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SHORT COMMUNICATIONS

Variations in the Chemical Composition of the Skeletons of Non-Zooxanthellate Scleractinian (Anthozoa: Scleractinia) Corals

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V.I. Vernadskii [1] was the first to attract attention to the concentrating ability of living matter, which results in the enrichment of chemical elements in the biomass and is of crucial importance for the geochemistry of the ocean. The processes of carbonate biological mineralization are among the oldest geochemical processes on earth, which started operating in the Early Cambrian (40–50 Ma) and continues until now. In oceanic and marine ecosystems, living organisms with carbonate-producing functions (coccolithophores, foraminifers, corals, echinoderms, mollusks, pteropods, and others) proceed heterogeneous accumulation, a process that produces carbonate skeletons, which serve as the basis for the biogenic carbonate sedimentation in the ocean, and that is significantly contributed by corals [2].

Nonreef-building scleractinian corals (which lack zooxanthellae, endosymbiotic algae) are known to have a carbonate skeleton [3–5], similarly to colonial reef-building corals living at depths of up to 50 m. However, in contrast to reef-building corals, these species are represented mostly by solitary forms inhabiting broad ranges of depths (from a few dozen to >6000 m) and temperatures (from 20 to –1.1°C). The average diameter of the cups of individual corals ranges from 1 to 4 cm. Much less non-zooxanthellate genera are colonial forms that produce cold-water coral banks at various latitudes and depths in the ocean. They occur mostly at depths from 60 to 900 m at high latitudes. In the tropics and subtropics, colder water species occur at depths of 1000–2600 m, mostly at the foots of seamounts [6–9].

It was experimentally demonstrated that shallow-water scleractinians posses all principal mechanisms of heterotrophic nutrition available for sedentary forms and feed on all types of nourishment except phytoplankton. These corals are active filter feeders and consume detritus (the species belong to sestonophages *per se*) and are highly specialized predators with a well-developed mechanism for capturing and ingestion of moving prey. In the early 1970s it was determined that corals are able to filtrate and consume plankton bacteria at their content in the water close to the naturally occurring values and can also efficiently utilize dissolved organic matter, with phytoplankton completely rejected by scleractinian corals [3, 4, 10, 11].

Starting in the 1930s, reef-building corals were employed in numerous experiments [3, 4, 12]. However, all of these experiments dealt with reef-building corals, whose number of species is much greater than that of scleractinian forms and which occur much more widely. It was determined that Ca, which is the basis of the skeletons of corals in the form of calcite or aragonite, is extracted from seawater [10, 11], whereas Fe is consumed by reef-building corals together with food and is then adsorbed in their skeleton [10]. The role of chemical elements was examined in the living activities of gorgonians [13], reef-forming corals [10], and brachiopods [14].

For example, it was demonstrated that the addition of small amounts of Ca or Sr accelerates the growth of reef-building corals, while excess concentrations of these elements, conversely, decelerates it [15]. The addition of any Mg amounts decelerates the growth of corals up to its complete termination. Obviously, an increase in the Mg/Ca ratio blocks the transport of Ca in their tissues and, hence, their growth [16]. Calcium can be adsorbed from water in the coral mucus [17]. The Ca concentrations in gorgonians usually does not vary with habitat depth or area, but any depth and area are characterized by remarkable variations in the Mg/Ca and Sr/Ca ratios [13]. Variations in the Sr/Ca ratio in coral skeletons is induced by its variations in seawater, the variability of the biological characteristics of the corals themselves, and variations in the water temperature, which controls the rate of Sr accommodation in the crystal structure of aragonite during the

Table 1. Sampling sites and species composition of material

NN	Depth, m	Research vessel, site	Coordinates latitude longitude	Seafloor topography	Species
1	60–120	"Moskovskii Universitet"-15 (11)	30°04 N. 12°52 W.	Shelf	*Balanophyllia regia*
2	370–400	"Ob"-460	61°15 S. 57°48 W.	Mordvinova Isl., slope	*Flabellum curvatum*
3	680	"Dmitrii Mendeleyev"-1265	34°18 S. 171°31 E.	High in the central part of the Fiji Basin	*Stephanophyllia complicata*
4	800	"Moskovskii Universitet"-1996	25°08 S. 99°25 W	No data (fishing trawl)	*Flabellum apertum*
5	950	"Vityaz'-2"-80B	35°30 N. 52°00 W.	Great Meteor Seamount, slope	*Madrepora oculata*
6	1060	"Akademik Kurchatov"-209	13°04 N. 63°06 W.	Aves Ridge	*Stephanocyathus diadema*
7	″	″	″	same	*Deltocyathus conicus*
8	1170	"Akademik Kurchatov"-1292	22°58 N. 85°46 W.	Mexico Basin	*Stephanocyathus laevifundus*
9	1750	"Akademik Mstislav Keldysh"-464	58°21 N. 31°35 W.	Foot of the slope of a high	*Solenosmilia variabilis*
10	1800	"Akademik Mstislav Keldysh"-385	58°27 N. 31°33 W.	Flat, slightly inclined seafloor	*Solenosmilia variabilis*
11	4300	"Akademik Kurchatov"-25	4°33 S. 63°12 E.	Eastern part of the Somali Basin, east of the Seychelles. Flat seafloor with small knolls around	*Fungiacyathus marenzelleri*
12	5070	"Vityaz'"-2119	46°07 N. 155°16 E.	Eastern slope of the central Kurile–Kamchatka Trench	*Fungiacyathus marenzelleri*
13	6117	"Vityaz'"-5633	44°07 N. 149°34 E.	Slope of the Kurile–Kamchatka Trench	*Fungiacyathus marenzelleri*

growth of the skeleton. High-resolution analytical techniques are applied to the analysis of the Sr/Ca ratio in reef-building corals to determine the temperatures of the surface waters and for paleoreconstructions [18, 19]. The correlation of ^{14}C,^{18}O, Ca, Mg, Sr, and Fe concentrations for various portions of the skeleton of the colonies of the reef-building coral *Montastraea annularis* formed in certain years with the water temperatures in the same years revealed significant seasonal fluctuations in the ^{14}C, Sr, and Mg concentrations related to variations in the growth rates. It is thereby thought that Fe detected in the skeletons is of detrital origin [15].

Practically no such experiments and data on the chemistries of nonreef-building deep-water scleractinian corals are known, because samples of low-bathyal and abyssal scleractinians are extremely scarce. In this sense, none of these collections is comparable with that housed at the Shirshov Institute of Oceanology, Russian Academy of Sciences. The absence of literature data on the chemical composition of scleractinians prompted us to analyze the major components of their chemical composition (including some trace elements) and the possible dependence of their concentrations on the parameters of the habitat, mostly on the depth. For this purpose, we used samples of nonreef-building scleractinian corals. It is pertinent to mention that it was demonstrated in earlier publications of one of the authors [20, 21] that significant oceanic depths (up to 6328 m) are inhabited solely by solitary scleractinians of three genera (*Fungiacyathus*, *Leptopenus*, and *Deltocyathus*), which have flat skeletons, whose volume is much lower than that of their body. The mass of the calcareous skeleton depends thereby on the amount of food in the ambient waters but not on the habitat depth. For example, the Kurile–Kamchatka Trench, which acts as a "trap" of food that sinks down its slope, hosts (at a depth of 6 km) *Fungiacyathus marenzelleri* individuals with much better developed and dense skeletons than individuals of the same species lifted from depths of 4–5 km from nearby barren abyssal plains. We also described analogous phenomena in the coral fauna of the Orkney Deep [21].

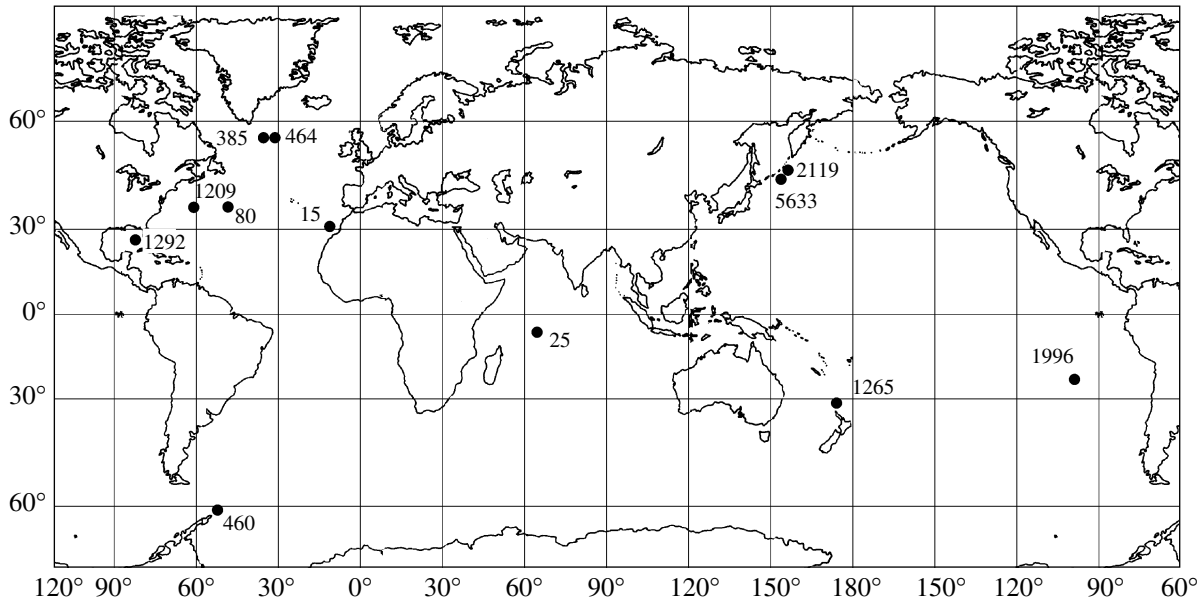

Fig. 1. Location of observation and sampling sites.

MATERIALS AND METHODS

This research was based on studying ten species of solitary and colonial corals of eight genera. Thirteen samples were collected during the cruises of Russian research vessels at twelve sites in the Atlantic and Pacific oceans, from depths ranging from 60 to 6117 m, i.e., from the shelf to abyssal plains (Table 1, Fig. 1). The samples were whole solitary forms and young living ends of branches from colonial forms. Coral samples were collected using various tools with the selection of only living individuals. Upon their extraction from the trawl, the samples were washed on a nylon net and dried at room temperature.

Major components (silicate analysis) were analyzed by XRF on a VRA-30 (Carl Zeiss). The detection limits ranged form 0.01 to 0.001% at errors of no higher than 15%. The quality of the analyses was controlled with the use of certified state standards with a carbonate matrix (standard SDO-3); the discrepancies with the tabulated values did not exceed 10%.

For analysis for trace elements, the samples were decomposed in Teflon containers with air-tight lids by concentrated reagent-grade nitric acid at temperatures no higher than 70°C for 3 h. The final volume of the analyte varied from 50 to 100 ml (depending on the mass of the sample).

The Cu, Zn, and Pb concentrations were determined by flame atomic absorption on a KVANT-2A spectrometer; Cd was analyzed by ET-AAS on a KVANT-Z.ETA spectrometer. The accuracy of the analyses was monitored using certified state standards (GSO) for ions of the analyzed metals; the completeness of decomposition was controlled using the OSO SADPP-10/5 soil standard and the GSD-2, GSD-4, and GSD-9 internationally certified standard samples of littoral bottom sediments. Replicate analyses demonstrate that the average deviations from the tabulated values for the standards were 5% for Zn, Cu, and Pb and 8% for Cd.

RESULTS

The results of our analysis include determinations of 13 elements (Ca, Si, Sr, Mg, Mn, K, Fe, Ti, Al, Zn, Cu, Pb, and Cd) in 13 samples (Table 2).

The Ca concentrations in the samples vary within a relatively narrow range: from 32.8 to 38.3% (anhydrous basis) for the whole examined depth range (from 90 to 6117 m). The average Ca concentration was 36.73% (anhydrous basis). The minimum Ca concentration was found at a depth of 5070 m, on the eastern slope in the central part of the Kurile–Kamchatka Trench. Calcium serves as the building material that maintains the calcification of organisms and forms the carbonate (aragonite) skeletons of corals.

The average Sr and Mg concentrations are 0.78 and 0.27%, i.e., are one to two orders of magnitude lower than the Ca concentrations. This fact is quite understandable, because Sr and Mg are isomorphous admixtures in calcite and aragonite [22]. The Mg and Sr concentrations vary from 0.18 to 0.4 and from 0.25 to 1.06%, respectively. The average Mg concentration is much lower than that in aragonite ooliths from the Mediterranean Sea (2.32% [23]). While the Mg concentration did not significantly vary within the depth range in question, the Sr concentration displays a pro-

Table 2. Chemical composition of the skeletons of scleractinian non-zooxanthelate corals

R/vessel	Site	Depth, m	*t*, °C	Ca, %	Sr, %	Mg, %	Si, %	Fe, %	Al, %	K, %	Ti, %	Mn, ppm	Zn, ppm	Cu, ppm	Pb, ppm	Cd, ppm
Vityaz'	2119	5070	1.5	32.8	0.81	0.27	0.6	0.063	0.06	0.17	0.015	23.3	73.6	7.12	0.92	0.386
Ob	460	385	0.5	36.4	0.94	0.38	0.25	0.045	0.031	0.05	0.008	8.5	70.9	4.04	1.98	0.115
Shtokman	1996	800	6.6	38.3	1.057	0.18	0.13	0.056	0.026	0.01	0.004	8.2	58.9	3.1	7.38	0.105
AMK	385	1800	3.3	36.9	0.97	0.29	0.19	0.046	0.026	0.014	0.007	5.1	32	1.8	3.08	0.117
MU	15	90	17.8	37.6	0.674	0.24	0.2	0.042	0.004	0.009	0.001	6.4	40.7	1	0.97	0.11
Kurchatov	1209	1060	5.5	37.1	0.792	0.22	0.4	0.059	0.052	0.011	0.009	4	8.4	1.46	0.52	0.025
Kurchatov	1292	1170	6.6	37.8	0.666	0.25	0.22	0.046	0.034	0.011	0.007	5.2	92	3.48	2.04	0.043
AMK	464	1750	3.3	36.4	0.831	0.28	0.24	0.049	0.029	0.007	0.005	7.8	8.55	1.61	1.94	0.101
Kurchatov	1209	1060	5.5	36.6	0.833	0.26	0.65	0.07	0.11	0.003	0.015	8	18.7	1.45	1.46	0.114
Kurchatov	25	4300	1.5	37.1	0.8	0.3	0.13	0.046	0.023	0.06	0.004	2.1	44.2	0.99	1.68	0.09
Mendeleyev	1265	680	7.2	36.3	0.252	0.4	2.47	0.154	0.226	0.058	0.04	16.3	17.9	0.23	0.6	0.059
Vityaz'	5633	6117	1.6	36.4	0.686	0.23	0.23	0.052	0.034	0.067	0.004	3.2	14.8	11.85	3.45	0.725
Vityaz'	80 B	950	8.0	37.8	0.797	0.26	0.22	0.049	0.05	0.014	0.005	4	19.2	4.21	1.42	0.08

Note: Abbreviations of research vessels: MU—Moskovskii Universitet; AMK—Akademik Mstislav Keldysh.

nounced minimum at a depth of 680 m. The average Sr concentration in coral skeletons (0.78% on anhydrous basis) is much higher than in deep-sea carbonate sediments (0.28% on anhydrous basis) and the shells of foraminifers (0.12% on anhydrous basis) [24].

The detected K concentrations are three orders of magnitude lower than the Ca concentrations. The average K concentration is equal to 0.037%, and the maximum (0.17%) occurs at a depth of 5070 m (site 2119) in the Kurile–Kamchatka Trench.

Silicon is contained in the skeletons of corals in amounts subordinate compared to those of Ca (0.13–2.47% on anhydrous basis, averaging at 0.45%) and shows a maximum at a depth of 680 m (like Sr).

Such an important major element as Al was detected in the skeletons of corals in an average concentration of 0.054%, which is thousands or hundreds of times lower than the Ca, Sr, and Mg concentrations. The significant scatter in the Al concentrations (from 0.004 to 0.226%, i.e., about two orders of magnitude) exceeds the variability of the concentrations of the elements discussed above. Note that a maximum in the Al concentration was detected at a depth of 680 m (like those of Sr and Si) (site 1265).

The Fe concentration varies from 0.042 to 0.154% at an average value of 0.0598%, which is close to the average Fe concentrations in the shells of foraminifers: from 0.05 to 0.32% [23]. It is interesting that the maximum of Fe, like those of Al, Si, and Sr, was detected in corals from the same site 1265, at a depth of 680 m.

The variations in the Ti concentrations do not differ from those of the aforementioned elements: its maxi-

Table 3. Average concentrations of chemical elements in scleractinian nonreef-building corals, oceanic water, and oceanic plankton

Parameter	Ca	Sr	Mg	Si	Fe	Al	K
Scleractinian corals*	36.73	0.777	0.274	0.456	6×10^{-2}	0.56×10^{-1}	3.7×10^{-2}
Oceanic water**	4×10^{-2}	8×10^{-4}	0.13	3×10^{-4}	6×10^{-9}	0.5×10^{-7}	3.7×10^{-2}
Oceanic plankton**	1.4	0.11	9.4	0.15	1.6×10^{-2}	0.62×10^{-2}	5.2
Enrichment factor	10^3	10^3	2	10^3	10^7	10^6	1

Parameter	Ti	Mn	Zn	Cu	Pb	Cd
Scleractinian corals*	1×10^{-2}	7.6×10^{-3}	4×10^{-3}	3×10^{-4}	2×10^{-4}	2×10^{-5}
Oceanic water**	1×10^{-7}	2.7×10^{-9}	0.4×10^{-7}	0.3×10^{-7}	2×10^{-10}	8×10^{-9}
Oceanic plankton**	1×10^{-3}	2×10^{-3}	0.4×10^{-2}	1.2×10^{-3}	0.9×10^{-3}	0.7×10^{-4}
Enrichment factor	10^5	10^6	10^5	10^4	10^6	10^4

Notes: * This publication.
** According to [26].

mum of 0.04% is restricted to a depth of 680 m, and the average concentration is 0.0095%, which is much lower than the concentrations of Ca, Sr, Mg, Mn, Si, Al, Fe, and K, i.e., Ti is, in fact, a trace element in corals.

The Mn concentration varies from 8.5 to 230 ppm (anhydrous basis) and averages at 76.5 ppm, which is roughly one order of magnitude lower than the Mn concentration in carbonate (predominantly coral) sediments of the Mediterranean Sea [23]. The maximum Mn concentrations in the scleractinians was detected at a depth of 5070 m in the Kurile–Kamchatka Trench (site 2119).

Other trace elements were found in coral skeletons in even lower concentrations (in ppm, on anhydrous basis): from 0.025 to 0.725 for Cd, from 0.52 to 7.38 for Pb, from 0.23 to 11.85 for Cu, and from 8.4 to 3.6 for Zn. The highest Zn concentrations were detected in the samples that contained the maximum Mn concentrations, which were collected at site 2119 from a depth of 5070 m in the Kurile–Kamchatka Trench, whereas peaks of Cd and Cu were detected at the deepest site 5633 (6117 m), also in the Kurile–Kamchatka Trench. The Pb concentration displays a maximum at a depth of 800 m (Nazca Plateau in the Pacific Ocean).

DISCUSSION

According to Perel'man's classification [25], which takes into consideration the biological importance of elements, Ca, Mg, Sr, and K belong to the group of elements that are actively biologically consumed and are vitally important for living organisms. Another group of chemical elements—Si, Al, Fe, and Ti—is characterized, according to Perel'man, by weak biological consumption, whereas trace elements—Mn, Zn, Cu, Pb, and Cd—belong to the group of intermediate biological accumulation and participate in various biochemical, fermentative, and redox reactions.

Scleractinian corals are, as was mentioned above, heterotrophic (and even predatory) organisms, and chemical elements can enrich in their bodies as a consequence of biological assimilation, physicochemical adsorption, and unselective filtration during feeding. The principal source of chemical elements is seawater, which contains elements in solute and suspended (including zooplankton) modes, and, to a lesser extent, organisms of higher trophic levels and bottom sediments. Comparing the concentrations of chemical elements in our samples of the skeletons of deep-sea corals with the average composition of oceanic waters [26], we calculated the enrichment factors K_e of the elements discussed in this publication with respect to oceanic water (Table 3). According to our data, the only element that is not accumulated by corals is K ($K_e = 1$). The Mg concentrations in corals are twice higher than in seawater, whereas other elements display K_e of the order of 10^3 and higher, with the highest $K_e = 10^7$ determined for Fe. This suggests that the process of biomineralization in scleractinian corals involves the biological concentrating of trace elements from the ambient seawater.

The concentrations of trace elements in corals are comparable in order of magnitude of their values with the average concentrations in oceanic plankton [26], and such elements as Ca, Fe, Al, and Ti have even higher contents. The succession of enrichment factors of individual elements in corals relative to seawater is as follows:

K < Mg < Sr, Ca < Si < Cd, Cu < Zn, Ti < Al, and Pb < Mn < Fe,

which differs from the succession of the clarkes of these elements and testifies to selective biological accumulation.

It is also interesting to consider the distributions of chemical elements in the skeletons of corals collected at various depths, from the shelf to abyssal plains (Tables 1, 2). As was mentioned above, the depth range in which corals were sampled is quite broad, with only one sample taken within the photosynthesis zone, at site 15, from a depth of 90 m.

Five elements (Si, Ti, Al, Fe, and Mg) show maxima of their concentrations within the upper 1200 m, and their concentration vary insignificantly below this depth (Tables 1, 2). The highest peak of the concentrations of each of these elements occurs at a depth of 680 m at a submarine high in the central part of the Fiji Basin. The reason for this can be the local upwelling of salt and trace element-enriched waters, which is commonly restricted to submarine highs (in contrast to offshore upwelling).

The distributions of the other three elements (Mn, K, and Ca) are different. Within the upper 1000 m, their concentrations vary, but the concentration maxima are pronounced not as clearly as those of the five elements discussed above. However, the depth range of 4300–6200 m is characterized by a minimum in the Ca concentrations and maxima in the K and Mn concentrations. Judging from the character of the distribution of values in Figs. 2a and 2b, the Ca and Mg concentrations in corals are prone to decrease with depth, which also follows from the significant negative correlation coefficients between depth and these values (R_{xy} = –0.55 and –0.51, respectively; Table 4). At the same time, Sr (Fig. 2c) does not show any significant correlation with depth. The partial dissolution of carbonate material at depths below the critical depth of carbonate accumulation likely transfers not only Ca but also Mg into solution, while Sr does not participate in this process, perhaps, because of its deeper setting in the aragonite structure, although this provisional conclusion should be further explored. Note also that our comparison of the Sr/Ca ratio and the water temperatures near the seafloor did not reveal any pronounced correlations.

The concentrations of some other elements (Si, K, Cu, and Cd) are, conversely, correlated with depth (R_{xy} from 0.64 to 0.81, Table 4). Since sediments at greater depths are predominantly fine-grained clayey, deep-sea corals have higher concentrations of K and Si, which are principal elements of aluminosilicates, and Cu and Cd, i.e., elements most readily adsorbed on clay particles. Moreover, Cd can substitute Ca in the calcite structure [22].

Based on the values of the correlation coefficients (Table 4), which display strong positive correlations in corals between Al, Si, Fe, and Ti and, to a lesser extent, between Mg and Al, Si, Fe, and Ti, it is reasonable to suggest that bottom sediments (namely, clayey oozes, whose main constituents are aluminosilicates) are a significant source of these elements for corals. No significant correlations were determined between Ca and trace elements, except Mn, which shows a significant negative correlation with Ca (R_{xy} = –0.79). According to [22, 27], Mn can be accommodated in the structure of biogenic carbonates and be, in a sense, an antagonist of Ca. Proceeding from the ionic radius values, Ca can also be substituted for Mg, Fe, Zn, and Cd in the crystal structure of calcite and for Sr and Pb in the structure of aragonite [22]; the last two exhibit significant positive correlations (Table 3). In the vicinity of seafloor, Mn typically forms thin oxide films on particles of bottom sediments, for example, carbonates, and it is thus reasonable to expect a positive correlation between Mn and Ca. However, our data reveal significant negative correlations in the pairs Ca–Mn and Ca–K, which agrees with literature data [22] and, for Mn, testifies that hydroxide films cannot be formed on living organisms (which were used in our research). At the same

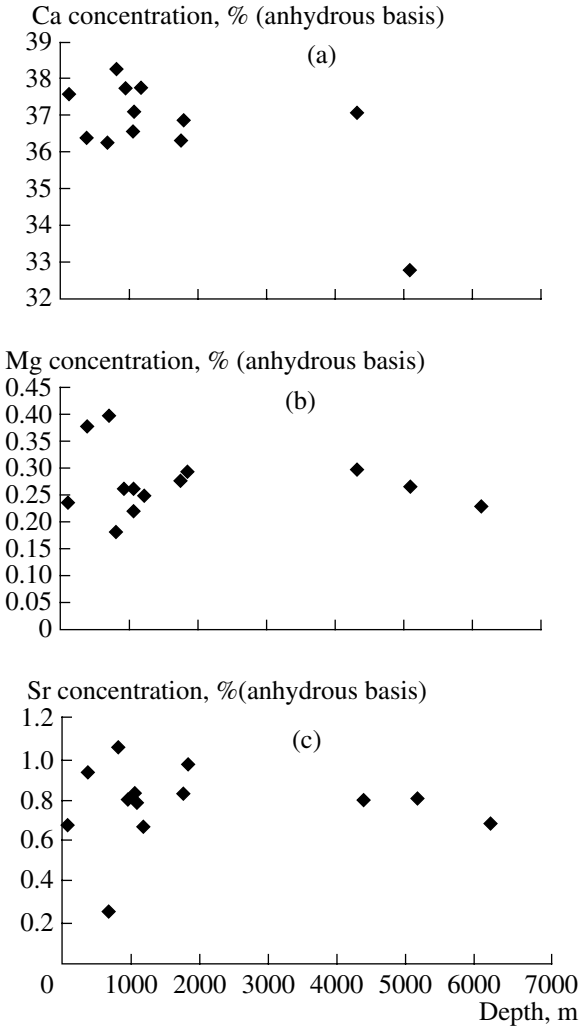

Fig. 2. Dependence of the distributions of chemical elements on depth.(a) Ca; (b) Mg; (c) Sr.

Table 4. Pair correlation coefficients (R_{xy}, $p < 0.05$) between components of the chemical composition of scleractinian corals depending on the depths

Element	Ca	Sr	Mg	Al	Fe	Mn	Depth
Ca	–	0.10	0.48	–0.23	–0.20	**–0.79**	**–0.55**
K	**–0.88**	**–0.72**	0.31	0.16	0.20	**0.72**	**–0.69**
Sr	0.10	–	–0.45	**–0.71**	**–0.75**	–0.26	0.05
Mg	0.48	–0.45	–	**0.55**	**0.53**	0.30	**–0.51**
Al	–0.23	**–0.71**	**0.55**	–	**0.97**	**0.51**	–0.16
Si	–0.26	**–0.80**	**0.60**	**0.97**	**0.99**	**0.57**	**0.64**
Fe	–0.20	**–0.75**	**0.53**	**0.97**	–	**0.53**	–0.14
Ti	–0.35	**–0.70**	**0.62**	**0.97**	**0.97**	**0.63**	–0.13
Mn	**–0.79**	–0.26	0.30	**0.51**	**0.53**	–	0.11
Zn	–0.13	0.09	–0.03	–0.29	–0.27	0.28	0.30
Cu	–0.37	0.09	–0.26	–0.24	–0.26	0.08	**0.71**
Pb	0.38	**0.55**	–0.47	–0.34	–0.25	–0.20	0.08
Cd	–0.46	–0.03	–0.20	–0.13	–0.11	0.12	**0.81**

time, a strong negative correlation of Sr (which can substitute Ca in aragonite) and Al, Si, Fe, and Ti (Table 3) seems to confirm that the latter four elements are contained in clay particles that are assimilated in coral skeletons during feeding. With reference to Si, this possibly suggests that the source of this element is zooplankton, for example, radiolarians with siliceous skeletons.

CONCLUSIONS

The first data on the chemical composition of non-reef-building non-zooxanthellate deep-sea corals presented in this publication allows us to identify the following tendencies manifested in the biomineralization process.

The comparison of the concentration levels of some chemical elements in scleractinian corals and ambient oceanic waters suggests that corals do not accumulate K in the process of biomineralization and weakly accumulate Mg, whereas Ca, Sr, Si, Al, Ti, Mn, Zn, Cu, Cd, Pb, and Fe are concentrated in the skeletons of corals with enrichment coefficients of 10^3 to 10^7.

Correlations between components contained in the skeletons of scleractinian corals suggest that the source of Al, Si, Fe, and Ti in them is the clayey constituent of bottom sediments and zooplankton, while trace elements are likely accumulated via bioassimilation from seawater. Such elements as Mn, Sr, Pb, and Cd can structurally substitute Ca in calcite and aragonite.

The variations in the concentrations of elements in coral skeletons depending on their habitat depths are fairly significant. As could be expected, the Ca and Mg concentrations are prone to decrease with depth (R_{xy} = –0.55 and –0.51, respectively), which can possibly be caused by the partial dissolution of the carbonate skeletons with increasing depth, whereas the Sr/Ca ratio does not depend on depth.

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