

Feeding of Roundnose Grenadier (*Coryphaenoides rupestris*) and its Trophic Relationships in the North Atlantic*

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Abstract

The food spectra of roundnose grenadier from the continental slope areas of eastern Canada, West Greenland, Iceland and Hatton Bank and from the thalassobathyal zones of Reykjanes Ridge and the northern part of the Mid-Atlantic Ridge are compared and changes in feeding by region and fish size are demonstrated. Roundnose grenadier from the continental slope areas of the North Atlantic are shown to be consumers mainly of the second order, their food consisting typically of crustaceans (amphipods, euphausiids, mysids, small decapods and copepods), with fish and cephalopods being generally of much less importance. In the thalassobathyal areas of the North Atlantic, roundnose grenadier are consumers of the third or fourth order, their food consisting mainly of various fish species (myctophids, bathylagids, serrivomerids, chauliodontids and searsiids) and large crustaceans (decapods). The differences are discussed in relation to the environmental conditions and the trophic structures of the communities in the different regions.

Introduction

Roundnose grenadier are found on the slopes of the continental shelves throughout the North Atlantic from about 37°N off the United States coast northward to Baffin Island, off West Greenland and Iceland, and in the Barents Sea (Savvatimsky, MS 1969). They occur in depths generally exceeding 400 m, and USSR investigations in the Northwest Atlantic have shown that commercial concentrations exist off Newfoundland and Labrador in 500-1,000 m. Recent studies have shown roundnose grenadier to be part of the ichthyofauna of Reykjanes Ridge and the northern part of the Mid-Atlantic Ridge (Gushchin and Kukuev, 1981), and on the continental slope off Northwest Africa (Golovan, 1978).

Various aspects of the biology of roundnose grenadier have been studied, e.g. age and growth by Savvatimsky (1971, 1972), parasites by Zubchenko (1981), reproduction by Grigorev (1972) and Geistdoerfer (1979), and food and feeding by Podrazhanskaya (1971), Konstantinov and Podrazhanskaya (1972) and Gushchin (1982a). Conflicting hypotheses have evolved from these and other studies on the extent of migrations and the population unity of roundnose grenadier in the North Atlantic. The absence of sexually mature individuals in Northwest Atlantic catches from depths to 1,000 m and the discovery of spawning grounds south of Iceland have led to the opinion that

eggs and larvae drift in the Irminger Current to West Greenland, from which the young are dispersed by the Baffin Land and Labrador Currents to settle off Labrador and northeastern Newfoundland, and that the maturing fish return to the Icelandic area for spawning (Podrazhanskaya, 1971). The capture of roundnose grenadier in the pelagial over great depths (Haedrich, 1974) is indirect evidence of migration opportunities for the species.

Despite the opinions of some researchers that grenadiers are poor swimmers due to their body shape and are unlikely to undertake extensive migrations (Savvatimsky, 1972; Parsons, 1976), some recent papers support, to a certain degree, the idea of population unity of roundnose grenadier throughout the North Atlantic (Alekseev *et al.*, 1979; Marti, 1980; Zubchenko, 1981). In this paper, with the use of data on feeding of roundnose grenadier in various regions, an attempt is made to show the position of the species in the trophic system of the North Atlantic.

Materials and Methods

The data in this paper were derived from analyses, by the authors and their colleagues, of the stomach contents of roundnose grenadier which were collected at different times by USSR research vessels in various areas of the North Atlantic (Fig. 1). The laboratory

* Based on a paper presented at the NAFO Special Session on "Trophic Relationships in Marine Species Relevant to Fisheries Management in the Northwest Atlantic", held at Leningrad, USSR, 14-16 September 1983.

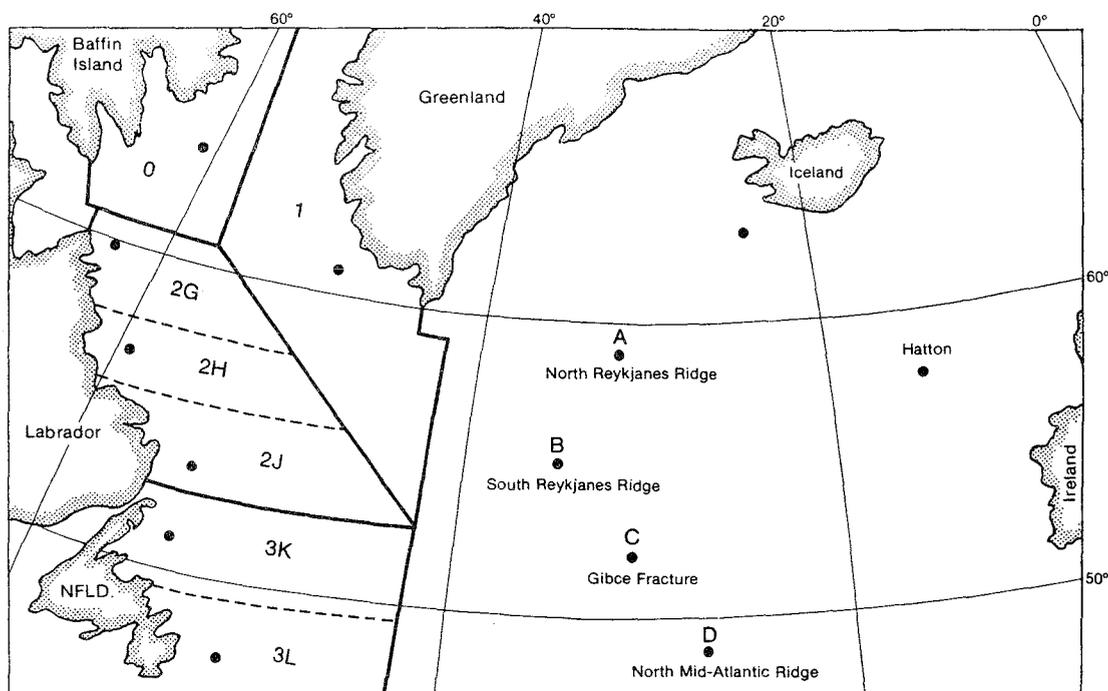


Fig. 1. The North Atlantic region showing the locations of roundnose grenadier samples used in this paper.

analyses involved 1,371 specimens from the Northwest Atlantic in areas extending from West Greenland and Baffin Island to the northern slope of Grand Bank off Newfoundland, 261 specimens from continental slope areas of the Northeast Atlantic (Iceland and Hatton Bank), and 1,330 specimens from Reykjanes Ridge and northern Mid-Atlantic Ridge.

The roundnose grenadier samples were examined according to traditional methods of studying feeding relationships in fishes (Borutskiy, 1974). At sea, the specimens without broken tails were measured as total length in centimeters and weighed in grams, the degree of stomach fullness was estimated by the traditional method used by Podrazhanskaya (1968, 1971), and the stomachs were extracted and preserved in 4% formalin for laboratory analysis. The samples contained specimens which ranged in length from 8 to 110 cm and had gonads at all maturity stages of the reproductive cycle. In the laboratory, each stomach was weighed, and the food items were separated into identifiable components and weighed to the nearest 0.1 g. For analysis by area and fish size, the weights of the various food components were expressed as percentages of the total weight of all food in the stomachs containing food. The total feeding index was calculated as the ratio of total weight of food to total weight of fish sampled, multiplied by 10,000 (expressed as ‰).

In addition to the data summarized in this paper, the feeding of roundnose grenadier has been studied

by field analysis (incidence of food items) of large numbers of stomachs from the Northwest Atlantic (>13,000) and from the Reykjanes Ridge and northern Mid-Atlantic Ridge in the Northeast Atlantic (>100,000 specimens) (Podrazhanskaya, 1968, 1969, 1971; Konstantinov and Podrazhanskaya, 1972; Gushchin, 1982a). Also, the feeding relationships of deepwater ichthyofauna have involved the field (>8,600 specimens) and laboratory (154 specimens) analyses of stomachs of other fishes which inhabit the same depth ranges and areas as roundnose grenadier in the North Atlantic (Konstantinov and Podrazhanskaya, 1972; Gushchin, 1982b). This paper incorporates information from those studies in evaluating the feeding relationships between roundnose grenadier and other species.

Results

Food composition by area

Northwest Atlantic slope areas. From the sampling of roundnose grenadier in various parts of the region, from Baffin Island and West Greenland southward to the Grand Bank, representatives of 74 different taxa belonging to nine major groups of invertebrates and four families of fishes were found in the stomachs (Table 1). Empty stomachs generally constituted less than 30% of those examined from the various areas, except in Div. 3K and 3L where 66 and 81% respectively were empty, the latter value being based on a very

TABLE 1. Food composition of roundnose grenadier (% by weight) from various areas of the North Atlantic. (See Fig. 1 for locations of areas sampled.)

Stomach contents	Northwest Atlantic areas												
	Northwest Atlantic slope areas							Northwest Atlantic areas					
	0	1	2G	2H	2J	3K	3L	Slope areas		Thalassobathyal ^a			
								Iceland	Hatton	A	B	C	D
Cephalopoda	5.4	8.7	9.4	2.9	8.2	3.3	1.1	2.6	9.0	7.0	24.6	4.3	5.5
Chaetognatha	0.6	1.8	1.3	5.8	2.4	0.2	—	0.3	—	0.2	0.0	0.1	0.0
Polychaeta	2.5	0.3	0.8	0.1	1.5	0.0	—	0.0	—	—	0.0	0.0	—
Scyphozoa	—	—	—	—	—	—	—	—	—	8.9	4.0	1.7	3.5
Tunicata	—	1.9	1.2	0.9	1.3	3.1	—	0.8	—	0.3	0.3	0.1	0.1
Crustacea	85.0	70.9	53.0	84.3	57.8	91.5	27.3	88.1	76.3	14.5	18.7	36.2	23.7
Amphipoda	49.0	28.2	35.9	76.6	25.4	3.8	0.4	1.0	—	0.8	0.6	1.3	0.1
Copepoda	5.1	1.6	8.5	0.8	6.6	1.5	4.6	0.1	0.5	0.1	0.2	1.3	0.3
Decapoda	4.4	12.9	2.1	2.3	13.2	84.5	18.5	51.4	55.9	7.8	12.7	19.8	18.9
Euphausiacea	5.4	9.8	6.5	4.6	12.6	1.7	—	35.5	—	0.4	1.2	0.4	0.4
Isopoda	—	—	—	—	—	—	—	—	0.1	0.0	—	0.4	0.1
Mysidacea	21.1	18.4	0.0	—	—	—	3.8	0.1	11.9	3.1	3.1	8.4	3.2
Ostracoda	—	—	—	—	—	—	—	—	0.4	—	0.3	0.3	0.0
Unidentified	—	—	—	—	—	—	—	—	7.5	2.3	0.6	4.3	0.7
Pisces	6.5	8.3	30.5	2.7	28.8	0.8	70.2	4.8	12.2	67.5	52.1	57.0	66.0
Bathylagidae	—	—	—	—	—	—	—	—	—	28.4	7.9	1.7	8.8
Chauliodontidae	—	—	—	—	—	—	—	—	—	3.4	2.5	5.4	4.0
Cottidae	—	2.8	—	—	—	—	—	—	—	—	—	—	—
Malacosteidae	—	—	—	—	—	—	—	—	—	—	—	5.8	5.8
Melamphaidae	—	—	—	—	2.0	—	—	—	—	—	1.9	3.5	0.9
Myctophidae	2.1	—	22.6	0.3	1.6	—	69.6	—	12.2	10.4	8.8	10.6	28.6
Paralepididae	—	—	—	—	—	—	—	—	—	10.9	—	—	—
Scorpaenidae	0.6	—	—	—	7.2	—	—	—	—	—	—	—	—
Searsiidae	—	—	—	—	—	—	—	—	—	—	4.3	1.5	11.8
Serrivomeridae	—	—	—	—	—	—	—	—	—	7.9	19.0	18.3	1.8
Unidentified	3.8	5.5	7.9	2.4	18.0	0.8	0.6	4.8	—	6.5	7.7	10.2	4.3
Unidentified food	—	8.1	3.8	3.3	—	1.1	1.4	3.4	2.5	1.6	0.3	0.6	1.2
Total stomachs	727	156	97	79	125	172	15	236	25	578	255	338	159
Empty stomachs (%)	29.2	25.6	24.7	18.9	8.8	66.3	81.0	6.8	40.0	44.2	14.2	27.2	17.0
Feeding index (‰)	64	28	20	34	35	7	20	43	36	35	39	27	32

^a A = North Reykjanes Ridge, B = South Reykjanes Ridge, C = Gibbs Fracture, D = North Mid-Atlantic Ridge.

small sample. The feeding index was highest in Subarea 0 and lowest in Div. 3K. Invertebrates predominated with considerably more than 50% of the food (by weight) consisting of crustaceans, mainly amphipods (*Parathemisto libellula*, *P. abyssorum*), copepods (*Calanus hyperboreus*, *C. finmarchicus*), euphausiids (*Meganyctiphanes norvegica*, *Nematoscelis megalops*), and decapods (shrimps). Other invertebrates consumed in small quantities in most areas were cephalopods, chaetognaths, polychaetes and tunicates. Fish were eaten in variable amounts in all areas, with myctophids being the most consistent group.

The composition of food organisms in the stomachs varied somewhat in different areas of the Northwest Atlantic (Table 1). In the northern areas (Subareas 0 and 1), the food consisted mainly of crustaceans, with amphipods (hyperiid) and mysids being the main components in both areas and decapods (shrimp) and euphausiids being also significant in Subarea 1. Off northern and southern Labrador (Div. 2G and 2J), the stomach contents were quite similar,

with crustaceans and fish being the major components. Among the crustaceans, amphipods were dominant in both divisions but decapods and euphausiids were also significant in Div. 2J. In contrast, the roundnose grenadier off central Labrador (Div. 2H) fed mainly on crustaceans (amphipods), with fish and other invertebrates being rather insignificant. Off northeastern Newfoundland (Div. 3K), the diet again consisted mainly of crustaceans but decapods replaced amphipods as the major food type. On the northeastern slope of Grand Bank (Div. 3L), fish (myctophids) was the main component in the very small number of specimens examined.

Northeast Atlantic slope areas. Like most of the Northwest Atlantic samples, crustaceans comprised the major food component in the specimens from Iceland and Hatton Bank (Table 1), with other invertebrates and fish being relatively unimportant. Crustaceans were represented by decapods and euphausiids in the Iceland sample and mainly by decapods with some mysids in the small sample from

Hatton Bank. Although the feeding index was similar in both cases, only 7% of the Iceland specimens had empty stomachs.

Northeast Atlantic thalassobathyal. The food composition of roundnose grenadier in the thalassobathyal of Reykjanes Ridge and the Mid-Atlantic Ridge included more than 90 different types of organisms which constitute the macroplankton and micronekton communities over the summits of the underwater mounts. In the four areas where samples were collected, representatives of 11 major groups of invertebrates and eight families of fish were found in the stomachs (Table 1). There were practically no bottom or near-bottom organisms. Empty stomachs constituted 14–44% of those examined from the different areas, and the feeding index varied over a relatively narrow range (27–39‰). Fishes were represented mainly by Myctophidae (*Benthosema glaciale*, *Lampanyctus crocodilus*), Serrivomeridae (*Serrivomer beani*) and Bathylagidae (*Bathylagus euryops*); crustaceans were represented mainly by shrimps (*Acantheephyra*, *Pasiphae*, *Gennades*, *Sergestes*); and cephalopods were represented by squids (*Mastegoteuthis agassizi*, *Gonatus fabricii*, *Todarodes sagittatus*).

Unlike roundnose grenadier from the Northwest and Northeast Atlantic continental slopes, those from the thalassobathyal fed mainly on various fishes, with crustaceans being second in importance (Table 1). Among the fish types consumed in the northern part of Reykjanes Ridge (area A), bathylagids were dominant with paralepidids, myctophids, serrivomerids and chauliodontids being of lesser importance. In the southern part of the Ridge (area B), serrivomerids were dominant, with myctophids and bathylagids being next in importance. In the Gibce Fracture sample (area C), fish food consisted mainly of serrivomerids and myctophids, whereas, farther southward on the northern part of the Mid-Atlantic Ridge (area D), myctophids followed by searsiids and bathylagids were the dominant types. Among the crustaceans, decapods (shrimps) were important in all four areas and mysids were found consistently in smaller quantities. Among the other invertebrates, cephalopods and scyphozocans were rather important in the Reykjanes Ridge samples.

Food composition by size-group

Northwest Atlantic and Iceland slope areas. The composition and quantity of food in the stomachs of roundnose grenadier varied considerably from the smallest to the largest specimens, but there was little variation among fish of intermediate sizes and data for 41–100 cm specimens were combined (Table 2). Also, the data for Iceland were included with those from the Northwest Atlantic because of the similarity of the food fauna in the samples from the two regions. Nearly all of

TABLE 2. Food composition (% by weight) of roundnose grenadier from the continental slope areas of the Northwest Atlantic and Iceland by size groups.

Stomach contents	Percent food by fish size (cm)		
	≤40	41–100	>100
Cephalopoda	—	6.6	9.2
Chaetognatha	0.4	1.2	—
Polychaeta	—	2.0	—
Tunicata	—	0.7	2.3
Crustacea	90.1	82.0	55.3
Amphipoda	66.3	22.8	2.6
Copepoda	10.2	5.1	0.9
Decapoda	—	16.4	35.3
Euphausiacea	4.7	14.9	16.1
Mysidacea	8.9	22.8	0.4
Pisces	—	7.5	33.2
Unidentified food	9.5	0.0	—
Total stomachs	111	1,449	47
Empty stomachs (%)	5.4	33.6	8.5
Feeding index (‰)	67	45	37

the food of small grenadier (<40 cm) consisted of crustaceans, with amphipods (hyperiidids) being the major component followed by copepods and mysids. Grenadier of intermediate sizes (41–100 cm) also fed mainly on crustaceans, with hyperiidids and mysids being the major components although decapods and euphausiids were also important. Fish and cephalopods were present in small quantities. The largest grenadier (>100 cm) fed mainly on crustaceans (decapods) and fish (mostly myctophids).

Northeast Atlantic thalassobathyal. In these areas (Table 3), young roundnose grenadier (8–20 cm) fed mainly on mysids, with chaetognaths and copepods being of much less importance. This may not be representative because the sample consisted of only 8 specimens. In larger juveniles (21–40 cm), although the proportion of mesoplankton crustaceans decreased significantly, mysids and copepods continued to be the major food components. Additionally, small mesopelagic fishes became important as food, the major types being melamphids and myctophids. The proportion of crustaceans increased slightly for larger fish (41–60 cm) due to the appearance of decapods (shrimps) in the diet. The overall proportion of fish food remained about the same for this size group as for the 21–40 cm group but more families were represented, the most significant ones being Melamphidae, Serrivomeridae and Bathylagidae. Grenadiers larger than 60 cm fed mainly on a variety of fishes (Myctophidae, Serrivomeridae, Bathylagidae and Chauliodontidae), but crustaceans (shrimps), cephalopods and scyphozocans were consistently found in smaller quantities.

TABLE 3. Food composition (% by weight) of roundnose grenadier from the thalassobathyal areas of the Northeast Atlantic by size groups.

Stomach contents	Percent food by fish size (cm)				
	8-20	21-40	41-60	61-80	81-100
Cephalopoda	—	—	4.9	12.8	6.0
Chaetognatha	14.9	7.1	0.7	0.1	0.0
Scyphozoca	—	—	—	3.3	7.3
Tunicata	—	—	0.5	0.3	0.0
Crustacea	85.0	51.8	53.9	14.2	15.0
Amphipoda	—	—	2.5	0.6	0.7
Copepoda	4.2	10.3	3.2	0.4	0.1
Decapoda	—	3.8	22.3	8.4	10.1
Euphausiacea	—	—	0.7	0.7	0.3
Isopoda	—	—	2.1	0.0	0.0
Mysidacea	77.0	36.0	12.7	2.9	3.3
Ostracoda	—	—	1.2	0.2	0.0
Unidentified	3.8	1.7	9.2	1.0	0.5
Pisces	0.1	41.1	39.8	69.3	71.7
Bathylagidae	—	—	6.2	11.8	12.1
Chauliodontidae	—	—	—	2.0	9.9
Malacosteidae	—	—	—	5.8	—
Melamphaidae	—	18.8	14.2	3.5	0.6
Myctophidae	—	10.1	1.1	12.3	26.5
Searsiidae	—	—	0.1	5.7	0.7
Serrivomeridae	—	—	13.9	13.9	14.1
Sternoptychidae	—	9.8	—	0.3	0.3
Unidentified	0.1	2.4	4.2	14.0	7.5
Total stomachs	8	52	66	393	282
Empty stomachs (%)	25.0	17.3	4.6	9.4	13.1
Feeding index (‰)	81	75	28	38	36

Discussion and Conclusions

The seasonal dynamics of roundnose grenadier feeding in the North Atlantic, as reported by Podrazhanskaya (1968, 1969, 1971) is manifested by an increase in the numbers of stomachs containing food from spring to autumn, with major feeding in September–November during the biological autumn (Semenova, 1964). Hepatosomatic indices closely coincide with the increase in feeding activity from spring to autumn (Podrazhanskaya, 1969). The feeding of roundnose grenadier on macroplankton, bathypelagic crustaceans and some fish in the Northwest Atlantic indicates that roundnose grenadier is a consumer of the second or third order (Fig. 2), i.e. it utilizes the energy from phytoplankton through one or two levels of prey organisms. The energy link to bottom organisms is mainly through shrimp (*Pandalus borealis*) which feed on polychaetes.

The seasonal dynamics of roundnose grenadier in the thalassobathyal is manifested by decreasing amounts of food in the stomachs from March to July–August, increasing amounts during spawning in September–October after which the autumn maximum is recorded, and decreasing amounts during the winter

TABLE 4. Variation in mean index of degree of stomach fullness of roundnose grenadier by month in the thalassobathyal of the North Atlantic, based on field examination of specimens.

Month	No. of specimens	Mean index	Standard deviation
Mar	2,900	1.27	0.16
Apr	12,500	1.14	0.10
May	14,900	0.84	0.08
Jun	19,600	0.75	0.07
Jul	20,100	0.74	0.07
Aug	9,900	0.86	0.09
Sep	10,500	0.95	0.11
Oct	7,200	1.12	0.11
Nov	2,600	0.83	0.23
Dec	2,400	0.54	0.14

(Table 4). Roundnose grenadier in this region are consumers of the third or fourth order (Fig. 3), i.e. their energy is derived mainly from eating fish in the bathypelagic zone and to a lesser degree from eating crustaceans and organisms of a stationary trophic complex. Meanwhile, roundnose grenadier are consumed by predators of higher trophic levels: dogfishes (*Etmopterus spinax*, *Centroscyllium fabricii*), northern wolffish (*Anarhichas denticulatus*), cutlassfish (*Aphanopus carbo*), deepsea angler (*Ceratias holboellii*), and toothed whales.

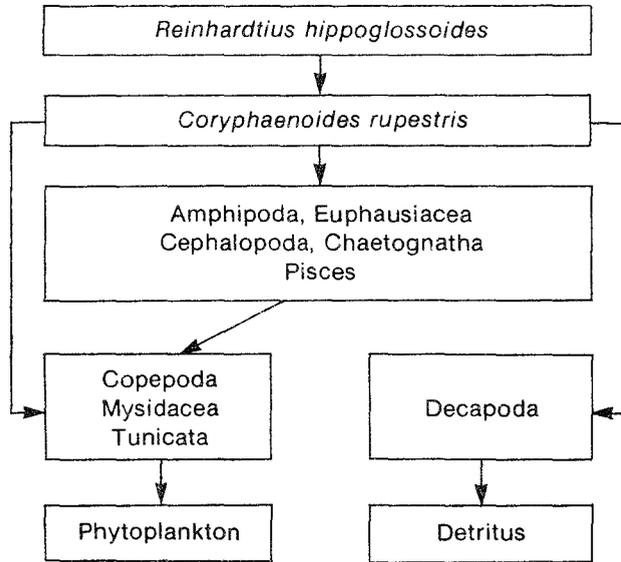


Fig. 2. Trophic relations of roundnose grenadier on the continental slopes of the Northwest Atlantic.

If roundnose grenadier on the continental slopes of the Northwest Atlantic and in the thalassobathyal of Reykjanes Ridge and northern Mid-Atlantic Ridge belong to the same population, as has been hypothesized by various researchers (Podrazhanskaya, 1971; Alekseev *et al.* 1979; Marti, 1980; Zubchenko, 1981), the area of distribution may be considered to consist of two functional parts (feeding and spawning migrations). From the spawning area of Reykjanes Ridge and northern Mid-Atlantic Ridge, developing eggs and larvae are transported by currents to the Northwest Atlantic via South Greenland, and the young settle on the continental slopes off Baffin Island, Labrador and eastern Newfoundland (Marti, 1980; Zubchenko, 1981). As they grow in size, the fish move northward along the slope towards Greenland and then eastward to Iceland where the larger maturing individuals aggregate and perform a spawning migration southward along Reykjanes Ridge.

Roundnose grenadier of the North Atlantic inhabit waters of the intermediate structural zone. In the Northwest Atlantic, this zone, according to Stepanov (1974), is represented by subarctic water which contains the arctoboreal fauna with an abundance of crustaceans (Beklemishev, 1969). This may account for the predominance of crustaceans in the food of roundnose grenadier in most areas of the Northwest Atlantic. However, on the northeastern slope of Grand Bank where the subarctic and transformed waters border upon the southern boundary of arctoboreal fauna, roundnose grenadier were found to feed mainly on fish (Table 1).

In the spawning area of Reykjanes Ridge and northern Mid-Atlantic Ridge, roundnose grenadier are

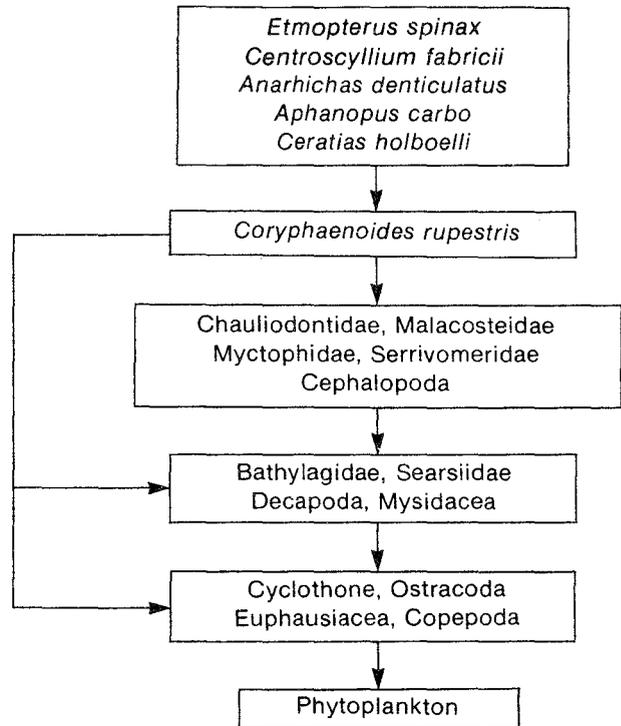


Fig. 3. Trophic relations of roundnose grenadier in the thalassobathyal areas of Reykjanes Ridge and northern Mid-Atlantic Ridge.

found in transformed water masses which are formed by the interaction of North Atlantic and Subarctic water masses (Mamaev, 1960; Stepanov, 1974), with a number of "zones of microproductivity" in the pelagial over the summits of the undersea mounts (Bezrukov and Natarov, 1976; Shomura and Barkley, 1979). These "zones", in combination with a number of frontal zones, according to Andriyashev (1979), create the high productivity of these thalassobathyal areas. Therefore, the fauna in these areas contain an abundance of tropical and subtropical oceanic species (Gushchin and Kukuev, 1981) with a complex structure of trophic chains. Roundnose grenadier feed mainly on fishes in this region, thus being consumers of the third or fourth trophic levels. It is noteworthy that roundnose grenadier in this region tend to be larger than those on the continental slopes of the Northwest Atlantic. Thus, roundnose grenadier rationally utilize the available food resources in both extremes of the distribution area in the North Atlantic.

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