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The strontium-calcium atom ratio in carbonate-secreting marine organisms

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Summary—The purpose of the present investigation was to study the distribution of strontium and calcium in the biosphere. The contents of strontium and calcium in 250 species of carbonate-secreting marine organisms were determined. The strontium-calcium atom ratio in calcareous portions of marine organisms ranged from 1·0 to 11 $\times$ 10^{-3}. With the exception of Nudibranchia and Madreporaria, the atom ratio in marine organisms was less than that of sea water, 8·9 $\times$ 10^{-3}. The strontium-calcium atom ratios in marine organisms appeared to be constant in accordance with their phylogenetic classification. Specimens of different species collected from a common ecological community showed diverse strontium-calcium atom ratios. On the other hand, the similar types of marine organisms living under different environmental conditions from arctic to tropical oceans, showed constant strontium-calcium atom ratios. Variations in salinity and temperature of sea water were apparently not the factors which influenced the strontium-calcium atom ratio in calcareous shells.

The mineralogical properties of calcium carbonate in marine organisms demonstrated a definite correlation with the occurrence of strontium. The marine organisms containing calcium carbonate as aragonite had strontium-calcium atom ratios greater than those as calcite. Samples of deep-sea sediments and *Clobigerina* ooze showed strontium-calcium atom ratios of 1·94 $\times$ 10^{-3} and 1·49 $\times$ 10^{-3}, respectively. The limestone deposits, which originated from marine organisms, had the smallest strontium-calcium atom ratio, 0·63 $\times$ 10^{-3}, of all materials examined. Apparently, the matrix of calcareous deposits of marine origin has lost strontium during geological time.

INTRODUCTION

THE PRESENT investigation was undertaken in order to study (1) the distribution of strontium in the carbonate-secreting marine organisms, (2) to ascertain possible correlations between the strontium and calcium contents of the calcareous skeletons, (3) to observe variations of the strontium-calcium atom ratio in accordance with the phylogeny of the marine organisms, (4) to note the extent of change in the atom ratio of marine organisms living in different natural environments, and (5) to determine the strontium content in relation to the mineralogical character of the calcium carbonate in the organisms.

The determination of small quantities of strontium in the presence of large amounts of calcium has been rather a laborious process. However, both of these elements can be determined readily by flame photometric methods recently described by CHOW and THOMPSON (1955 A and B).

REVIEW OF LITERATURE

The occurrence of calcium in marine organisms has been studied extensively, as it is the major constituent of many skeletal remains in calcareous marine sediments. An authoritative summary and discussion on the distribution of calcium in marine organisms has been presented by VINOGRADOV (1953). The investigations of LOWEN-

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STAM (1954 A and B) dealt with the effect of environmental factors upon the mineralogical character of the calcium carbonate in certain marine organisms.

Strontium has been detected in all phases of the biosphere. Due to the difficulty in analyzing trace quantities of strontium in the presence of calcium, only a few scattered analyses were reported in the early literature showing the existence of strontium in marine organisms (MORETTI, 1813; VOGEL, 1814; FORCHHAMMER, 1852; DIEULAFAIT, 1877; SCHMELCK, 1901). More recently, the role of strontium in the carbonate-secreting marine organisms has been the object of investigation, and several quantitative determinations were made on the distribution of strontium in various biological materials (FOX and RAMAGE, 1931; NOLL, 1934; MCCANCE and MASTERS, 1937; WEBB, 1937; TRUEMAN, 1944; TSUCHIYA, 1944, 1948; VINOGRADOV and BOROVIK-ROMANOVA, 1945; ASARI, 1950; ODUM, 1951 A). The relationship between the strontium content of fossils and that of recent marine organisms has also been studied (ODUM, 1951 B; KULP, *et al.*, 1952).

In summarizing the work of previous investigators, it may be said that strontium was found not only in the calcareous shells, but also in the tissues of marine organisms. It was also stated by some that the primary factor which determines the strontium-calcium atom ratio in the calcareous skeletons is the atom ratio of these elements occurring in the water in which the organisms lived. Experiments showed that large quantities of strontium could be taken into the calcareous shells of marine organisms grown under controlled conditions and that the relationship between the strontium-calcium atom ratio in the shells is almost directly proportional to the atom ratio of the environment. Since the strontium-calcium atom ratio in the calcareous skeletons reflects the chemical composition of the water, the analysis of the strontium-calcium atom ratio in unaltered fossils could be used as a valid method of measuring the strontium-calcium ratio of the ancient oceans. Such findings presented strong evidence that the strontium-calcium atom ratio of ocean waters has been of about the same order of magnitude since Palaeozoic times at least, because this atom ratio of the fossils resembles that of the modern counterparts.

In marine organisms the strontium-calcium atom ratio of the growing shells is apparently independent of the age of the organisms. No evidence was found that would indicate any seasonal fluctuations in the strontium-calcium atom ratio of marine organisms. It was also concluded that the temperature of the ocean waters is a relatively insignificant factor in affecting the strontium content of marine organisms.

Besides the chemical composition and the ecological environment, the mineralogical character, such as crystal lattice, of the calcareous skeletons was of some significance. It was found that there is always more strontium present when the calcium carbonate exists as aragonite rather than as calcite.

METHODS OF ANALYSIS

All chemicals used in the present investigation were of analytical grade and tested for traces of strontium and calcium. A stock solution of strontium, 6·00 mg-atoms per litre, was prepared by dissolving 0·886 gram of strontium carbonate in a limited volume of hydrochloric acid and then diluting to one litre; and that of calcium, 20·0 mg-atoms per litre, was prepared by dissolving 2·002 grams of calcium carbonate in hydrochloric acid and diluting to one litre. From such stock solutions, suitable aliquots were taken and diluted for the comparison standards. Polyethylene containers were used for storage of standard solutions in order to avoid possible contamination from the glassware.

The calcareous skeletons of the marine organisms were carefully cleaned and air-dried. Duplicate weighed samples (0·5 to 1·0 gram) of the dried materials were heated in an oven to a temperature of 350° C and then cooled. The loss in weight was designated as the organic matter. The samples were then further ignited at 1,100° C until all carbonates were decomposed. Upon cooling and weighing, the difference in weight was considered as carbon dioxide. The residues were treated with 10 ml of water, and 12 N hydrochloric acid was added dropwise until solution was complete. The solutions were then diluted to one litre, thoroughly mixed, and analyzed for strontium and calcium using the "internal standards" technique of flame photometry by CHOW and THOMPSON (1955 A and B).

RESULTS OF ANALYSIS

All analyses were made on the fresh calcareous skeletons (unless otherwise stated) which had been carefully cleaned and air-dried for several weeks. In order to obtain a general idea of the distribution of strontium in the biosphere, a large variety of species of carbonate-secreting marine organisms was analyzed, rather than concentrating on possible variations in just a few particular species.

In tables the calcium, strontium, carbon dioxide and organic matter content of the organisms are reported as percent of constituents in air-dried samples. To demonstrate more clearly the relation of the strontium to the calcium, it was deemed desirable to report this relationship as the atom ratio of strontium to calcium. For example, the calcareous alga, *Bossea orbigniana*, contains 0·199% of strontium and 29·2% of calcium. The strontium-calcium atom ratio would be:

$$\frac{0{\cdot}199/87{\cdot}63}{29{\cdot}2/40{\cdot}08} = 3{\cdot}12 \times 10^{-3}$$

and indicates that for every 1,000 atoms of calcium there are present approximately three atoms of strontium.

The mineralogical data cited in this paper were taken from the publications of BØGGILD (1930), VINOGRADOV (1953) and CHAVE (1954). However, the mineralogical properties of the specimens, which were analyzed chemically by the authors, will be studied further by Dr. R. G. BADER.

DISCUSSION

Phylogenetic Aspects:

1. *Marine Algae:* In most of the previous studies on calcareous algae, determinations of calcium and magnesium were given, the calcium carbonate in the skeletons being reported as calcite. Only one analysis of strontium was reported, which showed 0·26% of strontium in the ash of *Lithothamnion polymorphum* (NOLL, 1934).

The results of analysis of calcareous algae, Corallinaceae, are shown in Table I(A). The average strontium-calcium atom ratio was $3{\cdot}20 \times 10^{-3}$. The diatoms, *Coscinodiscus*, were also analyzed. As they are primarily of a silicious nature, only traces of calcium were found in the skeletons.

2. *Phylum Protozoa:* The calcium content of Foraminifera has been investigated extensively, especially its relation to the origin of calcareous marine sediments, but no strontium determinations appeared in the literature.

Analyses of calcareous Foraminifera (Table I (B)) by the authors showed an average strontium-calcium atom ratio of $3{\cdot}07 \times 10^{-3}$. The presence of magnesium in the skeletons was detected qualitatively. It has long been known that radiolarian skeletons are rich in strontium, but the authors were unable to collect sufficient material for a quantitative study.

3. *Phylum Porifera:* The classification of sponges is based on the chemical composition of the skeletons such as the Calcarea containing calcite spicules. FOX and RAMAGE (1931) noted the presence of strontium in Porifera when they examined the ash of *Clathrina* spectroscopically.

The average strontium-calcium atom ratio of calcareous sponges, Calcarea, containing measurable quantities of strontium, was $2 \cdot 99 \times 10^{-3}$ (Table I (C)). The calcium content in silicious sponges, Demospongiae, was minute; only traces of strontium were detected.

4. *Coelenterata:* The high strontium content in corals was observed by NOLL (1934). He reported the following results as percentage of strontium in their ash: hydrozoan *Millepora alcicornis*, 0·43%; alcyonarian *Corallium rubrum*, 0·17%; and madreporarian *Porites clavaria*, 0·42%. ODUM (1951 B) reported an average strontium-calcium atom ratio of $10 \cdot 6 \times 10^{-3}$ for corals. The calcium carbonate of Hydrozoa and Madreporaria was reported as aragonite, whereas that of Alcyonaria was calcite.

In Table I (D) are the results of analysis on calcareous portions of Coelenterata. In Hydrozoa, the Hydrocorallina possess calcareous skeletons. Except *Errinopora zarhyncha*, all the analyses yielded high strontium-calcium atom ratios which averaged $9 \cdot 49 \times 10^{-3}$.

The soft corals, Alcyonaria, contained less strontium than other corals, and magnesium was present in the skeletons. However, *Heliopora coerulea*, which has the calcium carbonate in the form of aragonite, showed a much higher atom ratio than other Alcyonaria. The *Heliopora* with their external tube-like skeletons differ morphologically from all other Alcyonaria. With the high content of organic matter and their strontium-calcium atom ratios comparable to Porifera (Calcarea), it is interesting to note that the skeletons of Alcyonaria also have much in common morphologically with those of Porifera.

The solitary corals, Madreporaria, were found to have consistently high strontium-calcium atom ratios with an average of $9 \cdot 86 \times 10^{-3}$. This is one of the orders of marine organisms to show the atom ratio equal to or greater than that of sea water, $8 \cdot 9 \times 10^{-3}$.

5. *Minor Phyla:* Specimens of these skeletonless marine organisms were analyzed. They were *Bolinopsis microptera* (Ctenophora), *Notoplana acticola* (Platyhelminthes), *Micrura verrilli* (Nemertea), *Urechis caupo* (Echiuroidea), *Phascolosoma agassizii* (Sipunculoidea), and *Phoronopsis viridis* (Phoronidea). Being non-carbonate secreting, these organisms contained 85 to 99% of organic matter which varied considerably among specimens. Calcium was always present in the ash of the organisms, and only traces of strontium could be detected.

6. *Phylum Annelida:* Many members of Annelida such as Polychaeta possess calcareous tubes which serve to shelter them. LOWENSTAM (1954 A) reported from 0·2 to 0·9% of strontium in the calcareous tubes of Serpulidae. CHAVE (1954) showed that the calcium carbonate in Polychaeta varies from pure calcite in specimens collected in the north Pacific and Behring Sea to almost pure aragonite in specimens collected in tropic areas.

Analyses of calcareous annelid tubes given in Table I (E) showed strontium-calcium atom ratios ranging from 3·86 to $8 \cdot 22 \times 10^{-3}$. This is the only group of marine organisms that demonstrated a wide range for the strontium-calcium atom ratio.

7. *Phylum Arthropoda:* The Arthropoda are represented in the ocean mainly by species of Crustacea. The majority of Crustacea possesses chitinous exoskeletons. The Cirripedia is the only group in this phylum which possesses calcareous skeletons

of calcite structure. Besides the Cirripedia, the Decapoda also contain calcite as well as an appreciable amount of phosphorite. VINOGRADOV and BOROVIK-ROMANOVA (1945) found 0·2% of strontium in the ash of *Balanus balanoides.* WEBB (1937) also reported 0·1% of strontium in the ash of the hermit crab *Eupagurus* (=*Pagurus*) *bernhardus*.

The results of analysis of calcareous portions of Arthropoda are given in Table I (F). The strontium-calcium atom ratios of Cirripedia averaged $4·45 \times 10^{-3}$, which is the highest value for the organisms containing calcite.

The canapace of Decapoda was found to contain more organic matter than Cirripedia, but their strontium contents were of the same order of magnitude, although the calcium content of Decapoda was much lower. Appreciable amounts of magnesium and phosphate were detected qualitatively. The strontium-calcium atom ratio was rather uniform with an average of $6·17 \times 10^{-3}$. The claws of *Cancer antennarius* were also analyzed, and showed no difference in chemical composition as compared to the carapace. The soft carapace of *C. productus* in its moulting stage was found to consist mainly of organic matter and only 0·44% of calcium. This may be cited as an illustration of the change in chemical composition of the exoskeletons during moulting.

8. *Phylum Mollusca:* The molluscs are widely distributed in the ocean and constitute the largest invertebrate group which possesses calcareous protective shells. The chemical composition, mainly calcium, of Pelecypoda and Gastropoda was studied by CLARKE and WHEELER (1922), FOX and RAMAGE (1931), NOLL (1934), MCCANCE and MASTERS (1937), WEBB (1937), ASARI (1951), ODUM (1951 B), KULP, *et al.* (1952) and VINOGRADOV (1953). The majority of Pelecypoda and Gastropoda possesses shells consisting chiefly of a calcite-aragonite mixture. Only three families (Anomiidae, Ostreidae and Pectinidae) were reported to have calcite shells. Aragonite was reported in calcareous portions of Amphineura, Scaphopoda, Cephalopoda and Nudibranchia.

Class Amphineura: The chitons are considered morphologically to constitute the most primitive class of living shell-bearing molluscs. Only a few calcium analyses on these organisms were reported and none on strontium.

The results of analysis of chiton plates are given in Table I (G). They were composed mainly of calcium carbonate with relatively high percentage of strontium. The strontium-calcium atom ratios averaged $8·06 \times 10^{-3}$ which was much higher than those in other classes of molluscs.

Class Pelecypoda: The results of analysis of 44 species of Pelecypoda are shown in Table I (H). Nine families (Myidae, Clinocardium, Saxicavidae, Tellinidae, Lyonsiidae, Mactridae, Periplomatidae, Pholadidae and Solenidae) had strontium-calcium atom ratios greater than $2·0 \times 10^{-3}$. The lowest strontium-calcium atom ratio was found in the families which were reported as having calcite shells, and that of the highest was Myidae.

Class Gastropoda: Forty-six species of subclass Prosobranchia shown in Table I (I) were analyzed. The strontium-calcium atom ratios among all families ranged from $1·31$ to $2·14 \times 10^{-3}$ and were less than that for Pelecypoda.

The Nudibranchia of subclass Opisthobranchia do not possess any calcareous protective shells. The body wall of *Anisodoris* and *Archidoris*, which contains calcareous materials, was analyzed (Table I (I)). The organisms were high in organic matter and gave an average strontium-calcium atom ratio of 10×10^{-3}. This appears to be in agreement with the finding of McCance and Masters (1937) that *Archidoris britannica* has a high strontium-calcium atom ratio. However, the strontium and calcium content occurs in such low concentrations that a slight experimental error in the determination of either one of the elements markedly affects the atom ratio.

Class Scaphopoda: The analysis of Scaphopoda was performed on *Dentalium* which was reported to have a strontium-calcium atom ratio of $2{\cdot}34 \times 10^{-3}$ (Odum, 1951 b). The specimen of *Dentalium entale* (Table I (J)) analyzed by the authors showed an atom ratio of $2{\cdot}35 \times 10^{-3}$.

Class Cephalopoda: Modern Cephalopoda, except *Nautilus*, usually possess an inner shell. In general, the calcareous inner shells contain more organic matter than the shells of Pelecypoda and Gastropoda. Odum (1951 b) reported a strontium-calcium atom ratio of $3{\cdot}87 \times 10^{-3}$ for a species of *Nautilus*. The inner shell of *Sepia* (Table I (J)) was found by the authors to have an atom ratio of $3{\cdot}74 \times 10^{-3}$. The chitinous plate of *Loligo opalescens* was found to contain chiefly organic matter and traces of calcium.

9. *Phylum Bryozoa:* The calcium content of Bryozoa studied by previous investigators was reported as calcite, but there was little information on the occurrence of other elements. In Table I (K) are the results of analysis of Bryozoa. The strontium-calcium atom ratios averaged $3{\cdot}41 \times 10^{-3}$. An appreciable amount of magnesium was present.

10. *Phylum Brachiopoda:* The calcareous shells of Class Articulata were reported as containing calcite. Odum (1951 b) found a strontium-calcium atom ratio of $1{\cdot}75 \times 10^{-3}$ for a species of *Terebratula*. The other class of Brachiopoda, Inarticulata, consists of apatite, and an atom ratio of $3{\cdot}60 \times 10^{-3}$ was reported for a species of *Crania* (Odum, 1951 b). Analyses by the authors showed that Articulata shells (Table I (L)) had strontium-calcium atom ratios ranging from $1{\cdot}20$ to $1{\cdot}57 \times 10^{-3}$.

11. *Phylum Echinodermata:* With the exception of Holothuroidea, the Echinodermata possess calcium-magnesium skeletons. The body wall of *Psolus* possesses calcareous plates. The calcium carbonate in skeletons was reported as calcite. Previous investigators reported the following results expressed as percentage of strontium in the ash: *Asterias rubens*, 0·8%; *Marthasterias glacialis*, 0·6%; and *Ophiocomina nigra*, 1% (Webb, 1937); *Asterias rubens*, 0·15%; *Gorgonocephalus eucnemis*, 0·2%; *Ophiopholis aculeata*, 0·2%; and *Strongylocentrotus dröbachiensis*, 0·15% (Vinogradov and Borovik-Romanova, 1945).

The results of analysis of calcareous portions of Echinodermata are shown in Table I (M). All five classes of Echinodermata showed remarkable uniformity in the strontium-calcium atom ratio which could be considered as a constant.

12. *Phylum Chordata:* The results of analysis are given in Table I (N). The organisms contained an undetermined amount of sand particles and only traces of strontium.

In Table II are the results of analysis of calcareous materials other than marine invertebrates. The relationship between the strontium-calcium atom ratios of marine Arthropoda and Mollusca and those of fresh water organisms, from the meagre data available for the latter, indicated an analogy: the fresh-water organisms having lower atom ratios.

A summary of all analytical results is presented phylogenetically in Table III. The data given for each column represent the average values obtained on various carbonate-secreting marine organisms as listed in foregoing tables. The strontium-calcium atom ratios are very constant in accordance with the phylogenetic classification. With the exception of Zoantharia (Madreporaria) and Opisthobranchia (Nudibranchia), the atom ratios in calcareous portions of marine organisms are less than that of sea-water, $8{\cdot}9 \times 10^{-3}$. In these instances and in that of radiolaria (Odum, 1951 a), it is apparent that strontium does play a physiological role in the development of calcareous shells of carbonate-secreting marine organisms. The mechanism of this selectivity presents an interesting physiological problem. Controlled laboratory experiments of growing marine organisms in artificial sea-water free of strontium, and further elaborating Odum's work with waters of varying strontium-calcium atom ratios, would probably yield fundamental information for explaining the role of strontium in marine organisms.

Ecological Aspects

1. *Habitat:* Organisms of various species are found associated together in an ecological niche. All species that have not adjusted themselves physiologically to the existing conditions will be eliminated from a given community. Since the environmental conditions influence the life of marine organisms, it is of interest to observe any variations of chemical composition of marine organisms which live in such a community. Various species were collected from two rocky shores near the Hopkins Marine Station, California, at the mid and the low inter-tidal levels. The results of analyses of calcareous portions of these organisms are listed in Table IV.

The strontium-calcium atom ratios of the organisms collected at the mid-tidal level varied from $1{\cdot}01 \times 10^{-3}$ (*Mytilus californianus*) to $7{\cdot}91 \times 10^{-3}$ (*Nuttallina californica*). The *Mytilus-Mitella-Pisaster* which were closely associated in the habitat, showed striking differences in the strontium-calcium atom ratio. The organisms collected at the low inter-tidal level had strontium-calcium atom ratios ranging from $1{\cdot}35 \times 10^{-3}$ (*Diodora aspera*) to 11×10^{-3} (*Anisodoris nobilis*). It appears that the marine organisms which live in the same ecological niche accumulate calcium and strontium in their calcareous shells in decidedly different proportions. On the other hand, a very definite relationship between the atom ratio and the phylogenetic classification of the organisms is indicated.

Another series of studies was carried out on the specimens of Echinodermata. Species of Echinodermata which lived in different habitats varying from inter-tidal rocky shore to deep-water, muddy substratum were collected near the Carmel-Monterey-Pacific Grove area. All Echinodermata given in Table V showed a remarkable constancy in their strontium-calcium atom ratios ranging from $2{\cdot}56$ to $2{\cdot}89 \times 10^{-3}$. Allowing for the individual variation and for experimental error, the atom ratios can be considered as identical for the whole phylum. Thus it may be concluded that some types of marine organisms will have a constant strontium-calcium atom ratio in their calcareous skeletons regardless of their habitats.

2. *Water temperature:* The water temperature as well as the salinity affect the solubility of the calcium and strontium carbonates in sea water. Wattenberg and Timmermann (1936) demonstrated that the solubility of calcium carbonate in sea water increased with increasing salinity and with decreasing temperature. The

strontium and calcium carbonates had identical solubility products of 5×10^{-7} in sea water at a temperature of 20° C and a salinity of 35 ‰ (WATTENBERG and TIMMERMANN, 1938).

BOGGILD (1930) stated that ecological variations are not effective on the form of calcium carbonate in marine organisms. ODUM (1951 B) and KULP, *et al.* (1952) have also concluded that the sea water temperature is not an important factor in determining the chemical composition of calcareous skeletons. However, LOWENSTAM (1954 B) demonstrated that the environmental factors, principally temperature, greatly influence the mineralogical properties of calcium carbonate in some marine organisms.

The data obtained by the authors (see Table I) showed that some types of marine organisms collected from arctic to tropical oceans always consisted of a nearly constant strontium-calcium atom ratio in their calcareous shells regardless of the water temperature of the environment.

3. *Salinity:* In their studies of strontium in fossils and limestones, KULP, *et al.* (1952) stated that " the primary factor which determines strontium-calcium ratio in the shell or limestone is the strontium-calcium ratio of the water from which these are deposited. The strontium-calcium ratio of the water in turn is related to the salinity and the source." ODUM (1951 B), who used artificial sea waters of varying strontium-calcium atom ratios, demonstrated that this ratio in the calcareous shell of *Physa* is directly proportional to that of artificial sea water. He also reported an atom ratio of $9{\cdot}23 \times 10^{-3}$ for the Atlantic Ocean water. Later investigations by CHOW and THOMPSON (1955 A and B) showed that samples of sea water collected from various oceans have a constant ratio between strontium and chlorinity, and calcium and chlorinity. Thus, the strontium-calcium atom ratio would be a constant ($8{\cdot}9 \times 10^{-3}$) regardless of the salinity of ocean waters. From these findings and the experiments of ODUM (1951 B), it may be concluded that dilution or concentration of sea water within the tolerance of marine organisms would not be an influential factor on the strontium-calcium atom ratio of calcareous skeletons.

Mineralogical Aspects

NOLL (1934) concluded from his investigations that there is always more strontium associated with aragonite limestones than with calcite limestones. KULP, *et al.* (1952) substantiated this by stating that calcite has a crystal lattice which is less amenable to strontium than the aragonite lattice. VINOGRADOV (1953) implied that NOLL'S rule cannot be applied strictly to calcareous shells of marine organisms, but that the rule is valid, in general, for many of them.

The analytical results obtained by the present authors together with the mineralogical data secured by previous investigators are summarized in Table VI. The majority of the specimens studied apparently had calcium carbonate existing as calcite. The calcite group includes Algae (Corallinaceae), Protozoa (Foraminifera), Porifera (Calcarea), Coelenterata (Alcyonaria), Arthropoda (Cirripedia), Mollusca (Anomiidae, Ostreidae and Pectinidae of Pelecypoda), Bryozoa, Brachiopoda (Articulata) and Echinodermata. The average strontium-calcium atom ratio of this group ranged from $1{\cdot}22$ to $4{\cdot}45 \times 10^{-3}$. In phylum Mollusca, the Pelecypoda (except three families mentioned above) and the Gastropoda (Prosobranchia) had a calcite-aragonite mixture in their shells. The strontium-calcium atom ratios of this group were $1{\cdot}94 \times 10^{-3}$ and $1{\cdot}49 \times 10^{-3}$, respectively.

Aragonite was reported only in the calcareous portions of Coelenterata (Hydrozoa and Madreporaria) and Mollusca (Amphineura, Scaphopoda, Cephalopoda and Nudibranchia). The strontium-calcium atom ratios of the aragonite group ranged from $2{\cdot}35$ to 10×10^{-3}. Scaphopoda and Cephalopoda which contain aragonite had atom ratios of $2{\cdot}35 \times 10^{-3}$ and $3{\cdot}74 \times 10^{-3}$, respectively. When comparisons are made mineralogically among molluscs, there is demonstrated a very definite trend for the occurrence of strontium, that is, aragonite Mollusca (10, 8·06, 3·74 and $2{\cdot}35 \times 10^{-3}$), aragonite-calcite mixture Mollusca (1·94 and $1{\cdot}68 \times 10^{-3}$) and calcite Mollusca (1·31 and $1{\cdot}22 \times 10^{-3}$). It appears logical to conclude, therefore, that marine skeletons consisting of aragonite contain more strontium than those of calcite.

The mineralogical structure of calcium carbonate in Polychaeta (Annelida) is not certain. It was reported (CHAVE, 1954) that species of *Serpula* contained calcium carbonate that varies from pure calcite in one specimen to pure aragonite in another. The Polychaeta shown in Table I (E) had an average strontium-calcium atom ratio of $5{\cdot}86 \times 10^{-3}$, and thus it may be concluded that for most specimens examined, the calcium carbonate is predominantly aragonite.

The Decapoda (Arthropoda), which were found to contain an appreciable amount of phosphorite as well as calcite, showed an average strontium-calcium atom ratio of $6{\cdot}17 \times 10^{-3}$. This is in agreement with ODUM'S findings (1951 B) on the phosphate in Brachiopoda, and with the statement of KULP, *et al.* (1952) that the presence of phosphate in the shells tends to yield a high strontium-calcium atom ratio.

Analyses (Table II) on *Globigerina* ooze of the Pacific Ocean which consists mainly of calcium carbonate, showed a strontium-calcium atom ratio of $1{\cdot}49 \times 10^{-3}$. The calcareous deep-sea sediments from the Indian Ocean showed an atom ratio of $1{\cdot}94 \times 10^{-3}$. These values are in marked contrast to those obtained by KULP, *et al.* (1952) but are in excellent agreement with an average value of $1{\cdot}86 \times 10^{-3}$ given by ODUM (1951 B).

The matrix of Permian limestone deposits from Roche Harbour, Washington, showed the lowest strontium-calcium atom ratio, $0{\cdot}63 \times 10^{-3}$, of all materials examined. This finding is comparable to the average atom ratio of $0{\cdot}71 \times 10^{-3}$ on a number of limestone samples obtained by KULP, *et al.* (1952) and to the value cited by RANKAMA and SAHAMA (1949). The matrix of strontionite deposits from Anacortes, Washington, contained 3·56% of calcium and 52·5% of strontium respectively, equivalent to an atom ratio of $6{,}750 \times 10^{-3}$.

Most of the analyses of calcareous portions of living marine organisms showed strontium-calcium atom ratios greater than those obtained on marine sediments. The strontium-calcium atom ratio for these marine sediments in turn was greater than those for the matrix of geologically older limestone deposits of marine origin. Furthermore, calcium carbonate deposited originally as aragonite should contain more strontium than that of calcite, as evidenced by analyses given above. Aragonite limestones are metastable and, in geological time, eventually change into calcite limestones which have a strontium-calcium atom ratio much less than that of marine organisms. Thus it seems logical to conclude that the strontium content of calcareous deposits decreases as the result of geological aging.

To explain the elimination of strontium from calcareous deposits, the following is postulated: the solubility products of calcium and strontium carbonates are about the same order of magnitude, 5×10^{-7}, in sea water at a temperature of 20° C and a salinity of 35‰ (WATTENBERG and TIMMERMANN, 1938). When marine organisms die and disintegrate, there is a tendency for calcareous materials to halmyrolyze and go into solution. Should strontianite ($SrCO_3$) be present, it would dissolve slowly because sea water is not saturated with respect to strontium carbonate. On the other hand, the ionic strength of calcium in sea water is such that the re-solution of calcium carbonate is exceedingly limited. Should celestite ($SrSO_4$) be present in such marine organisms which have a high strontium-calcium atom ratio, it would leach much more readily from the calcareous matrix, as strontium sulphate is about ten times more soluble than strontium and calcium carbonates. To partially substantiate this hypothesis, the experiments of ODUM (1951 A) are cited. He demonstrated that strontium existed as celestite and not strontianite as previously assumed in radiolaria. It is the intention of the authors to investigate this problem further and to determine the actual chemical composition of the strontium compound in such marine organisms as Madreporaria.

ACKNOWLEDGEMENT

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Table I.—Chemical composition of calcareous portions of carbonate-secreting marine organisms

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \cdot 1000$
(A) MARINE ALGAE						
DIVISION RHODOPHYTA						
FAMILY CORALLINACEAE						
Bossea orbigniana	Calif.*	29·2	0·199	36·5	14·6	3·12
Bossea sp.	Calif.	27·0	0·201	34·7	18·0	3·41
Calliarthron cheilosporioides	Calif.	23·6	0·151	30·8	29·8	2·93
Corallina chilensis	Calif.	26·8	0·180	34·7	19·1	3·06
C. gracilis	Calif.	26·2	0·195	34·2	19·5	3·39
C. officinalis	N. H.	29·2	0·196	35·1	14·0	3·07
Corallina sp.	N. H.	26·6	0·186	33·1	19·1	3·19
Lithophyllum sp.	Calif.	29·2	0·203	34·5	16·3	3·18
Lithothamnion conchatum	Calif.	29·0	0·219	34·2	16·4	3·45
DIVISION CHRYSOPHYTA						
Coscinodiscus sp.	Wash.	trace	trace	4·1	18·9	–
(B) PHYLUM PROTOZOA, CLASS SARCODINA, ORDER FORAMINIFERA						
Calcarina sp.	Ifalik Atoll†	31·6	0·193	40·8	6·72	2·78
Baculogypsina sp.	Ifalik Atoll†	31·4	0·217	40·8	9·40	3·16
Foraminifera (unidentified)	Bermuda	33·3	0·239	40·1	5·19	3·28

* The California specimens of algae were identified by Dr. G. J. HOLLENBERG.

† The Foraminifera specimens were collected by Professor DONALD ABBOTT and were identified y Mr. FRANK SULLIVAN.

Table I (cont.)

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca} \times 1000$
(C) PHYLUM PORIFERA						
CLASS CALCAREA						
ORDER HOMOCOELA						
Leucosolenia eleanor	Calif.	1·29	trace	3·24	20·2	—
Leucosolenia sp.	Maine	13·6	0·099	23·3	25·0	3·33
Sponge (unidentified)	Beaufort Sea	13·5	0·098	34·4	22·8	3·34
ORDER HETEROCOELA						
Leuconia heathi	Calif.	1·00	trace	2·28	30·3	—
Rhabdodermella nuttingi	Calif.	29·6	0·149	35·8	12·7	2·30
CLASS DEMOSPONGIAE						
SUBCLASS TETRAXONIDA, ORDER EPIPOLASIDA						
Tethya aurantia	Calif.	0·06	trace	6·30	42·3	—
SUBCLASS CORNACUSPONGIDA						
ORDER POECILOSCLERINA						
Esperiopsis originalis	Calif.	0·08	trace	2·12	38·2	—
Ophlitaspogia pennata	Calif.	0·05	trace	1·97	40·8	—
ORDER HAPLOSCLERINA						
Haliclona permollis	Calif.	0·07	trace	6·57	42·2	—
ORDER KERATOSA						
Euspongia sp.	Unknown	0·05	trace	12·6	85·0	—
(D) PHYLUM COELENTERATA*						
CLASS HYDROZOA, ORDER MILLEPORINA						
Millepora tenera	Ifalik Atoll	38·1	0·686	41·4	3·15	8·22
ORDER STYLASTERINA						
Allopora californica	Calif.	36·5	0·778	38·5	8·46	9·74
A. campyleca paragea	Gulf of Alaska	35·7	0·768	40·6	4·47	9·83
A. porphyra	Calif.	38·8	0·580	41·1	2·91	6·83
A. venusta	Calif.	37·0	0·808	40·4	5·38	9·97
Cryptohelia trophostega	Bering Sea	37·8	0·930	41·1	3·42	11·2
Distichopora violacea	Marshall Is.	37·6	0·640	41·2	3·54	7·77
Errinopora zarhyncha	Aleutian Is.	37·5	0·224	43·1	2·50	2·73
Stylaster elegans	Marshall Is.	37·4	0·852	41·3	3·84	10·4
S. sanguineus	Hawaii	37·7	0·843	41·2	3·88	10·2
CLASS ANTHOZOA, SUBCLASS ALCYONARIA						
ORDER STOLONIFERA						
Tubipora sp.	Unknown	31·1	0·225	41·8	2·38	3·30
ORDER ALCYNACEA						
Eunephthya rubiformis	Beaufort Sea	4·72	0·039	12·4	30·4	3·78
ORDER PENNATULACEA						
Stylatula elongata	Calif.	22·7	0·128	28·5	33·0	2·64
ORDER GORGONACEA						
Psammogorgia arbuscula	Calif.	21·4	0·136	30·0	37·5	2·90
ORDER COENOTHECALIA						
Heliopora coerulea	Ifalik Atoll	37·3	0·618	40·0	6·60	7·57

* Some of the specimens were contributed by the Hopkins Marine Station from the collection of the late Professor W. K. FISHER.

Table 1 (cont.)

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca} \times 1000$
SUBCLASS ZOANTHARIA, ORDER MADREPORARIA						
Acropora sp.	Ifalik Atoll	37·3	0·810	41·1	3·85	9·92
Astrangia sp.	Calif.	37·0	0·868	41·3	3·43	10·7
Balanophyllia elegans	Calif.	32·3	0·666	37·5	8·84	9·41
Caryophyllia sp.	Calif.	37·4	0·850	41·4	2·90	10·4
Meandrina sinuosa	Bermuda	36·5	0·802	41·2	3·25	10·1
Pocillopora sp.	Ifalik Atoll	37·9	0·735	41·5	3·13	8·85
Porites sp.	Ifalik Atoll	37·3	0·790	40·7	5·38	9·67
(E) PHYLUM ANNELIDA, CLASS POLYCHAETA						
FAMILY CIRRATULIDAE						
Dodecaceria pacifica	B.C., Canada*	32·5	0·574	40·6	5·38	8·07
D. fistulicola	Calif.	35·4	0·530	40·3	5·20	6·84
FAMILY SERPULIDAE						
Salmacina tribranchiata	Calif.	33·2	0·596	36·5	6·35	8·24
Serpula vermicularis	B.C., Canada	32·4	0·288	40·7	4·51	4·06
S. vermicularis	Calif.	32·1	0·289	42·5	4·60	4·12
Spirorbis sp.	N. H.	29·2	0·247	34·2	15·0	3·86
(F) PHYLUM ARTHROPODA, SUBPHYLUM MANDIBULATA, SUPERCLASS CRUSTACEA						
CLASS CIRRIPEDIA, ORDER THORACICA						
Balanus amphitrite	Florida†	37·0	0·428	41·8	5·00	5·28
B. balanoides	N. H.	37·6	0·382	41·7	3·27	4·64
B. balanoides	N. H.	34·1	0·336	39·8	7·76	4·50
B. cariosus	Wash.	39·1	0·324	42·2	1·80	3·78
B. crenatus	Beaufort Sea	36·1	0·337	41·7	3·24	4·27
B. eburneus	Florida	36·7	0·381	41·8	4·80	4·74
B. eburneus	Florida	36·6	0·345	41·7	2·39	4·32
B. glandula	Wash.	37·0	0·358	41·6	3·12	4·42
B. glandula	Calif.	37·4	0·371	41·5	2·88	4·53
B. nubilis	Calif.	35·6	0·334	39·6	7·18	4·29
B. nubilis	Wash.	34·2	0·282	36·7	12·3	3·77
Balanus sp.	Wash.	37·4	0·364	41·8	2·72	4·45
Balanus sp.	B.C., Canada	36·1	0·337	41·2	3·80	4·27
B. tintinnabulum	Calif.	37·2	0·381	41·4	1·88	4·67
Chthamalus fragilis	N. C.	32·4	0·328	37·3	8·33	4·62
Mitella polymerus	Calif.	36·8	0·344	40·7	4·48	4·27
Tetraclita squamosa	Calif.	35·6	0·381	41·2	4·07	4·88
CLASS MALACOSTRACA, SUBCLASS EUCARIDA, ORDER DECAPODA						
Cancer antennarius	Calif.	27·2	0·363	30·2	32·7	6·12
C. antennarius‡	Calif.	28·0	0·371	32·5	20·0	6·05
C. borealis	N. H.	24·0	0·322	29·3	27·2	6·13
C. magister	Wash.	24·0	0·351	28·1	28·1	6·69
C. productus	Calif.	23·3	0·308	30·2	30·0	6·04
C. productus **	Calif.	0·44	trace	8·6	85·5	—
Hemigrapsus nudus	Wash.	26·0	0·349	29·3	28·7	6·13
Pugettia producta	Calif.	21·2	0·278	25·7	33·3	6·00
(G) PHYLUM MOLLUSCA						
CLASS AMPHINEURA, ORDER POLYPLACOPHORA						
Cryptochiton stelleri	Calif.	38·2	0·736	40·3	6·10	8·80
C. stelleri	Wash.	37·1	0·751	41·4	3·66	9·25
Cyanoplax hartwegii	Calif.	38·3	0·716	41·3	5·70	8·55
Nuttallina californica	Calif.	38·2	0·662	41·2	4·69	7·91
Tonicella lineata	Calif.	37·6	0·640	41·4	4·83	7·79

* The specimens from British Columbia were provided by Mr. Cyril Berkeley of the Pacific Biological Station.
† The Florida specimens were provided by Mr. C. S. Yentsch.
‡ Claw ** Moulting

Table I (cont.)

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca} \times 1000$
(G) PHYLUM MOLLUSCA (*continued*)						
CLASS AMPHINEURA, ORDER POLYPLACOPHORA						
Ischnochiton heathiana	Calif.	38·7	0·636	41·4	3·63	7·52
I. mertensii	Calif.	38·6	0·636	41·3	3·95	7·55
Ischnochiton sp.	Wash.	38·8	0·680	41·8	3·06	8·02
Katharina tunicata	Calif.	38·7	0·687	39·6	3·91	8·12
Mopalia ciliata	Calif.	37·2	0·626	41·1	4·83	7·69
M. lignosa	Calif.	37·9	0·664	41·2	4·26	8·01
M.muscosa	Calif.	37·9	0·608	41·0	4·74	7·32
M. muscosa	Wash.	37·8	0·709	42·2	3·31	8·57
M. wosnessenskii	Calif.	37·6	0·606	41·4	3·88	7·37
Chiton (unidentified)	Beaufort Sea	37·0	0·680	41·5	4·00	8·41
(H) PHYLUM MOLLUSCA, CLASS PELECYPODA						
ORDER FILIBRANCHIA						
FAMILY ANOMIIDAE						
Pododesmus macroschisma	Calif.	38·6	0·103	42·6	1·75	1·22
FAMILY MYTILIDAE						
Botula falcata	Calif.	38·6	0·196	38·9	5·67	2·32
Modiolus capax	Calif.	37·5	0·103	41·1	5·10	1·25
M. modiolus	N. H.	37·8	0·125	41·8	3·97	1·52
M. modiolus	N. H.	38·8	0·116	42·7	2·39	1·37
M. modiolus	N. H.	37·5	0·112	41·3	5·58	1·37
M. modiolus	N. H.	37·8	0·132	41·1	4·20	1·60
Modiolus sp.	Wash.	38·2	0·099	42·1	3·96	1·19
Mytilus edulis	N. H.	37·2	0·176	42·5	3·10	2·16
M. edulis	N. H.	37·9	0·110	42·0	3·32	1·33
M. edulis	Maine	38·3	0·128	42·1	3·30	1·53
M. edulis	Maine	37·2	0·116	42·4	3·52	1·43
M. edulis	Wash.	38·6	0·106	42·2	3·24	1·26
M. edulis	B.C., Canada	38·6	0·154	41·4	4·42	1·82
M. edulis	Beaufort Sea	36·6	0·117	41·2	5·53	1·46
M. edulis	Calif.	36·5	0·118	42·2	3·87	1·48
M. californianus	Calif.	39·0	0·086	43·1	1·54	1·01
M. californianus	Calif.	38·5	0·086	43·1	1·70	1·02
FAMILY PECTINIDAE						
Pecten hindsii	Wash.	38·2	0·111	41·8	1·91	1·33
P. hericius	Wash.	37·8	0·107	42·1	1·75	1·29
ORDER EULAMELLIBRANCHIA						
FAMILY OSTREIDAE						
Crassostrea virginica	N. H.	33·7	0·092	42·4	2·16	1·25
C. virginica	N. C.	37·8	0·107	41·8	2·34	1·29
Ostrea gigas	B.C., Canada	34·6	0·097	37·6	13·3	1·28
O. gigas	B.C., Canada	36·2	0·100	42·5	1·71	1·26
O. lurida	Calif.	38·6	0·085	42·5	1·68	1·01
FAMILY SPONDYLIDAE						
Spondylus sp.	unknown	38·0	0·128	41·6	1·67	1·54
FAMILY CHAMIDAE						
Chama pellucida	Calif.	36·8	0·142	42·3	2·47	1·76
FAMILY TELLINIDAE						
Macoma irus	Calif.	38·7	0·153	40·8	2·42	1·81
M. nasuta	Calif.	38·0	0·215	38·9	2·27	2·59
M. secta	Calif.	38·9	0·248	42·5	2·17	2·91
Tellina sp.	B.C., Canada	37·1	0·173	42·1	2·50	2·14

Table I (cont.)

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio Sr/Ca × 1000
FAMILY SOLENIDAE						
Ensis directus	N. H.	37·0	0·164	41·9	3·47	2·03
Siliqua costata	N. H.	38·4	0·182	42·4	2·46	2·17
S. patula	Wash.	38·4	0·207	42·0	2·88	2·46
Solen sicarius	Calif.	38·1	0·116	42·9	1·66	1·39
FAMILY MACTRIDAE						
Mesodesma deauratum	N. H.	37·6	0·164	42·0	3·31	2·00
Schizothaerus nuttallii	Wash.	37·8	0·195	41·6	4·00	2·36
S. nuttallii	Calif.	39·1	0·177	42·6	1·79	2·07
Spisula solidissima	N. H.	38·2	0·216	42·0	2·58	2·58
FAMILY PLEUROPHORIDAE						
Cyprina islandica	N. H.	39·2	0·135	42·7	1·93	1·57
FAMILY CLINOCARDIIDAE						
Clinocardium nuttallii	Wash.	37·6	0·245	41·9	2·98	2·98
C. nuttallii	Wash.	38·5	0·188	41·8	3·68	2·23
C. nuttallii	Calif.	38·0	0·185	41·8	3·55	2·22
FAMILY VENERIDAE						
Compsomyax subdiaphana	Wash.	38·6	0·180	42·2	3·07	2·13
Irus lamellifer	Calif.	37·6	0·134	41·6	3·20	1·63
Protothaca staminea	Wash.	39·4	0·179	41·8	3·30	2·08
P. staminea	Calif.	38·2	0·149	42·0	2·45	1·78
P. tenerrima	Wash.	37·3	0·175	42·0	2·94	2·14
Saxidomus giganteus	Wash.	38·6	0·192	42·3	2·23	2·27
S. nuttallii	Calif.	37·8	0·125	42·2	2·63	1·52
Tivela stultorum	Calif.	38·8	0·120	42·0	3·34	1·41
Venus mercenaria	Canadian Atlantic	38·6	0·148	42·5	2·38	1·75
FAMILY PERIPLOMATIDAE						
Periploma sp.	B.C., Canada	37·9	0·183	42·0	2·60	2·20
FAMILY LYONSIIDAE						
Mytilimeria nuttallii	Calif.	36·6	0·188	39·8	7·63	2·35
FAMILY MYIDAE						
Mya arenaria	Maine	38·6	0·246	42·2	2·44	2·91
M. arenaria	Wash.	38·7	0·238	42·3	2·28	2·81
M. arenaria	Oregon	38·8	0·181	42·3	2·48	2·12
M. arenaria	Wash.	38·3	0·181	42·2	2·22	2·16
FAMILY SAXICAVIDAE						
Panope generosa	Wash.	38·2	0·207	42·3	2·03	2·48
Saxicava sp.	Beaufort Sea	37·9	0·196	40·5	4·98	2·36
FAMILY PHOLADIDAE						
Pholadidea penita	Calif.	37·0	0·147	41·2	3·63	1·82
P. ovoidea	Calif.	38·7	0·192	42·2	2·36	2·27
Zirfaea crispata	N. H.	38·3	0·148	41·2	3·63	1·77
Z. pilsbryi	Calif.	39·0	0·230	42·5	2·30	2·70
(I) PHYLUM MOLLUSCA, CLASS GASTROPODA						
SUBCLASS PROSOBRANCHIA						
ORDER ASPIDOBRANCHIA, SUBORDER ZYGOBRANCHIA						
FAMILY FISSURELLIDAE						
Diodora aspera	Calif.	38·5	0·114	41·5	3·54	1·35
Fissurella volcano	Calif.	39·5	0·108	42·6	1·86	1·25
Megathura crenulata	Calif.	38·0	0·104	42·8	2·03	1·25
Megatebennus bimaculatus	Calif.	39·0	0·117	42·1	2·74	1·38

Table I (cont.)

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca} \times 1000$
FAMILY HALIOTIDAE						
Haliotis cracherodii	Calif.	37·1	0·123	42·2	3·87	1·52
H. rufescens	Calif.	38·8	0·130	41·7	3·82	1·54
SUBORDER PATELLACEA						
FAMILY ACMAEIDAE						
Acmaea digitalis	Calif.	38·5	0·199	42·6	2·51	2·37
A. digitalis	Calif.	37·6	0·204	42·1	2·79	2·48
A. insessa	Calif.	37·8	0·183	42·4	2·84	2·21
A. limatula	Calif.	38·2	0·168	42·0	3·03	2·01
A. mitra	Calif.	37·2	0·161	42·4	2·61	1·98
A. mitra	Wash.	38·2	0·162	42·3	2·48	1·94
A. pelta	Calif.	37·6	0·151	40·4	3·39	1·84
A. persona	Calif.	37·6	0·201	42·0	3·16	2·45
A. scabra	Calif.	37·3	0·180	42·5	1·97	2·21
A. t. scutum	N. H.	38·4	0·180	41·8	3·28	2·14
A. t. scutum	Calif.	37·6	0·164	41·7	3·65	2·00
Lottia gigantea	Calif.	37·4	0·170	42·2	2·71	2·08
SUBORDER TROCHACEA						
FAMILY TROCHIDAE						
Calliostoma canaliculatum	Calif.	37·2	0·129	41·0	4·95	1·59
C. costatum	Calif.	37·0	0·122	41·2	2·96	1·51
C. gloriosum	Wash.	36·3	0·131	41·7	4·73	1·65
Tegula brunnea	Calif.	37·5	0·124	40·6	4·06	1·51
T. funebralis	Calif.	37·4	0·113	41·9	3·64	1·38
T. montereyi	Calif.	38·2	0·121	41·5	3·99	1·45
FAMILY TURBINIDAE						
Astraea inaequalis	Calif.	36·7	0·120	41·0	5·37	1·50
ORDER PECTINIBRANCHIA						
SUBORDER TAENIOGLOSSA						
FAMILY EPITONIIDAE						
Epitonium groenlandicum	Atlantic	37·0	0·118	41·9	3·07	1·46
Epitonium sp.	Calif.	36·8	0·120	41·2	4·80	1·49
FAMILY VERMETIDAE						
Petaloconchus montereyensis	Calif.	35·6	0·144	40·2	7·10	1·85
FAMILY LITTORINIDAE						
Littorina litorea	Maine	38·4	0·107	42·5	2·27	1·27
L. litorea	N. H.	38·7	0·107	42·8	1·84	1·26
L. palliata (= *L. obtusata*)	N. H.	37·2	0·142	41·0	2·72	1·74
L. planaxis	Calif.	37·8	0·155	42·4	2·62	1·87
L. rudis (= *L. saxatilis*)	N. H.	38·6	0·140	41·8	1·50	1·66
L. rudis	N. H.	37·5	0·125	41·7	4·39	1·53
L. scutulata	Calif.	38·4	0·121	42·5	2·77	1·44
FAMILY CALYPTRAEIDAE						
Crepidula adunca	Calif.	37·7	0·140	42·0	3·22	1·70
C. fornicata	Mass.	38·0	0·149	42·3	2·37	1·79
C. nummaria	Calif.	38·5	0·153	42·3	2·36	1·82
FAMILY NATICIDAE						
Polinices Heros	Mass.	37·7	0·121	42·2	2·96	1·47
P. draconis	Wash.	38·8	0·137	42·5	2·28	1·61
Natica sp.	Beaufort Sea	37·8	0·108	41·8	3·54	1·31
SUBORDER STENOGLOSSA						
FAMILY OLIVIDAE						
Oliva litterata	Florida	39·6	0·145	42·8	1·61	1·67
Olivella biplicata	Calif.	38·9	0·113	42·4	1·84	1·33

Table 1 (cont.)

	Locality	*Calcium* %	*Strontium* %	*Carbon dioxide* %	*Organic matter* %	*Atom ratio* $\frac{Sr}{Ca} \cdot 1000$
FAMILY FUSINIDAE						
Fusinus monksae	Calif.	35·5	0·115	40·1	4·27	1·48
FAMILY NASSARIIDAE						
Nassa obsoleta	N. H.	36·4	0·151	40·9	6·46	1·89
FAMILY MURICIDAE						
Acanthina spirata	Calif.	38·6	0·131	42·3	2·66	1·55
Murex pume	Florida	39·9	0·172	41·7	2·30	1·97
M. triolatus	Calif.	38·0	0·131	42·6	1·68	1·58
Thais canaliculata	Calif.	38·1	0·128	42·8	2·26	1·54
T. emarginata	Calif.	37·6	0·138	42·3	3·03	1·68
T. lamellosa	Wash.	38·8	0·129	42·8	1·45	1·52
T. lapillus	N. H.	38·5	0·126	42·7	1·13	1·50
T. lapillus	N. H.	36·5	0·128	39·4	3·68	1·60
SUBCLASS OPISTHOBRANCHIA, ORDER NUDIBRANCHIA						
Anisodoris nobilis	Calif.	2·60	0·063	3·25	67·2	11
Archidoris montereyensis	Calif.	3·16	0·062	4·68	78·0	9
Triopha grandis	Calif.	0·25	trace	(———91·3——)		—
(J) PHYLUM MOLLUSCA CLASS SCAPHOPODA						
Dentalium entale	Wash.	38·2	0·196	42·3	1·81	2·35
CLASS CEPHALOPODA, SUBCLASS DIBRANCHIATA, ORDER DECAPODA						
Loligo opalescens	Calif.	trace	trace	trace	99·5	—
Sepia sp.	unknown	35·8	0·293	40·1	7·35	3·74
(K) PHYLUM BRYOZOA, CLASS ECTOPROCTA ORDER CYCLOSTOMATA						
Idmonea sp.	Calif.	35·6	0·307	38·1	7·90	3·94
Crisia sp.	Calif.	35·7	0·282	38·2	6·28	3·61
Bryozoa (unidentified)	Beaufort Sea	34·3	0·256	40·2	7·30	3·41
Bryozoa (unidentified)	Beaufort Sea	30·6	0·209	35·0	16·5	3·12
Bryozoa (unidentified)	Beaufort Sea	25·3	0·181	31·8	23·2	3·27
ORDER CHEILOSTOMATA						
Bugula californica	Calif.	18·2	0·124	23·7	36·0	3·12
Hippodiplosia insculpta	Calif.	29·4	0·247	35·8	13·8	3·84
Phidolopora pacifica	Calif.	33·7	0·221	40·0	6·37	3·00
(L) PHYLUM BRACHIOPODA, CLASS ARTICULATA, ORDER TESTICARDINES						
Hemithyris psittacea	Beaufort Sea	37·7	0·113	42·2	3·02	1·37
*H. psittacea**	Beaufort Sea	38·9	0·102	42·8	1·94	1·20
Terebratalia transversa	Wash.	38·0	0·130	41·3	2·02	1·57
Terebratulina unguicala	Calif.	37·8	0·113	42·5	1·81	1·37
Brachiopoda (unidentified)	Calif.	38·7	0·108	42·7	1·79	1·28
(M) PHYLUM ECHINODERMATA CLASS CRINOIDEA						
Antedon sp.	Calif.	25·8	0·145	38·2	13·3	2·56
CLASS ASTEROIDEA ORDER FORCIPULATA						
Asterias forbesi	Mass.	18·6	0·113	24·9	39·4	2·78
A. vulgaris	N. H.	22·5	0·141	27·9	33·6	2·86
A. vulgaris	Mass.	20·2	0·128	28·6	34·4	2·89
Leptasterias aequalis	Calif.	20·9	0·127	32·7	31·0	2·78
L. pusilla	Calif.	25·5	0·146	37·7	20·4	2·61
Mediaster aequalis	Calif.	27·3	0·158	36·1	19·0	2·60

* Remains.

Table I (cont.)

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca} \times 1000$
CLASS ASTEROIDEA (*continued*)						
ORDER FORCIPULATA						
Pisaster brevispinus	Calif.	22·7	0·131	33·6	28·5	2·64
P. giganteus	Calif.	17·2	0·101	31·9	37·2	2·69
P. ochraceus	Calif.	24·6	0·148	34·0	24·4	2·76
Pycnopodia helianthoides	Calif.	20·0	0·114	31·8	33·5	2·60
ORDER SPINULOSA						
Henricia leviuscula	Wash.	23·1	0·136	30·3	28·6	2·69
H. leviuscula	Calif.	25·2	0·155	33·3	25·8	2·81
H. sanguinolenta	N. H.	18·4	0·112	28·6	38·2	2·78
Henricia sp.	Beaufort Sea	20·6	0·125	29·0	34·0	2·78
Solaster papposus	Beaufort Sea	23·2	0·131	31·0	28·8	2·60
Patiria miniata	Calif.	26·8	0·162	36·1	21·2	2·77
ORDER PHANEROZONIA						
Hippasteria spinosa	Wash.	22·7	0·137	30·8	29·6	2·76
Luidia sp.	Calif.	24·1	0·142	34·1	19·3	2·69
CLASS OPHIUROIDEA						
ORDER EURYALAE						
Gorgonocephalus sp.	Beaufort Sea	26·6	0·158	33·4	21·8	2·72
ORDER OPHIURAE						
Amphipholis squamata	Calif.	24·7	0·146	33·2	23·5	2·70
Ophiopholis aculeata	Maine	24·5	0·146	32·6	24·4	2·72
O. aculeata	N. H.	25·9	0·149	34·5	19·7	2·63
Ophiothrix spiculata	Calif.	20·4	0·118	28·9	33·4	2·64
Ophioplocus esmarki	Calif.	27·1	0·165	36·9	17·0	2·79
Ophiura sarsii	Wash.	31·2	0·185	39·2	11·0	2·71
O. sarsii	Beaufort Sea	30·2	0·175	38·0	13·5	2·65
CLASS ECHINOIDEA						
ORDER CENTRECHINOIDA						
Strongylocentrotus dröbachiensis	N. H.	34·8	0·214	41·0	5·68	2·81
S. dröbachiensis	Wash.	35·5	0·214	42·0	3·33	2·76
S. dröbachiensis	Wash.	35·6	0·210	42·0	3·05	2·70
S. fragilis	Calif.	32·7	0·188	39·6	9·28	2·63
S. franciscanus	Wash.	36·4	0·218	42·8	2·97	2·74
S. pallidus	Beaufort Sea	32·2	0·191	40·0	8·10	2·71
S. purpuratus	Wash.	35·4	0·215	43·8	2·18	2·78
S. purpuratus	Calif.	33·2	0·210	41·4	6·96	2·89
Heterocentrotus trigonarius	Ifalik Atoll	31·6	0·180	43·9	1·20	2·60
ORDER CLYPEASTROIDA						
Dendraster excentricus	Calif.	33·5	0·205	43·5	2·85	2·79
Echinarachnius parma	N. H.	31·8	0·178	41·4	5·62	2·56
ORDER SPATANGOIDEA						
Brisaster sp.	Wash.	30·5	0·164	40·1	8·77	2·46
CLASS HOLOTHUROIDEA						
ORDER DENDROCHIROTIDA						
Cucumaria curata	Calif.	0·8	trace	7·5	84·0	—
Psolus chitonoides	Wash.	29·1	0·173	38·3	12·2	2·72
P. peroni	Beaufort Sea	25·2	0·153	32·1	25·8	2·78
P. sp.	Calif	28·6	0·170	34·5	18·0	2·72
(N) PHYLUM CHORDATA, CLASS ASCIDIACEA						
Polyclinum planum	Calif.	0·30	trace	13·8	70·0	—
Synoicum par-fustis	Calif.	0·38	trace	13·5	69·1	—

Table II.—The occurrence of calcium and strontium in substances other than marine organisms

	Locality	Calcium %	Strontium %	Carbon dioxide %	Organic matter %	Atom ratio $\frac{Sr}{Ca}$ 1000
Walrus (*Odobenus rosmarus*) ivory	Alaska	21·0	trace	2·96	36·8	—
Fresh water clam (unidentified)	Wash.	38·0	0·085	41·4	5·53	1·02
Fresh water clam (unidentified)	Wash.	36·4	0·072	41·3	6·02	0·90
Potamobius sp.	Wash.	19·8	0·077	21·7	45·5	1·78
Deep sea sediments*	Indian Ocean (Swedish Deep Sea Expedition 1948–1949)	29·4	0·125	37·7	2·95	1·94
Globigerina ooze†	Pacific Ocean	37·5	0·122	41·8	1·46	1·49
Coquina rock (cemented shells)	Florida	37·8	0·153	41·7	1·57	1·85
Limestone deposits	Wash.	38·1	0·052	42·5	0·68	0·63
Strontianite deposits	Wash.	3·56	52·5	31·5	0·26	6,750
Sea water	Over-all					8·90

* Specimen was provided by Mr. Taivo Laevastu.

† Specimen was provided by Dr. Howard R. Gould.

Table III.—Summary of results arranged in accordance with the phylogenetic classification of marine organisms

Classification	Calcium mean %	Strontium mean %	Carbon dioxide mean %	Organic matter mean %	Mean atom ratio $\frac{Sr}{Ca}$ · 1000
Marine Algae, Corallinaceae	27·4	0·193	34·2	18·5	3·20
Protozoa, Foraminifera	32·1	0·216	40·6	7·10	3·07
Porifera, Calcarea	11·8	0·069	19·8	22·2	2·99
Demosponiae	0·06	trace	5·91	49·7	—
Coelenterata, Hydrozoa	37·4	0·711	41·0	4·16	8·69
Anthozoa					
Alcyonaria	23·2	0·229	30·5	22·0	4·04
Zoantharia	36·5	0·789	40·7	4·40	9·86
Annelida, Polychaeta	32·5	0·421	39·1	6·84	5·87
Arthropoda, Cirripedia	36·3	0·354	40·8	4·65	4·45
Decapoda	24·6	0·328	29·3	27·8	6·17
Mollusca, Amphineura	38·0	0·669	41·2	4·30	8·06
Pelecypoda	37·9	0·154	41·8	3·18	1·85
Gastropoda					
Prosobranchia	37·8	0·139	41·8	3·14	1·68
Opisthobranchia	2·38	0·062	3·97	72·6	10
Scaphopoda	38·2	0·196	42·3	1·81	2·35
Cephalopoda	35·8	0·293	40·1	7·35	3·74
Bryozoa, Ectoprocta	30·4	0·228	35·4	14·7	3·41
Brachiopoda, Articulata	38·4	0·113	42·3	2·12	1·36
Echinodermata, Crinoidea	25·8	0·145	38·2	13·3	2·56
Asteroidea	22·4	0·134	31·8	29·3	2·73
Ophiuroidea	26·3	0·153	34·6	20·5	2·69
Echinoidea	33·6	0·199	41·8	5·00	2·70
Holothuroidea	27·8	0·166	35·0	18·3	2·74
Chordata, Ascidiacea	0·34	trace	13·7	69·6	

Table IV.—Strontium-calcium atom ratio of marine invertebrates collectea at different tide levels

Mid-tidal Level	Atom ratio $\frac{Sr}{Ca} \times 1000$	Low Inter-tidal Level	Atom ratio $\frac{Sr}{Ca} \times 1000$
Mytilus californianus	1·01	*Diodora aspera*	1·35
Littorina scutalata	1·44	*Rhabdodermella nuttingi*	2·30
Pisaster ochraceus	2·76	*Henricia leviscula*	2·81
Mitella polymerus	4·27	*Tetraclita squamosa*	4·88
Balanus glandula	5·06	*Pugettia producta*	6·00
Cancer antennarius	6·12	*Cryptochiton stelleri*	8·80
Nuttallina californica	7·91	*Balanophyllia elegans*	9·41
		Anisodoris nobilis	11

Table V.—Strontium-calcium atom ratio of Echinodermata in relation to their habitats

Habitat	Specimen	Atom ratio $\frac{Sr}{Ca} \times 1000$
Wharf Piling	*Pisaster giganteus*	2·69
Mid-tidal Level Rocky Shore	*P. ochraceus*	2·76
Low Inter-tidal Rocky Reef	*Henricia leviscula*	2·81
Burrowing	*Strongylocentrotus purpuratus*	2·89
Sandy Flat	*Dendraster excentricus*	2·79
Sandy-mud Substratum	*Ophioplocus esmarki*	2·79
Inter-tidal Zone	*Psolus* sp.	2·72
Deep water	*Strongylocentrotus fragilis*	2·63

Table VI.—Strontium-calcium atom ratio in relation to the mineralogical character of calcium carbonate in marine organisms

Calcite	Atom ratio $\frac{Sr}{Ca} \times 1000$	Calcite–Aragonite Mixture	Atom ratio $\frac{Sr}{Ca} \times 1000$	Aragonite	Atom ratio $\frac{Sr}{Ca} \times 1000$
Algae, Corallinaceae	3·20	Mollusca,		Coelenterata,	
Protozoa,		Pelecypoda	1·94†	Hydrozoa	9·49‡
Foraminifera	3·07	Gastropoda		Zoantharia	9·86
Porifera, Calcarea	2·99	Prosobranchia	1·68	Mollusca,	
Coelenterata,				Amphineura	8·06
Alcyonaria	3·16*			Gastropoda	
Arthropoda,				Nudibranchia	10
Cirripedia	4·45			Scaphopoda	2·35
Mollusca,				Cephalopoda	3·74
Pelecypoda					
Anomiidae	1·22				
Ostreidae	1·22				
Pectinidae	1·31				
Bryozoa, Ectoprocta	3·41				
Brachiopoda,					
Articulata	1·36				
Echinodermata	2·71				

* Does not include the aragonite *Heliopora*.

† Does not include the calcite Anomiidae, Ostreidae and Pectinidae.

‡ Does not include the calcite *Errinopora*.

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