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DISTRIBUTION OF DEMERSAL FISHES OF THE CARIBBEAN SEA FOUND BELOW 2,000 METERS

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ABSTRACT

Abyssal fishes of the Caribbean Sea are known from the work of six research vessels, yet only one of these collections has been reported. The most recent collection, that of the USNS BARTLETT in 1981, contains 13 new records of rare fish to the Caribbean, including two undescribed species. Twelve species accounts are given, documenting the new finds, along with some taxonomic changes from previous reports. Zoogeographical analysis revealed that the abyssal fish fauna of the Caribbean basins reflects a depauperate, tropical, western Atlantic subunit of a broader, circumglobal pattern of the world's abyssal fish fauna.

Knowledge of the composition and structure of the world's demersal deep-sea fish fauna has greatly increased in the past 20 years. Studies in the western North Atlantic Ocean have been concentrated off New England (Haedrich et al., 1980), the Middle Atlantic Bight (Musick, 1979), the Bahamas (Staiger, 1970; Sulak, 1982) and the Gulf of Mexico (Bright, 1968). Collections from the Caribbean Sea have been made by a number of vessels, but to date no attempt has been made to consolidate knowledge of the demersal fish fauna of the Caribbean basins. Data from only 16 stations below 1,000 m have been reported previously (Nielsen, 1975a; Rass et al., 1975).

Among Caribbean collections are fishes from a 1981 cruise of the USNS BARTLETT which made 19 successful trawls between 3,411 and 5,057 m. Results of the BARTLETT collections are reported herein. Meristic and morphometric data on rare species from BARTLETT samples are presented, along with resolution of some dubious identifications in the literature. Based on all known samples below 2,000 m in the Caribbean (54 trawl collections), the species composition of the abyssal fish fauna of that basin is summarized and characterized taxonomically. Finally, we discuss observable differences between the composition of the deep-demersal fish fauna of the Caribbean and adjacent regions of the western Atlantic.

METHODS AND MATERIALS

Caribbean Sea collections made by the U.S. Fish Commission Steamer BLAKE, R/V JOHN ELLIOTT PILLSBURY, R/V JAMES M. GILLISS, R/V ALAMINOS and USNS BARTLETT, as well as published collections of the Soviet AKADEMIK KURCHATOV form the basis of this paper. Station locations are shown in Figure 1 and listed in Table 1. Although the U.S. National Marine Fisheries Service vessels OREGON, OREGON II and SILVER BAY conducted extensive sampling in deep waters in the Gulf of Mexico and Caribbean Sea (Springer and Bullis, 1956; Bullis and Thompson, 1965; G. Miller and E. Gutherz, pers. comm.), only eight trawl stations were from depths exceeding 2,000 m and all eight were conducted in the Gulf of Mexico. All specimens examined for meristics and morphometrics are maintained at the National Museum of Natural History, Washington, D.C. (USNM), the Virginia Institute of Marine Science, Gloucester Pt., Virginia (VIMS), Texas A&M University, College Station, Texas (TAMU), and the Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida (UMML). Additional material has been deposited at the Zoological Museum, University of Copenhagen (ZMUC). Hauls from the BARTLETT were made with a 13.5-m semi-balloon trawl. We quantified the BARTLETT hauls by use of a time-depth recorder, but as comparable data are lacking for all other collections, our 19 samples are considered too few to report catch estimates.

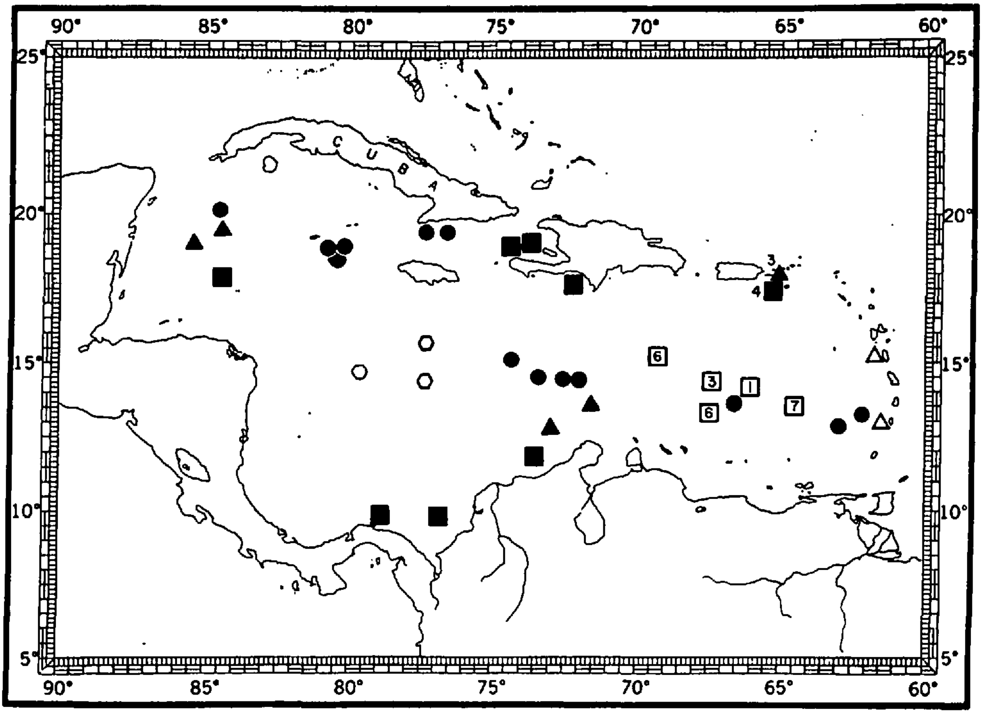

Figure 1. Chart of the Caribbean Sea showing trawl stations below 2,000 m. Symbols are collections of the BARTLETT (□); BLAKE (△); ALAMINOS (○); PILLSBURY (■); GILLISS (▲) and AKADEMIK KURCHATOV (●).

RESULTS

At least 35 demersal fish species have been taken in the Caribbean Sea between 2,068 and 6,845 m (Table 2). Of these, *Bathyprion danae* and *Leptochilichthys agassizi* may be bathypelagic (Markle, 1976). Caribbean deep water fish collections were dominated by ophidiiforms (17 species; two families) and alepocephaloids (seven species). Ophidiiforms comprised 86.6% by number the total BARTLETT collections; alepocephaloids made up 7.2% of the catch. The eurybathic ophidiid *Bathyonus laticeps* numerically predominated the BARTLETT samples (332 specimens), whereas two other ophidiids, *Apagesoma edentatum* (represented by two specimens weighing 7,399 g) and *Bassozetus* sp. B (33 specimens weighing 6,413 g) made up 65% of the ophidiiform biomass.

The following species accounts present new data on rare species or new records for the Caribbean Sea.

Synaphobranchidae

Haptenchelys texis Robins and Martin, 1976

Two species (USNM 26438; 245 and 378 mm SL) from BARTLETT station E039 in 3993–4064 m represent the first reporting of the species since its description (Robins and Robins, 1976). *Haptenchelys texis* was originally described from the Bahamas, Gulf and Mexico and Caribbean on the basis of six specimens taken in 2350–4086 m.

Table 1. Data for 54 bottom trawl stations yielding demersal fishes in the Caribbean Sea at depths exceeding 2,000 m

Vessel	Station No.	Latitude, N	Longitude, W	Depth, m	Date
Blake	182	15°27′	61°37′	2,068	26 I 1879
Blake	235	12°57′	61°25′	2,756	21 II 1879
Pillsbury	328	09°58′	79°36′	2,070	07 VII 1966
Pillsbury	346	09°54′	77°03′	2,977	10 VII 1966
Pillsbury	576	18°20′	84°34′	2,212	21 V 1967
Pillsbury	782	11°57′	73°32′	2,365	30 VII 1968
Pillsbury	1180	18°55′	73°53′	3,343	01 VII 1970
Pillsbury	1181	18°51′	74°30′	2,518	01 VII 1970
Pillsbury	1266	17°53′	71°59′	2,846	17 VII 1970
Pillsbury	1397	17°54′	65°10′	4,359	11 VII 1971
Pillsbury	1401	17°51′	65°04′	4,180	12 VII 1971
Pillsbury	1402	17°55′	64°47′	3,943	12 VII 1971
Gilliss	26	19°44′	84°26′	4,434	24 VII 1972
Gilliss	27	19°04′	85°40′	4,417	25 VII 1972
Gilliss	39	12°51′	73°02′	2,648	03 VIII 1972
Gilliss	41	13°46′	71°25′	4,186	04 VIII 1972
Gilliss	63	17°50′	65°25′	4,050	22 I 1973
Gilliss	64	17°54′	65°10′	4,371	23 I 1973
Gilliss	118	17°55′	65°08′	4,325	17 VII 1975
Alaminos	70A10-28	14°33′	79°40′	2,340	14 VII 1970
Alaminos	70A10-48	14°30′	77°29′	4,086	24 VII 1970
Alaminos	70A10-50	15°50′	77°24′	2,678	25 VII 1970
Kurchatov	1207	13°18′	61°59′	3,000	18 II 1973
Kurchatov	1208	12°59′	62°59′	2,655	19 II 1973
Kurchatov	1212	14°10′	66°40′	5,030	21 II 1973
Kurchatov	1224	14°41′	73°24′	2,400	01 III 1973
Kurchatov	1231	15°20′	74°20′	4,140	04 III 1973
Kurchatov	1232	14°42′	72°24′	4,020	04 III 1973
Kurchatov	1233	14°38′	72°32′	3,500	04 III 1973
Kurchatov	1242	18°59′	80°30′	6,800	06 III 1973
Kurchatov	1243	19°00′	80°38′	6,845	20 III 1973
Kurchatov	1259	19°05′	80°29′	6,150	— III 1973
Kurchatov	1266	19°44′	76°12′	6,770	24 III 1973
Kurchatov	1267	19°38′	76°39′	6,750	24 III 1973
Kurchatov	1272	20°08′	84°30′	4,580	28 III 1973
Bartlett	E038	15°07′	69°17′	3,985	27 X 1981
Bartlett	E039	15°08′	69°13′	4,032	27 X 1981
Bartlett	E040	15°08′	69°20′	3,981	28 X 1981
Bartlett	E058	13°45′	67°43′	5,054	04 XI 1981
Bartlett	E060	13°48′	67°47′	5,046	06 XI 1981
Bartlett	E062	13°50′	67°35′	5,053	07 XI 1981
Bartlett	E063	13°49′	67°55′	5,046	08 XI 1981
Bartlett	E065	13°52′	67°52′	5,046	09 XI 1981
Bartlett	E066	13°23′	67°30′	4,442	10 XI 1981
Bartlett	E087	13°36′	64°43′	3,494	25 XI 1981
Bartlett	E088	13°34′	64°47′	3,536	25 XI 1981
Bartlett	E090	13°27′	64°43′	3,440	26 XI 1981
Bartlett	E091	13°27′	64°47′	3,479	27 XI 1981
Bartlett	E092	13°31′	64°45′	3,499	28 XI 1981
Bartlett	E093	13°32′	64°41′	3,438	28 XI 1981
Bartlett	E094	13°32′	64°42′	3,441	28 XI 1981
Bartlett	E096	14°17′	67°06′	5,057	30 XI 1981
Bartlett	E097	14°34′	67°26′	5,057	01 XII 1981
Bartlett	E099	14°52′	67°28′	4,981	02 XII 1981

Table 2. List of demersal fishes taken in the Caribbean Sea below 2,000 m. (Depths for Caribbean captures only)

Species	Depth range, m
Synaphobranchidae	
Haptenchelys texis Robins and Martin, 1976	2,678–4,086
Halosauridae	
Aldrovandia affinis (Günther, 1878)	2,212
Aldrovandia gracilis Goode and Bean, 1896	2,070–2,518
Alepocephalidae	
Bathyprion danae Marshall, 1966*	5,046
Bathytroctes microlepis Günther, 1878	3,979–3,984
Conocara salmoneum (Gill and Townsend, 1897)	3,478–5,057
Nomoctes koefoedi (Parr, 1951)	3,411–4,180
Nomoctes michaelsarsi (Koefoed, 1927)	2,341
Rinoctes nasutus (Koefoed, 1927)	3,411–3,476
Leptochilichthyidae	
Leptochilichthys agassizi Garman, 1899*	3,499
Chlorophthalmidae	
Bathypterois grallator (Goode and Bean, 1896)	2,977–3,980
Bathytyphlops sewelli (Norman, 1939)	3,459–4,186
Ipnops murrayi Günther, 1878	1,345–3,518
Synodontidae	
Bathysaurus mollis Günther, 1878	3,499–4,359
Thaumatichthyidae	
Thaumatichthys binghami Parr, 1927	3,536–4,032
Aphyonidae	
Aphyonus rassi Nielsen, 1975	2,655–5,057
Aphyonus sp. A	4,878–5,057
Nybelinella erikssoni (Nybelin, 1957)	5,046–5,057
Ophidiidae	
Acanthonus armatus Günther, 1878	2,518–4,417
Apagesoma edentatum Carter, 1983	4,152–5,057
Barathrites iris Zugmayer, 1911	5,046
Bassozetus sp. A	2,068–2,365
Bassozetus sp. B	3,428–5,057
Bathyonus laticeps Günther, 1878	2,341–5,057
Cataetyx laticeps Koefoed, 1927	2,365
Dicrolene kanazawai Grey, 1958	2,070–2,342
Holcomycteronus squamosus (Roule, 1916)	3,033–5,057
Leucicorus atlanticus Nielsen, 1975	4,590–6,845
Penopus macdonaldi Goode and Bean, 1896	3,440–3,536
Porogadus catena (Goode and Bean, 1885)	3,234–3,440
Porogadus miles Goode and Bean, 1885	4,208–5,054
Porogadus silus Carter and Sulak, 1984	3,508
Macrouridae	
Coryphaenoides macrocephalus (Maul, 1951)	3,459–3,508
Zoarcidae	
Pachycara sp. A	3,476–3,518

* May be bathypelagic (see text).

We originally identified the specimens as *Ilyophis arx* Robins, 1976 on the basis of their lack of scales, low, overlapping number of vertebrae, incomplete lateral line and crescentic, horizontal gill slit. However, *H. texis* is chiefly distinguished from *Ilyophis* by its low-set pectoral fin, fleshy snout tip, smaller teeth, shorter trunk length and several osteological features (Robins and Robins, 1976).

Alepocephalidae

Bathyprion danae Marshall, 1966

One specimen of this rare fish (USNM 264640; 359 mm SL) was taken at BARTLETT station E063 in 5,046 m. Only three specimens have been reported previously: the holotype from off Australia, one in the South Atlantic and one in the Norwegian Sea (Marshall, 1966; Markle, 1976). *Bathyprion danae* has been taken 600–2,300 m off the bottom and is thought to be bathypelagic (Markle, 1976). Meristics: D 26; A 25; Pel. 9/9; Pect. (damaged); pyloric caeca 7; branchiostegal rays L 10, R 11; gill rakers 3 + 1 + 13.

Nomoctes Parr, 1952

The genus *Nomoctes,* as recognized by Markle (1976), contains two species, *N. michaelsarsi* (Koefoed, 1927) and *N. koefoedi* (Parr, 1951). Neither species has been reported previously from the Caribbean Sea. Counts and measurements of all our specimens are within the ranges reported by Markle (1976).

The BARTLETT captured 15 specimens of *Nomoctes koefoedi* (VIMS 06941–06948; 108–272 mm SL) in 3,411–4,013 m at stations E038, E040, E087, E088, E091, E092, E093 and E094. Two specimens (TAMU 3355.8; 195 and 228 mm SL) were taken at ALAMINOS station 70A10-48 in 4,152 m and another (UMML, uncat., PILLSBURY station P-1401) in 4,180 m. *Nomoctes koefoedi* was previously known from 20 specimens taken off the Azores and in the Gulf of Mexico between 2,865 and 5,850 m (Markle, 1976).

Two Caribbean specimens of *Nomoctes michaelsarsi* are known, one from ALAMINOS station 70A10-28 in 2,343 m (TAMU 3350.3; 284 mm SL), the other from BARTLETT station E097 in 5,057 m (USNM 264855; 234 mm SL). The species was previously known from seven specimens taken between 2,010 and 2,993 m; six from the eastern Atlantic and one from the western Atlantic off Virginia (Markle, 1976).

Rinoctes nasutus (Koefoed, 1927)

All Caribbean captures of this species are from the BARTLETT cruise in which seven specimens (VIMS 06969–06971; 110–217 mm SL) were taken in 3,411–3,476 m at stations E090, E093 and E094. Most of these are badly damaged and some unidentifiable alepocephalids from the BARTLETT collections may be this species. *Rinoctes nasutus* has been known previously from 22 eastern Atlantic and two Gulf of Mexico specimens, all taken in 2,000–4,156 m (Markle and Merrett, 1980). Markle and Merrett provided counts and measurements, as well as a thorough osteological description of this species.

Ophidiidae

Apagesoma edentatum Carter, 1983

Two specimens of this species (USNM 260456, 260457; 756 and 780 mm SL) were captured at BARTLETT stations E096 and E063, respectively, in depths of

Table 3. Counts and measurements on selected deep-sea ophidiids from BARTLETT collections. (Measurements on *Bassozetus* sp. B based on 33 specimens, counts on 13)

Characters	*Holcomycteronus squamosus*	*Barathrites iris*	*Bassozetus* sp. B	*Apagesoma edentatum*
Counts				
Vertebrae	18+51 = 69	18+42–44 = 60–62	13+54–58 = 67–71	14+50 = 64
Dorsal fin rays	–	108–110	122–124	111–116
Anal fin rays	–	78	101–106	92–96
Pectoral fin rays	18	24	23–27	25–26
Caudal fin rays	6	8	8	6
Pelvic fin rays	2	2	1	1
Branchiostegal rays	8	7	8	8
Gill rakers	3+IV+4	3+VI–VIII+3	3–4+XII–XVI+4–6	3+VIII–X+4
Measurements, % SL				
Predorsal length	21.5	22.6–23.0	17.5–21.6	21.3–24.9
Preanal length	40.0	42.2–44.3	32.0–37.8	39.2–42.0
Head length	18.7	13.8–15.3	17.8–22.0	19.3–24.2
Body depth at anal origin	14.0	15.1–16.1	12.6–15.4	17.4–24.9
Maxillary length	10.6	6.2–7.1	7.6–10.9	11.0–13.2
Snout length	5.2	5.0–5.8	3.3–5.3	6.3–7.0
Eye diameter	2.0	<1.0	1.0–1.3	1.0
Pelvic fin length	5.0	5.4–6.4	14.5–16.1	8.9–14.9

5,046–5,057 m. Another specimen (TAMU 3355.12; 486 mm SL) was found among the ALAMINOS material from station 70A10-48 in 4,152 m. *Apagesoma edentatum* was known previously only from the holotype taken in 5,082 m east of the Bahamas (Carter, 1983). Counts and measurements of the three new specimens are given in Table 3. The single specimen of *Typhlonus* sp. reported by Rass et al. (1975), Hureau et al. (1979), Shcherbachev and Tsinovsky (1980), and Hureau and Nielsen (1981), now apparently lost, probably also pertains to *Apagesoma.*

Barathrites iris Zugmayer, 1911

Two specimens of this species (USNM 260458; 560 and 625 mm SL) were taken at BARTLETT station E063 in 5046 m. *Barathrites iris* is known only from the North Atlantic, but the genus is known in the tropical eastern Pacific at depths comparable to those from which *B. iris* occurs in the Atlantic (D. Cohen, pers. comm.). Our specimens represent only the second capture of the species in the western Atlantic (Nybelin, 1957) and the first record from the Caribbean Sea. Counts and measurements of both fish are given in Table 3.

Bassozetus Gill, 1884

The genus *Bassozetus* Gill is currently being studied by J. G. Nielsen and H. J. Carter. The genus presently includes nine nominal and at least one undescribed species (Cohen and Nielsen, 1978). These fishes inhabit bathyal and abyssal depths beneath tropical and temperate seas.

Two species of *Bassozetus* are known from Caribbean Sea collections. Pending a generic revision, we refer to these as *Bassozetus* sp. A and *Bassozetus* sp. B.

Bassozetus sp. A occurs at depths less than 2,500 m and has been taken by the BLAKE (sta. 182) and PILLSBURY (sta. 2365). *Bassozetus* sp. B was captured by the BARTLETT at depths between 3,428 and 5,057 m and was the third most frequently taken fish on the cruise (33 specimens). This species has been captured at similar abyssal depths adjacent to the Bahamas as well (Sulak, 1982). Preliminary examinations indicate that *Bassozetus* sp. B closely resembles the holotype of *B. normalis* Gill (J. G. Nielsen, pers. comm.). However, Nielsen (1975a), Hureau and Nielsen (1981) and Sulak (1982) identified Caribbean and Bahamian specimens from below about 2,500–2,900 m as *B. taenia* (Günther) (depths in the Bahamas for this species spanned 1,559–5,267 m). Counts and measurements for our *Bassozetus* sp. B are given in Table 3.

Holcomycteronus squamosus (Roule, 1916)

The genus *Holcomycteronus* Garman is being revised by J. G. Nielsen. The circumglobal genus presently contains six nominal species that live in bathyal to hadal depths (Cohen and Nielsen, 1978).

One species of *Holcomycteronus*, identified as *H. squamosus* by J. Nielsen, has been captured in the Caribbean Sea. New records consist of four specimens, 145–264 mm SL, from ALAMINOS station 70A10-48 in 4,152 m (TAMU 3355.7), BARTLETT stations E087 and E096 in 3,482–5,077 m (ZMUC P77758 and USNM 264639, respectively), and PILLSBURY station P-1180 in 3303 m (UMML 28536). *Holcomycteronus squamosus* was previously known only from the holotype taken off the Azores in 4,261 m (Roule, 1916; 1919). Counts and measurements of our 145 mm SL specimen are given in Table 3; others are currently being studied by J. Nielsen.

Leucicorus atlanticus Nielsen, 1975

Rass et al. (1975) reported the first capture of this species and concluded it was the "characteristic, unique hadal fish species of the Caribbean region," found in depths of 5,800–6,800 m. They considered an abyssal record from 4,590 m as uncharacteristic for the species. However, three specimens have since been taken from the Silver Abyssal Plain in 5,303–5,563 m (Nielsen, 1975a; 1975b; COLUMBUS ISELIN cruise 8113, sta. D018, ZMUC P77759-60), and another has been taken in the central Atlantic in 5,100 m (Hureau and Nielsen, 1981).

Zoarcidae

Pachycara sp.

A single specimen of the eelpout genus *Pachycara* Zugmayer, a juvenile female (USNM 233627; 161 mm SL), was taken at BARTLETT station E092 in 3,476–3,518 m. Prior to Anderson (1984), *Pachycara* was based on one species known from two specimens. Our specimen agrees well with *Pachycara* as Anderson redefined it, and represents an undescribed species, which will be described elsewhere by M. E. Anderson.

DISCUSSION

The nomenclature of several deep demersal fish species has been updated since the work of Rass et al. (1975). Some of these changes have been addressed in the previous sections. Additional name changes pertinent to previous species records are listed in Table 4, along with the source of the change.

Although Rass et al. (1975) attempted to address faunal zonation among Caribbean deep-sea fishes, their general characterization of the composition of the abyssal fish fauna should be considered inadequate due to the paucity of their samples. The AKADEMIK KURCHATOV completed 13 successful abyssal stations, yielding only 30 specimens of 9 demersal species. Moreover, the small nets (2.5–6 m) used by the KURCHATOV fished selectively, missing most large species capable of net avoidance; thus Rass et al. underestimated the richness of this fauna (Sulak, 1982: 115). In most KURCHATOV samples, only a few numerically dominant species were captured. The data of Rass et al. on the distribution of *Ipnops murrayi* also tends to contradict the strict zonation they reported (Tables 2 and 4).

The combined collections from all 35 samples known (but largely unpublished) prior to the BARTLETT cruise totaled 175 specimens representing 24 species. The BARTLETT collections made a substantial addition to the Caribbean material, adding 519 specimens representing 28 species, and bringing the overall abyssal faunal list to 35 species. That this large increase in specimens resulted in only a moderate increase in the number of species known for the Caribbean fauna suggests that additional sampling would result in few new species. Thus, the available collections seem sufficient to represent the taxonomic richness of the Caribbean abyssal fauna, and to enable a general characterization of that fauna. They appear adequate as well to enable fundamental comparisons with the abyssal faunas of other previously studied areas of the North Atlantic.

The combined samples from the Caribbean reveal a fauna dominated in numbers of species and individuals by neobythitine ophidiids (14 species) and alepocephaloids (seven species). Also, together contributing prominently to the fauna in number of species (10) are ipnopine chlorophthamids, halosaurs, synaphobranchids and aphyonids. Macrourids are poorly represented (one species, four individuals); morids are absent. Thus, at the family level, the Caribbean fauna appears closely aligned with the Bahamian-southern Sargasso Sea bathyal-abyssal fauna (Sulak, 1982), and strikingly dissimilar from the abyssal fauna characteristic of temperate latitudes in the western North Atlantic (Musick, 1979; Haedrich et al., 1980; Sulak, 1982). At those latitudes the abyssal fauna is characterized by the macrourids *Coryphaenoides armatus, C. leptolepis,* and *C. carapinus,* the morid *Antimora rostrata,* the alepocephalid *Alepocephalus agassizi,* the halosaur *Halosauropsis macrochir,* the ophidiids *Porogadus miles* and *Spectrunculus grandis,* the skate *Bathyraja richardsonii* and the chimaera *Hariotta raleighana.* Of these species only *P. miles* has been recorded in the Caribbean.

Regional faunal differentiation can arise either by events operating on a historical geological time scale (e.g., vicariance, differential extinction) or by those operating on a contemporary ecological time scale (e.g., trophic interactions, competition, locally limiting environmental conditions). With respect to the deep-sea, our understanding of processes controlling faunal structure on either time scale is poorly developed. However, regions of endemism are much less apparent for the abyssal fish fauna than for the littoral, shelf and slope faunas (Briggs, 1974; Anderson, 1984). Many abyssal species are circumglobal, or nearly so, including *C. armatus, C. leptolepis, A. rostrata, S. grandis, Acanthonus armatus, Abyssobrotula galathaea, H. macrochir, Narcetes stomias, Bathypterois longipes, B. grallator, Bathysaurus ferox, B. mollis* and *H. raleighana.* This is indeed instructive in view of the very limited number of samples available from the Indo-West Pacific. The widely scattered localities of many other less frequently obtained species, known mostly from Atlantic records, are also indicative of a general abyssal pattern of very broad distributions. Included here are *Coryphaenoides*

Table 4. Nomenclatural changes of some deep-sea fishes since Rass et al. (1975)

Previous name (Rass et al., 1975)	Valid name	Source
Aldrovandia pallida Goode and Bean	*A. affinis* (Günther)	McDowell (1973)
Macdonaldia sp.	*Polyacanthonotus merritti*	Sulak et al. (1984)
Leptoderma springeri Mead and Bohlke	*L. macrops* Vaillant	Markle 276)
Ipnops agassizi Garman†	*I. murrayi* Günther†	Sulak (in press)
Cariburus mexicanus Parr	*Coryphaenoides mexicanus* (Parr)	Marshall and Iwamoto (1973)
Grenurus grenadae Parr	*Sphagemacrurus grenadae* (Parr)	Marshall and Iwamoto (1973)
Nezumia hildebrandi Parr	*N. aequalis* (Günther)	Marshall and Iwamoto (1973)
Squalogadus intermedius Grey	*S. modificatus* (Gilb. and Hubbs)	Marshall and Iwamoto (1973)
Mixonus pectoralis Goode and Bean‡	*Bathyonus laticeps* (Günther)‡	Hureau and Nielsen (1981)

† *Ipnops agassizi* is known only from the eastern Atlantic and Indo-Pacific in 1,392–4,163 m (Sulak, in press). *Ipnops murrayi* has been taken only in the western Atlantic in 1,206–3,518 m.

‡ Hureau and Nielsen (1981) synonymized *Mixonus* with *Bathyonus*. Without addressing other western Atlantic records, they identified one specimen as *B. laticeps*, thereby tacitly synonymizing the western Atlantic *M. pectoralis* with the eastern Atlantic *B. laticeps*. All our specimens agree with *B. laticeps*, as did theirs, in having 11–13 long gill rakers and having a snout length 25.5–27.0% head length.

macrocephalus, Bathyonus laticeps (incl. *B. pectoralis*; see Table 4), *Leucicorus atlanticus, Bassozetus taenia, Porogadus catena, Holcomycteronus profundissimus, H. squamosus, Halosaurus attenuatus, Conocara salmoneum, Rinoctes nasutus, Bathytyphlops sewelli, Bathymicrops regis, Ipnops agassizi, Sciadonus pedicellaris, Aphyonus gelatinosus, Nybelinella erikssoni* and *Pachycara obesum.* Only a few abyssal species from the Caribbean are possibly endemic to the Pan-Caribbean region (e.g., the eel *Haptenchelys texis,* the aphyonid *Aphyonus rassi* and the eelpout *Pachycara* sp.). It would seem then that classical geographical "barriers" operating on a historical time scale are much less trenchant for the abyssal fish fauna than for the littoral, shelf and slope faunas. The apparent ineffectiveness of such barriers with respect to the abyssal fauna strongly suggests that processes operating on an ecological time scale are a better starting point from which to analyze contemporary regional faunal differentiation.

Given a probable circumglobal nature for the abyssal fish fauna, it is instructive to examine not only what species are present regionally, but also what species are absent. As argued above, but allowing for some absences of rare species due to sampling artifact (see below), species absences might best be evaluated within the context of ecological processes. Thus, among Caribbean samples we note numerous species absences compared to the faunas known for other regions of the North Atlantic. These absences are briefly considered below—in the light of available hypotheses pertinent to limitation of species ranges—as a first step toward understanding processes controlling composition of the Caribbean abyssal fish fauna.

First, sampling artifact needs to be considered. It is possible that this accounts for the apparent absence from the Caribbean of certain species known from the adjacent western Atlantic, but previously obtained there only infrequently. Likely species here include the skate *Raja purpuriventralis,* the eel *Synaphobranchus bathybius,* the halosaurs *Halosaurus attenuatus* and *Aldrovandia rostrata,* the ophidiids *Holcomycteronus profundissimus* and *Bassogigas gillii,* and the alepocephalids *Alepocephalus australis* and *A. productus.*

It is much more difficult to invoke mere artifact to account for the absence from Caribbean samples of species taken frequently from nearby regions, and known to be widely distributed as well. In contrasting the composition of the bathyal-abyssal fish faunas of the Bahamas and the Middle Atlantic Bight, Sulak (1982) invoked an hypothesis of regional species replacement in response to energy availability. Energy availability on the bottom at abyssal depths varies as a function of local water mass primary productivity (Rowe, 1971). Only species with energetically stringent life histories would be predicted to inhabit low productivity regions. Those with energetically expensive life histories (e.g., active predators, continual swimmers, species with very high relative fecundities) would be rare or absent under conditions of low food availability. The region of the Caribbean and Gulf of Mexico has been characterized as one of generally very low mean annual primary productivity (Corwin, 1969; Koblentz-Mishke et al., 1970; Rowe, 1971; El-Sayed et al., 1972), and of correspondingly very low macrofaunal prey biomass and density (Moskalev and Pasternak, 1970; Rowe, 1971; Rowe et al., 1974; Pasternak et al., 1975; Richardson, 1983). Food resources on the bottom at abyssal depths may be insufficient to support species with relatively great food intake requirements. The absence or rarity in the Bahamas-southern Sargasso Sea of species prominent in the abyss of the much more productive, temperate Middle Atlantic Bight has been rationalized, in part, on this basis (Sulak, 1982). A parallel argument may be advanced for Caribbean samples with respect to the absence of the macrourids *C. armatus, C. leptolepis* and *C. carapinus,* the morid *A. rostrata* and other species, including *H. macrochir, A. agassizi* and *S. grandis.* All of these are wide-ranging, eurybathic, eurythermal species whose apparent absence from the Caribbean is very difficult to reconcile (see Iwamoto, 1975, regarding the "enigmatic" absence of *Antimora rostrata* from the region). Most are also large, active foragers which differ dramatically in mode of existence from the passively hovering and drifting species typical of the Bahamian abyssal fauna (Sulak, 1982). The passive, drifting mode has been suggested to be energetically less expensive for benthopelagic abyssal organisms than one involving active, directed locomotion (Ingram and Hessler, 1983).

An alternative hypothesis to account for the rarity of certain species in the tropical Atlantic involves a life cycle tied to high latitude spawning. For example, a life cycle involving cyclic ontogenetic migration between boreal feeding grounds and subarctic spawning grounds has been documented in the bathyal macrourid *Coryphaenoides rupestris* (Pechenik and Troyanovskii, 1970; Podrazhanskaya, 1971). In this species, early life history stages are known only from high latitudes. Unripe adults occur abundantly in trawl catches as far south as Virginia (Musick, 1979; Haedrich et al., 1980), but only a few individuals have been recorded from as far south as the Bahamas (Sulak, 1982). Based on the absence of small juveniles and ripe adults off Virginia, Wenner and Musick (1977) suggested that the abyssal species *Antimora rostrata* may also spawn at high latitudes. Thus, with a life cycle involving southward drift of larvae and early juveniles, followed by a progressive northward return migration of maturing fish, few individuals might be expected to reach and regularly inhabit low latitude basins. Moreover, in a high latitude spawner, pelagic larvae will probably be adapted to develop successfully in low temperature surface waters unavailable at lower latitudes. Accordingly, the general southward limits of adults might tend to be restricted as well as species upper temperature tolerance limits are approached with decreasing latitude. Despite the probability of high latitude spawning in *A. rostrata,* an hypothesis of subsequent exclusion of adults from low latitudes fails. This circumglobal species (replaced in the North Pacific by *A. microlepis*) is known from a number of captures in the tropical eastern Pacific (Small, 1981), despite the limited number of samples available from the region. The occurrence of *A. rostrata* in a tropical region of high productivity (resulting from coastal upwelling), in contrast to its absence from the Caribbean and rarity in the Bahamas (i.e., general absence from areas of low productivity), rejects a restriction from tropical latitudes due to life history limitations inherent in the reproduction-migration cycle. Instead, its occurrence in the tropical upwelling region favors Sulak's (1982) ecological hypothesis of faunal differentiation and replacement in response to energy availability and the requirements of the species. Like *A. rostrata,* certain other abyssal species absent from Caribbean samples, are known from more productive tropical regions. Among these are *C. carapinus* and *A. agassizi,* both known from the tropical eastern Atlantic (Nybelin, 1957; Golovan', 1976).

Neither energetic limitations of adults nor limiting surface temperatures for adults or larvae can readily be invoked to account for the absence from Caribbean samples of another set of species characteristic of the adjacent tropical Atlantic and typical of very great depths (exceeding 4,000 m). Such species include the chlorophthalmids *Bathypterois longipes* and *Bathymicrops regis* and the ophidiid *Abyssobrotula galatheae,* all typical of the open Atlantic and Bahamian faunas (Nielsen, 1969; 1975a; Sulak, 1982). It must be assumed that all of these small, microphagous, deep-abyssal forms are characterized by accommodations to an extremely stringent energy supply. Given their known bathymetric ranges, they may also be characterized, however, as cold-stenothermal species. It has been previously hypothesized (Sulak, 1977) that *B. longipes* is excluded from the Gulf and Caribbean by unusually warm bottom temperatures at abyssal depths (uniformly warmer than ca. 4°C in all areas: Fuglister, 1960). An inability to tolerate water temperatures warmer than 4°C may exclude the adult stages of cold-stenothermal abyssal species from the Caribbean, even if surface temperatures are appropriate for developing epipelagic larvae.

More perplexing is the absence from Caribbean abyssal samples of a final set of species that are generally typical of tropical, abyssal waters of the North Atlantic. These are broadly eurybathic (thus apparently eurythermic) and are well represented among Bahamian samples (Sulak, 1982). Notable here are the eels *Synaphobranchus brevidorsalis* and *Ilyophis brunneus* (the latter known in the Caribbean only from bathyal depths: Robins, 1971), and the alepocephalids *Conocara niger* and *Narcetes stomias*—all of which might reasonably be expected to inhabit the Caribbean abyss, and occur fairly frequently there. Curiously the absence of some of these species is offset by the occurrence of closely related confamilials that are rare or absent in the adjacent tropical Atlantic (e.g., *Haptenchelys texis* and *C. salmoneum,* respectively, for the first three species listed above). Between-region faunal replacement recognizable within sets of closely related species with otherwise overlapping ranges is suggestive of competitive exclusion (King, 1964; MacArthur, 1965). Sulak (1982) presented substantial, if indirect, evidence of competitive exclusion in sets of species from the Bahamas and Middle Atlantic Bight bathyal-abyssal faunas. It is presently impossible to obtain direct evidence of competitive interactions in the deep-sea where controlled ecological experiments with fishes are logistically excluded. However, differential patterns of occurrence inside versus outside the Caribbean within sets of closely related species are indeed suggestive of competitive exclusion.

In conclusion, Rass et al. (1975) stated that the "majority of depths of the Caribbean Sea are lacking in Atlantic species." Our findings tend to refute this view. On the contrary, the abyssal fish fauna of the Caribbean appears continuous with that of the entire tropical Atlantic. There is scant evidence of a particular affinity with the "Panamanian-Peruvian" fauna as suggested by Rass et al. Of the fishes they cited to support such an opinion, only the geminate species pairs in *Bathypterois* and *Leucicorus* depict the amphi-American relationship between the Caribbean and tropical Pacific. We view the distributions of most other "amphi-American" species groups they cited as more reflective of a general circumglobal pattern among species comprising the world's abyssal fish fauna.

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