Fauna and Zoogeography of Deep-Benthic Chondrichthyan Fishes around the Japanese Archipelago

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Abstract The deep-benthic chondrichthyan fishes collected by 584 hauls of otter-trawl from the Okinawa Trough, Kyushu-Palau Ridge, Pacific continental slope off northern Honshu Island ("Tohoku Slope") and continental slope of Okhotsk Sea off Hokkaido ("Okhotsk Slope") were analyzed. Sixty-one species were recorded from 200 to 1,520 m in depths; 37 species from the Okinawa Trough, 10 from the Kyushu-Palau Ridge, 18 from the Tohoku Slope, and nine from the Okhotsk Slope.

The Okinawa Trough has the most varied composition, with many species of the Squalidae, Scyliorhinidae, and Rajidae (genus Raja). The Kyushu-Palau Ridge has a relatively high number of squalid species, but no species of the Rajidae or Chimaeriformes. The Tohoku Slope fauna is relatively varied, comprising six families, of which the Rajidae (genus Bathyraja) is the most numerous, followed by the Squalidae. The Okhotsk Slope has the least number of species, and is characterized by a remarkable dominance of the Rajidae (genus Bathyraja).

In addition, the Japan Sea was included in the analyses, based on literature records, enabling coverage of all the main regions around the Japanese Archipelago.

The distributional characteristics of the major taxonomic groups, i.e. Scyliorhinidae, Squalidae, Rajidae and Chimaeriformes, were discussed, and the Shichito-Iojima Ridge, which runs from the Izu Peninsula southward to the Ogasawara Islands and Iojima Islands, was proposed as an effective barrier for deep-benthic chondrichthyan fishes at least, especially for those of the northern regions.

From 1978 through 1980, the Fisheries Agency of Japan conducted intensive deep-sea investigations around the Japanese Archipelago. Four research regions were selected for study, and numerous experimental bottom trawls were made and bottom lines set on the deep-sea ridges, troughs, and continental slopes down to a depth of nearly 1,600 m. These regions were the Okinawa Trough in the East China Sea, Kyushu-Palau Ridge, Pacific off northern Honshu Island, and Okhotsk Abyssal Plain off Such extensive bathy-benthic surveys Hokkaido. have never been done around Japan, and the research has already resulted in a series of publications, including a great many new findings, i.e. on fishes (Okamura et al., 1982; Amaoka et al., 1983; Okamura and Kitajima, 1984; Okamura, 1985), and on invertebrates (Baba et al., 1986; Okutani et al., 1987, 1988a, b; Imaoka et al., 1990).

The present authors were involved in the identification of fish species and noticed pronounced faunal differences in deep-sea chondrichthyan fishes among these four research regions. In addition, the Japan Sea, which was not included in the present

deep-sea investigation, is well known by a unique fauna (Nishimura, 1965a, 1965b, 1966, 1968, 1969), and the inclusion of the Japan Sea in the present consideration makes it possible to compare the local deep-benthic chondrichthyan faunas of all the main regions around the Japanese Archipelago.

The purposes of this paper are to summarize the occurrence of the deep-sea benthic chondrichthyans that occur below 200 m in depth, to discuss the faunal differences of the regions, and to infer the distributional characteristics of the major chondrichthyan taxonomic groups around the Japanese Archipelago.

Methods and data

The regions studied were the Okinawa Trough in the East China Sea, Kyushu-Palau Ridge, Pacific continental slope of northern Honshu (mainly Tohoku District) from off Ibaragi Prefecture to Aomori Prefecture (referred to below as "Tohoku Slope"), and the slope of the Okhotsk Abyssal Plain off Hokkaido ("Okhotsk Slope"). In addition to

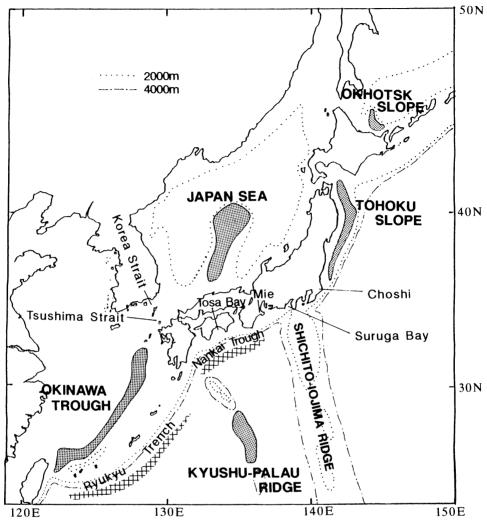


Fig. 1. Research regions (dotted areas) and topographic features around the Japanese Archipelago.

these, we include a fifth region, Japan Sea, based on data from Ogata et al. (1973) in the faunal analyses. These five study regions, ranging from warm to cold waters, represent the major areas around the Japanese Archipelago (Fig. 1).

Bottom otter-trawl and bottom lines were deployed, but only the fishes caught by trawls were used for direct regional comparisons, in order to have a homogeneous basis for discussion, because bottom lines were not operated in some regions. The trawl surveys in the four regions were conducted by the same type of commercial bottom trawlers that originally operated in the North Pacific Ocean. The survey in the Japan Sea was operated by R/V Kaiyo Maru of the Fisheries Agency of Japan. The trawl nets used

were: 72.9 m in circumferential length at the net mouth and 34.6 m in net length for the Okinawa Trough, 66.9 m and 28.8 m respectively for the Tohoku Slope, and 72.8 m and 32.7 m for the Okhotsk Slope. Although exact dimensions of the trawl nets used for the Kyushu-Palau Ridge and the Japan Sea surveys were not available, similarly sized nets to those above were used also in these regions. The number of trawl hauls and average time per haul are summarized in Table 1.

Bottom trawls were done in 200-1,180 m over stone, sand or mud in the Okinawa Trough, in 310-910 m over rock, stone or sand on the Kyushu-Palau Ridge, in 580-1,520 m over mud on the Tohoku Slope, in 400-1,420 m over mud on the Okhotsk

Slope, and in 200-1,200 m over mud or sand in the Japan Sea. The number of specimens caught in each survey was not counted. Some species were, however, apparently represented by a single specimen. These species were not included in the faunal discussion, unless their occurrence was substantiated either by the literature or an alternative source.

Results and discussion

Although the depths surveyed differ in each region, it seems valid to make comparisons of the deep-sea chondrichthyan faunas of the five regions, considering the broad overlap in depths trawled and general eurybathic distribution of deep-sea chondrichthyans (Forster et al., 1970; Pearcy et al., 1982; Yano and Tanaka, 1983; Clark and Kristof, 1990; McEachran and Miyake, 1990b).

A. Regional Comparison

Okinawa Trough. One hundred and twenty hauls of the bottom trawl were conducted below 200 m, of which the deepest was 1,180 m (Table 1). Fifteen families, 29 genera and 37 species were recorded (Tables 2 and 3). Compared with the Tohoku Slope, where a relatively high number of species were also collected, the Okinawa Trough has much more than twice as many families, genera and species (Table 3). Taxonomic richness, which is defined as the relative number of families, genera and species per one 60-minute haul (Table 4), are also by far the highest for all three taxonomic ranks. Therefore, the Okinawa Trough is characterized by having the most diverse deep-benthic chondrichthyan fauna of the regions surveyed.

Among the families, Squalidae were most numerous in number of species (nine species), and other main catches were Scyliorhinidae (seven species), Rajidae (five species) and two species each of Urolophidae, Triakididae, Chimaeridae and Rhinochimaeridae (Table 5). The species of the former three families contributed more than half of the total species in this region, characterizing the deep benthic chondrichthyan fauna of the Okinawa Trough.

The Okinawa Trough has some species in common with the Kyushu-Palau Ridge and/or the Tohoku Slope, suggesting some faunal relationship. On the other hand, the Japan Sea, which is geographically the closest region to the Okinawa Trough, is the farthest faunistically without any deep-benthic chondrichthyan fishes in common. The geographically

most distant region, Okhotsk Slope, also has no species in common.

Kyushu-Palau Ridge. One hundred and eighteen bottom trawls were operated between depths of 310 m and 910 m (Table 1). Ten species belonging to five families were collected, and the numbers of families, genera and species on the Kyushu-Palau Ridge rank third among the five regions (Tables 2 and 3). Sharks of the family Squalidae were most numerous in number of species (five species), occupying half of the total species in this region (Table 5). Other catches were Scyliorhinidae (two species), Hexanchidae (one species), Dasyatididae (one species) and Urolophidae (one species). The remarkable features of the Kyushu-Palau Ridge are the presence of a relatively high number of squalid species and the complete absence of raiid and chimaeriform species.

The Kyushu-Palau Ridge differs from the other regions in being located on the Philippine plate, whereas the others are on the Eurasian plate. This difference in geological history of these two plates might have caused the faunal difference between them. The Kyushu-Palau Ridge is located on the nonmarginal portion of the Philippine plate, and is separated from the continental plate by abyssal areas, i.e. the Ryukyu Trench (6,000–7,000 m deep) and the Nankai Trough (4,000–4,800 m deep).

Table 1. Number of trawl hauls in corresponding depths, and average time per haul. Depth range of each haul was averaged.

Depth (m)	Okinawa Trough	Kyushu Palau	Tohoku Slope	Okhotsk Slope	Japan Sea*
200-	40				1
300-	30	63			3
400-	15	18		4	4
500-	9	9		3	6
600-	7	15	6	3	
700-	7	11	20	14	12
800-	4		55	5	7
900-	6	2	34	31	1
1000-			26	12	3
1100-	2		28	19	5
1200-			26	12	1
1300-			19	9	
1400-			15		
1500-			5		
Total	120	118	234	112	43
Time**	43	120	117	65	31

^{*} From Ogata et al. (1973).

^{**} Average time (min.) of one haul.

Table 2. Species and depths (in meters) collected. Depths in parentheses indicate capture by bottom lines.

FAMILY Species	Okinawa Trough	Kyushu Palau	Tohoku Slope	Okhotsk Slope	Japan Sea*
CHLAMYDOSELACHIDAE					
Chlamydoselachus anguineus	750				
HEXANCHIDAE	,50				
Heptranchias perlo	240-515	370			
•	240 313	370			
SCYLIORHINIDAE	225				
Cephaloscyllium umbratile Scyliorhinus torazame	335				
Apristurus japonicus	320 820–915				
Apristurus japonicus Apristurus macrorhynchus	220-1140				
Apristurus longicephalus	600-1140				
Apristurus herklotsi	520-910				
Apristurus fedorovi	320 710		810-1430		
Galeus eastmani	330-900		010 1430		
Galeus nipponensis	330 700	362-540			
Parmaturus pilosus	(360-400)	685-710			
TRIAKIDIDAE	(500 100)	005 /10			
	140-220				
Proscyllium habereri Proscyllium venustum	140–320 205				
	203				
SQUALIDAE	1				
Squalus mitsukurii	unknown				
Squalus japonicus	330–340	450 (05	050 030		
Etmopterus lucifer	430–550	450-695	850–930		
Etmopterus pusillus		450-710	015 1100		
Etmopterus unicolor Centroscyllium ritteri			815-1100		
Centroscyllium kamoharai	560-1000		1000-1100		
Miroscyllium sheikoi	300-1000	340-370			
Centroscyllium sp.		694-910			
Zameus squamulosus	520-750	054-510	810-980		
Centrophorus squamosus	320 730		1000		
Centrophorus acus	600-810		1000		
Centrophorus scalpratus	300-330				
Deania calcea	780-810				
Squaliolus laticaudus	295-385	355-360			
SQUATINIDAE	2/3/303	333 300			
Squatina nebulosa	280-330				
•	200-330				
TORPEDINIDAE	220		4400		
Torpedo tokionis	220		1100		
RHINOBATIDAE					
Rhinobatos schlegelii	135-230				
RAJIDAE					
Raja kwangtungensis	155-240				
Raja macrocauda	unknown				
Raja gigas	300-1000				
Raja badia			1120-1165	1300-1420	
Notoraja tobitukai	505-1000				
Bathyraja abyssicola			1070-1100		
Bathyraja diplotaenia			800-1000		
Bathyraja matsubarai			800-1205		
Bathyraja caeluronigricans			800-1000	1310-1340	
Bathyraja notoroensis				650-700	

Table 2. (continued)

FAMILY Species	Okinawa Trough	Kyushu Palau	Tohoku Slope	Okhotsk Slope	Japan Sea*
Bathyraja aleutica	11046		800-850	470-950	
Bathyraja violacea			800 830	400-520	
Bathyraja minispinosa				470-1420	
Bathyraja lindbergi				900-950	
Bathyraja smirnovi				470-950	255-1125
Bathyraja isotrachys	790		1170-1520		
Rhinoraja longicauda			810-980		
ANACANTHOBATIDIDAE					
Anacanthobatis borneensis	630-990				
DASYATIDIDAE					
Dasyatis violacea		330-381			
UROLOPHIDAE					
Urolophus aurantiacus	155-205				
Urotrygon daviesi	205-300	350-395			
HEXATRYGONIDAE					
Hexatrygon longirostra	710				
MYLIOBATIDIDAE					
Myliobatis tobijei	220				
CHIMAERIDAE	220				
			000 1100	470 520	
Hydrolagus barbouri			900-1100 1120-1430	470–520	
Hydrolagus purpurescens Hydrolagus mitsukurii	600-830		1120-1430		
Chimaera phantasma	360-500				
*	300-300				
RHINOCHIMAERIDAE	700 700		000 020		
Rhinochimaera pacifica Harriotta raleighana	700–790 unknown		800-930		

^{*} From Ogata et al. (1973).

Table 3. Number and abundance of families, genera and species.

	Okinawa Trough	Kyushu Palau	Tohoku Slope	Okhotsk Slope	Japan Sea*	Total
Family	15	5	6	2	1	16
(%)	(93.8)	(31.3)	(37.5)	(12.5)	(6.3)	(100)
Genus	29	8	11	3	1	34
(%)	(85.3)	(23.5)	(32.4)	(8.8)	(2.9)	(100)
Species	37	10	18	9	1	61
(%)	(60.7)	(16.4)	(29.5)	(14.8)	(1.6)	(100)

^{*} Data from Ogata et al. (1973).

Table 4. Relative abundance of families, genera and species per 60 minute haul.

Region	Okinawa Trough	Kyushu Palau	Tohoku Slope	Okhotsk Slope	Japan Sea*	Total
(No. trawl)	(120)	(118)	(234)	(112)	(43)	(627)
Family	10.7	1.0	0.8	1.0	2.8	1.0
Genus	9.1	0.9	0.7	0.7	1.2	1.0
Species	6.5	0.6	0.6	1.1	0.7	1.0

^{*} Data from Ogata et al. (1973).

These abyssal areas probably also influence the distribution of weak swimmers or benthic species lacking a mesopelagic life stage, and we believe that some of the faunal differences between the Kyushu-Palau Ridge and the other regions are caused by the presence of such abyssal waters. The absence of rajids from the Kyushu-Palau Ridge may be a good example of this (see below). Squalids, some of which are mesopelagic and stronger swimmers, seem to be little affected by such abyssal waters.

Tohoku Slope. Two hundred and thirty four bottom trawls were made between depths of 580 m and 1,520 m. The numbers of families, genera and species (six, 11 and 18, respectively) rank second among the five regions, and the fauna is rather diverse in composition, similar to that of the Okinawa Trough. Among the families represented, the species of Rajidae are most abundant (eight species), followed by Squalidae (Table 5). The rajid species are those of the genera Raja (Amblyraja) and Bathyraja, and the Tohoku Slope is close to the Okhotsk Slope in that rajid species are most dominant, with members of the same genera or subgenus, and with some species common. However, the rajids of the Okinawa Trough are mostly members of different phyletic groups (McEachran and Miyake, 1990a), suggesting that the Tohoku Slope has rather lower affinities with the Okinawa Trough. On the other hand, the Tohoku Slope has a relatively high number of squalid species with some common species, suggesting that the Tohoku Slope has closer affinities with the Okinawa Trough and Kyushu-Palau Ridge in this regard.

Okhotsk Slope. One hundred and twelve bottom trawls were made between depths of 400 m and 1,420 m. The Okhotsk Slope is conspicuous for its poor representation of families (Tables 2 and 3), only two being represented by the species obtained. Of the nine species collected, seven belong to the rajid genus *Bathyraja*, showing a remarkable dominance of the genus below 200 m in depth. As discussed above, some species commonly occur both on the Tohoku Slope and in this area, suggesting closer faunal relationships.

Japan Sea. The Japan Sea chondrichthyan fauna is the poorest of the five regions, consisting of only one species, *Bathyraja smirnovi* (Tables 2 and 3). This species, which is abundant and occurs in a wide range of depths (Ogata et al., 1973; Okiyama, 1982), was also collected on the Okhotsk Slope. The Japan Sea is well known for its distinctive deep-water fauna, which is derived from the Okhotsk and Bering

Table 5. Dominant families, number of species and abundance (percent of total species in each region).

	Okinawa Trough	Kyushu-Palau	Tohoku Slope	Okhotsk Slope	Japan Sea*
1	Squalidae (9 spp, 24.3%)	Squalidae (5 spp, 50%)	Rajidae (8 spp, 44.4%)	Rajidae (8 spp, 88.8%)	Rajidae (1 sp, 100.0%)
2	Scyliorhinidae (7, 18.9%)	Scyliorhinidae (2, 20%)	Squalidae (5, 27.7%)	Chimaeridae (1, 11.1%)	
3	Rajidae (5, 13.5%)	Hexanchidae Dasyatididae Urolophidae (1, 10% each)	Chimaeridae (2, 11.1%)		
4	Triakididae Urolophidae Chimaeridae Rhinochimaeridae (2, 5.4% each)		Scyliorhinidae Torpedinidae Rhinochimaeridae (1, 5.6% each)		
	Chlamydoselachidae Hexanchidae Squatinidae Torpedinidae Rhinobatidae Anacanthobatididae Hexatrygonidae Myliobatididae				
	Myliobatididae (1, 2.7% each)				

^{*} From Ogata et al. (1973).

seas, with which it has many species in common (Nishimura, 1968). With presence of common species, some faunal relation are also indicated in this survey between this region and the Okhotsk and Tohoku slopes, but none is evident with the Kyushu-Palau Ridge or the Okinawa Trough in the deep benthic chondrichthyan fauna (see below for further discussion).

B. Distributional analyses of major groups

Scyliorhinidae. Scyliorhinid species are most abundant in the Okinawa Trough. In contrast, only two species were taken on the Kyushu-Palau Ridge and one on the Tohoku Slope. None were recorded from the Okhotsk Slope or Japan Sea. In spite of their close geographical position at the same latitudes, there is a sharp contrast between the Okinawa Trough and Kyushu-Palau Ridge. Generally, the composition of scyliorhinid sharks is similar at the Tosa Bay (Kamohara, 1958; Nakaya, 1975, 1988a, b), Mie (Kobayashi et al., 1982; Taniuchi, 1984), Suruga Bay (Tanaka, 1984), Choshi (Taniuchi, 1984; Nakaya, 1988b) and the Okinawa Trough (present study). Therefore, scyliorhinid species are considered to occur rather uniformly in composition along the southern coasts of the Japanese Archipelago. These facts show that there is a remarkable difference in scyliorhinid fauna between the Kyushu-Palau Ridge and the other regions. This may be due to the Kyushu-Palau Ridge being located on the Philippine plate and the other regions on the Eurasian plate. In addition, scyliorhinid sharks are generally sluggish swimmers and benthic in the mode of life, and they are considered to have difficulty in surmounting abyssal areas, which are deeper than their normal habitat. Therefore, the abyssal areas between the Kyushu-Palau Ridge and the Japanese Archipelago, i.e. the Ryukyu Trench and Nankai Trough, may well serve as barriers to their movement to the Kyushu-Palau Ridge. Our survey, however, discovered two species of genera Parmaturus and Galeus from the Kyushu-Palau Ridge. In addition, Ivanov (1986) reported Apristurus longicephalus (correctly A. herklotsi, see Nakaya, 1991) from the southern part of the survey area on the Kyushu-Palau Ridge. One paratype of Apristurus fedorovi came from the Emperor Sea Mounts (39°N, 171 °E) on the Pacific Plate (Dolganov, 1985 a). Though Springer (1982) noted that scyliorhinid sharks are restricted to the continental plates, with the exception of Apristurus spongiceps from Hawaii, these facts suggest that some of them occur on the

non-continental plates. Lee (1969), Jones and Geen (1977), and Cross (1988) reported the occurrence of juveniles and adolescents of Parmaturus xaniurus and Apristurus brunneus in midwater between 10-500 m above the sea bottom. Cross (1988) also noted the conspicuous absence of the young of these two species in benthic collections. If juveniles and adolescents have mesopelagic stages, as suggested by Cailliet (1981, abstract of ASIH meeting, Corvallis, Oregon), it may be reasonaly inferred that they have a better chance than other scyliorhinid species, that lack a mesopelagic stage, to expand their distribution across great depths and to settle on distant sea mounts or ridges. This may explain the occurrence of some sluggish scyliorhinid sharks on the Kyushu-Palau Ridge.

A. fedorovi is a very abundant species in the Tohoku region and is also known from the southern waters of Hokkaido (unpublished data, Nakaya), and the Emperor Sea Mounts (Dolganov, 1985a), but no specimens have been recorded from southern Japan. There are five other species of Apristurus in Japanese and adjacent waters, but they are known only from southern Japan, the northern-most records being Choshi (Nakaya, 1975, 1988b; Taniuchi, 1984). Therefore, the available information to date suggests that A. fedorovi is the only northern species, and that this species and the other five species are allopatric in distribution. With regard to Galeus, only a single species, G. nipponensis, has been recorded from Choshi and southern waters, but none has been collected from the Tohoku region. These facts, together with rajid distribution features discussed below, may suggest a discontinuity of the deep-benthic chondrichthyan fauna between the Tohoku and more southern regions.

The cold Oyashio Current is dominant along the Pacific coast of northern Japan and the warm Kuroshio Current flows along southern Japan, with a boundary at around Cape Inubo near Choshi. As these currents influence depths to some 800 m only (Sverdrup et al., 1961), this faunal discontinuity seen in some deep-benthic chondrichthyan fishes must result from other factors, because these species mostly inhabit deeper waters. One possible factor is the presence of the relatively shallow Shichito-Iojima Ridge, which is a huge elevation, running southward from the Izu Peninsula to Iojima Island, between the Shikoku Abyssal Basin and the Izu-Ogasawara Trench. The Ridge is shallower than 1,000 m in the northern part, and becomes deeper southwards. The

warm Kuroshio current flows north-eastward over the northern end of the ridge. As far as can be ascertained, A. fedorovi is the deepest species (at least down to 1,430 m) among the Japanese species of the genus, and the other more southern species of the genus and Galeus are known from depths of 900-1,100 m and 330-900 m, respectively. It may be easier for the southern species to cross the ridge, because of the presence of the Kuroshio Current and their rather shallower distribution. However, the northern deeper-benthic species, including the species of Bathyraja, are considered to have difficulty in surmounting the ridge, because they have, in a sense, a huge wall on the southwestern side of their habitat and, moreover, the top areas of the ridge are influenced by the warm current. Therefore, the Shichito-Iojima Ridge, combined with the effect of the Kuroshio Current, could be a more effective barrier for the northern deepbenthic species. The presence of southern deepbenthic species at Choshi (north-eastern side of the Shichito-Iojima Ridge), and absence of northern species on the western side of the ridge may support this consideration. The distribution of deep-sea teleosts might be also explained in this way. Some northern deep-benthic teleosts, i.e. some members of the macrourid, cottid and liparidid fishes, have similar distributions, confined to the eastern and/or northern sides of the Ridge (pers. comm. with Drs. O. Okamura, M. Yabe and K. Kido). Although this hypothesis needs verification from different standpoints of view, we consider that the Shichito-Ioiima Ridge functions as a mechanical barrier for deepbenthic fishes, and that associated with the warm Kuroshio Current on the top, it is particularly effective against movements of northern species.

No scyliorhinid is known from the Okhotsk Slope or the Kurile Islands, and various oceanographic and topographic conditions seem to have prevented scyliorhinids from entering the Okhotsk Sea. The Japan Sea and Okinawa Trough are geographically closest among the surveyed regions, but the deep-water scyliorhinid fauna in these regions is markedly different. Ogata et al. (1973) reported no species from the Japan Sea, but many species are known from the Okinawa Trough. However, Cephaloscyllium umbratile and Scyliorhinus torazame, which were collected in the Okinawa Trough, have been reported also from the Japan Sea (Mori, 1956; Honma and Kitami, 1977). These two species are known to enter very shallow coastal waters (Nakaya, 1975; Yamada,

1986), and the Tsushima Strait (120 m in depth) and Korea Strait (140 m) between the Okinawa Trough and the Japan Sea do not act as barriers for them. In contrast, the complete absence of *Apristurus* and *Galeus* from the Japan Sea may imply that these straits function as a physical barrier for the typical deep-water scyliorhinids.

Squalidae. Species of Squalidae are relatively abundant in the Okinawa Trough and on the Kyushu-Palau Ridge and Tohoku Slope, but no species was recorded from the Okhotsk Slope or Japan Sea. The number of species does not so obviously decrease on the Kyushu-Palau Ridge or Tohoku Slope, when compared with the Okinawa Trough, as did in scyliorhinid species. As squalid sharks are generally more buoyant (Bone and Roberts, 1969) and are stronger swimmers than scyliorhinid sharks, the abyssal areas and the ridges do not seem to function as barriers for squalid sharks. Similarly, the Shichito-Iojima Ridge does not seem to influence the distribution of squalid sharks. On the other hand, despite the presence of many squalid sharks in the Okinawa Trough, typical deep-water squalids, such as Centrophorus and Centroscyllium, do not occur in the Japan Sea. They, especially species of these genera, whose preferred depths are deeper than 150 m (Kobayashi et al., 1982; Yano and Tanaka, 1983), seem to be obstructed by the shallow Tsushima and Korea Straits, as seen also for some of the scyliorhinid sharks. Only a few species of Squalus and Somniosus have been reported from the Japan Sea (Mori, 1965; Ueno, 1971; Honma and Kitami, 1977). Squalus acanthias and Somniosus pacificus (Ueno, 1971; pers. com. with Mr. K. Maeda) are the only squalids in the Okhotsk region, and they are widely distributed in the north Pacific south to the East China Sea (Chu, 1960). Species of Squalus are relatively shallow-water inhabitants (Yamada, 1986), and Somniosus pacificus is sometimes caught by set net at 50-60 m in depths (Amaoka et al., 1989). The shallow Tsushima and Korea Straits, and the channels of the Kurile Islands do not form a barrier for them. However, the absence of deepwater squalids in the Okhotsk Sea may suggest that the Kurile Islands and its shallow areas have obstructed their invasion to the Okhotsk Sea from the Pacific Ocean.

Rajidae. The species of Rajidae show an interesting distribution pattern around Japan. No rajid species were collected from the Kyushu-Palau Ridge, but five or more species were collected from each of

the other regions considered. Tosa Bay and Mie are also reported to have five or six common species (Kamohara, 1958, 1959; Ishiyama, 1967; Taniuchi, 1984), suggesting a rather uniform rajid fauna along the Pacific coast of southern Japan. These facts suggest a remarkable faunal gap between the Kyushu-Palau Ridge and the other regions, paralleling the situation seen in scyliorhinid sharks. The strongly benthic habit of rajids and the presence of abyssal areas much deeper than their normal habitat (2,900 m at the deepest, McEachran and Miyake, 1990b) may explain the discontinuity between these two regions.

Species of the genera Raja and Bathyraja were numerously collected in the present study. Three of the four Raja species from the Okinawa Trough were members of the subgenus Dipturus. Species of this subgenus have been reported from various parts of Japan, including Tohoku, Okhotsk and Japan Sea regions (Lindberg and Legeza, 1967; Maruyama, 1971; Ueno, 1971; Honma and Kitami, 1977; pers. com. with Mr. K. Maeda).

The occurrence of the species of genus Bathyraja is apparently different in the regions surveyed. Six and seven species occurred on the Tohoku Slope and Okhotsk Slope, respectively, but only one species each was seen at the Okinawa Trough (B. isotrachys) and the Japan Sea (B. smirnovi). It is generally known that species of Bathyraja are especially numerous in northern Japan (Ishiyama, 1967), and at least 11 species have been reported from the Pacific side of northern Honshu (Maruyama, 1971; Dolganov, 1985b; Ishihara and Ishiyama, 1985; present study). Very few species are, however, found in southern Honshu; B. aleutica (Tanaka and Kubota, 1988) and B. isotrachys seem to be the only member of the genus there. Therefore, the distribution of most Bathyraja species appears to be confined to northern Japan north of Choshi. In fact, Taniuchi (1984) reported some species of Bathyraja from Choshi, but only one specimen of B. aleutica has been observed in Suruga Bay (Tanaka and Kubota, 1988). As noted for scyliorhinids, Choshi appears to mark a break in the distribution of Bathyraja. Species of Bathyraja are distributed at various depths from shallow to very deep bottom (McEachran and Miyake, 1990b), and all of the species at the Tohoku Slope were caught from depths greater than 800 m in this survey. Considering the vertical distribution and the sudden disappearance of Bathyraja species from middle latitude waters of Japan, the Shichito-Iojima

Ridge and the Kuroshio current seem to play an important role in their distribution, as inferred also for the scyliorhinid sharks.

The distribution of *Bathyraja isotrachys* is, however, rather strange and remains unexplained, because it is the only species distributed the length of the Pacific coast of Japan, including the East China Sea (Ishihara and Ishiyama, 1985). Occurrence of *B. aleutica* in Suruga Bay might be explained by its extremely wide geographical distribution (amphi-Pacific distribution: Ishihara and Ishiyama, 1986).

Chimaeriformes. Chimaeriform fishes were not collected from the Kyushu-Palau Ridge, although some species occurred in the Okinawa Trough and on the Tohoku and Okhotsk Slopes. Maruyama (1971) reported three more species of chimaeroid and rhinochimaeroid fishes from the Tohoku Slope. Mori (1956), Kamohara (1958) and Tanaka (1984) noted the presence of a few species from the Japan Sea, Tosa Bay, and Suruga Bay. Chimaeriform fishes are generally considered to be benthic dwellers (Krefft, 1973), or pelagic to benthopelagic fishes (Stehmann and Bürkel, 1984). The available data of their distribution show that they live around the upper continental slope down to at least 3,149 m (Merrett and Marshall, 1981), and close to land (Compagno, 1986), although some species are reported from oceanic islands, such as Hawaii (Gilbert, 1905) and the Azores (Stehmann and Bürkel, 1984). Despite trawling for more than 236 hours, chimaeriform fishes were not collected from the Kyushu-Palau Ridge. Therefore, it will be reasonable to conclude that chimaeriform fishes do not occur on the Kyushu-Palau Ridge. If they are at least pelagic or benthopelagic (Stehmann and Bürkel, 1984), the opportunity would seem to exist for their expanding distribution over abyssal areas, as seen in some scyliorhinid sharks.

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Literature cited

- Amaoka, K., K. Nakaya, H. Araya and T. Yasui. 1983. Fishes from the north-eastern sea of Japan and the Okhotsk Sea of Hokkaido. Japan Fisheries Resource Conservation Association, Tokyo, 371 pp.
- Amaoka, K., K. Nakaya and M. Yabe. 1989. Fishes of Usujiri and adjacent waters in southern Hokkaido, Japan. Bull. Fac. Fish., Hokkaido Univ., 40(4): 254– 277.
- Asahida, T., H. Ida and T. Inoue. 1988. Karyotypes and cellular DNA contents of two sharks in the family Scyliorhinidae. Japan. J. Ichthyol., 35(2): 215-219.
- Baba, K., K. Hayashi and M. Toriyama. 1986. Decaped crustaceans from continental shelf and slope around Japan. Japan Fisheries Resource Conservation Association, Tokyo, 336 pp.
- Bone, Q. and B. L. Roberts. 1969. The density of elasmobranchs. J. Mar. Biol. Ass. U.K., 49: 913-937.
- Chu, Y. T. 1960. Classification of Chondrichthyes of China. Scientific Press, Peking, 225 pp.
- Clark, E. and E. Kristof. 1990. Deep-sea elasmobranchs observed from submersibles off Bermuda, Grand Caymen, and Freeport, Bahamas. Pages 269–284 in H. L. Pratt, Jr., S. H. Gruber and T. Taniuchi, eds. Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech. Rep. NMFS 90, 518 pp.
- Compagno, L. J. V. 1986. Subclass Holocephali, Order Chimaeriformes. Pages 144-147. in M. M. Smith and P. C. Heemstra, eds. Smith's Sea Fishes. Springer-Verlag, Berlin, xx+1047 pp.
- Cross, J. N. 1988. Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California. Fish. Bull., 86(4): 691–702.
- Dolganov, V. N. 1985a. A new species of shark from the North-West Pacific Ocean. Biol. Morya, (3): 64-65. (In Russian)
- Dolganov, V. N. 1985b. New species of skates of the family Rajidae from the Northwestern Pacific Ocean. Voprosy Ikhtiologii, 25(3): 415-425.

- Forster, G. R., J. R. Badcock, M. R. Longbottom, N. R. Merrett and K. S. Thomson. 1970. Results of the Royal Society Indian Ocean deep slope fishing expedition, 1969. Proc. Roy. Soc. London, B. 175: 367–404.
- Gilbert, C. H. 1905. The aquatic resources of the Hawaiian Islands. The deep-sea fishes. Bull. U.S. Fish Comm., 23 (2): 575-713.
- Honma, Y. and T. Kitami. 1977. Fauna and flora in the waters adjacent to the Sado Marine Biological Station,
 Niigata University. Ann. Rep. Sado Mar. Biol. Sta.,
 Niigata Univ., (8): 7-81.
- Imaoka, T., S. Irimura, T. Okutani, C. Oguro, T. Oji, M. Shigei and H. Horikawa. 1990. Echinoderms from continental shelf and slope around Japan. Vol. I. Japan Fisheries Resource Conservation Association, Tokyo, 159 pp.
- Ishihara, H. and R. Ishiyama. 1985. Two new North Pacific skates (Rajidae) and a revised key to *Bathyraja* in the area. Japan. J. Ichthyol., 32(2): 143–179.
- Ishihara, H. and R. Ishiyama. 1986. Systematics and distribution of the skates of the North Pacific (Chondrichthyes, Rajoidei). Pages 269–280 in T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds. Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyol. Soc. Japan, Tokyo, xii+985 pp.
- Ishiyama, R. 1967. Fauna Japonica, Rajidae (Pisces). Tokyo Electrical Engineering Coll. Press, Tokyo, vi+84 pp.
- Ivanov, O. A. 1986. A new capture of the rare catshark, *Apristurus longicephalus* (Scyliorhinidae). Voprosy Ikhtiologii, (5): 862-864.
- Jones, B. C. and G. H. Geen. 1977. Observations on the brown cat shark, *Apristurus brunneus* (Gilbert), in British Columbia coastal waters. Syesis, British Columbia Provincial Museum, 10: 169–170.
- Kamohara, T. 1958. A catalogue of fishes of Kochi Prefecture (Province Tosa), Japan. Rep. Usa Mar. Biol. Sta., 5(1): 1-76.
- Kamohara, T. 1959. New Records of fishes from Kochi Prefecture, Japan. Rep. Usa Mar. Biol. Sta., 6(2): 1-8.
- Kobayashi, H., Y. Yamaguchi, T. Nonoda, K. Izawa and H. Ban. 1982. The sharks caught on the continental shelf and slope in Kumano Nada region along the Pacific coast of Japan. Bull. Fac. Fish., Mie Univ., (9): 101-123.
- Krefft, G. 1973. Chimaeridae. Rhinochimaeridae. Pages 78-80 in J. G. Hureau and Th. Monod, eds. Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean. United Nations Educational, Scientific and Cultural Organization, Paris, xxii+683 pp.
- Lee, R. S. 1969. The filetail catshark, *Parmaturus xaniurus*, in midwater in the Santa Barbara Basin off California. Calif. Fish and Game, 55(1): 88-90.
- Lindberg, G. U. and M. I. Legeza. 1967. Fishes of Sea of Japan and the adjacent areas of the Sea of Okhotsk and

- the Yellow Sea. Part 1. Academia Nauk SSSR, Moskva (Translated, Israel Prog. Sci. Trans., Jerusalem), iv+198 pp.
- Maruyama, K. 1971. A catalogue of fishes of Iwate Prefecture, Japan. Bull. Iwate Pref. Fish. Exp. Sta., (1): 1-70.
- McEachran, J. D. and T. Miyake. 1990a. Phylogenetic interrelationships of skates: a working hypothesis (Chondrichthyes, Rajoidei). Pages 285-304 in H. L. Pratt, Jr., S. H. Gruber and T. Taniuchi, eds. Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech. Rep. NMFS 90, 518 pp.
- McEachran, J. D. and T. Miyake. 1990b. Zoogeography and bathymetry of skates (Chondrichthyes, Rajoidei). Pages 305–326 in H. L. Pratt, Jr., S. H. Gruber and T. Taniuchi, eds. Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech. Rep. NMFS 90, 518 pp.
- Merrett, N. R. and N. B. Marshall. 1981. Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08–27°N). Prog. Oceanog., 9: 185–244.
- Mori, T. 1956. Fishes of San-in District including Oki Islands and its adjacent waters (Southern Japan Sea). Mem. Hyogo Univ. Agr., 2(3): 1-62.
- Nakaya, K. 1975. Taxonomy, comparative anatomy and phylogeny of Japanese catsharks, Scyliorhinidae. Mem. Fac. Fish., Hokkaido Univ., 23(1): 1–94.
- Nakaya, K. 1988a. Morphology and taxonomy of Apristurus longicephalus (Lamniformes, Scyliorhinidae). Japan. J. Ichthyol., 34(4): 431-442.
- Nakaya, K. 1988b. Records of Apristurus herklotsi (Lamniformes, Scyliorhinidae) and discussion on its taxonomic relationships. Japan. J. Ichthyol., 35(2): 133-141.
- Nakaya, K. 1991. A review of the long-snouted species of Apristurus (Chondrichthyes, Scyliorhinidae). Copeia, 1991(4): 992-1002.
- Nishimura, S. 1965a. The zoogeographical aspects of the Japan Sea. Part I. Publ. Seto Mar. Biol. Lab., 13(1): 35-79
- Nishimura, S. 1965b. The zoogeographical aspects of the Japan Sea. Part II. Publ. Seto Mar. Biol. Lab., 13(2): 81-101.
- Nishimura, S. 1966. The zoogeographical aspects of the Japan Sea. Part. III. Publ. Seto Mar. Biol. Lab., 13(5): 365-384.
- Nishimura, S. 1968. The zoogeographical aspects of the Japan Sea. Part IV. Publ. Seto Mar. Biol. Lab., 15(5): 320-352
- Nishimura, S. 1969. The zoogeographical aspects of the Japan Sea. Part V. Publ. Seto Mar. Biol. Lab., 17(2): 67–142.
- Ogata, T., M. Okiyama and Y. Tanino. 1973. Diagnoses of the animal populations in the depths of the Japan Sea,

- chiefly based on the trawling experiments by the R/V Kaiyo-Maru. Bull. Japan Sea Reg. Fish. Res. Lab., (24): 21-51.
- Okamura, O. (ed.) 1985. Fishes of the Okinawa Trough and the adjacent waters. II. Japan Fisheries Resource Conservation Association, Tokyo, p. 418-781.
- Okamura, O., K. Amaoka and F. Mitani (eds.). 1982. Fishes of the Kyushu-Palau Ridge and Tosa Bay. Japan Fisheries Resource Conservation Association, Tokyo, 435 pp.
- Okamura, O. and T. Kitajima. 1984. Fishes of the Okinawa Trough and the adjacent waters. I. Japan Fisheries Resource Conservation Association, Tokyo, 414 pp.
- Okiyama, M. 1982. Elasmobranch fishes in the Sea of Japan, with special reference to the deep sea skate, *Bathyraja smirnovi*. Biological notes on the dominant fish in the deep waters of the marginal sea based on the material collected by the R/V "Kaiyomaru" in 1970. Rep. Japan. Gr. Elasmobranch Studies, (9): 55-56.
- Okutani, T., M. Tagawa and H. Horikawa. 1987. Cephalopods from continental shelf and slope around Japan. Japan Fisheries Resource Conservation Association, Tokyo, 194 pp.
- Okutani, T., M. Tagawa and H. Horikawa. 1988a. Bivalves from continental shelf and slope around Japan. Japan Fisheries Resource Conservation Association, Tokyo, 190 pp.
- Okutani, T., M. Tagawa and H. Horikawa. 1988b. Gastropods from continental shelf and slope around Japan. Japan Fisheries Resource Conservation Association, Tokyo, 203 pp.
- Pearcy, W. G., D. L. Stein and R. S. Carney. 1982. The deep-sea benthic fish fauna of the northeastern Pacific Ocean on Cascadia and Tufts abyssal plains and adjoining continental slopes. Biol. Oceanogr., 1(4): 375-428.
- Springer, V. G. 1982. Pacific plate biogeography, with special reference to shorefishes. Smithsonian Contr. Zool., (367): 1–182.
- Stehmann, M. and D. L. Bürkel. 1984. Chimaeridae, Rhinochimaeridae. Pages 212-218 in P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen and E. Tortonese, eds. Fishes of the north-eastern Atlantic and the Mediterranean. Vol. 1. United Nations Educational, Scientific and Cultural Organization, Paris, 510 pp.
- Sverdrup, H. U., M. W. Johnson and R. H. Fleming. 1961. The Oceans. Prentice-Hall, New Jersey, x + 1087 pp.
- Tanaka, S. 1984. Chondrichthyes of Suruga Bay and adjacent waers. Report of a preliminary investigation on sharks and rays in the Western Pacific Ocean. Japan. Gr. Elasmobranch Studies, Spec. Publ. (1): 25-35.
- Tanaka, S. and T. Kubota. 1988. Observation on the behavior of some deep-sea fishes in the Suruga Bay using the submersible "Shinkai 2000". JAMSTECTR Deepsea Res., (1988): 111-118.
- Taniuchi, T. 1984. Distribution of elasmobranchs in

Choshi, Izu Islands, and Ogasawara Islands. Report of a preliminary investigation on sharks and rays in the Western Pacific Ocean. Japan. Gr. Elasmobranch Studies, Spec. Publ. (1): 14–24.

Ueno, T. 1971. List of the marine fishes from the waters of Hokkaido and its adjacent regions. Sci. Rep. Hokkaido Fish. Exp. Sta., (13): 61-102.

Yamada, U. 1986. Scyliorhinidae, Squalidae. Pages 8-11, 21-25 in O. Okamura, ed. Fishes of the East China Sea and the Yellow Sea. Seikai Regional Fisheries Research Laboratory, Nagasaki, xxvi+501 pp.

Yano, K. and S. Tanaka. 1983. Biological studies on squaloid sharks from Suruga Bay, Japan. Proc. 2nd N. Pac. Aquacul. Symp., p. 405-413.

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日本周辺海域の深海底生性軟骨魚類相および動物地理 仲谷一宏・白井 滋

1978年から3年間,沖縄舟状海盆,九州一パラオ海嶺,茨城県から青森県に至る本州北部太平洋の陸棚斜面("東北冲")および北海道のオホーツク海陸棚斜面("オホーツク沖")において大規模な深海魚類調査が実施された。

この中で著者らは軟骨魚類の分類を担当し、水深 200-1,520 m で行われた 584 回のトロール漁獲物から 61 種の深海底生性軟骨魚類を確認した。また、これら 4 調査海域に加え、尾形他 (1973)

による日本海でのトロール結果を含めて軟骨魚類相を検討した結果、各々の海域が極めて特徴的な深海底生性軟骨魚類相を有することが判明した。沖縄舟状海盆は非常に多様性に富んだ海域で、多くの分類群に含まれる37種が出現し、中でもッノザメ科、トラザメ科、ガンギェイ科(ガンギェイ属)の種が優占した。九州一パラオ海嶺には10種が出現し、その構成は比較的単純で、ツノザメ科の種が多く、ガンギェイ科の手が当りの種が出現し、がンギェイ科(ソコガンギェイ属)の種が最も多く、ツノザメ科の種がこれに次いだ。オホーツク沖では軟骨魚類の構切はメメ科の種がこれに次いだ。オホーツク沖では軟骨魚類の構切はガンギェイ属)の種であった。日本海で見られた深海底生性軟骨魚類はガンギェイ科(ソコガンギェイ属)のドブカスベー種で、他の海域に比較して極めて貧弱な軟骨魚類相であることを再確認した。

これらの深海底生性軟骨魚類の分布は琉球海溝等の超深海や対馬海峡等の浅海域の存在により大きな影響を受けているものと考えられる。また、多くの種が出現した分類群について日本周辺での分布の特徴を調査した結果、伊豆半島から南下する巨大な七島・硫黄島海嶺が深海底生性軟骨魚類の分布に大きな影響を与えているものと考えられた。すなわち、中浅海部を黒潮で復われた七島・硫黄島海嶺は、特に北方産の深海底生性軟骨魚類の多くにとって越え難い障壁となっており、さらに、北方深海底生性の魚類一般についてもこの考えを拡大できる可能性が示唆された。

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