND METHODS

Sources of data for this study were eight groundfish surveys of the continental shelf (27 to 366 m) from LaHave Bank, off southeastern Nova Scotia and the Gulf of Maine to Cape Hatteras conducted by the Biological Laboratory of the National Marine Fisheries Service at

Woods Hole, Massachusetts. A total of 2247 fishing stations were made aboard the R/V Albatross IV and R/V Delaware II during the winters of 1968, 1969, and 1970; the summer of 1969; the autumn of 1967, 1968, 1969, and 1970 (Table 1). Each cruise except for part of 70-06 was conducted by the R/V Albatross IV. The survey area was divided into 58 sampling strata according to depth and geographical area and three or more stations were randomly selected within each stratum per cruise (Fig. 13). A number 36 Yankee trawl with a cod-end liner of 0.25 in. was towed at 3.5 k for 0.5 hr. The ground rope of the net was equipped with 18 in. rollers. Grosslein (1969) described the sampling design in detail.

The survey area was divided into five ecological subareas according to hydrography and substratum. The southern section of the mid-Atlantic Bight consisted of strata 61 to 76; the northern mid-Atlantic Bight was comprised 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 Nova Scotian Shelf consisted of strata 31 to 35, 41 to 42. All four depth strata (27-55, 56-110, 111-183, 184-366 m) were sampled in the three former subareas, the three deeper strata were surveyed in the Gulf of Maine, and only two strata, 56-110 and 111-183 m, were sampled on the Nova Scotian shelf.

Ancillary distributional data were obtained from the Exploratory Fishing and Gear Research Base of the National Marine Fisheries Service at Pascagoula, Mississippi for the area from the Straits of Florida to Cape Hatteras; from the Biological Station of the Fisheries

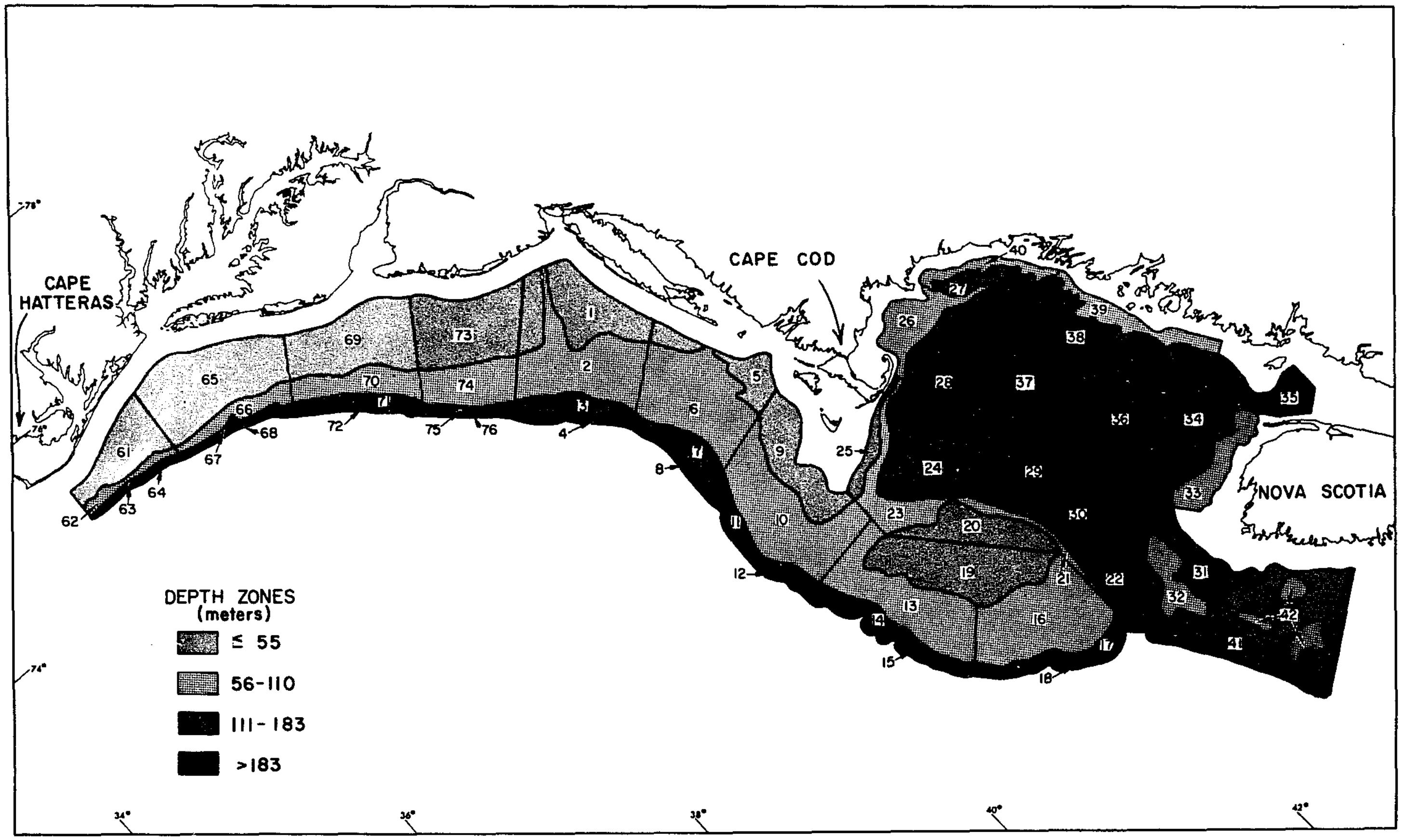
TABLE 1

GROUNDFISH SURVEYS CONDUCTED BY THE BIOLOGICAL LABORATORY OF THE NATIONAL MARINE FISHERIES SERVICE AT WOODS HOLE, MASS.

Cruise	Date	Season	Number of Stations
67-21	Oct. 17-Dec. 9, 1967	Autumn	271
68-03	Mar. 4-May 16, 1968	Winter	262
68-17	Oct. 10-Nov. 26, 1968	Autumn	275
69-02	Mar. 5-Apr. 10, 1969	Winter	266
69-08	Jul. 14-Aug. 28, 1969	Summer	267
69-11	Oct. 8-Nov. 23, 1969	Autumn	276
70-03	Mar. 12-Apr. 29, 1970	Winter	289
70-06	Oct. 15-Nov. 20, 1970	Autumn	341
		Total number of stations	2247

Fig. 13

Strata sampled by the R/V Albatross IV and Delaware II, 1967-1970. Strata 43-60 were not included in the surveys.


CAPE HATTERAS
CAPE COD
NOVA SCOTIA
DEPTH ZONES
(meters)
≤ 55
56-110
111-183
>183
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
34°
36°
38°
40°
42°
74°
76°

Research Board of Canada 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; and from the Virginia Institute of Marine Science (VIMS) for Chesapeake Bight (38 43'N latitude to 35 13'N latitude).

The distributional data from south of Cape Hatteras and from northeastern Nova Scotia and the Gulf of St. Lawrence, collected from 1961 to 1968 and 1960 to 1970 respectively, were based on numerous surveys which employed a number of vessels outfitted with several types of trawling gear. No statistical estimates of abundance were drawn from these data.

Statistical estimates of abundance (geometric means) were computed for the skate data obtained from the VIMS survey of Chesapeake Bight. Five seasonal surveys were made during 1967 and 1968 aboard the same vessel equipped with an Atlantic western trawl. The survey area covered the area between 9 and 274 m (Musick and McEachran, 1972). The trawl was not equipped with rollers as was the trawl used aboard the Albatross IV, so was more efficient in capturing skates (Edwards, 1968). Chesapeake Bight was divided into two areas, one north and the other south of the Virginia Capes (37°N latitude) for analysis of the skate data.

Features of the Study Area:

The mid-Atlantic Bight is a broad, gently-sloping portion of the continental shelf which is widest off New York and constricted to the north at Nantucket Shaols and to the south at Cape Hatteras.

The relatively smooth bottom is intersected by five canyons. Hudson Canyon, the largest, divides this bight into a northern and a southern section. Isotherms tend to parallel the coastline; however, in summer a pool of cool water, surrounded by warm water, extends as far south as the offing of Chesapeake Bay (Bigelow, 1933). The greatest extremes in bottom water temperature are in the shoaler areas. The coldest temperatures occur in late February to early March and the warmest bottom temperatures occur in August for shallow water but not until the end of October for water of intermediate depth (Bigelow, 1933). The deeper areas of the bight are influenced by slope of water and have little seasonal fluctuations (Bigelow, 1933). A steep thermal gradient develops at Cape Hatteras during the autumn and breaks down in the spring, and a thermal gradient develops at Nantucket Shoals in the spring and breaks down in the autumn (Parr, 1933). The sediments of the bight are predominately sand (Uchupi, 1963).

Georges Bank separates the Gulf of Maine from the open sea and is separated from adjacent shoal areas by deep channels. The shoaler areas of Georges Bank have wide seasonal fluctuations in bottom temperatures and the extremes in temperature are reached at about the same time as the shoal areas of the mid-Atlantic Bight. The deeper sections have more constant temperatures. The deeper areas of the northeastern region are influenced by warm slope water (Bigelow, 1927) and have more moderate temperatures than areas of the western sector at the same depth. The sediments of Georges Bank consist of coarse sand and scattered patches of gravel (Uchupi, 1963).

The Gulf of Maine is a broad, irregular depression separated from the open sea by Georges Bank and the Nova Scotian shelf (Uchupi, 1970). East Channel, between Georges Bank and Browns Bank, joins the basin of the Gulf (183 m and deeper) to the open sea. The basin is influenced by slope water which enters the Gulf through East Channel (Bigelow, 1927). The topographic highs of the Gulf are covered by sand and gravel, sediments of the basin consists of silty sand and sandy silt to silt and clay, and East Channel is blanketed by coarse sand and gravel (Uchupi, 1963).

The Nova Scotian shelf, except for a series of banks, is deep. The inshore areas have seasonal temperature fluctuations. The banks are under the influence of a cold intermediate water mass and the slope water; bottom water temperatures are below 5 C when the intermediate mass is thick and temperatures are above 5 C when the intermediate water layer is less thick, (McLellan, 1954). The deeper areas of the shelf are under the influence of slope water and temperatures are more stable (McLellan, 1954).

Data Analyses:

Raja erinacea and *R. ocellata* are difficult to distinguish (Part I). Field personnel often misidentified them and, occasionally, the other species. Records of species not verified by the author were evaluated with discretion. Records were discarded when it was not possible to determine the correct species.

Taylor (1953) and Roessler (1965) demonstrated that groundfish counts are contagiously distributed and preliminary examination of the skate data also suggested contagion. Both a logarithmic and a negative binomial transformation tend to normalize contagious distributions (Pereyra *et al.*, 1967; Bartlett, 1947). Counts were transformed to log (x + 1) in the present study. Transformed values were used to determine the geometric mean numbers (index of abundance) of skates per stratum per cruise. The stratum estimates were weighted to correct areal differences between strata and thus facilitate comparisons of abundance between strata.

Index of abundance for all stations, within temperature intervals of one degree C within each subarea, was calculated for each species. Length frequencies were computed by strata sets (27-55, 56-110, 111-183, 184-366 m) within each of the subareas. This analysis gave the percentage that each 3 cm length increment contributed to the total catch of a species within each of the strata sets of the subareas. Index of abundance was computed for each of the species (*R. eglanteria*, *R. garmani*, *R. erinacea*, and *R. ocellata*) captured during the VIMS survey of Chesapeake Bight, both by temperature intervals of one degree C and by depth strata (0-18, 19-37, 38-73, 74-110, 111-165, 166-274 m), north and south of 37°N latitude separately.

Data collected during the Albatross IV and Delaware II cruises were used to determine the level of interspecific relationships between the species. Index of association (Hurlbert, 1969) was calculated for all of the possible species combinations to determine if any of the species co-occurred. This index is based on the presence or 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 in competition with one another (Hurlbert, 1969). The correlation indices were computed from transformed abundance values [log (x+1)] at stations where the two species co-occurred. According to Hurlbert (1969) a significant negative slope shows an inverse relationship in numbers of individuals between the species and indicates that the two species are in competition for the same resources.

RESULTS AND DISCUSSION

Seasonal bottom isotherms were plotted from the R/V Albatross IV surveys of 1969 because this was the only year in which a summer cruise was made, and the winter and autumn temperature profiles appeared typical. Temperatures were lowest during the winter survey and in the mid-Atlantic Bight isotherms tended to parallel the coast line (Fig. 14) 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 (Fig. 15), a condition previously described by Bigelow (1933). Temperatures were warmest during the autumn survey (Fig. 16). The summer survey was conducted during July and August and the autumn survey during October and November (Table 1). Intermediate waters of both the mid-Atlantic Bight and Georges Bank reach their maximum temperatures in October (Bigelow, 1933; 1927, respectively).

The length frequencies by strata sets revealed that small to large specimens of each species were found together except that small

Fig. 14

Bottom isotherms for the winter, 1969 survey of the R/V Albatross IV. Temperatures in degree C.

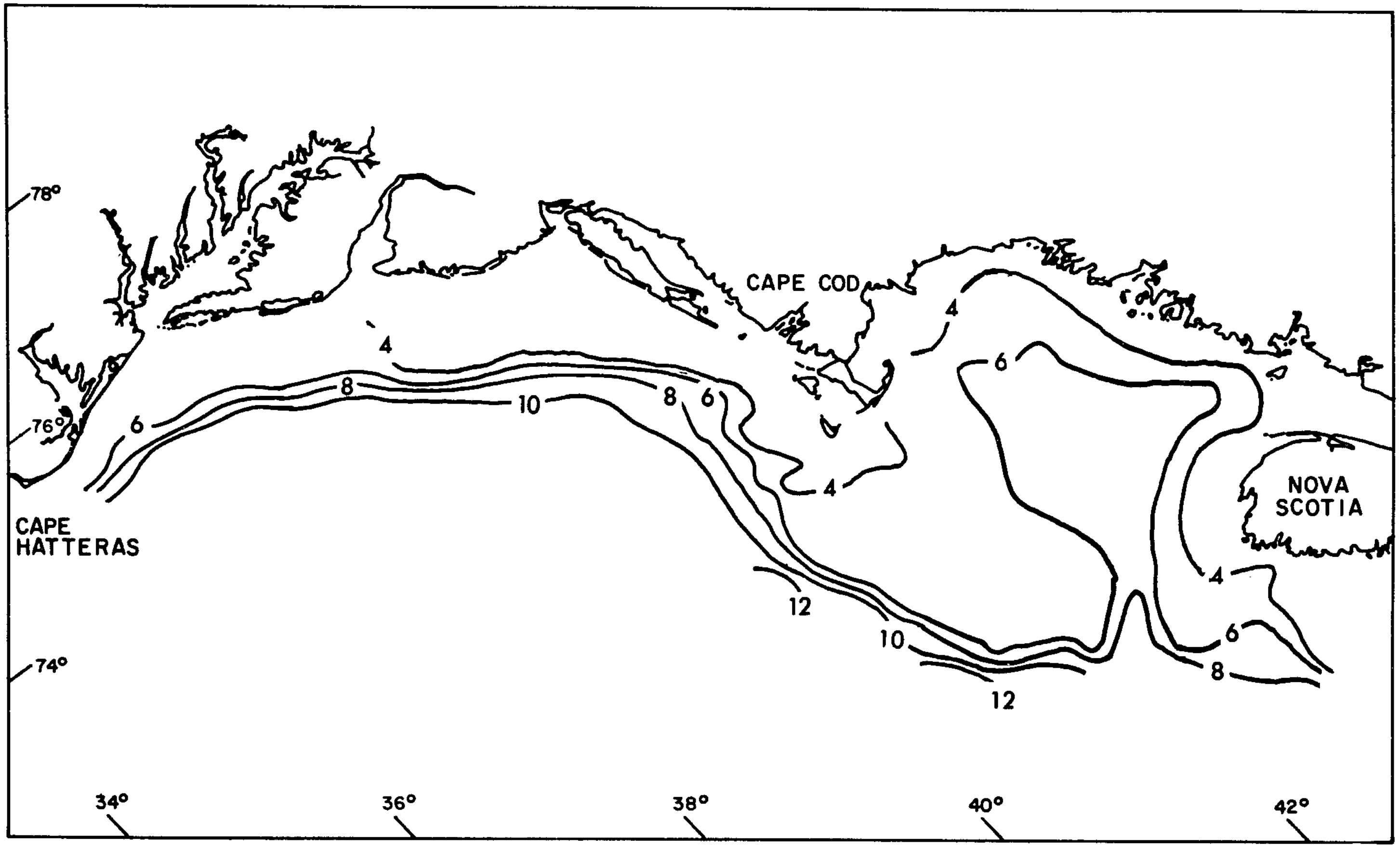
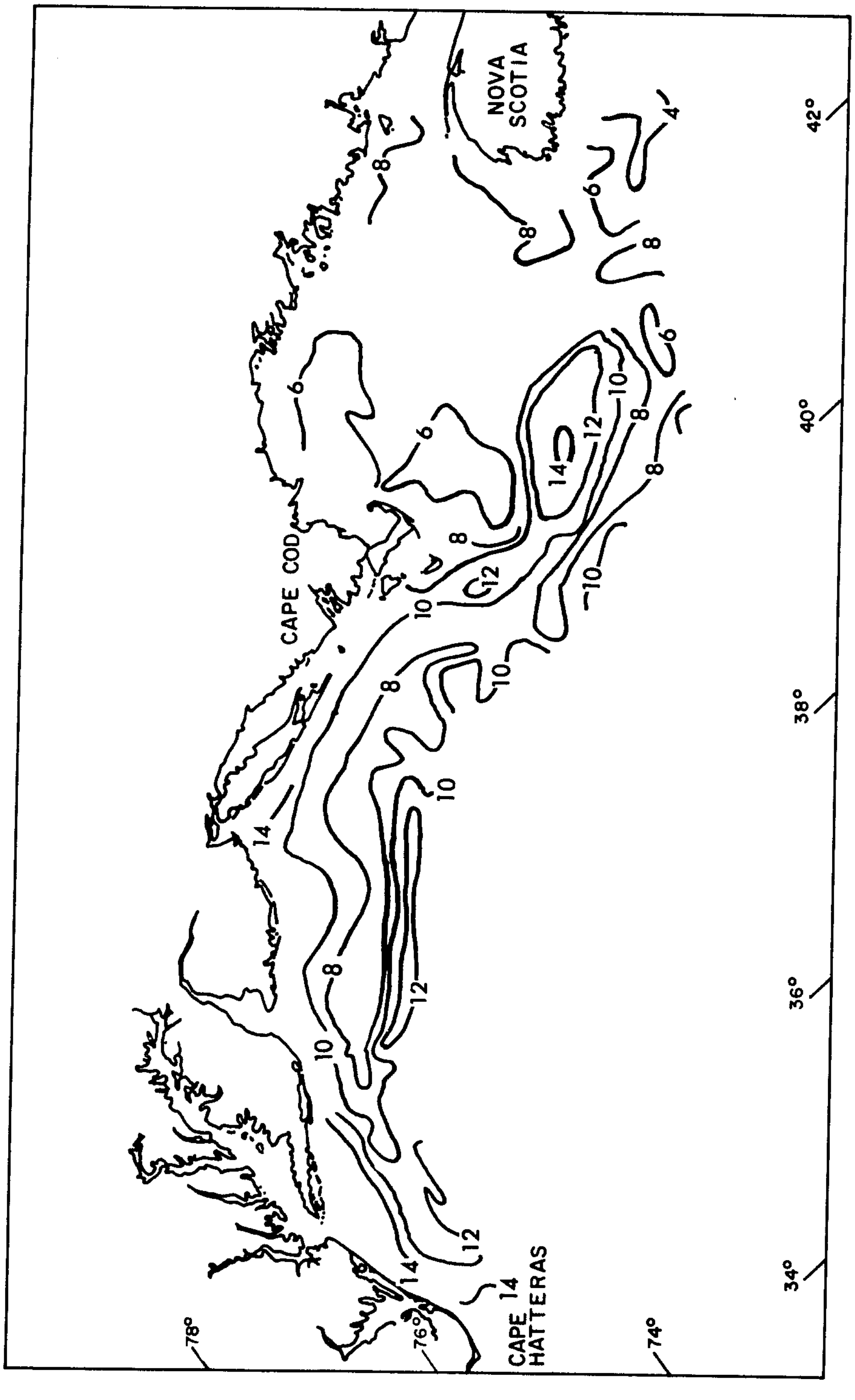
78°
76°
74°
CAPE HATTERAS
CAPE COD
NOVA SCOTIA
4
6
8
10
12
34°
36°
38°
40°
42°

Fig. 15

Bottom isotherms for the summer, 1969 survey of the R/V Albatross IV. Temperatures in degree C.


NOVA SCOTIA
CAPE COD
CAPE HATTERAS
78°
76°
74°
34°
36°
38°
40°
42°
4
6
6
6
6
8
8
8
8
8
8
8
10
10
10
10
10
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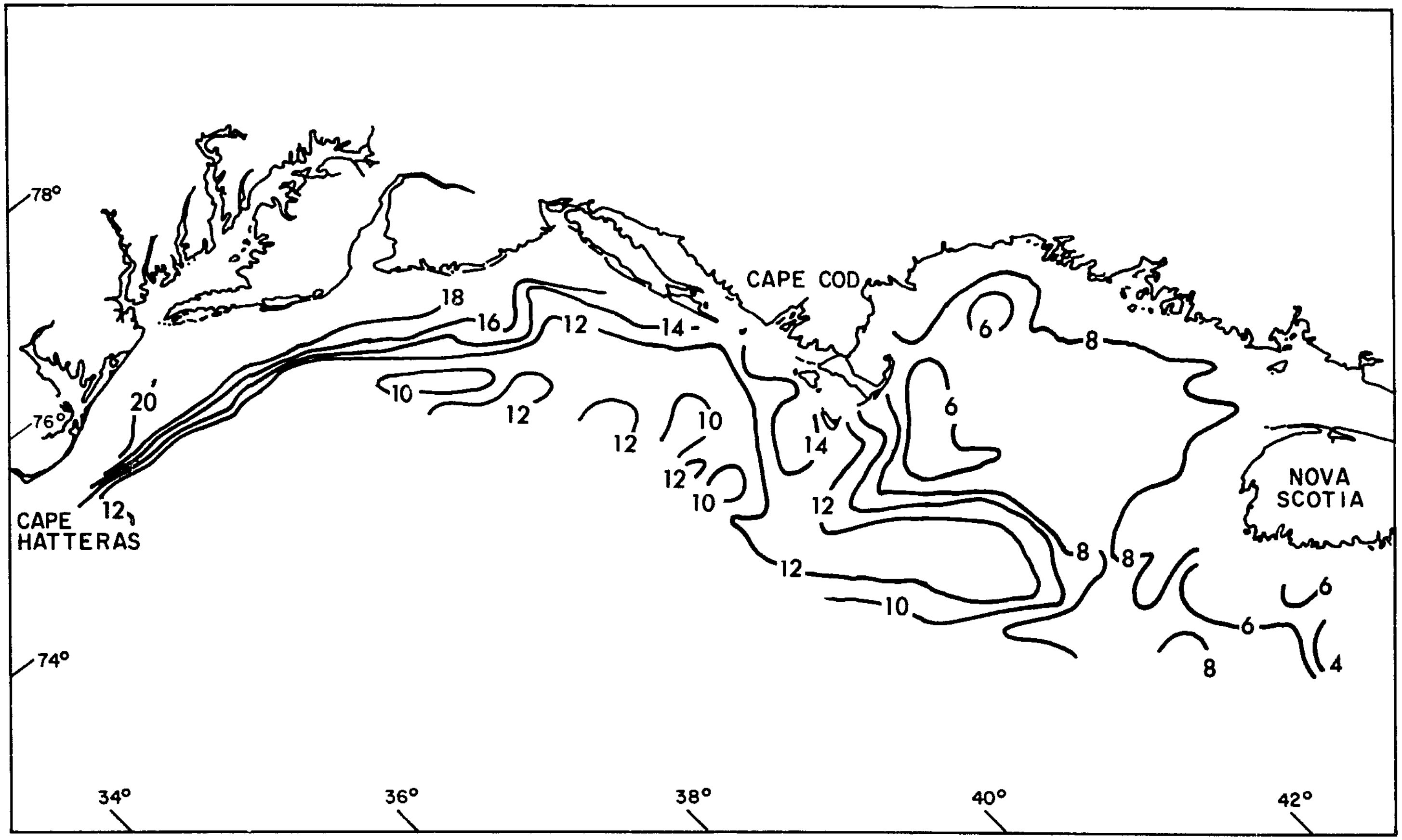
12
12
12
12
14
14
14
14

Fig. 16

Bottom isotherms for the autumn, 1969 survey of the R/V Albatross IV. Temperatures in degree C.



78°
76°
74°
34°
36°
38°
40°
42°
CAPE HATTERAS
CAPE COD
NOVA SCOTIA
20
18
16
14
12
10
8
6
4

specimens of *R. erinacea* and *R. ocellata* were seldom captured. The young of these two species may have different distributional patterns than the older fish or may be less vulnerable to the gear used. Data were pooled for the distributional analyses of each species.

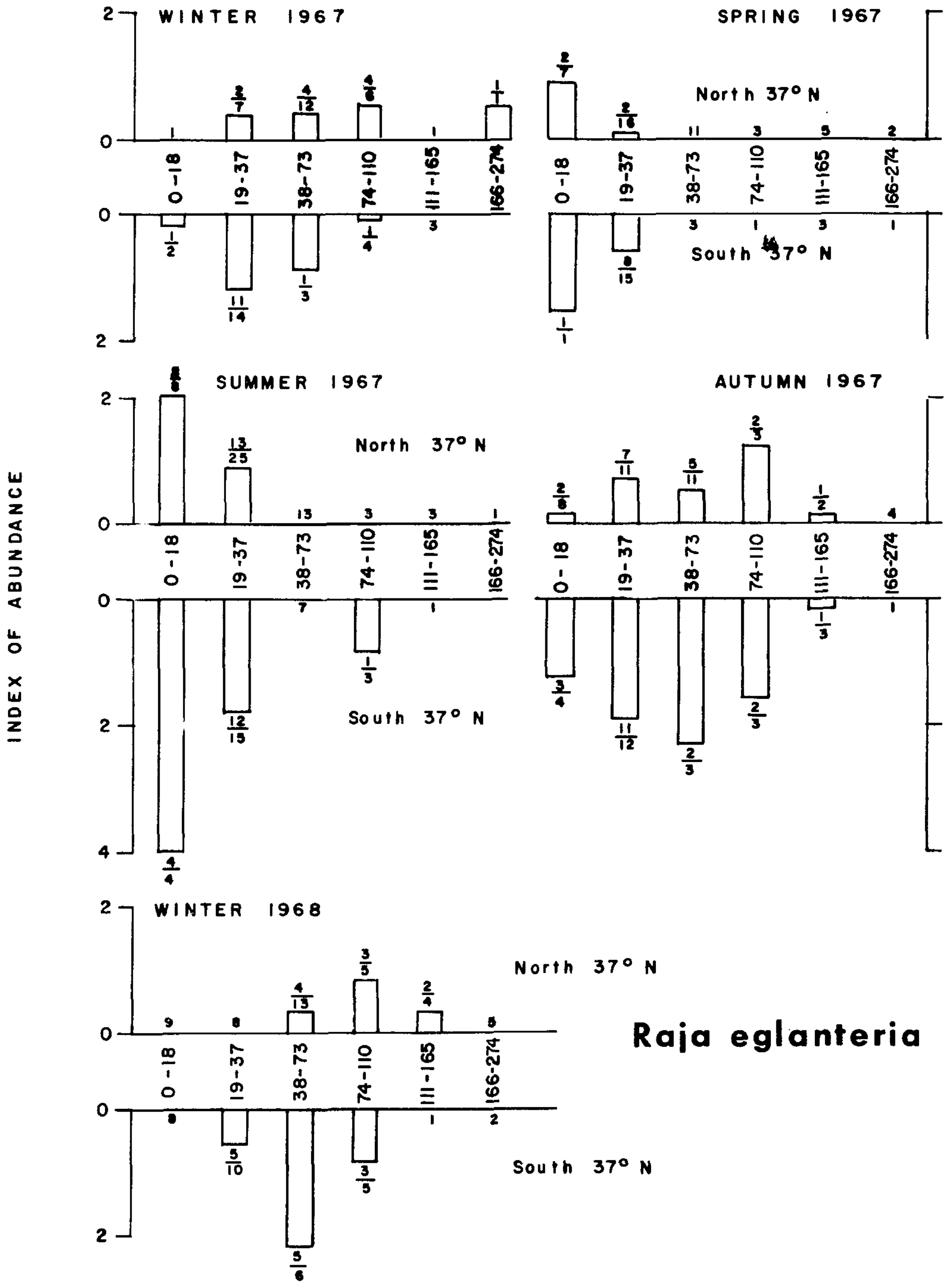
Charts showing the distribution by strata and histograms showing the distribution by temperature were illustrated for the Albatross IV cruises of 1969. Only the four most abundant species (*R. erinacea*, *R. ocellata*, *R. senta*, and *R. radiata*) were included. Distribution by temperature and depth strata were illustrated for two species (*R. eglanteria* and *R. garmani*) captured during the VIMS survey of 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. Small numbers of this species were taken in the southern section of the mid-Atlantic Bight on all Albatross IV cruises except in the summer, 1969 and the winter, 1970. During the VIMS survey of Chesapeake Bight *R. eglanteria* was more abundant in shoal water during the spring and summer than during the autumn and winter (Fig. 17). It was more abundant in both sectors of Chesapeake Bight in the summer and autumn than in the winter and spring. *R. eglanteria* was captured between 5 and 26 C in Chesapeake Bight and was most abundant between 9 and 20 C (Fig. 18). 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.

Fig. 17

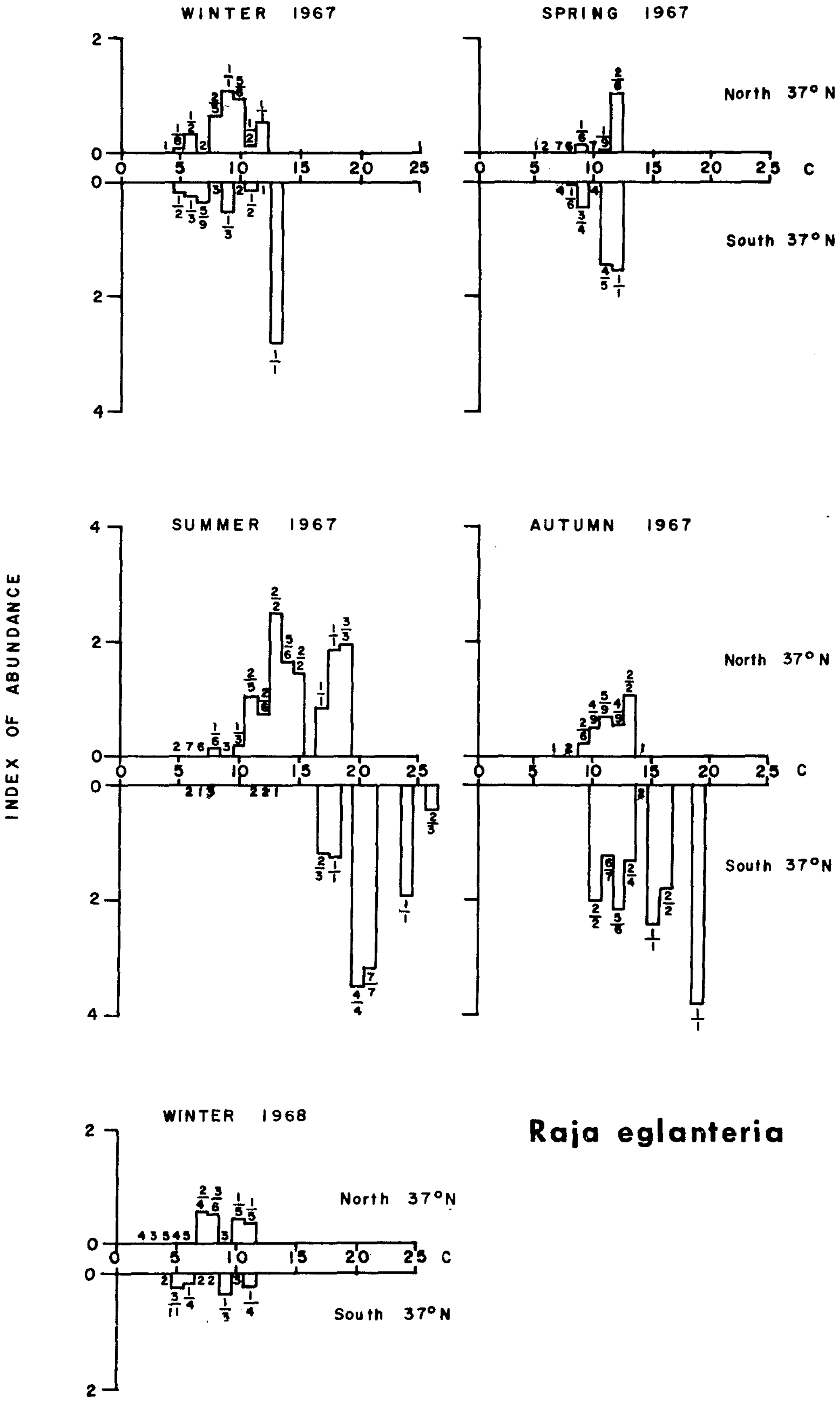
Index of abundance (geometric mean) of *R. eglanteria* captured in Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of 37°N were analyzed separately. The fraction over each bar is the ratio of the number of stations at which the species was captured to the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



INDEX OF ABUNDANCE
WINTER 1967
SPRING 1967
SUMMER 1967
AUTUMN 1967
WINTER 1968
North 37° N
South 37° N
0-18
19-37
38-73
74-110
111-165
166-274
0
2
4
Raja eglanteria

Fig. 18

Index of abundance (geometric mean) of *R. eglanteria* captured in Chesapeake Bight during each cruise within temperature intervals of one degree C. Data collected north and south of 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.



Raja eglanteria

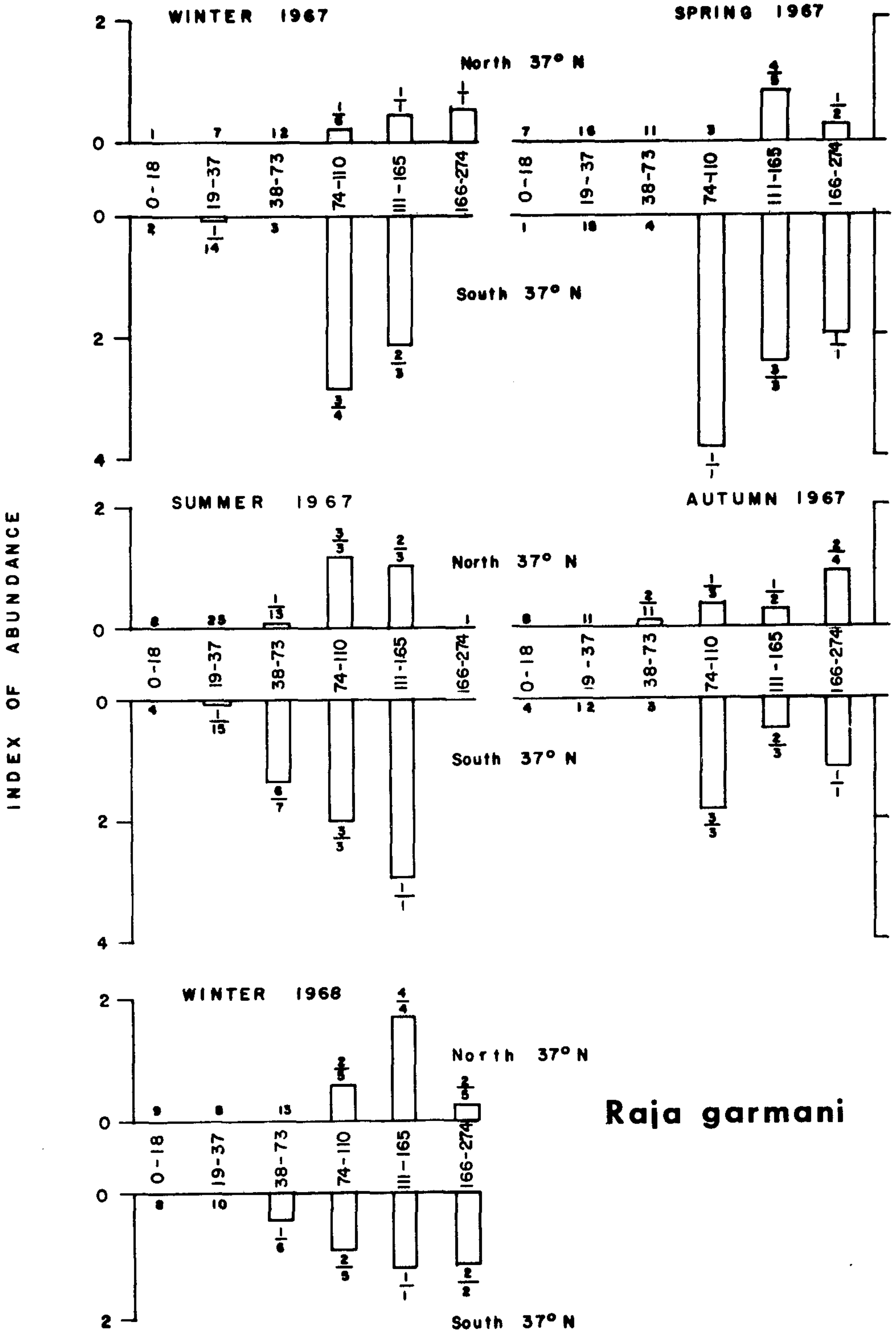
Raja eglanteria, a Carolinian species in the sense of Johnson (1934) and Hedgpeth (1957) occurs north of Cape Hatteras all year but is abundant there only during the warmer months. Bigelow and Schroeder (1953) stated that it is most abundant from the sublittoral zone to about 55 m, however, Edwards *et al.* (1962) captured it in 280 and 329 m off Cape May, New Jersey during the winter. In autumn *R. eglanteria* leaves the embayments and shallow areas of the mid-Atlantic Bight (Bigelow and Schroeder, 1953; Schwartz, 1961; Massmann, 1962; Fitz and Daiber, 1963: and 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 then is concentrated at depths shoaler than 27 m. Apparently part of the individuals that summers in the southern part of Chesapeake Bight moves 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 Chesapeake Bight it was found between 33 and 196 m and generally deeper than 73 m (Fig. 19), and appeared to move shoreward in the summer. In Chesapeake Bight *R. garmani* was captured at temperatures

Fig. 19

Index of abundance (geometric mean) of *R. garmani* captured in Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of 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.



Raja garmani

of 6 to 17 C and was most abundant between 9 and 13 C (Fig. 20). Between Cape Hatteras and Georgia it was found in 66 to 123 m at 17C, 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.

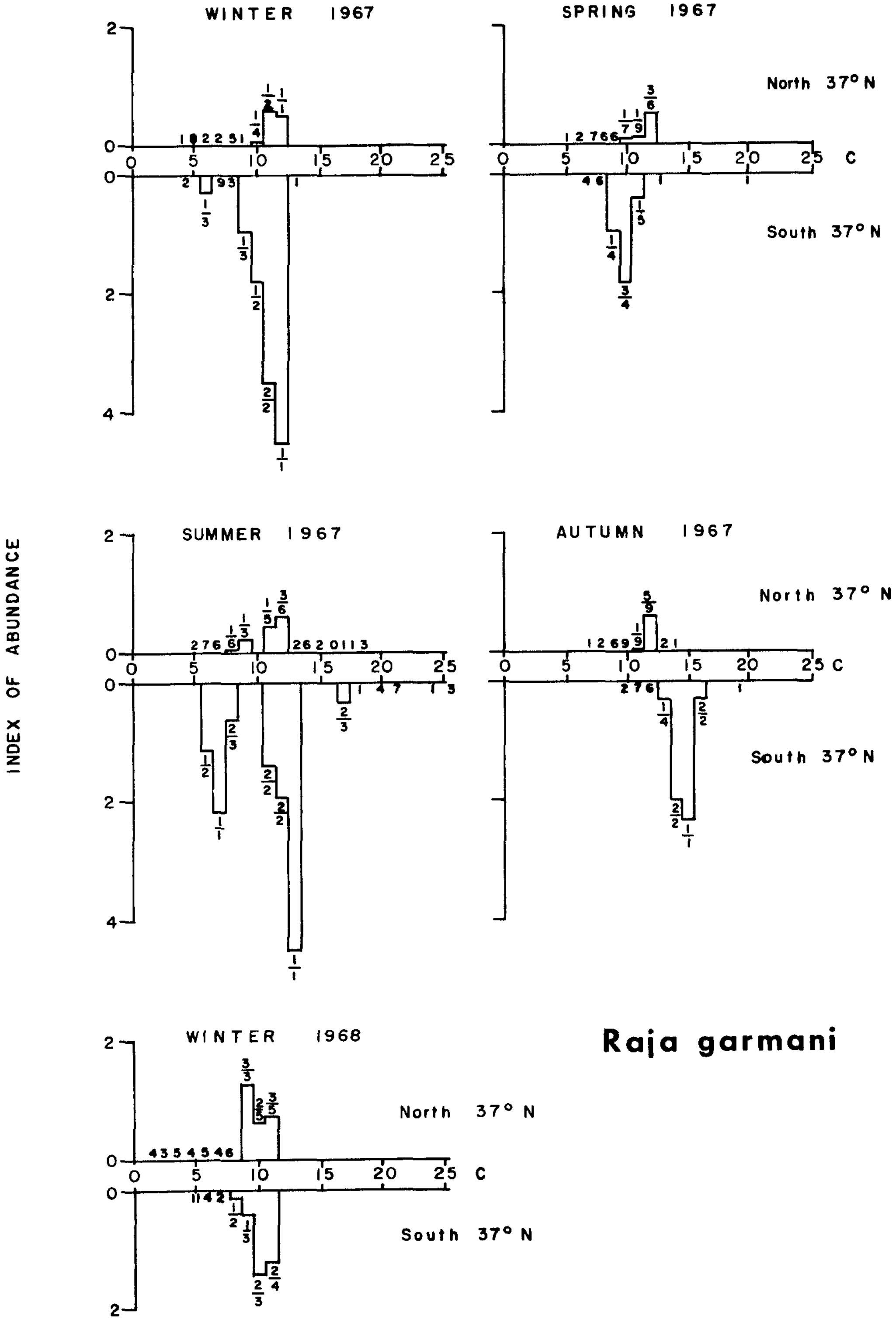
Raja garmani probably does not regularly occur on the eastern slope of Georges contrary to Schroeder (1955), because no specimens were captured there during the Albatross IV cruises. The depth and temperature ranges of 51 to 494 m and 5.3 to 15 C given by Bigelow and Schroeder (1953) are close to those for the area north of Cape Hatteras in the present study. It has a more limited depth range and higher temperature preferences in the southern part of its range than it does in the northern part of its range as stated by Bigelow and Schroeder (1953). Staiger (1970) stated that it is found between the 119 and 366 meter 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 (McEachran, unpub. data). The differences in temperature preferences 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

Fig. 20

Index of abundance (geometric mean) of *R. garmani* captured in Chesapeake Bight during each cruise within temperature intervals of one degree C. Data collected north and south of 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.



Raja garmani

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. *R. laevis* was caught in 302 to 368 m off northeastern Florida.

Raja laevis is the most ubiquitous 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 tide mark 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, North Carolina to Dry Tortugas, Florida (Bigelow and Schroeder, 1968). *R. 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*. Also *R. laevis* does not occur in the species lists of Struhsaker (1969) or Staiger (1970). Thus it is likely that many 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 (Fig. 21, 22,23). *R. 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 occured 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 (Fig. 24, 25, 26). The recorded temperature range of the species is 1.2 C (Tyler, 1971a) 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. In the southern section of the mid-Atlantic Bight it was usually caught

Fig. 21

Index of abundance (geometric mean) of *R. erinacea* captured by sampling strata during the winter, 1969 cruise of the R/V Albatross IV.

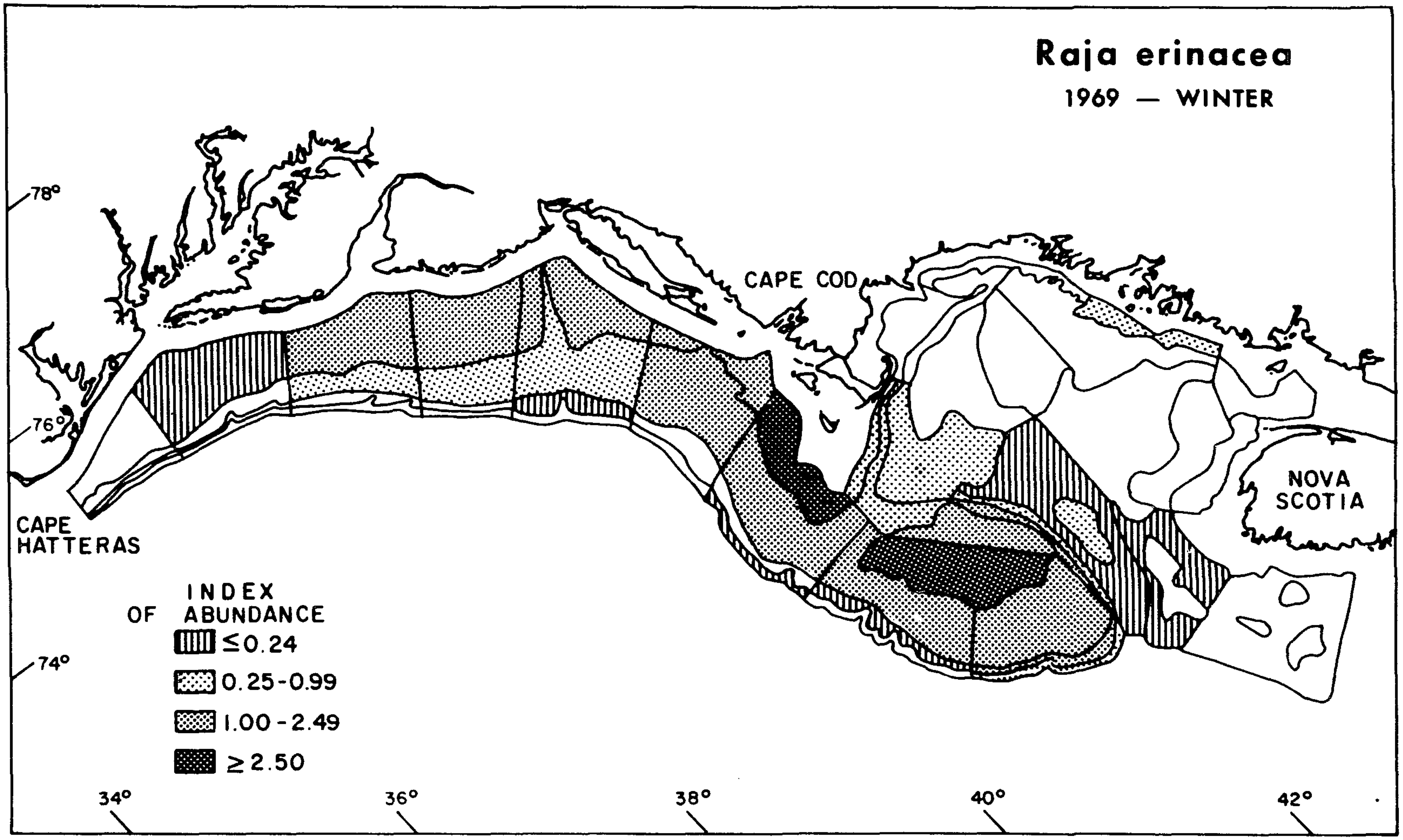

Raja erinacea
1969 — WINTER
78°
76°
74°
CAPE COD
NOVA SCOTIA
CAPE HATTERAS
INDEX OF ABUNDANCE
≤0.24
0.25-0.99
1.00-2.49
≥2.50
34°
36°
38°
40°
42°

Fig. 22

Index of abundance (geometric mean) of *R. erinacea* captured by sampling strata during the summer, 1969 cruise of the R/V Albatross IV.

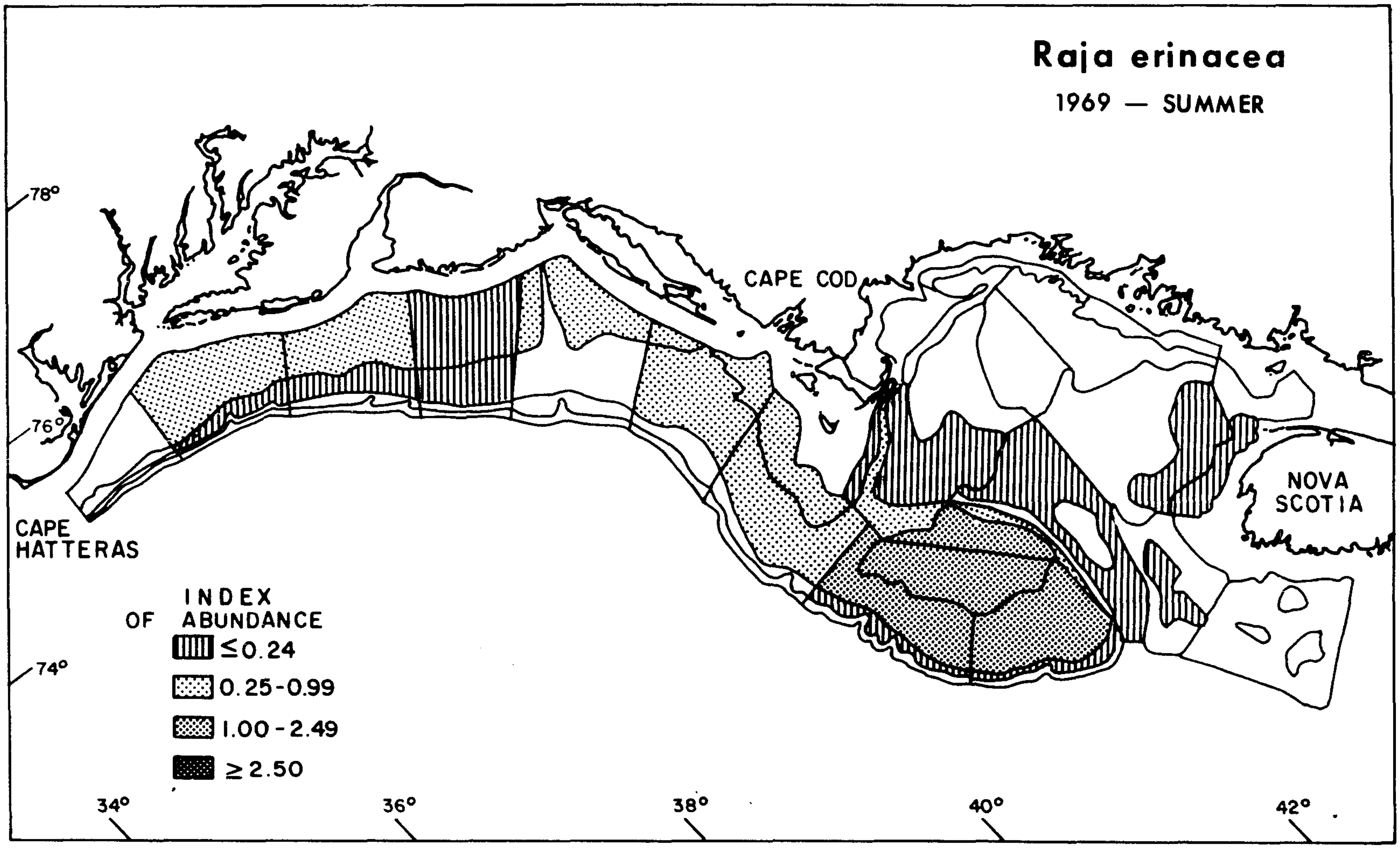
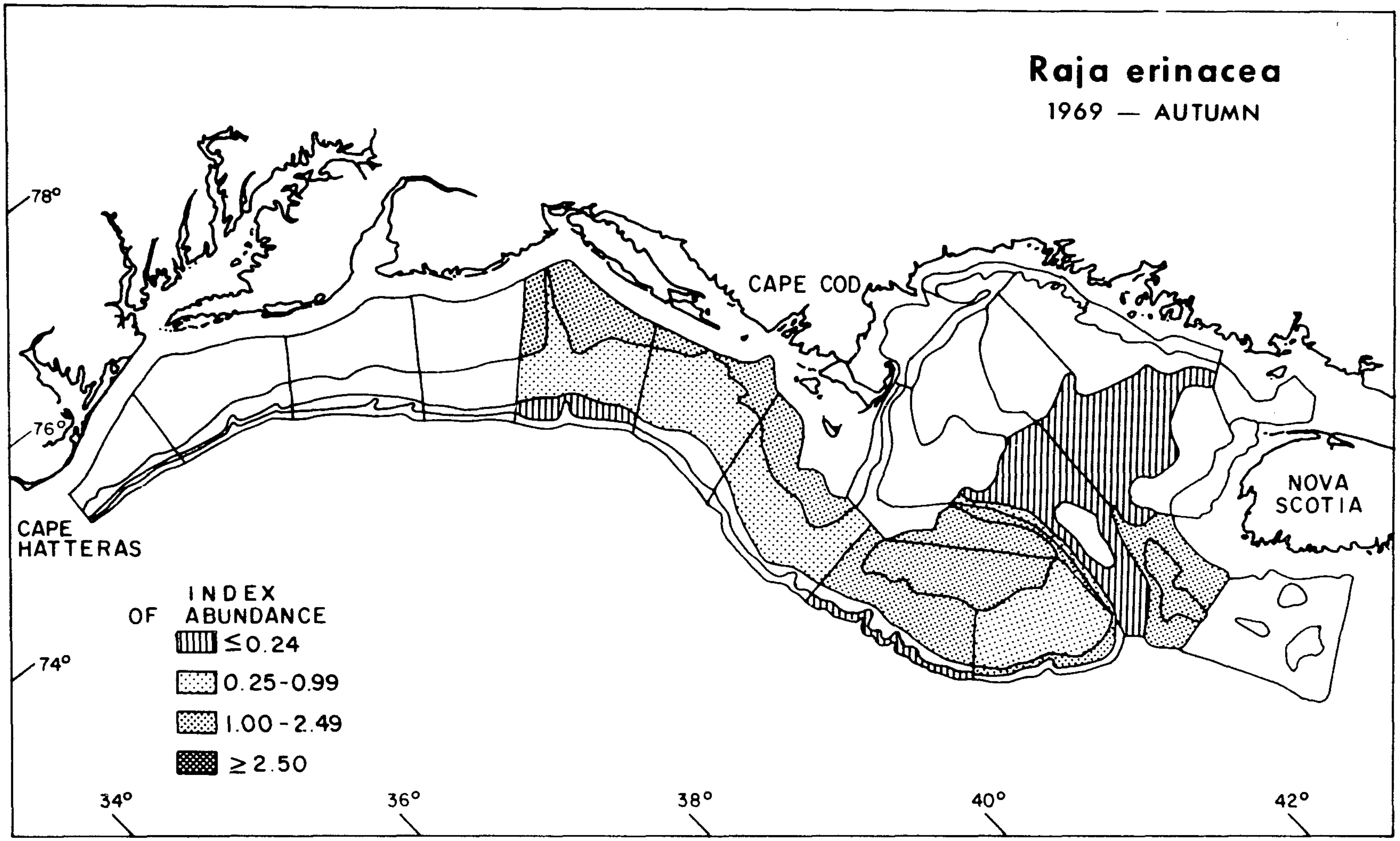

Raja erinacea
1969 — SUMMER
78°
76°
74°
CAPE COD
CAPE HATTERAS
NOVA SCOTIA
INDEX OF ABUNDANCE
≤0.24
0.25-0.99
1.00-2.49
≥2.50
34°
36°
38°
40°
42°

Fig. 23

Index of abundance (geometric mean) of *R. erinacea* captured by sampling strata during the autumn, 1969 cruise of the R/V Albatross IV.



Raja erinacea

1969 — AUTUMN

Fig. 24

Index of abundance (geometric mean) of R. *erinacea* captured in each subarea during winter 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja erinacea
WINTER 1969

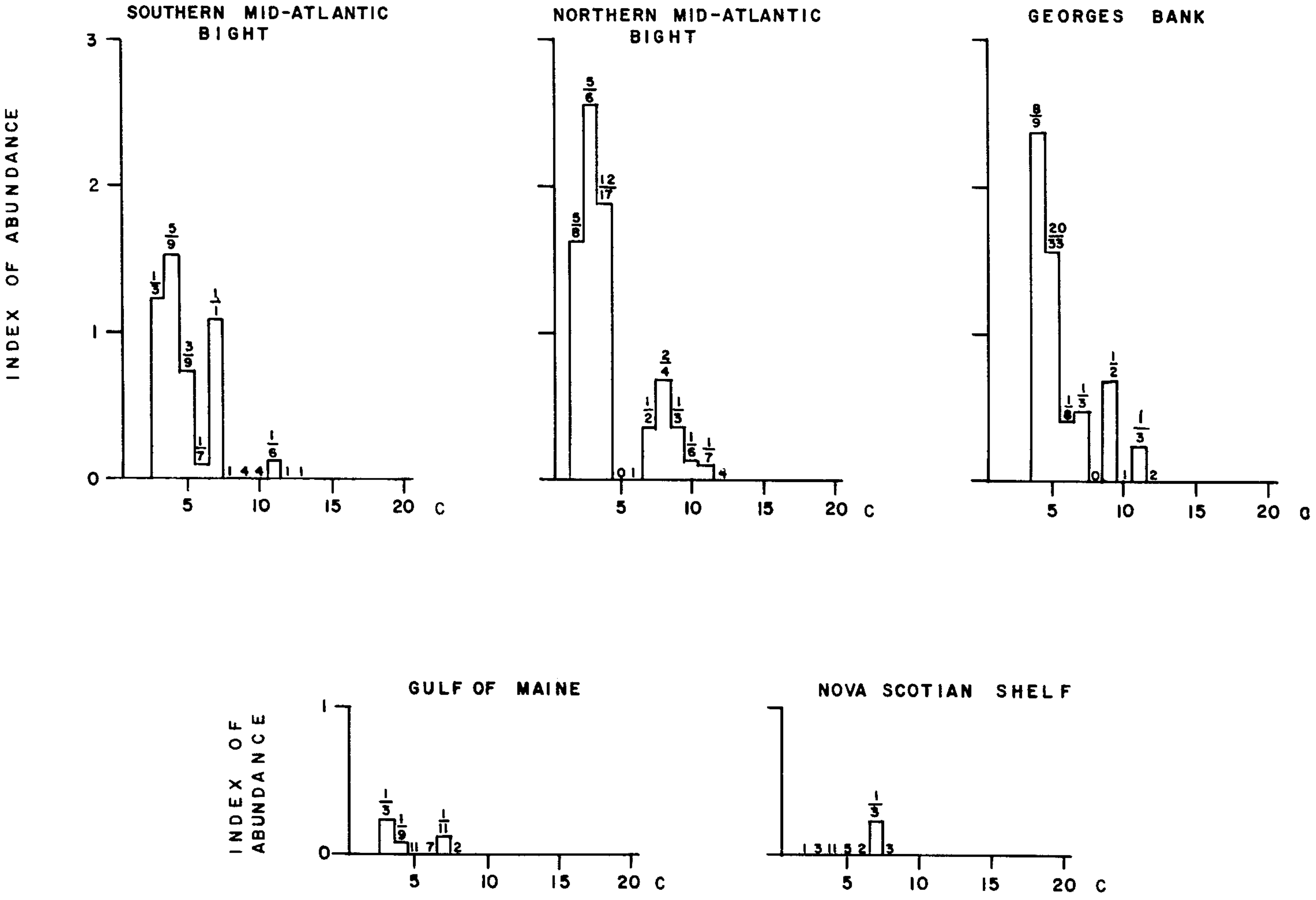


Fig. 25

Index of abundance (geometric mean) of *R. erinacea* captured in each subarea during summer, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja erinacea
SUMMER 1969

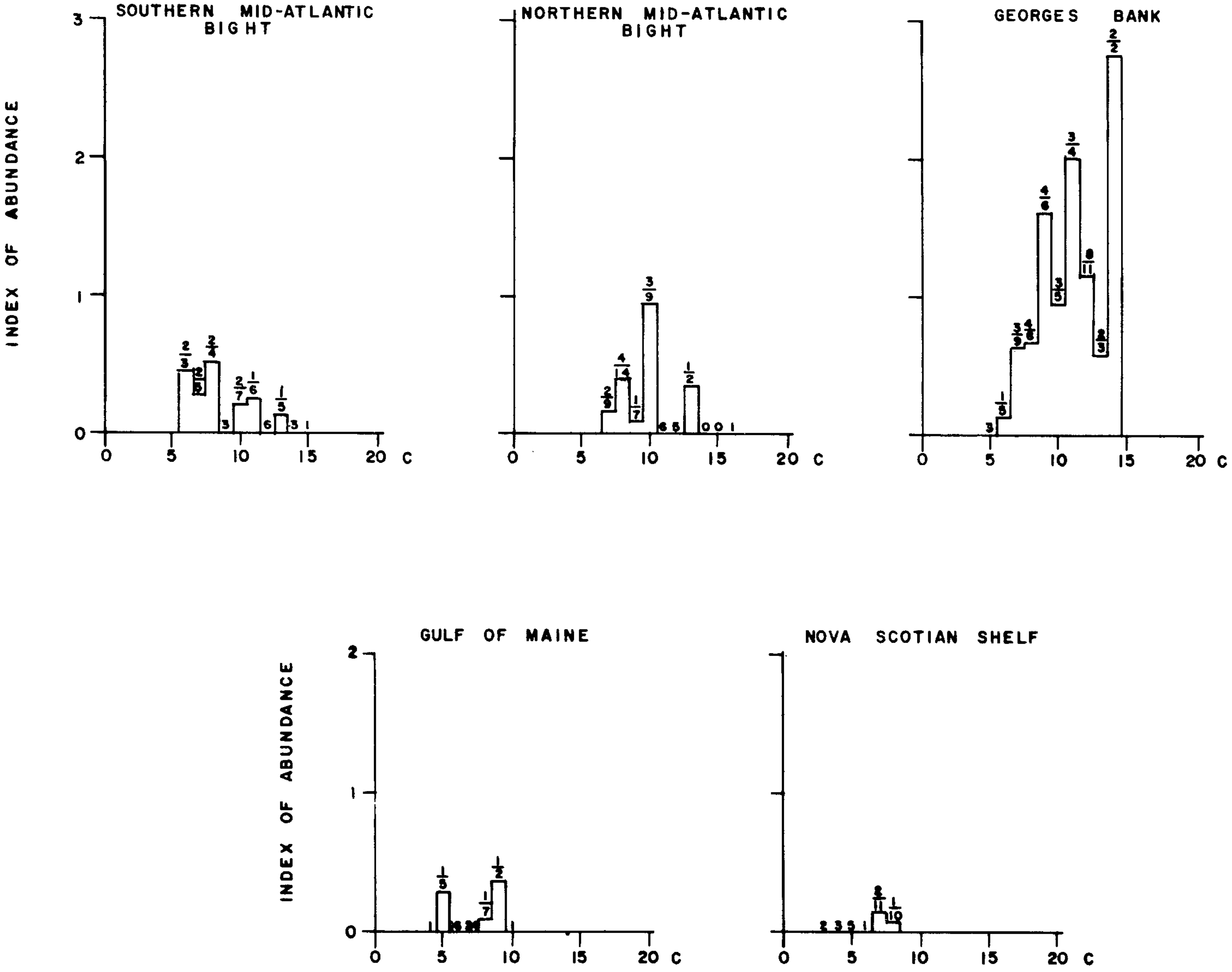
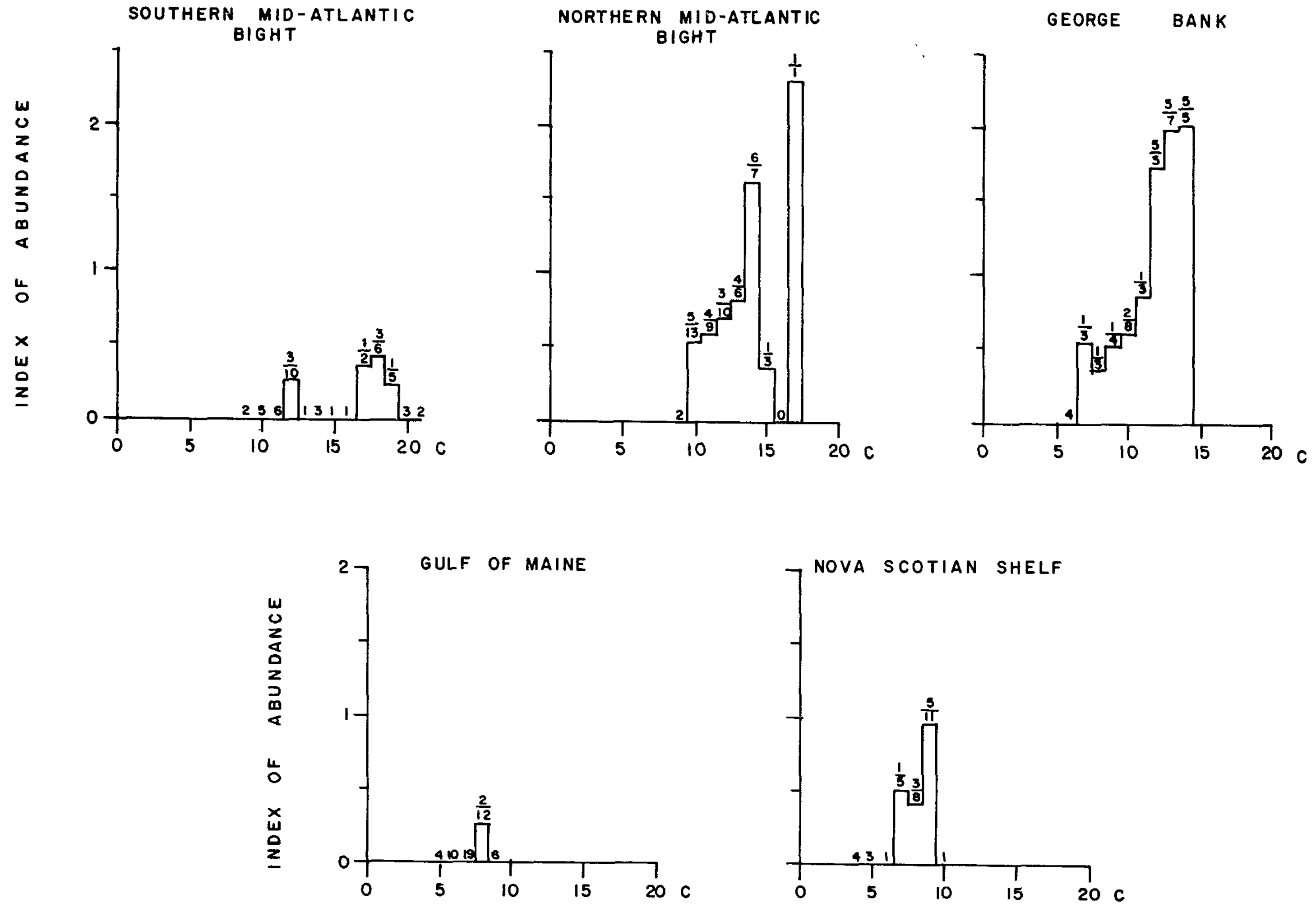


Fig. 26

Index of abundance (geometric mean) of *R. erinacea* captured in each subarea during autumn, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja erinacea
AUTUMN 1969



over the lower part of the temperature range for the area and on the Nova Scotian shelf over the upper part of the temperature range.

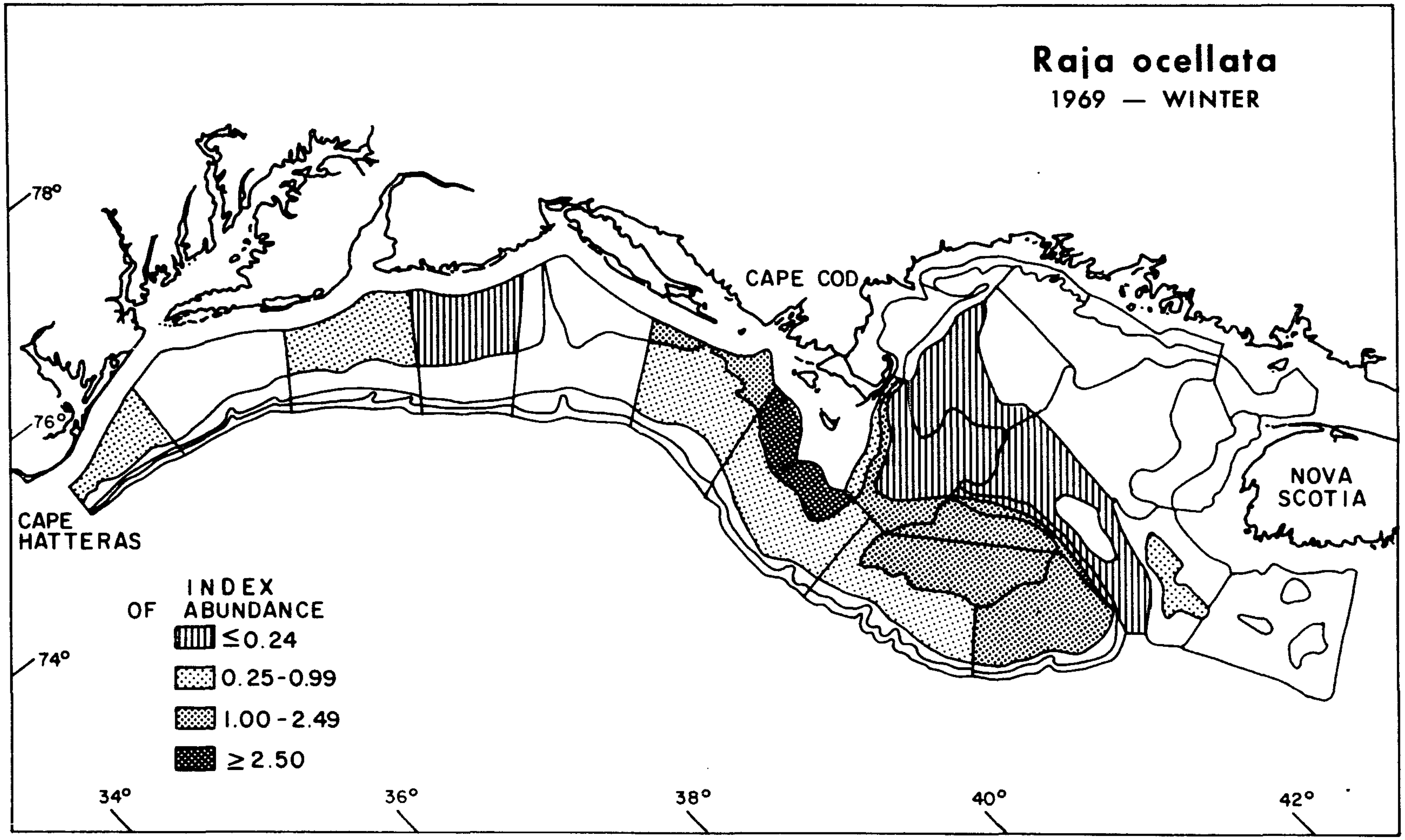
Along the inshore fringe of its range the species moves onshore and offshore with seasonal temperature changes as stated by Bigelow and Schroeder, (1953); Merrimen *et al.* (1953); Fitz and Daiber (1963); Richards (1963); Schaefer (1967); and Tyler (1971a, 1971b). *Raja erinacea* also moves north and 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 (Part I).

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 (Fig. 27, 28, 29). *R. 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 shoaler than 111 m, but it 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. Lawrence it was taken 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

Fig. 27

Index of abundance (geometric mean) of *R. ocellata* captured by sampling strata during the winter, 1969 cruise of the R/V Albatross IV.



Raja ocellata
1969 — WINTER

Fig. 28

Index of abundance (geometric mean) of *R. ocellata* captured by sampling strata during the summer, 1969 cruise of the R/V Albatross IV.

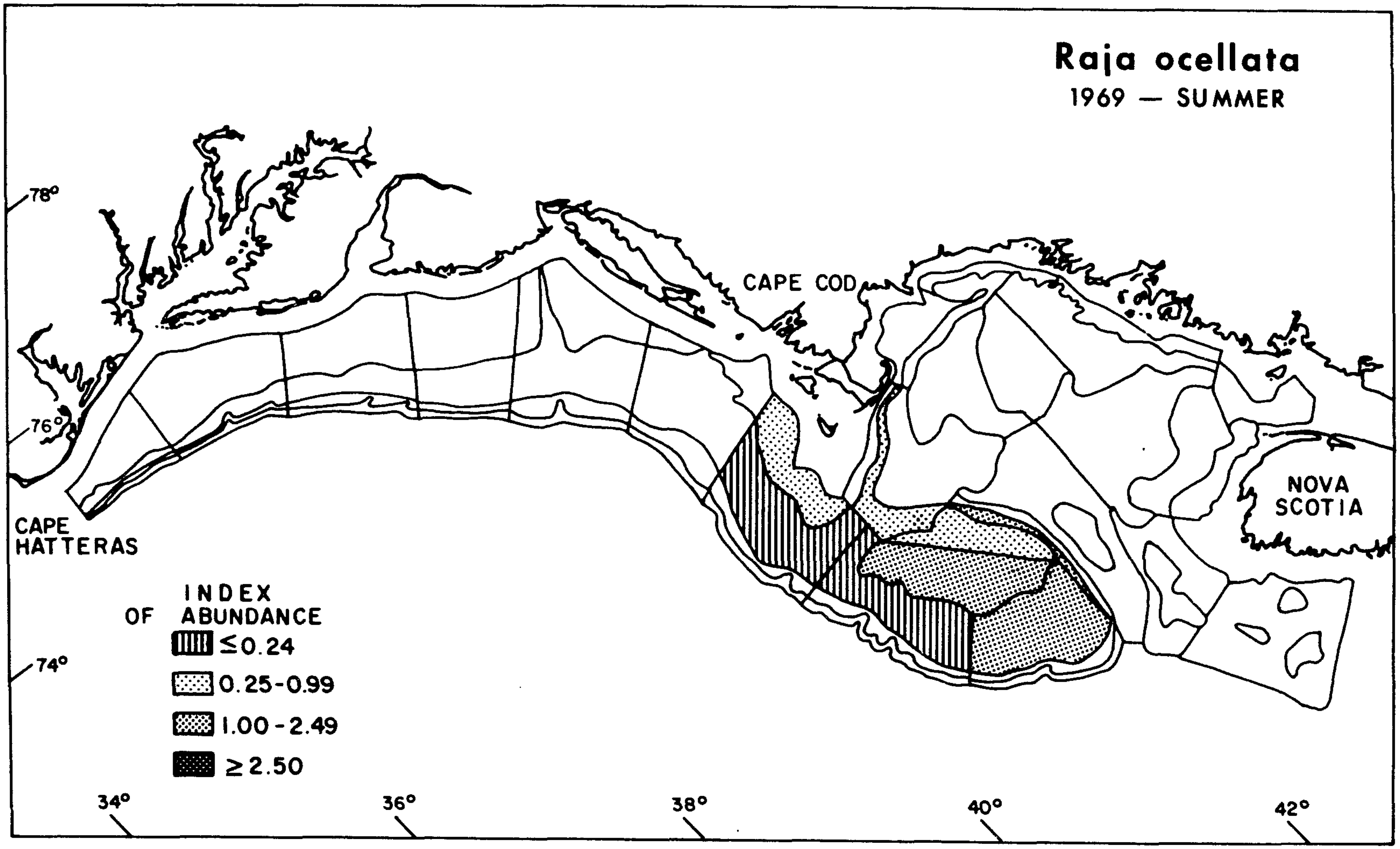

Raja ocellata
1969 — SUMMER

Fig. 29

Index of abundance (geometric mean) of R. *ocellata* captured by sampling strata during the autumn, 1969 cruise of the R/V Albatross IV.

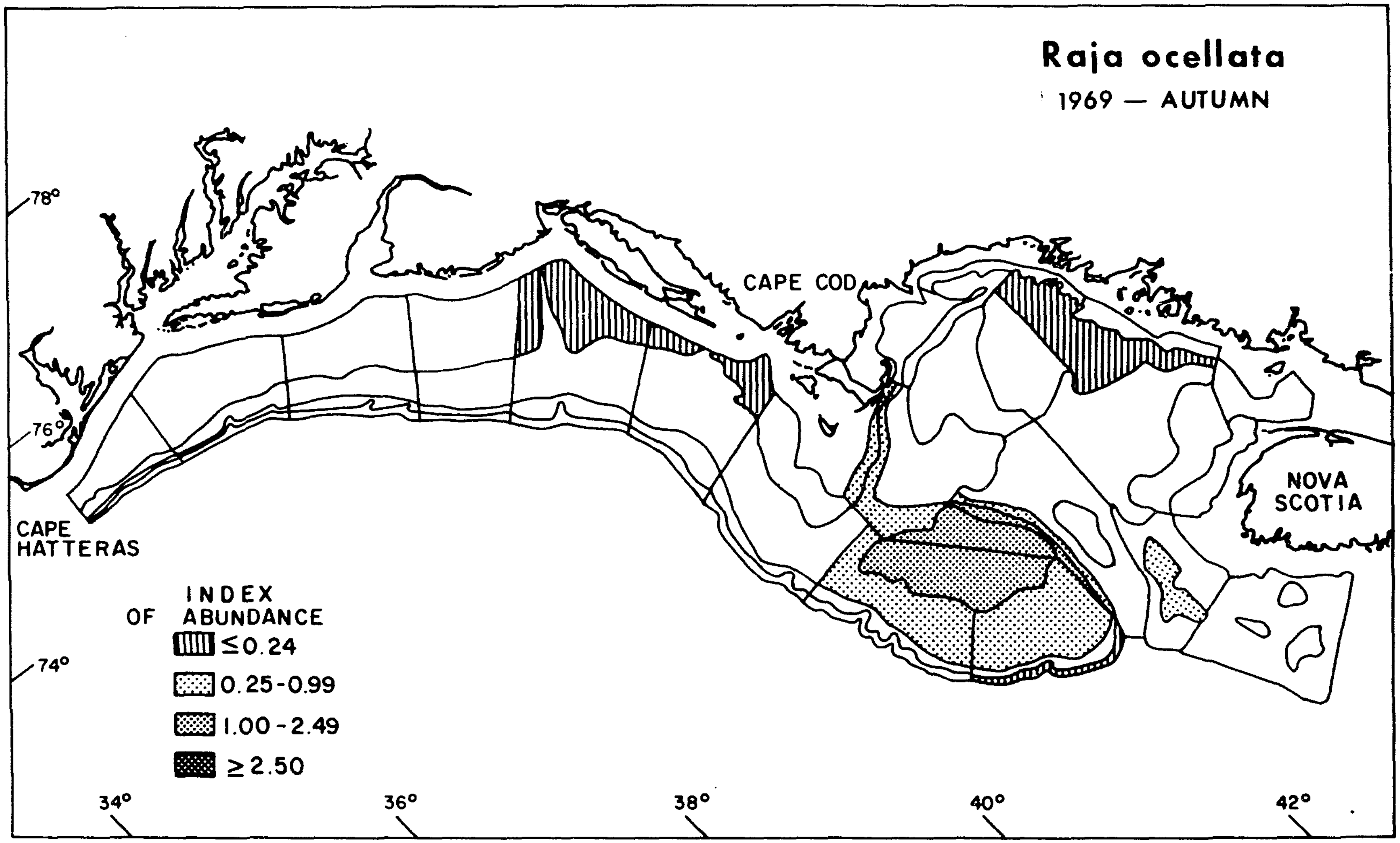

Raja ocellata
1969 — AUTUMN
78°
76°
74°
CAPE COD
NOVA SCOTIA
CAPE HATTERAS
INDEX OF ABUNDANCE
▥ ≤0.24
▒ 0.25-0.99
▒ 1.00-2.49
▓ ≥2.50
34°
36°
38°
40°
42°

Fig. 30

Index of abundance (geometric mean) of *R. ocellata* captured in each subarea during winter, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja ocellata
WINTER 1969

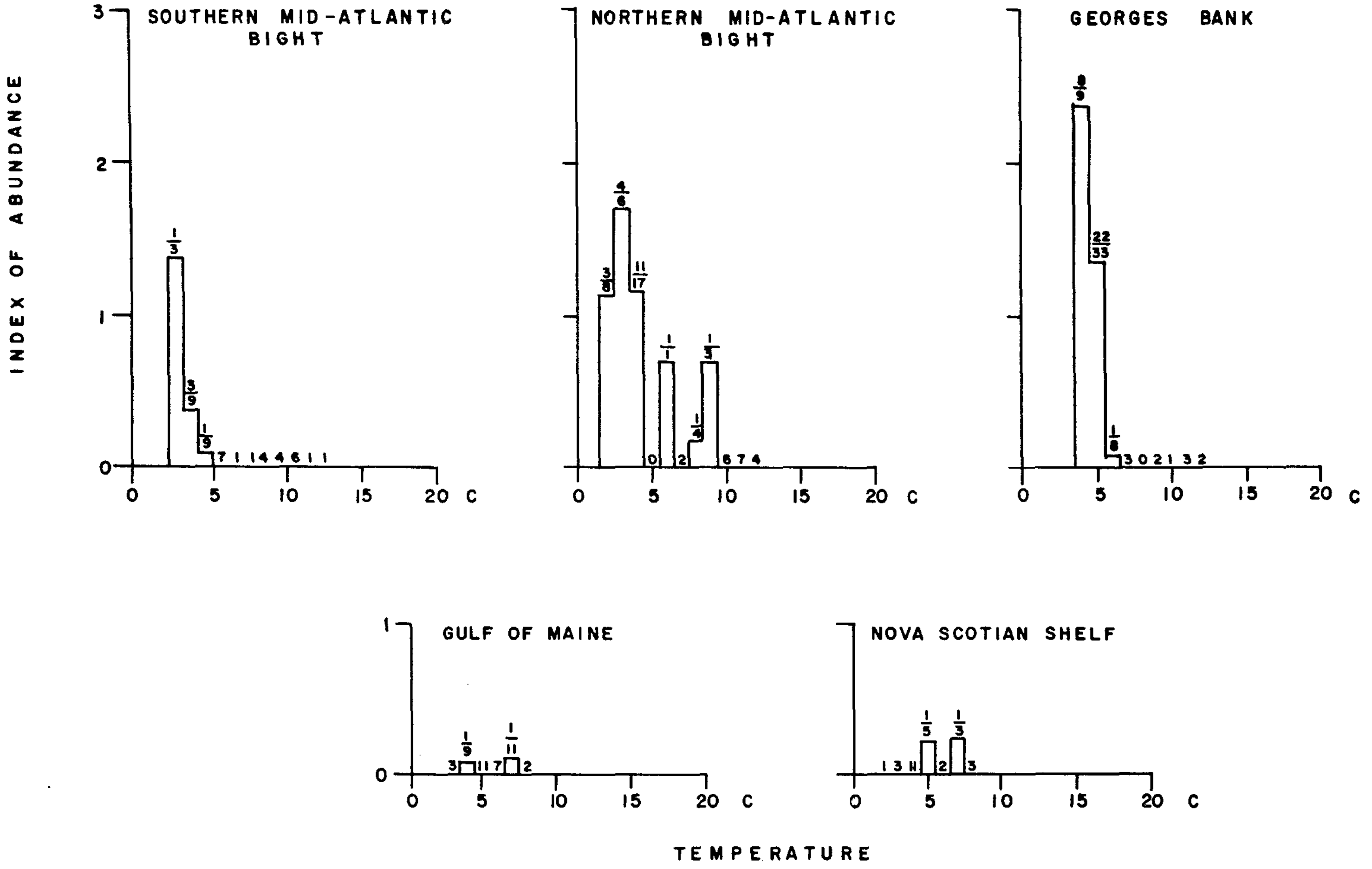


Fig. 31

Index of abundance (geometric mean) of *R. ocellata* captured in each subarea during summer, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja ocellata
SUMMER 1969

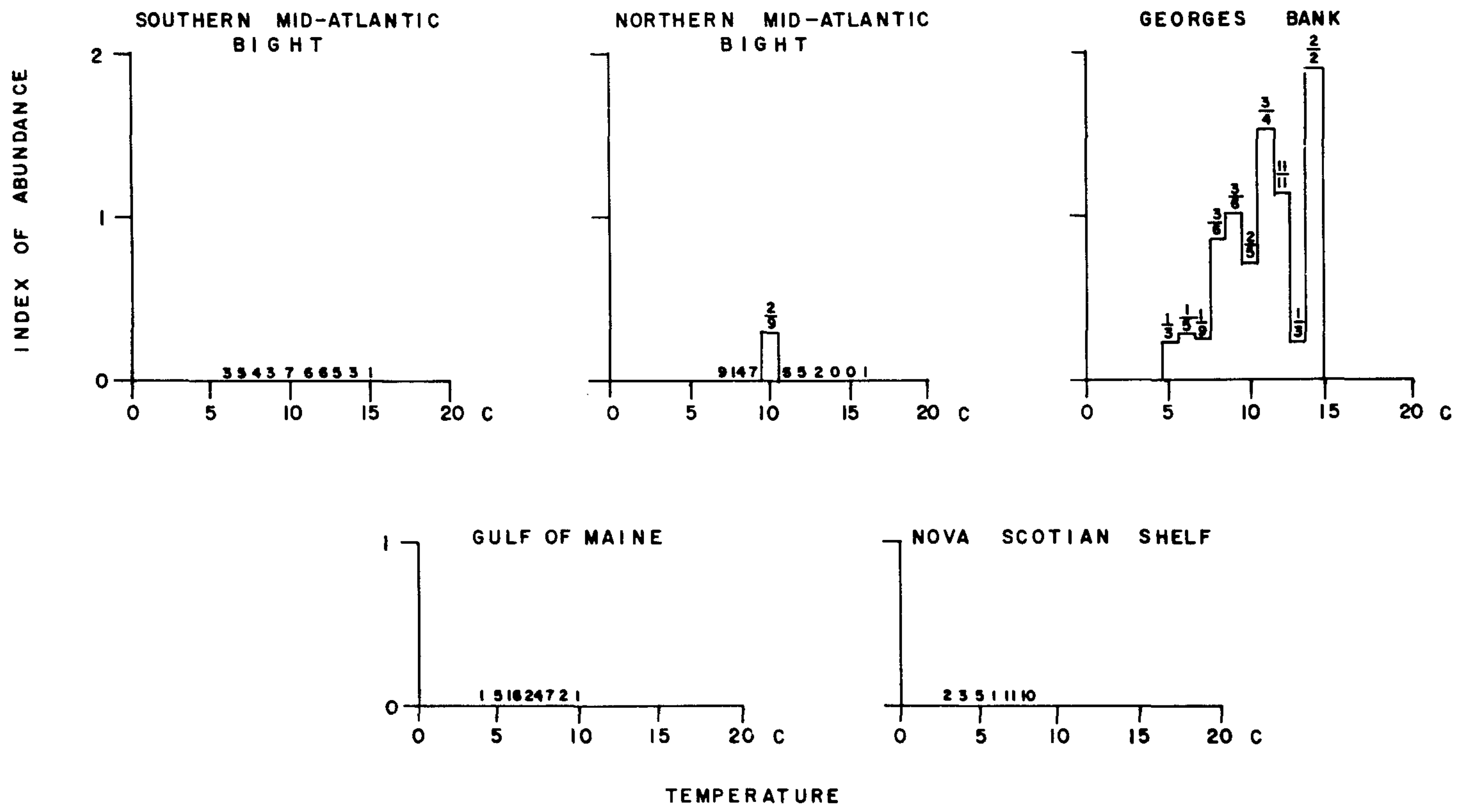
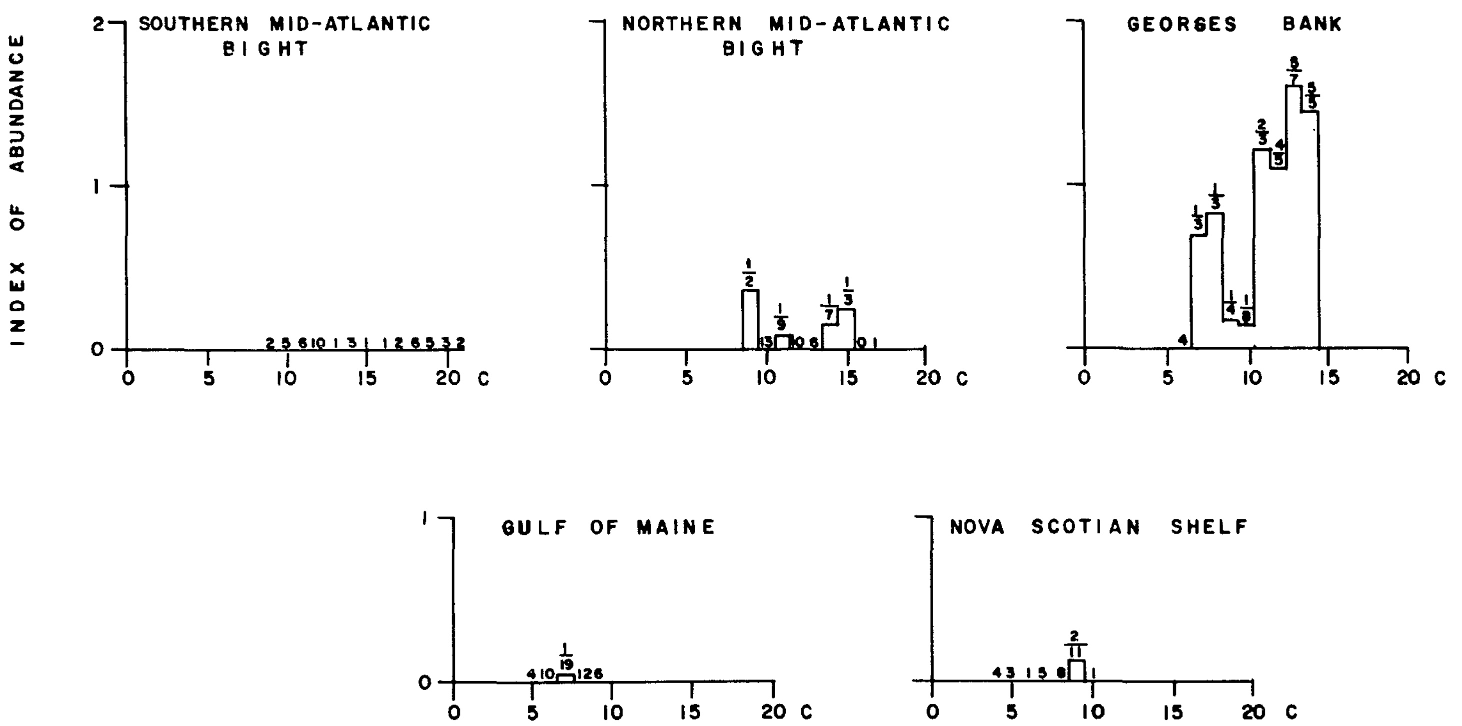


Fig. 32

Index of abundance (geometric mean) of *R. ocellata* captured in each subarea during autumn, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja ocellata
AUTUMN 1969



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 (Tyler, 1971a) 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 (Fig. 30, 31, 32). 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*.

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 (Fig. 33, 34, 35). No seasonal trends in its abundance were noted. Depth of capture ranged from 31 to 413 m but it was most abundant below 110 m. Bigelow and Schroeder (1953)

Fig. 33

Index of abundance (geometric mean) *R. senta* captured by sampling strata during the winter, 1969 cruise of the R/V Albatross IV.

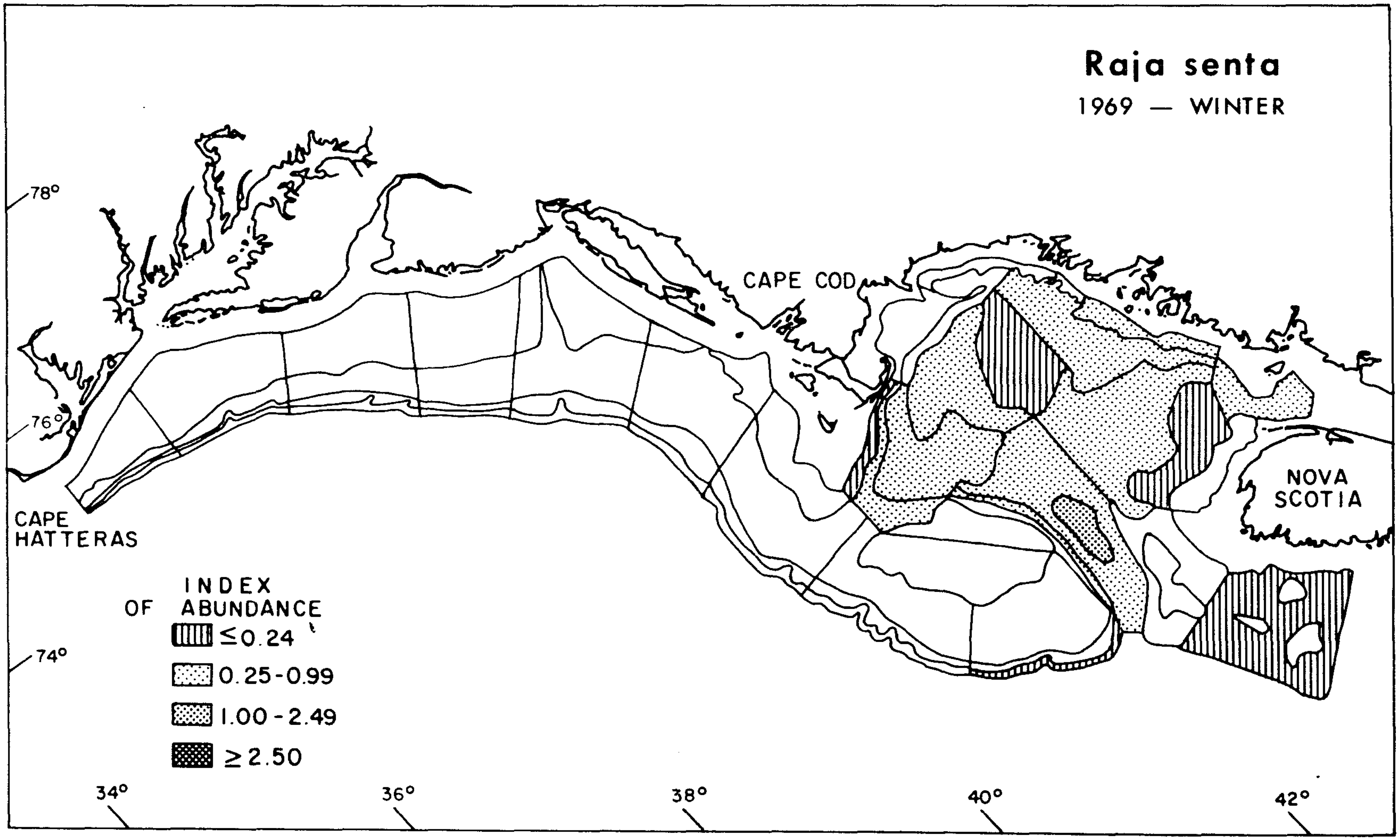
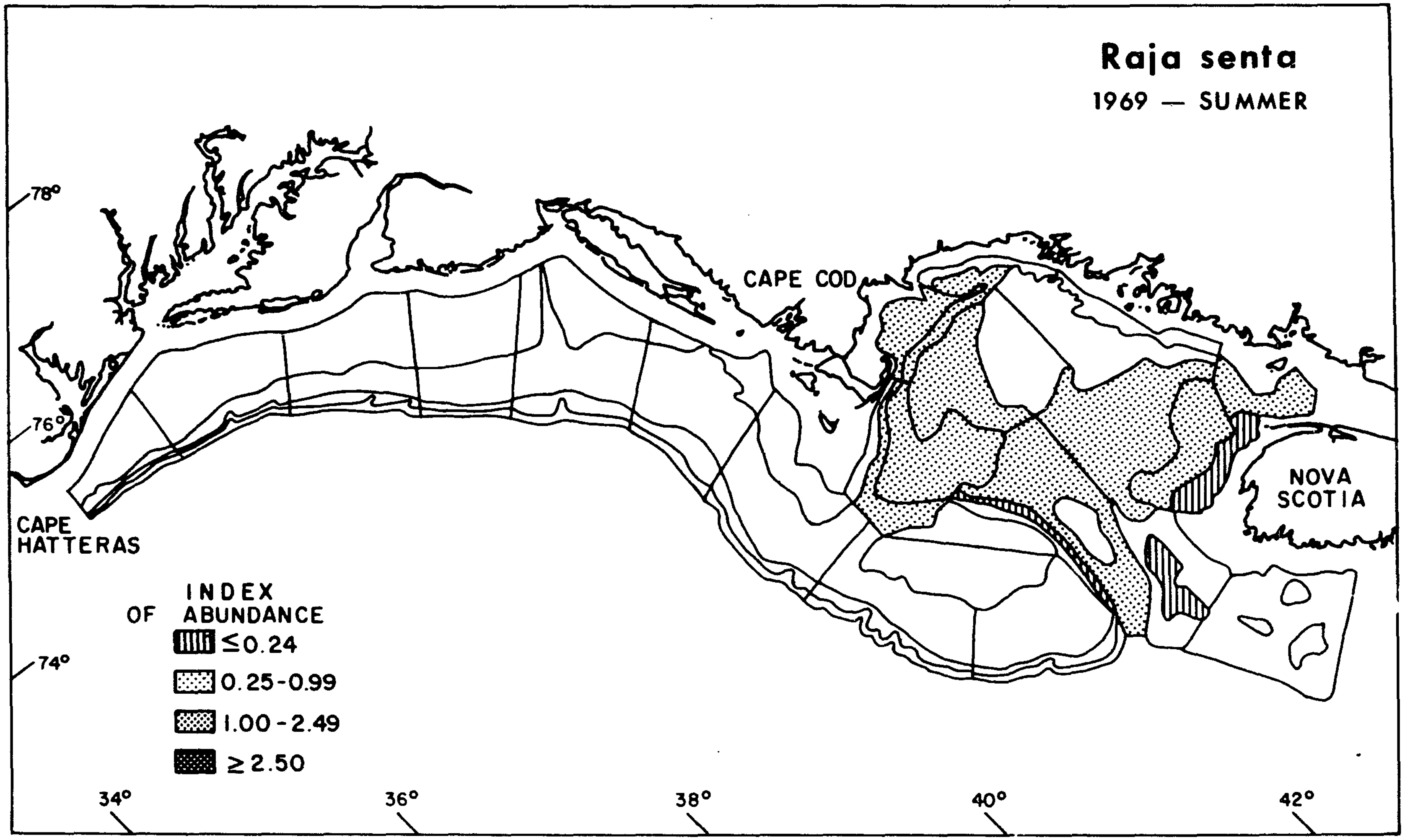

Raja senta
1969 — WINTER
CAPE COD
NOVA SCOTIA
CAPE HATTERAS
INDEX OF ABUNDANCE
▥ ≤0.24
░ 0.25-0.99
▒ 1.00 - 2.49
▓ ≥2.50
78°
76°
74°
34°
36°
38°
40°
42°

Fig. 34

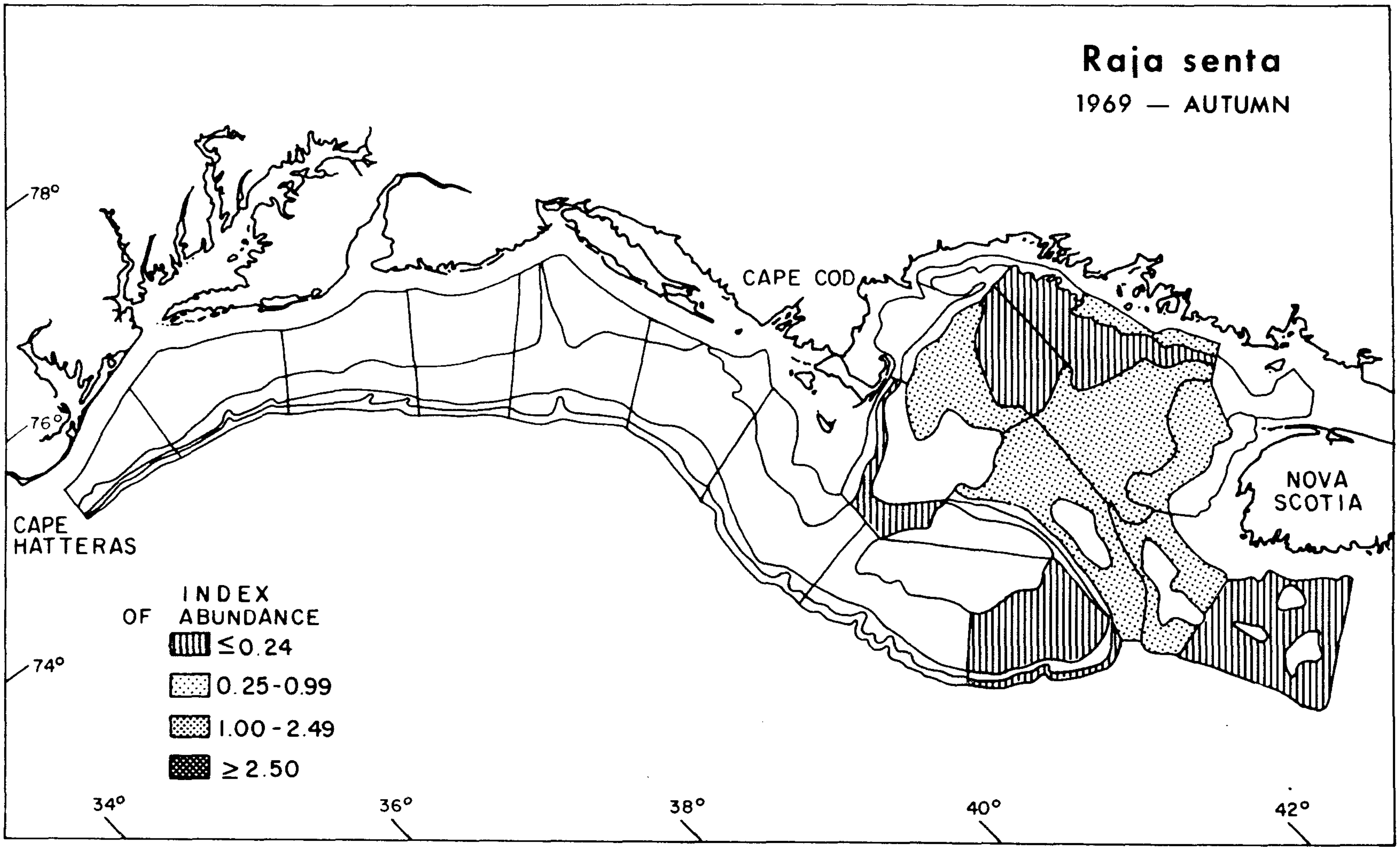
Index of abundance (geometric mean) of *R. senta* captured by sampling strata during the summer, 1969 cruise of the R/V Albatross IV.



Raja senta
1969 — SUMMER
78°
76°
74°
CAPE HATTERAS
CAPE COD
NOVA SCOTIA
INDEX OF ABUNDANCE
▥ ≤0.24
░ 0.25-0.99
▒ 1.00-2.49
▓ ≥2.50
34°
36°
38°
40°
42°

Fig. 35

Index of abundance (geometric mean) of *R. senta* captured by sampling strata during the autumn, 1969 cruise of the R/V Albatross IV.



Raja senta

1969 — AUTUMN

Fig. 36

Index of abundance (geometric mean) of R. *senta* captured in each subarea during winter, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja senta
WINTER 1969

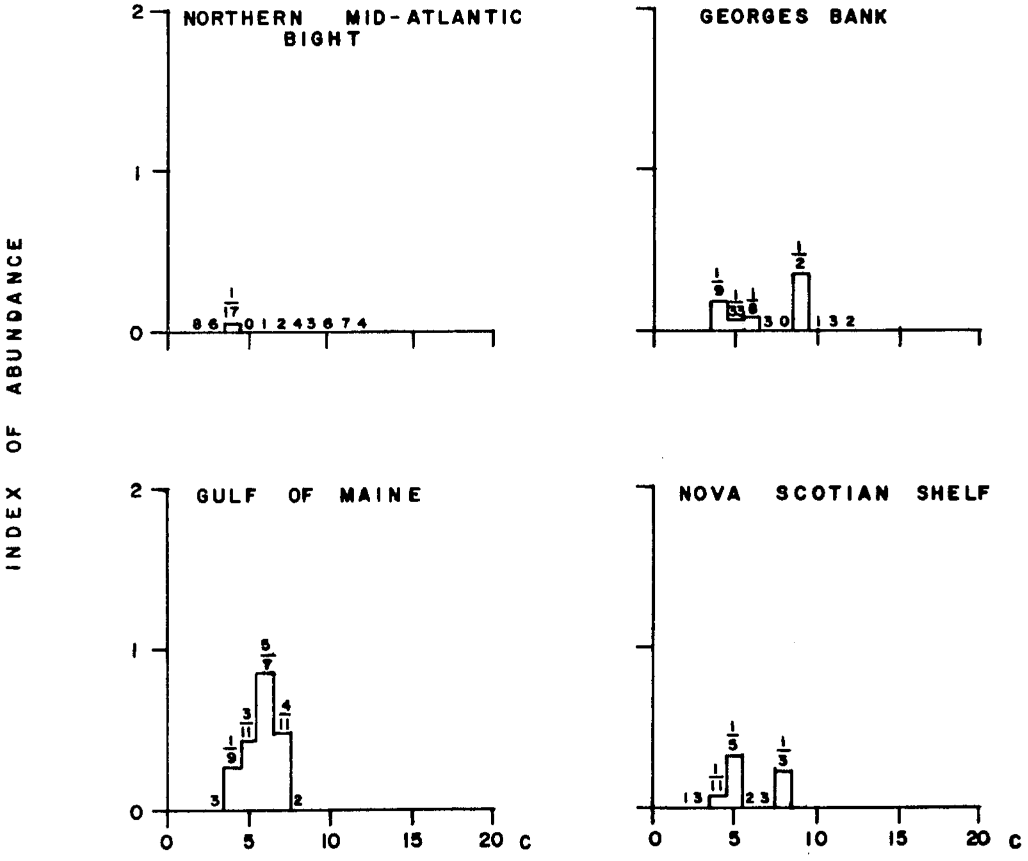


Fig. 37

Index of abundance (geometric mean) of *R. senta* captured in each subarea during summer, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja senta
SUMMER 1969

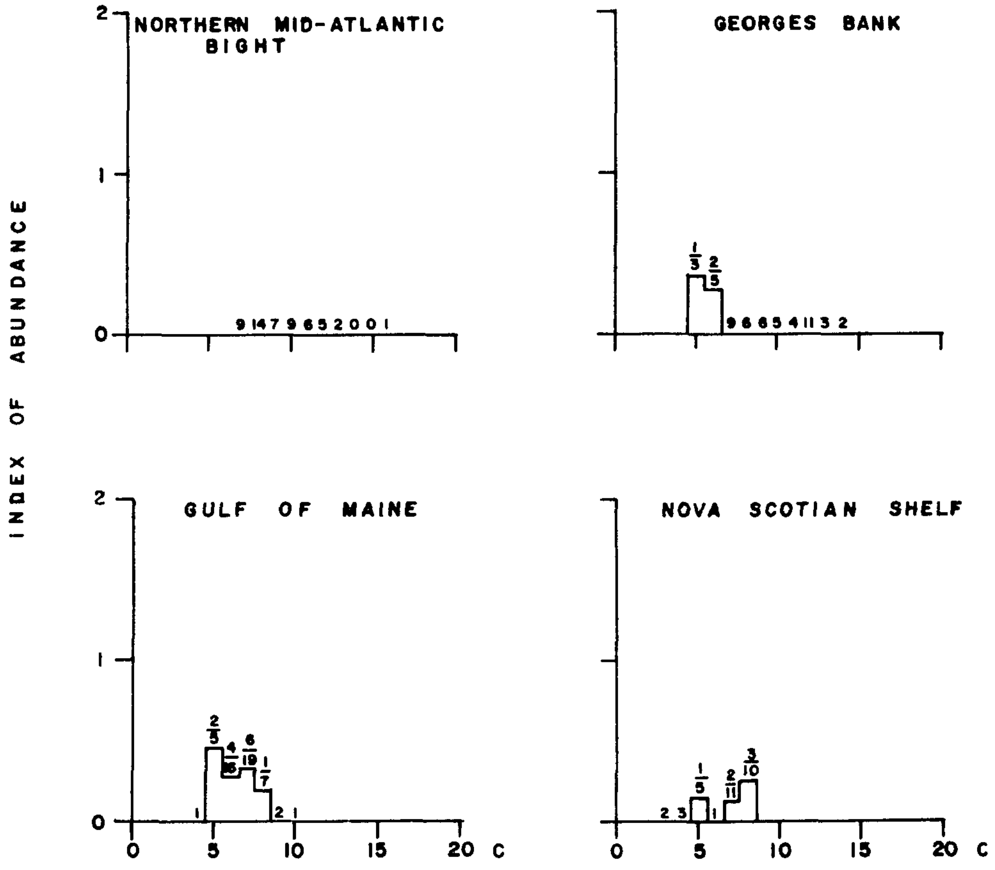
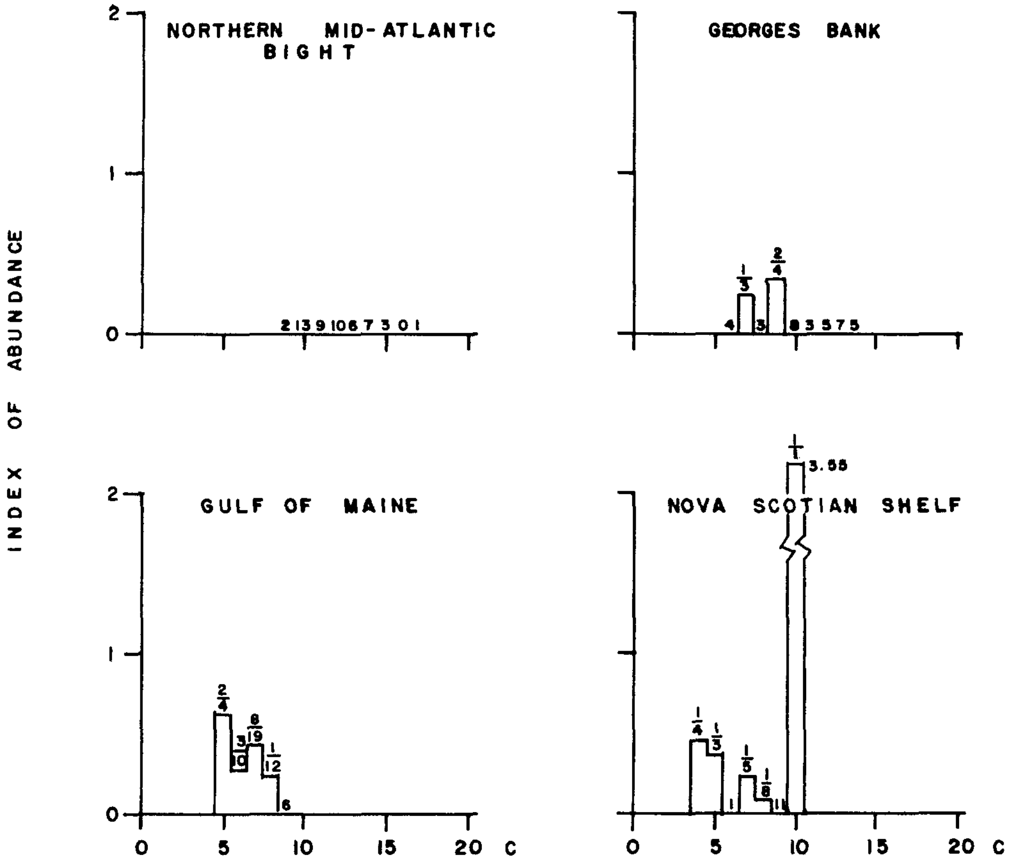


Fig. 38

Index of abundance (geometric mean) of *R. senta* captured in each subarea during autumn, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja senta

AUTUMN 1969



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 is occasionally caught at temperatures less than 2 C, which Bigelow and Schroeder (1953) stated is 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 (Fig. 36, 37, 38). It is found only at the lower part of the temperature range on Georges Bank.

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 (Fig. 39, 40, 41). *R. 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 extends northward from the Gulf of Maine probably as far as the Gulf of St. Lawrence. It was found almost over the entire

Fig. 39

Index of abundance (geometric mean) of *R. radiata* captured by sampling strata during the winter, 1969 cruise of the R/V Albatross IV.

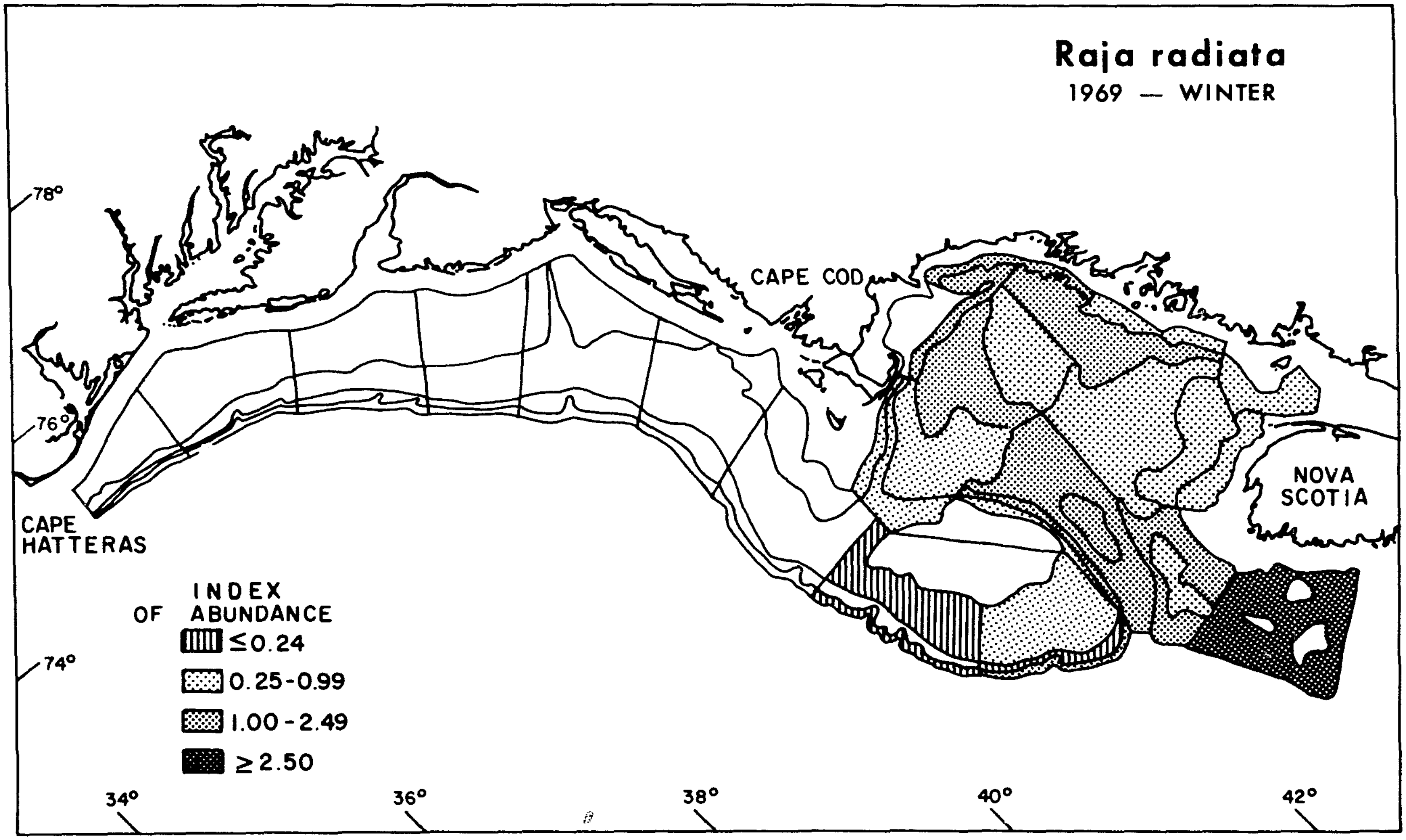

Raja radiata
1969 — WINTER
CAPE COD
NOVA SCOTIA
CAPE HATTERAS
78°
76°
74°
34°
36°
38°
40°
42°
INDEX OF ABUNDANCE
▥ ≤0.24
░ 0.25-0.99
▒ 1.00-2.49
▓ ≥2.50

Fig. 40

Index of abundance (geometric mean) of R. *radiata* captured by sampling strata during the summer, 1969 cruise of the R/V Albatross IV.

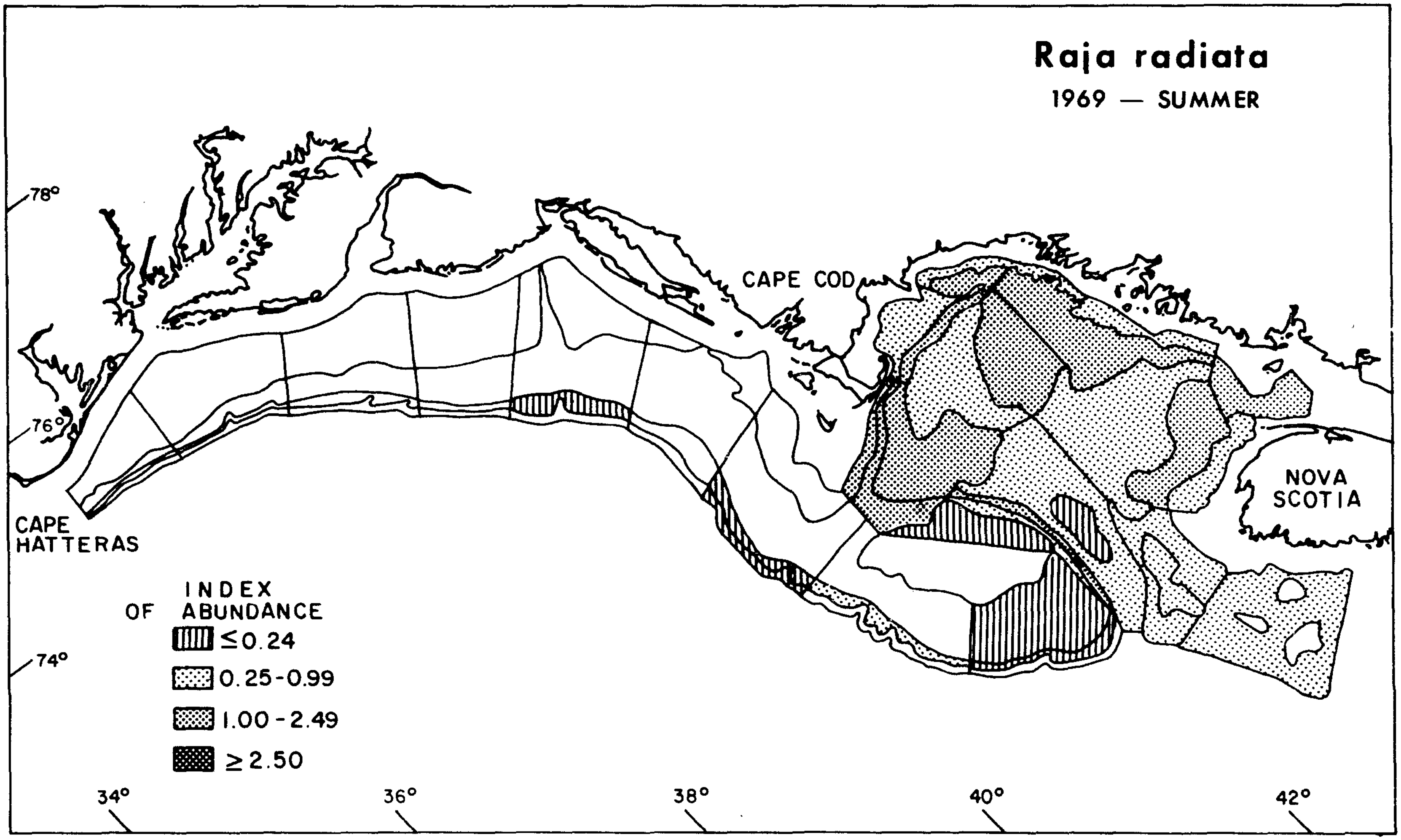
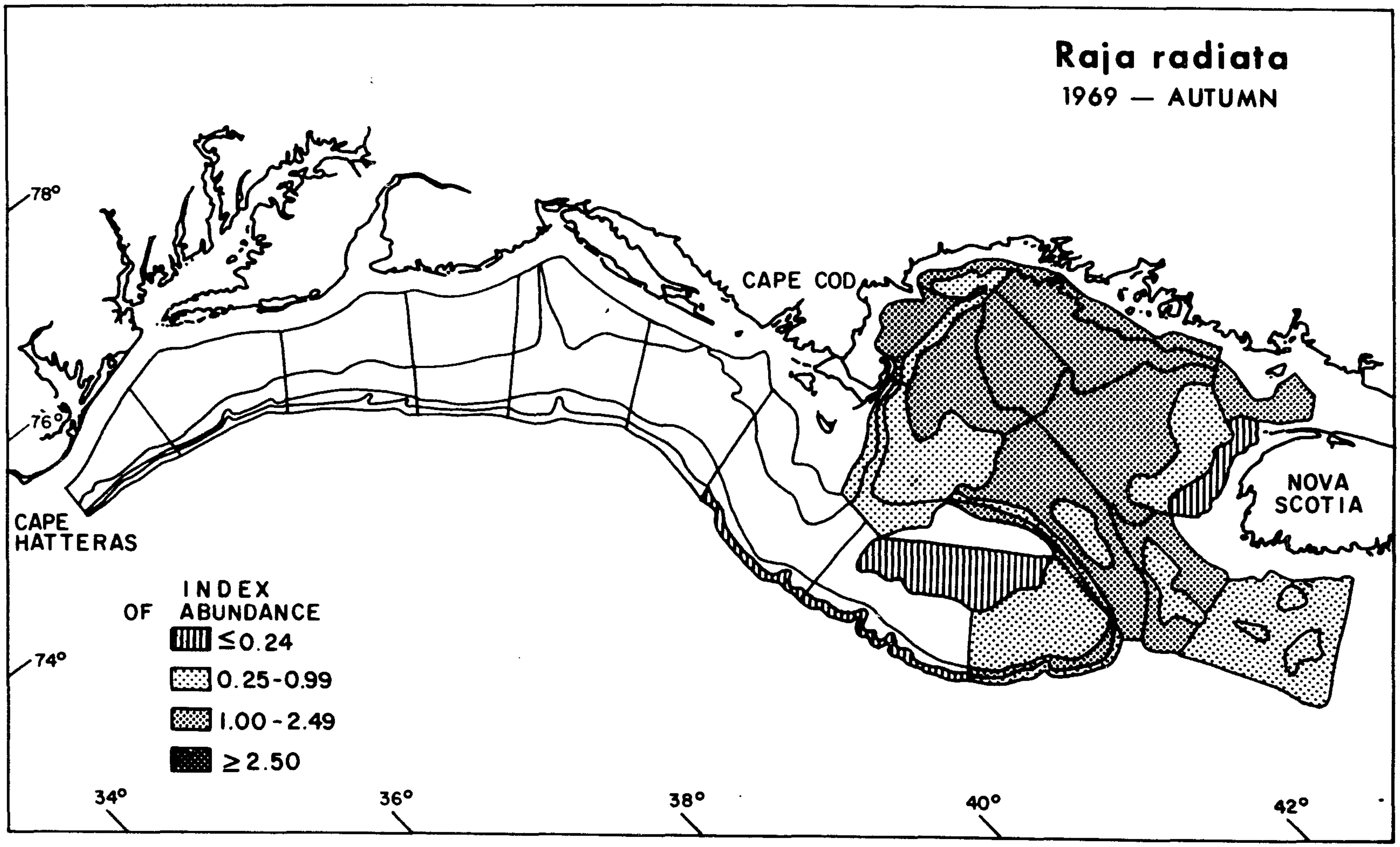

Raja radiata
1969 — SUMMER
78°
76°
74°
CAPE COD
NOVA SCOTIA
CAPE HATTERAS
INDEX OF ABUNDANCE
▥ ≤0.24
░ 0.25-0.99
▒ 1.00-2.49
▓ ≥2.50
34°
36°
38°
40°
42°

Fig. 41

Index of abundance (geometric mean) of *R. radiata* captured by sampling strata during the autumn, 1969 cruise of the R/V Albatross IV.



Raja radiata

1969 — AUTUMN

Fig. 42

Index of abundance (geometric mean) of R. *radiata* captured in each subarea during winter, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja radiata

WINTER 1969

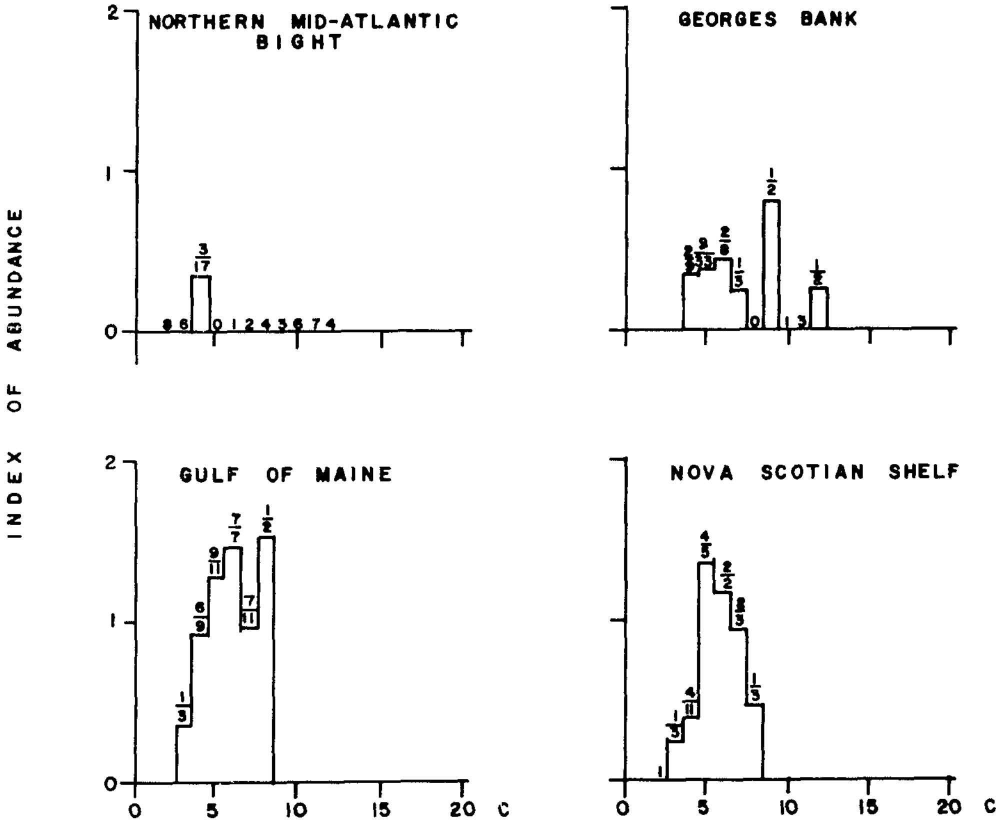


Fig. 43

Index of abundance (geometric mean) of R. *radiata* captured in each subarea during summer, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja radiata
SUMMER 1969

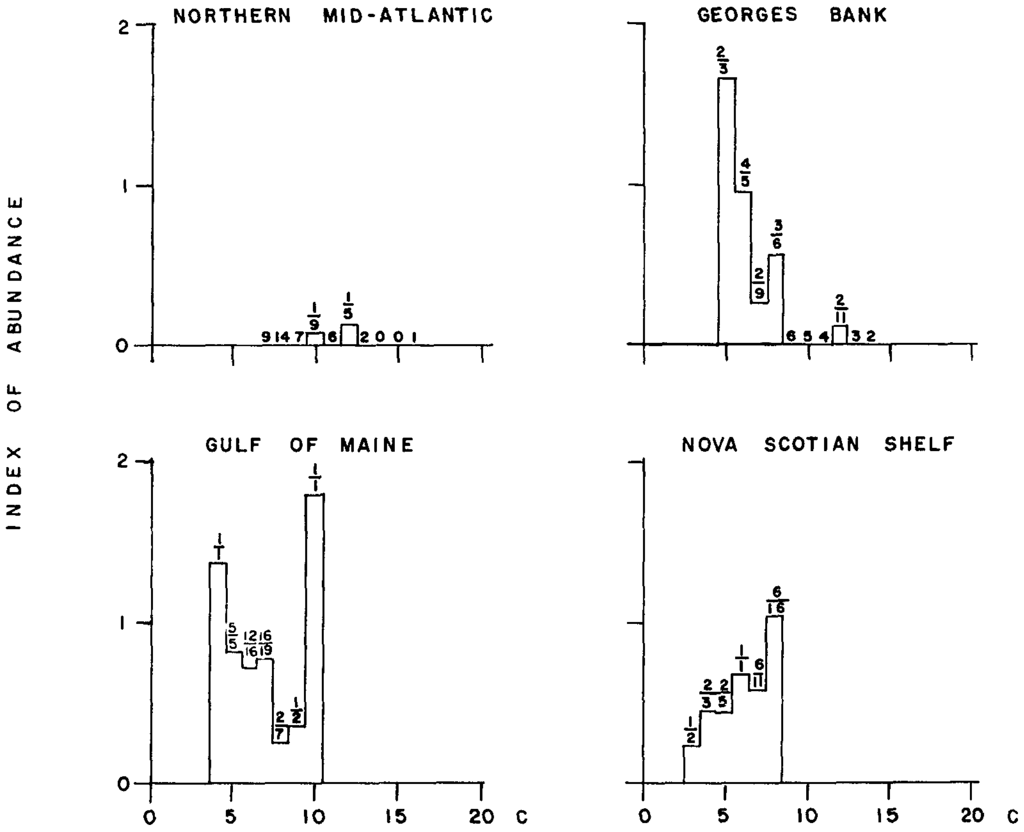
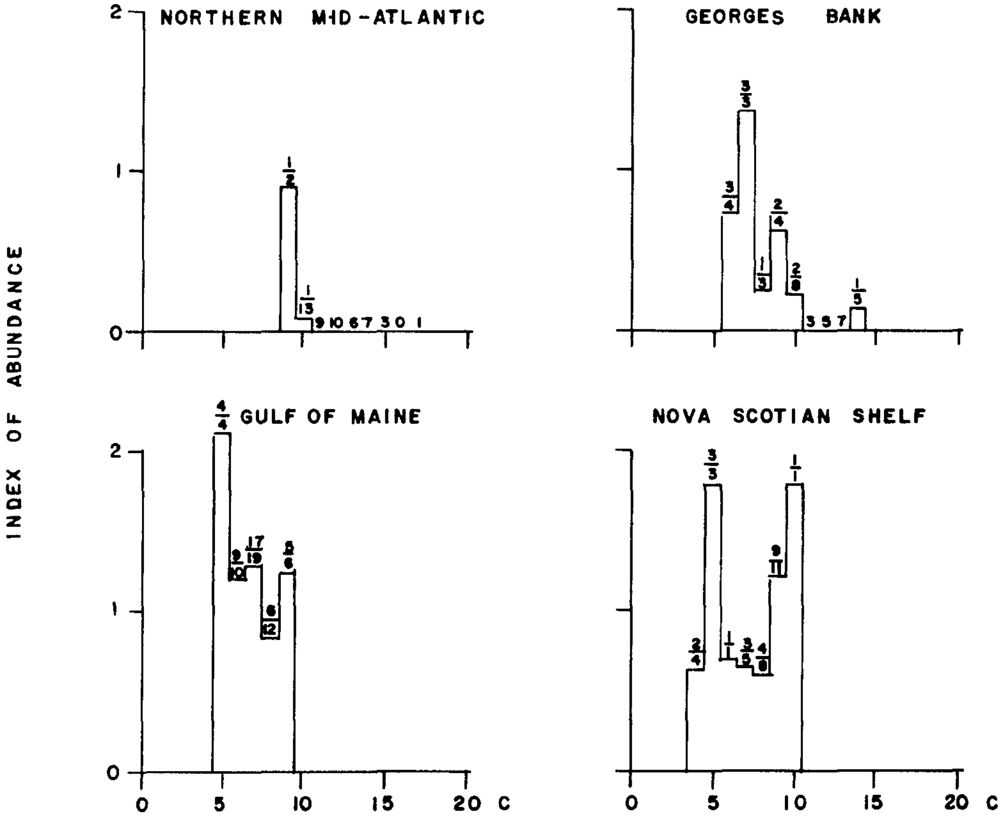


Fig. 44

Index of abundance (geometric mean) of *R. radiata* captured in each subarea during autumn, 1969 within temperature intervals of one degree C. 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 at each degree C. Whole numbers represent the number of stations at temperatures at which no specimens were captured.

Raja radiata
AUTUMN 1969



temperature range in the Gulf of Maine and off southeastern Nova Scotia. (Fig. 42, 43, 44)

Interspecific Relationships:

Five of the species co-occurred significantly with one or more of the other species (Table 2). R. *laevis* was associated with both R. *erinacea* and R. *ocellata* for one half or more of the Albatross IV cruises. R. *erinacea* and R. *ocellata* were positively associated during all of the survey cruises. R. *senta* and R. *radiata* had the highest coefficient of association and these two species were often negatively associated with R. *erinacea* and R. *ocellata*. R. *erinacea* and R. *ocellata* were also 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. R. *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 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 predominately found in the areas covered with sand or gravel (Uchupi, 1963) at depths less than 111 m. They have similar responses to seasonal temperature changes. In the southern periphery of their ranges they move southward during

TABLE 2

COEFFICIENTS OF INTERSPECIFIC ASSOCIATION FOR *R. OCELLATA*, *R. ERINACEA*, *R. SENTA*, *R. RADIATA*, AND *R. LAEVIS*

Cruise 67-21				
Species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
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				
Species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
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				
Species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
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				
Species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
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				
Species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
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

TABLE 2 (Continued)

Cruise 69-11

Species	R. *ocellata*	R. *erinacea*	R. *senta*	R. *radiata*
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

	R. *ocellata*	R. *erinacea*	R. *senta*	R. *radiata*
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

	R. *ocellata*	R. *erinacea*	R. *senta*	R. *radiata*
R. *erinacea*	0.41**	-	-	-
R. *senta*	-0.82**	-0.84	-	-
R. *radiata*	-0.61**	-0.44	0.80**	-
R. *laevis*	0.01	0.01	0.10	0.51

---

* Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

the colder months of the year and off shore and northward during the warmer months of the year. Within their centers of abundance neither species undergo seasonal migrations, each of the species is able to tolerate the seasonal temperature extremes. *R. ocellata* appears to have slightly lower temperature preferences, 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 stratum (27 to 55 m) which is covered with sand, gravel, and rock (Uchupi, 1963) 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.

Raja laevis is found in the same areas as the above species pair but has wider substratum and depth preferences. The lack of habitat specialization of *R. laevis* may account for its low abundance.

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 covered with sandy silt to silt and clay (Uchupi, 1963). 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. *R. radiata* appears to have a wider temperature range and the lower temperature preference and 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.

CONCLUSIONS

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, Florida. North of Cape Hatteras it is found in 37 to 366 m at 6 to 17 C and south of Cape Hatteras 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 at least North Carolina. It is found from shore to 375 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 shoaler 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 shoaler 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 Laborador, West Greenland, Hudson Bay, Grand Banks, and Gulf of St. Lawrence to South Carolina. It occurs from 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. *R. ocellata* has slightly lower temperature preferences than *R. erinacea* and occurs farther to the north than the latter. *R. senta* and *R. radiata* are sympatric species, *R. radiata* has a wider temperature range and is more widespread than *R. senta*.

PART III

FOOD HABITS OF THE SYMPATRIC SPECIES PAIRS (*RAJA ERINACEA-R. OCELLATA* AND *R. RADIATA-R. SENTA*)

INTRODUCTION

This section compares the food habits of the two sympatric species pairs of skates. One pair, *R. erinacea* and *R. ocellata* are sibling species (Part I). The other pair, *R. radiata* and *R. senta*, though morphologically quite different co-occur in the same habitats and have similar ranges. The distributions of the species pairs are complementary (Part II).

The food habits of these species have been studied (Smith, 1950; Bigelow and Schroeder, 1953; Fitz and Daiber, 1963; Richards, 1963; Richards, *et al.*, 1963; Tyler, 1968, 1972) but each study was limited to a small area in the total geographical ranges of the species and gave little insight into the competitive interaction within the species pairs.

In the present study food habits were compared over large portions of the ranges of all species. Also, some *R. erinacea* and *R. radiata* were obtained from areas where the other member of the respective species pair was rare which might reveal whether *R. ocellata* was excluding *R. erinacea* and *R. senta* was excluding *R. radiata*. Unfortunately *R. ocellata* and *R. senta* from areas where the other member of the respective species pair was rare were unavailable so that the reciprocal effect of modification could not be studied (Nilsson, 1967).

MATERIALS AND METHODS

A total of 1637 stomachs were collected for this study during four cruises aboard the R/V Albatross IV (Part II) (Table 3). Stomachs were usually taken from all of the individuals of a species captured at a station, but individuals were randomly selected when many were captured. Efforts were made to obtain stomachs from all periods of the day and from as large a geographical area as possible. The anterior and posterior section of each stomach were tied off prior to removing it from the fish to prevent loss of contents, each stomach was individually wrapped with pertinent data in cheese cloth, preserved in 10% buffered formalin, and stored in 40% isopropyl alcohol after soaking in water.

The contents of each stomach were sorted to species or species group, when possible, and the number and displacement volume of each taxon were recorded. All organisms of a taxon were placed in a calibrated vial filled to the calibration mark with a self-leveling burette. The volume was obtained by subtracting the amount of water used to fill the vial to the calibration mark from the volume to which the vial was calibrated. For small organisms, i.e. amphipods, cumaceans, and mysids one volume was obtained for major taxon. A separate volume was obtained for each species or species group of the large organisms.

Data Analysis:

Food habits were determined for each species of skate per cruise for the entire survey area and for subareas (mid-Atlantic Bight,

TABLE 3

NUMBER OF FISH OF EACH SPECIES EXAMINED IN THE FOOD STUDY IN EACH OF THE SUBAREAS PER CRUISE. TOTAL LENGTH RANGE OF FISH IS IN PARENTHESIS

Cruise 69-02	Mid-Atlantic Bight		Georges Bank		Gulf of Maine		Nova Scotian Shelf	
R. *erinacea*	35	(11-50)	109	(10-52)	3	(34-47)	1	(47)
R. *ocellata*	21	(15-88)	94	(12-98)	-	-	3	(86-93)
R. *radiata*	8	(26-52)	24	(35-95)	45	(18-108)	21	(25-89)
R. *senta*	-	-	9	(44-63)	37	(24-60)	1	(34)
69-08								
R. *erinacea*	40	(12-53)	57	(11-63)	-	-	-	-
R. *ocellata*	6	(39-88)	89	(14-99)	-	-	-	-
R. *radiata*	-	-	-	-	-	-	-	-
R. *senta*	-	-	-	-	-	-	-	-
69-11								
R. *erinacea*	131	(9-53)	180	(10-54)	5	(24-47)	34	(20-59)
R. *ocellata*	9	(56-88)	114	(22-86)	1	(67)	2	(86-97)
R. *radiata*	2	(14-78)	47	(25-93)	112	(14-117)	54	(12-93)
R. *senta*	-	-	3	(36-62)	34	(12-65)	23	(16-60)
70-03								
R. *erinacea*	46	(10-21)	127	(10-53)	1	(53)	16	(34-64)
R. *ocellata*	4	(57-88)	87	(15-91)	2	(59-62)	9	(67-114)
R. *radiata*	-	-	-	-	-	-	-	-
R. *senta*	-	-	-	-	-	-	-	-

Georges Bank, Gulf of Maine, and Nova Scotian shelf) at a higher taxonomic level (order or class) and at a lower taxonomic level (species or species group). The higher taxonomic level included gastropods, bivalves, cephalopods, polychaetes, cumaceans, isopods, amphipods, mysids, euphausids, decapods, and fishes. The relative importance of each of these categories to the predator species was determined by computing the index of relative importance (Pinkas *et al.*, 1971).

$$(N+V)\ F = IRI$$

Where N = Numerical percentage

V = Volumetric percentage

F = Frequency of occurrence percentage

IRI = Index of relative importance

Stomach data from each cruise for each skate were divided into four time periods based on the hour of collection: 0-0559, 0600-1159, 1200-1759, 1800-2358. The arithmetic mean number and volume of food organisms was computed in each time period and the percent comprised by each higher taxon was computed to examine feeding periodicity. Tyler's (1969) test for relating heterogeneities to predator size was used to determine if the skates changed their diets as they grew. The stomach data for each cruise were stratified into 10 cm increments of predator length and the mean number and volume of food organisms and percent comprised by each higher taxon were computed for each increment and compared with the results of the heterogeneity test. H' diversity (Shannon and Weaver, 1949) was computed for the assemblage of prey species of each predator species within each of the subareas per cruise. Dominance affinities were computed (Sanders, 1960) between the diets of each species within a sympatric pair using higher taxonomic categories, all subareas combined, and lower taxonomic categories, within subareas.

RESULTS AND DISCUSSION

The number of stomachs from each subarea varied depending on sampling intensity and species abundance. Only the northern most section of the mid-Atlantic Bight was sampled during cruises 69-02 and 70-03 and the Gulf of Maine and the Nova Scotian shelf were not sampled during cruise 69-08 (Table 3). Stomach samples of *R. radiata* and *R. senta* were examined only from cruises 69-02 and 69-11.

Raja erinacea:

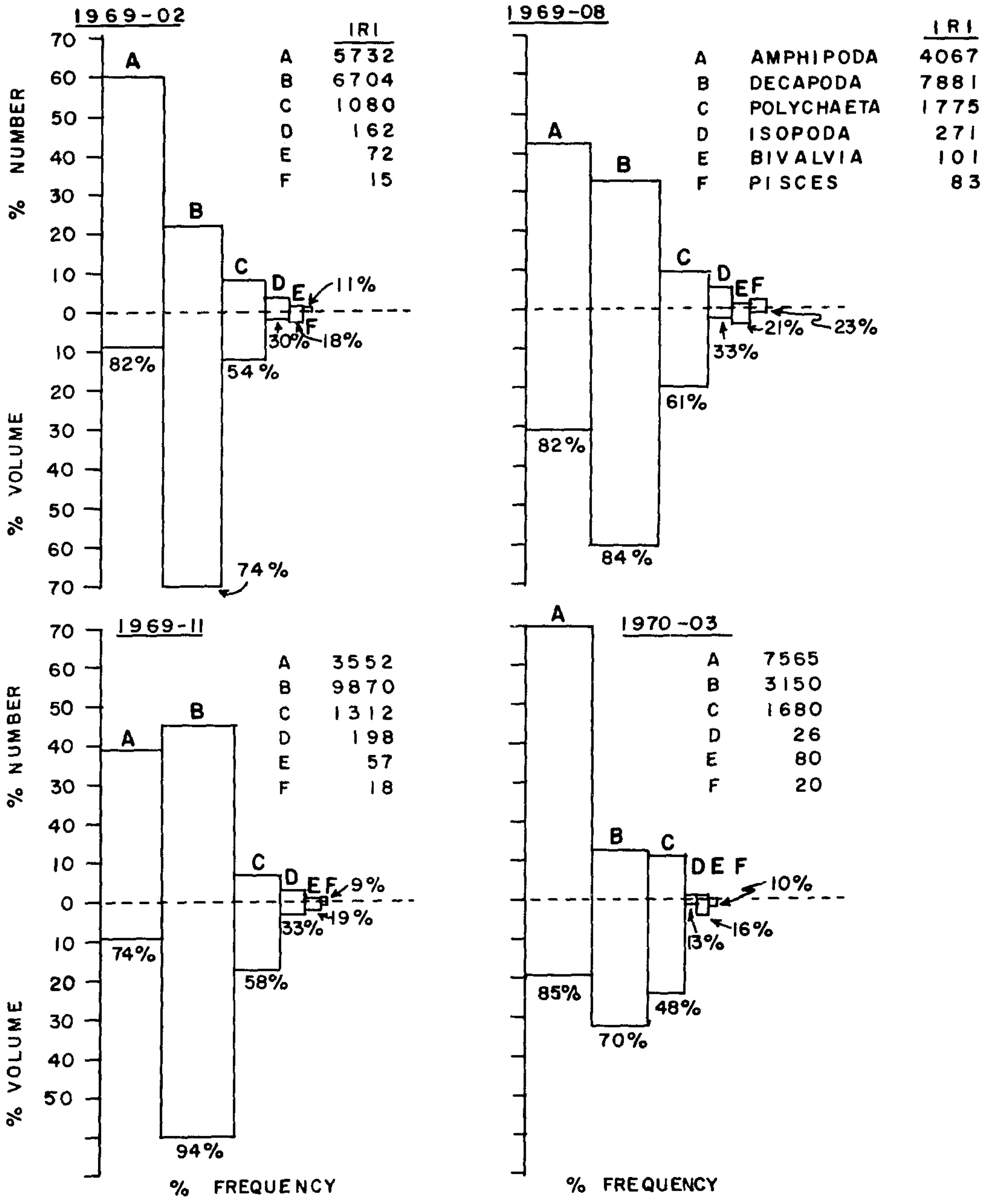
Decapod crustaceans and amphipods had the highest index of relative importance (IRI) for *R. erinacea*. Decapods comprised the largest volume and amphipods were third in volume and first in numerical abundance (Fig. 45). Polychaetes had the third highest IRI and made up the second greatest volume of food organisms. Isopods, bivales, and fishes were of minor importance.

There were no apparent differences in the relative numbers of the high taxonomic categories consumed among the subareas, however, there were differences in the species eaten. *Crangon septemspinosa*, *Pagurus acadianus*, *Cancer irrorata*, and *Dichelopandalus leptocerus* were the most frequently eaten decapods in the mid-Atlantic Bight and on Georges Bank. *C. septemspinosa* was the most numerous while *P.*

Fig. 45

Percent composition of food by high taxonomic groups in number, volume, and frequency of occurrence for *R. erinacea* during each of the seasonal surveys. The numbers within the rectangles are the indices of relative importance.

Raja erinacea



acadianus and *C. irrorata* accounted for most of the volume of decapods. In the Gulf of Maine and on the Nova Scotian shelf *Pagurus pubescens*, *Crangon septemspinosa*, *Hyas* sp., and *Eualus pusiolus* were the most frequently eaten decapods. *Monoculodes* sp., *Unciola* sp., *Leptocheirus pinguis*, ampeliscids, haustoriids, and *Dulichia monacantha* were the most frequently consumed amphipods in the mid-Atlantic Bight and on Georges Bank. *L. pinguis* predominated in the mid-Atlantic Bight and *Monoculodes* sp. and *Uniciola* predominated in the Georges Bank samples. Haustoriids were found in relatively few stomachs but when present they occurred in large numbers. *Pleustes panopla*, *L. pinguis*, *Hippomedon serratus*, *Monoculodes* sp., and *Unciola* sp. were the most frequently eaten amphipods in the Gulf of Maine and on the Nova Scotian shelf. The major polychaetes consumed on Georges Bank and in the mid-Atlantic Bight were *Nereis* spp., *Nephtys* spp., *Lumbrineris fragilis*, *Aphrodite hastata*, maldanids, (mostly *Clymenella torquata*), *Glycera* spp., and *Pherusa affinis*. The polychaetes *Ophelia denticulata*, *Nothria conchylega*, and *Pectinaria* sp. predominated in stomachs from the Gulf of Maine and the Nova Scotian shelf. *Cirolana polita* and *Chiridotea tuftsi* were the most frequently eaten isopods. The former species accounted for almost the entire volume of isopods. Most of the identifiable bivales were in the family Solenidae. *Ensis directus* was the only species of this family that could be identified. *Solemya* sp. was the only other form recognized. *Limanada ferruginea*, *Leptoclinus maculatus*, and *Myoxocephalus octodecemspinosus* were the most numerous fishes.

Fitz and Daiber (1963) and Smith (1950) found that *R. erinacea* from Delaware Bay and Block Island Sound depended more upon a single prey species than specimens included in this study. *Crangon septemspinosa* made up 74% of the number of food organisms of *R. erinacea* from Delaware Bay and *Leptocheirus pinguis* comprised 52% of the wet weight of the food of *R. erinacea* from Block Island Sound. The difference between the earlier studies and the present study may be attributable to differences in the faunal composition or degree of heterogeneity of the survey areas. The estuarine and inshore areas sampled by the previous authors may have been less diverse faunas and thus offered less variety of prey to *R. erinacea* than the area sampled in the present study. The former studies were limited to small areas each of which may have been occupied by a single community. Each subarea of the present study may have been occupied by several communities. Wigely (1956) found that Georges Bank was inhabited by at least three benthic communities. In either case the food habits of *R. erinacea* are fairly generalized and, to some extent, appear to be adaptable to the availability of prey organisms.

Except for the dependence upon a single prey species the diet of *R. erinacea* from Block Island Sound was similar to that of *R. erinacea* in the present study. *Cancer irrorata*, *Crangon septemspinosa*, nekton, *Upogebia affinis* (a burrowing crab), *Glycera dibranchiata*, *Byblis serrata* (an ampeliscid). *Unicola irrorata*, *Nephtys incisa*, and *Ensis directus* followed *L. pinguis* in abundance in Block Island Sound (Smith, 1950).

H'diversity values for the assemblage of prey species ranged from 1.81 to 4.20 in the present study (Table 4). The highest values were found in samples from Georges Bank and the lowest values from the Gulf of Maine.

Tyler's heterogeneity test revealed that the diet of *R. erinacea* was size dependent. Specimens < 41 cm TL consumed considerably fewer decapods and more amphipods than those ≥ 41 cm TL. With few exceptions all of the decapods eaten by specimens ≤ 30 cm TL were *C. septemspinosa*. Haustoriids and *Dulichia monacantha* were almost exclusively limited to *R. erinacea* ≤ 30 cm TL. Cumaceans and copepods were also limited to the smaller specimens. All sizes fed on fish but the frequency of occurrence increased with size of the predator. Consumption of polychaetes was independent of predator size.

Earlier authors also noted that the diet of *R. erinacea* is size dependent. Richards (1963) found as in the present study that amphipods and *C. septemspinosa* were more important to smaller specimens than to larger specimens. Tyler (1968, 1972) stated that in Passamaquoddy Bay specimens ≤ 44 cm TL consumed significantly more amphipods than those > 44 cm TL.

Comparison of stomach contents collected at different times of the day revealed no feeding periodicity. Also only 30 of the 780 stomachs examined were empty thus offering further support that *R. erinacea* feeds at any time of the diel cycle. There was no indication of difference in feeding intensity between the seasonal cruises. Variation in the mean volume per 10 cm increment of skate length varied

TABLE 4

RELATIVE DIVERSITY OF DIETS OF THE FOUR SPECIES OF SKATES

Cruise 1969-02 Species	Mid-Atlantic Bight H'	Georges Bank H'	Gulf of Maine H'	Nova Scotian Shelf H'
R. *erinacea*	2.59 (35)[1]	4.20 (109)	-	-
R. *ocellata*	3.34 (21)	3.70 (94)	-	-
R. *radiata*	2.61 (8)	2.99 (24)	2.47 (45)	3.41 (21)
R. *senta*	-	2.33 (9)	0.69 (37)	-
Cruise 1969-08 Species				
R. *erinacea*	2.67 (40)	3.44 (57)		
R. *ocellata*	-	3.37 (89)		
R. *radiata*	-	-		
R. *senta*	-	-		
Cruise 1969-11 Species				
R. *erinacea*	2.98 (131)	3.40 (180)	1.81 (5)	3.58 (34)
R. *ocellata*	2.60 (9)	3.12 (114)	-	-
R. *radiata*	-	3.89 (47)	3.43 (112)	3.50 (54)
R. *senta*	-	-	2.64 (34)	2.59 (22)
Cruise 1970-03 Species				
R. *erinacea*	2.25 (46)	3.13 (127)		2.14 (16)
R. *ocellata*	1.79 (4)	3.14 (87)		2.95 (9)
R. *radiata*	-	-		-
R. *senta*	-	-		-

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[1] Numbers within parenthesis stand for number stomachs examined.

more between the two winter cruises (69-02 and 70-03) than between any other combination of cruises.

Raja ocellata:

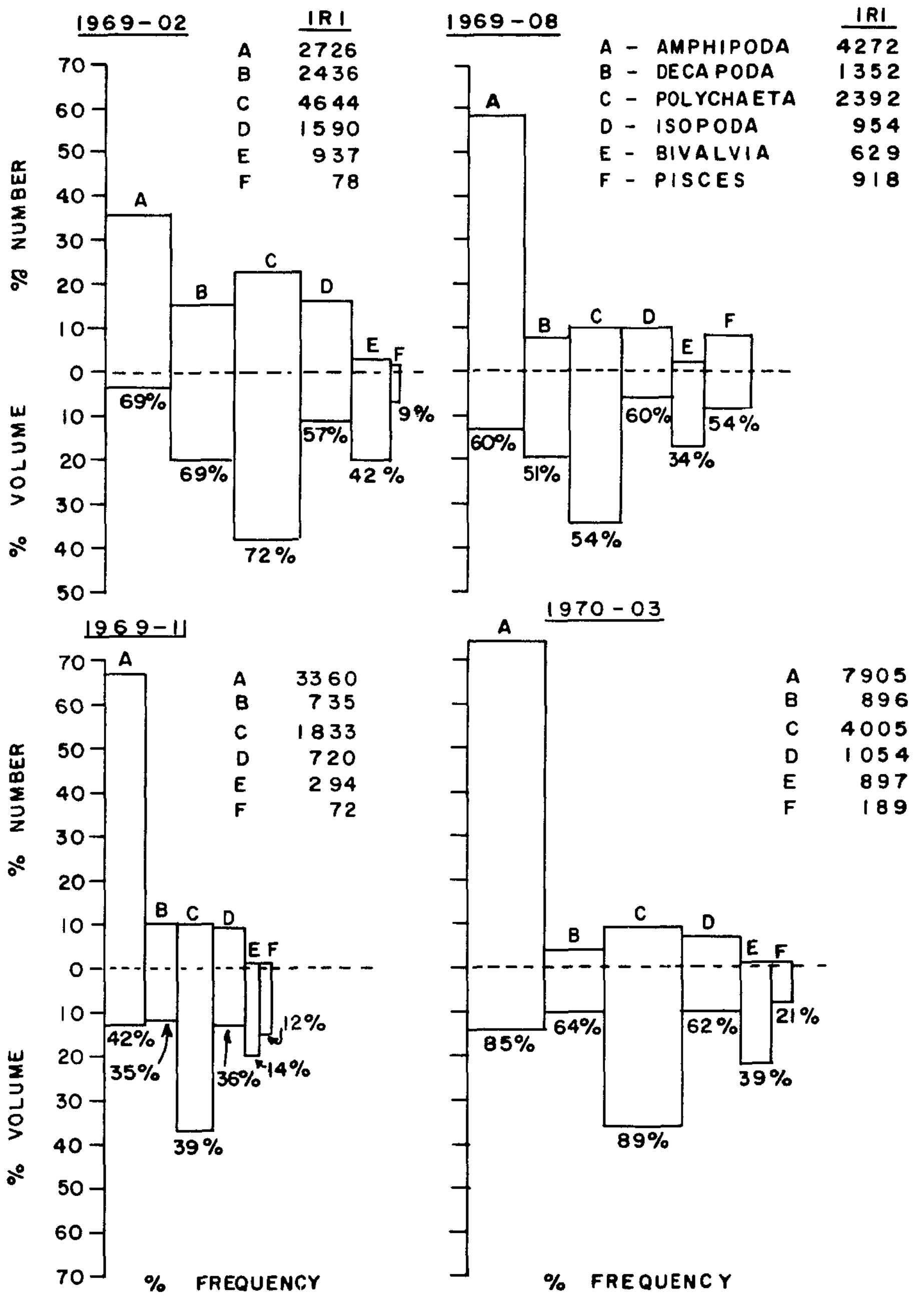
Amphipods and polychaetes had the highest IRI for *R. ocellata.* Polychaetes comprised the largest volume and amphipods the greatest number of prey organisms (Fig. 46). Decapods contributed slightly more to the volume of food organisms than isopods. Bivalves were the third largest taxon by volume but had a lower frequency of occurrence than the above taxa.

There were no differences in the relative numbers of the high taxonomic categories consumed among the subareas but there were differences at the species level. *Nephtys* spp., *Nereis* spp., *Lumbrineris fragilis*, *Ophelia denticulata*, and maldanids (mostly *Clymenella torquata*) were the most abundant polychaetes in the mid-Atlantic Bight and Georges Bank samples. *Nephtys* spp. *Pectinaria* sp., *Ophelia denticulata*, and *Aphrodite hastata* were the most frequently consumed forms in the Gulf of Maine and on the Nova Scotian shelf. Haustoriids, *Leptocheirus pinguis*, *Monoculodes* sp., *Hippomedon serratus*, ampeliscids, *Paraphoxus* sp., and *Tmetonyx* sp. were the most frequently eaten amphipods over the survey area. *Crangon septemspinosa* was by far the most abundant decapod in the diet. *Cancer irrorata*, *Dichelopandalus leptocerus*, *Pagurus acadianus* and *Hyas* sp. were consistently eaten but only in small numbers. *Cirolana polita* was the dominant isopod prey in both numbers and volume. *Chiridotea tuftsi* and *Edotea triloba* were also eaten but they contributed little to the

Fig. 46

Percent composition of food by high taxonomic groups in number, volume, and frequency of occurrence for *R. ocellata* during each of the seasonal surveys. The numbers within the rectangles are the indices of relative importance.

Raja ocellata



volume of food. *Solemya* sp. and *Ensis directus* were the only bivalves that were identifiable. *Ammodytes* sp. was the most frequently eaten fish and it comprised a greater part of the volume of fishes. *Limanda ferruginea* and *Myoxocephalus octodecimspinosus* were occasionally eaten.

Nekton were much more and isopods much less important to *R. ocellata* in Block Island Sound than in the present study. The major food items of *R. ocellata* in Block Island Sound were nekton, *Leptocheirus pinguis*, *Nephtys incisa*, *Ensis directus*, *Crangon septemspinosa*, *Nereis* sp., *Cancer irrorata*, *Lumbrineris* sp., and *Monoculodes edwardsi* (Smith, 1950).

Specimens from Georges Bank had the most diverse diet and those from the mid-Atlantic Bight the least diverse diet in the present study (Table 4). The H' values were similar to but generally slightly lower than those of *R. erinacea*.

The heterogeneity test indicated that there was no significant change in the diet of *R. ocellata* with increase in size. However, comparison of the relative abundance of prey taxa per 10 cm increment of fish length revealed that the numbers of polychaetes gradually increased and amphipods gradually decreased with increase in predator size. The number of fish and bivalves increased with predator size and above 79 cm TL the two taxa comprised the major part of the diet. Ingestion of decapods was independent of predator size. Apparently the heterogeneity test shows only rapid changes in diet over short length increments. In Passamaquoddy Bay the heterogeneity test revealed no significant differences between the diets of small and large *R. ocellata* (Tyler, 1968, 1972).

There was no indication of either diel or seasonal periodicity in intensity of feeding. Fifty-nine of the total 437 stomachs were empty.

Raja radiata:

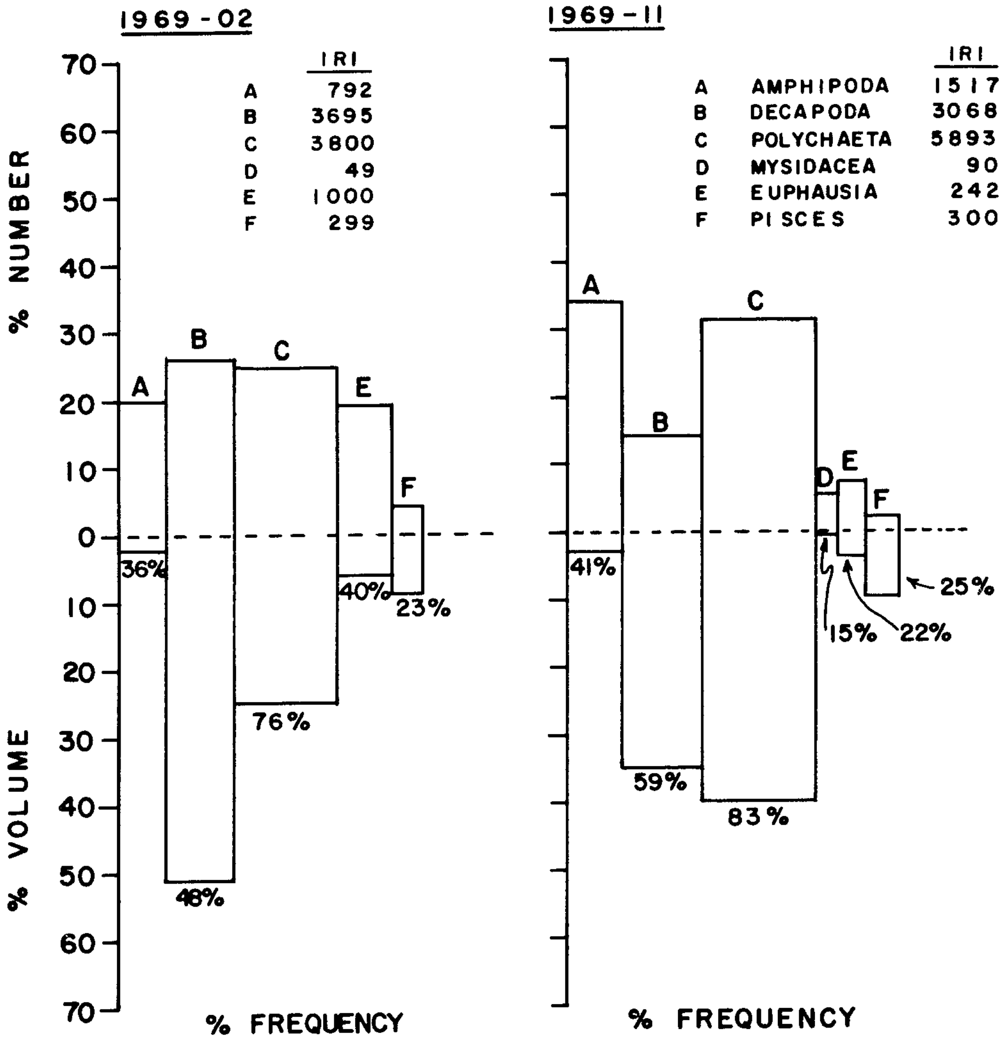
Polychaetes and decapods had the highest IRI for *R. radiata*. Amphipods had the third highest IRI in the autumn sample (69-11) but had the fourth highest behind euphausids in the winter sample (69-02). Fishes and mysids contributed little to the diet (Fig. 47).

There were no differences in the relative numbers of the high taxonomic categories consumed among the subareas but there were some differences at the specific level. *Nephtys* spp. and *Glycera* were the most frequently eaten polychaetes on Georges Bank. *Nephtys* spp., *Eunice pennata*, and *Aphrodite hastata* were the most abundant forms in the Gulf of Maine on the Nova Scotian shelf. On Georges Bank *Hyas* sp., *Eualus pusiolus*, *Dichelopandalus leptocerus*, and *Crangon septemspinosa* were the most frequently eaten decapods. *Pandalus* spp., *Pagurus pubescens*, *Axius serratus*, and *Pasiphaea* sp. predominated in the Gulf of Maine. *Hyas* sp., *Pagurus pubescens*, *Eualus pusiolus*, *Axius serratus* were the major forms eaten on the Nova Scotian shelf. *Leptocheirus pinguis*, ampeliscids, and *Orchomonella* sp. were the most frequently ingested amphipods on Georges Bank. *Pontogeneia inermis* and *Tmetonyx* sp. were most abundant in the Gulf of Maine. On the Nova Scotian shelf ampeliscids and *L. pinguis* were the most frequently eaten amphipods. *Meganyctiphanes norvegica* was the only euphausid represented

Fig. 47

Percent composition of food by high taxonomic groups in number, volume, and frequency of occurrence for *R. radiata* during two of the seasonal surveys. The numbers within the rectangles are the indices of relative importance.

Raja radiata



in the diet. Mysids eaten were *Neomysis americana*, *Erythrops erythrophthalma*, and an unknown species. The most commonly eaten fishes were *Ammodytes* sp., *Myoxocephalus octodecemspinosus*, and *Myxine glutinosa*.

The diet of *R. radiata* was size dependent. Specimens ≤40 cm TL fed mostly on amphipods while those >40 cm TL fed chiefly on polychaetes and decapods. Mysids decreased in the diet while fishes increased with increase in size of the skate. Fishes were a major component of the diet of skates above 70 cm TL. Consumption of euphausids was independent of predator size.

In Passamaquoddy Bay there was also a significant difference in the food habits between specimens of *R. radiata* ≤40 cm TL and those >40 cm TL (Tyler, 1968, 1972). The principle prey of the smaller specimens were *Meganyctiphanes norvegica*, *Mysis stenolepis*, *Aphrodite aculeata*, *Lumbrineris fragilis*, *Nephtys incisa*, *Clymenella torquata*, and *Unciola leucopis*. The larger specimens at *Hyas araneus*, *Aphrodite aculeata*, and *Nephtys incisa*. As in the present study amphipods decreased and decapods increased in importance with increase in predator size, however, unlike the present study, euphausids were important to only the smaller specimens and polychaetes were important to both size groups.

There was no indication of periodicity in intensity of feeding, although most of the euphausids were observed in specimens which were collected during the night or early morning (0-1200). Twenty of the 313 stomachs were empty.

Raja senta:

Decapods and euphausids had the highest IRI for *R. senta.* Euphausids were more frequently eaten during the winter than during the autumn (Fig. 48). Amphipods and mysids were frequently eaten but fishes and polychaetes contributed little to the diet.

There were no differences in the relative numbers of the high taxonomic categories consumed among the subareas but the species of prey varied among the subareas. *Pagurus pubescens*, *Dichelopandalus leptocerus*, *Crangon septemspinosa*, and *Eualus pusiolus* were the major decapods eaten on Georges Bank. In the Gulf of Maine and on the Nova Scotian shelf *Pagurus pubescens*, *Pandalus* spp., and *Crangon septemspinosa* were the most numerous decapod prey. *Meganytiphanes norvegica* was the only euphausid eaten. *Monoculodes* sp. was the major amphipod eaten on Georges Bank and *Dulichia monacantha* and *Pontogeneia inermis* were the most frequently eaten forms in the Gulf of Maine and on the Nova Scotian shelf. The mysids *Erythrops erythrophthalma*, *Neomysis americana*, and an unknown species were consumed in large numbers.

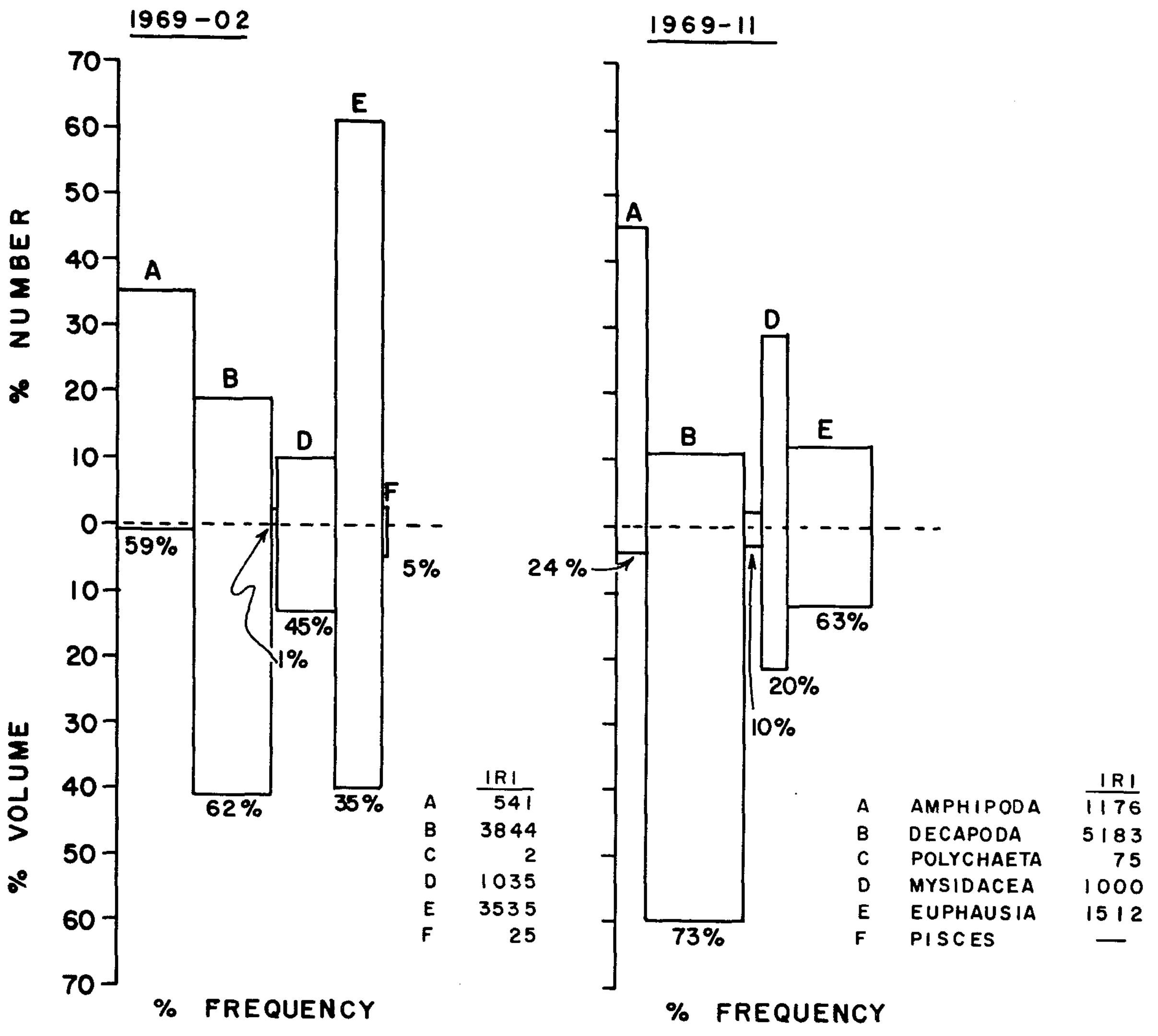
Raja senta had the lowest H' diversity for the assemblages of prey species of the four skates. The lowest and highest values were from specimens captured in the Gulf of Maine. The lowest values were for the winter sample when *R. senta* fed largely on *Meganytiphanes norvegica.*

The heterogeneity test indicated that there was no change in the diet of *R. senta* with increase in size. However, plots of the relative abundance of food taxa per 10 cm increment of fish length

Fig. 48

Percent composition of food by high taxonomic groups in number, volume, and frequency of occurrence for *R. senta* during two of the seasonal surveys. The number within the rectangles are the indices of relative importance.

Raja senta


1969-02
1969-11
% NUMBER
% VOLUME
% FREQUENCY
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
A
B
C
D
E
F
59%
62%
1%
45%
35%
5%
24%
73%
10%
20%
63%
IRI
A 541
B 3844
C 2
D 1035
E 3535
F 25
IRI
A AMPHIPODA 1176
B DECAPODA 5183
C POLYCHAETA 75
D MYSIDACEA 1000
E EUPHAUSIA 1512
F PISCES —

revealed that ingestion of decapods, amphipods, and mysids were size dependent. Amphipods and mysids were important only to skates <40 cm TL and decapods were important only to those ≥ 40 cm TL. Consumption of euphausids was independent of predator size.

Raja senta collected during the night and early morning (0-1200) had greatest volumes of food. This trend was especially apparent during the winter sample when *R. senta* fed largely on *M. norvegica*. Very few euphausids were found in specimens which were collected during the day. Eight of the 107 stomachs that were examined were empty.

Interspecific Comparisons:

Raja erinacea and *R. ocellata* consumed largely the same large taxonomic groups (Table 5). Their diets consisted mostly of amphipods, decapods, and polychaetes, however, *R. ocellata* consumed relatively more polychaetes and less decapods than *R. erinacea*. Isopods and, to a lesser extent, bivalves were major items of the diet of *R. ocellata* but not *R. erinacea*.

The two skates ate many of the same prey species. Within the same subareas *R. ocellata* had 38 to 94% of the same prey species as *R. erinacea* and *R. erinacea* had 30 to 72% of the same prey species as *R. ocellata*. However, there were marked differences in the relative abundance of prey consumed by the two skates. Dominance affinities were less than 50% within all of the subareas; those of Georges Bank were the highest (Table 6). Haustoriids were prevalent in the diet of *R. ocellata*, but except for the autumn sample were of little importance to *R. erinacea*. In the autumn sample a few specimens of

TABLE 5

SANDER'S INDEX OF AFFINITY VALUES OF LARGE TAXA OF PREY AMONG THE FOUR SKATES

Cruise 69-02

	R. erinacea	*R. ocellata*	*R. radiata*
R. erinacea	-	-	-
R. ocellata	66%	-	-
R. radiata	52%	49%	-
R. senta	28%	25%	48%

Cruise 69-08

	R. erinacea	*R. ocellata*	*R. radiata*
R. erinacea	-	-	-
R. ocellata	72%	-	-
R. radiata	-	-	-
R. senta	-	-	-

Cruise 69-11

	R. erinacea	*R. ocellata*	*R. radiata*
R. erinacea	-	-	-
R. ocellata	62%	-	-
R. radiata	59%	56%	-
R. senta	55%	59%	60%

Cruise 70-03

	R. erinacea	*R. ocellata*	*R. radiata*
R. erinacea	-	-	-
R. ocellata	87%	-	-
R. radiata	-	-	-
R. senta	-	-	-

TABLE 6

SANDER'S INDEX OF AFFINITY VALUES OF SPECIES OF PREY AMONG THE FOUR SKATES

Cruise 69-02

Mid-Atlantic Bight

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	38%	-	-
R. *radiata*	28%	19%	-
R. *senta*	-	-	-

Georges Bank

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	45%	-	-
R. *radiata*	23%	20%	-
R. *senta*	15%	10%	7%

Gulf Of Maine

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	-	-	-
R. *radiata*	-	-	-
R. *senta*	-	-	64%

Cruise 69-08

Georges Bank

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	41%	-	-
R. *radiata*	-	-	-
R. *senta*	-	-	-

TABLE 6 (Continued)

Cruise 69-11

Mid-Atlantic Bight

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	10%	-	-
R. *radiata*	-	-	-
R. *senta*	-	-	-

Georges Bank

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	45%	-	-
R. *radiata*	23%	32%	-
R. *senta*	-	-	-

Gulf of Maine

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	-	-	-
R. *radiata*	2%	-	-
R. *senta*	4%	-	28%

Nova Scotian Shelf

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	-	-	-
R. *radiata*	15%	-	-
R. *senta*	3%	-	33%

Cruise 70-03

Mid-Atlantic Bight

	R. *erinacea*	R. *ocellata*	R. *radiata*
R. *erinacea*	-	-	-
R. *ocellata*	12%	-	-
R. *radiata*	-	-	-
R. *senta*	-	-	-

TABLE 6 (Continued)

Cruise 70-03

Georges Bank

	R. erinacea	*R. ocellata*	*R. radiata*
R. erinacea	-	-	-
R. ocellata	49%	-	-
R. radiata	-	-	-
R. senta	-	-	-

Nova Scotian Shelf

	R. erinacea	*R. ocellata*	*R. radiata*
R. erinacea	-	-	-
R. ocellata	6%	-	-
R. radiata	-	-	-
R. senta	-	-	-

R. erinacea consumed large numbers of haustoriids. *R. ocellata* ate more *Tmetonyx* sp., *Hippomedon serratus*, and *Paraphoxus* sp. than *R. erinacea*. *R. erinacea* consumed more *Unciola* sp. and ampeliscids than *R. ocellata*. The two skates ate about equal numbers of *Leptocheirus pinguis* and *Monoculodes* sp. *Crangon septemspinosa* was the most frequently eaten decapod by both species. *Pagurus* spp. (especially *P. acadianus*) were eaten in large numbers by *R. erinacea* but not by *R. ocellata*. *R. ocellata* ingested more *Nephtys* spp. and *Ophelia denticulata* than *R. erinacea* and *R. erinacea* ate more *Aphrodite hastata* and *Glycera* spp. than *R. ocellata*. *Pherusa affinis* was eaten only by *R. erinacea*. The two skates ate about equal numbers of *Nereis* spp., *Lumbrineris fragilis*, and maldanids.

An index of dominance affinity of 49% was computed for the prey species of *R. erinacea* and *R. ocellata* reported by Smith (1950) for Block Island Sound. This index is comparable to those obtained from Georges Bank but is higher than the indices obtained from the mid-Atlantic Bight in the present study. Insufficient sampling may be responsible for the low indices obtained in the present study. Small samples of *R. ocellata* from a limited area of the mid-Atlantic Bight were obtained for all cruises but 69-02. Tyler (1968, 1972) found more overlap between *R. ocellata* and *R. erinacea* ≤44 cm TL than between *R. ocellata* and *R. erinacea* > 44 cm TL. The former pair had two of four principal prey in common while the latter pair had two of seven prey in common. However, Tyler's results are difficult to evaluate because they are based on very small sample sizes. Tyler obtained 90 specimens of *R. erinacea* and only 7 specimens of *R. ocellata* with food in their stomachs.

Raja ocellata tended to feed on infauna and *R. erinacea* tended to feed on epifauna. Large burrowing polychaetes and bivalves were consumed more frequently by *R. ocellata* and epifaunal decapods were more frequently eaten by *R. erinacea*. *R. ocellata* ate more haustoriid amphipods while *R. erinacea* consumed more *Unciola* sp. and ampeliscids. Haustoriids are sand burrowing amphipods (Sameoto, 1969). *Unciola* sp. is active on the bottom surface and ampeliscids build their tudes above the level of the bottom surfact (Smith, 1950). The division of food resources between the skates is not complete because some individuals of *R. erinacea* consumed large numbers of infauna and some *R. ocellata* ate large numbers of epifauna. Both species ate considerable numbers of *Leptocheirus pinguis*, a tubicolous amphipod, that is active on the bottom surfact (Smith, 1950) and *Crangon septemspinosa*, an epifaunal decapod. *R. erinacea* occasionally fed on haustoriids and deep burrowing nereids, *Nephtys* spp., and *Glycera* spp. were regular items of its diet. The infaunal and epifaunal preferences of the two skates may be more distinct in areas where they coexist than in areas where they occur separately because in Delaware Bay (Fitz and Daiber, 1963) *R. erinacea* consumed relatively more infauna than it did in the areas sampled in Smith's (1950) study or the present study. In Delaware Bay *Crangon septemspinosa*, *Ensis directus*, *Eucramus praelongus* (a burrowing crab), *Nereis limbata*, *Pagurus* spp., and *Neomysis americana* were the most abundant prey. *R. ocellata* does not regularly occur in

Delaware Bay.

Part of the overlap in species of prey of the two skates may be explained by high abundance of a prey species. When a prey species is very abundant it becomes a nonlimiting food source and may also support less well adapted secondary predators. Tyler (1968) stated that in Passamaquoddy Bay during the summer *M. norvegica* is very abundant and is an important food source of seven predators, in the winter *M. norvegica* is scarce and is important to only two predators. High abundance of haustoriids during cruise 69-11 may have been the reason why *R. erinacea* fed heavily on them at this time but not at the other times of the year.

The difference in the shape of the mouth and number of tooth rows may be related to the food habits of the two skates. The mouth of *R. ocellata* is less arched and has a greater number of tooth rows than that of *R. erinacea* (Part I, Fig. 8, 10). Interspecific competition in the area of sympatry may have led to divergence in food habits and associated morphology of the mouth.

There does not appear to be a high degree of competitive interaction between *R. erinacea* and *R. ocellata* because they are positively correlated by abundance and where the two species are most abundant (Georges Bank) they have the most similar diets and highest diversity of assemblages of prey species. If competitive interaction was high the two species would not reach their highest abundance at the same localities, their food habits would be more dissimilar in areas where both species were abundant, or the diets of one or both of the species would be low in diversity. Competition for food is minimized, because both species are euryphagous; one seems to be slightly more efficient at capturing infauna, the other at capturing epifauna. Thus food resources rarely become limiting. Consequently, because both species are euryphagous their diets may overlap greatly when a prey species becomes very abundant.

Raja radiata and *R. senta* also had similar food habits at the high taxonomic level (Table 5). Decapods were consumed in large numbers by both species but *R. radiata* ate more polychaetes and fewer mysids than *R. senta*. Euphausids were a major food item of both skates but they were more frequently eaten by *R. senta* than by *R. radiata*.

Within the same subareas the diet of *R. senta* included many of the same species that were eaten by *R. radiata*. Sixty to eighty percent of the species eaten by *R. senta* were also eaten by *R. radiata* whereas only 15 to 38% of the prey species eaten by *R. radiata* were eaten by *R. senta*. Quantitatively the diets of the two skates were very different except for the winter samples from the Gulf of Maine (Table 6). *M. norvegica* was the dominant prey of both species from these samples. *Dulichia monacantha* was the most abundant amphipod in the diet of *R. senta* and *Leptocheirus pinguis* and ampeliscids were the most numerous forms in the diet of R. radiata. Both skates consumed large numbers of *Pontogeneia inermis*. *Hyas* sp., *Eualus pusiolus*, and *Axius serratus* were frequently eaten by *R. radiata* but only occasionally by *R. senta*. *Crangon septemspinosa* was the decapod most frequently eaten by *R. senta*.

Raja radiata has a less specialized diet than *R. senta*, both in terms of the total number of organisms consumed and the type of habitats in which the prey occur. Epifaunal and infaunal elements are about of equal importance to *R. radiata* whereas the diet of *R. senta* is almost entirely limited to epifauna. *R. senta* appears to specialize on several species of amphipods, two mysids, a euphausid, and several species of decapods.

Competitive interaction may be more severe between *R. radiata* and *R. senta* than between *R. erinacea* and *R. ocellata* because the diet of *R. senta* is very low in diversity and *R. senta*, over its entire range, is much less abundant than *R. radiata*. Nilsson (1967) has shown that species with similar food habits tend to become more specialized when they are sympatrically distributed than when they are allopatrically distributed. The low abundance and low diversity of prey species of *R. senta* indicate that it is more severely affected by competitive interaction than is *R. radiata*.

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