

# THE ABUNDANCE AND DISTRIBUTION OF THE FAMILY MACROURIDAE (PISCES: GADIFORMES) IN THE NORFOLK CANYON AREA<sup>1</sup>

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## ABSTRACT

The Norfolk Canyon off Virginia and the adjacent slope areas were sampled with 13.7 m otter trawls in June 1973, November 1974, September 1975, and January 1976. Trawl depths ranged from 75 to 3,083 m, and 22 species of macrourids were captured during the study. *Coryphaenoides rupestris* demonstrated seasonal movement to shallower water (ca. 750 m) during winter. *Nezumia bairdii*, *N. aequalis*, and *Coryphaenoides carapinus* exhibited a significant positive correlation between head length and depth ( $r^2 = 0.47, 0.37, \text{ and } 0.35$ , respectively). *Nezumia bairdii* apparently spawns in July or August, and reaches an age of about 11 years. New size records were established for *Nezumia aequalis* (64 mm head length (HL)) and *N. bairdii* (66 mm HL). New depth records were established for *Coelorinchus c. carminatus* and *N. aequalis* (884 and 1,109 m, respectively). The known geographic ranges for *Coelorinchus caribbeus*, *C. ocea*, *Nezumia cyrano*, *Coryphaenoides colon*, *Hymenocephalus gracilis*, *H. italicus*, *Bathygadus macrops*, *Macrourus berglax*, and *Gadomus dispar* were extended to the Norfolk Canyon area.

The Macrouridae (Pisces: Gadiformes) includes some of the most abundant archibenthic deep-sea fish species (Marshall 1965, 1971; Marshall and Iwamoto 1973; Iwamoto and Stein 1974) and attains greatest abundance and diversity on the continental slopes of the world oceans (Marshall and Iwamoto 1973). Present knowledge of the life history and ecology of macrourids has been accrued piecemeal from faunal lists and taxonomic works (Gunnerus 1765; Gunther 1887; Gilbert and Hubbs 1920; Farron 1924; Iwamoto 1970; Okamura 1970; Marshall and Iwamoto 1973; Iwamoto and Stein 1974), or from studies on physiology, anatomy, and life history (Kulikova 1957; Marshall 1965; Phleger 1971; Rannou 1975; Rannou and Thiriot-Quiereaux 1975; Haedrich and Polloni 1976; McLellan 1977; Merrett 1978; Smith et al. 1979). The meager literature on reproduction and growth of macrourids and other deep-sea anacanthine fishes has recently been reviewed by Gordon (1979). With the advent of increasing expertise in deepwater trawling, some macrourid species, such as *Coryphaenoides rupestris* and *Macrourus berglax*, have become commercially

important in the western North Atlantic. Experimental commercial trawling was initiated by the Soviet Union in 1962, and many studies directly related to the commercial fishing of macrourids have been subsequently published by Soviet workers (Podrazhanskaya 1967, 1971; Savvatimskii 1971, 1972; Grigor'ev 1972) and to a lesser extent by Polish researchers (Stanek 1971; Nodzinski and Zukowski 1971).

The present study examines the seasonal distribution and abundance of the macrourid species captured in the Norfolk Canyon area. In addition aspects of age, growth, and reproduction of selected dominant species are also described.

## MATERIALS AND METHODS

### Gear

The data presented in this paper were obtained on four cruises to Norfolk Canyon and the adjacent open slope to the south (Fig. 1) conducted by the RV *Columbus Iselin* (June 1973) and RV *James M. Gillis* (November 1974, September 1975, January 1976). On all cruises a 13.7 m semiballoon otter trawl with 1.3 cm (stretched) mesh in the cod end liner and 5.1 cm (stretched) mesh in the wings and body was employed. Steel "china V" doors at the end of 22.9 m bridles were used to permit spreading of the net from a single warp (Musick et al. 1975).

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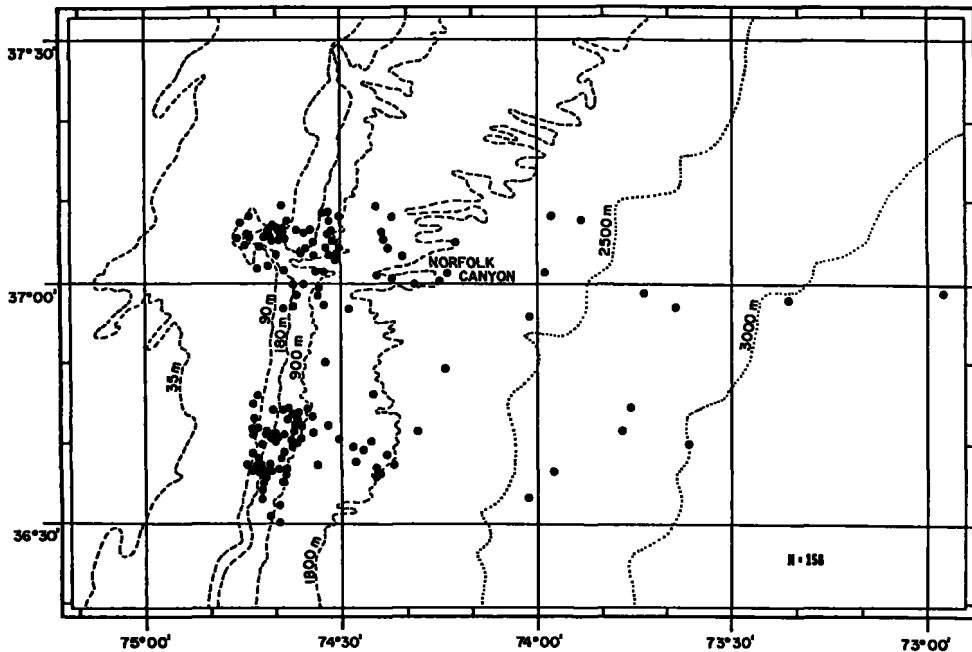


FIGURE 1.—Map of the Norfolk Canyon study area with station locations indicated.

### Sampling Design

Norfolk Canyon and an adjacent open slope were divided into five sampling strata: 75-150 m, 151-400 m, 401-1,000 m, 1,001-2,000 m, and 2,001-3,000 m. Six stations were then randomly assigned in each depth stratum. The duration of all tows in depths of <2,000 m was 0.5 h (bottom time). Where the depth exceeded 2,000 m, the tow times were extended to 1 h. Station depth was determined from a sonic precision depth recorder when the net was set and then every 3 min for the duration of the 0.5 h tows (every 6 min for the 1-h tows). Mean station depth was then determined by averaging the 11 resultant values.

### Data Collection and Analysis

Head lengths instead of total lengths were measured because macrourids have slender whiplike tails that are easily damaged during trawling. The head length (HL) was measured to the closest millimeter, from the tip of the snout to the posterior edge of the opercle using Helios<sup>4</sup> dial calipers. The fish were weighed with an Ohaus dial-a-gram scale. Calibration showed the scale to be accurate within

1.0-1.5 g under all typical shipboard conditions.

The sex and gonadal conditions of freshly captured specimens were noted. Gonadal samples for histological processing were stored in Davidson's preservative and later mounted using standard paraffin techniques. Sections (5 mm) were stained with Mayer's hematoxylin and eosin counterstain.

Saccular otoliths and a scale sample were removed from all *Nezumia bairdii* and stored dry. Representative otolith samples were chosen randomly from individuals over the entire size range of fish captured.

The length-weight relationships for *Nezumia bairdii*, *Coryphaenoides armatus*, and *C. rupestris* were analyzed using log transformed weights regressed against head length (Fig. 2).

Regression analysis of head length on depth of capture was performed for each species to determine any significant change in head length with change in depth. Testing of the hypothesis that  $\beta = 0$  for the regression line ascertained whether there was a significant change of size with changing depth. The coefficient of determination ( $r^2$ ) was also calculated to determine what proportion of the variance of head length could be attributed to change in depth.

The a posteriori Student-Newman-Keuls analysis of means was used as a second method for interpreting the size/depth relationship. This method calculated the mean depth of capture of each head-

<sup>4</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

length interval, combined the head lengths in subsets whose mean depths did not differ significantly from each other, and defined the constituents of each subset.

Due to the large size and thickness of the macrourid otoliths, standard age determination techniques proved unsuccessful (Christensen 1964; McEachran and Davis 1970). Therefore, a thin section was removed from each otolith and, using a dissecting microscope, the number of bands presumed to be annual were counted and recorded.

Gonads of the specimens were classified into reproductive stages for analysis. The criteria for these stages were as follows:

**Stage 1—Undeveloped.** The gonads were immature and no development was evident. The reproductive organs were difficult to distinguish within the body cavity.

**Stage 2—Early Immature.** The reproductive organs had enlarged slightly. The sex could be determined, but no vascularization of the ovaries was apparent. The organs of both sexes had a highly translucent appearance.

**Stage 3—Immature.** The ovaries were enlarged and vascularization had begun. The testes had become discernibly "sausage shaped". The organs of both sexes were opaque.

**Stage 4—Late Immature.** The reproductive organs of both sexes were full size. The ovaries were about 90% vascularized. The testes had become milky white in color.

**Stage 5—Mature.** The reproductive organs were developed completely. Ovaries were fully vascularized and had a granular appearance.

**Stage 6—Ripe.** Advanced spermatogenesis or

oogenesis was evident. The oocytes were fully developed in the females and the male testes contained milky-white seminal fluid.

**Stage 7—Spent.** The testes and ovaries were spent. The reproductive organs were flaccid and had recently released sperm or eggs.

## RESULTS AND DISCUSSION

### Species Accounts

#### *Coelorinchus c. carminatus* (Goode 1880)

*Coelorinchus c. carminatus* is a relatively shallow water macrourid reported from depths of 89-849 m (Marshall and Iwamoto 1973). In the study area this species was captured in depths of 210-884 m (Fig. 3). Marshall and Iwamoto (1973) reported *C. c. carminatus* from northern Brazil to the Grand Banks, but absent in the Bahama Island chain. The largest specimen captured in our study had a head length of 70 mm, while Marshall and Iwamoto (1973) reported specimens with 73 mm HL.

During our study, a maximum of 188 individuals and 4 kg of *C. c. carminatus* were captured in a 0.5-h trawl. This species also contributed as much as 34.2% of the number and 27.8% of the biomass of benthic fishes captured in individual samples.

Figure 4 shows the depth distribution of *C. c. carminatus* incremented by 2 mm size groups. A slight increase in head length with increase of depth was apparent. The slopes of the regression lines were shown to be significantly different from zero. The coefficient of determination (Table 1) also showed a correlation between head length and depth. There was variability among cruises, but this may be at-

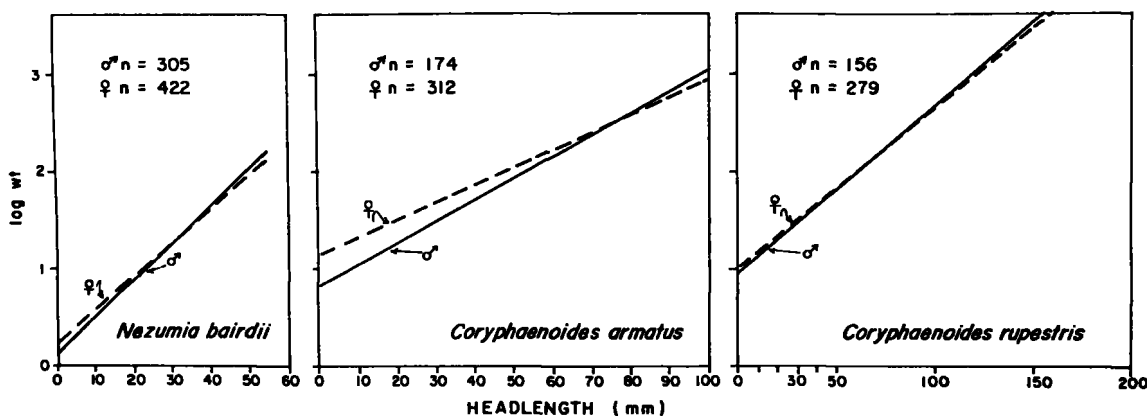


FIGURE 2.—The log (wt) versus head length regressions for *Nezumia bairdii*, *Coryphaenoides armatus*, and *Coryphaenoides rupestris*.

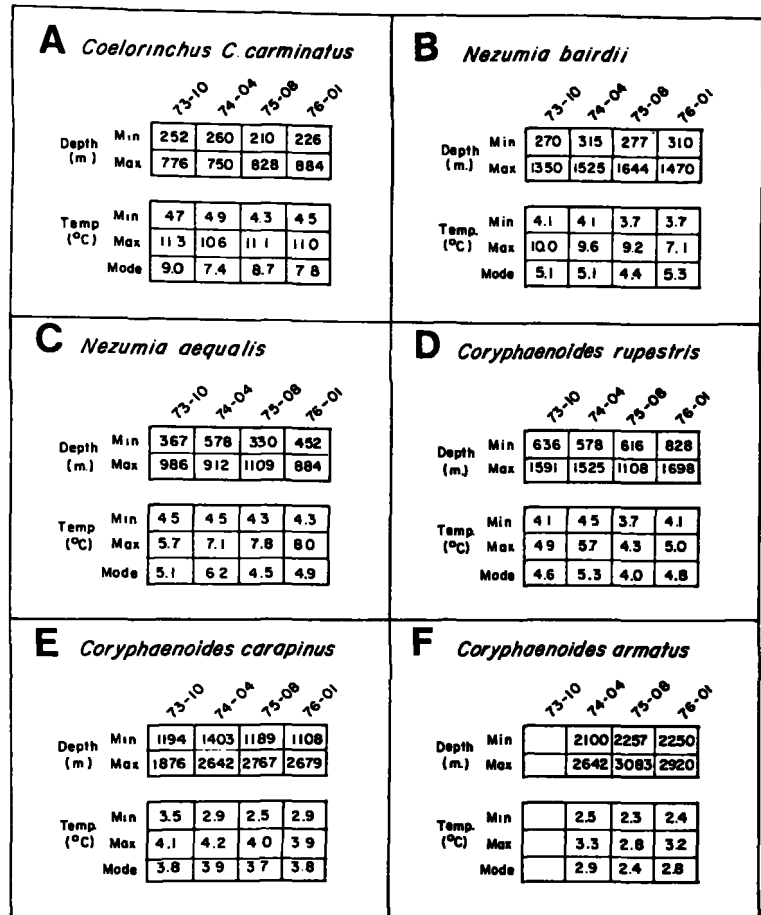


FIGURE 3.—Minimum and maximum depth of capture, with minimum, maximum, and modal temperatures of capture for each species and each cruise.

TABLE 1.—The coefficient of determination ( $r^2$ ) for the change in head length with change in depth regression lines.

| Species                           | Cruises    |            |             |            | Combined cruises |
|-----------------------------------|------------|------------|-------------|------------|------------------|
|                                   | Jan. 76-01 | June 73-10 | Sept. 75-08 | Nov. 74-04 |                  |
| <i>Coelorinchus c. carminatus</i> | 0.006      | 0.23       | 0.13        | 0.44       | 0.23             |
| <i>Nezumia aequalis</i>           | 0.45       | 0.15       | 0.62        | 0.14       | 0.37             |
| <i>Nezumia bairdii</i>            | 0.12       | 0.50       | 0.44        | 0.49       | 0.47             |
| <i>Coryphaenoides rupestris</i>   | 0.04       | 0.19       | 0.08        | 0.11       | 0.02             |
| <i>C. carapinus</i>               | 0.59       | 0.005      | 0.30        | 0.37       | 0.35             |
| <i>C. armatus</i>                 | 0.000      | —          | 0.05        | 0.000      | 0.14             |

tributed to sampling artifacts and the relatively narrow depth range (674 m) of this species.

The analysis of variance showed a significant difference in mean depths of the head length groups ( $F = 35.9$ ,  $F(\text{table}; \alpha = 0.01) = 1.79$ ). The Student-Newman-Keuls test divided the group into two

significantly different subsets; one 10-50 mm HL and the other 51-70 mm HL.

Other macrourids (*N. bairdii* and *N. aequalis*) had high biomass but low numerical abundance at the deep end of their ranges, indicating the presence of a few large specimens there. This was not the case for *C. c. carminatus* (Fig. 5). The occurrence of fish distributing by size can be obscured if the larger members of the population traverse the entire range. The biomass of the species would be elevated at the shallower depths so that a consistent biomass level is present throughout the depth range. Comparison of Figure 4 with Figure 5 shows that although the mean depth of capture for this species increased with head length, the larger fish occurred over the entire depth range. This pattern is important because it shows that for some fishes the "bigger-deeper" phenomenon described by Polloni et al. (1979) may really be a "smaller-shallower" phenomenon. A plot of mean fish weight against depth as used by Polloni

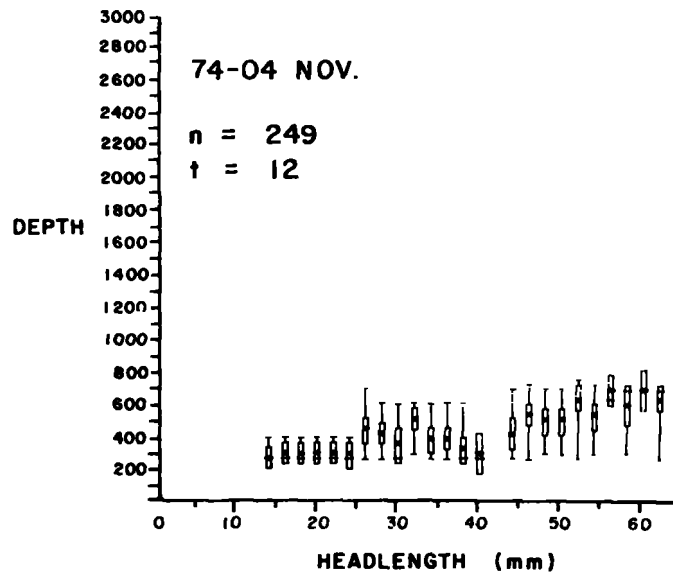
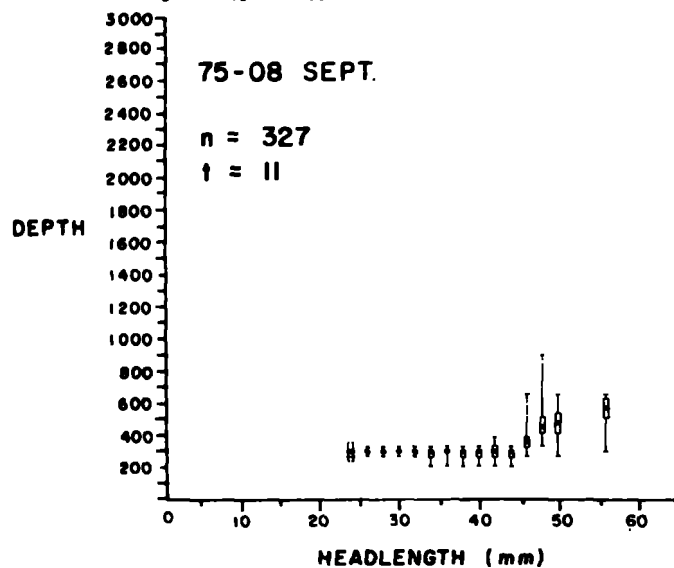
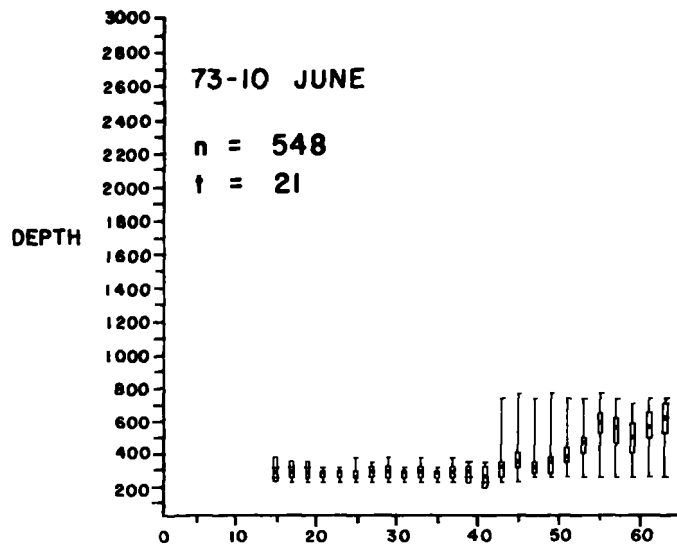
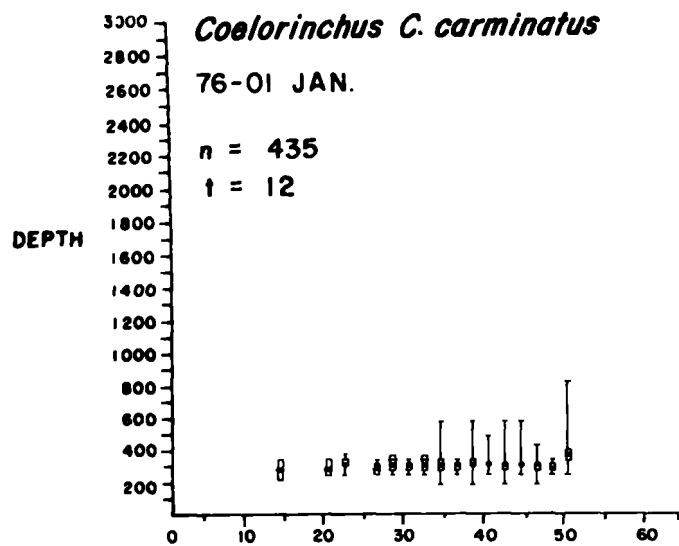


FIGURE 4.—Graph of head length versus depth, by cruise, for *Coelorinchus c. carminatus*. The dot is the mean, the rectangle is the 95% confidence interval, and

the lines each enclose the range.  $n$  = the number of specimens and  $t$  = the number of trawls.

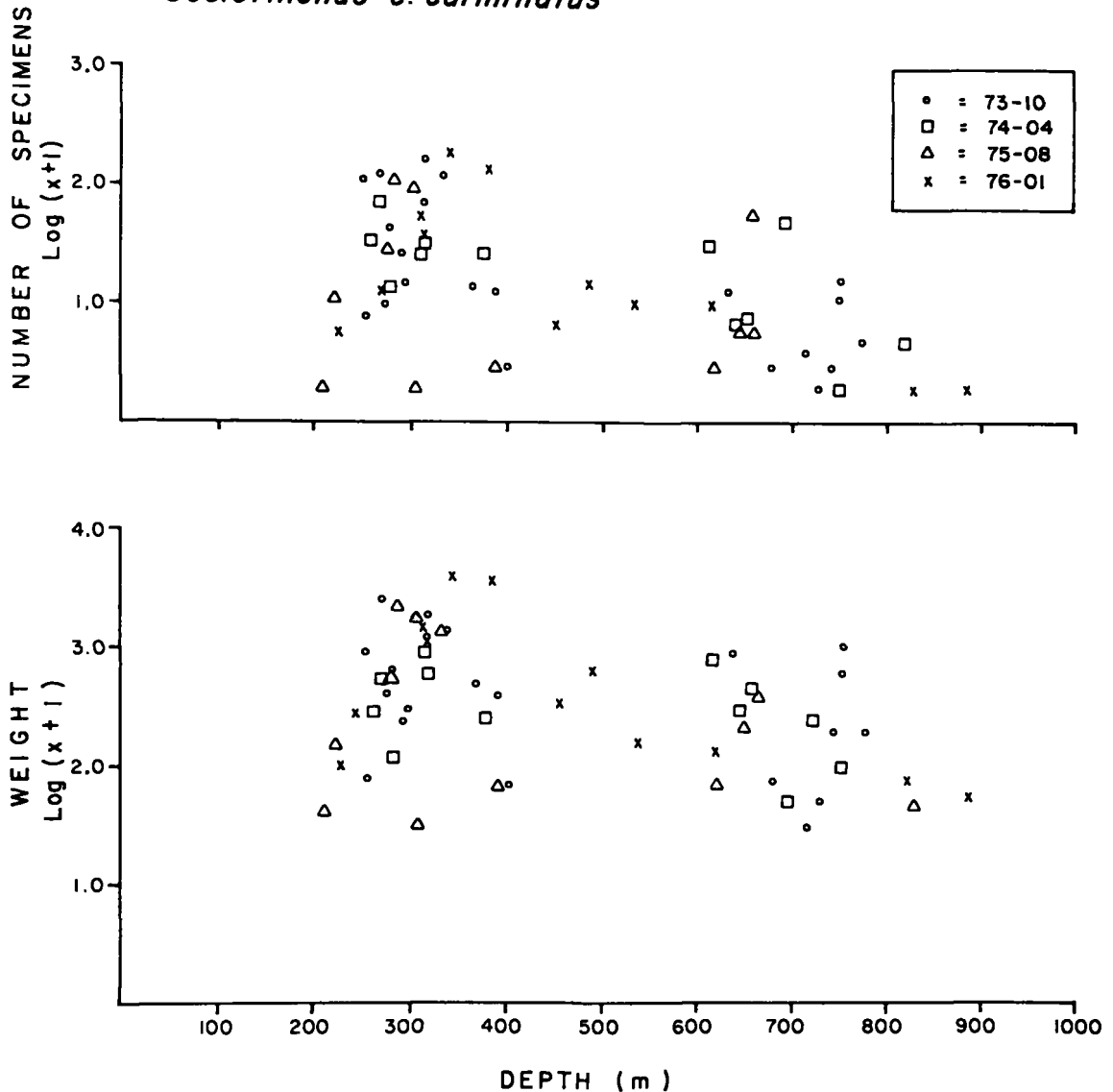
*Coelorinchus c. carminatus*

FIGURE 5.—The distribution of log transformed ( $\log(x+1)$ ) abundance and weight of *Coelorinchus c. carminatus* at each station, plotted against depth.

et al. (1979) may have a highly positive slope, but these data are impossible to interpret without information about length-frequency patterns with depth.

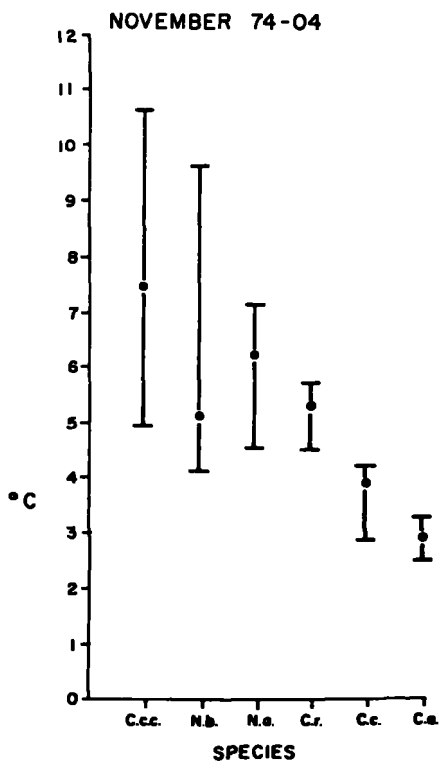
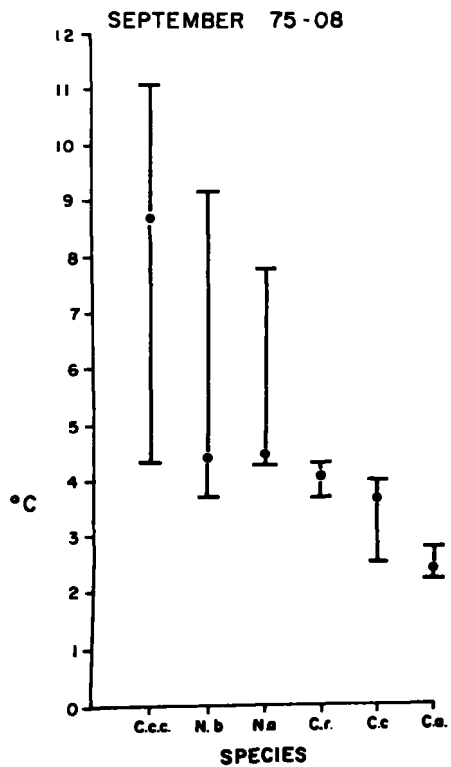
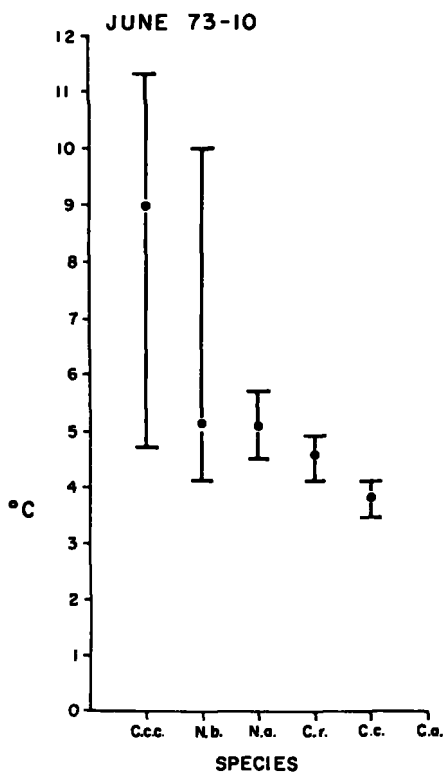
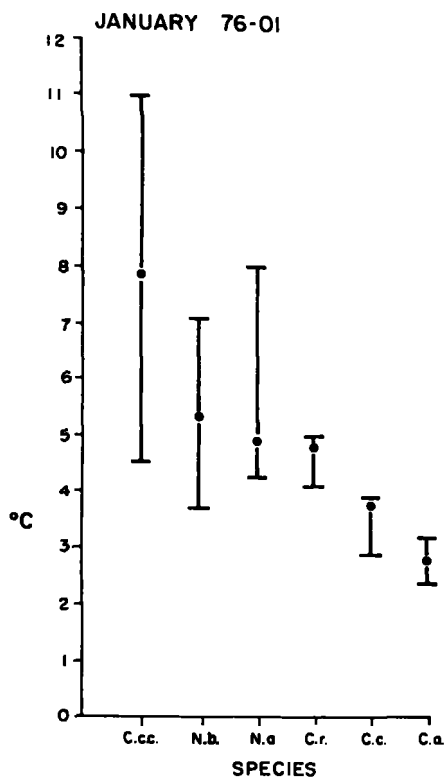
The temperatures at which *C. c. carminatus* were captured varied from 4.3° to 11.3°C (Fig. 6). The average temperature of collection was 7.6°C.

*Nezumia aequalis* (Günther 1878)

*Nezumia aequalis* is a closely related congener of

*N. bairdii* and is found primarily south of the study area (Marshall and Iwamoto 1973). *Nezumia aequalis* attains a head length of at least 53 mm and has a depth distribution of 200-1,000 m. Its

FIGURE 6.—The temperature range for each species, by cruise. The dot designates the modal temperature, Ccc - *Coelorinchus c. carminatus*, N.b. - *Nezumia bairdii*, N.a. - *Nezumia aequalis*, C.r. - *Coryphaenoides rupestris*, C.c. - *Coryphaenoides carpinus*, C.a. - *Coryphaenoides armatus*.



geographic range is listed as from the Faroe bank to northern Angola in the eastern Atlantic, the Mediterranean, and from Davis Straits to northern Brazil in the western Atlantic (Marshall and Iwamoto 1973).

In the Norfolk Canyon area the depth of capture of *N. aequalis* was from 330 to 1,109 m. The greatest number in a trawl was 40 in November of 1974, and the highest biomass per trawl was 300 g in September 1975. *Nezumia aequalis* comprised up to 8.9% of a trawl catch by number and 3.1% by weight. The analysis of variance of the mean depths of the head length groups gave a *F* value of 3.32 (*F*(table;  $\alpha = 0.01$ ) = 2.11). The Student-Newman-Keuls analysis showed only one subset, probably because of the low sample size. Examination of Figure 7 suggests head length increased with depth, and the slope of the line was significantly different from zero.

Although its bathymetric range was extensively sampled, densities were low and few mature specimens were captured (Fig. 8). These findings are in contrast to the distribution and abundance of its congener, *N. bairdii*, suggesting competitive exclusion. Alternately, Norfolk Canyon populations of *N. aequalis* may represent expatriation from denser populations in the Gulf of Mexico or on the Blake Plateau.

The temperature range for *N. aequalis* captured in the Norfolk Canyon area was from 4.3° to 8.0°C (Fig. 6). The average temperature of collection was 5.3°C.

#### *Nezumia bairdii* (Goode and Bean 1877)

*Nezumia bairdii* is a relatively small macrourid with a reported head length of up to 60 mm (Marshall and Iwamoto 1973). During our study the head lengths varied from 12 to 66 mm with the weight of the largest specimen being 295 g. The geographic range of *N. bairdii* extends from the Straits of Florida north to the Grand Banks (Marshall and Iwamoto 1973). *Nezumia bairdii* is captured commonly between 90 and 183 m in the northern part of its range and appears to undergo tropical submergence because it is found primarily between 548 and 731 m in the southern parts of its range. The inclusive depth range is 90-2,285 m (Goode and Bean 1885; Marshall and Iwamoto 1973). One anomalous catch at a depth of 16.5 m was recorded in Vineyard Sound (Bigelow and Schroeder 1953), but this was most likely a discard from a commercial fishing vessel.

Within the study area the depth of capture ranged from 270 to 1,644 m (Fig. 3). The largest catch in

a half hour tow was 76 fish and the greatest biomass per half hour tow was 5.7 kg. *Nezumia bairdii* comprised up to 30% of the demersal fish catch in number and up to 15% of the biomass.

In the January plot (Fig. 9), the head length increased slightly with depth. The regression line of the mean depth of each head length class showed a positive slope significantly different than zero. By June (Fig. 9) the regression line showed a highly significant positive slope and three distinct size groups separated by depth were evident. The first group included those fish <30 mm HL, the second group was from 30 to 42 mm HL, and the third group was >43 mm HL. The head lengths at the start of maturity for females (27 mm) and males (32 mm) correspond well with the dividing line between size groups one and two, as defined by depth distribution. Also, *N. bairdii* females and males can be fully mature at 44 and 45 mm HL, respectively (Fig. 10). These values are close to the division between the second and third size groups noted above. The three size groups appear to reflect maturity stages as well as size differences, and this may contribute to the bathymetric differences. The first group consisted of all immature fish that were not found in deep water in June. The second group could be termed the transitional group because it included fish that were just starting to mature and those more highly developed. Since this group included such a diverse spectrum of maturity, it encompassed portions of the depth ranges of both immature and mature fish. The third group consisted of all mature fish and was not found in water shallower than approximately 600 m in June. In September, the larger fish had reached their deepest limit, and immature *N. bairdii* were virtually absent deeper than 1,000 m. By November (Fig. 9), the largest fish were returning to shallower water to complete what appears to be a seasonal migration cycle.

Examination of histological sections of gonads showed that the only spent *N. bairdii* were captured on the September cruise. Although no ripe fish were caught on any cruise, these spent fish suggest that *N. bairdii* spawns in July or August, coincident with the time when the mature fish are inhabiting their deepest level.

Marshall's (1965) hypothesis concerning reproduction of certain macrourids states that fertilization takes place at the bottom. Subsequently the eggs, which are buoyant, develop and hatch on their way upward to the seasonal thermocline. The larvae then maintain themselves just below the thermocline, in order to take advantage of the plankton that tends to accumulate there in the density gradient. In con-



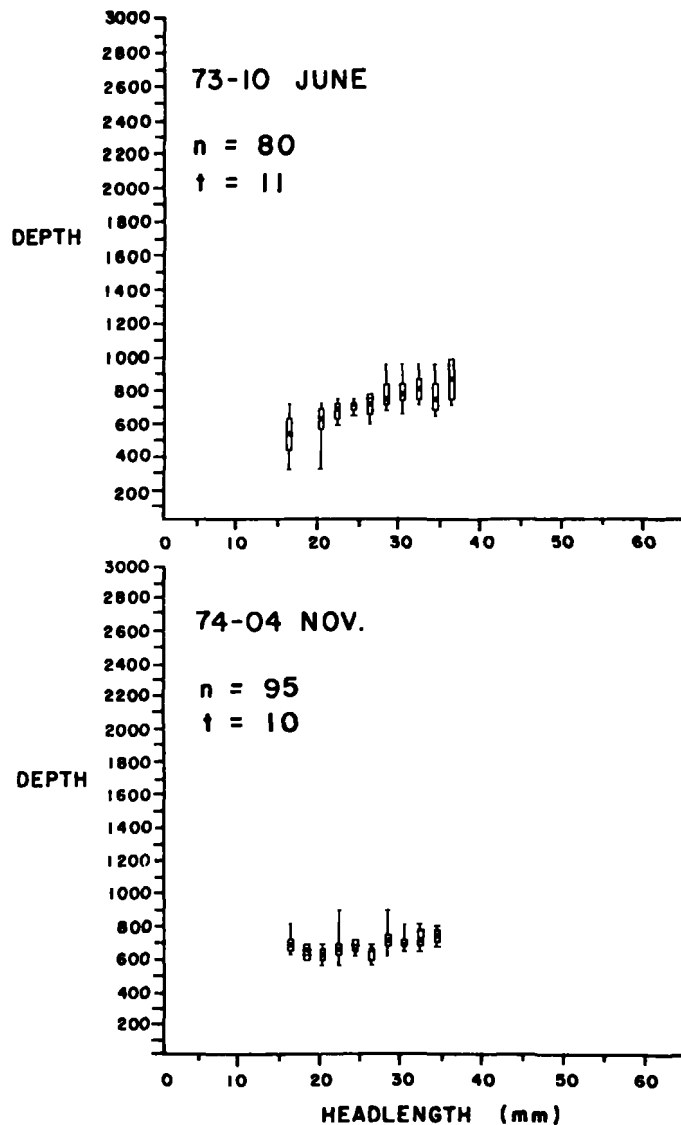
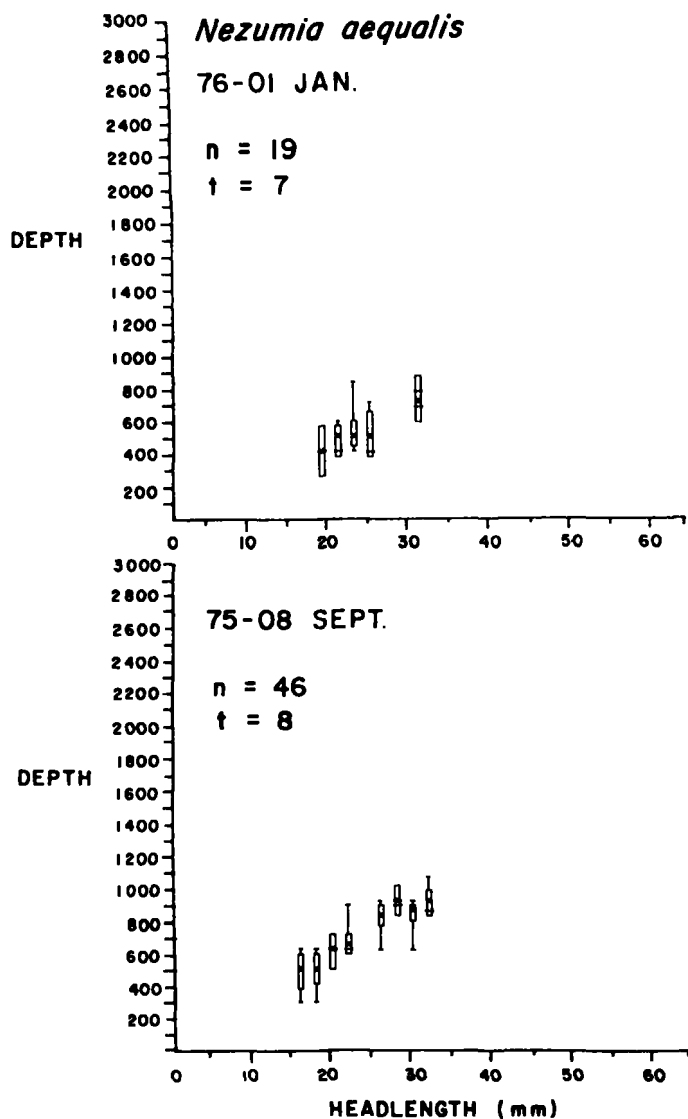


FIGURE 7.—Graph of head length versus depth, by cruise, for *Nezumia aequalis*. The dot is the mean, the rectangle is the 95% confidence interval, and

the lines enclose the range. n = the number of specimens and t = the number of trawls.

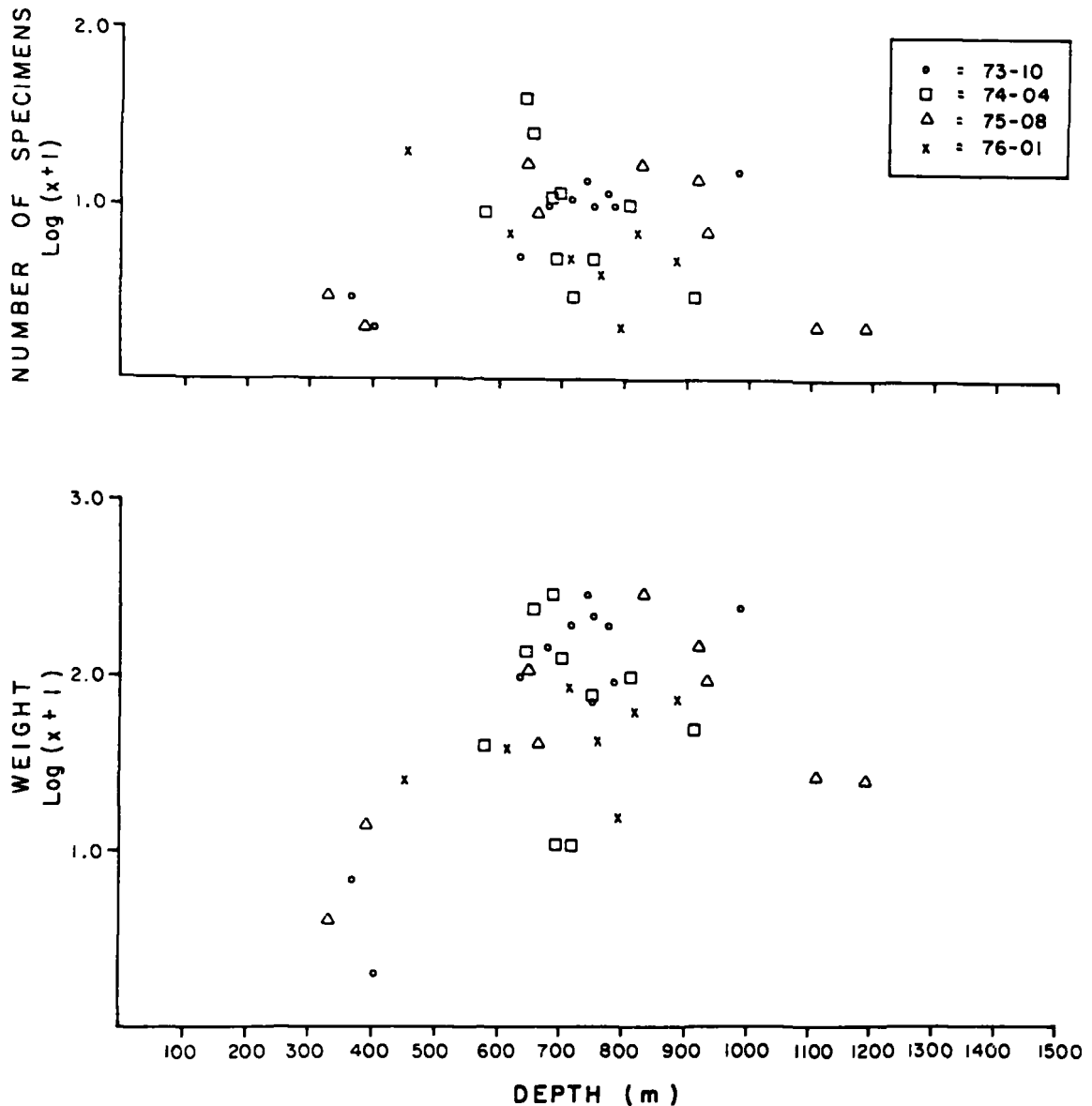
*Nezumia aequalis*

FIGURE 8.—The distribution of log transformed ( $\log (x + 1)$ ) abundance and weight of *Nezumia aequalis* at each station, plotted against depth.

junction with Marshall's hypothesis, the advantages of the type of seasonal migration suggested by our data are twofold. First, the migration concentrates the reproductively mature fish in a limited area thereby increasing the probability of a sexual encounter. Second, it allows additional time for development of eggs on their rise to the upper layers, and concurrently lessens the chance that the egg will

travel through the thermocline and be removed from the area by the more active surface currents (although egg density could be such that neutral buoyancy occurs at the thermocline). If these suggestions hold true, it would be expected that the larvae would benefit from the high productivity and warmer temperatures of the surface waters and have enhanced growth. As productivity declines in the late

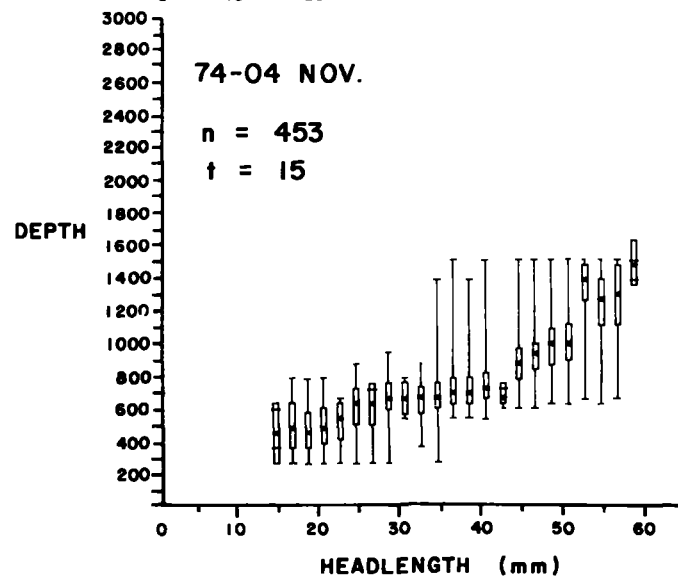
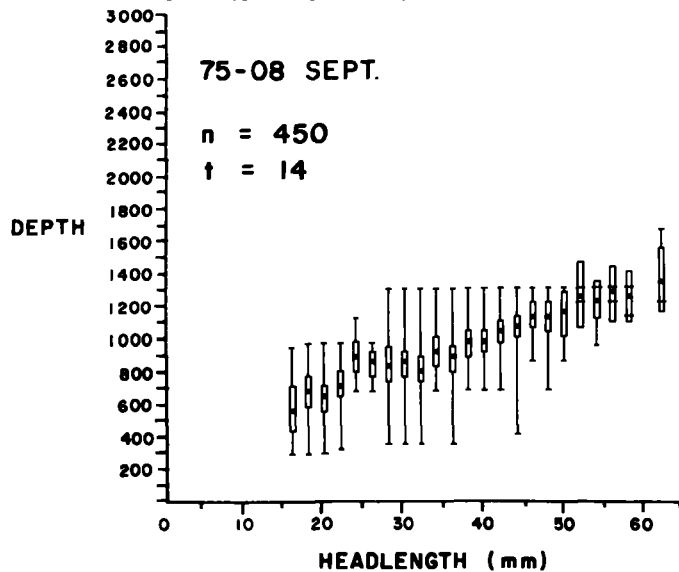
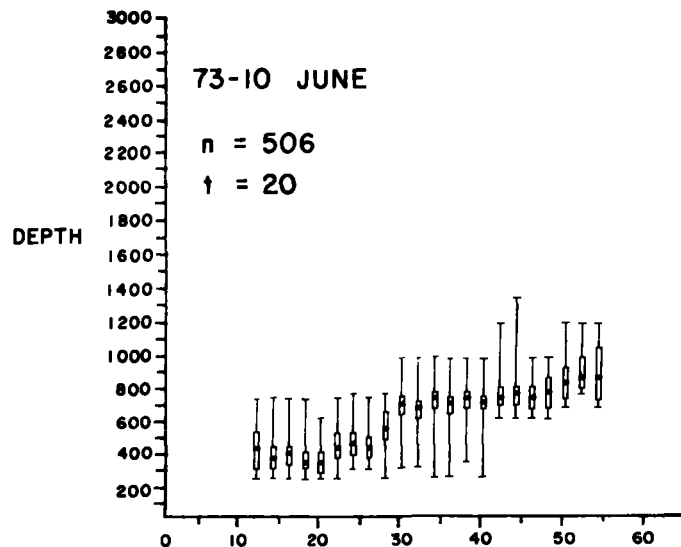
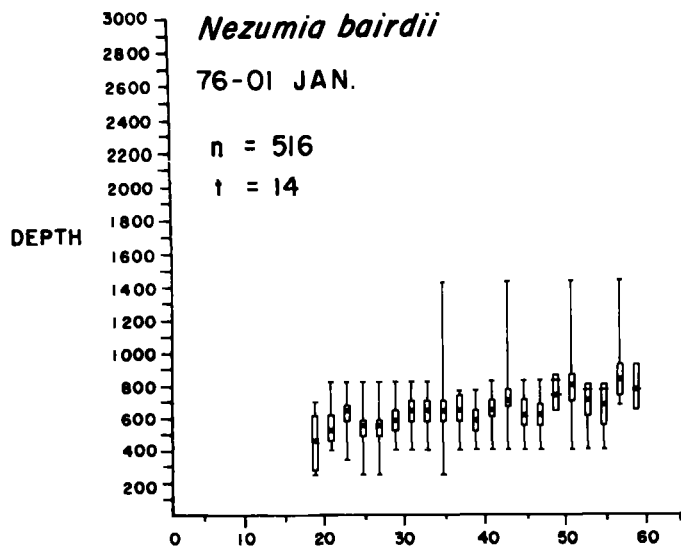


FIGURE 9.—Graph of head length versus depth, by cruise, for *Nezumia bairdii*. The dot is the mean, the rectangle is the range. n = the number of specimens and t = the number of trawls.

fall and the larvae become larger, they would drop out of the water column to the bottom. Length frequencies of *N. bairdii* (Fig. 11) suggested that

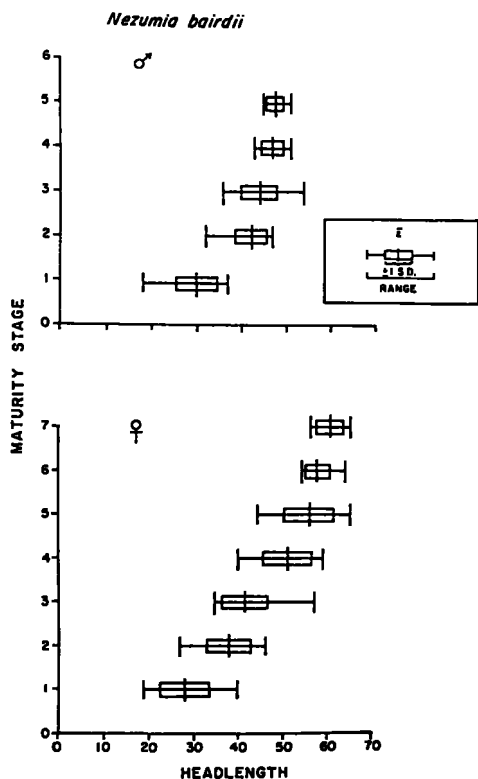


FIGURE 10.—The gonadal maturity stages plotted against head length for *Nezumia bairdii*.

recruitment of young occurred between the months of November and January. No small *N. bairdii* were captured benthically between the proposed deep-water spawning time and the shallower January recruitment spike.

The larger *N. bairdii* occurred deeper than the small ones (Figs. 9, 12) demonstrating the "larger-deeper" phenomenon.

The age and growth analysis of *N. bairdii* presented many problems. Due to the thickness of the sacculus otolith a thin cross section had to be removed from each. After examination of the thin sections, two problems became apparent. First, all of the smaller specimens had two hyaline zones. Because the specimens were obtained on the winter (January; 76-01) cruise, all had hyaline zones around the perimeter as expected. There was, in addition, a well-defined hyaline zone in the interior of all the otoliths obtained from the smallest fishes available ( $\leq 27$  mm HL). Subsequently two hypotheses were proposed: 1) a period of hyaline zone formation (slow growth) occurred between June-July (spawning) and January, and 2) young *N. bairdii* were not available to our trawl until the second winter hyaline zone was forming (age about 1.5 yr).

The first hypothesis was discarded because a period of slow growth within the first 6 mo would have no apparent selective advantage. It should be noted, however, that since the larvae of *N. bairdii* were probably pelagic, a change from planktonic feeding to benthic feeding would have occurred during that time. Such an ontogenetic change occurs in related gadid fishes. Musick (1969) described the

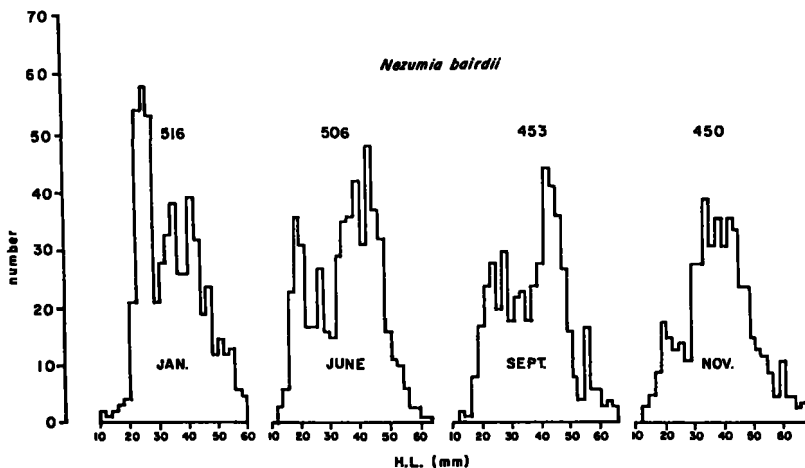


FIGURE 11.—Head length frequency distribution for *Nezumia bairdii* by cruise. The number above each cruise indicates the number of specimens.

ontogenetic transition for *Urophycis chuss* and suggested that the transition from pelagic to demersal adaptations in morphology and behavior occurred within a period of 12-24 h. This short time span would be unlikely to be reflected in macroscopic hyaline band formation. Therefore, the second hypothesis appeared more likely, and led to the conclusion that the juvenile *N. bairdii* remained pelagic until the second winter and then descended from the water column to the bottom where they were captured.

The second problem was that in the older fish (>4 yr) the outer bands were very difficult to define with any degree of confidence. The percentage of unreadable otoliths increased from about 5% in fish <4 yr to about 50% in fish >4 yr. The mean head length of *N. bairdii* with four bands was 42.7 mm, the size at the onset of sexual maturity. Growth may have slowed down to compensate for the energy needed for reproduction, and produced spatially close and obscure hyaline zones. Therefore spawning checks may have had considerable influence on

*Nezumia bairdii*

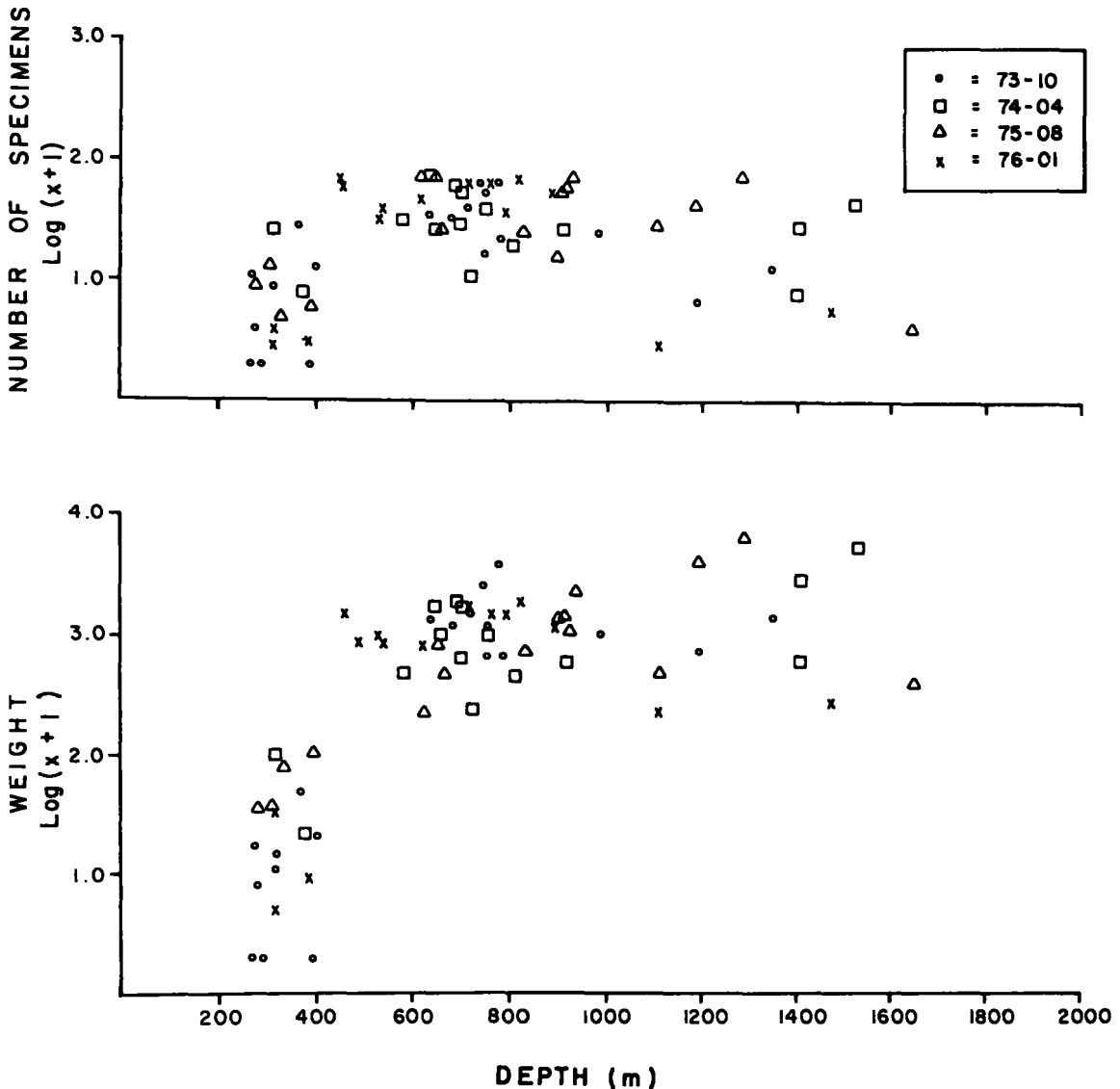


FIGURE 12.—The distribution of log transformed ( $\log(x+1)$ ) abundance and weight of *Nezumia bairdii* at each station plotted against depth.

the interpretation of the hyaline zones.

Using the length at age data, a Walford growth transformation graph was plotted (Beverton and Holt 1957). Instead of calculating the  $L_{\infty}$ , we used our largest specimen (66 mm HL). The estimate of Brody's coefficient ( $K$ ) obtained from this graph was 0.276. Using the Walford graph, the head lengths for those presumed ages >4 yr could be iteratively generated. This method gave a maximum age of approximately 11 yr. The von Bertalanffy growth equation for length was

$$L_t = 66 (L - e^{-0.276 (T+0.16)}).$$

Rannou (1976) studied the age and growth of a congener (*N. sclerorhynchus*) that occupies a similar depth range in the western Mediterranean. He calculated a  $K$  coefficient of 0.16 and an  $L_{\infty}$  of 42.31 mm HL. Thus, although this species is smaller than *N. bairdii*, it has a much slower growth rate, probably attributable to lower productivity in the western Mediterranean compared with the slope off the mid-Atlantic coast of the United States (Koblentz-Mishke et al. 1970).

The length-weight regression for *N. bairdii* (Fig. 2) was analyzed. The solution of the line for *N. bairdii* males was  $\log(\text{weight}) = 0.038(\text{head length}) + 0.083$ ,  $r^2 = 0.810$ , and for females it was  $\log(\text{weight}) = 0.035(\text{head length}) + 0.216$ ,  $r^2 = 0.760$ .

These length-weight relationships are not unlike those summarized by Gordon (1979) for other small macrourids (*Coelorinchus coelorinchus*, *C. occa*, and *Nezumia aequalis*).

In summary, larger *N. bairdii* were captured deeper and the minimum and maximum depths of capture off the mid-Atlantic coast were 270 m and 1,644 m. The fish seasonally migrated to deeper water with the mature fish occurring deeper than immature fish. The males matured at about 45 mm HL and the females became mature at 44 mm HL. *Nezumia bairdii* probably spawned pelagic eggs in July and August and the young apparently remained pelagic until the second winter (January), when they first appeared in bottom trawls. The maximum age of *N. bairdii* was presumed to be 11 yr. The temperature range for *N. bairdii* was from 3.7° to 10.0°C, with the average temperature of capture being 5.3°C (Fig. 6).

#### *Coryphaenoides rupestris* (Gunnerus 1765)

*Coryphaenoides rupestris* is a large macrourid that reaches a total length of about 100 cm (Savvatimskii 1971; Nodzinski and Zukowski 1971; Marshall

and Iwamoto 1973), and is found on both sides of the North Atlantic. In the eastern North Atlantic it ranges from the Trondhjem area to the Bay of Biscay. In the western North Atlantic it is reported to occur from Davis Strait to ca. lat. 37°N (Marshall and Iwamoto 1973), although two specimens (81 and 100 mm HL) were captured by C. Richard Robins<sup>6</sup> at lat. 23°29.8-32.0'N, long. 77°05.5'W. The depth distribution of *C. rupestris* varies from about 180 to 2,200 m (Leim and Scott 1966) with highest abundance occurring between 400 and 1,200 m (Marshall and Iwamoto 1973).

*Coryphaenoides rupestris* is rarely used as a food fish in the United States, but the German Democratic Republic, the Soviet Union, and Poland fish commercially for it in the western North Atlantic. In 1968, the Soviets recorded a harvest of 30,000 tons of *C. rupestris* off Labrador, Baffin Island, and Greenland (Nodzinski and Zukowski 1971). The catches of this macrourid were reported to increase during the second half of the year as the catches of redfish and cod decreased (Savvatimskii 1971).

*Coryphaenoides rupestris* was captured in the Norfolk Canyon area at depths of 578-1,698 m (Fig. 3). Savvatimskii (1971) reported that *C. rupestris* is known to form dense aggregations off the coast of Labrador. In November 1974 an anomalous catch of over 6,000 *C. rupestris* with a total weight >1,000 kg was obtained in a half hour tow in the Norfolk Canyon area. A random subsample of 1,000 specimens was examined and no sexually mature fish were found. Although the head length ranged from 59 to 110 mm, the length-frequency curve was strongly unimodal at 76 mm. The greatest number and biomass of *C. rupestris* caught in "normal" half hour tows was 128 fish comprising 39% of the individuals and 68 kg, and representing 65% of the total catch by weight. The largest specimen captured had a head length of 155 mm.

The head length distribution by depth and by cruise (Fig. 13) suggested a mass movement of *C. rupestris* toward deeper water during the summer months, and a reciprocating movement to shallower water in the winter. In January, the majority of *C. rupestris* was captured between 700 and 800 m, while in June and September there appeared to be a movement toward deeper water. By November the depths of capture decreased and were similar to those of January, and the slope of the head length-depth regression for *C. rupestris* was significantly

<sup>6</sup>C. Richard Robins, Rosenstiel School of Marine and Atmospheric Science, Division of Biology and Living Resources, 4600 Rickenbacker Causeway, Miami, FL 33149.

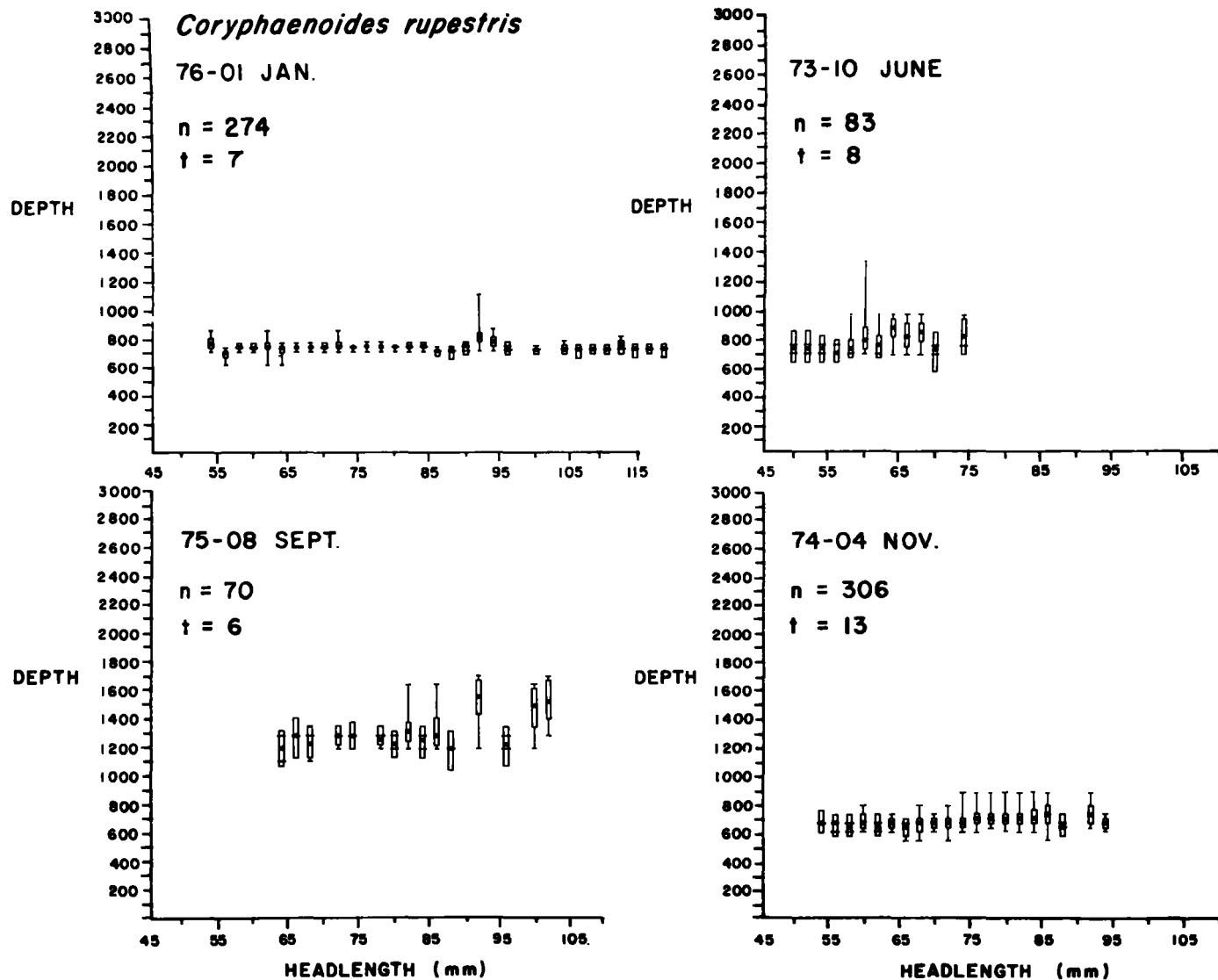


FIGURE 13.—Graph of head length versus depth, by cruise, for *Coryphaenoides rupestris*. The dot is the mean, the rectangle is the 95% confidence interval,

and the lines enclose the range. n = the number of specimens and t = the number of trawls.

different from zero. There was no apparent seasonal size segregation evident as in *Nezumia bairdii*, but the graph of numerical abundance against depth also indicated a general seasonal movement down slope in September (Fig. 14). Similar seasonal movements have been shown by Savvatimskii (1971) off Newfoundland.

Females may be mature from about 104 mm HL and males from 71 mm HL (Fig. 15).

Podrazhanskaya (1971) supported Zarkharov and Mokanu's (1970) theory that *C. rupestris* spawns in Icelandic waters. She stated that *C. rupestris* spawn near Iceland and the Irminger Current could transport the eggs and larvae to Greenland. From Greenland the western branch of the West Greenland Current would transport larvae to Baffin Island where the Labrador Current would move the fish down to the Newfoundland banks. When the fish in the Newfoundland area attain a size of 40-50 cm total length (TL), they start to migrate back to Iceland. Podrazhanskaya gave the modal lengths for *C. rupestris* in each area. The smallest fish (modal TL of 45-47 cm) were found on the Northern Newfoundland bank and the largest (modal TL of 98-100 cm) were found around Iceland. Fish from between Baffin Island and West Greenland had modal lengths

of 60-62 and 78-80 cm, respectively. Podrazhanskaya's (1971) modal-length data for each area in conjunction with Savvatimskii's (1971) age and growth data reveal that the modal-length fish off the Newfoundland banks are about 6 yr old, off Baffin Island they are 9-10 yr, around Greenland they are 15-16 yr, and at Iceland they are over 20 yr. If a spawning migration occurs, it does not preclude spawning by some members of the population not undergoing migration, thereby accounting for the small percentage of ripening fish to be found outside of their primary spawning area.

If Podrazhanskaya's migration theory is valid, some interesting observations can be made. First, the *C. rupestris* found on the east coast of the United States may be derived from the larvae that failed to metamorphose by the time they reached the Newfoundland banks and continued to drift southwest. The predominant currents move south and west from Newfoundland to Cape Hatteras (Worthington 1964; Webster 1969; Gatién 1976), thereby affording a means of transport for unmetamorphosed larvae (Wenner and Musick 1979). Additionally, the modal length for the 7,011 *C. rupestris* caught in the Nor-

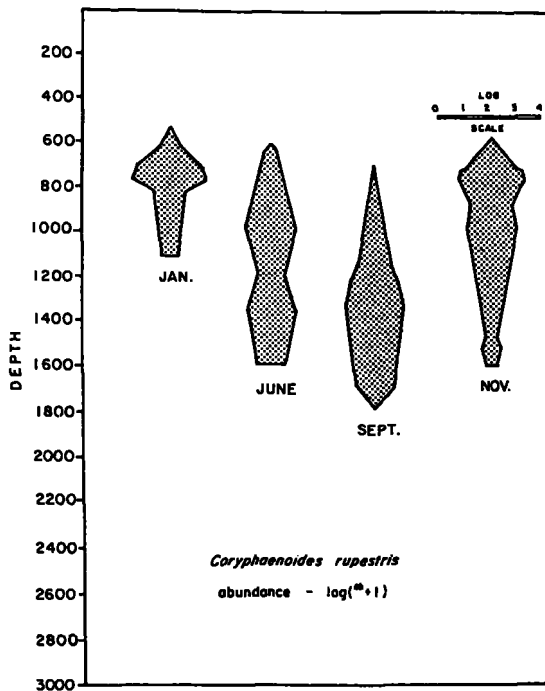


FIGURE 14.—Diagram of depth plotted against the log transformed ( $\log(s + 1)$ ) numerical abundance, by cruise, for *Coryphaenoides rupestris*.

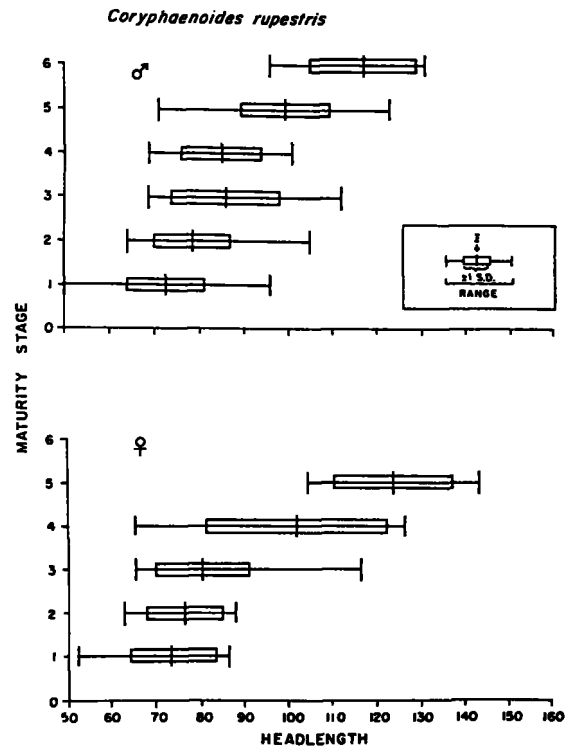


FIGURE 15.—The gonadal maturity stages plotted against head length for *Coryphaenoides rupestris*.



folk Canyon area was 46 cm, exactly that which was found for *C. rupestris* in the Newfoundland bank area. However, no small *C. rupestris* were captured in the Norfolk Canyon area. We found only 2 fish with a head length <40 mm (24 cm TL) and only 10 fish with head length <50 mm (30 cm TL).

The regression line for head length against log (weight) (Fig. 2) was analyzed. The solution for *C. rupestris* males was  $\log(\text{weight}) = 0.023(\text{head length}) + 0.82$ ,  $r^2 = 0.898$ , and for females it was  $\log(\text{weight}) = 0.018(\text{head length}) + 1.16$ ,  $r^2 = 0.885$ .

Unfortunately these length-weight data cannot be compared directly with those summarized by Gordon (1979) because we measured head lengths in our study and he gave standard lengths. We do not have the data at present to compute the regression for head length on standard length for this species.

Temperatures at which *C. rupestris* were captured near Norfolk Canyon ranged from 3.7° to 5.7°C (Fig. 6). The average temperature was 4.9°C.

*Coryphaenoides rupestris* does not follow the "larger-fewer-deeper" pattern shown for *N. bairdii* in Norfolk Canyon because it migrates seasonally (Fig. 16) and the larger specimens traverse the entire bathymetric range (Fig. 13).

In summary, *C. rupestris* migrated seasonally to shallower water in the fall and early winter. Catch per unit effort increased in the fall and winter, and a dense aggregation was found in the fall. Podrazhanskaya's (1971) spawning and migration theory appears feasible but further intensive study is needed. No ripe, running, or spent fish were captured in the Norfolk Canyon area out of 7,011 individuals examined. There was a trend for the larger *C. rupestris* to range deeper but not to the degree that was found in *N. bairdii*. It appears that the distribution of *C. rupestris* was more closely related to temperature than to depth, the species being found mostly within the 4°-5°C range.

#### *Coryphaenoides carapinus* (Goode and Bean 1883)

*Coryphaenoides carapinus* is another small macrourid which grows to about 390 mm TL, and is found on the lower slope and abyss from 1,000 to 3,000 m (Haedrich and Polloni 1976). In the western North Atlantic it has been found between Nova Scotia and Cape Hatteras (lat 37°N) and in the eastern Atlantic from lat. 50°N to the Equator. *Coryphaenoides carapinus* has also been reported from the mid-Atlantic ridge (Marshall and Iwamoto 1973).

In the Norfolk Canyon area *C. carapinus* was cap-

tured at 1,108-2,767 m (Fig. 3). The largest number caught in one trawl was 37 (total weight 550 g). These were captured in September 1975 at a depth of 1,803 m. *Coryphaenoides carapinus* comprised up to 23.4% of a catch in number, but only 4.3% in biomass. The maximum size captured was 90 mm HL.

*Coryphaenoides carapinus* tended to be larger at the lower end of its depth range (Fig. 17). The slope of the regression line for head length with depth was significantly different than zero. The coefficient of determination was 0.346.

Figure 18 displays low numbers and high variability in the capture of *C. carapinus* in relation to depth. The phenomenon of fewer, larger fish at the deeper part of the bathymetric range was evident but obscured because of the relatively small size of *C. carapinus*, low numbers, and contagious distribution.

*Coryphaenoides carapinus* was taken at temperatures of 2.5°-4.2°C with the average temperature being 3.7°C (Fig. 6). Some overlap in distribution with depth and temperature occurred among *C. carapinus*, *C. armatus*, and *C. rupestris*. Because *C. carapinus* is a small species and mostly a benthic feeder (Haedrich and Polloni 1976) and *C. armatus* and *C. rupestris* are large species that forage into the water column (Podrazhanskaya 1971; Haedrich and Henderson 1974; Smith et al. 1979), competitive interaction is probably low.

#### *Coryphaenoides armatus* (Hector 1875)

*Coryphaenoides armatus* is cosmopolitan in distribution, being found in all oceans except the Arctic. It commonly is found from 2,200 to 4,700 m, with a few specimens being captured as shallow as 282 m (Marshall and Iwamoto 1973). Larger individuals have been shown to forage off the bottom for pelagic prey (Haedrich and Henderson 1974; Percy 1975; Smith et al. 1979). *Coryphaenoides armatus* attains a size of 165 mm HL and over 870 mm TL (Iwamoto and Stein 1974). The largest specimen captured in Norfolk Canyon was 146 mm HL. Although *C. armatus* is one of the deepest living macrourids, it is rather well-known biologically because of its broad distribution and availability to deepwater trawls (Haedrich and Henderson 1974; Percy and Ambler 1974; McLellan 1977; Smith 1978).

*Coryphaenoides armatus* was taken in every successful trawl from 2,100 m to our deepest trawl of 3,083 m in the Norfolk Canyon area and virtually was confined to below the 3°C isotherm (Fig. 3). In

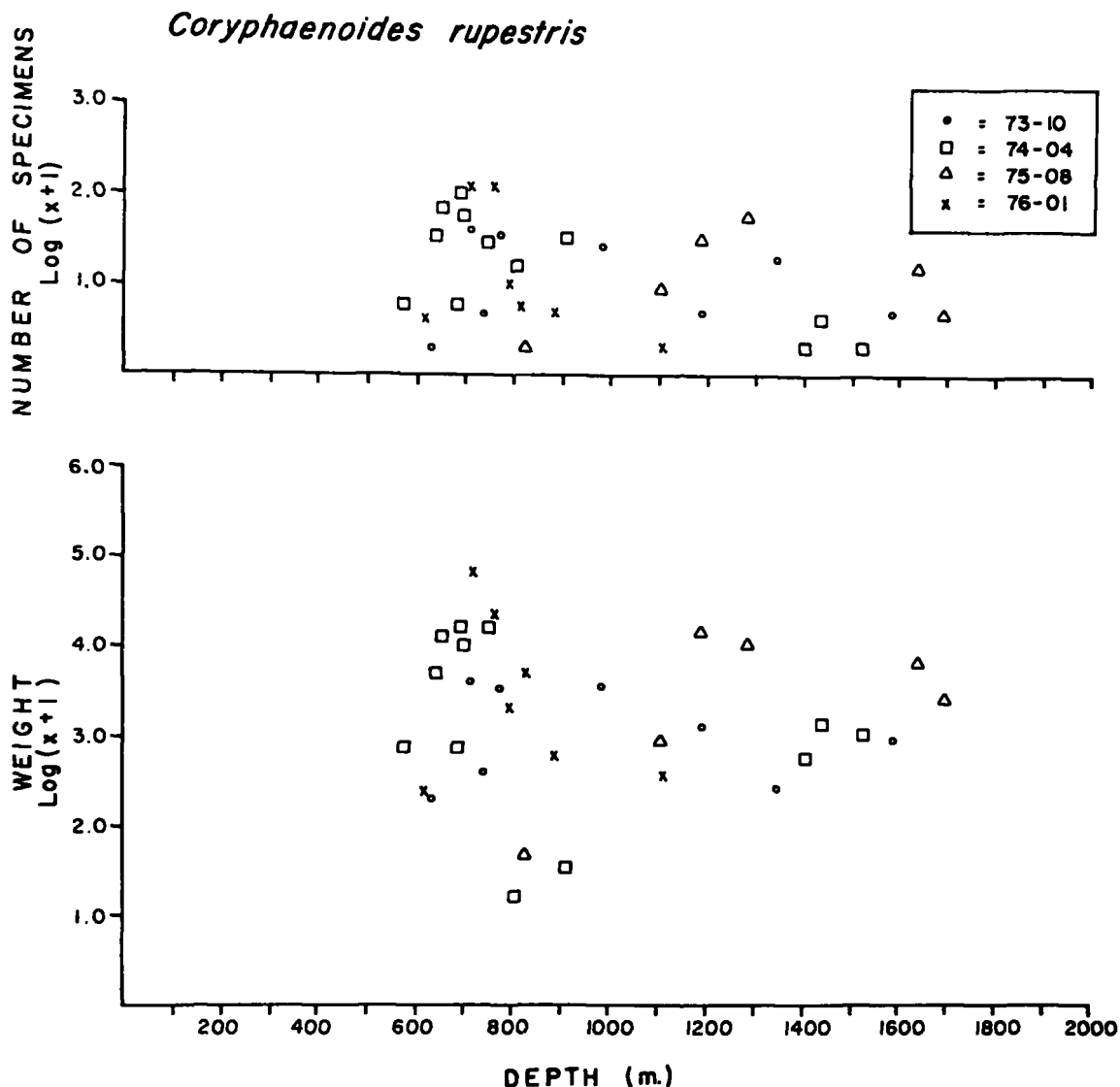


FIGURE 16.—The distribution of log transformed ( $\log(x + 1)$ ) abundance and weight of *Coryphaenoides rupestris* at each station, plotted against depth.

one trawl *C. armatus* comprised 92.7% of the benthopelagic fish numbers and 93.4% of the biomass. In a 1-h trawl the maximum number captured was 76 and the maximum biomass was 21.2 kg.

No increase in fish size with increased depth was evident in the data (Fig. 19) (Table 1), and the slope of the regression line for head length with depth was not significantly different from zero. However, known depth range of *C. armatus* was incompletely sampled in this study, and further samples from greater depth may lead to other conclusions.

The distribution of numerical abundance and weight with depth are shown in Figure 20. *Coryphaenoides armatus* increased in abundance from 2,100 to 2,600 m, beyond which its abundance remained constant.

The regression lines for head length against log (weight) were analyzed (Fig. 2). The solution for males was  $\log(\text{weight}) = 0.017(\text{head length}) + 0.956$ ,  $r^2 = 0.967$ , and for females it was  $\log(\text{weight}) = 0.016(\text{head length}) + 1.029$ ,  $r^2 = 0.972$ .

The maturity stages of *C. armatus* against head

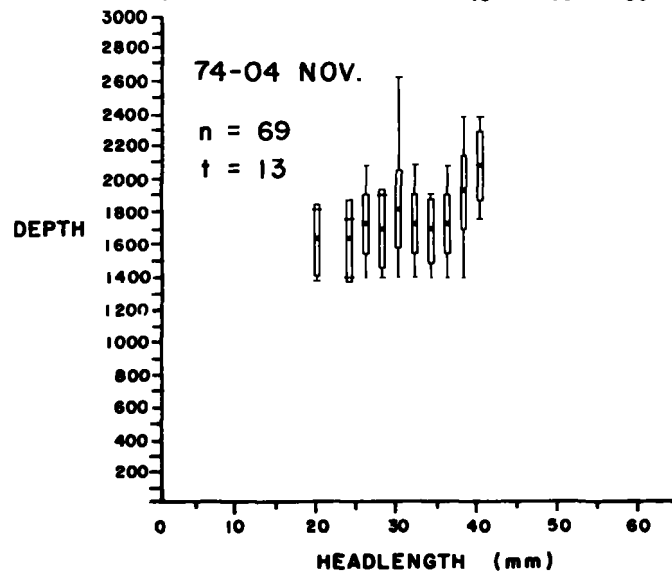
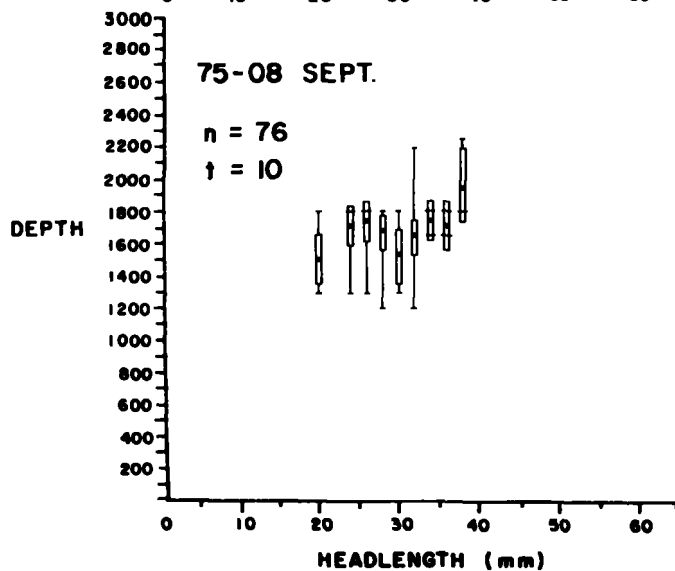
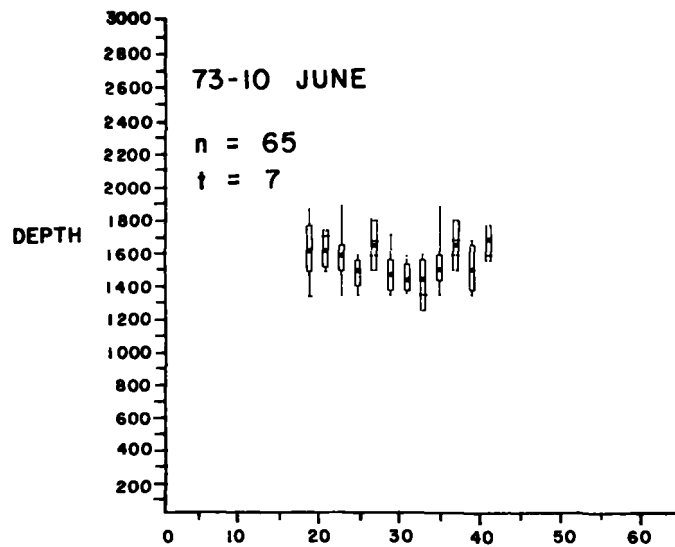
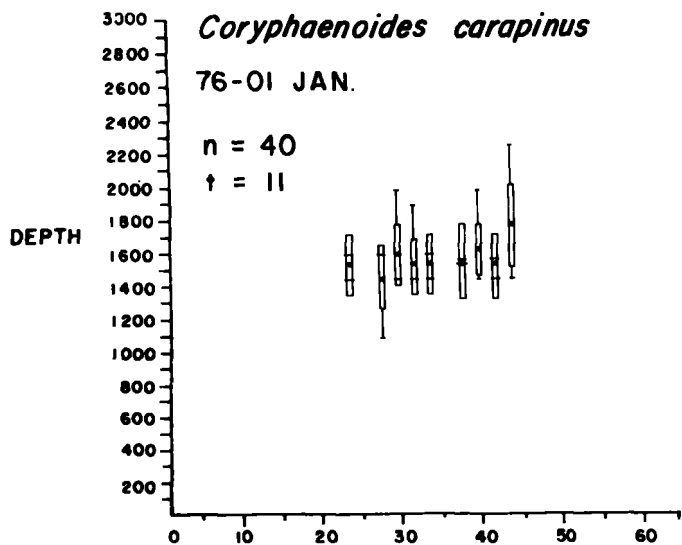


FIGURE 17.—Graph of head length versus depth, by cruise, for *Coryphaenoides carapinus*. The dot is the mean, the rectangle is the 95% confidence interval,

and the lines enclose the range. n = the number of specimens and t = the number of trawls.

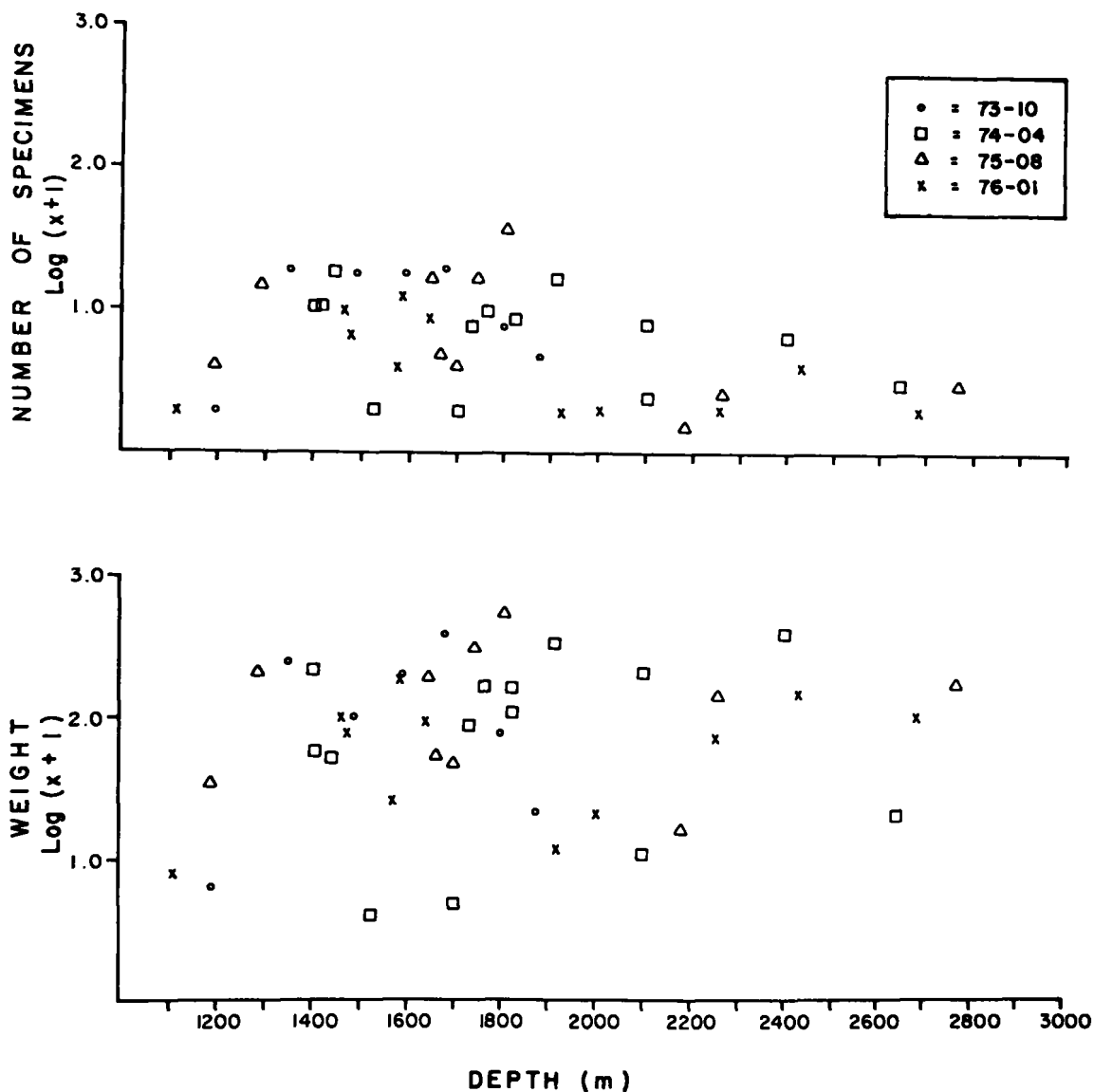
*Coryphaenoides carapinus*

FIGURE 18.—The distribution of log transformed ( $\log(x+1)$ ) abundance and weight of *Coryphaenoides carapinus* at each station plotted against depth.

lengths are shown in Figure 21. No mature males were found, but the females matured at about 78 mm HL. *Coryphaenoides armatus* was captured in temperatures ranging from 2.3° to 3.3°C (Fig. 6). The majority of individuals, however, were caught between 2.4° and 2.9°C during the study and the average temperature was 2.6°C.

#### Distribution of Macrourids With Temperature

Depth distribution has been used commonly throughout the literature to delineate the habitat of various fishes, including macrourids (Macpherson 1981). The temperature ranges for each species in

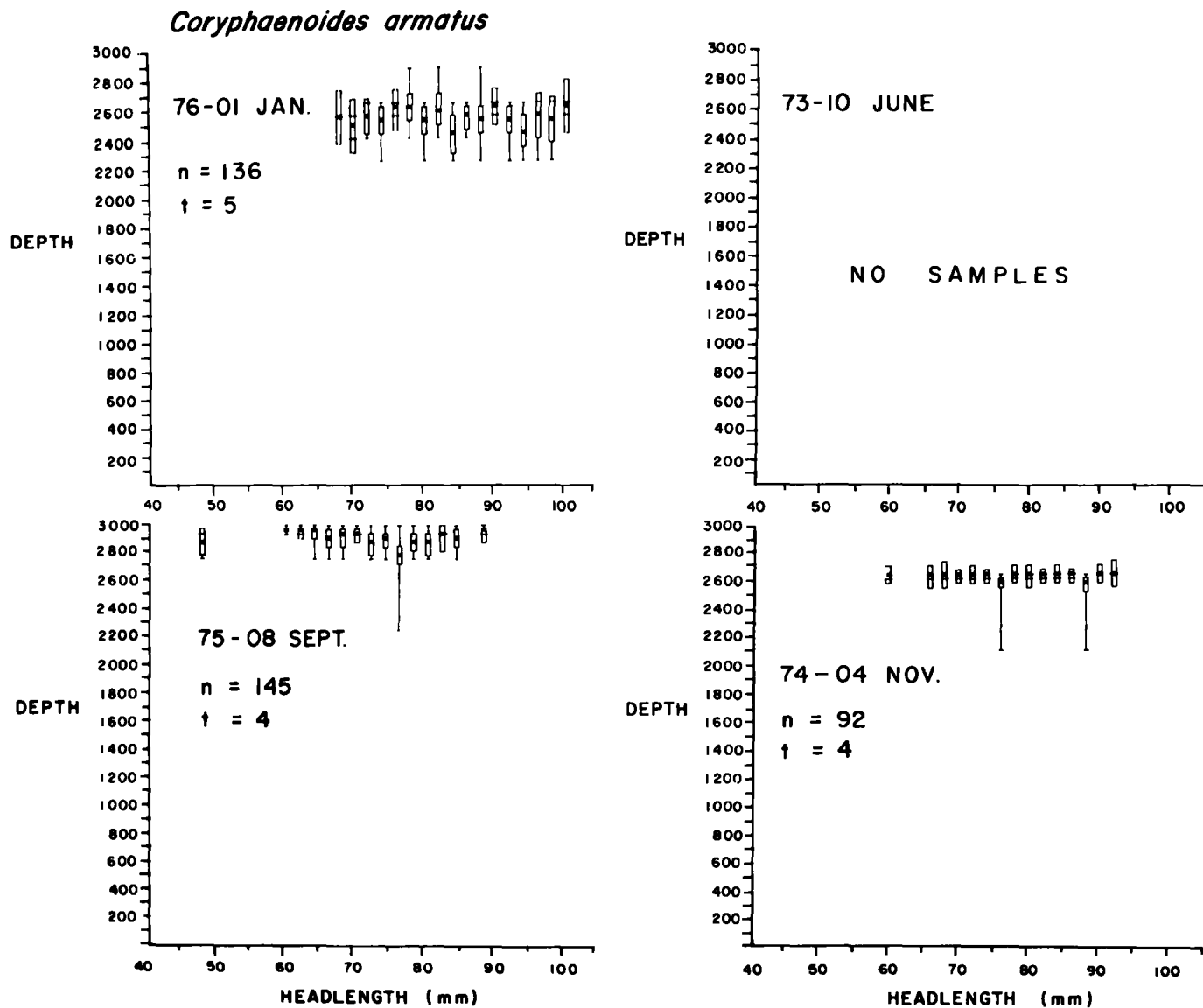


FIGURE 19.—Graph of head length versus depth, by cruise, for *Coryphaenoides armatus*. The dot is the mean, the rectangle is the 95% confidence interval, and

the lines enclose the range. n = the number of specimens and t = the number of trawls.

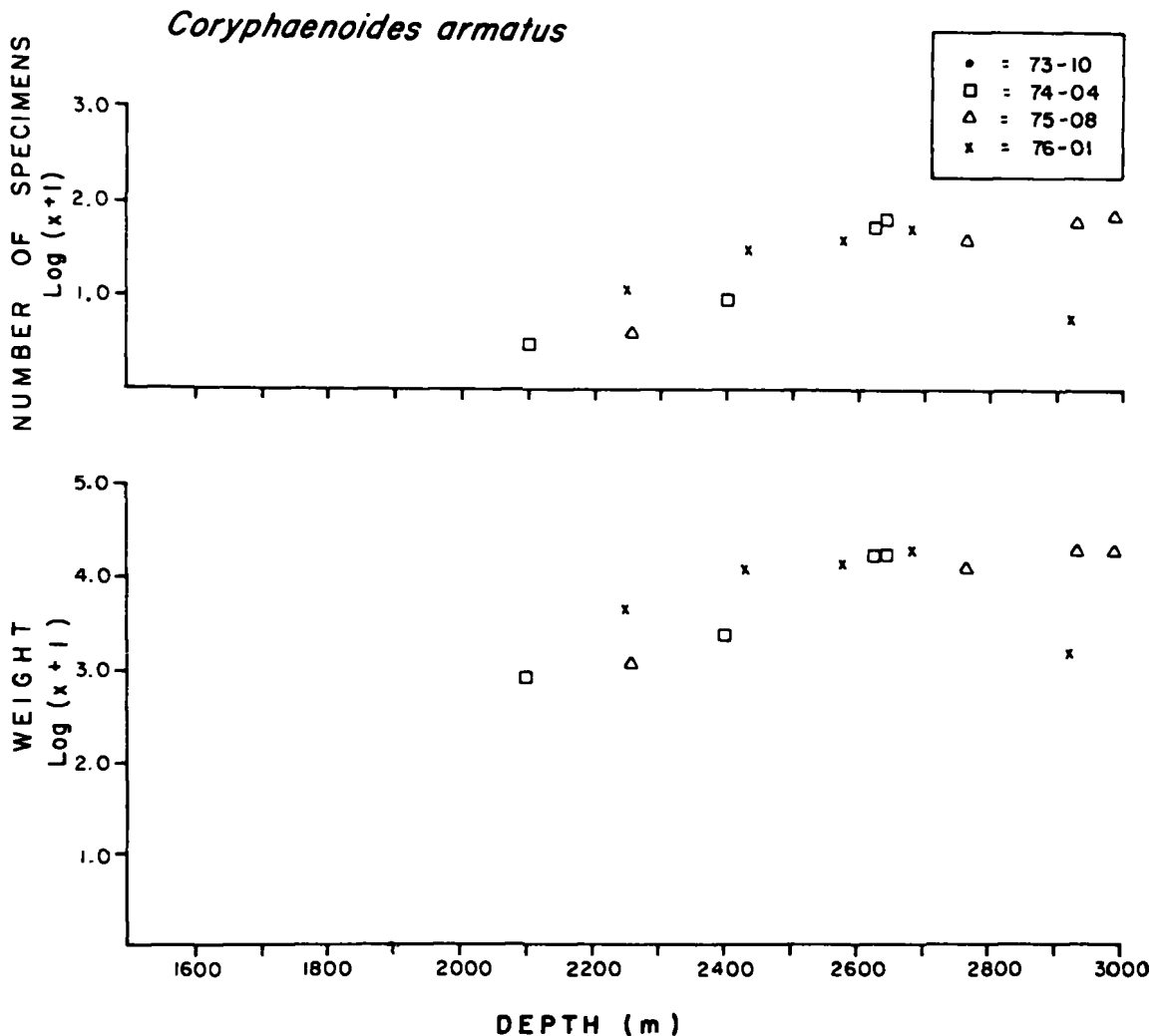


FIGURE 20.—The distribution of log transformed ( $\log(x+1)$ ) abundance and weight of *Coryphaenoides armatus* at each station plotted against depth.

the present study showed some overlap, but the temperatures at which the population modes were found were fairly discrete except for *Nezumia aequalis*, *Nezumia bairdii*, and *Coryphaenoides rupestris*.

In Figure 6 the relationship of species with temperature is more clearly defined. The minimum temperature of each species remained fairly constant as did the maximum and modal temperature for those species in which there was no indication of seasonal migratory patterns (*Coelorinchus carminatus*, *Coryphaenoides carapinus*, *C. armatus*). The 3.5°C minimum temperature found for *C. carapinus* in June was probably not accurate since

the deepest trawl of that cruise did not encompass the entire range of *C. carapinus*. Similarly, the minimal temperatures for *C. armatus* may not be representative.

#### Competition Among Macrourids

Competition among macrourids in the Norfolk Canyon region is probably minimal because the species differ in body size and feeding strategies or, if feeding strategies are similar, the species have different distributions with temperature and depth. Close congeners such as *Nezumia bairdii* and *N. aequalis* might be expected to occupy similar depth

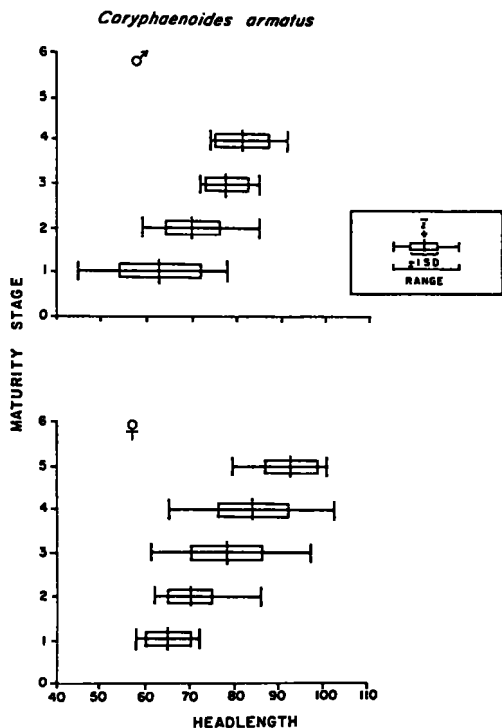


FIGURE 21.—The gonadal maturity stages plotted against head length for *Coryphaenoides armatus*.

and temperature ranges; however, the *N. aequalis* in this area were at the northern limit of their geographic range, occurred in small numbers, and may have been in direct competition with *N. bairdii*. Although *C. rupestris* also occupied the lower section of the two *Nezumia* spp. temperature and depth regimes, direct competition was probably low because of their dissimilarity in mouth size and morphology and related differences in diet (Podrazhanskaya 1971; Geistdoerfer 1975; McLellan 1977).

### Abundance and Density of the Family Macrouridae

In the study area the abundance of macrourids, in water shallower than 2,000 m, was fairly constant with respect to other bottom fishes. The average percent of macrourids by number in each cruise was 16.6% in cruise 73-10 (June), 15.0% in 74-04 (December), 14.6% in 75-08 (September), and 18% in 76-01 (January). The major peaks of abundance were found between 300 and 400 m, where *Coelorinchus c. carminatus* was present, and around 800 m where the complex comprised of *Nezumia aequalis*,

*N. bairdii*, and *Coryphaenoides rupestris* dominated (Fig. 22). In depths of over 2,000 m the numerical dominance of *C. armatus* was evident. Some of the minor inflections can be attributed to the contagious distributions displayed by these fishes.

The graph of macrourid biomass (Fig. 23), as percent of the catch, was similar to that for numerical abundance except for a shift in biomass from 800 m to below 1,000 m between January and June. This was probably because of the seasonal movement of the larger macrourid *Coryphaenoides rupestris*. Between about 1,400 and 2,200 m, macrourids made up a very small portion of the biomass, although their percent by number was comparable with lesser depths. The dominant macrourid in this area, *C. carapinus*, was small, and *Antimora rostrata*, a large morid, was the most abundant member of the benthic fish community from 1,300 to 2,500 m (Wenner and Musick 1977). In depths >2,200 m the biomass of *C. armatus* steeply increased with depth, until it was the predominant member of the benthic community.

All the macrourid species, with the exception of *C. rupestris*, maintained a fairly constant numerical distribution from cruise to cruise. There was apparent variability for *C. carapinus* and *C. armatus*, but this was due to the small number of samples from deeper areas. Distribution of macrourids as the percent of catch revealed a gradual replacement of species with depth, and the predominance of *C. armatus* in depths >2,500 m.

Macrourids made up a major numerical portion of the benthic fish community from 300 m to the deepest station at 3,083 m. Macrourids were also a main component of the biomass of the communities from 300 to 3,083 m, excluding the 1,300-2,500 m range where the morid, *A. rostrata*, dominated.

Although Macrouridae is a dominant family in the Norfolk Canyon area, the potential for a fishery is essentially nonexistent. *Coryphaenoides rupestris* is the only species which attains an appreciable size in the mid-Atlantic area; a modal length of 46 cm TL. However, this size is much smaller than typically found in the North Atlantic and the density of organisms is generally low (normally <0.86 individuals/100<sup>2</sup>). In addition, *C. rupestris* demonstrates a tropical submergence, being found deeper in lower latitudes. The depth range of this species in the Norfolk Canyon area (578-1,698 m), combined with smaller size and lower density of organisms, indicate that a commercial fishery would not be economically feasible.

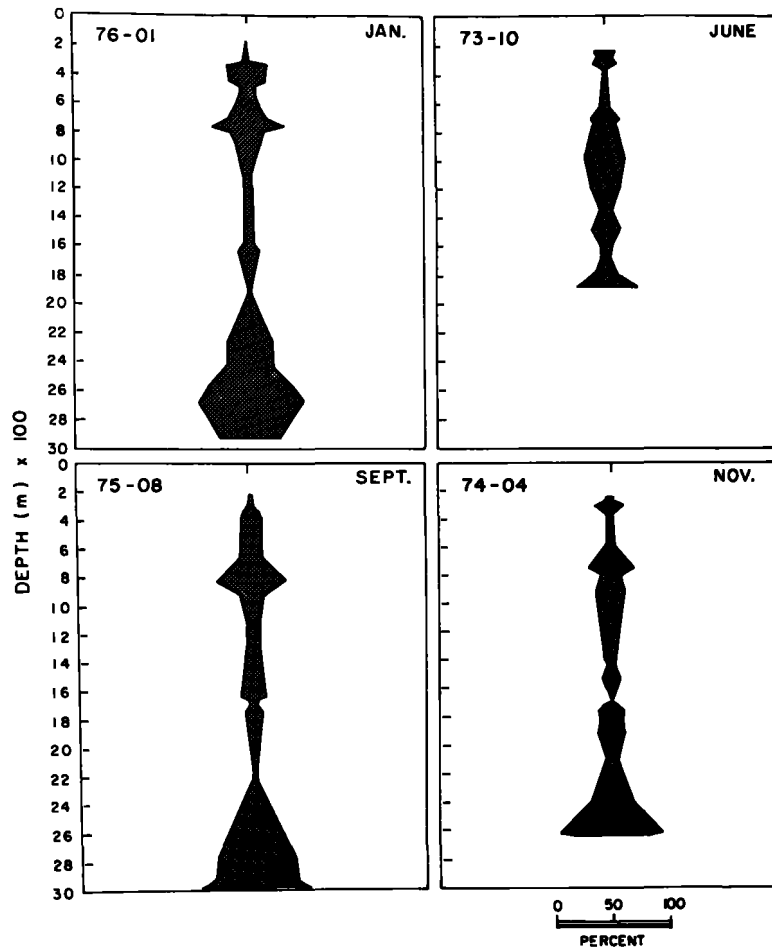


FIGURE 22.—Depth versus relative abundance (as percent, by number, of total capture) for the family Macrouridae, by individual cruise.

### Comparison With Other Studies

The comparison of this study with others in the North Atlantic lends support to Marshall and Iwamoto's (1973) hypothesis that the greatest diversity of macrourids is in the bathyal tropical regions. The number of macrourid species declines from tropical to boreal regions. Marshall and Iwamoto (1973) reported 32 macrourid species from the Caribbean and Gulf of Mexico, but only 22 species were captured during our study (Table 2). Bullis and Struhsaker (1970) found that Macrouridae was one of the dominant families on the western Caribbean slope between 201 and 400 fathoms (368-732 m). The deepest stratum sampled was 451-500 fathoms (825-914 m), and macrourids (9 species) comprised about 67% of the individuals captured within these depths. Within the same depths in the Norfolk Can-

yon area the dominant macrourids (4 species) contributed about 31% to the total catch.

Merrett and Marshall (1981) remarked on the high diversity (and apparent resource partitioning) of macrourids from a tropical upwelling area off northwest Africa and reported 26 species from there. They found 18 species on the slope ( $\leq 1,600$  m), including four species of *Nezumia*. Bathygadine macrourids were important off Africa but virtually absent in our study area. Thus macrourid diversity is probably highest on the continental slope in the tropics, particularly in areas of higher productivity. In addition, high diversity is manifested there at several taxonomic levels, from the species to the subfamily.

Haedrich et al. (1975) reported the capture of 121 macrourid specimens (3 species) in 29 trawls off Southern New England. Their trawl depths ranged from 141 to 1,928 m. Their findings were similar to



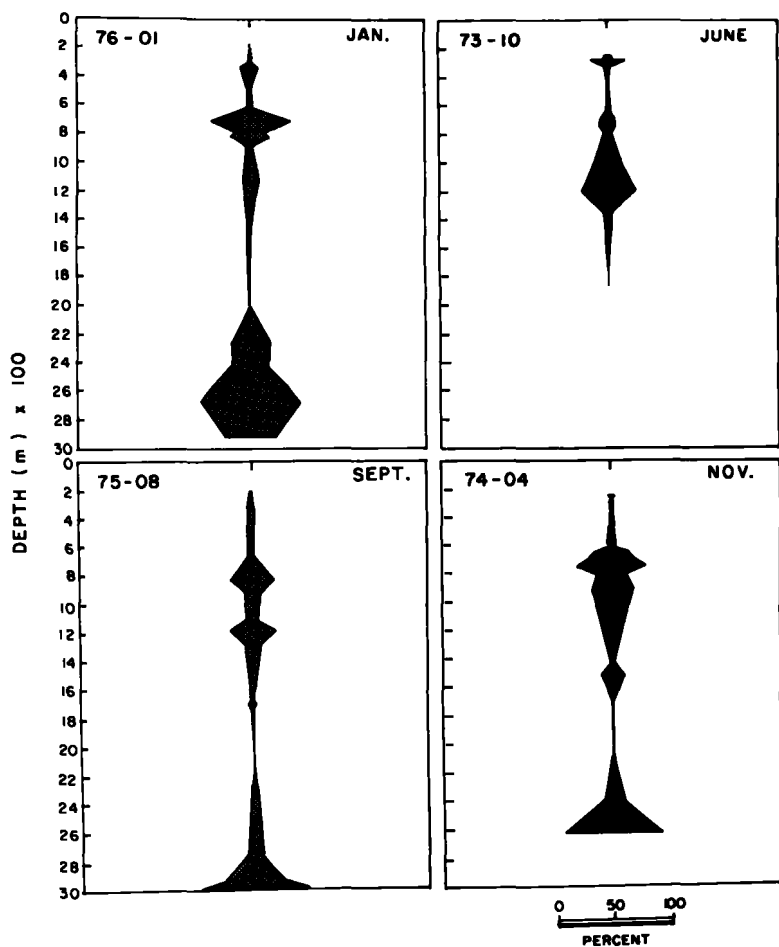


FIGURE 23.—Depth versus relative abundance (as percent, by biomass, of total capture) for the family Macrouridae, by individual cruise.

TABLE 2.—Species captured during study, with total number and total weight.

| Species                                     | Total number | Total weight (g) | Species                                     | Total number | Total weight (g) |
|---|--------------|------------------|---|--------------|------------------|
| <i>Coelorinchus c. carminatus</i>           | 1,827        | 38,597           | <i>Coryphaenoides colon</i> <sup>1</sup>    | 1            | 20               |
| <i>Coelorinchus caribbaeus</i> <sup>1</sup> | 10           | 419              | <i>Coryphaenoides leptolepis</i>            | 12           | 4,922            |
| <i>Coelorinchus occa</i> <sup>1</sup>       | 1            | 2                | <i>Ventrifossa occidentalis</i>             | 60           | 1,449            |
| <i>Nezumia aequalis</i>                     | 285          | 4,041            | <i>Ventrifossa macropogon</i>               | 1            | 8                |
| <i>Nezumia bairdii</i>                      | 2,222        | 72,865           | <i>Hymenocephalus gracilis</i> <sup>1</sup> | 1            | 1                |
| <i>Nezumia longebarbatus</i> <sup>2</sup>   | 12           | 1,299            | <i>Hymenocephalus italicus</i> <sup>1</sup> | 1            | 12               |
| <i>Nezumia sclerorhynchus</i>               | 1            | 8                | <i>Bathygadus favosus</i>                   | 2            | —                |
| <i>Nezumia cyrano</i> <sup>1</sup>          | 1            | —                | <i>Bathygadus macrops</i> <sup>1</sup>      | 1            | 22               |
| <i>Coryphaenoides rupestris</i>             | 7,120        | 1,229,304        | <i>Sphagemacrus grenadae</i> <sup>2</sup>   | 4            | 30               |
| <i>Coryphaenoides carapinus</i>             | 213          | 4,703            | <i>Macrourus bergi</i> <sup>3</sup>         | 2            | 4,470            |
| <i>Coryphaenoides armatus</i>               | 391          | 120,456          | <i>Gadomus dispar</i> <sup>1</sup>          | 1            | —                |

<sup>1</sup>Range extension from the Gulf of Mexico-Caribbean area.

<sup>2</sup>Also reported by Haedrich and Polloni (1974).

<sup>3</sup>Range extension from Boreal Northwest Atlantic.

those in the present study within the 350-1,100 m depth interval. Respectively, the family Macrouridae accounted for 21% and 22.4% of the fishes captured in these depth intervals.

Haedrich and Krefft (1978) studied the fish fauna in the Denmark Strait and Irminger Sea. In the five fish assemblages that they reported, macrourids were abundant in the 2,026-2,058 m assemblage (22.4%) and very dominant in the 763-1,503 m (48.3%) and 493-975 m (55.4%) assemblages. Macrourids were conspicuously absent from their group three assemblage, although it was well within macrourid depth and temperature range (280-776 m, 1.4°-7.4°C). An interesting aspect of Haedrich and Krefft's (1978) study was evident in their group two assemblage. *Coryphaenoides rupestris* was the highly dominant fish (48.3%) in this group, and the temperature range of this group (3.9°-5.6°C) corresponded closely to the temperature range we found for *C. rupestris* in the present study (3.7°-5.7°C).

Pearcy et al. (1982) summarized data on deep-sea benthic fishes collected over several years off Oregon (Day and Pearcy 1968; Pearcy and Ambler 1974). Iwamoto and Stein (1974) reported 11 species of macrourids from the northeast Pacific and Pearcy et al. (1982) recorded 8 of these off Oregon. A comparison of these data with ours shows that the greatest contrast in the two areas is on the upper and middle slope (500-1,000 m) where five common species are regularly encountered in the western Atlantic (*Coelorinchus c. carminatus*, *Nezumia bairdii*, *C. aequalis*, *Coryphaenoides rupestris*, and *Ventriofossa occidentalis*), but Pearcy et al. (1982) recorded no macrourid as common. This faunal difference may be due to the high density off Oregon of scorpaeniform and lycodine fishes, many of which may fill niches on the upper slope occupied by macrourids elsewhere. The macrourid fauna in depths >2,000 m have many similarities to our study. *Coryphaenoides armatus* becomes increasingly dominant below this depth and often is the only species captured deeper than 3,000 m in both areas (see also Musick and Sulak 1979). Among other macrourid species *Coryphaenoides leptolepis* is usually second or third in abundance at abyssal depths in both regions (Musick and Sulak 1979).

This distribution pattern is very different from that reported for the continental rise in the tropics off west Africa (Merrett and Marshall 1981) where *C. armatus* and other large rat tails were very rare. Marshall and Merrett (1981) speculated that the rarity of large predatory scavengers in the upwelling area they studied might be because of the competitively superior fishes of small size which were

better adapted to use the constant abundant food supply there. This speculation is not supported by data from the southern Sargasso Sea and Bahamas (Musick and Sulak unpubl. data), a tropical region quite low in productivity, in which large rat tails, such as *C. armatus*, are also very rare. The virtual absence of *C. armatus* from tropical abyssal areas may be due instead to some restriction on the life history of the species. Musick and Sulak (1979) have suggested that this species (along with some other large species of predator/scavenger such as *C. rupestris* and *Antimora rostrata*) may migrate to boreal areas to spawn. The tropics may be too far removed from such spawning areas for individuals to successfully return.

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