

The First Data on the Structure of Vulnerable Marine Ecosystems of the Emperor Chain Seamounts: Indicator Taxa, Landscapes, and Biogeography

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Abstract—The first comprehensive study of the deep-sea ecosystems of the Emperor Chain seamounts (the northwestern Pacific Ocean) was conducted in July–August 2019 by A.V. Zhirmunsky National Scientific Center of Marine Biology, FEB RAS. The expedition, using a remote-operated underwater vehicle *Comanche 18*, was aimed at the study of distribution of typical underwater landscapes and key taxa of Octocorallia corals and Hexactinellida sponges in the vulnerable marine ecosystem of the seamounts. New data on the macrobenthos biodiversity and biogeographic characteristics of deep-sea corals and sponges, which are the dominant animals in the studied area, are presented. The survey has shown changes of the coral fauna in the latitudinal direction and obtained new data on the biogeographic boundary in the area of the Emperor Chain seamounts.

Keywords: Emperor Chain, seamounts and guyots, vulnerable marine ecosystems, deep-water Octocorallia, deep-water sponges Hexactinellida, biogeographic boundary

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INTRODUCTION

Seamounts, including the raisings of the Emperor Chain, are areas with high biological productivity of benthic and pelagic communities, including industrially important accumulations of marine organisms that support commercial fishery [1, 12, 25]. Uncontrolled commercial fishery in the neutral waters of the North Pacific seriously threatens the natural balance, as at least 75% of the fish stocks on the seamounts are decreasing [13]. In order to ensure the rational use of bioresources in the high seas of the World Ocean, international regional fishery management organizations operate in eight oceanic zones to develop quotas for fishing and prevent damage to vulnerable marine ecosystems (VMEs) of seamounts. In the Atlantic, the North-East Atlantic Fisheries Commission (NEAFC) established a fishery restriction regime and introduced a complete ban on bottom fishery in several areas. It is proposed to use deep-sea corals and sponges as indicator groups of VMEs; the critical catch values for them determine the regime of fishing limits on seamounts (<https://www.neafc.org>). Since 2012, the North Pacific Fisheries Commission (NPFC) has been operating on the basis of the Convention on the Conservation

and Management of High Seas Fisheries Resources with participation of the countries of the region, including the Russian Federation (<https://www.npfc.int>). The Commission and the Convention are focused on deep-sea bottom VMEs, including accumulations of soft coral and the gorgonians (“coral gardens”) of the Emperor Chain as sources and indicators of the high productivity of the region. At a meeting in March 2018 (Yokohama, Japan) the Commission recognized the lack of information on the distribution and the population density of bottom organisms in the region and the need to study them closely (<https://www.npfc.int/npfc-yearbook-2017>).

The deep-sea bottom ecosystems of the seamounts are classified as VMEs, since their recovery after mechanical damage by bottom trawls or resulting from overfishing is proceeding extremely slowly [5, 15, 23]. Large and slowly growing gorgonians and sponges are the longest-living representatives of the deep-sea biota. These corals and sponges are of great importance for the existence of bathyal communities, since they serve as a substrate for numerous benthic organisms (echinoderms, worms, associated microorganisms, etc.) and thereby fulfill the important habitat-forming function [6–8, 33].

Data on the biodiversity and biogeographical characteristics of eight-rayed corals (Anthozoa: Octocorallia) of the Emperor Chain are scarce and have been presented only in two publications [11, 20]. The authors list eight families and six species of the subclass Octocorallia in the southern part of the seamount chain and thus give just the initial information about the Octocorallia of the entire region. There are no publications on the sponges of the Emperor Chain. A significant gap exists in the study of the biogeography, the history of the fauna formation, and the pathways of dispersal of corals and sponges in the northwestern and central parts of the Pacific. Seamounts and guyots (flat-topped seamounts) are of interest from a biogeographic point of view, since various communities of bottom and pelagic fauna are associated with them [19, 24, 25]. According to the modern concepts, oceanic risings can be “stepping stones” for resettlement and enrichment of deep-sea fauna, as well as refuges and faunal centers; they can become biogeographic barriers and have a significant impact on the formation of the oceanic fauna [3, 24, 34]. In the northwestern part of the Pacific, marine species carried by currents meet seamounts and guyots of the Emperor Chain on their way; however, the biogeographic role of this process is unclear. However, we expect that these corals and sponges, as important representatives of deep-sea communities, could make a significant contribution to understanding the pathways of the dispersal of deep-sea species in the North Pacific and serve as markers of the distribution of bottom organisms in the latitudinal direction and to the depths.

The aim of this study was to obtain information on the structure, distribution, and biogeographic characteristics of the macrobenthic population of the vulnerable marine ecosystems of the Emperor Chain, and especially on their indicator taxa, that is, corals and sponges.

MATERIALS AND METHODS

The material was collected during the expedition of the A.V. Zhirmunsky National Scientific Center of Marine Biology, Far East Branch, Russian Academy of Sciences (FEB RAS) with participation of the P.P. Shirshov Institute of Oceanology (RAS) aboard the R/V *Akademik M. Lavrentyev* (cruise no. 86) in July–August 2019 (Fig. 1). The main research methods were collection of bottom fauna, visual observations, as well as photo and video recording with a remotely operated underwater vehicle (ROV) *Comanche 18*. The landscape-ecological situation and the bottom fauna were studied in the depth range from 2182 to 338 m. Visual observations were accompanied by continuous video recording, selective photographing, and targeted sampling. Video transects were performed to quantify the abundance of some dominant groups of hydrobionts. A 10-cm laser scale was used to

determine the size of animals and to assess the density of their settlements; 1789 photographs and more than 49 h of video records were obtained and studied. The collection of biological samples equaled 679 storage units.

RESULTS

The substrate in the studied areas was mostly built of the alternation of sedimentary and rocky facies. Loose soils were represented by washed calcareous sand (rarely pteropod sediments) interspersed with small fragments of sedimentary and volcanic rocks. Solid substrates were represented by tuffs, tuff-sandstones, limestone, as well as pillow lava and cover lavas of various degrees of fragmentation, covered with a more or less thick iron–manganese crust.

The populations of sedimentary and rocky facies were different, as expected. However, some taxa were very plastic in this regard. On the one hand, many detritus-collecting forms (small brittle-stars and some holothurians) were numerous on stones devoid of visible sediments. Animals that were previously considered as inhabitants of soft soils (for example, sea urchins of the genus *Aspidodiadema*) were numerous on stony facies. On the other hand, the mere presence of even small stones and outcrops of the underlying rock created conditions for the development and dominance of attached sestonophages on external “sedimentary” facies. The near-top area was characterized by active near-bottom hydrodynamics. The pronounced signs of ripples formed on the sediment in different directions, the drift of turbid suspensions and the behavior of the ROV showed the presence of rather strong currents in the area of study. The variety of substrate forms, the presence of currents, and the depth differences determined an intricate pattern of distribution of biotic complexes. Nevertheless, based on direct observations, we identified and localized the main types of the landscapes characteristic of the top parts and the upper slopes of the investigated seamounts for the first time (Table 1).

We recorded corals of the subclass Octocorallia and “glass” sponges belonging to the class Hexactinellida, which are widely distributed on the studied risings, during almost all ROV dives. The distribution of corals and sponges was very uneven. Representatives of both groups were rarest on sedimentary facies, although there were enough small stones or outcrops of the underlying rock for these animals, which usually attach on a thin sedimentary cover. Many sponge species were found on strewn small fragments. On stony facies, both animal groups preferred massive relief forms and did not occur on small fragments. Bottom hydrodynamics appears to be the first determining factor in the distribution of corals and sponges. Moreover, it seems that the conditions that were optimal for corals were not always the same for sponges, and vice

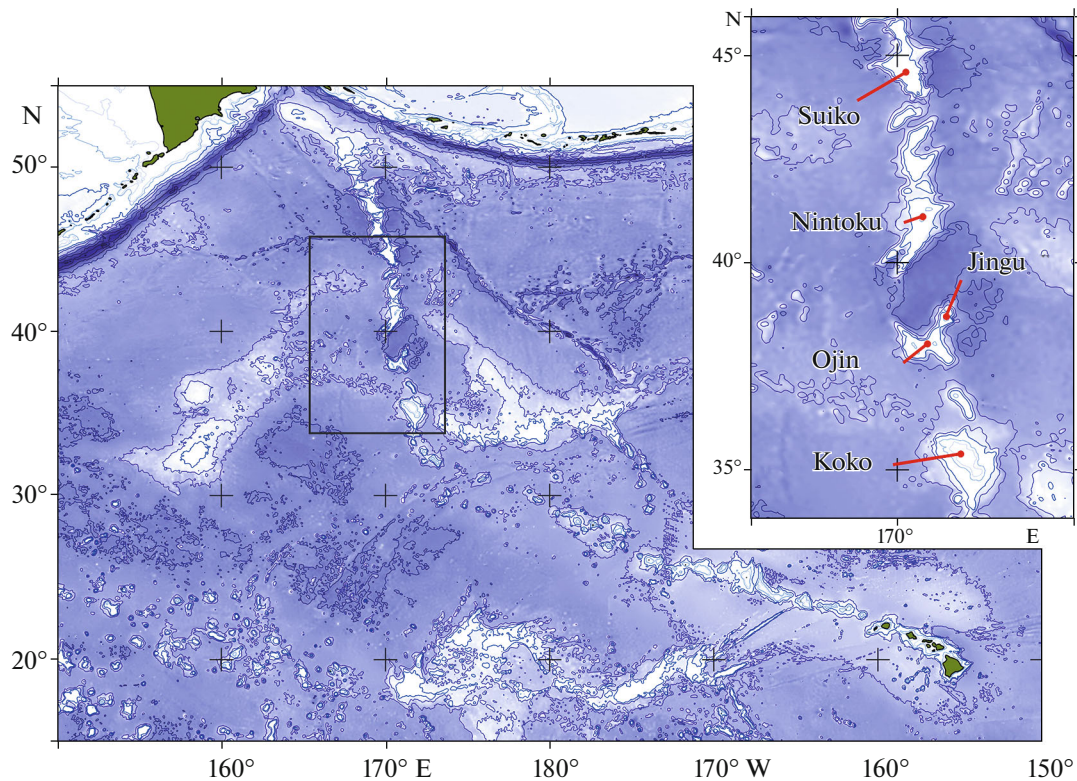


Fig. 1. A map of the area of study.

versa. Our surveys with the ROV showed dense coral settlements on the northern top and in the northwestern part of the plateau on the Koko Guyot (Fig. 2a). However, in many biotopes of this guyot, sponges were not among the dominant forms. The opposite situation was observed on the slopes of Jingu Seamount, where we recorded the highest density and variety of sponges on the northern slope, but Octocorallia were few (Table 1).

In the studied areas of the Emperor Chain, the Octocorallia population was dominated by gorgonians, mainly of the Primnoidae family, they were represented by the largest number of genera (Table 2). On the Koko Guyot, located in the southern part of the ridge, we found 24 genera of Octocorallia, more than on the guyots located northwards. Among them three genera belong to the order Pennatulacea (sea pen) and 21 genera belong to the order Alcyonacea (including three genera of soft corals and 18 genera of gorgonians). Northwards, on the Ojin Guyot and Jingu Seamount, Octocorallia were significantly less diverse: only two genera of soft corals and four genera of gorgonians were found (Fig. 1, Table 2); *Paragorgia coralloides* Bayer, 1993 was not found here, but *P. arborea* (Linnaeus, 1758) was recorded; the latter is a characteristic inhabitant of high latitudes with a bipolar range [16].

Seven families of sponges occurred in the studied area: Aulocalycidae, Euplectellidae, Euretidae, Far-

reidae, Leucopsacidae (?), Rossellidae, and Tretodictyidae. The highest number of the detected genera belong to the Euplectellidae family: *Amphidiscella* and *Bolosoma* of the subfamily Bolosominae; *Atlantisella*, *Dictyaulus*, and *Walteria* of the Corbitellinae subfamily (two known species of the genus *Walteria* were recorded: *W. flemmingi* Schulze, 1886 and *W. leuckarti* Ijima, 1896), as well as a representative of a new genus and species. The Rossellidae family was represented by both subfamilies: Rossellinae by *Acanthascus* [*A. (Rhabdocalyptus)* and *A. (Staurocalyptus)*] and Lanuginellinae by *Lanuginella pupa* Schmidt, 1870. The Leucopsacidae family was represented by the *Leucopsacus* genus; the Farreidae family was represented by several species of the *Farrea* genus. Two genera of the Tretodictyidae family were recorded: *Hexactinella* and *Tretocalyx*. In the studied guyots, the Aulocalycidae and Euretidae families were represented by several new species belonging to new genera (Table 3). Endemic genera that are new to science were found on Jingu Seamount and on the Ojin Guyot. The representatives of the genus *Hexactinella* and several species of the genus *Farrea* occurred most frequently (Fig. 2b). The species *Walteria leuckarti*, which have an uncommon dichotomously branching form (Fig. 2d), was found on almost all guyots.

On the slopes of the investigated guyots, in addition to Hexactinellidae sponges, we found encrusting

Table 1. The main communities discovered in the Emperor Chain area in July–August 2019 with the ROV *Comanche 18*

ROV dive no.	Coordinates	Depth, m	Type of substrate	Landscape-forming taxa
Koko Guyot				
4	35.5836 N; 171.2460 E	492–507	Solid	Octocorallia + Stylasteridae + Decapoda
8	35.7155 N; 171.0714 E	593–581	"	Octocorallia + Stylasteridae + Scleractinia + Echinothurioida + Decapoda with purple carapace
9	35.6557 N; 171.0560 E	386–365	"	Octocorallia + Stylasteridae + Decapoda
16	35.4038 N; 171.3192 E	391–397	"	Octocorallia + Stylasteridae + Scleractinia + Echinothurioida + Decapoda
3	35.3552 N; 171.6040 E	338–341	Soft	Decapoda: Portunidae + Echinoidea: Cidaridae + Asteroidea: Goniasteridae cf. <i>Ceramaster</i>
5	35.6032 N; 171.2232 E	779–768	"	Ophiuroidea small + Holothuroidea: Elpidiidae small
6	35.7909 N; 171.0636 E	2182–1969	"	Ophiuroidea big white + Holothuroidea varia
11	35.0724 N; 171.2883 E	1882–1853	"	Ophiuroidea big white + Holothuroidea varia
10	35.0957 N; 171.3194 E	1366–1383	Solid	Octocorallia + Echinoidea: <i>Caenopedina</i> sp. + Holothuroidea: cf. Elpidiidae transparent
17	35.0948 N; 171.3179 E	1429–1358	"	Octocorallia + Echinoidea: <i>Caenopedina</i> sp. + Holothuroidea: cf. Elpidiidae transparent
7	35.7718 N; 171.0677 E	1621–1341	"	Ophiuroidea small white + Echinoidea: <i>Aspidodiadema</i> sp.
Jingu Seamount				
12	38.7811 N; 171.0917 E	2152–1579	Solid	Hexactinellida + Ophiuroidea big white
14	38.7653 N; 171.0854 E	1616–1329	"	Hexactinellida + Ophiuroidea red on stones
13	38.7665 N; 171.0988 E	1290–862	"	Hexactinellida + Ophiuroidea red on stones
15	38.7563 N; 171.0975 E	865–847	"	Hexactinellida + Echinoidea: <i>Gracilechinus</i> aff. <i>lucidus</i>
Ojin Guyot				
18	38.0333 N; 170.2138 E	1527–1460	Soft	Ophiuroidea red half-buried + Echinoidea: <i>Gracilechinus</i> aff. <i>lucidus</i>
19	38.0412 N; 170.2938 E	1065–961	Solid	Ophiuroidea pink under stones + Actiniaria small + Hexactinellida
20	38.1903 N; 170.9142 E	1274–1104	"	Ophiuroidea red half-buried + Echinoidea: <i>Gracilechinus</i> aff. <i>lucidus</i>
Nintoku Guyot				
21	40.9992 N; 170.7247 E	1154–1147	Soft/solid	Sediment: Ophiuroidea red half-buried + Holothuroidea: Elpidiidae small Stones: Hexactinellida + Stylasteridae

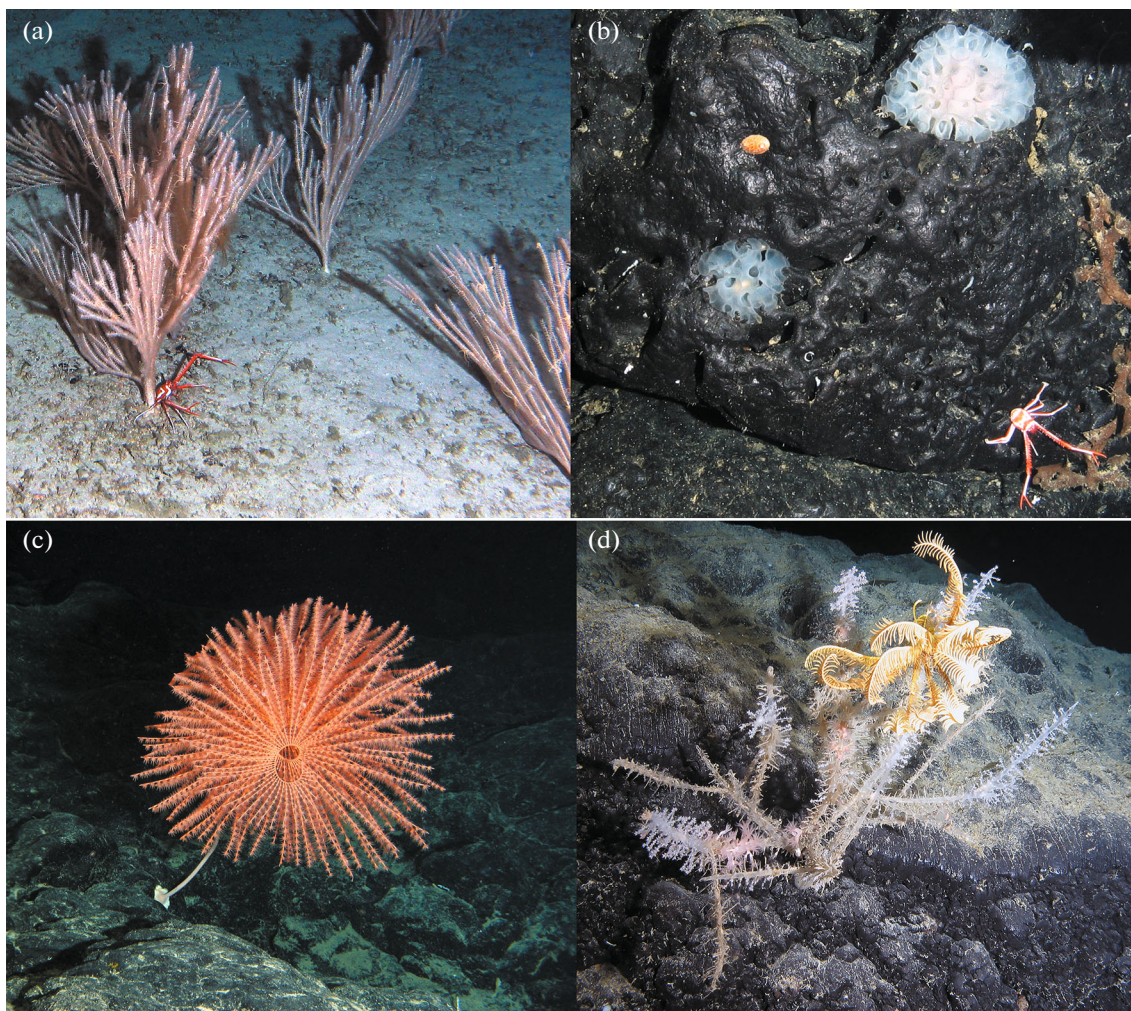


Fig. 2. Typical representatives of the deep-sea fauna of the area of study: (a) dense settlements of the coral *Narella* sp., Koko Guyot, depth of 343 m; (b) the sponges *Farrea*, Jingu Seamount, depth of 1267 m; (c) the coral *Iridogorgia* sp., Koko Guyot, depth of 1312 m; (d) the sponge *Walteria leuckarti*, Jingu Seamount, depth of 2060 m.

Demospongiae, including their small representatives previously described as belonging to the predatory Cladorhizidae family (see: [17]).

DISCUSSION

The main factors that determine the state of seamount communities are the depth, temperature, and gradients of dissolved oxygen, suspended organics, and nutrients [21, 22]. The data obtained in the present research regarding the intricate distribution of the biotic complexes and key taxa of the Octocorallia and Porifera in the studied areas of the Emperor Chain seamounts indicate the importance of such local conditions as substrate diversity and a complicated system of currents, which, in combination with depth, determine the state of the community.

Gorgonians play an essential role in the deep-sea communities of the Octocorallia of the Hawaiian

Ridge: the Plexauridae and Primnoidae families contain 46% of the species recorded here, the second largest group is gorgonian Chrysogorgiidae family (*Chrysogorgia*, *Iridogorgia*, and *Metallogorgia* (see: [10]). The faunistic complex of Octocorallia on the Koko Guyot can be characterized as very close to that of the Hawaiian Ridge, with a significant participation of members of the gorgonian Chrysogorgiidae family, including the *Iridogorgia* and *Metallogorgia* genera (Fig. 2c), and the Isididae family (Table 2). The genus *Chrysogorgia* was not previously recorded for the Pacific Ocean northwards of the Hawaiian Islands. We found three species of this genus on the Koko Guyot, including the *Ch. stellata* Nutting, 1908, earlier known only in the Hawaii [9], and the species *Ch. ramosa* Ver-sluis, 1902, previously recorded only in the Philippines [9]. The finding of the *Paragorgia coralloides* Bayer, 1993 on the Koko Guyot, which was previously found in the Pacific only in the Philippine Sea near

Table 2. Octocorallia from different areas of the Emperor Chain (based on materials of this survey) and from adjacent areas of the Northwest Pacific

Genus, species	Alaska and Aleutian islands ¹	Emperor Chain		
		Ojin Guyot	Jingu Seamount	Koko Guyot ²
Order Alcyonacea				
<i>Acanthogorgia</i>	–	+	+	+
<i>Calcigorgia</i>	+	–	–	–
<i>Anthomastus</i>	+	+	+	+
<i>Chrysogorgia</i>	–	+	–	+
<i>Iridogorgia</i>	–	–	–	+
<i>Metallogorgia</i>	–	–	–	+
<i>Clavularia</i>	+	+	–	+
<i>Sarcodictyon</i>	+	–	–	–
<i>Corallium</i>	–	–	–	+
<i>Hemicorallium</i>	+	–	–	–
<i>Bathygorgia</i>	+	–	–	–
<i>Isidella</i>	–	+	–	+
<i>Keratoisis</i>	–	–	–	+
<i>Lepidisis</i>	–	+	+	+
<i>Keroeides</i>	–	–	–	+
<i>Gersemia</i>	+	–	–	–
<i>Siphonogorgia</i>	–	–	–	+
<i>Paragorgia arborea</i>	–	+	+	–
<i>P. coralloides</i>	–	–	–	+
<i>P. regalis</i>	–	+	–	–
<i>Paragorgia</i> sp.	+	–	–	–
<i>Sibogagorgia</i>	+	–	–	–
<i>Echinomuricea</i>	–	–	+	+
<i>Alaskagorgia</i>	+	–	–	–
<i>Cryogorgia</i>	+	–	–	–
<i>Muriceides</i>	+	–	–	–
<i>Swiftia</i>	+	+	–	+
<i>Arthrogorgia</i>	+	–	–	–
<i>Callogorgia</i>	–	–	–	+(+)
<i>Calyptrophora</i>	+	–	–	–
<i>Candidella</i>	–	–	–	(+)
<i>Fanellia</i>	+	–	–	+(+)
<i>Narella</i>	+	–	–	+(+)
<i>Parastenella</i>	+	–	–	–
<i>Plumarella</i>	+	–	–	+
<i>Primnoa</i>	+	–	–	–
<i>Thouarella</i>	+	–	–	+
Pennatulacea				
<i>Anthoptilum</i>	+	–	–	–
<i>Halipteris</i>	+	–	–	–
<i>Kophobelemnion</i>	–	–	–	+
<i>Pennatula</i>	–	–	–	+

Table 2. (Contd.)

Genus, species	Alaska and Aleutian islands ¹	Emperor Chain		
		Ojin Guyot	Jingu Seamount	Koko Guyot ²
<i>Ptilosarcus</i>	+	—	—	—
<i>Umbellula</i>	+	—	—	+
<i>Cavernularia</i>	+	—	—	—
<i>Stylatula</i>	+	—	—	—
<i>Virgularia</i>	+	—	—	—
Total number of genera	28	8	5	24

¹According to [18, 28, 35]. ²Data from: [2, 11 (in brackets)].

Palau Island, is also noteworthy [26]. On the Ojin Guyot and Jingu Seamount, the composition of the Chrysogorgiidae family at the studied sites was depleted; we recorded a single species, *Ch. stellata*. The composition of the family Isididae was also noticeably poorer than on the Koko Guyot (Table 2). The occurrence of *P. arborea* on the Ojin Guyot and the Jingu Seamount extends the range of this species in the northwestern Pacific, which is in conformity with its previous findings near the eastern coast of Kamchatka and the Aleutian Islands [18, 28].

Based on the findings mentioned above, we can conclude that the boreal Pacific species (including deep-sea corals) spread along the Emperor Chain southwards, while deep-sea species of tropical genesis spread northwards, along with the movement of deep water mass. This is also confirmed by the distribution of deep-sea Antarctic mollusk species along the Hawaiian-Emperor Chain toward the North Pacific [27] (Sirenko, 2019). The biogeographic boundary between the coral faunas in the area of the Emperor seamount area seems to occupy the area of 37°–39° N (Fig. 1). Here, on the Ojin Guyot and Jingu Seamount, we discovered a mixed fauna of Octocorallia, including both temperate representatives and a few deep-water elements of tropical origin. Our observation data coincide with the suggestion about the position of the biogeographic boundary between the boreal and the West Pacific biogeographic regions in the area of the Emperor Chain; this statement is based on data on the fauna of brittle-stars (Ophiura) in the bathyal zone [4].

The Emperor Chain area is a biogeographically important region of the Pacific, but the little knowledge of its fauna was, until recently, based only on data about trawl by-catch (see review: [14]). Japanese researchers presented a general list of Octocorallia genera of the southern part of the Emperor Chain area, without the characteristics of the faunas of each seamount [20]. The role of the Emperor Chain in the distribution of corals in the North Pacific can be very important, because of its significant length northwards in the meridional direction.

The fauna of Hexactinellidae sponges in the studied areas of the Emperor Chain belongs to the Indo-West Pacific with typical bathyal taxa, including representatives of the genera *Amphidiscella*, *Atlantisella*, and *Walteria*, confined to guyots and mid-ocean ridges [30]. One unexpected feature of the studied region was the absence of sponges attaching exclusively by anchor-like spicules (Phoronematidae, Hyalonematidae, Euplectellidae—Euplectellinae), which are common in the Indo-West Pacific bathyal zone and inhabit silty, sandy, and rocky substrates [29–32]. In order to draw clear zoogeographic boundaries based on the distribution of Hexactinellidae sponges, species definitions and further surveys of the Emperor Chain area are required (in particular, it is necessary to expand work on the guyots north of the Jingu Seamount).

Bottom populations of hydrobionts on the seamounts of the northern part of the Emperor Chain were not previously investigated. The research cruises performed from the 1960s to this area aboard the TINRO-Center vessels were aimed at studying ichthyofauna, while the large-scale cruises of the R/V *Vityaz* (USSR Academy of Sciences) did not reach areas of mid-ocean ridges and seamounts. With the development of deep-sea surveys and the use of ROVs, the bottom communities of the seamounts of the North Pacific and the Emperor Chain have become the subject of active study in the last 10 years. The use of deep-sea vehicles allowed us to significantly expand the list of the genera of the sea pen Pennatulacea that inhabit the Emperor Chain area, as well as to make unique and biogeographically important records of corals. Our studies have confirmed the prospects of faunal and biogeographic surveys of Octocorallia in the Emperor Chain area and, at the same time, demonstrated the extremely low level of the knowledge of this region. In the near future, complex biological studies of VMEs in the area of the Emperor Chain are required, together with hydrological, geological and geophysical surveys, to obtain pioneering data on the state of biological and other resources in the North Pacific. This will make a significant contribution to the work of the North

Table 3. Hexactinellida from different areas of the Emperor Chain (from materials of this survey) and in the World Ocean

Taxa	Studied regions				World Ocean
	Koko Guyot	Jingu Seamount	Ojin Guyot	Nintoku Guyot	
Family Rossellidae					
Subfamily Rossellinae					
<i>Acanthascus (Rhabdocalyptus)</i> sp.	+	-	-	+	North Pacific, South Africa, West Australia, Antarctic, Circum Pacific (from Indonesia to South America)
<i>Acanthascus (Staurocalyptus)</i> sp.	+	+	-	-	
Subfamily Lanuginellinae					
<i>Lanuginella pupa</i>	+	-	-	-	Indo-West Pacific and East-Central Atlantic
Family Euplectellidae					
Subfamily Bolosomininae					
<i>Amphidiscella</i> sp.	-	+	-	-	North Atlantic (ridges), South Atlantic (Falkland Islands) South Pacific (New Caledonia and New Zealand), Indian Ocean (Western Australia)
<i>Bolosoma</i> sp.	+	+	+	-	Indo-West Pacific
Subfamily Corbitellinae					
<i>Dictyaulus</i> sp.	-	-	+	-	Indo-West Pacific (western Indian Ocean, New Caledonia and New Zealand), North and West Atlantic (northern Mid-Atlantic Range, Atlantic coast of Canada and Brazil)
<i>Atlantisella</i> sp.	-	+	-	-	North Atlantic (ridges), Central Pacific (Hawaii), South Pacific (New Zealand)
<i>Walteria flemmingi</i>	+	+	+	-	Indo-West Pacific (South-West Pacific)
<i>W. leuckarti</i>	+	+	+	-	Indo-West Pacific (including Hawaii and Japan)
Gen. nov., sp. nov.	-	+ ¹	-	-	Endemic
Family Euretidae					
Gen. nov., sp. nov.	-	+ ¹	+ ¹	-	Endemic
Family Tretodictyidae					
<i>Hexactinella</i> sp.	+	+	+	+	Indo-West Pacific (except Indian Ocean), Atlantic, near Kerguelen
<i>Tretocalyx</i> (?) sp. nov.	+	-	+	-	Indo-West Pacific (Red Sea)
Family Leucopsacidae (?)					
<i>Leucopsacus</i> (?) sp.	+	-	-	-	Indo-West Pacific, North Pacific, North and East Atlantic
Family Farreidae					
<i>Farrea</i> sp.	+	+	+	+	Cosmopolitan (except Arctic)
Family Aulocalycidae					
Gen. nov., sp. nov.	-	+ ¹	-	-	Endemic

“-” means taxon not found; “+¹” means endemic genus.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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