

COLD WATER BIOTA

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ABSTRACT

A cold water biota is here defined as organisms living in water with an annual mean temperature of nearly 0°C. Since such cold water is present in both the polar oceans and deep seas (approximately 2000 meters in depth), both polar cold water biota and deep sea cold water biota are differentiated. Either biota can be used as an indicator of low temperature. In the geological record, owing to its remarkable latitudinal dependence, the polar cold water biota may be more easily recognized than the deep sea cold biota.

The recognition of deep sea cold water biota is approached by uniformitarianism in that we can infer the environment and mode of life of fossils from the knowledge of living representatives. However the polar cold water biota can be recognized either by a uniformitarian approach or by a paleobiogeographic approach. The reconstruction of paleobiogeography is based on (1) Large scale morphological gradients, including the coiling directional ratio of foraminifers, the apical features of gastropods and growth rate of corals, (2) Large scale diversity gradients which utilize the absolute number of taxa in each sample, (3) Large scale geochemical gradients, including isotope ratios and differences of mineralogical composition, and (4) Biotic similarity which involves the degree of resemblance of biotic content according to the presence and absence of taxa.

INTRODUCTION

One of the great achievements in science is the finding of a close correlation between any two variables. Such a correlation is termed a regression line. If one variable happens to be known, it can be used to predict another variable whenever

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both are with a causal relationship. For instance, the cold water biota has a close relationship with low temperature, if they are found as fossils, they will indicate an ancient polar environment or a deep sea environment of low temperature. Through the analysis of Lower Permian ammonoid faunal provinciality, a polar realm which includes boreal and austral provinces (Fig.1) has been recognized (Lee, 1981). Since the water existing in the polar region is generally cold or low in temperature, I will deal with the cold water biota (mainly fauna) in the present paper and will emphasize the problem of how to recognize the cold water biota.

T-D SPACE CONFIGURATION FOR LOWER PERMIAN(SAKHARIAN) AMMONOID FAUNAL PROVINCIALITY(GENUS LEVEL)

STRESS = 0.1246

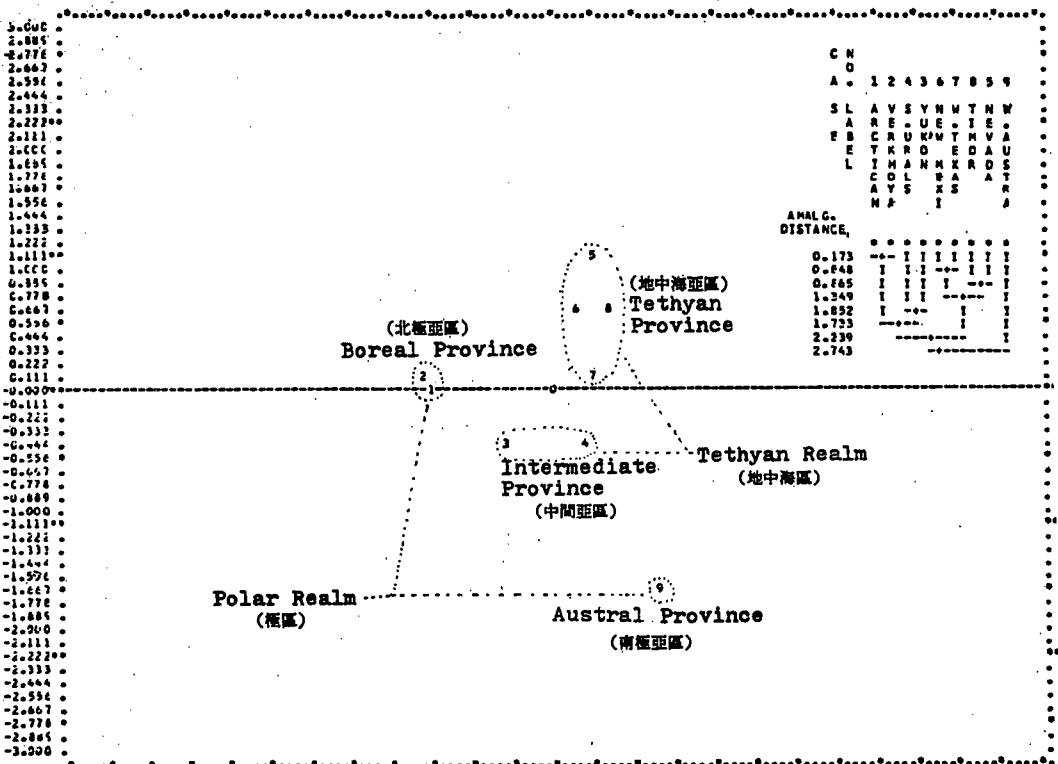


Fig. 1 Recognized polar realm in an analysis of Lower Permian ammonoid fauna provinciality (Lee, 1981).

Causality can not be deduced with certainty from correlation alone, unless other related factors are held constant or controlled in some fashion. For the present, I largely confine my discussion to temperature and take it as the primary limiting factor controlling cold water biota with little or no influence by extraneous factors, therefore we should keep in mind that some important factors other than temperature are definitely not to be overlooked.

DEFINITION OF COLD WATER AND COLD WATER BIOTA

Though water has a very high specific heat than any other substance without raising its temperature very far and likewise can give off heat in larger amounts without reducing its temperature much, there are two regions, one is in polar oceans and another is in deep seas where remain near freezing. Therefore a nearly 0°C can be served as a good definition for the cold sea water. Biota living in cold water will be defined as cold water biota. Inevitably they will fall into two categories : deep sea cold water biota and polar cold water biota. An universally accepted definition of below which depth is the territory of deep sea remains to be developed. But if temperature near 0°C (ranging up 4°C) is taken as cold and warm water boundary, it corresponds to about 2000 m. in depth from the current temperature profile in either the Pacific or the Atlantic Ocean (Valentine, 1973).

Deep Sea Cold Water Biota

Some relevant data in regarding to deep sea cold water biota follows:

1. Bruun (1965) applied the term Psychral to the fauna living in the sea at temperature below 10°C.

Menzies (1963) has proposed the term Hypopsyschral for the fauna inhabiting water of temperature less than 0°C. The temperature of sea water below 2000 m. in the Mediterranean sea is 14°C, in the Antarctic and Arctic it is -1.2°C and in the Caribbean sea is 6°C, but in the rest of the world's oceans, it ranges mostly between 1°C and 3°C.

2. Zonation of benthonic foraminiferal faunas are recognized (Phleger, 1960). One of them do occur at approximately 2000 meters in depth.

3. Hulsemann (1963) finds radiolaria in the deeper parts of the Arctic which secrete opaline silica tests and contribute to the deep sea sediment.

4. Menzies and Imbrie (1958) noted that siliceous sponges in the modern deep sea (abyssal realm).

5. Deep water genera of bryozoans are identical to shallower shelf forms but the species are different. Menzies and Imbrie (1958) reported that only geologically younger forms (cheilostomes) of bryozoans (Tertiary-Recent) are found in the abyssal depths.

6. Abyssal species of brachiopoda that are permanent inhabitants at such depths include Pelagodiscus atlanticus to 5000 meters and Abyssothyris wyvillei to 5500 meters (Menzies and Imbrie, 1958).

7. Living halothuroids are distributed at all depths and occur in all latitudes. Nevertheless, it is in the deep water of ocean trenches from 4000 to 8500 meters that they constitute 50% to 90% of the total mass (Bruun, 1956).

8. Most living crinoids prefer shallow water. Of less than 3000 meter depth where 19 crinoid species are found, then the number of species decrease thereafter to depths of 9000 meters (Zenkevitch, 1959).

9. Arkell et al. (1957) thought that generally complex suture of ammonoids probably reflected deep sea forms while simplified suture denoted a shallower

habit or sluggish benthonic existence. However the complexity of the suture is more related to pressure than temperature.

A modern distribution of major fossilizable nonvertebrate groups relative to water depth was assembled in Fig. 2.

Polar Cold Water Biota

The biota of the polar regions are known in sufficient detail that their composition can be approximated. Antarctic planktonic organism generally are dominated by diatoms, dinoflagellates and some kinds of crustaceans but the benthonic organisms consist mainly sponges and echinoderms.

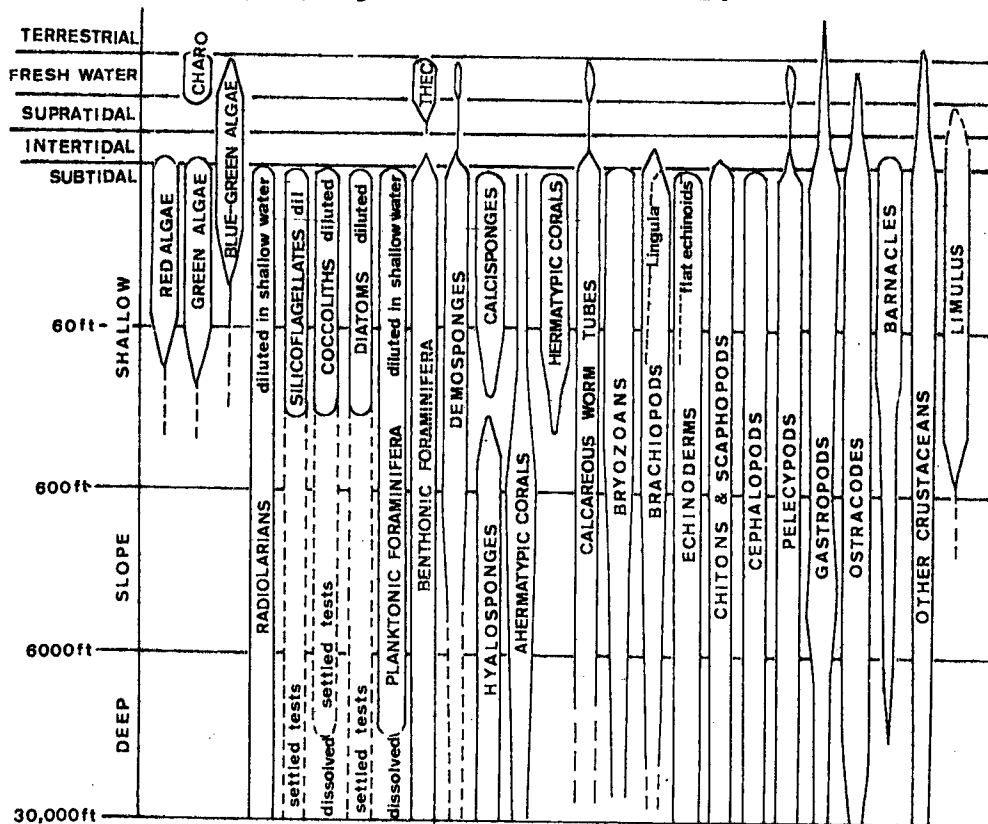


Fig. 2 Modern distribution of major fossilizable nonvertebrate groups relative to water depth (Heckel, 1972).

Some relevant data for polar cold water fauna are listed below:

1. Diatoms are found in abundance in the deposits of high latitudes in both hemispheres (Riedel, 1971). They live in the upper 200 meters of ocean water and are particularly abundant in cold water where a large upwelling belt is situated.

2. Many cold water species of living planktonic foraminifers have a bipolar distribution inhabiting both the northern and southern cold water provinces. Their present disjunct distribution indicates a former continuous distribution. The recent isolation of bipolar species is caused by warming of the ocean water since the Wisconsin glacial epoch. This has consequently resulted in the reduction of their geographical range. Stenothermal cold water species, such as Eukrohnia hamata which achieves a continuous distribution by "submerging" below the tropical-subtropical waters are very rare. None of the planktonic foraminiferal species are known to exhibit deep tropical submergence. Even rarer are the eurythermal cosmopolitan species that have a worldwide distribution in all water types. Globigerina glutinata is a rare example in this category (Be and Tolderland, 1971).

3. Warm subtropical crinoids generally have many arms but Antarctic crinoids generally have few arms (Fell, 1966).

HOW TO RECOGNIZE THE COLD WATER BIOTA

Uniformitarian Approach

Comparison of fossil assemblages with living assemblages is mainly a "present is the key to the past" approach. However, we should apply

uniforitarianism carefully as Menzies and Imbrie (1958) noted that the siliceous sponges apparently migrated to inhabit to greater depths probably no earlier than Tertiary time. As certain aspects of ecological tolerance have changed through geological time, the farther back in age, the more careful we must be. The same geological reasoning can be used for polar cold water biota. Past positions of marine winter isotherms along the Pacific Coast, estimated from fossil occurrences of molluscs and reef corals may be different from those of today.

Paleobiogeography Approach

Because paleoclimate trends are large scale as opposed to salinity trends, etc., the reconstruction of paleobiogeography will permit inference of the possible distribution of paleoclimate trends. Additionally, the paleobiogeographic study will help us to locate two paleopoles as well as paleoequators. If the polar cold water biota was restricted to polar areas where were as well differentiated dramatically as they are today through all geological time, the recognition of paleopoles by other methods such as paleomagnetism will help us to recognize polar cold water biota.

The reconstruction of paleobiogeography is generally based on following methods: (1) Large scale morphological gradients, (2) Large scale diversity gradients, (3) Large scale geochemical gradients and (4) Biotic similarity. The gradient is defined as rate of variation which generally increases or decreases in a given direction.

1. Large scale morphological gradients. Although many rules such as Allen's, Bergmann's etc., state the relationship between morphology and temperature within the species range, the application of such rules to fossils are rather limited by the great biases of preservation.

The coiling direction of recent planktonic foraminifers has been proven to be largely controlled by the temperature of the water in which they live. Globigerina pachyderma and Globorotalia truncatulinoides have shown the predominance of left-coiling forms in cold water and of right-coiling forms in warm water (Bandy, 1960).

Other large scale morphological gradients are found in shelf gastropods. In tropical seas, about 85% of species have a pelagic larval stage, this generally drops to zero wherever approaching the Arctic or Antarctic seas. Because gastropod species bearing a planktonic pelagic larval stage have a large apex and such morphological features are preservable in the fossil record, they are quite useful to determine which is cold water fauna as assemblage of snails all with large apex means living in cold water (Thorson, 1952).

Unfortunately it is not known why coiling direction of foraminifers changes (Bandy, 1960) and why bearing a pelagic larval stage in snails relates to the temperature.

The common warm water biota can be used to locate the possible paleotropical belts. A series study of growth rates of corals was done by Ma (1954) who found that coral with regularly arranged dissepiments not grouped in rings are likely to have lived near the equator since season growth is only away from tropics. From large number of observations, Ma (1954) deduced a supposed equator for most of the geological systems. Thereafter two corresponding paleopoles will be located afterwards and consequently the biota restricted to polar area can be inferred to be polar cold water biota.

2. Large scale diversity gradients. Biotic diversity is defined as the absolute number of taxa represented in a given sample (Hessler and Sanders, 1971). The larger the scale, the closer relationship

between diversity and temperature. Along the east coast of North America, diversity of shallow water gastropods species decreases northwards (Fisher, 1960). In general, diversity gradients show the maximum diversity at or near the equator, dropping off gradually toward the poles. This generality can be applied as well as for all Recent benthonic marine invertebrates (Fig. 3).

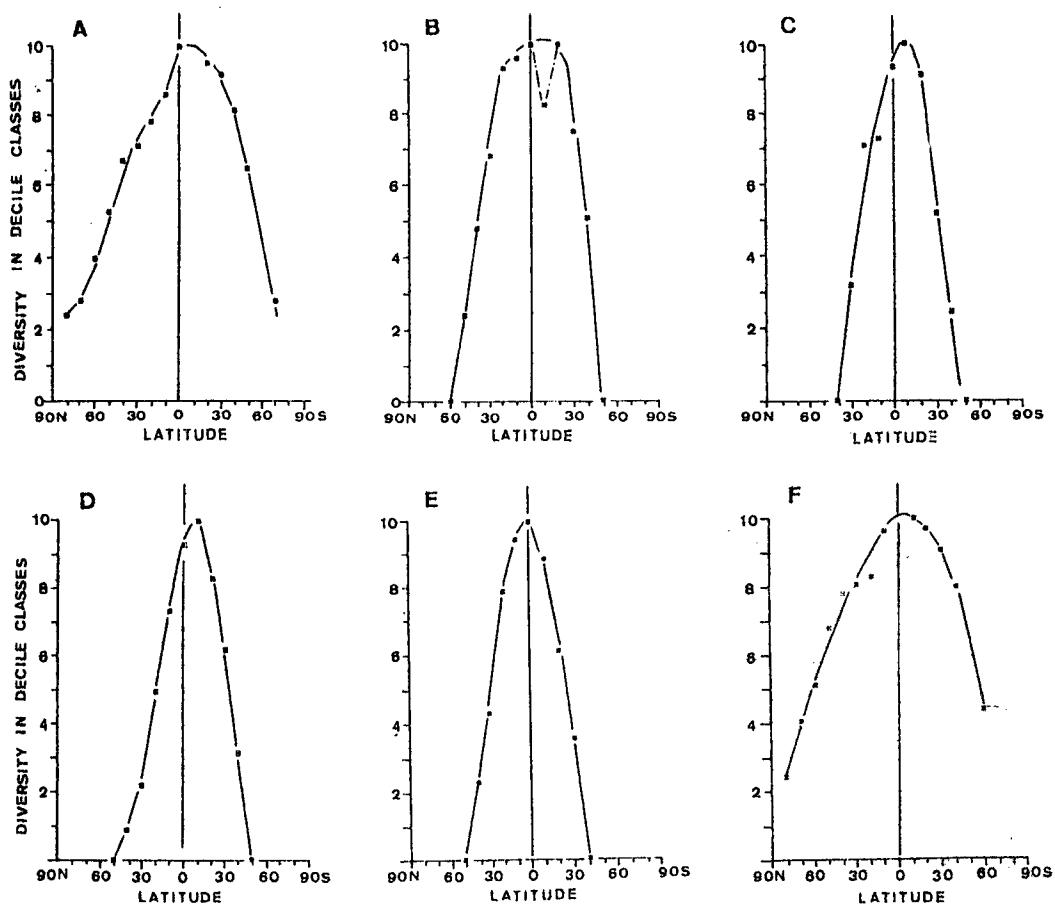


Fig. 3 Diversity gradients of Recent benthonic marine invertebrates plotted on present-day latitudes. The data shown refers to the following groups of organisms: A. genera of pelecypods; B. species of cypraeid gastropods; C. Species of Strombus (gastropods); D. species of the family pinnidae (pelecypods); E. families of pelecypod; F. genera of hermatypic corals (Stehli, 1968).

The intensive application of biotic diversity gradients to the geological record was carried out by Stehli (1968). He plotted the diversity gradients of Permian brachiopods including families Terebratulidae and Orthotetacidae, respectively and estimated positions of the Permian north poles. Although the poles positions suggested by brachiopod groupings are nearly identical, the coincidence with the present pole position is not compatible with one based on paleomagnetic data of Permian. However serious challenge is to against the use of diversity gradients as support for the case of the statistical techniques have concluded the North pole was located differently during the Permian than it is today.

Several serious limitation need to be considered when applying this diversity gradients method. In general, the epifaunal elements and groups with cosmopolitan distribution are preferable because the temperature exerts a strong control whereas diversity change is less marked with infauna.

3. Large scale geochemical gradients. Chave (1954) demonstrates that warm water members of a group of organisms have a relative higher percentages of magnesium in the skeleton. This is true for aragonitic corals as well as calcitic echinoderms.

The oscillation of aragonite/calcite ratio with consecutive growth increments in living polychaete worm Eupomatus gracilis suggests seasonal temperature control of this ratio (Lowenstam, 1954). Since aragonite and high-magnesium calcite are not stable and revert to low-magnesium calcite with time. Thus meaningful paleotemperature will be impossible to determine from such ratios. Generally oxygen isotope ratios now appear to be better suited for paleotemperature determination than do mineral composition (Weber, 1973). Three oxygen

isotope O^{16} , O^{17} , O^{18} , occur naturally in an abundance ratio of 99.76%, 0.04%, and 0.20% respectively. However the ratio of O^{18} to O^{16} increases as water temperature drops. It is maintained that the oxygen isotope ratio of the sea water is incorporated into the calcium carbonate of the marine organism skeletons. Urey et al. (1951) began to apply this principle to the fossil record. Bowen (1961) studied the oxygen isotope of Cretaceous belemnite rostra and inferred paleotemperatures. Later research revealed that salinity is another important factor in controlling O^{18} / O^{16} ratio. This reduced the strength of possible inferences for paleotemperatures.

4. Biotic similarity. Biotic similarity calculates the degree of resemblance of biotic content according to the presence and absence of taxa.

The commonly used coefficients for such similarity measurements are the provincity index of Johnson ($=c/2E$) (Johnson, 1971), Jaccard's coefficient ($=C/N_1+N_2-C$) and Simpson's coefficient ($=C/N_1$), in which C, E, N_1, N_2 represent common taxa, smaller total taxa and larger total taxa respectively. All coefficient except Johnson's are reviewed by Cheetham and Hazel (1969)

Through clustering analysis which is based on different similarity coefficient, it is possible to delineate all possible faunal provinces. The faunal provinces which are located near or at paleopolar area will contain potentially a cold water biota.

The above method has been applied extensively in recent investigation of paleobiogeographic reconstruction since the highly developed computer program will render the difficult of the clustering techniques and other calculation problems. For instance, Table 1 is the similarity matrix for the Artinskian ammonoid of Lower Permian at generic level and Table 2 is the minimum stress for the similar

subject at family level. Through clustering technique, Arctic Canada clusters Verkhoyan is assigned as "Boreal province" and western Australia is assigned as "Australian province". Both provinces is termed as polar realm. The most excellent endemic genera are Neouddenites and Sverdrupites for the Boreal province and Queenslandoceras for the Austral province (Lee, 1975).

Tale. 1 Similarity matrix for Artinskian (genus level)

SIMILARITY MATRIX FOR ARTINSKIAN (GENUS LEVEL)

1. ARCTICAN											
2. VERKHOYA	0.400										
3. URALS	0.136	0.045									
4. PAMIRS	0.111	0.000	0.550								
5. TRANSALA	0.067	0.000	0.389	0.354							
6. NEVADA	0.120	0.083	0.321	0.400	0.273						
7. NC. TEXAS	0.250	0.059	0.318	0.417	0.333	0.391					
8. W. TEXAS	0.148	0.036	0.379	0.500	0.240	0.303	0.346				
9. S. CHINA	0.000	0.000	0.150	0.120	0.167	0.083	0.125	0.115			
10. TIMOR	0.088	0.000	0.353	0.500	0.233	0.289	0.367	0.368	0.094		
11. W. AUSTRALIA	0.000	0.000	0.111	0.087	0.222	0.095	0.154	0.083	0.125	0.103	
	1. ARCTICAN	2. VERKHOYA	3. URALS	4. PAMIRS	5. TRANSALA	6. NEVADA	7. NC. TEXAS	8. W. TEXAS	9. S. CHINA	10. TIMOR	11. W. AUSTRALIA

Table.2 Minimum stress for the Artinskian (Lower Permian ammonoid (familial level, one dimension)

1. Arctic Canada	-1.691
2. Verkhoyan	-1.735
3. Urals	0.152
4. Pamirs	0.172
5. Transalai Range	0.215
6. Nevada	0.183
7. NC. Texas	0.188
8. West Texas	0.171
9. South China	0.213
10. Timor	0.168
11. W. Australia	1.965

CONCLUSIONS

1. Though water has very high specific heat of around 1.0 to regulate heat easily without raising or reducing its temperature much, there are two regions in the world oceans where water remains nearly freezing: one is in polar oceans and another is in deep seas. If water remains near freezing is termed as cold water biota. Inevitably, there are differentiated into polar cold water biota and deep sea cold water biota. In the geological record, owing to its remarkable latitudinal dependence, the polar cold water biota are generally more easily recognized than the deep sea cold water biota.

2. Based on uniformitarian approach of pleobiogeographic reconstruction through the analysis data of large scale morphological, diversity, geochemical gradients and biotic similarity, the cold water biota can be recognized. Among those methods, the large scale diversity and biotic similarity are better methods since they are counting the presence and absence of taxa from a handy faunal list. This is more convenient than counting the morphological and geological gradients which are usually not given from the same faunal list.

3. Perhaps the temperature of nearly 0°C is not a good definition of cold water. The recognition of cold water biota through above methods in this paper indicates a relatively low temperature or temperature trend rather than an absolute temperature.

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冷水生物群

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節要

居住在年平均溫度通常接近 0°C 的冷水體的一群生物，稱為冷水生物群。通常這樣的冷水體存在於極區的海洋及任何海洋之深處(約超過2000公尺)。所以冷水生物群又可再細分為極區冷水生物群及深海冷水生物群二類。二者均具有指示低溫之意義存在。在地質記錄中，極區一定靠近高緯度，所以極區冷水生物群比深海冷水生物群，易於辨認。

在地質記錄中之深海冷水生物群依「均變說」之原理，可嘗試利用其現生代表種之有關知識，逆推出化石種之生活習性及環境而加以確認。但是極區冷水生物群除了藉助於「均變說」外，亦可利用重建古生物地理之方法來確認。一般古生物地理之重建則基於(1)大規模之形態變化梯度，像有孔蟲之左、右旋之比例，腹足類之殼頂的特徵及珊瑚之生長速率。(2)大規模之多樣變化梯度，此取決於一個樣本中有多少相異種類(3)大規模之地化變化梯度，像同位素之比及礦物成分變異等，及(4)生物之相似性，此取決於生物成員之出現或不出現，以便計算出相似程度之高低。