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The biogeographic zonation of the South American Shelf
based on a classification of the ranges
of bottom-dwelling invertebrate species

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The Biogeographic Zonation of the South American
Shelf Based on a Classification of the Ranges of
Bottom-Dwelling Invertebrate Species

(Translated from Russian)

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The Biogeographic Zonation of the South American Shelf Based on a Classification of the Ranges of Bottom-Dwelling Invertebrate Species**

V.N. Semenov

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The zoogeography of the South American Shelf has been the subject of numerous studies, both special, with respect to taxonomic groups and comparatively small regions [Madsen, 1956; Menzies, 1962; Boschi, 1964; Lopez, 1964; Stuardo, 1964; Vannucci, 1964; Kusakin, 1967; Zarenkov, 1968; Zezina, 1973] and general, with respect to the region as a whole and manifold groups of the bottom-dwelling population [Ekman, 1935,1953; Balech, 1954, 1964; Pérèž, 1961; Gur'yanova, 1964, 1974; Zenkevich, 1968; Briggs, 1974]. Of the latter, many are generalisations of individual schemes. The discrepancies which were manifested there (figs. 1-6)

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* The figures in the right-hand margin are page numbers of the original (Tr.).

** This study is an adapted and heavily augmented portion of a thesis for the degree of Candidate of Biological Sciences [Semenov, 1979]. The Introduction, Sections 7, 9 and 10 and the Conclusion have been re-written. Important achievements by Soviet far eastern mathematicians in the theory of measures of similarity are taken into consideration.

demonstrated that by using only definitive results obtained by different investigators it is impossible to construct a common biogeographic scheme that is reliable from the standpoint of detail. The reasons for this are, firstly, because the various authors used dissimilar approaches and principles of zonation, and, secondly, because schemes constructed with respect to individual taxonomic groups characterise first and foremost the taxonomic group in question, and not the living cover in its entirety.

We selected another method of generalising. From the studies of our predecessors, chiefly from special taxonomic studies (totalling more than 200 sources [see Semenov, 1979]), it is not the definitive results (schemes) that are used, but only the source data on the distribution of species. With the addition of our own data, collected during the first and third voyages of the Scientific Patrol Vessel "Akademik Knipovich" in the Antarctic and on the Patagonian-Uruguayan

** (Cont'd) Certain biogeographic concepts are defined: the co-range, the syntopic element, the type of range, the region, the α -region, the minimal region, the boundary pressure, etc. More attention has been devoted to explaining the boundary effect, the symmetry of biological structure and some other questions.

I am deeply grateful to all of the colleagues who supported and assisted me so generously: to A.A. Neiman and A.P. Andriyashev for their constant attention and advice tendered, to K.N. Nesis, who undertook the difficult task of editing the manuscript, and to K.V. Beklemishev, O.N. Zezina, I.A. Vanchurov, D.E. Gershanovich, A.I. Kafanov, V.V. Krylov, O.G. Kusakin, V.V. Murina, B.I. Semkin, O.A. Skarlato, Ya.I. Starobogatov and Z.A. Filatova for their valuable comments and opinions when discussing the questions touched upon in the study. I express my heartfelt gratitude to V.G. Averintsev, N.A. Zarenkov, B.G. Ivanov, R.Ya. Levenshtein, R.R. Makarov, L.I. Moskalev, A.F. Pushkin, I.S. Smirnov and E.P. Turpaeva for their invaluable help as specialist taxonomists in the course of determining the collections of the Scientific Patrol Vessel "Akademik Knipovich" and selecting the source data.

Shelf, in our sampling there are 1,545 species, assigned to the following higher taxa: the Polychaeta Errantia, 333 species; the Bivalvia Taxodonta and the Dysodonta, 119; the Gastropoda Fissurellidae, 42; the Crustacea: Isopoda, 133, Decapoda, 619 and Stomatopoda, 42; the Pantopoda, 54; the Brachiopoda, 14; the Asteroidea, 83; the Echinoidea, 38 and some others. Included in the sampling are species inhabiting what in the broad sense are referred to as the temperate waters of South America [Briggs, 1974] and also inhabitants of warm waters, which occur as far south as the Equator in the Pacific and reach latitude 18-20° South in the Atlantic. Warm water species which do not range as far as these boundaries are not taken into account. All of the species found on the Shelf and at depths of less than 300m are treated, although manifestly bathyal species are excluded.

In the vast majority of cases, no complete separation of ranges along the vertical is observed in the Shelf zone. The ranges of the species making up the various vertical groupings of benthos living on the Shelf partly or fully overlap. This is the premise for constructing a unified scheme of zonation for the entire Shelf zone, rather than singling out the littoral as a separate scheme. The majority of the species occurring on the littoral are also distributed in the upper sub-littoral and at greater depths.

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A zonation is begun by elucidating the natural chorological structure of the benthos. This is done by distinguishing similar types of distribution and through a classification of ranges. The principal

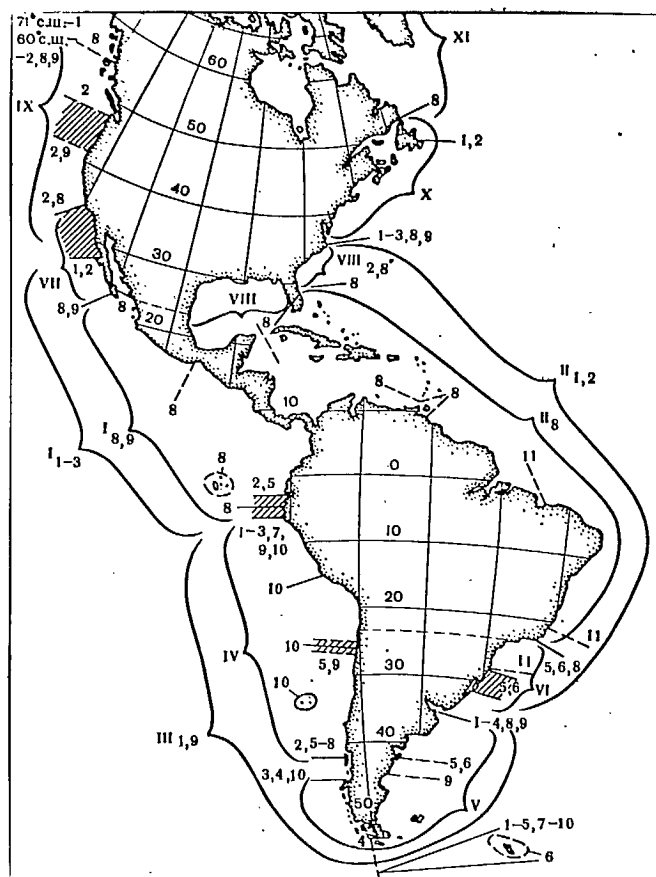


Fig. 1. Schemes of zoogeographic zonation of the western hemisphere constructed by Ortmann [1896] and Ekman [1935, 1953] and their subsequent development.

I, II - regions of warm waters (tropical regions) distinguished by Ortmann, Ekman and Briggs [1974], and Gur'yanova's region [1964]; III - the South American (Notalian) region of temperate waters distinguished by Ortmann, Zenkevich and Gur'yanova [1974]; IV - Ekman's region of warm-temperate waters, Brigg's and Gur'yanova's [1964] region, Zarenkov's Peruvian-Chilean subregion (?) [1968]; V - Ekman's region of "Antiboreal South America"; Gur'yanova's [1964], Balech's [1964] and Bernasconi's [1966] region, Zarenkov's subregion [1968], Brigg's Magellan province; VI - the subtropical (Bernasconi) and "warm-temperate" (Briggs) regions, Balech's [1954] and Coelho's and Ramos's [1972] provinces; VII-XI - the "regions", regions and subregions* of the northern hemisphere distinguished by Ortmann, Ekman,

*Translator's note. More detailed information on the meanings of these terms is given in footnote No. 3 (p.17) and the translator's note which follows it.

Gur'yanova and Briggs. Boundaries between the units according to 1 - Ortmann [1896], Zenkevich [1946]; 2 - Ekman [1935, 1953]; 3 and 9 - Gur'yanova [1964, 1974]; 4 - Zarenkov [1968]; 5 - Balech [1964]; 6 - Bernasconi [1964]; 7 - Garth [1957], Soot-Ruen [1959] and Dahl [1954]; 8 - Briggs [1974]; 10 - Menzies [1962]; 11 - Coelho and Ramos [1972]. The solid lines are the boundaries between the "regions", regions and subregions; the broken lines - the boundaries between the provinces. In figs. 2-6, identical symbols are used to denote the boundaries.

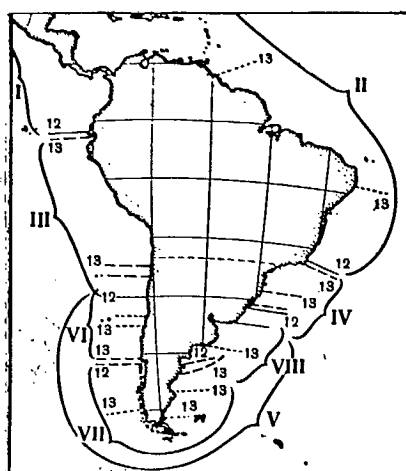


Fig. 2

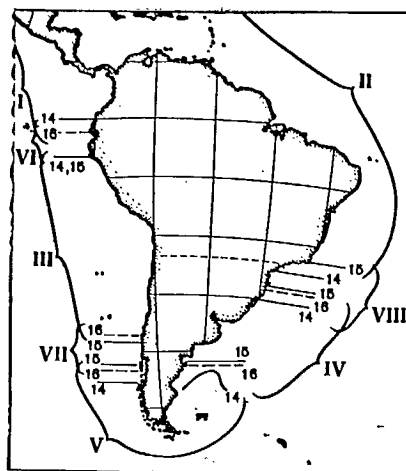


Fig. 3

Fig. 2. Schemes of zoogeographic zonation of the coastal waters of South America constructed by Knox [1960] and Balech [1954].

I - Balech's Panamanian province (extending to the Californian Peninsula in the north); II - Balech's Antilles province with the Caribbean, Guianian and Bahian districts; III - Balech's Peruvian province and Knox's "warm-temperate" region, including a single province; IV - Balech's Southern Brazilian province and Knox's "warm-temperate" region; V - Knox's "cold-temperate" region, including the Central Chilean (VI), Magellan (VII) and Argentinian (VIII) provinces; 12 - Knox's boundaries, 13 - Balech's boundaries. The boundaries between the districts are denoted by a broken line.

Fig. 3. The zoogeographic zonation of the South American coastal waters according to Pérès [1961], the malacologists Carcelles and Williamson [1951] and Stuardo [1964].

I, II - Pérès's zone of the "tropical community" and the malacologists' (Panamanian and Antillean) warm water provinces; III, IV - Pérès's "warm-temperate" regions and the malacologists' Peruvian and Argentinian provinces, amalgamated [Stuardo, 1964] in accordance with the latitudinal-

zonal principle into a single region. V - Pérès's zone of the "antiboreal community" and the malacological Magellan province, included [Stuardo, 1964] in a "cold-temperate" region; VI-VIII - transitional zones (VIII is the subtropical transitional region distinguished by Vanucci in 1964). The boundaries of the regions and provinces according to: 14 - Pérès [1961], 15 - Stuardo [1964], 16 - Carcelles and Williamson [1951].

unit of classification is the co-range, or the group of coincident ranges of those species which constitute the syntopic element of the fauna. V.V. Alekhin's [1944] geographic elements (flora) are differentiated from the syntopic by the fact that, in the course of distinguishing them, there is no mention of a matching vertical distribution of species (in a marine environment - affiliation with a single bathymetric zone) or degree of coincidence of the ranges. In distinguishing the syntopic elements, use is made of the concept of a distinctive (or differentiative) level of classification - based on the criterion of estimating the probability of a cartographic coincidence of ranges with respect to the overall length (n) of the Shelf of North America and South America [Krylov and Semenov, 1977]. The type of probability formula is identical to the subradical expression in formula (3a) in fig. 13 (see below), if instead of the number of species we substitute the areas of the ranges of the two species and the degree (C) of their coincidence. The threshold value of this criterion is taken to be 0.02 (2%). The criterion of the differentiative level is the complementing to unity of the probability value. The formula is analogous to a simple paired coefficient (see 3b in fig. 13). The threshold value of the latter is accordingly 0.98 (98%).

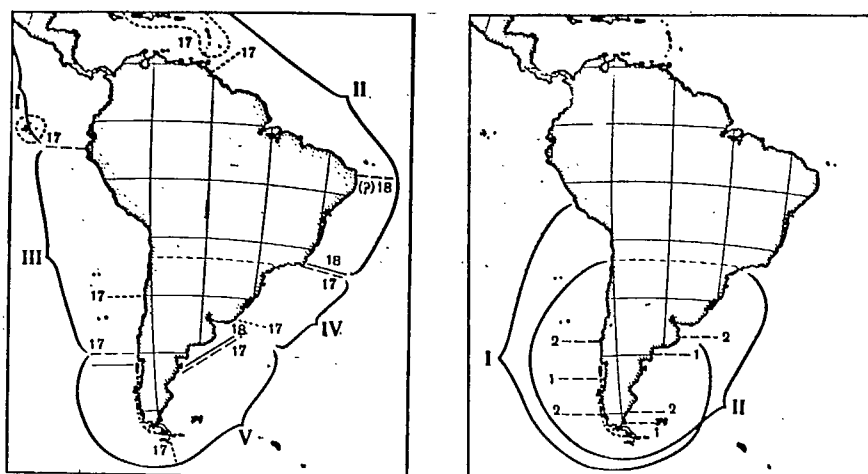


Fig. 4. The zoogeographic zonation according to Lopez [1964], Boschi [1964, 1966] and Scelzo and Boschi [1973].

I - Lopez's Panamanian province with the Lower Californian, Panamanian and Galapagos districts; II - Lopez's West Indian province with the Mexican-Caribbean, Antillean and Brazilian districts; III - Lopez's Peruvian-Chilean province with the Peruvian and Central Chilean districts; IV - Lopez's Argentinian province with the Southern Brazilian and Buenos Aires districts and Boschi's and Scelzo's "cold-temperate (Notalian)" region. The boundaries of the "regions", provinces and districts according to : 17 - Lopez [1964], 18 - Boschi [1964, 1966] and Scelzo and Boschi [1973].

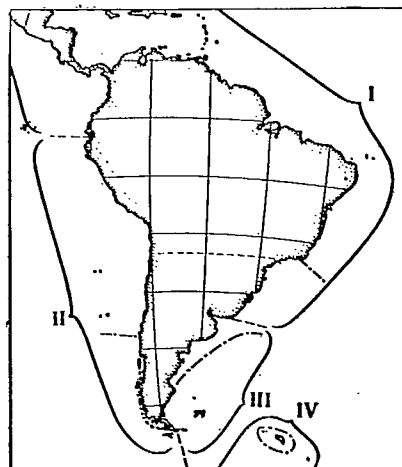
Fig. 5. T.F. Shchapova's South American Austral region [cit. after Zenkevich, 1951] (I,1) and Kusakina's Magellan (Patagonian) region [1967] (II,2).

The boundaries between the provinces are denoted by a broken line.

Fig. 6. S.D. Boltovskoi's [1964] zonation of the South American coastal waters, based on the Foraminifera.

I - The West Indian province, including the Pacific Panamanian district; II - The South American Pacific province with the Southern Brazilian and Patagonian subprovinces; IV - The Antarctic province.*

* The explanation for III on the chart is missing from the caption (Tr.).



On the chart, the range of the syntopic element (the co-range), is represented by the type of range¹. As a rule, the limits of distribution of dissimilar groups of species - the syntopic elements, coincide with the extreme summer and winter boundaries between the water masses, the same hydrological boundaries determining the limits of distribution of many syntopic elements. Some groups of species (about one-fifth of all the species on the Shelf) live only in the border zones between water masses. The presence of these species gives rise to certain difficulties in zonation. In this event, a juxtapositioning of the actual and potential ranges [Kryzhanovskii and Starobogatov, 1974] can hardly be furnished, since some (if not many) of the bordering, endemic species are in all probability relict forms. Hereafter, in a faunistic zonation, we shall adhere strictly to the principle of distinguishing biogeographic units on the basis of empirically determined contemporary types of distribution of groups of species, irrespective of the causes that led to this distribution and regardless of what it might have been, in the event of these causes being removed.

¹Previously, instead of the term "type of range" I used the term "range-type" [Semenov, 1978], since various range configurations (ribbon-shaped, disconnected, etc) are referred to as types of ranges in the literature. This innovation has brought forth many critical remarks.

The necessity for strictly differentiating between a faunistic
zonation and a latitudinal-zonal division

Two systems of zonation are used in contemporary biogeography: a faunistic and a latitudinal-zonal. The two systems have often been confused with each other. Even L.S. Berg indicated this in the course of a dispute with P.Yu. Shmidt [see: Andriyashev, 1955]. Regrettably, they are insufficiently differentiated in many modern studies also. The point at issue is not merely that diverse zoogeographic regions with a dissimilar faunistic composition are merged into large latitudinal zones. Much worse is the fact that latitudinal-zonal characteristics of species are frequently put forward as a decisive argument when drawing boundaries between faunistic regions to which a definite rank (region, subregion, etc.) and a proper name have been assigned. 191

With such a confusion, two errors are possible: either the implicit use of physico-geographic (climatic) criteria, which may be introduced through a scheme of latitudinal zonation when distinguishing faunistic units, or a vicious circle in the course of determining the main zoogeographic boundaries. The error of the vicious circle consists in the fact that faunistic subdivisions (territories = water areas) are distinguished, ab initio, often intuitively, "by rule of thumb", following which, on the basis of affiliation with the territory in question, latitudinal-zonal characteristics are ascribed to the species or genera, whereupon, by correlating taxa with particular characteristics, the boundaries between large regions are "more precisely defined".

Table 1. Distribution of species with dissimilar zoogeographic (latitudinal-zonal) characteristics in a zonation according to the principle of hierarchic closure of the South American temperal region.

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1 Группа видов	2 Всего видов	3 Северотропический, 2°-5°-12°-14° ю. ш.	4 Южнобразильско-уругвайский, 23°-24°-35°-38° ю. ш.	5 Южноперуанский, 12°-14°-18°-30°-20° ю. ш.	6 Северочилийский, 18°-30°-26°-33° ю. ш.	7 Центральночилийский, 33°-41°-26°-43° ю. ш.	8 Севераргентинский, 35°-38°-42°-43° ю. ш.	9 Южночилийско-Южноаргентинский район к югу от 42°-43° ю. ш.	
								10 весь район	11 Огненная Земля и Фолклендские (Мальвинские) острова
12 Тепловодные	316	146	170						
13 Тропические	221	56%	71%						
14 Битропические	95	65*+48	39*+69						
15 Теплых и умеренных вод	192	31*+2	27*+35	101	95	62	38	47	34
		44%	28%	67%	40%	25%	23%	9%	8%
16 Темперо-тропические ** (тропического происхождения)	38	25	16	19	13	8	4	4	3
17 Битропическо-темперальные (вероятно, тропического происхождения)	55	2*+26	4*+16	19	22	14	10	14	10
18 Нототропическо-темперальные распространены севернее 1-5° ю. ш. в Тихом океане и 23-24° ю. ш. в Атлантическом (тропического происхождения) не идут севернее указанных пограничных зон (вероятно, тропического происхождения, хотя их и нет в эвтропических подзонах)	99	62	31	63	60	40	24	29	21
	29	15	5	19	16	9	5	4	2
19 Умеренных вод	70	47	26	44	44	31	19	25	19
	494	—	—	47	126	158	88	320	246
				31%	52%	63%	54%	60%	56%
20 Нототемперальные	481	—	—	44	121	150	88	314	240
21 Битемперальные	13	—	—	3	5	8	—	6	6
22 Холодных и умеренных вод	180	—	3***	3	19	30	37	163	159
			1%	1%	8%	12%	23%	31%	36%
23 Южноамерикано-антарктические (нототемперо-полярные)	166	—	3	1	11	22	33	155	147
24 Битемперо-полярные	14	—	—	2	8	8	4	8	12
25 Всего видов	1182	261	240	151	240	250	163	530	439

* Circatropical species... living only in the boundary regions (1-5° S. lat. in the Pacific and 23-25° S. lat. in the Atlantic), and other species possessing micropopulations in these regions.

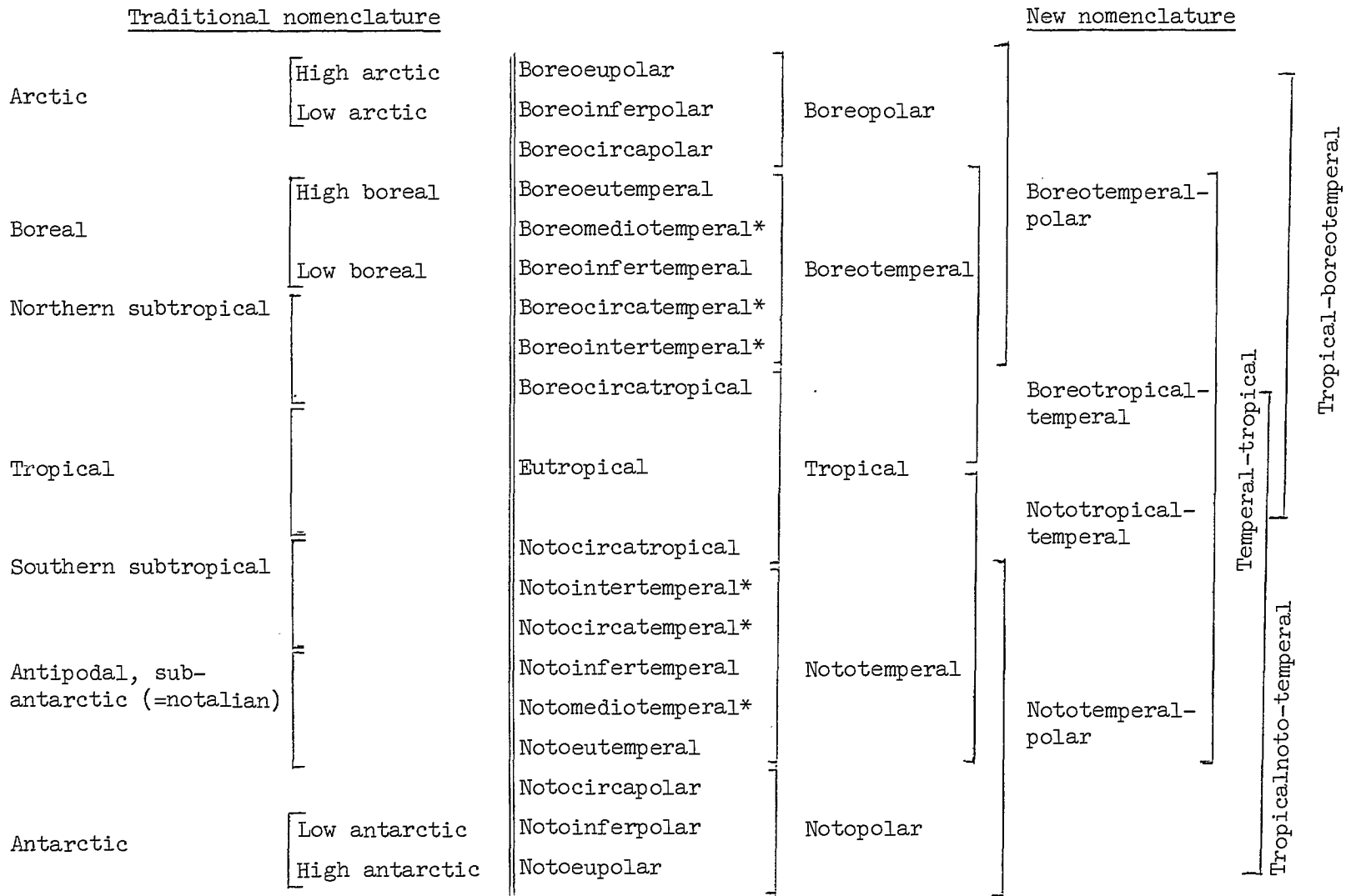
** Fourteen species have been excluded from this group: they occur only in the temperal zone and the circatropical subzone of the northern hemisphere; in the southern hemisphere they live only in the eutropical subzone.

*** Including three species living in the Atlantic circatropical subzone.

- Numbered key:
1. Group of species.
 2. Total number of species.
 3. Northern Peruvian, 2-5° - 12-14° S. lat.
 4. Southern Brazilian-Uruquayan, 23-24° - 35-38° S. lat.
 5. Southern Peruvian, 12-14° - 18°30' - 20° S. lat.
 6. Northern Chilean, 18°30' - 20° - 33° S. lat.
 7. Central Chilean, 33° - 41°26' - 43° S. lat.
 8. Northern Argentinian, 35-38° - 42-43° S. lat.
 9. Southern Chilean-Southern Argentinian region southwards of 42-43° S. lat.
 10. The whole region.
 11. Tierra del Fuego and the Falkland Islands (Malvinas).
 12. Warm water species.
 13. Tropical.
 14. Bitropical.
 15. Of warm and temperate waters.
 16. Temperal-tropical** (of tropical origin).
 17. Bitropical-temperal (probably of tropical origin).
 18. Nototropical-temperal species distributed northwards of 1-5° S. lat. in the Pacific and 23-24° S. lat. in the Atlantic (of tropical origin) do not occur to the north of these boundary zones (probably of tropical origin even though they are also absent in the eutropical subzones).
 19. Of temperate waters.
 20. Nototemperal.
 21. Bitemperal.
 22. Of cold and temperate waters.
 23. South American-Antarctic (nototemperal-polar).
 24. Bitemperal-polar.
 25. Total number of species.

In the zonation of the far eastern seas this error was discovered more than 10 years ago by B.G. Ivanov (personal communication), but he refrained from publishing comments. What has been stated here as regards the vicious circle in the definition of boundaries is, of course, yet another basis for introducing a new terminology which would be independent of the latitudinal-zonal system and free of such customary words as "arctic", "boreal", "notal" and the like, the use of which for naming units of a faunistic zonation has become a habit that is difficult to eradicate.

Fig. 7. Schematic representation of new latitudinal-zonal nomenclature and its conformity with the traditional terminology.



*Only off the west coasts of the continents. Off the coasts of South America a mediotemperal subzone is not distinguished.

Despite the need for strict differentiation, a definite relationship exists between latitudinal zonation and faunistic structure. A latitudinal-zonal scheme is, as a rule, constructed in conformity with a faunistic zonation, so that the boundaries between biological and latitudinal zones in a particular part of the World's ocean conform to the boundaries between faunistic regions situated in dissimilar climatic zones.

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In order to facilitate the systematisation of types of distribution in the early stages of the classification of ranges, a preliminary latitudinal-zonal scheme was adopted as a working hypothesis [Semenov, 1977a]. In this scheme, which is used here in the course of presenting data on the composition of the fauna (table 1), the boundaries between the latitudinal zones are given in conformity with the boundaries of zoogeographic regions distinguished on the basis of species-determinants (see fig. 9). Based on this latitudinal-zonal scheme the tropical zone off both the Pacific and the Atlantic coasts is subdivided into 3 subzones: a central (eutropical) and two peripheral (circatropical) - a northern and a southern. The temperal (temperate) zone off the Pacific coast of South America is subdivided into 4 subzones: a eutemperal, a medio-, an infer- and a circatemperal, and off the Atlantic coast - into two subzones: a eutemperal and an infertemperal. In the Atlantic this division remains unchanged. All the refinements pertain only to the Pacific portion of the South American Shelf situated northwards of the eutemperal subzone.

A definitive latitudinal-zonal scheme can be furnished only after matching it with results of a faunistic zonation that take into consideration the species similarities and differences between regions. A new scheme is presented at the conclusion of the article (see fig. 17).* The names of all the latitudinal zones and subzones are given in accordance with the new latitudinal-zonal nomenclature [Semenov, 1977a] - fig. 7. The types of amphiequatorial (bipolar in the traditional sense of the word) distributions not shown in fig. 7 are denoted by the addition of the prefix "bi". Five types of amphiequatorial distribution are distinguished: a bipolar (only in the cold waters of the Arctic and Antarctic; not a single bipolar species was found among the ~1,500 species in the sampling), a bitemperal-polar, a bitemperal, a bitemperal-tropical and a bitropical (a tropical distribution with an interruption of the range in the central tropical or equatorial zone).

Some chorological methods of zonation
which have not been used previously

Based on types of ranges, at least two methods of faunistic zonation² are possible. The first is the distinguishing of regions by the co-ranges of the species-determinants [Semenov, 1972]. The distinguishing of territories by this method is objective but difficult when there is a complex pattern of intersecting co-ranges.

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* Author error for fig. 18 (Tr.).

² Here and subsequently, zonation is discussed only at the species level.

Frequently, an unambiguous demarcation of them is impossible.

Similarly, a natural separation of regions based on the criterion of their hierarchic subordination is by no means always feasible, since in a number of cases a single small territory may be included in two neighbouring ones, distinguished by types of ranges partially superposed on one another. At the same time, when analysing the hierarchic subordination of territories, it is relatively easy to arrange them in order of the ascending (or descending) rank of the biogeographical subdivision (unit).

Another method of zonation, which is very tempting on account of its simplicity and is the most used of all in zoogeography (but is usually provisional, there being no precise count kept of the number of taxa) is the division of territories on the basis of the most significant biogeographic boundaries, that is, the matching boundaries of the ranges of the largest number of species and the co-ranges (the most significant boundaries coincide moreover with the principal temperature boundaries of the environment). An unambiguous division of territories by this method can be performed very easily, but there is always the possibility that territories with dissimilar faunistic elements may be amalgamated into a single large region. Here, also, a tacit preference for a zonation based on physico-geographic (climatic) data is possible, since the most sharply defined climatic boundaries usually limit the distribution of the greatest number of species.

And finally, there are mathematical methods, based on the paired comparison of lists of taxa of any two regions and estimating the faunistic similarity between regions. One such highly popular method in biogeography is the Preston method [Preston, 1962]. Like the first two methods, it can be used in a chorological analysis in order to compare regions distinguished by the types of ranges or the co-ranges. In this case, the method can furnish more natural results than are obtained when arbitrarily or intuitively comparing the selected regions with provisional boundaries.

While the second and third of the above-mentioned methods of zonation are frequently used and are quite well known, the first needs to be discussed in greater detail.. In order to make the transition from chorological units, viz. co-ranges and types of ranges, we will introduce and strictly define the concept of the aforementioned α -region and also the concept of the species-determinant.

A biogeographic unit (territory) of any rank, which is determined by the type of range, is called an α -region, i.e., corresponding to each particular α -region there must of necessity be its own type of range (or co-range), the boundaries of which completely coincide with this α -region. In a system of biogeographic subdivisions there may be other territories of indeterminate rank, for which the type of range cannot be established in a one-to-one correspondence. Such biogeographic units are known simply as regions, without the addition

of the index "alpha".³ The latter, in addition to being the method of distinguishing, simultaneously indicates affiliation with the species level of the faunistic (floristic) zonation. Each particular region and α -region has its proper name, which is written with the first letter capitalised.

Although the boundaries of the type of range and the similarly named α -region coincide graphically (on the chart), from the standpoint of meaning these concepts are different. For example, included with the species of a given type of range, let us say AB (fig. 8,a), are only those species that have comparatively closely coinciding ranges and are amalgamated into a single syntopic element, which is similarly represented by the type of range AB. It is also possible

³The term "region" (from the Latin regio meaning region or oblast') is consequently the most common designation of any for indicating the size of a biogeographic unit of indeterminate rank in a system of faunistic and/or floristic zonation. N.V. Parin [1968] was the first to introduce this term in Soviet literature in precisely this sense. In Ekman [1953], "region" is a freely used term for raion or oblast' and denotes a unit of biogeographic zonation without indicating the rank. In Ortmann [1896] "Littoralregion" and "Subregion" are closer in meaning to the categories "oblast'" and "podoblast'" in the hierarchic system of biogeographic units. In recent literature published in the English and Spanish the term "Region", with the first letter capitalised [Balech, 1964; Boschi, 1964; Briggs, 1974, et al.], or occasionally "Province" [Hedgpeth, 1969], most closely corresponds to the Russian term "oblast'".*

*Translator's note. Throughout this translation the Russian terms region and raion are rendered as 'region', the terms oblast' and podoblast' - as 'region' and 'subregion', okrug as 'district'; provintsiya as 'province', and zona and podzona as 'zone' and 'subzone'. Some difficulty was encountered in distinguishing between the terms oblast' and region (Cyrillic characters) as the author uses them interchangeably in an hierarchic sense. Statements appearing on pages 215 and 248 of the text indicate that the words are synonyms. It is shown clearly in fig. 19 (p.238) that region (Cyrillic) is a term denoting any and all of the various biogeographic units, including oblast'. The latter is therefore translated as 'region', except when it would result in difficulty in interpretation, in which case it is rendered as 'oblast''.

to include with the species of a given α -region (AB), besides the species of the type of range AB determining this α -region, the species of other syntopic elements, the co-ranges of which fully or partly overlap the type of range AB, or conversely, are themselves fully or partly overlapped by it, for example, AC and AD (fig. 8,a) or CB and CD (fig. 8,d). The species of the syntopic element (type of range, co-range) determining the given α -region are known as the species-determinants of this α -region. Thus, the species having the type of range AB (8,d) are the determinants of the α -region AB; the species of the group CB are (like the former), endemic forms but not the determinants of it, while the species comprising the syntopic element CD, simply inhabit the territory of the α -region AB, inasmuch as they occupy a part of its area, but are neither endemic forms nor determinants of the α -region in question.

Thus, it turns out that at least as many α -regions can be distinguished in a given region as there are continuous types of ranges. When there is a sufficiently distinctive level of classification, this number, as we have seen, can be very large and it would be exceptionally difficult to adjust the pattern without performing a computer-assisted statistical analysis. In the present context, a statistical analysis means a ranking of the α -regions, or a cluster analysis, based on the use of various criteria; such indices as the degree of endemism, the determinant of the α -region, etc.; can be used in this capacity. [Semenov, 1975, 1977a].

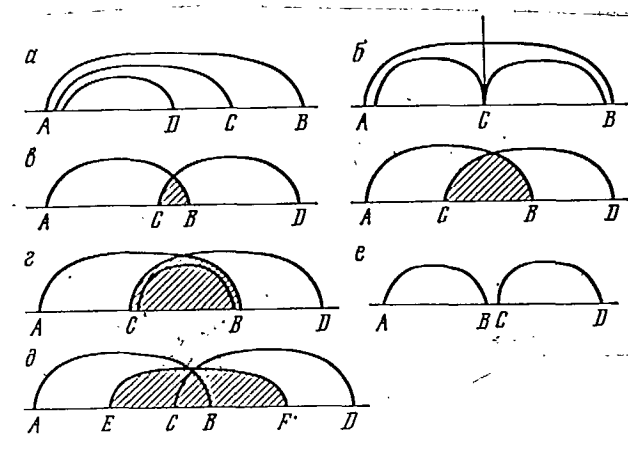


Fig. 8. Simple cases of the relative positions of α -regions.

Nevertheless, even in our case an attempt can be made to discriminate between large and small α -regions in the complex pattern of intersection, having in mind the discrete character of distribution of the groups of species and some simple cases of relative positions of α -regions, which can be encountered in nature in various complex combinations (see fig. 8).

In the first place, two different types of inclusion (subordination) of α -regions are distinguished.

1. A large α -region includes an α -region of smaller area and the latter, in turn, includes one of smaller area still, and so on (fig. 8,a). If this type of inclusion predominates, then the presence of a single faunistic centre or nucleus can apparently be inferred. In the present case, the fact that the subordination of the α -regions is of the hierarchic type affords a basis for speaking of their rank ascending with transition from a smaller to a larger region. In the process, the degree of endemism increases.

2. A large α -region AB includes two or more contiguous small α -regions AC and CB, the rank of which is one step lower than the rank of the α -region AB.

Secondly, dissimilar cases of intersection of the boundaries of α -regions are possible. Ordinarily, such an ideal coincidence of boundaries as is depicted in fig. 8,b for the α -regions AC and CB, does not exist or is seen very rarely. More often, dissimilar types of transitional zones occur.

3. A first-order transitional zone CB (fig. 8,c) forms as a result of the intersection of the boundaries of two neighbouring α -regions of approximately equal rank AB and CD. The size of the transitional zone can differ markedly in the various situations.

4. The transitional zone CB (fig. 8,d) has its own group of species-determinants and the appropriate type of range can be indicated for it. Such a territory, in contradistinction to ordinary first-order transitional zones, which do not have species-determinants, will be called a transitional α -region (first-order). Simultaneously, this is a further type of territorial subordination of α -regions: the transitional α -region CB (a zone in case 3) can be included with equal justification in either of the two higher ranking intersecting α -regions AB and CD. Sometimes, a first-order transitional zone (or α -region) is completely excluded from both neighbouring regions, which seems an excessively artificial step. It would appear completely acceptable to include it in either of the two regions, depending on which of the boundaries is considered to be the main one.

5. The small α -region EF (fig. 8,e) partly overlapping the two neighbouring large α -regions AB and CD, is also regarded as a transitional region. In this case, besides the first-order transitional zone CB, second-order transitional zones: EB and CF respectively, are distinguished on the territory of the α -regions AB and CD. In the event that it had been possible to indicate the species-determinants for these zones, as in case 4, they also would have had to have been considered α -regions.

6. Finally, two neighbouring α -regions of the same rank may be separated by a gap or by an insurmountable barrier: by ocean deeps or dry land (fig. 8,f).

The faunistic zonation of the South American Shelf according to species-determinants.

In discussing the bottom-dwelling population of the South American Shelf, the vast majority of zoogeographers distinguish off the coasts of South America three independent faunas which are more or less unified in terms of origin: two warm water faunas (a Pacific and an Atlantic) and one in temperate waters [Ekman, 1935, 1953; Pérès, 1961; Zenkevich, 1968; Gur'yanova, 1974; Briggs, 1974, et al.].

For a zonation to be natural and at the same time convenient for practical purposes, it is necessary first and foremost to distinguish precisely the α -regions (regiony^{*}) corresponding to these three faunas,

* Russian terms inserted by translator and underlined both here and subsequently as an aid to interpretation (Tr.).

which by tradition can be assigned the rank of region (oblast'). Here, the boundaries of these latter " α -regions" must not intersect. Besides the condition of total isolation (non-intersection of boundaries) of the α -regions, it is necessary to fulfill one further requirement which we shall designate as the principle of hierarchic closure of a large region (region). When performing a zonation based on species-determinants it is impossible to integrate several small α -regions into a large biogeographic unit if, for this large unit (oblast'), there are no species-determinants integrating all these small α -regions (regiony) and no corresponding type of range.

Given that all of these conditions exist off the coasts of South America, the easiest solution is to select the largest range by which an α -region (oblast') can be distinguished, initially in temperate waters, because there the choice is limited to several possibilities as compared with warm waters. In temperate waters the most extensive type of range (and the corresponding α -region) stretches southwards from 12-14° S. lat., in the Pacific and from 32-33° S. lat., in the Atlantic, 198 including the Falkland Islands region (the Malvinas) (fig.9). However, of the ~1500 species in our sampling, including 500 species living only in the temperate waters off the coasts of South America, there are no more than two species with such a range. They are Aulacomya ater (Molina, 1782) and the crab Eurypoidus latreillei Guérin, 1828. The thus defined boundary of the temperate α -region off the Atlantic coast of the South American continent more or less corresponds to generally accepted

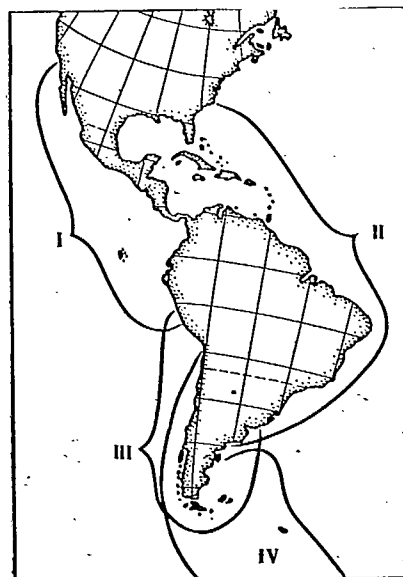
ideas. Off the Pacific coast, however, it lies much further to the south than is customarily believed (usually it is drawn in the region between 2 and 5° S. lat.). It has not proved possible to distinguish a suitable group of species-determinants from among the species comprising the fauna of the temperate waters which are distributed northwards to this latitude. There is only one Pacific-Atlantic species with a continuous range which is in any way suitable. This is the bivalve mollusc Brachidontes purpuratus Lamarck, 1819. Off the Atlantic coast, however, it does not occur northwards of latitude 42° S, and off the Pacific coast the most northerly occurrences of adult individuals of this species were at 8° 15' S. lat. Further north, off the coasts of Ecuador (3° S. lat.), only small, sexually immature individuals are found. The corresponding α -region (region), distinguished by this species alone, turns out to be smaller than the preceding one and exhibits a worse fit with the faunistic (and hydrological) data for the region considered as a whole (tables 1 and 2).

Northwards of the South American temperate α -region (oblast'), two tropical α -regions (regiony), a Pacific and an Atlantic, which perhaps also qualify for the rank of region (oblast'), are distinguished (fig. 9). The Western American (Eastern Pacific) tropical α -region extends northwards from 12-14° S. lat., as far north as 32-34° North lat. The nucleus of the Eastern Pacific tropical fauna lies within narrower limits: between 23-24° N. lat., and 2-5° S. lat., which

roughly corresponds to Ekman's [1935, 1953] and Briggs; [1974] tropical region (see fig. 1) and to our eutropical subzone. The Eastern American (Western Atlantic) tropical α -region is situated between 35° N. lat., and $35-38^{\circ}$ S. lat., and the nucleus of the Eastern American tropical fauna extends from $25-27^{\circ}$ N. lat., off the coasts of Florida and the Yucatan Peninsula to 23° S. lat. off southern Brazil [Briggs, 1974; our data].

Fig. 9. Zonation of the South American Shelf according to species-determinants (large α -regions).

I and II - Tropical α -regions;
 III - South American temperate α -region;
 IV - Austral super-region.



Clearly distinguished to the south of the South American temperate region (oblast') is the Antarctic (cold water) region (region) of the shelf fauna which inhabits the deep waters of Drake Passage and the Antarctic convergence zone.

The South American temperate region is (partly) integrated with the Antarctic region into a South American-Antarctic α -region (region)

with a higher rank, possibly that of super-region. Its Pacific boundary runs close to 20° S. lat. in the north, and the Atlantic boundary - close to $37-38^{\circ}$ S. lat. (along the outer part of the Shelf). Numbered among the species-determinants are the polychaetes Phyllodoce (Anaitides) patagonica (Kinberg, 1866), whose depths of habitation are 0-225 m off the coasts of South America and as great at 598-919 m (maximum 3,076 m) in Antarctica, and Typosyllis brachycola (Ehlers, 1897), living near the coasts of South America at depths of 0-250 (300) m and in Antarctica, as deep as 641 m. Off the coasts of Northern Argentina both these species are found at depths of 100-202 m. The α -region (region) determined by these species extends over a very large area, integrating the regions (oblasti) of the cold and temperate waters of the southern hemisphere. As we shall see later (see Table 6), the areas comprising Kergelen Island and southern New Zealand, together with the immediate offshore islands, can also be included in it.

The warm water American regions can also be integrated with part of the South American temperate region into larger α -regions (regiony), possibly ranking higher than region (oblast'). Thus, portions of the Western American tropical- and the South American temperate regions can be integrated into a Western American tropical-nototemeral α -region (region). It can be confidently stated that three species-determinants of this α -region are distributed from the shores of the Californian Peninsula (approx. $27-30^{\circ}$ N. lat.) to Magellan Strait

and Tierra del Fuego without any significant interruption of the ranges. These are the polychaete Lumbrineris tetraura (Schmarda, 1861), living at depths of 0-73 m, and two supralittoral sympatric species of crustacean Decapoda belonging to the Anomura: Coenobita compressus H. Milne-Edwards, 1837, and C. rugosus H. Milne-Edwards, 1837. In the south, the polychaete ranges all the way to the Falkland Islands and there may be yet another isolated micropopulation of it in the north in the boundary region off southern California, at 32° 30' N. lat.

Off the Atlantic coast an analogous α -region (region) integrates a large part of the Eastern American tropical region (oblast') and a small part of the South American temperate region. It extends from Florida (27° N.) to Argentina (42° S.) (fig. 9). There are two species-determinants: the bivalve molluscs Pododesmus rubis (Broderip, 1834) and Plicatula spondiloidea (Menschen, 1781), which evidently live in the upper sublittoral. Moreover, there is the rather rare crab Metasesarma rubripes (Rathbun, 1897), distributed from Nicaragua (15° N. lat.) to Argentina (41° 09' S. lat.) to depths of 150-320 m on the Shelf. These are species belonging to the tempero-tropical group in our classification. There are a further three or four bitropical-nototemeral species with ranges that are disconnected in the equatorial zone; they range southwards as far as latitude 41-42° S. These 6 or 7 species all live near the coasts of northern Argentina, mainly in the offshore zone. Accordingly, the large α -region (region) determined by them hardly intersects at all

with the South American-Antarctic region. As a rule, off the coasts of northern Argentina, the species of the nototempero-polar group by which this latter region is distinguished, are not found at depths less than 70-80 m [Semenov, 1971].

Off the Pacific coast, no such clear separation in terms of the depth of habitation of the temperotropical and nototempero-polar species is seen, as their ranges partly overlap. Thus, the Pacific part of the South American temperate α -region extending from 20° S. lat., to the area of Tierra del Fuego and the Falkland Islands can be regarded as a transitional first-order α -region (region) between large α -regions ranked as super-regions (nad-oblasti). Four species-determinants of this transitional region can be indicated: the polychaete Perinereis falklandica Ramsay, 1914, the isopod Munna (Uromunna) nana (Nordenstam, 1933), the shrimp Nauticaris magellanica (A. Milne-Edwards, 1891) and the bryozoan Membranipora hyadesi Jullien, 1888. They are all distributed off the Pacific coast from northern Chile (20° S. lat.) to Tierra del Fuego and the Falkland Islands in the Atlantic at depths of between 0 and 100-150 m.

Inasmuch as non-traditionally intersecting large α -regions of the super-region type are both unusual and at all times unsuitable for practical purposes, here also a prohibition can be placed on an intersection, just as is the case with α -regions (oblasti), separating large α -regions along one of the natural boundaries at which the species of the tempero-tropical and nototempero-polar groups of our classification are represented in the sampling by the same number.

Table 2. Distribution of species with modified latitudinal-zonal characteristics, if the boundary between the temperal and tropical faunas is taken to extend between 1-5° S. lat., in the Pacific and between 23-24° S. lat., in the Atlantic.

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1 Группа видов	2 Всего видов	3 Североперуанский, 2-5°-12-14° ю. ш.	4 Южнобразильско-уругвайский, 23-24°-35-38° ю. ш.	5 Южноаргентинский, 12-14°-18-30°-20° ю. ш.	6 Северочилийский, 18°30'-20°-33° ю. ш.	7 Центральночилийский, 33°-41°26'-43° ю. ш.	8 Североаргентинский, 35°-38°-42-43° ю. ш.	9 Южночилийско-Южноаргентинский к югу от 42-43° ю. ш.	10 Весь район	11 Огненная Земля и Фолклендские (Мальвинские) острова
12 Тепловодные*	168*	98*	70*							
(исключены из расчета процентного соотношения видов)										
13 Тропические (циркатропические виды пограничных зон: 1-5° ю. ш. в Тихом океане и 23-25° ю. ш. в Атлантическом)	104	65	39							
14 Битропические (только те, которые не идут южнее указанных пограничных областей: имеют там обособленные популяции)	58	31	27							
15 Битропическо-темперальные (только те, которые в южном полушарии распространены как битропические)	6	2	4							
16 Теплых и умеренных вод	196	77	109	51	44	28	18	18	13	
		47%	64%	34%	18%	11%	11%	3%	3%	

Table 2. Continued.

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17	Темперо-тропические **	38	25	16	19	13	8	4	4	3
18	Тропические (голо- и нототропические, приравнены к темперо-тропическим) и соответствующие им амфиамериканские	55	18	38						
19	Битропические (только идущие южнее указанных выше пограничных зон, приравнены к битропическо-темперальным)	35	2	35						
20	Битропическо-темперальные (только те, которые распространены в экваториальных подзонах)	39	17	15	13	15	11	9	10	8
21	Нототропическо-темперальные (только распространенные в экваториальных подзонах)	29	15	5	19	16	9	5	4	2
22	Умеренных вод	638	86	58	97	177	192	108	349	267
23	Тропические (циркулярные, идущие южнее указанных выше пограничных областей, приравнены к нототемперальным)	58	53%	34%	64%	74%	77%	66%	66%	61%
24	Битропическо-темперальные (только те, которые не заходят в экваториальные подзоны, приравнены к нототемперальным)	16	9	1	6	7	3	1	4	2
25	Нототропическо-темперальные (только те, которых нет в экваториальных подзонах, приравнены к нототемперальным)	70	47	26	44	44	31	19	25	19

Table 2. Continued.

202

Группа видов	Всего видов	Североперуанский, 2-5°-12-14° ю. ш.	Южнобразильско-уругвайский, 23-24°-35-38° ю. ш.	Южноперуанский, 12-14°-18-30° ю. ш.	Северочилийский, 18-30°-20°-33° ю. ш.	Центральночилийский, 33°-41°-26°-43° ю. ш.	Североаргентинский, 35°-38°-42-43° ю. ш.	Южночилийско-Южноаргентинский к югу от 42-43° ю. ш.	
								Весь район	Огненная Земля и Фолклендские (Мальвинские) острова
26 Нототемперальные	481	—	—	44	121	150	88	314	240
27 Битемперальные	13	—	—	3	5	8	—	6	6
28 Холодных и умеренных вод	180	—	3	3	19	30	37	163	159
29 Южноамерикано-антарктические (нототемперо-полярные, в том числе 3 вида циркуатропическо-полярных атлантических)	166	—	2%	2%	8%	12%	23%	31%	36%
30 Битемперо-полярные	14	—	3***	1	11	22	33	155	147
31 Всего видов	1014 (1182)	163 (261)	170 (240)	151	240	250	163	530	439

* Circatropical species living only in boundary regions (1-5° S. lat., in the Pacific and 23-25° S. lat., in the Atlantic), and other species that have micropopulations in these regions.

** A total of 14 species of this group are excluded: they occur in the temperal zone and circatropical subzone of the northern hemisphere only. In the southern hemisphere they live only in the eutropical subzone.

*** Including three species living in the Atlantic circatropical subzone.

Table 2. (Continued)

- Key:
1. Group of species.
 2. Total number of species.
 3. Northern Peruvian, 2-5°-12-14° S. lat.
 4. Southern Brazilian-Uruquayan, 23-24°-35-38° S. lat.
 5. Southern Peruvian, 12-14° - 18°30'-20° S. lat.
 6. Northern Chilean, 18°30' - 20-33° S. lat.
 7. Central Chilean, 33°-41°26'-43° S. lat.
 8. Northern Argentinian, 35°-38°-42-43° S. lat.
 9. Southern Chilean-Southern Argentinian southwards of 42-43° S. lat.
 10. Entire region.
 11. Tierra del Fuego and Falkland Islands.
 12. Warm water* (excluded from the calculation of the percentage ratio of the species).
 13. Tropical (circatropical species of the boundary zones: 1-5° S. lat., in the Pacific and 23-25° S. lat. in the Atlantic).
 14. Bitropical (only those which do not occur to the south of these boundary regions; isolated populations exist there).
 15. Bitropico-temperal (only those which are distributed in the southern hemisphere as bitropical).
 16. Of warm and temperate waters.
 17. Tempero-tropical.**
 18. Tropical (holo- and nototropical, equated to tempero-tropical) and the amphi-American species corresponding to them.
 19. Bitropical (only those occurring to the south of the above-indicated boundary zones, equated to bitropical-temperal).
 20. Bitropical-temperal (only those which are distributed in eutropical subzones).
 21. Nototropical-temperal (distributed only in eutemperal subzones).
 22. Of temperate waters.
 23. Tropical (circatropical, occurring to the south of the above-indicated boundary regions, equated to nototemperal).
 24. Bitropical-temperal (only those which do not enter eutropical subzones, equated to nototemperal).
 25. Nototropical-temperal (only those which are absent in eutropical subzones, equated to nototemperal).
 26. Nototemperal.
 27. Bitemperal.
 28. Of cold and temperate waters.
 29. South American-Antarctic (nototempero-polar, including 3 species of the circatropical-polar-Atlantic groups).
 30. Bitempero-polar.
 31. Total number of species.

It is better still if a boundary is selected at which the species of these groups occur in a ratio that is proportional to the total number of them in a sufficiently representative sampling [Semenov, 1972]. In any case, off the Pacific coast a boundary at 42° S. lat. proves to be the most suitable. This boundary is also characterised by the greatest value of the biotic and species pressure as compared with the proximate boundaries (at 37° or 33° S. lat.).

Second-order transitional α -regions (regiony) are distinguished in relation to α -regions (oblasti) by the types of ranges of the group of nototropical-temperal species which intersect the boundaries of the α -regions, there being 5 types of intersection (fig. 8,e). Thus, in this particular system of division the Northern Peruvian α -region extending from 2-5 to 12-14° S. lat. can be regarded as a second-order transitional region (species-determinants: the polychaete Nereis veleronis Hartman, 1940, and the crustacean decapods Callianassa (C.) islagrande Schmitt and Pachycheles crinimanus Haig, 1960). The adjacent second-order α -region stretching southwards of 12-14° S. lat., to the area of Tierra del Fuego and the Falkland Islands has 16 species-determinants: the polychaetes Glycera papillosa Grube, 1857, Notocirrus lorum Ehlers, 1897; the gastropods Fissurella limbata Sowerby, 1834, F. maxima Sowerby, 1834, F. nigra Lesson, 1830; the bivalve mollusc Choromytilus chorus (Molina, 1782); the crustacean decapods Liopetrolisthes mitra (Dana, 1852), Gomeza serrata Dana, 1852, Pseudocorystes sicarius Poëppig, 1836, Pinnixa valdiviensis (Rathbun, 1907), Pinnotherelia laevigata

Milne-Edwards and Lucas, 1843, Pisoides edwardsi (Bell, 1835), Taliepus dentatus (H. Milne-Edwards, 1835); and the starfishes Luidia magellanica Leiboldt, 1895, Stichaster striatus Müller and Troschel, 1840. Only the mitilid Ch. chorus ranges all the way to the Falkland Islands. The species of the integrating range EF (fig. 8,e), distributed from 2-5° S. lat. to Tierra del Fuego and the Falkland Islands are as follows: the polychaete Hemipodus simplex (Grube, 1857); the gastropods Fissurella crassa Lamarck, 1822, F. picta (Gmelin, 1791); the crustacean decapods Paguristes weddelli (H. Milne-Edwards, 1848), Gaudichaudia gaudichaudi (H. Milne-Edwards, 1834), Pilumnoides perlatus (Poeppig, 1836); Cancer edwardsi Bell, 1835, Eurypanopeus crenatus (H. Milne-Edwards and Lucas, 1843), Homolaspis plana (H. Milne-Edwards, 1834), Pinnaxodes chilensis (H. Milne-Edwards, 1837); and the sea-urchin Loxechinus albus (Molina, 1782), totalling 11 species in all, of which F. picta ranges all the way to the Falkland Islands.

Off the Atlantic coast the Southern Brazilian-Uruquayan, and the Uruquayan-Northern Argentinian α -regions (regiony), coinciding with the circatropical and infertemperal sub-zones, are second-order (relative to α -regions (oblasti)) transitional α -regions.

The species-determinants of the Southern Brazilian-Uruquayan α -region are: the bivalve mollusc Hormomya darwiniana (d'Orbigny, 1846); the stomatopods Squilla brasiliensis Calman, 1917, Hemisquilla brasiliensis (Moreira, 1903); the crustacean decapods

Penaeus paulensis Perez-Farfaite, 1967; Scillarides deceptor Holthuis, 1963; Nephrops rubellus Moreira, 1903, Pagurus exilis (Benedict, 1892), Uca uruguayensis Nobili, 1901, Fabia emiliae (de Mello Leitao, 1971), Pinnixa rapax Bouvier, 1917, Parthenope (Platylambrus) aylthoni (Righi, 1967); the brachiopod Bourchardia rosea (Mawe, 1823); and the starfish Anthenoides brasiliensis Bernasconi, 1956.

The species-determinants of the Uruquayan-Northern Argentinian α -region extending from 33-35° to 42-43° S. lat. are: the polychaetes Eunice argentinensis (Treadwell, 1929), Marphysa atlantica (Kinberg, 1865) Lumbrineris quinquentata (Kinberg, 1865), the gastropod Lucapinella hassleri Perez-Farfaite, 1943; the bivalve molluscs Chlamys felipponei (Dall, 1922), Musculus viator (d'Orbigny, 1846), Pododesmus leloiri Carcelles, 1941, the stomatopod Heterosquilla (H.) platensis (Berg, 1900), the crustacean decapods Betaeus lilianae Boschi, 1966, Pachycheles chubutensis Boschi, 1963; Platyxanthus crenulatus A. Milne-Edwards, 1879, P. patagonicus A. Milne-Edwards, 1879, Cyrtograpsus altimanus Rathbun, 1898, Pinnothere garthi Fenucci, 1975; and the starfish Luidia patriae Benasconi, 1943.

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The species-determinants of the integrating α -region extending from 23-24° S. lat. to 42-43° S. lat. are: the gastropod Fissurella hiantula (Lamarck, 1822); the bivalve molluscs Glycymeris longior (Sowerby, 1832); Chlamys tehuelcha d'Orbigny, 1846; the crustacean decapods Artemisia longinaria Bate, 1888, Blepharipoda

doelloi Schmitt, 1942, Pinnixa patagoniensis Rathbun, 1918, Chasmagnathus granulata Dana, 1851, Collodes rostratus A. Milne-Edwards, 1878, Libinia spinosa H. Milne-Edwards, 1834; the pantopod Achelia (Pigrolavatus) besnardi Sawaya, 1951, and the starfish Allostichaster hartii (Rathbun, 1879).

In distinguishing the foregoing second-order transitional regions, the absolute number of species-determinants, both of the EF type of range (fig. 8,e) and also of the EB and CF types of ranges, is taken into account. Generally speaking, if it is only an intersection of a given geometric type that is regarded as such, then very disparate variants are possible in the distinguishing of second-order transitional α -regions in relation to pairs of biogeographic units of any rank [Semenov, 1978, figs. 1-4].

In contrast to large and medium-sized α -regions, the distinguishing of very small biogeographic units gives much less cause for doubt. These units can easily be distinguished solely on the basis of a classification of the ranges of the maximal and the 98-99%-th differentiative level. The rank of district (okrug) is assigned to these very small and well isolated (little intersecting) α -regions, which correspond to our elementary biotopes in the biogeographic sense [Semenov, 1978] (fig. 10). The boundaries of districts, like those of other units (see table 5) closely coincide with the climatic boundaries of the environment (summer or winter), or with the boundaries segregating saliferous modifications of water masses, which ultimately also form under the influence of climate.

Strictly speaking, the boundary regions (oblasti) can also be considered α -regions with the rank of district (subdistrict?). A sufficient and necessary attribute is the presence of species-determinants. Some of the relatively extensive boundary regions are included in the list presented in table 5. In fig. 10 and table 5, Roman numerals are used to denote units distinguished by species-determinants.

Distinguished on the territory of certain districts are some further α -regions of lower rank (subdistrict). These tend to disrupt the linear linking of the individual territories: units XVII, XX and XXI (fig. 10). Their distinguishing is unrelated to any significant difference between species in terms of depth of habitation. The reasons for such an arrangement of very small co-ranges are not completely clear. It is possible that, in addition to large-scale hydrology, a definite role is played here by geological factors: the large- and intermediate facies arrangement of soil types and bottom sediments. In terms of scale, the very small biogeographic units may even be commensurate with the biotopes of biocoenoses distinguished by the quantitative abundance of the species and by index fossils; the distribution of these latter depends in large measure on the small- and intermediate facies arrangement of the soils and on local hydrodynamic peculiarities. The relationship between chorological and synecological units is not discussed in the present study. Let us now return to the distinguishing of large territories.

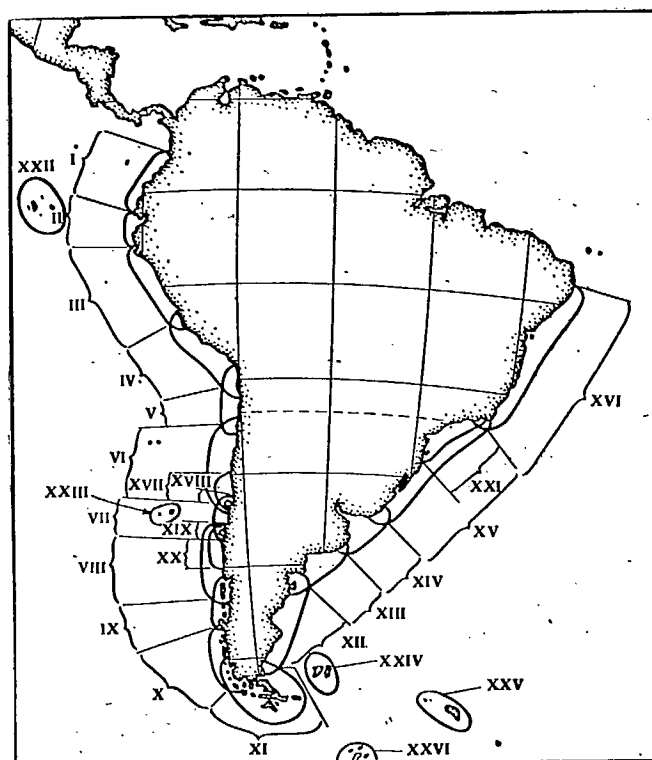


Fig. 10. Coverage of the biotope system by types of ranges of minimal extent.

I-XVI, XXII-XXIV are elementary biotopes in the biogeographic sense (some units which are not completely distinct are indicated but not marked in). The elementary biotopes correspond to α -districts in the system of zonation by species-determinants.

Insofar as the South American temperate α -region (oblast') is concerned, if we ignore the requirement of hierarchic closure of a large α -region, and the fact that one large α -region corresponding to the fauna of the temperate waters must, of necessity, be identified, then another variant of zonation by species-determinants is possible. One of the evident rules with respect to this variant is to take the number of species-determinants into account even when distinguishing

a particular large α -region. This is a more effective approach, because ordinarily, spatially limited types of ranges (as a rule, the boundary and insular groups), are represented by the largest number of species, whereas territorially large - both the continuous and disconnected types of ranges, especially the latter - are represented in a random sampling by a small number of species. In our sampling in temperate waters, they are normally represented by two or three species. Therefore, if an extensive range is represented by a noticeably large number of species (let us say ≥ 10) in comparison with other ranges of the same area, then this can serve as an argument in favour of distinguishing the large α -region by precisely this type of range in the first place.

It is by the number of species-determinants off the coasts of South America in the specifically temperate waters, that the Southern Peruvian-Chilean α -region, extending from 12-14° S. lat., to the area of Tierra del Fuego, is distinguished, there being 15 species-determinants (16 species, together with the one that ranges as far as the Falkland Islands). They are listed above as the determinants of the Southern Peruvian-Chilean transitional second-order α -region. These are mainly littoral-sublittoral species. It is by the types of ranges of species belonging to the nototropical-temperal group, dispersed northwards off the Pacific coast of South America as far as 2-5° S. lat. and by the number of species-determinants, that we also distinguish the extensive Peruvian-Chilean (Andean) α -region, which stretches from 2-5° S. lat. to Tierra del Fuego and

the Falkland Islands. It is distinguished by 11 species-determinants (see above). In terms of the number of determinants this α -region is second only to Southern Peruvian-Chilean region (16 species), so that in the zonation by species-determinants, the boundary between the tropical fauna and the fauna of the temperate waters remains valid at 12-14° S. lat., even when failing to observe the principle of hierarchic closure of a single temperate α -region off the coasts of South America. The next large α -region in terms of the number of species-determinants is the Argentinian, extending from 34-38° S. lat. to Tierra del Fuego, including the Falkland Islands. Up to 19 species-determinants, with depths of habitation within the Shelf zone varying within wide limits, can be indicated. Of these, the following 9 species are distributed throughout the area extending from La Plata (35-38° S. lat.) to Tierra del Fuego and the Falkland Islands: Drilonereis tenuis (Ehlers, 1900); the molluscs Lithophaga patagonica (d'Orbigny, 1846), Chlamys (Zygochlamys) patagonica (King, 1831) and Limopsis hirtella Mabille et Rochebrune, 1899; the crustacean decapod Pseudolithodes zenkevitchi Birstein et L. Vinogradov, 1972, the pantopod Pycnogonum magellanicum Hoek, 1898; the bryozoan Pseudidmonea fissurata (Busk, 1886); the sea-urchin Austrocidaris canaliculata (A. Agassiz, 1863), and the starfish Ctenodiscus australis Lütken, 1871. The following four species do not occur near the Falkland Islands: Lepidasthenia gigas (Johnson, 1897), the isopods Cleantis granulosa Heller, 1865 and Edotia doellojuradoi Giambiagi, 1925, and the starfish Hippasteria argentinensis Bernasconi. A further four species, also non-occurring

off the Falkland Islands, are dispersed slightly further north than the remainder, as far as $32-34^{\circ}$ S. lat.: the bivalve mollusc Chamys lischkei (Dunker, 1850); the crab Pilumnoides hassleri A. Milne-Edwards, 1880; the pantopod Pallenopsis boehmi Schimkewitsch, 1930 and the starfish Poraniopsis mira (de Loriol, 1904).

Thus, two α -regions (oblasti) are distinguished in the temperate zone of the South American Shelf by the number of species-determinants: a Pacific and an Atlantic. But if the principle of hierarchic closure remains in force and if the South American temperate α -region (oblast') distinguished earlier by the two species-determinants is unitary, then it has to be subdivided into two α -subregions: a Pacific and an Atlantic. The boundary between them lies in the vicinity of Tierra del Fuego.

Distinguished in the temperate waters off the coasts of South America are several additional α -regions (regiony) with a fairly large number of species-determinants, but it is difficult to determine the rank of these units. I am referring to the Southern Peruvian-Northern Chilean α -region, stretching from 12° to 37° S. lat., with 11 littoral-upper sublittoral species-determinants. The Northern Chilean and Central Chilean regions (raiony) are integrated into the Tarapaca-Chiloe α -region on the basis of two co-ranges, lying (i) between $18^{\circ}30'-20^{\circ}13'$ S. lat., and $40^{\circ}47'-42^{\circ}57'$ S. lat., - 8 species, and (ii) between $18^{\circ}30'-20^{\circ}13'$ S. lat., and $44^{\circ}7'-45^{\circ}15'$ S. lat., - 6 species. As we shall see subsequently, this α -region proves to be very homogeneous faunistically.

The less extensive South American α -regions, corresponding to zoogeographic provinces, which many investigators distinguish, have from 5 or 6 to 10 species-determinants. In general, it should be noted that the unambiguous distinguishing of α -regions corresponding approximately to provinces is almost impossible on the basis of species-determinants. Previously Semenov [1972], had suggested the distinguishing of the following three strongly intersecting α -provinces in the temperate waters: a Chilean, between 12-14° S. lat., and 42-43° S. lat.; a Magellan, southwards of 30-33° S. lat. in the Pacific and 42-43° S. lat. in the Atlantic; and an Argentinian, between 33-35° S. lat., and Tierra del Fuego and the Falkland Islands. But a comparison of the faunal composition is more conveniently made with respect to individual units. For this purpose we will use the relatively small units corresponding to our previously distinguished latitudinal subzones [Semenov, 1977a], even though they are certainly of unequal value as faunistic units. Two of these regions (raiony) correspond to the α -districts of the faunistic zonation by species-determinants (II, XV and IV respectively in fig. 10), three regions (raiony) each include two α -districts (V-VI, VII-VIII and XIII-XIV) and one - the largest region (the eutemperate subzone) - 4 α -districts or 5, if the Tierra del Fuego boundary region is considered to be a district (IX-XII and XXIV in fig. 10).

Translator's note: As mentioned in my Note on p. 17, the Russian term oblast' is being translated as 'region', notwithstanding the fact that the author is using region (Cyrillic characters) as a generic term for all of the various zoogeographic units, including oblast', in his hierarchic system of classification. This was explained in his footnote 3.

Information contained in Ricker's Russian-English Dictionary for Students of Fisheries and Aquatic Biology suggests that when used in a marine zoogeographic context, oblast' may mean 'zone'. According to Dr. Ricker, the word does mean a zoogeographic region when a land situation is being discussed. Otherwise, he cites a counterpart term: zoogeograficheskaya zona okeana (zoogeographic zone of the ocean).

In the present text, however, the terms zona and podzona (subzone) are used in reference to climatic and latitudinal zones and subzones, with oblast' and podoblast' usually (see below) referring to faunistic geographic units. This distinction, together with the fact that the author himself equates oblast' to "region" (Latin characters) (footnote 3, p. 17 and p. 50), citing Briggs and other authors as his source, has led me to continue to render oblast' as 'region'. This can, however, lead to repetition, as, for instance, when he speaks of "the Southern Brazilian-Uruguayan α -region (region) being distinguished as an independent superprovince forming part of the Western Atlantic (Columbian) tropical region (oblast'), p. 82. It would seem that in this particular context he is using oblast' as a synonym of zona. The position of an oblast' in the hierarchic classification of the regions is shown graphically in fig. 19.



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The biogeographic zonation of the South American Shelf
based on a classification of the ranges of
bottom-dwelling invertebrate species

(Translated from Russian)

Second of Three Installments

(Pages 42-86)

Data on the composition of the fauna by regions

The distribution of species in respect of which the types of dispersion exhibit regional differences, thus reflecting the composition of the fauna, is presented in tables 1 and 2. From 99 to 100% of the fauna of the Northern Peruvian and Southern Brazilian regions (table 1) consists of warm water species and of species inhabiting warm and temperate waters, which means that it is obviously of tropical origin. The fauna of the Southern Brazilian region is more of a warm water fauna than is the Northern Peruvian (table 1). Two-thirds of the fauna of the Southern Peruvian region (from $12-14^{\circ}$ to $18^{\circ}30'-20^{\circ}$ S. lat.) consist of widely dispersed elements of manifestly tropical origin. Although the faunas of the Northern Chilean (from $18^{\circ}30'-20^{\circ}$ to 33° S. lat.) and Northern Argentinian regions (from $35-38^{\circ}$ to $42-43^{\circ}$ S. lat.) have almost the same proportions of species inhabiting temperate waters (the first region is somewhat larger - table 1), they differ very little in terms of the percentage ratio between widely dispersed elements, that is, the species of the warm and temperate waters (the temperotropical group) and the species of the cold and temperate waters (the temperopolar group). Considered as a whole, the fauna of the Northern Argentinian region is much more of a cold water fauna than is the Northern Chilean, and the number of the most cold water elements in it (the South American-Antarctic or Nototempero-polar elements) is almost the same as that of the widely dispersed species of tropical origin (table 1). In the relative number of these latter the Northern Argentinian region approximates to the Central Chilean (33° S. lat.- $41^{\circ}26'-43^{\circ}$ S. lat).

A remarkable fact, which still requires explaining, is the comparatively small total number of species constituting the faunas of the Southern Peruvian and Northern Argentinian regions. Whereas for the first of these regions (α -district IV) this might have been attributed to the fact that, in comparison with the adjacent regions, the fauna has been investigated to a much lesser extent, the benthos off the Northern Argentinian coasts has been studied no less fully than has the Southern Brazilian or Patagonian benthos. In our sampling the total number of species in each of these two regions proved to be only three-quarters of the number in the adjacent regions, due to the sharp decrease in the number of species of manifestly warm water origin (the temperal-tropical, nototropical-temperal and bitemperal-tropical species). Tropical and bitropical species are absent (in the Atlantic only 19 of the 170 species in our sampling are found in the La Plata boundary region as far as 38° S. lat). There are also fewer temperal species in these regions. Moreover, there is an abrupt decrease in the number of temperal-polar species (the nototemperal-polar and bitemperal-polar group) in the Southern Peruvian region in comparison with the more southerly Northern Chilean region.

Now, we have considered the main results of a zonation based on species-determinants and the information which pertains to the percentage ratio between species with dissimilar latitudinal-zonal characteristics in the different regions. On the basis of the ratio between the warm water-- and the cold water elements, the Northern Argentinian and Central Chilean regions, situated in the zones of the modified

(relatively warmer) waters of the sub-Antarctic structure, proved to be the most similar. On the basis of faunal composition these regions ought to be included in the same latitudinal subzone.

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Zonation-according to the boundaries of co-ranges

We shall now consider the results of a zonation based on the second chorological method, when faunistic units of a particular rank are distinguished in relation to the degree of significance* of the biogeographic boundaries separating them. With this method of zonation, for each boundary region an estimate is made of the number of species and co-ranges which reach the boundary in question from the north and the south.⁴ It will be recalled that in a projection to the coast, narrow zones of dense thickening of the dispersion boundaries of species alternate with more extensive regions of boundary thinning. And if a species has "transited" a particular boundary zone (region of boundary thickening), then with very few exceptions, it will proceed to the next boundary, without stopping midway. Such is the actual nature of the discreteness of the living cover. A plus sign is provisionally assigned to the number of species and co-ranges which reach a particular boundary from the north, from the regions of warmer waters, and a minus sign, to the number of species reaching

*Znachimost' in the original text, which is a synonym of vazhnost', also meaning 'importance' (Tr.).

⁴V.I. Sauskan [1979] also determines the significance of the boundary on the basis of the number of species having the designated dispersion boundary, but without indicating the number of species approaching the boundary from different directions.

that boundary from the south. The Tierra del Fuego and Falkland Islands region, where the Pacific species are designated by a plus sign and the Atlantic species by a minus sign, constitutes an exception.

Thus, the relative significance of each biogeographic boundary with respect to a given sampling, is evaluated by two pairs of numerals: by the number of species and the number of co-ranges. The characteristics of the different zoogeographic boundaries are presented in table 3 and (in less detail) in fig. 11 with respect to the Shelf fauna as a whole and separately for the fauna of the upper part of the Shelf (littoral + upper sub-littoral). The most important boundaries lie between $20-21^{\circ}$ and $27-28^{\circ}$ S. lat., in the Atlantic (the Paulian-Catharinian region) and in the area extending from $1^{\circ}15'$ to $5^{\circ}05'$ S. lat., in the Pacific (the Guayaquilian region). Two narrowly localised boundaries are distinguished off the Atlantic coast. The more important of the two lies near $23-24^{\circ}$ S. lat., the second, with well-defined compression from the north, near $27-28^{\circ}$ S. lat. Off the Pacific coast, four very important local boundaries lie very close to each other in the Guayaquilian district.

These boundaries, especially near $2^{\circ}10'-5^{\circ}05'$ S. lat., in the Pacific and near $23-24^{\circ}$ S. lat., in the Atlantic, can be taken to be boundaries of zoogeographic regions in the case of the second method of zonation which is based on types of ranges (fig. 12). They completely correspond to the boundaries between the tropical and "warm-temperate" regions which were adopted by Briggs [1974]. But as

Table 3. Significance of the zoogeographic boundaries off the coasts of South America and the boundary compression on the basis of the number of species and co-ranges.

1 Тихоокеанское побережье (широта южная)	2 Виды	3 Коаралы
0°40'—1°(2°)	+11 -3	+4 -3
(0°20')1°15'—1°20'	+38 -26	+38 -21
2°10'—2°15'(3°)	+72 -12	
3°23'—4°5'	+54 -3	+38
4°30'—5°5'(5°40')	+69 -25	-14
4 Около 6°57'	+4 -9	0 -2
Около 9°	+3 -12	+2 -3
12—14°	+35 -51	+22 -19
18°30'	+5 -10	+12
20°10'—20°13'	+20 -32	-21
22°—23°30'	+3 -6	+3 -5
25°25'—25°30'	+2 -9	+2 -4
29°—30°	+5 -25	+4 -14
32°57'—33°20'	+34 -32	+19 -17
Около 34°56'	+2 -5	+1 -2
36°40'—37°14'	+43 -20	+21 -14
38°16'(39°)	+4 -8	+4 -3
39°50'—40°	+9 -6	+1 -4
41°30'—42°57'	+56 -63	+25 -31
45°—46°	+21 -4	+9 -3
48°—49°	+2 -4	+2 -2
5 Огненная Земля (52—56°)	+108 -130	+55 -47
6 Атлантическое побережье	Виды	Коаралы
20—21°	+27 -3	+10 -3
23—24°(25°)	+112	+52

Key: (a) Entire shelf zone; (b) Littoral and upper sublittoral

1. Pacific coast (south latitude)
2. Species
3. Co-ranges
4. Near
5. Tierra del Fuego
6. Atlantic coast
7. Falkland Islands

Table 3 (Continued)

6	Атлантическое побережье	2	Виды	3	Коареалы
	27—28°	-44	} +218 ↓ -48	-17	} +100 ↓ -21
		+79		+38	
4	Около 32°	-1	} +9 ↓ -9	-1	} +3 ↓ -2
		+9		+3	
	33°—34°30' (35°35')	+23	} +56 ↑ -106	+19	} +35 ↑ -46
		-38		+14	
	35°35'—38°30'	+24	} -59 ↓ -23	+14	} -22 ↓ -46
		-59		-23	
	Около 40°	+2	} +4 ↓ -4	+1	} +1 ↓ -1
		-4		-1	
	41°—42°30' (43°40')	+44	} +50 ↑ -67	+15	} +16 ↑ -38
		-46		-28	
	44°15'—46°	+6	} +6 ↓ -21	+1	} +1 ↓ -10
		-21		-10	
	47°45'—49°30'	+9	} +9 ↓ -15	+5	} +5 ↓ -8
		-15		-8	
5	Огненная Земля (52—56°)	+130	} +130 ↓ -108	+47	} +47 ↓ -55
		-108		-55	
7	Фолклендские (Мальвинские) острова	+55	} +55 ↓ -80	+21	} +21 ↓ -34
		-80		-34	

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б) Литораль и верхняя сублитораль

1	Тихоокеанское побережье	Виды	Коареалы
	0°40'—1°(2°) с. ш.	+4	+2
		0	0
	(0°20') 1°15'—1°20'	+20	+5
		-20	-8
	2°10'—2°15'(3°)	+47	+17
		-9	-8
	3°23'—4°5'	+30	+8
		-1	-1
	4°30'—5°5'(5°40')	+64	+20
		-14	-13
	Около 6°57'	0	0
		-2	-2
	Около 9°	+2	+2
		-9	-3
	12°—14°(15°)	+26	+17
		-41	-14
	18°30'—20°13'	+19	+13
		-26	-12
	22°—23°30'	+2	+1
		-6	-2
	25°25'—25°30'	+2	+2
		-3	-3
	29°—30°	+2	+2
		-12	-7
	32°57'—33°20'	+27	+16
		-20	-10
	36°40'—37°14'	+35	+19

Table 3 (Continued)

1 Тихоокеанское побережье	2 Виды	3 Коареалы
38°16' (39°)	-15 + 1 0	-13 + 1 0
39°50'—40°	+ 1 - 1	+ 1 - 1
41°30'—42°57'	+39 -16	+20 - 7
(44°) 45—46°	+18 - 3	+ 8 - 2
48°—49°	+ 1 - 3	+ 1 - 1
Огненная Земля	+67 -25	+36 -15
6 Атлантическое побережье	Виды	Коареалы
18°	+ 3 - 2	+ 3 - 2
20—21°	+ 5 - 3	+ 5 - 3
23—24° (25°)	+80 -38	+43 -14
27°—28°	+66 0	+39 0
Около 32°	+ 5 - 8	+ 4 - 2
33°—34°30' (35°35')	+18 - 6	+10 - 4
35°35'—38°30'	+23 -10	+10 - 4
Около 40°	+ 1 - 1	+ 1 - 1
41°—42°30' (43°40')	+28 -13	+10 - 7
45°	0 - 1	0 - 1
47°45'—49°30'	+ 3 - 1	+ 2 - 1
5 Огненная Земля (52—56°)	+25 -67	+15 -36
7 Фолклендские (Мальвинские) острова	+ 4 -26	+ 3 -13

regards the further subdivision of the region of temperate waters, there proves to be nothing in common, either with what Briggs suggests or with what was concluded by Ekman [1953] and the other authors who conceive of a single "cold-temperate" fauna and one or two "warm-temperate" faunas off the coasts of South America together with units with the rank of region (oblast') or subregion (podoblast') corresponding to them (figs. 1,3).

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The next most important zoogeographic boundary on the basis of the number of species and co-ranges which is equivalent to the two preceding ones lies off the South American coasts in the vicinity of Tierra del Fuego and Falkland Islands. In significance, this boundary corresponds to the boundaries between zoogeographic regions (oblasti) or subregions at the least.

A boundary which is less significant than the three aforementioned ones but is nevertheless very well defined and localised, lies off the Pacific coast at $41^{\circ}26' - 43^{\circ}$ S. lat. It corresponds to Ekman's boundary between the faunas of the "warm" and "cold-temperate" waters. An additional, fairly important boundary, which actually amalgamates two very closely situated local boundaries, lies off the Atlantic coast in the vicinity of La Plata (table 3). It is analogous to the Pacific boundary and corresponds to the boundary between the faunas of the "warm" and "cold-temperate" waters, although not that of Ekman [1953] and Briggs [1974]. We can now see clearly that in their schemes, both Ekman and Briggs used the zonal-geographic principle and the data on the most important climatic boundaries in the marine environment,

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to which their boundaries between oblasti ("Regions") correspond, and that they did not note a single one of the most important boundaries off the coasts of South America: those in the vicinity of Tierra del Fuego and the Falkland Islands.

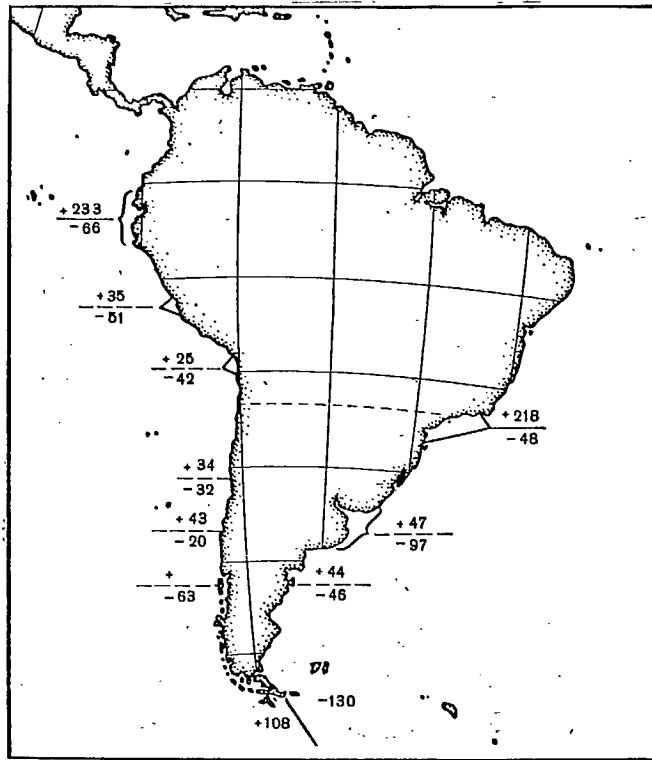


Fig. 11. Principal biogeographic boundaries off the coasts of South America.

The numerals denote the number of species reaching the particular boundary from the north (shown with a plus sign) and from the south (with a minus sign).

In terms of their significance, the boundaries at $41^{\circ}26' - 43^{\circ}$ S. lat. in the Pacific and in the vicinity of La Plata (in sum, based on the following two sets: at $33^{\circ} - 35^{\circ}35'$ and at $35^{\circ}35' - 38^{\circ}30'$ S. lat.) in the Atlantic,

roughly correspond to the boundaries between superprovinces or even subregions, if the Pacific and Atlantic temperate regions off the coasts of South America are considered to be independent (fig. 11).

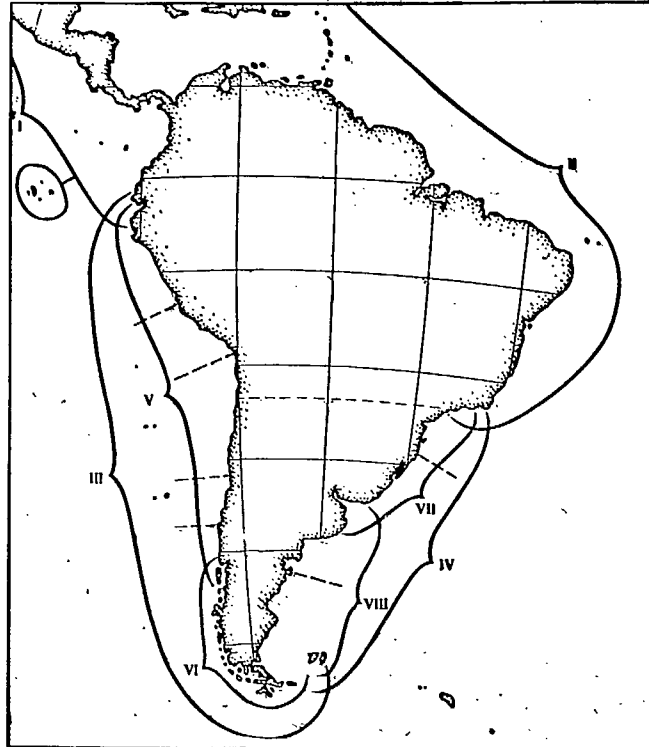


Fig. 12. Zonation of the South American Shelf on the basis of the degree of significance of the zoogeographic boundaries.

I, II - Tropical regions (Eastern Pacific and Western Atlantic);
 III, IV - Pacific and Atlantic temperate regions;
 V, VI - Peruvian-Chilean and Southern Chilean subregions (or superprovinces?);
 VII, VIII - Southern Brazilian-Uruguayan and Argentinian subregions.
 The boundaries between the provinces are denoted by a broken line.

Highly important boundaries, which are approximately provincial in rank, lie near $12-14^{\circ}$, $18^{\circ}30'-20^{\circ}13'$, $32^{\circ}57' -33^{\circ}20'$ and $36^{\circ}40'-37^{\circ}14'$

S. lat. off the Pacific coast and near $41^{\circ}-43^{\circ}40'$ S. lat. off the Atlantic side of the continent.

The distinguishing of very small units by means of the second chorological method also gives a somewhat different picture than when species-determinants are used. The minimal region (region) is that region the territory of which is not traversed by the boundary of a single syntopic element or type of range at the particular differentiative level of classification of the ranges. If, being guided by this rule, minimal regions are distinguished between adjacent zoogeographic boundaries that stand out with any degree of clarity, then such units will prove to be larger than the minimal α -regions distinguished on the basis of species-determinants. Thus, distinguished on the territory of the districts obtained by the first method are regions which have no species-determinants but are nevertheless differentiated from adjacent territories on the basis of species composition. Numbered among such regions are, for example, the Tarapacan, Antofagastan and Saladan subdistricts off the coast of Northern Chile, the Rio Grande region in the Atlantic and others (see Table 5).

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The main differences of the scheme of zonation based on the second chorological method (the boundaries of the co-ranges) are as follows. It is not one, but two zoogeographic regions of the temperate fauna - a Pacific and an Atlantic - that are distinguished. The boundaries between the tropical and the temperate regions are displaced much further northward over a distance of at least one

elementary biotope.⁵ Clearly distinguished in the temperate waters off both the Pacific and the Atlantic coasts are two units, evidently with rank of subregion or superprovince. A zonation by small units is obtained in more detailed form. The medium-sized units - the provinces - are distinguished with a much greater degree of definiteness.

Additional data on faunal composition,
taking into account variations in the latitudinal-zonal
characteristics of the species.

We shall now consider to what extent the results of a zonation based on the second method correspond to data on the composition of the fauna. When making a comparison of faunal composition we take the same regions (raiony) as in the first case. But we alter to some extent the latitudinal-zonal characteristics of the species, because the boundary between the tropical and the temperate (nototemperal) zones must be shifted northwards in order for it to correspond to the boundaries between the new zoogeographic regions (oblasti). Thus, the endemic species of the Northern Peruvian and Southern Brazilian regions (raiony) which form part of the tropical group of species, having regard to the displacement of the boundaries between zones, are assigned to the South American nototemperal group. The holo-tropical species found within these subzones are transferred to the tempero-tropical group, the nototropical, which occur southwards of 5-6° S. lat. in the Pacific and southwards of 23-24° S. lat. in the

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⁵For a further discussion of this concept, see Semenov [1978].

Atlantic, to the nototropical-temperal group, and so on. The percentage ratio of the species with modified (altered*) latitudinal-zonal characteristics within the confines of these regions is furnished in table 2.

On comparing the data in tables 1 and 2, it can be seen, for example, that in the Southern Brazilian-Uruguayan region the ratio between the species with dissimilar latitudinal-zonal characteristics had altered abruptly. With the exception of those which do not occur southwards of the boundary region between 23 and 25° S. lat., the warm water species had disappeared, the share of the inhabitants of the warm and temperate waters had increased by more than 200% (at the expense of part of the former warm water species), and the species of temperate waters had made an appearance. Hitherto, however, there had been a marked predominance (63%) of species of warm and temperate waters (the tempero-tropical group of species) which are undoubtedly of tropical origin. Thus, on the basis of the faunal composition the Southern Brazilian-Uruguayan region should be placed within the tropical latitudinal zone and within the Western Atlantic tropical region (oblast!), as is also the case with a zonation by species-determinants. The boundary between the latitudinal zones, as also between the faunistic regions, having regard to the origin of the fauna, should be not the most important of the boundaries off the coast of South America (near 23-24°), but a less important one:

* Inserted by translator.

near $33-35^{\circ}35'$ S. lat., or $35^{\circ}35'-38^{\circ}30'$ S. lat., in the vicinity of La Plata. On the basis of the number of co-ranges, preference should be given to the more northerly of these two boundaries, near $33-35^{\circ}35'$ S. lat.

A somewhat different situation obtains with respect to the Northern Peruvian region between $2^{\circ}10'-5^{\circ}05'$ S. lat. and $12-14^{\circ}$ S. In this region an inverse relationship obtains between the faunal elements of the temperate waters (taking into account the variations in the latitude zone characteristics) - the temperal and tempero-tropical species (living in both warm and temperate waters): 53 and 47% respectively. As we shall see, here there is no marked predominance of species of any major group; the relationship between the elements is close to parity. Formally, however, this region should be included in the temperal zone, since it is derived both from the composition of the fauna and from a comparative estimation of the zoogeographic boundaries. It therefore seems more reasonable to draw the boundary between the zones (and latitude zones) on the basis of the most significant zoographic boundary in this region: near $2^{\circ}10'-5^{\circ}05'$ S.

In conclusion we notice once again the high degree of localisation and the density of the thickening between the boundaries of dispersion of many species, which only become manifest when the classification of ranges is at its most minute. Sometimes there is an unusually precise indication in the literature of the boundaries of dispersion, which may be given to within minutes of latitude, and in the case of

many species a coincidence between these boundaries appears unreal. For instance, the very narrowly localised species dispersion boundaries in the vicinity of Valparaiso, near $32^{\circ}57'$ and $33^{\circ}20'$ S. lat., are conceivably associated with the activity of the major research centre at Vina del Mar. But similar boundaries are also distinguished further south: in the vicinity of Talcahuano, near $36^{\circ}40'$ and $37^{\circ}14'$ S. lat, as well as in other places where it would be difficult to postulate a man-made cause (both pairs of boundaries lie near a little-indented coastline). The boundaries off the coasts of Ecuador and Northern Peru are very strictly localised. There, in the Guayaquilian boundary zone, several secondary boundaries with a diminishing degree of significance from the middle of the region to the periphery are distinguished (table 3). It is difficult to explain these secondary boundaries as resulting from the confinement of species to a particular type of terrain, since species belonging to dissimilar life forms are amalgamated naturally into the same syntopic elements. A marked discrepancy between the species with respect to depth of habitation is also far from always the case, even though the secondary boundary near $38^{\circ}16'$ S., off the coasts of Central Chile is associated with precisely this circumstance. The Cautinian and Osorno regions (regiony) (table 6) are distinguished by the types of ranges, principally of the middle- and lower sublittoral species. The existence of the secondary boundaries is possibly associated with stable, local peculiarities in the hydrology which are unknown to us and perhaps reflects periodic and long-standing fluctuations of

boundaries between water masses, inasmuch as we are dealing with data that are disconnected in time and were collected over a period of decades, it frequently being impossible to establish the exact time when the samplings were taken.

The use of estimates of faunistic similarity between regions when performing a zonation (see below) sometimes makes it possible to state a preference for one of several equivalent secondary boundaries, for example, in the Guayaquilian (near $4^{\circ}30' - 5^{\circ}05'$ S. lat.) and the La Platan (near $33 - 34^{\circ}30'$ S.) first-order transitional α -regions.

A correction which allows for the similarity
between faunas, and a new scheme of faunistic zonation

Thus far, the two methods of zonation based on the chorological approach have led to essentially different results. In one case a single faunistic region (oblast') is distinguished in South American temperate waters. In the other, two large regions (regiony) with the rank of region (oblast') or at the very least, subregion, are distinguished in these waters. Here, their northern boundaries are situated much further north than in the first case. Off the Atlantic coast it proves possible to select a matching position of the boundary if coordinating data on faunal composition are used (i.e., the range- and genetic principle). Off the Pacific coast this method does not yield a clear advantage as to a particular boundary. Moreover, the question of the rank of the boundary in the vicinity of Magellan Strait and Tierra del Fuego remains only partly resolved. How much

significance should be attached to it and to what extent are the Pacific and Atlantic faunas of the South American temperate waters disconnected?

In these and analogous unresolved cases it is possible to draw upon additional arguments in favour of a particular solution, by using quantitative estimates of similarity between faunas with the help of various measures of similarity and difference. We use estimates of faunistic similarity (difference) as basic correcting data when refining the boundaries and determining the rank of regions at the species level of zonation.

Presented in fig. 13 are some symmetrical measures of similarity and difference which are used in biogeography, synecology and systematics. The value of the symmetrical measures does not change with rearrangement from time to time of the sizes of the lists of species N_A and N_B of the two regions (raiony) being compared. The exponents $1a, b$ and $2a, b$ and the exponents $3a, b$ and $4a, b$ pertain to two different groups. We designate the first group as measures of relative or partial similarity or difference. When using them, only the taxa which are present in both regions are taken into consideration. Not taken into account are the taxa of the sampling which are absent in the two regions. The similarity or difference is estimated solely in relation to the given pair of regions. But the absence of particular species can be regarded as a typical feature of the regions. The species of the sampling which are absent in both regions are considered to be on a par with those that are present in the

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exponents of the second group (3a, b and 4a, b in fig. 13), which we designate as measures either of absolute similarity or difference for the sampling in question or of the similarity or difference which is common to all of the regions being compared.

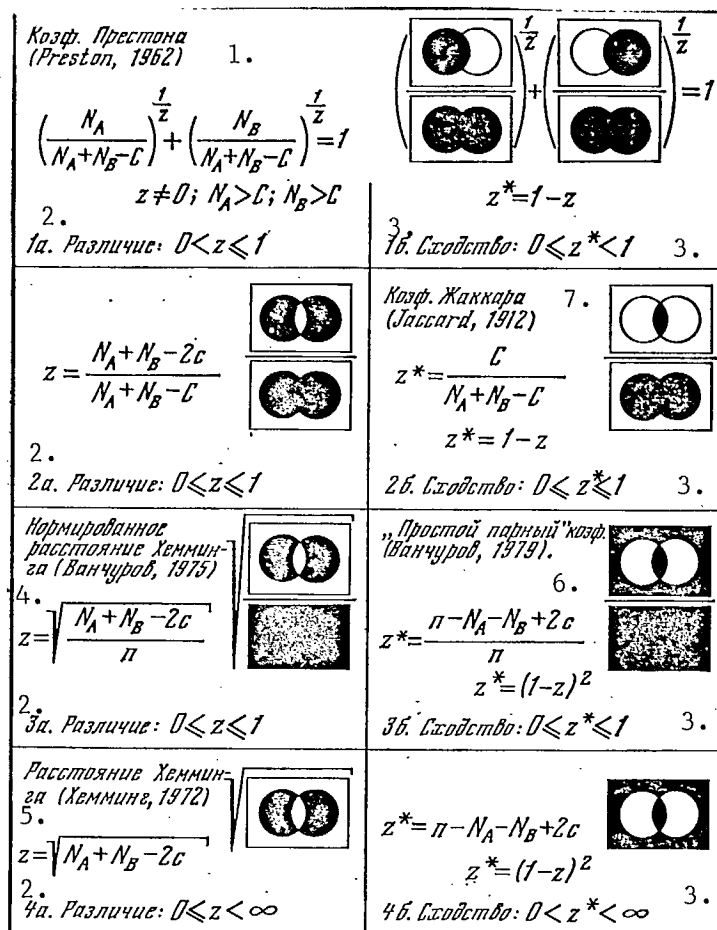


Fig. 13. Some symmetrical measures of similarity (z^*) and difference (z) used in biogeography and systematics.

- Key:
1. Preston's coefficient (Preston, 1962)
 2. Difference.
 3. Similarity.
 4. Khemming's normalised distance (Vanchurov, 1975).
 5. Khemming's distance (Khemming, 1972).
 6. Simple paired "coefficient" (Vanchurov, 1979).
 7. Jaccard's coefficient (Jaccard, 1912)

From the formally mathematical point of view, the exponents of the second group are considered preferentially to the exponents of the first group [Vanchurov, 1975, 1979; Karelina and Pecherskii, 1978]. While not denying this, we note that these indices are based on another, wider definition of similarity. When they are used, an aggregate of values can be obtained which rules out any possibility of a biological interpretation. For example, two islands which are very far apart each have a small number of species and not a single species in common. Against the background of a large sampling these two islands, according to the coefficients of the second group, will have a very small difference (even making it possible to amalgamate them into one zone), which is solely on account of the absence of a large number of identical species. The position of an investigator who wishes to use these exponents will be roughly as follows: formal estimates of similarity or difference, while impeccable in themselves, have no relevance to hypotheses concerning the genesis and paths of evolution of the faunas, nor are they relevant to other biologically interesting explanations. The one is not a criterion for judging the other. For purposes of comparison we shall cite the values of the exponents of both groups when referring to our regions, but will keep in mind that the exponents of the first group are less dependent on the absolute number of species in each of the two regions and on the unequal degree of representativeness of the source data for the different regions. The two pairs of regions being compared, while having the same proportion of common species and like similarity

according to Jaccard, but differing from one another with respect to the number of species, will have unlike similarity according to the simple paired coefficient (the greater the number of species, the greater the similarity). These two measures (2,b and 3,b in fig. 13), like measures 2a and 3a, are not equivalent.⁶ It is not only measures 3a and 4a that are equivalent, but also 3b and 4b, since division by the size of the sampling n , which is the same for all of the regions being compared, in principle changes nothing.

Also assembled in fig. 13 are pairs of coequivalent measures (a is the difference, b - the similarity). There is no fundamental difference between the two coequivalent measures. If the value of the difference is known, then in order to find out the similarity there is no need to go to the source data. It is sufficient to know the dependence by which the coequivalent measures of the pair in question are related. Measures 1a and 1b, like measures 2a and 2b, are related by a decreasing linear dependence, mutually complementing one another to unity, while measures 3a and 3b, like measures 4a and 4b, are related by a decreasing quadratic dependence. Finding the root in case 3a makes the measure more sensitive in comparison with 3b, while in case 4a, the values of the derived differences are more readily visible.

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⁶On the notion of the equivalence and coequivalence of measures of similarity, see also Semkin and Dvoichenkov [1973] and Andreev [1979, 1980].

Preston's coefficients $1a$ and $1b$ are not directly related by a functional dependence with Jaccard's coefficient and measure $2a$ which is derived from the latter. Therefore, they cannot be considered equivalent in the strict sense of the word. In our material, however, it is established that a definite empirical dependence between these exponents nevertheless exists (cf. figs. 16 and 18). The spread of the points on the graphs (see fig. 16) is comparatively minor and they are arranged lengthwise along the curve in a manner reminiscent of a very gentle symmetrical parabola (if the graph is turned 45° in a clockwise direction), or a catenary. These measures, related by a readily noticeable empirical, but not strictly functional, increasing dependence, can be called quasiequivalent.

In the literature one can come across the statement that Preston's method gives more reliable results than does Jaccard's, since when estimating the difference according to Preston [Preston, 1962] the criterion which is used for determining the reliability of the differences is 0.27. This threshold value $z=0.27$ (or in the case of a similarity: $z^*=0.73$) was established by Preston on the basis of certain theoretical considerations, viz., the hypothesis of the lognormal distribution of the number of species N in relation to the area of the region A , i.e., $N=kA^z$, where k and z are constants (z also enters into Preston's fundamental equation - see fig. 13). So in actual fact the reliability of the difference between two aggregations of taxa when $z > 0.27$ bears no relation whatsoever to the reliability of the results of measuring the similarity or difference which are

derived by the use of Preston's measures. The reliability of those results, as is the case when using other measures, depends on the volume and representativeness of the sampling, irrespective of whether we accept or do not accept Preston's theoretical justification of the threshold value z which was selected by him. The table [Preston, 1962, p. 419] for calculating the exponent z does not contain any corrections for the representativeness or size of the sampling.

Sometimes, objections are raised to the use of Preston's equation on the basis that it is complicated, lacks visual clarity and is mathematically incorrect, and that even in the event of it being correct, it is not so in all conditions (Vanchurov and Semkin, personal communication). For instance, when $z=0$ the sum of the left portions of the equation (see fig. 13) equals not 1, but 2. It is impossible to use this equation in those instances when a list of the taxa of one region is fully incorporated in a list of another (here, the sum of the left portions of the equation is greater than 1), that is, in those cases in which Jaccard's coefficients or the unsymmetrical measures of Simpson and Braun-Blanke et al., are operative (for details of these and other measures, see Vanchurov [1975, 1979] and Andreev [1979, 1980]). All the same, despite the criticisms and having regard to these limitations, Preston's method has the advantage of being one of the most sensitive. Although the hypothesis of a lognormal distribution of the number of species as a function of the area of the region has not been verified in the case of the South American Shelf, it appears altogether probable.

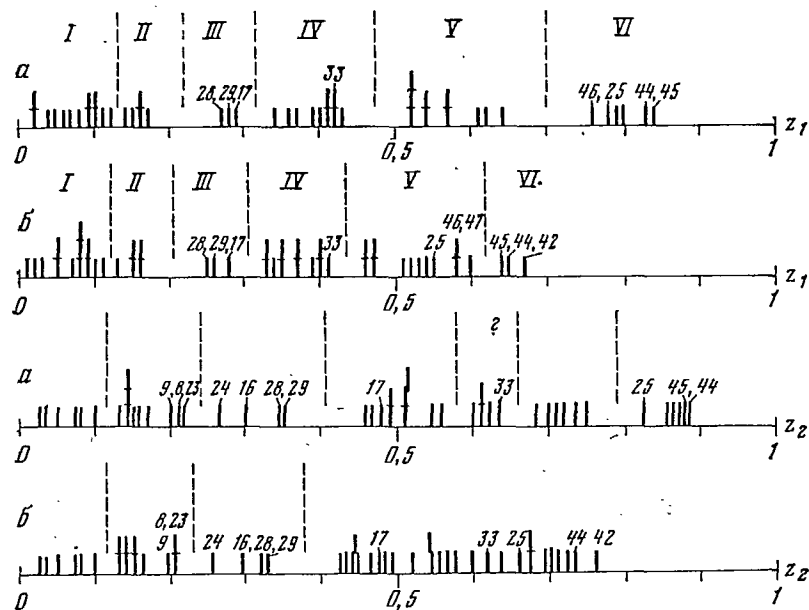


Fig. 14. Distribution along the number scale of the values of the exponents of the difference between the faunas (z_1 and z_2) of 47 pairs of adjacent regions of the South American Shelf.

a - without taking into account and b - taking into account the boundary species. The 6 groups of values of the Preston exponent (z_1) correspond to the following units of differing biogeographic rank (table 5): I - different districts and subdistricts, II - superdistricts, III - subprovinces, IV - provinces, V - superprovinces and subregions, VI - different regions.

When using any of the measures of similarity that have been cited the assumption is made that the species completely occupy the entire territory of the region. This assumption is not true at all times, even when comparing very small regions. Moreover, the matter is complicated by the boundary effect.

It was stated above that approximately one-fifth of the shelf species off the coasts of South America have a "punctate" range and that they live in the zones of thickening of the boundaries between the ranges of other species, that is, at the boundaries between the faunistic regions. Besides the endemic boundary species, there are species with wider ranges, of which small, detached populations also live in the boundary zones [Semenov, 1977b, 1978].

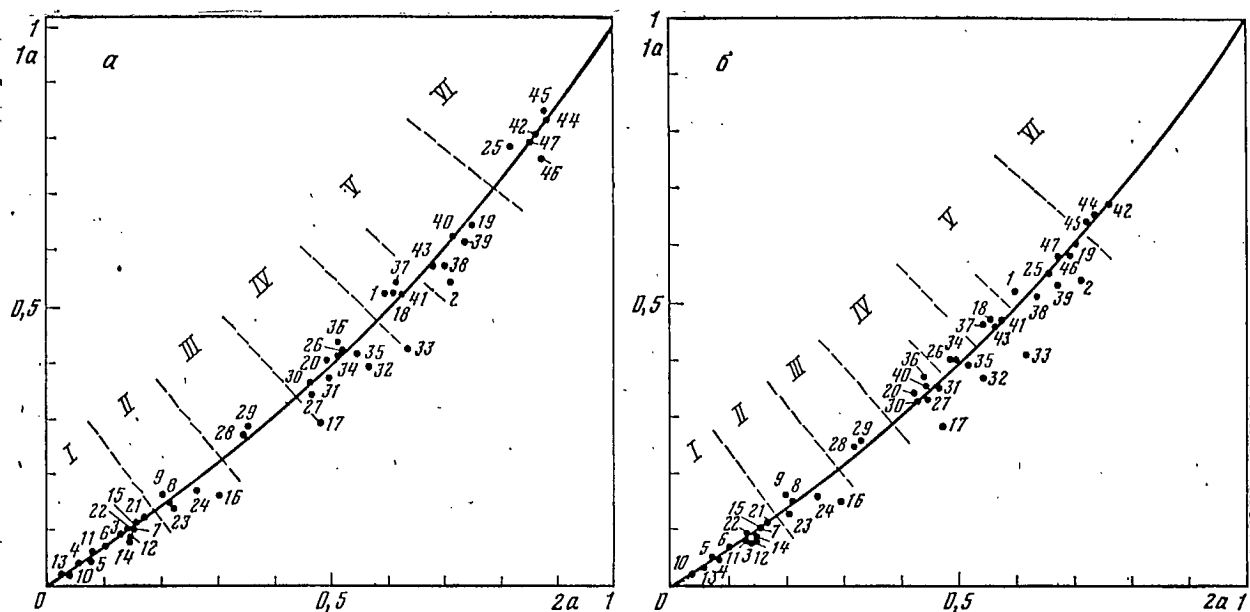


Fig. 15. Two-dimensional representation of a set of values of Preston's quasiequivalent measures of difference ($1a, z_1$) and of the exponent ($2a, z_2$) derived from Jaccard's coefficient, for 47 pairs of adjacent regions of the South American Shelf (the regions illustrated in fig. 14 and in table 4).

a - without taking into account, and b - taking into account the boundary species.

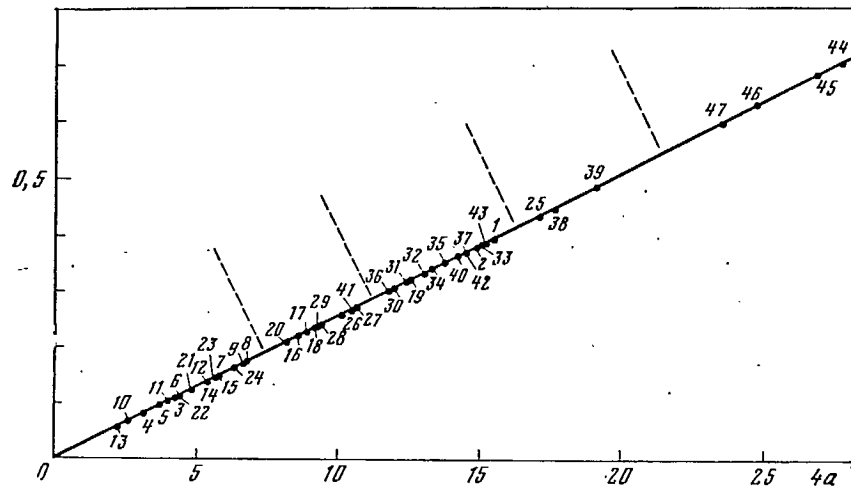


Fig. 16. Distribution of the values of two equivalent measures of difference $3a$ and $4a$.

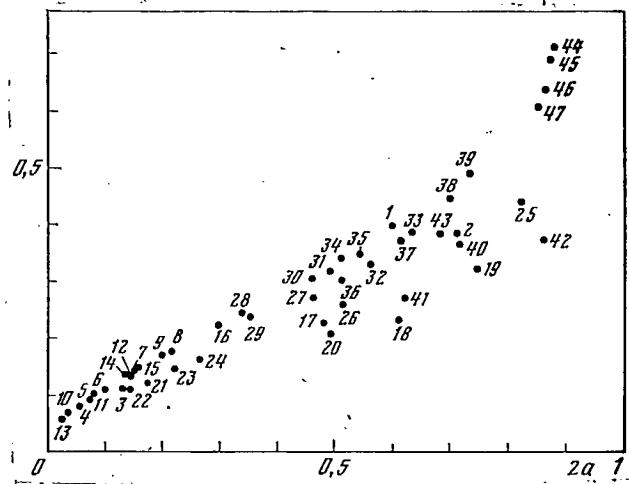


Fig. 17. Distribution of the values of two non-equivalent measures of difference $-2a$ and $3a$.

A possible interpretation is that the boundary species do not inhabit the territories of either the first or the second region, but another way of thinking is as follows: that they belong to the fauna of each of the two regions separately and at the same time are species

common to both. In a number of cases it is quite impossible to ignore the boundary species, for example, in the Tierra del Fuego and Falkland Islands region, where they constitute almost half of the fauna. In the calculation of the exponents of the first group the results depend on whether or not the boundary species are taken into consideration. Therefore, our calculations with respect to Preston and Jaccard (of exponents 1a and 2a) are performed in two variants (see table 4). The addition or subtraction of the boundary species when calculating the exponents of the second group (3a and 4a) changes nothing.

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Table 4. Values of the exponents of the difference between the faunas (z_1, z_2, z_3) for 47 pairs of adjacent regions off the coasts of South America.^{**}

- Key:
1. Pairs of regions being compared
 2. Boundaries of the regions (south latitude)
 3. Without taking the boundary species into account
 4. Taking into account the boundary species
 5. Number of species
 6. Values of the difference between the faunas
 7. Of each region (N_A, N_B)
 8. Common to two regions (C)
 9. Pacific coast
 10. Tierra del Fuego
 11. Atlantic coast
 12. Pacific Ocean
 13. Falkland Islands
 14. Atlantic Ocean

^{**} The Roman numerals correspond to the groups of values of z_1 in fig. 14 and table 5.

*If the 45 boundary species are assumed to form part of the fauna of the Chonos-Chiloe region (41°30'–45° S. lat.).

Таблица 4

Величины показателей различия фаун (z_1 , z_2 и z_3) для 47 пар смежных районов у берегов Южной Америки.

Римские цифры соответствуют группам величины z_1 на рис. 14 и в табл. 5

1	2 Границы районов (широта южная)	3 Без учета пограничных видов					4 С учетом пограничных видов				
		5 Число видов		6 Величины различия фаун			5 Число видов		6 Величины различия фаун		
		7	8	z_1	z_2	z_3	7	8	z_1	z_2	
Пары сравниваемых районов	Границы районов (широта южная)	каждого района (N_A, N_B)	общих для двух районов (C)	z_1	z_2	z_3	каждого района (N_A, N_B)	общих для двух районов (C)	z_1	z_2	
9 Тихоокеанское побережье											
	3—6° с. ш.	275					275				
1	1—2° ю. ш.	285	161	0,52 (V)	0,60	0,39	285	161	0,52 (V)	0,60	
	5°5'—6°57'	285					285				
	1—2°	285					285				
2	5°5'—6°57'	122	92	0,54 (V)	0,71	0,38	122	92	0,54 (V)	0,71	
	9°	122					127				
	5° (6°57')	122					127				
3	9°	132	118	0,09 (I)	0,13	0,11	137	123	0,08 (I)	0,13	
	12—14°	174					176				
	18°30'—20°	174					176				
4	22—23°30'	178	171	0,04 (I)	0,05	0,08	180	173	0,03 (I)	0,05	
	25°30'	178					181				
	22—23°30'	178					181				
5	25°30'	182	173	0,05 (I)	0,08	0,10	185	176	0,05 (I)	0,07	
	29—30°	183					186				
	18°30'—20°	183					186				
6	25°30'	182	173	0,07 (I)	0,10	0,11	185	176	0,07 (I)	0,10	
	29—30°	182					184				
	25°30'	182					184				
7	29—30°	201	176	0,10 (I)	0,15	0,14	203	178	0,09 (I)	0,15	
	33°	183					186				
	18°30'—20°	183					186				
8	25°30'	209	173	0,15 (II)	0,21	0,17	212	176	0,15 (II)	0,21	
	33°	209					212				

Таблица 4 (продолжение)

Пара сравняемых районов	Границы районов (широта южная)	Без учета пограничных видов					С учетом пограничных видов				
		Число видов		Величины различия фаун			Число видов		Величины различия фаун		
		каждого района (W, N, B)	общих для двух районов (C)	z ₁	z ₂	z ₃	каждого района (W, N, B)	общих для двух районов (C)	z ₁	z ₂	

9 Тихоокеанское побережье

9	18°30'—20°	195				197			
	29—30°	176	0,16 (II)	0,20	0,17	178	0,16 (II)	0,20	
10	33°	201				203			
	33°	204				204			
10	34°56'	201	0,02 (I)	0,03	0,07	201	0,02 (I)	0,03	
	37°	205				205			
11	37°	194				197			
	39°50'—40°	186	0,06 (I)	0,08	0,10	189	0,05 (I)	0,08	
12	41°30'—43°	194				194			
	41°30'—43°	198				203			
12	45—46°	174	0,09 (I)	0,14	0,14	179	0,08 (I)	0,14	
	(48) 49°	179				184			
13	45—46°	179				179			
	(48) 49°	177	0,02 (I)	0,03	0,06	177	0,01 (I)	0,03	
14	Огненная Земля 10	180				180			
	41°30'—43°	203				203			
14	(48) 49°	177	0,08 (I)	0,14	0,14	177	0,08 (I)	0,14	
	Огненная Земля 10	180				180			
15	41°30'—43°	198				203			
	45—46°	174	0,11 (I)	0,16	0,14	179	0,10 (I)	0,15	
16*	(48) 49°	182				187			
	Огненная Земля 10	243				248			
16*	41°30'—43°	243				248			
	45—46°	174	0,16 (II)	0,30	0,22	179	0,15 (II)	0,29	
16*	(48) 49°	179				184			

Таблица 4 (продолжение)

Пары сравниваемых районов	Границы районов (широта южная)	Без учета пограничных видов					С учетом пограничных видов			
		Число видов		Величины различия фаун			Число видов		Величины различия фаун	
		каждого района (N, N _B)	общих для двух районов (C)	z ₁	z ₂	z ₃	каждого района (N, N _B)	общих для двух районов (C)	z ₁	z ₂
9 Тихоокеанское побережье										
40	41°30'—43° Тихий океан	12	208				385			
	Огненная Земля	10		81	0,62	0,72	0,36	258	0,35	0,44
	Фолклендские (Мальвинские) острова	13			(V)				(IV)	
	42°, Атлант. океан	14	158				335			
Атлантическое побережье										
41	Огненная Земля									
	Фолклендские (Мальвинские) острова		145				160			
42	42°		102	68	0,52	0,62	0,27	117	83	0,47
	35—38°				(V)				(V)	0,57
43	42°		102				134			
	35—38°			34	0,80	0,86	0,37	66	0,67	0,76
44	23—24°		175		(VI)		207		(VI)	
	35—38°						244			
45	23—24°		175	107	0,57	0,68	0,39	176	0,46	0,56
	13°		267		(V)		336		(V)	
46	1—5° Тихий океан	12	544				721			
	Огненная Земля	10		105	0,83	0,88	0,71	282	0,65	0,73
47	Фолклендские (Мальвинские) острова	13			(VI)				(VI)	
	23—24°, Атлант. океан	14	434				611			

Таблица 4 (окончание)

Пары сравниваемых районов	Границы районов (широта южная)	Без учета пограничных видов					С учетом пограничных видов			
		Число видов		Величины различия фаун			Число видов		Величины различия фаун	
		каждого района (WA, NB)	общих для двух районов (C)	z_1	z_2	z_3	каждого района (WA, NB)	общих для двух районов (C)	z_1	z_2
11 Атлантическое побережье										
45	12—14°, Тихий океан	12	487				664			
	Огненная Земля	10								
	Фолклендские (Мальвинские) острова	13	101	0,84 (VI)	0,88	0,68	278	0,64 (VI)	0,72	
46	23—24°, Атлант. океан	-14	434				611			
	1—5°, Тихий океан	12	544				721			
	Огненная Земля	10								
47	Фолклендские (Мальвинские) острова	13	94	0,76 (VI)	0,87	0,63	271	0,58 (V)	0,69	
	35—38°, Атлант. океан	14	255				432			
	12—14°, Тихий океан	12	487				664			
47	Огненная Земля	10								
	Фолклендские (Мальвинские) острова	13	94	0,79 (VI)	0,85	0,60	271	0,58 (V)	0,67	
	35—38°, Атлант. океан	14	255				432			

* Если считать 45 пограничных видов в составе фауны Чоно-Чилотского региона (41°30'—45° ю. ш.).

Table 5. Empirical range of the values of the exponents of the difference (z_1 and z_2) corresponding to units of different biogeographic rank.

1	Величины различий	2 Округ, подок- руг	3 Надок- руг	4 Под- провин- ция	5 Провинция	6 Надпровинция, подобласть	7 Область	
8	Без пограничных видов	z_1	0,01— 0,12	0,14— 0,17	0,27— 0,29	0,34— 0,43	0,52—0,62	0,78— 0,84(?)
		z_2	0,03— 0,17	0,20— 0,30	0,34— 0,35	0,45— 0,57	0,59—0,75	0,82— 0,86(?)
9	С пограничными видами	z_1	0,01— 0,11	0,13— 0,16	0,25— 0,28	0,33— 0,41	0,46—0,58	0,64— 0,67(?)
		z_2	0,03— 0,16	0,19— 0,30	0,32— 0,33	0,42— 0,58(?)	0,59—0,71(?)	0,72— 0,76(?)

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Key: 1. Values of the differences 2. District, subdistrict
 3. Superdistrict 4. Subprovince
 5. Province 6. Superprovince, subregion
 7. Region 8. Without the boundary species
 9. With the boundary species

In order to achieve maximum agreement between the scheme of faunistic zonation and the actual chorological structure, it is necessary to find the natural range of the values of similarity or difference, if such exists, and to correlate it with the adopted categories of the biogeographic scheme. We are using the most universally adopted hierarchic type of scheme. We are arranging the values of the exponents of the difference between the faunas (z) of the various pairs of large and small adjacent regions of the South American Shelf (table 4) in ascending order along a number scale (fig. 14) and in two-dimensional diagrams in a rectangular system of coordinates (figs. 15-17). Closely similar values of z are amalgamated into individual groups, separated by more or less definite intervals

and roughly corresponding to units the rank of which ranges from subdistrict and district to region (oblast') (table 5).

If, for example, the difference between the regions (regiony) lies in the range $z_1 = 0.33 - 0.43$ according to Preston (coefficient 1a in fig. 13) or in the range $z = 0.42 - 0.59$ according to coefficient 2a, derived from Jaccard's coefficient, then these regions belong to different provinces. We recall the theoretical interpretation of Preston's exponent (z_1): when $z_1 = 1$ the faunas are absolutely different and exist in total isolation, when $z_1 = 0.27$ the faunas are in equilibrium - a more or less free exchange of taxa occurs between the territories, and when $z_1 = 0$ the fauna is absolutely unitary, which can only be the case within units of very low rank. The agreement between the groups of z_1 values on the number scale (see fig. 14) and the units of definite rank is found to be such that even for very large territories, belonging to the same province, the values of this exponent of the difference lie close to the point of equilibrium. It is interesting to note that here, the values of the quasiequivalent measure z_2 , derived from Jaccard's coefficient, were found to be in almost the same range as that pertaining to the land fauna ($\sim 0.40-0.60$) [Neronov and Lushchekina, 1980]. These authors give values of $z_2 \approx 0.60-0.78$ (on conversion from Jaccard's coefficient to our measure 2a) for the various subprovinces, $z_2 \approx 0.78-0.90$ for the subregions and $z_2 \approx 0.92-1$ for the regions (oblast'). This range of measure 2a, the more so of Preston's 1a, would have been clearly excessive in the case of the adjacent regions of Shelf-inhabiting marine fauna.

As already indicated, the difference between the faunas according to coefficients 1a and 2a depends on whether or not the boundary effect is taken into consideration. The greatest disparity between the groups of values z_1 and z_2 in table 5 and fig. 14 occurs with regions of high rank, since it is precisely these regions which are separated by the most significant boundaries, where the greater part of the boundary species are concentrated.

We will now consider some concrete examples with respect to refinement of the rank of the regions. If we compare the difference between the faunas of the 8th and 9th pairs of regions (table 4, figs. 15, 16), it will be seen that the water area extending from $18^{\circ}30'$ - 20° to 33° S. lat., off the Pacific coast must be subdivided into two superdistricts. However, it is not clear along which boundary this should be done, $25^{\circ}30'$ or $29-30^{\circ}$ S. lat., ("according to Preston", preference can be given to one boundary, according to coefficients 2a and 3a - to another). We then compare the other pairs of regions: 4, 5 and 7 (table 4), which are distinguished in the water area extending from $18^{\circ}30'-20^{\circ}$ to 33° S. lat. It follows from the diagrams (figs. 15, 16) that the boundaries near $22^{\circ}-23^{\circ}30'$ and $25^{\circ}30'$ S., corresponding to pairs 4 and 5, separate water areas with the rank of subdistrict, and the boundary near $29-30^{\circ}$ S., corresponding to the 7th pair, separate minimal regions with the rank of district (this boundary is also more significant with respect to the relation between the number of boundaries of the species ranges - fig. 12). Consequently, in the water area extending from $18^{\circ}30' - 20^{\circ}$ S., a single, Coquimbian, district (from $29-30$ to 33° S.) must be distinguished, with the following minimal regions: the Tara-

pacan (from $18^{\circ}30' - 20^{\circ}$ to $22^{\circ} - 23^{\circ}30'$ S.), the Antofagastan (from $22^{\circ} - 23^{\circ}30'$ to $25^{\circ}30'$ S.), and the Saladan (from $25^{\circ}30'$ to $29 - 30^{\circ}$ S.), being distinguished as subdistricts. Earlier, however, we found that the 8th and 9th pairs of regions (both are within the above indicated large water area - the Atacaman subprovince) are distinguished as superdistricts. Accordingly, the three subdistricts that we enumerated are integrated into a Tarapacá - Saladan superdistrict (see table 6). Thus, the Atacaman subprovince consists of one superdistrict, including three subdistricts, and a separate Coquimbian district (see fig. 19 and table 6).

In a number of cases the estimates of rank fully correspond to the results obtained in the classification of boundaries according to their significance (the second chorological method), while in some cases there is no correspondence. For example, it turns out that the boundaries ranked as provincial off the Pacific coast and situated near 33° and 37° S., do not separate provinces, but subprovinces which are more similar with respect to fauna (cf. the 28th and 29th pairs of regions in figs. 15, 16 and tables 4-5). It is not five, but only three provinces which are distinguished in the temperate waters off the Pacific coast of South America (see figs. 19 and 20 below).

We will consider yet another incompletely clear case: the sub-
division of the Southern Brazilian-Uruguayan region (superprovince) into the Catarinan-Paulian and Rio Grandian regions (table 4, 17th pair). If the difference between the corresponding faunas is estimated according to Preston (fig. 14, table 5) or according to

coefficient 3a (fig. 16), this region is subdivided into two sub-provinces, but if according to coefficient 2a (fig. 14), then it is subdivided into two provinces. If we turn now to the two dimensional representation of the difference between the faunas according to coefficients 1a and 2a (fig. 15), then the division obtained, like that based on coefficient 2a, is into provinces. It is important to note that a two dimensional representation of the difference or similarity on number scales is, in general, more graphic than a one dimensional. The difference in this case is read off along the diagonal of the diagram, or more precisely, along the line indicating the relation between the two measures.

The use of estimates of the difference between faunas for correlating the results of a zonation makes it possible to arrive at the following conclusions:

1. The fauna of the Northern Peruvian α -region between 2-5° and 12-14° S. lat. more closely resembles the faunas of the temperate waters than the tropical fauna (table 4, pairs 25, 26). Therefore, the boundary between the corresponding zoogeographic regions is taken to be almost the same as it is with the second method of zoning, near 4°30'-5°05' S.⁷ This is also the case when it is based on the relation

⁷The values of the indices 3a and 4a (fig. 16) of the difference between the faunas of the South American temperate region and adjacent tropical regions proved to be lower than those for the regions, due to the fact that it was not entire tropical regions, but only parts of them, that were compared. As mentioned earlier, in such cases these exponents are useless.

between species with a dissimilar type of distribution and presumed origin.

2. Conversely, the fauna of the Southern Brazilian-Uruguayan α -region lying between $23-24^{\circ}$ and $35-38^{\circ}$ S. lat. more closely resembles the tropical fauna than it does the Northern Argentinian fauna of the temperate waters (table 4, pairs 42, 43). This is also supported by the numerical relation between species with a dissimilar origin and type of distribution. On the basis of these considerations the boundary between the Western Atlantic tropical and the South American temperate zoogeographic regions (and the corresponding latitude zones in that region) is taken to be not near $23-24^{\circ}$ S. (the preeminent boundary), but near (the less significant) $33^{\circ}-35^{\circ}35'$ S. lat.

3. Subdivisions with the rank of subregion and superprovince are indistinctly differentiated with respect to lists of species. The corresponding values z_1 and z_2 are grouped on the number scale (fig. 14) and on the diagrams (fig. 15) without being sufficiently isolated. Two subregions are distinguished: the Pacific and the Atlantic South American. On the basis of the significance of the boundaries these water areas are distinguished as regions. They are also distinguished as independent regions on the basis of the faunas (all four indices) without taking into account the boundary - and insular species of Tierra del Fuego and the Falkland Islands (figs. 15-16). When the boundary species are taken into consideration, these water areas are distinguished (according to the Preston index and the index derived from Jaccard's coefficient) only as subregions.

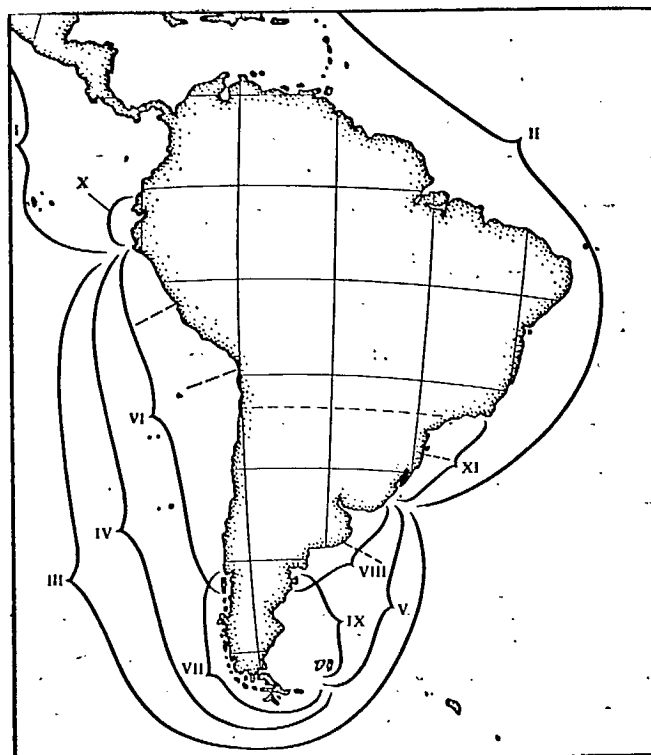


Fig. 18. Scheme of zoogeographic zonation of the South American Shelf taking into account the faunistic similarity - difference.

- I, II - Tropical regions (Eastern Pacific and Western Atlantic);
- III - South American temperate (Magellan) region;
- IV, V - Pacific (Andean) and Atlantic (Malvinian) South American subregions;
- VI, VII - Peruvian-Northern Chilean and Southern Chilean superprovinces;
- VIII, IX - Uruguayan-Northern Argentinian and Southern Argentinian superprovinces;
- X - Guayaquilian transitional region (superprovince?);
- XI - Southern Brazilian-Uruguayan superprovince.

Boundaries between the provinces denoted by a broken line. The complete scheme of zoogeographic zonation and the system of subordination of the regions will be found in fig. 19.

4. The Pacific South American (Andean) subregion is subdivided in the region between 41° and 43° into two superprovinces: a Peruvian-Northern Chilean (consisting of three provinces - a Northern Peruvian,

a Southern Peruvian and a Northern Chilean) and a Southern Chilean, which is not subdivided into provinces (figs. 18,19). The Atlantic South American (temperate) subregion is also subdivided - approximately between 41° and 43° - into two superprovinces: an Uruguayan-Northern Argentinian and a Southern Argentinian, or Patagonian (not including the Falkland Islands region). The Uruguayan-Northern Argentinian superprovince consists of two provinces: a La Platan transitional (from $32^{\circ}-34^{\circ}30'$ to $37^{\circ}-38^{\circ}30'$ S.) and a Buenos Airean (Northern Argentinian). The Southern Argentinian superprovince, like the Southern Chilean, is subdivided into water areas ranking no higher than superdistrict (fig. 19). The Southern Brazilian-Uruguayan α -region (region), extending from $23-24^{\circ}$ to $32^{\circ}-34^{\circ}30'$ S., is distinguished as an independent superprovince forming part of the Western Atlantic (Columbian) tropical region. It consists of two provinces or subprovinces - the Catarino-Paulian and the Rio Grandian, with the boundary between them situated along $27-28^{\circ}$ S. lat. These regions are not subdivided further.

5. Taken to be units of lower rank (subdistrict) are the smallest water areas, distinguished by the species-determinants, or the areas lying between the proximate zones of thickening of the boundaries of the species ranges (with the exception of certain secondary boundaries in the border zones), which are differentiated from the adjacent areas by the indices of difference $z_1 \leq 0.07$ and $z_2 \leq 0.10$. The values of z_1 with respect to the various adjacent districts are in the 0.08-0.12 range, of z_2 - in the 0.13-0.17 range. The complete scheme of zonation and subordination of regions differing in rank is presented in fig. 19 (see also table 6).

Table 6. Faunistic units distinguished off the coasts of South America

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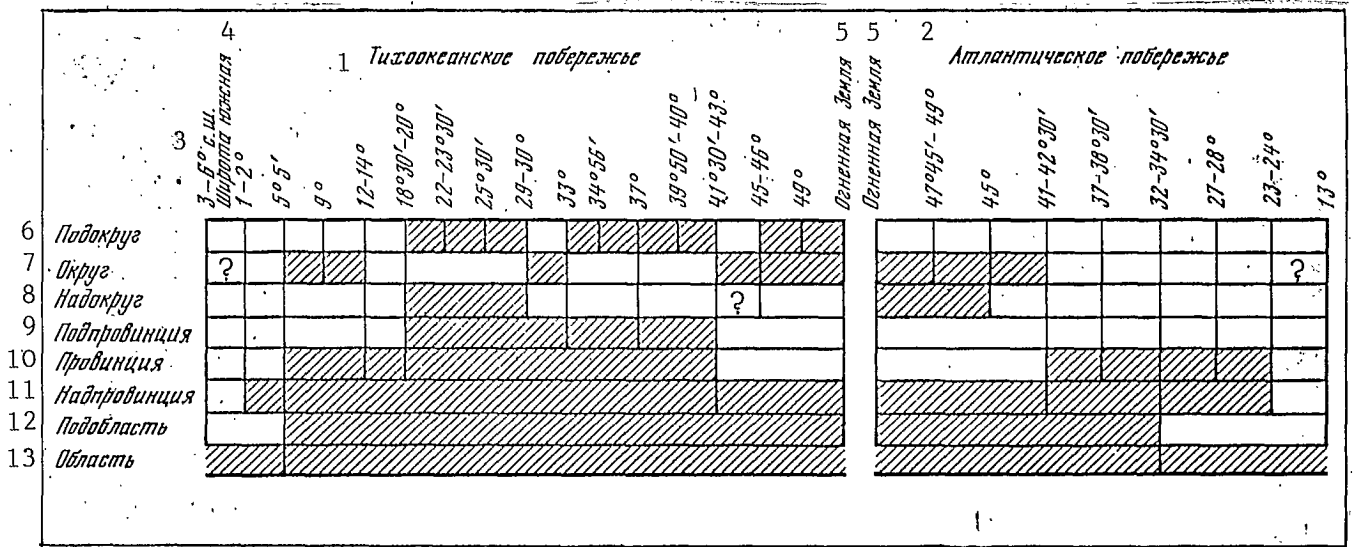
Region	Rank of Regions after correct- ion	Number of species N	Number of end- emic species			Number of Determinants	
			E	E%	D	D%	
(a) <u>Pacific coast (south latitude)</u>							
I Columbian-Ecuadorian, 5-6° N. lat., - 1-2°	District (?)	275	3	1,1	2	0,7	
II Guayaquilian, 1-2° - 5°05'(6°56')	Superprovince	285	65	23	5	1,8	
Libertadian, (4°30') 5°05'-6°57'-9°	District	122	1	0,8	1	0,8	
Liman, 9°-12-14°	District	132	5	3,8	5	3,8	
III Northern Peruvian, (4°30') 5°05'-6°57'-12-14°	Province	144	18	13	3	2,1	
IV Southern Peruvian, 12-14° - 18°30'-20°	"	155	2	1,3	3	1,3	
Tarapacan, 18°30'-20°-22-23°30'	Subdistrict	174	0	0	0	0	
Antofagastan, 22-23° - 25°30'	"	178	0	0	0	0	
V Tarapacan-Antofagastan, 18°30'-20° - 25°30'	"	183	1	0,5	1	0,5	
Saladan, 25°25'-29-30°	"	182	0	0	0	0	
Tarapacan-Saladan, 18°30'- 20°-30°	Superdistrict	195	5	2,6	0	0	
XVII Coquimbian, 29-30°-32°57'-33°20'	District	201	1	0,5	1	0,5	
VI Saladan-Coquimbian, 25°25'- 33°	"	209	2	1	3	1,4	
Atacaman, 18°30'-20°-33°	Subprovince	222	12	5,4	2	0,9	
Santiagosan, 32°57'-33°20'-34°56'	Subdistrict	204	1	0,5	1	0,5	
Maulean, 34°56'-36°40'-37°14'	"	205	0	0	0	0	
VII Central Chilean, 33°-37°	Subprovince	208	3	1,4	3	1,4	
XX Cautinian, 37°8'-38°16' - 39°50'-40°	Subdistrict	194	3	1,5	3	1,5	
Osornian, 39°50'-40°9'-41°30'-42°57'	"	194	3	1,5	3	1,5	
VIII Arauco-Chiloen, 37°-41°30'-42°57'	Subprovince	205	19	9	9	4,4	
Northern Chilean, 18°30'-20°-41°30'-43°(with the Juan Fernandez Islands)	Province	356	108	30	9	2,7	
Peruvian-Northern Chilean, 2-5°-41°30'-43°	Superprovince	425	183	43	7	1,6	
IX Chonos-Chiloen, 41°30'-43°-45-46°	District	198	5	2,5	1	0,5	
The same with the boundary group, 41°24'-43°	Superdistrict	243	31	13	1	0,4	
Taitao-Penasian, 45°-(48)49°	Subdistrict	179	0	0	0	0	
Magallanesian, 49°8'-49°24'- Tierra del Fuego	"	180	2	1,1	2	1,1	
X Taitao-Magallanesian, 45° - Tierra del Fuego	District	182	3	1,6	1	0,6	
Southern Chilean, 41°30' - Tierra del Fuego	Superprovince	253	46	18	12	4,7	
Pacific (Andean), 2-5° - Tierra del Fuego	Subregion	544	273	50	11	2	

Table 6 (continued).

(b) Atlantic coast

XVI	Bahian, 13°-23°-24°	District (?)	267	3	1,1	2	0,8
XXI	Catarino-Paulian, 23°-24°-27-28°	Subprovince	158	7	4,4	5	3,2
	The same with the boundary group, 23°-25°	"	235	38	16	5	2,1
	Rio Grandian, 27°-28°-32°-34°	"	93	2	2,2	0	0
XV	Southern Brazilian-Uruguayan, 23-24°	Superprovince	244	52	21	14	5,7
	Uruguayan-Northern Argentinian, 32-34°30'-41°30'-42°	"	158	36	23	15	9,5
XIV	La Platan, 32-34°30'-37°-38°30'	Province	134	23	17	3	2,2
XVIII	Buenos Airean, 37°-38°-41°30'-42°	"	108	13	12	11	10
	Montemayorian, 41°30'-42°-45°	District	119	3	2,5	0	0
	Jorgian, 45°-47°45'-49°	"	128	0	0	0	0
	Santa Cruzian, 47°45'-49° - Tierra del Fuego	"	121	4	3,3	3	2,5
	Southern Patagonian, 45° - Tierra del Fuego	Superdistrict	145				
XII	Patagonian, 41°30'-42° - Tierra del Fuego	Superprovince	158	18	11	3	1,9
	Southern Argentinian, 41°-42°30' - Tierra del Fuego, Falkland Islands	"	171	30	18	9	5,3
	Atlantic (Malvinian), 32-34°30' - Tierra del Fuego, Falkland Islands	Subregion	277	91	33	10	3,6
XXIV	Falklandian.	District (?)	259	24	9	35	14
XI	Tierra del Fuegan transitional	?	373	43	12	48	13
	Tierra del Fuegan - Falklandian	?	439	83	19	19	4,3
	South American temperate (Magellans) southwards of 2-5° in the Pacific and 32-34°30' in the Atlantic.	Region	1004	478	48	0	0

Note: I-XVI and XXIV are elementary biotopes and α -districts, distinguished on the basis of species-determinants; XVII, XX and XXI are α -subdistricts (some are undesignated, see fig. 1).



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Fig. 19. Scheme of subordination of regions differing in rank, distinguished off the coasts of South America.

- Key:
- | | |
|----------------------|--------------------|
| 1. Pacific coast. | 8. Superdistrict. |
| 2. Atlantic coast. | 9. Subprovince. |
| 3. N. lat. | 10. Province. |
| 4. S. lat. | 11. Superprovince. |
| 5. Tierra del Fuego. | 12. Subregion. |
| 6. Subdistrict. | 13. Region. |
| 7. District. | |

The rank of the first order Guayaquilian and La Platan α -regions, which are distinguished as α -districts according to the species determinants (table 6), proves to be unexpectedly high. The Guayaquilian border region together with all the border groups of species is distinguished from the adjacent regions as a superprovince or even a subregion ($z_1 = 0.52-0.54$, $z_2 = 0.60-0.71$, $z_3 = 0.38-0.39$: see table 4, pairs 1 and 2), the similarity of this fauna to the tropical being greater than it is to the temperate. This region is also distinctive

for the high degree of endemism (about 23%), compared with the average level of endemism of the fauna of the superprovinces (22.5% according to table 6). The La Platan transitional region belongs to the South American temperate (notalial) region (oblast') (figs. 18, 19) and is differentiated from the neighbouring Buenos Airean, as a province on the basis of Preston's and Jaccard's indices ($z_1 = 0.34-0.40$, $z_2 = 0.42-0.49$) and as a province or subprovince on the basis of Vanchurov's coefficient ($z_3 = 0.21$). The degree of endemism (17%) corresponds to the average degree of endemism of the fauna of the provinces ($\sim 16.5\%$). The status of the Tierra del Fuegan and Falklandian transitional regions, both jointly and separately, is almost impossible to determine, since the distribution of the vast majority of the species in this region is not indicated with a sufficient degree of precision in the literature.





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The biogeographic zonation of the South American Shelf
based on a classification of the ranges of
bottom-dwelling invertebrates

(Translated from Russian)

Third of Three Installments

(Pages 87-142)

Links between the South American Shelf
fauna and the faunas of other oceanic regions

A list of the regions having benthic species in common with the coastal regions of South America is presented in table 7. There are 32 of these, with more than half of them oceanic islands. Certain of the regions and also the types of distribution of a small proportion of the species are indicated inaccurately in the literature, for example, the "Indo-Pacific" or "Cosmopolitan".

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Mathematical estimates involving the use of measures of similarity or difference are not cited for the other oceanic regions. This is because species of other regions which are not found in the South American Shelf zone do not enter into our sampling.

Of the tropical and bitropical species living near the coasts of South America and falling within our sampling which is limited to the tropical regions (see above), most are species common to islands of the tropical zone situated close to the South American mainland: the Galapagos Islands (71 species), the Bermudas (51), and the islands of Fernando de Noronha and Rocas (29 species). More remote habitats are tropical West Africa (23 species), Revilla Gigedo and Clipperton Islands (14), the Cocos Islands (11), the Mediterranean and Black Seas (9), Zelenyy Mys Island (8), and the islands of Saint Helena and Ascension (8).

As regards the species of the next major group, living in both the tropical and the temperal (temperate) zones - the tempero-tropical, bitropical-temperal and nototropical-temperal zones - among the other

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regions where they are noted are first and foremost the Galapagos Islands (35 species) and also the following islands of the temperate zone situated immediately proximate to the mainland: Juan Fernandez, San Felix and San Ambrosio (18). More distantly situated are the Mediterranean and Black Seas and Western Europe (Atlantic coast) - each with 12 species; and tropical West Africa, South Africa and Japan and China, each with 10 species. The Bermudas and the "Indo-Pacific" are each accounted for by 8 species.

With respect to the nototemeral species of the other regions of the World Ocean, the following regions situated between 33° and 50° S., in the zone of influence of the westerlies are in the lead: New Zealand and the adjacent islands - Macquarie, Chatham, Campbell, Auckland, the Antipodes and Bounty (30 species), South Africa (23), Kerguelen and Heard Islands (22), Southeastern and Southwestern Australia (18), the islands of Juan Fernandez, San Felix and San Ambrosio (15), Tristan-da-Cunha and Gough Islands (10), and Prince Edward Island (9).

A third of the 165 South American-Antarctic species (55 species) are found near Kerguelen and Heard Islands. Of the other regions where the species of this group occur, in first place are the following regions, also in the zone of influence of the Westerlies: New Zealand and the offshore islands (28 species), South Africa (4), Southeastern and Southwestern Australia (5), Prince Edward Island and Crozet Island (19), Bouvet Island (11) and the Eastern Pacific Rise (7).

A very remarkable fact is the threefold reduction in the number of South American-Antarctic species near Prince Edward and Crozet Islands, as compared to Kerguelen and Heard Islands which are situated relatively close to them and at almost the same latitude: 19 species as compared to 55. This is only partly explained by the fact that Kerguelen is located in the Antarctic Convergence Zone (Heard Island is even further south), with Prince Edward Island and Crozet Island situated slightly to the north of it. It is more probable that the difference in the numbers of species is a consequence of the geological youthfulness of Prince Edward and Crozet Islands as compared with Kerguelen and Heard Islands [Frost et al., 1976]. The region occupied by Kerguelen and Heard Islands is included in the South American-Antarctic (Austral) superregion, distinguished on the basis of species-determinants. Juan Fernandez, San Felix and San Ambrosio Islands are included in the South American temperate region. Apparently also to be included in this region are Tristan da Cunha and Gough Islands [Briggs, 1974]. In terms of the benthic fauna, the Galapagos Islands, Revilla Gigedo Island, Clipperton Island and the Cocos Islands belong to the Eastern Pacific tropical region, and the Bermudas and Fernando de Noronha, to the Western Atlantic tropical region. The latter region has a fairly large number of elements in common with the Eastern Atlantic tropical region (tropical West Africa). Assuming that the tropical and bitropical species are autochthonous, have relatively small ranges and are in general younger than the tempero-tropical, bitropical-temperal and nototropical-temperal species with

a more extensive distribution, it can be postulated that there has been a relatively recent exchange of faunistic elements between the west and east coasts of the tropical zone of the Atlantic.

The latitudinal zoning of the South American benthos

The distinction between a faunistic and a latitudinal division into zones* was discussed at the outset of this study. The faunistic division is primarily directed at identifying and describing the unique, inimitable characteristics and peculiarities of the chorological structure of a biota. With the zonal method, everything is subordinated to the task of singling out similar and regularly recurring units, whether they be types of distribution of taxa or the regular patterns of alternation of faunistic elements, entire faunas and regions. These patterns can also be studied from the ecological perspective - the dependence on environmental and climatic factors - and in more abstract terms, from the perspective of the spatial symmetry of organisation of the living cover. Although our faunistic zonation is based on the natural chorological structure, it would have been impossible to dispense with certain assumptions. A zonal division is even more tentative than a faunistic. In this system of units, even though faunistic data and data on the nature of the environment, the latter dictating the distribution of the species, are combined into a single scheme, a zonal division does not by itself substitute for a division based on geographic landscape, remaining as it does a domain of biological science [Neiman et al., 1977].

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* Used here as a synonym of 'zonation' (Tr.).

Table 7

Number of species comprising the sampling of the South American fauna which are common to other regions of the World Ocean.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Группы видов	Всего видов	Новая Зеландия и район от о. Чатем до о. Маккуори	Юго-восточная и юго-западная Австралия	Южная Африка	Острова Кергелен и Херд	Острова Принс-Эдуард и Крозе	О-в Буве	Острова Тристан-да-Куния и Гоф	Острова Фернанду-ди-Норонья и Рокас	Бермудские острова	Острова Хуан-Фернандес, Сан-Феликс и Сан-Амбросио	Восточно-Тихоокеанское поддугие, 54—55° ю. ш.	Острова Сен-Поль и Амстердам	Красное море, Персидский залив	Средиземное и Черное моря	Тропическая западная Африка	«Космополиты» *	Гавайские острова
37 Тропические	615	—	?	—	—	—	—	—	18	32	2	—	—	3	6	15	5	2
38 амфиамериканские	21	—	?	—	—	—	—	—	1	7	1	—	—	2	3	3	3	—
39 тихоокеанские	270	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	2	2
40 атлантические	166	—	—	—	—	—	—	—	17	25	—	—	—	—	—	—	—	—
41 Битропические	158	1	?	1	—	—	—	—	11	19	—	—	—	1	3	11	1	—
амфиамериканские	13	—	?	1	—	—	—	—	1	2	—	—	—	3	2	8	—	—
тихоокеанские	40	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
атлантические **	105	—	—	—	—	—	—	—	10	17	—	—	—	2	2	6	—	1
42 Темперо-тропические	49	—	—	4	—	—	—	—	3	5	—	—	—	—	2	2	1	1
амфиамериканские	7	—	—	1	—	—	—	—	2	2	—	—	—	—	—	1	1	1
тихоокеанские	25	—	—	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—
атлантические	17	—	—	1	—	—	—	—	1	3	—	—	—	—	2	—	—	—
43 Битропическо-темперальные	55	2	3	5	1	1	—	2	1	3	8	—	—	2	7	5	5	5
амфиамериканские	12	—	—	2	—	—	—	—	1	3	4	—	—	1	2	3	4	1
44 циркум-южноамериканские	1	1	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
тихоокеанские	25	1	2	2	—	—	—	2	—	—	4	—	—	1	1	1	1	4
атлантические	17	—	?	1	—	—	—	—	—	—	—	—	—	4	1	—	—	—

Table 7 (Continued)

45	Нототропическо-темперальные	100	1	3	1	—	—	—	1	—	—	10	—	1	2	3	3	—	—
44	циркум-южноамериканские	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
38	амфиамериканские	10	—	1	1	—	—	—	1	—	—	2	—	1	—	1	1	—	—
39	тихоокеанские	65	1	2	—	—	—	—	—	—	—	8	—	—	2	2	—	—	—
40	атлантические	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
46	Нототемперальные	499	30	18	23	22	9	—	10	—	—	15	—	4	4	3	2	—	—
	амфиамериканские	8	2	2	2	—	—	—	—	—	—	—	—	—	1	—	—	—	—
44	циркум-южноамериканские	138	13	4	8	14	5	—	3	—	—	3	—	2	—	1	—	—	—
	тихоокеанские	256	14	11	12	6	3	—	5	—	—	12	—	—	3	—	—	—	—
	атлантические	97	1	1	1	2	1	—	2	—	—	—	—	2	—	2	2	—	—
47	Битемперальные	15	3	1	2	—	—	—	—	—	—	1	—	—	3	4	—	2	—
48	южноамерикано-антарктические	166	28	5	4	55	19	11	7	—	—	8	7	3	—	—	—	—	—
44	циркум-южноамериканские	97	18	3	2	29	11	5	2	—	—	4	3	2	—	—	—	—	—
	тихоокеанские	31	6	2	1	15	3	3	4	—	—	2	2	—	—	—	—	—	—
	атлантические	38	4	—	1	11	5	3	1	—	—	2	2	1	—	—	—	—	—
49	Битеперо-нотополлярные	11	2	2	4	3	—	—	2	—	—	—	—	—	1	5	1	1	—
50	Битеперо-полярные	3	—	—	2	1	2	—	2	—	—	—	1	—	—	—	—	—	—

Table 7 (Continued)

1	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Группа видов	Острова Ревилья-Хи-хедо и Клиппертон	О-в Кокос	Острова Галапагос	«Индо-Пацифика»	Восточная Африка, о-в Мадагаскар	«Южные моря», северная Австралия, Филиппины	Япония, Китай	Дальневосточные моря (Умеренные широты)	Центральная и южная Пашифика	О-в Пасхи	Арктика, Гренландия	Северная Атлантика, Баренцево и Белое моря	Западная Европа	Азорские острова	Канарские острова и о-в Madeira	Острова Зеленого Мыса	Острова Святой Елены и Вознесения
37 Тропические	10	9	59	2	1	3	1	—	1	—	—	—	2	—	1	5	5
38 амфиамериканские	2	—	9	1	1	2	1	—	1	—	—	—	—	—	—	—	1
39 тихоокеанские	8	9	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—
40 атлантические **	—	—	—	1	—	1	—	—	—	—	—	—	1	—	1	5	4
41 Витропические	4	2	12	2	2	3	2	—	3	—	—	—	1	1	1	3	3
амфиамериканские	—	—	4	—	1	1	1	—	1	—	—	—	—	—	—	—	1
тихоокеанские	4	2	8	2	—	1	1	—	1	—	—	—	—	—	—	—	—
атлантические	—	—	—	—	1	1	—	—	1	—	—	—	1	1	1	3	2
42 Темперо-тропические	1	—	11	4	—	—	2	—	—	—	—	—	3	2	1	—	—
амфиамериканские	—	—	3	3	—	—	1	—	—	—	—	—	1	1	—	—	—
тихоокеанские	1	—	8	1	—	—	1	—	—	—	—	—	—	—	—	—	—
атлантические	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	—
43 Витропическо-темперальные	3	2	14	3	4	2	7	2	2	2	—	—	7	2	1	1	1
амфиамериканские	2	—	5	3	1	—	—	—	1	1	—	—	5	1	—	1	1
44 циркум-южноамериканские	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
тихоокеанские	1	2	9	—	2	1	6	1	1	1	—	—	—	—	—	—	—
атлантические	—	—	—	—	1	1	1	—	—	—	—	—	2	1	1	—	—

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Table 7 (Continued)

45	Нототропическо- темперальные	1	—	10	1	—	—	1	—	—	1	—	1	2	—	—	—	—
44	циркум- южноамериканские	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
38	амфиамериканские	—	—	1	—	—	—	1	—	—	1	—	1	1	—	—	—	—
39	тихоокеанские	1	—	9	1	—	—	—	—	—	—	—	—	1	—	—	—	—
40	атлантические	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
46	Нототемперальные амфиамериканские	—	—	4	—	—	2	4	—	3	—	—	—	1	—	—	1	1
44	циркум- южноамериканские	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	1	1
	тихоокеанские	—	—	4	—	—	2	2	—	3	—	—	—	—	—	—	—	—
	атлантические	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
47	Битемперальные	—	—	—	?	—	—	?	—	3	—	—	—	3	—	—	—	1
48	южноамерикано- антарктические	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
44	циркум- южноамериканские	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	тихоокеанские	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	атлантические	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
49	Битемперо-нотополлярные	—	—	—	—	—	—	—	3	—	—	—	2	3	—	—	—	—
50	Битемперо-полярные	—	—	—	—	1	—	2	—	—	3	—	3	3	—	—	—	—

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* Without a precise indication of the place.

** In all, 11 species of this group are noted for the banks of the outer Shelf of southern Brazil off the coasts of Bahia and Espirito Santo, the benthos of which has hardly been studied at all.

Table 7 (Continued)

- Key:
1. Groups of species.
 2. Total number of species.
 3. New Zealand and the region extending from Chatham Island to Macquarie Island.
 4. Southeastern and southwestern Australia.
 5. South Africa.
 6. Kerguelen Island and Heard Island.
 7. Prince Edward Island and Crozet Island.
 8. Bouvet Island.
 9. Tristan da Cunha and Gough Islands.
 10. Fernando de Noronha Island and Rocas Island.
 11. The Bermuda Islands.
 12. Juan Fernandez, San Felix and San Ambrosio Islands.
 13. Eastern Pacific Rise, 54-55° S.
 14. Saint Paul Island and Amsterdam Island.
 15. Red Sea and Persian Gulf.
 16. Mediterranean Sea and Black Sea.
 17. Tropical West Africa.
 18. "Cosmopolitans".
 19. Hawaiian Islands.
 20. Revilla Gigedo and Clipperton Islands.
 21. Cocos Islands.
 22. Galapagos Islands.
 23. "Indo-Pacific".
 24. East Africa and Madagascar Island.
 25. "South Seas", northern Australia, the Philippines
 26. Japan and China.
 27. Far Eastern seas (temperate latitudes).
 28. Central and South Pacific.
 29. Easter Island.
 30. Arctic and Greenland.
 31. North Atlantic, Barents and White Seas.
 32. Western Europe.
 33. Azores.
 34. Canary Islands and Madeira Island.
 35. The islands of Zelenyy Mys.
 36. Ascension Island and the Island of Saint Helena.
 37. Tropical.
 38. Amphi-American.
 39. Pacific.
 40. Atlantic.
 41. Bitropical.
 42. Tempero-tropical.
 43. Bitropical-temperal.
 44. Circum-South American.
 45. Nototropical-temperal.
 46. Nototemperal.
 47. Bitemperal.
 48. South American-Antarctic.
 49. Bitempero-notopolar.
 50. Bitempero-polar.
-

Apart from the configuration of the continents, the main external factor on which the geographic distribution of species in a marine environment depends is the climate, operating through the distribution of the water masses. In the continental zone, the principal characteristics of the water masses, on the basis of which they also are singled out (temperature and salinity), vary according to the geographic latitude. It is this that accounts for the latitudinal zoning of the distribution of shelf species and faunas⁸.

We formulate below certain traditionally established postulates of the latitude zone system of division, which can be regarded as generally accepted in marine biology.

1. The latitude zone division, as is the faunistic, is performed in a single bathymetric zone only (in our case, of the littoral and sub-littoral, i.e., of the Shelf and the uppermost part of the Slope).

2. On the planetary scale, it is possible to include in one zone regions with completely different aggregations of species, for example, off the opposite shores of a continent or ocean. The unification of regions into a single zone or subzone is based on biotopical similarity

⁸In the open sea the zoning of the benthos, which in the final analysis is also dependent on the overall geomorphology and climate, is due to a longer chain of causes and effects. In the abyssal zone, the foremost of these is the trophic circumcontinental-oceanic zoning, with the principal characteristics of the water masses, temperature and salinity, in second place [Sokolova, 1977, 1978; Neiman et al., 1977; Kucheruk, 1979]. As regards the benthic zone of the entire ocean, an annular scheme of zonation, a combination of the circumcontinental-oceanic and latitudinal, would seem to be the most appropriate [Semenov, 1981].

and faunistic analogy⁹, rather than on the similarity between faunas in the above-described sense.

3. In any given region the boundaries between the latitudinal zones are drawn along the boundaries of the major biotic (faunistic) units (usually with the rank of region) (oblast') and, as a rule, they coincide with the sharpest of the climatic boundaries. Having regard to the latter, third principle and if the zones (without the subzones) are taken to extend from pole to pole, a latitude zone scheme of the shelf benthos can only be five-membered, as in the schemes elaborated by Zinova [1962], Zenkevich [1968] and others. It cannot be seven-membered [Kusakin et al., 1975], for there are no faunistic regions corresponding to the northern and southern subtropical zones, nor can it be nine-membered, as in Forbes [Briggs, 1974].

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Overall, off the coasts of South America, only one latitudinal zone is distinguished: the nototemperal (=southern temperate, Notalian), within which the entire South American notalian region is included.

⁹We define a faunistic analogy as a similarity of arrangement and structure, but not of function. With respect to latitudinal zoning we are considering only the spatial, or topical, analogy between the faunas and regions from the following two perspectives:
 (1) their similar positioning as components and their symmetry in space, i.e., compatibility on being rotated relative to the axes and planes of symmetry of the biogeographic structure;
 (2) the structure of faunas consisting of analogous, geographically symmetrical syntopic elements. These latter faunas may have a dissimilar history of evolution and consist of diverse genetic and historic elements [Semenov, 1980].

The boundary between the tropical and temperal zones off the Pacific coast should not be drawn through 12-14° S., as might be assumed on the basis of the zonation by species-determinants [Semenov, 1977a], but much further to the north, through 5° S., (fig. 20). Off the Atlantic coast the boundary between these zones remains unchanged: through 32°-34°30' S. In the Pacific this corresponds to the normal position of the tropical-equatorial front (when there is no reinforcement of the warm El-Nino Current*), and in the Atlantic - to the sub-Antarctic-Subtropical Front [Semenov and Berman, 1978]. The nototemperal and notopolar zones of the Shelf are separated by the abyssal deeps and the Antarctic Convergence which passes through Drake Passage and northwards of South Georgia Island.

The further subdivision of the temperal zone into subzones and also smaller units is a question which has still to be fully elucidated. It is evident that any solution to it will be, at best, tentative. The most simply subdivided is the temperal zone off the Atlantic coast of South America: into the eutemperal and the infertemperal subzones with a corresponding faunistic boundary through 41-42°30' S., between the Uruguayan-Northern Argentinian and Southern Argentinian superprovinces and the hydrological boundary separating the waters of the sub-Antarctic and the transitional sub-Antarctic-temperate structures. The difficulties begin when subdividing the temperal zone off the Pacific coast. The faunistic structure of the benthos and the scheme of zonation there is much more complicated than it is off the Atlantic coast (fig. 19 and table 6). It is impossible to draw a meridional plane of bilateral

* Tentative spelling; not found in any reference work consulted (Tr.).

symmetry across the continent. The question arises: should the division into subzones reflect the absence of this symmetry or, to this end, should fractional units be inserted in the subzones (which would further complicate an already complex terminology)? At least two approaches are possible. If the usual and most simple (although not the most correct) division of the temperate zone off the Pacific coast into two subzones is accepted, then the boundary between them should be drawn at $41^{\circ}30' - 43^{\circ}$ S., as with the Atlantic coast, that is, so as to coincide with the boundary between the Peruvian-Northern Chilean and the Southern Chilean superprovinces. The Southern Chilean and Southern Argentinian superprovinces belong to the eutemperate subzone. These superprovinces resemble each other in the proportion of faunistic elements with a dissimilar type of distribution, and also in the properties of the biotopes, but their water masses belong to waters of sub-Antarctic structure. The eutemperate subzone remains unchanged even in the event of the temperate zone off the Pacific coast of South America being subdivided into 4 rather than 2 subzones. But we would then need to find an analogue of the Atlantic infertemperate subzone within the Pacific Peruvian-Chilean superprovince.

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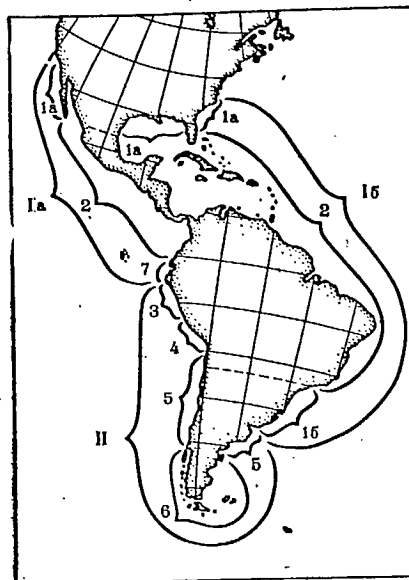
With respect to plankton, K.V. Beklemishev [1969] established the rule of the homologousness of the biotopes, according to which, in species with disconnected ranges, each population complex existing in isolation from the others is situated in a similarly named water mass. Arising from this, the suggestion was advanced that in the benthos also the homologousness of the biotopes (or, according to our terminology,

the analogousness of the faunas and regions) can be established for parts of disconnected ranges - in this case, of amphi-American species.

Fig. 20. Latitudinal zoning of the benthos of the South American Shelf

Zones: I - (holo)tropical (1a - Western American or Balboan, 1b - Eastern American or Columbian, biogeographic regions); II - nototemperate (corresponds to the South American biogeographic region of temperate waters).

Subzones: 1 - circatropical (1a - boreo-circatropical, 1b - notocircatropical), 2 - eutropical, 3 - intertemperate, 4 - circatemperate, 5 - infertemperate, 6 - eutemperate, 7 - Guayaquilian transitional region, analogous to the Southern Brazilian-Uruguayan (circatropical subzone 1b). Off the coasts of North America the boundaries of the zones and subzones are given hypothetically. The boundaries of the eutropical subzone coincide with the boundaries of Briggs's Eastern Pacific and Western Atlantic tropical zoogeographic "regions" [Briggs, 1974].



In actual fact it turned out that this rule is by no means always applicable, even with respect to the benthos of similarly named latitudinal zones, to say nothing of subzones. Even among the most manifold tropical amphi-American ranges, it would be difficult to select any specific type for this purpose, since there exist very different variants of an amphi-American distribution: there are almost as many species as there are types of distribution. Often a species is distributed in the tropical zone off the Pacific coast and in temperate waters off the Atlantic coast, and conversely. In some cases of this type, with respect to species with continuous ranges a hypothesis was advanced

concerning the role of biocoenotic links and competitive relationships (in the broad sense) in the colonisation of homologous biotopes [Beklemishev, 1969, p. 251]. While there is no possibility of checking this hypothesis, we can, however, state an empirical rule which governs the distribution of the benthic species of a shelf zone with both disconnected and continuous ranges. This is the principle of combinatorial filling of a biotopic system [Semenov, 1978]. A larger number of disconnected ranges of a particular type is a consequence of historical causes combined with the excessive climatic deformation of the biota during the present geological epoch [Semenov, 1978]. Similarly, a relatively small number of ideally symmetrical disconnected ranges is indicative of constancy of the combinatorial tendency even under conditions of climatic deformation.

Very roughly an analogy can be established with respect to the region (regiony) using data on the proportions of the number of species inhabiting them which belong to the various (main) types of distribution: in the warm, temperate and cold waters (see tables 1, 2). According to the data in table 1, off the Pacific coast of South America, in its faunal composition the Central Chilean region (extending from 33° to $41^{\circ}30'$ - 43° S.) most closely resembles the Atlantic Uruguayan-Northern Argentinian superprovince (= Northern Argentinian region, infertemperal subzone). But since the boundary between the tropical and temperal zones is drawn at 5° S., rather than at $12-14^{\circ}$ S., as was done previously when compiling table 1, the data on the proportion of the various groups of species off the

Pacific coast must be taken from table 2 with correspondingly changed latitudinal zone characteristics of the species. We are taking the proportion of the species off the Atlantic coast from table 1, since the boundary between the latitudinal zones has remained unchanged there. According to the relative number of tempero-tropical species (elements, in all probability of tropical origin), the Northern Argentinian region then proves to be closest to the Northern Chilean (from $18^{\circ}30'$ - 20° to 33° S.), whereas, according to the proportion of the relatively cold water (tempero-polar South American-Antarctic and bitempero-polar) elements, it is closest to the Central Chilean region. These two regions - the Northern and the Central Chilean - constituting a single province and based on the proportion of various groups of species differing little from one another, can be integrated, together with the Northern Argentinian region off the Atlantic coast, into a single infertemperal subzone (fig. 20). There are no analogues of the Northern Peruvian and Southern Peruvian provinces off the Atlantic coast of the South American continent. These provinces differ markedly in the proportion of the faunistic elements (table 2) and belong to dissimilar subzones of the nototemperal zone (fig. 20). Distinguished within the tropical latitude zone is a southern circatropical (or notocircatropical) subzone, to which the small Guayaquilian region and the Southern Brazilian-Uruguayan region belong.

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The asymmetry of the faunistic structure of the benthos off the west and east coasts of the continent, which is also reflected in the scheme of the latitudinal zonation, is attributable to the distribution

of the coastal water masses [for a detailed discussion of this, see Semenov and Berman, 1977]. The eutemporal subzone fully corresponds to the area of distribution of the water masses of the sub-Antarctic structure, the temperature of which ranges from 4-4.5° to 8-11° C and, with rare exceptions, does not exceed this. The infertemporal subzone is almost wholly a consequence of the area of distribution of the waters of the transitional, sub-Antarctic-temperate structure. The temperature of the water masses of this structure, in contrast to the preceding structure, is subject to more abrupt seasonal variations, and ranges from 6-7 to 10-20° at various depths. In salinity, these freshened waters are almost indistinguishable from the waters of the sub-Antarctic structure: in the open sea, the salinity above the Shelf and the Slope ranges from 33.4-33.5 to 34.2-34.5‰. Off the Atlantic coast, sub-Antarctic-temperate waters are distributed as far as La Plata. Off the coasts of Central and Northern Chile, at the surface, depending on the time of year, they reach latitudes of 23-25° or 33-34° S., and in the 25-50 to 100 m layer - 22-23° S., or possibly range further north. It is probable that with this water, the South American-Antarctic species even reach Northern Chile (as far as 20° S.). These coastal water masses together with the subtropical¹⁰ waters, distributed to the north of them and further out

¹⁰It should be borne in mind that the hydrological terminology (the meanings of the terms "tropical", "subtropical", "temperate", etc.), does not coincide with the traditional latitudinal zone terminology of the biologists [Zinova, 1962; Zenkevich, 1968; Kusakina et al., 1975]. For further details, see Semenov [1977a].

to sea, form part of the cold Peruvian Current. As already mentioned [Beklemishev, 1963; Semenov and Berman, 1977], the Peruvian Current is, in the main, the eastern peripheral part of the southern subtropical (anticyclonic) gyral of the Pacific. Off the Atlantic coast of South America the waters of the similarly named oceanic gyral are transported not from south to north, but from north to south by the warm Brazilian Current. It is for this reason that the southern subtropical water masses off the Atlantic coast resemble the Pacific waters only in name. These are the much warmer ($24-29^{\circ}\text{C}$) and more saline ($35-37\text{‰}$) waters of the tropical latitudinal zone. Off the Pacific coast the temperature of the southern subtropical water masses (of the nototemperate zone), is between $8-11$ and $16-17^{\circ}$, depending on the depth, reaching a maximum of 20°C , with the salinity ranging from 34.6 to $34.8-35.2\text{‰}$. As we shall see, their values do not differ very markedly from the corresponding characteristics of the sub-Antarctic-temperate water masses, which evidently explains the higher biotic permeability of the boundaries off the Pacific coast. The water masses of the southern subtropical structure are distributed within the Southern Peruvian province (the circatemperate subzone) and, in part, within the Northern Chilean province (not to the south of $33-35^{\circ}$ S.). The water masses of the southern tropical structure (the Eastern Pacific "neutral zone") which are distributed in the Northern Peruvian province (the intertemperate subzone) are somewhat warmer and more saline than the southern subtropical waters, and also have no analogue off the Atlantic coast of South America. The Northern Peruvian transitional province is

characterised by unstable hydrological conditions. Periodically (every 7 or 8 years) the warm, desalinated equatorial waters of the El Nino Current penetrate there from the north. At times, due to intensive upwelling, the temperature is seen to fall to 4-5°C below normal.

Thus, within the nototemperal zone off the east and west coasts of South America, differences exist even in the biotopical substrate, Off the west coasts of the continent the diversity of the water masses of the temperate zone is greater than off the east coasts and the faunistic structure of the benthos is more complicated, which is also reflected in our latitude zone scheme. In constructional plan, leaving aside the concrete units and nomenclatural differences, this scheme closely resembles the phytogeographic zonal scheme proposed by A.D. Zinova [1962] with respect to bottom-dwelling macrophytes. Our circatropical subzones (boreo- and noto-) correspond to her peripheral subtropical subzones (northern and southern), which form part of the tropical zone. In contrast to our nototemperal, Zinova's austral zone is subdivided into 3 rather than 4 subzones, as is the boreal (= boreo-temperal) zone of the northern hemisphere, equally off the west and east coasts of the continents (and oceans), that is, without taking the asymmetry into account. It is not only in the temperal zone, however, that a biogeographic meridional asymmetry is manifested. O.N. Zezina [1979] has recorded an asymmetry of distribution of brachyopods in the tropical zone as well, which is also due to hydrological factors.

Discussion

A comparison of the three methods of zonation used in this study in terms of their underlying principles and the main results achieved is presented in table 8. The results of the zonation based on the difference or similarity of the faunas are not in full agreement with the schemes of zonation based on the first and second chorological methods. Thus, the boundary between the Western Atlantic tropical (Columbian) and South American temperate region when Preston's and Jaccard's methods are used is drawn in the vicinity of La Plata, just as it is in the zonation based on species-determinants, rather than near Rio de Janeiro, which is where the most significant faunistic boundary off the Atlantic coast lies, the latter separating regions distinguished by the second method. Off the Pacific coast, the reverse situation obtains: the greatest differences between the faunas substantiate the most significant boundary between the Eastern Pacific tropical (Bulboan) and South American temperature regions, but, not the boundary ascertained from the species-determinants.

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The very large intersecting units, with the rank of superregion, are distinguished solely by the first chorological method. The tentatively accepted boundaries between them ($41-43^{\circ}$ S. in the Pacific and $35-38^{\circ} - 41-43^{\circ}40'$ in the Atlantic) coincide with the boundaries between the superprovinces and regions (oblast'). Kerguelen and Heard Islands are included in the South American-Antarctic (Austral) superregion, since it is not only the corresponding species-determinants but also approximately one-third of the South-American-Antarctic species of our sampling which inhabit the waters near these islands.

Table 8 Comparison of the chorological methods of zonation used in the present study.

Method of Zonation	I By species-determinants	II By the degree of significance of the zoogeographic boundaries.	III Coordinating, taking into account faunistic similarity-difference.
1. The underlying basis of the zonation.	1. The distinguishing of α -regions by the types of ranges of the determining species, and also by the number of species in the syntopic elements (co-ranges).	1. The drawing of zoogeographic boundaries through zones of thickening between the boundaries of the geographic distribution of species and groups of species (syntopic elements).	1. Calculating the indices of similarity (1-z) or difference (z) between faunas of regions distinguished by the first two methods, taking into account and not taking into account the boundary effect.
	2. Analysis of the subordination and intersection of α -regions.	2. The distinguishing of zoogeographic boundaries by the differing degree of significance (by the number of species and co-ranges), corresponding to units of differing biogeographic rank (at the species level). Determining the boundary pressure by the difference between the number of species and co-ranges at the boundary in question.	2. Empirical determination of natural threshold values of the z indices for units of differing biogeographic rank, taking into account and not taking into account the boundary effect.
	3. The principle of hierarchical integrity (closure) of a large α -region (region, superregion, subregion).		
	4. The principle of total isolation, or placing a ban on the intersection of boundaries of large α -regions.		
	(Additional use is made of data on the distribution by regions of species with dissimilar types of distribution and which are hypothetically of diverse origin.),		

2. Particular characteristics of the zoogeographic zonation of the South American Shelf.	<p>1. Off the coasts of South America one temperate zone; its boundaries with the tropical zones displaced as far to the south as possible.</p> <p>2. The division of the South American temperate α-region (<u>oblast'</u>) into a Pacific and an Atlantic subregion is projected from the number of species-determinants of certain types of ranges.</p> <p>3. An Austral (South American-Antarctic) superregion, including Kerguelen and Heard Islands, is distinguished.</p> <p>4. In all, 17 α-districts, corresponding to elementary biotopes, are distinguished.</p>	<p>1. Off the coasts of South America two temperate zones: a Pacific and an Atlantic. Their boundaries displaced as far to the north as possible.</p> <p>2. The Pacific and the Atlantic temperate regions each consists of two subregions (or?) superprovinces which, in turn, are subdivided into provinces.</p> <p>3. A larger number of minimal units (districts and subdistricts) is distinguished than with method I.</p>	<p>1. One temperate zone. Off the Pacific coast its northern boundary coincides with the boundary established by method II, off the Atlantic coast - by method I.</p> <p>2. The South American temperate (Magellan) region is subdivided into 2 subregions - a Pacific and an Atlantic, each is subdivided into 2 subprovinces. The system of subordination of the regions (<u>regiony</u>) of the Pacific subregion is more complex than with those of the Atlantic. The Peruvian-Northern Chilean superprovince consists of 3 rather than 5 provinces, as with method II.</p> <p>3. Some small units, especially transitional (ecotones), have a higher rank than with methods I and II.</p>
3. Overall results of the zonation.	<p>1. The lowest ranking units (district), corresponding to elementary biotopes, are distinguished unequivocally.</p> <p>2. Units with the rank of region (<u>oblast'</u>) and superregion are more or less definitely distinguished.</p> <p>3. First- and second-order transitional zones (and regions) are distinguished. It is possible to form an opinion as to the probable routes of exchange of faunistic elements.</p> <p>4. Units of intermediate rank (provinces) are not distinguished unequivocally.</p>	<p>1. The lowest ranking units (district and subdistrict) are distinguished unequivocally. The system of these units is more fractional than according to method I.</p> <p>2. Regions and subregions (not coinciding with those according to method I) are more or less definitely distinguished, as are provinces.</p> <p>3. The probable direction of migration of the faunistic elements and the degree of definiteness of this trend are determined from the sign and magnitude of the boundary pressure.</p>	<p>1. The results of the zonation do not fully coincide with the results of zonation methods I and II.</p> <p>2. Distinguished more definitely are units of differing biogeographic rank extending from subdistrict to region (<u>oblast'</u>). The system of subordination of the regions is most fully elucidated.</p> <p>3. With a larger number of boundary groups the rank of the units may depend more heavily on whether or not the boundary effect is taken into consideration.</p>

According to the second chorological method the Pacific and the Atlantic parts of the South American temperate region (the Peruvian-Chilean and Uruguayan-Argentinian α -regions (regiony)) are separated by the boundary in the vicinity of Tierra del Fuego at the level of regions (oblasti) or at the very least, of subregions. This result is also supported by the third method - entailing the use of various, non-equivalent estimates of the difference between the faunas, and when the boundary effect is taken into account a more definite conclusion can be reached, namely, that the said regions (regiony) are distinguished as two subregions (podoblasti). According to species-determinants this result is derived (and not completely clearly at that) only when the number of species is compared with the various determining types of ranges.

The faunistic provinces are distinguished in a first approximation by the boundaries of the co-ranges and are subsequently refined on the basis of the degree of difference between the species constituting them. The fauna of the Northern and Central Chilean regions proves to be unitary and is placed within a single Northern Chilean province, despite the fact that biogeographic boundaries corresponding in significance to provincial boundaries (table 3, fig. 11) are situated in the middle of this province (near 33 and 37° S.). Here, as with the boundaries near Rio de Janeiro and La Plata, there is evidence of an actual or apparent paradox of faunistic zonation: the similarity or difference between the species constituting the faunas of neighbouring regions may not correspond to the degree of

significance of the boundaries, as estimated on the basis of the absolute number of species of the sampling and the co-ranges at each boundary. Such a discrepancy is obtained in those regions where there is a strong reciprocal (or unidirectional, as at 23° S., in the Atlantic) penetration of dissimilar faunistic elements. It may be that the way out of this paradox and the further development of the method will be the use, when estimating the significance of boundaries, not of absolute (in relation to the entire sampling), but of relative values, in relation to the number of species which freely cut across a particular boundary, i.e., a methodological analogy with the absolute and relative criteria of similarity or difference (see above).

The distinguishing of the very small territories can be based both on species-determinants and on the boundaries of co-ranges. According to the second method the number of the units with an independent status is greater, since the territories with no species-determinants are also taken into consideration. The estimates of the difference between the faunas make it possible to establish more definitely the biogeographic rank of very small regions. In some cases it proves to be very high: territories initially determined as districts are elevated to the rank of provinces and even super-provinces.

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The Central-Northern Chilean nucleus of the fauna and the Falklandian-Tierra del Fuegoan faunistic centre are readily discerned, both from the species-determinants (the number of species in the

co-ranges) and the degree of endemism (table 6). The degree of endemism of the fauna and the number of determinants off the coasts of northern Argentina are fairly high. In their fauna and hydrology both the Northern Chilean and the Northern Argentinian centres are ecotones or zones of intermixing. In general, a whole series of hierarchically subordinate ecotones of differing extent and degree of distinctness can be distinguished off the coasts of South America. Almost all of the South American temperate region is an ecotone (a zone of intermixing of widely dispersed tempero-tropical and tempero-polar species). This also applies to all transgressive hydrological zones situated between the extreme summer and winter boundaries of water masses [Semenov and Berman, 1977]. The Guayaquilian and La Platan boundary regions are numbered among the most clearly defined ecotones.

The Central-Northern Chilean faunistic centre is characterised by a large number of species in each of the local syntopic elements (distinguished on the basis of the co-ranges). Littoral and upper sublittoral species predominate. The predominance here of species inhabiting shallow water may be partly on account of the difficulty of accessing the lower sublittoral of this region for research purposes: the Shelf off the coasts of Southern Peru, Northern and Central Chile is very narrow, from 4 to 10 miles wide, and passes abruptly into a steep continental slope. The edge of the Shelf is at a depth of only about 50 m [Udintsev, 1972]. The region is situated in the zone of influence of waters of subtropical structures, typical of which is a pronounced vertical temperature stratification.

The warm surface layer extends the full depth of the edge of the Shelf. Thus, the large number of species in the littoral-upper sublittoral vertical grouping may be due not only to the macrorelief of the bottom, but also to the warm surficial water mass. Southwards of 37-42° S., where the Shelf becomes wider, more gently sloping and deep, and probably also because of a general slackening of the vertical stratification of the waters of sub-Antarctic structure, there is evidence of submergence of certain of the species which live in the littoral or upper littoral further to the north: the polychaete Lumbrineris bifurcatus (Ehlers, 1901), the isopods Jaeropsis bidens Menzies, 1962 and Edotia dahli Menzies, 1962; Munna (Uromunna) nana (Nordenstam, 1933) and others. This submergence is especially noticeable in the modified waters of the so-called Chiloe Basin (Ancud and Corcovado Bays). The modification of the hydrological structure in this region is due to intra-shelf depressions of the bottom to depths of up to 400-450 m., the hydrological isolation of the region and the continental run-off [Brattström and Dahl, 1951]. Numerous endemic species with small local populations live in the waters of Chiloe Basin.

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In the region of Tierra del Fuego and the Strait of Magellan there are also numerous isolated intrashelf depressions in the bottom which could explain the abundance of endemic and, probably autochthonous, elements of the fauna. Many species of demersal fishes, known to be present from reports of occasional or single occurrences in this region, are described from precisely these small,

isolated, intrashelf (pseudobathyal according to Andriyashev [1979]) intermontane valley-like depressions. The hypothesis advanced by Andriyashev [1979] concerning parallel and polytopic speciation in these depressions is evidently not without foundation. It remains, however, incompletely clear as to how much time is required for this process to yield noticeable results. For purposes of comparison it is interesting to note that there are also numerous intrashelf depressions in the northern hemisphere: off Labrador, Greenland and Norway, and in the Barents Sea. Such is also the case in almost the whole of the White Sea¹¹. In them, however, in contrast to the depressions recorded in the southern regions of South America (and the Shelf of Antarctica), there are very few or no endemic species, probably by reason of the continuous sheet glaciation of the shelves of North America and Europe in the Pleistocene [Flint, 1963; Grosval'd, 1980]. The White Sea, for example, became free of ice, which had occupied almost the whole of its basin, between 10,500 and 13,000 years ago [Deryugin, 1928; Nevesskii et al., 1977] - a period which would obviously have been insufficient for the evolution of new species. Consequently, provided that the same rates of speciation obtained, the intrashelf depressions in the southern part of South America must have existed for a longer period of time or have been at least partly free of ice during the periods of maximal Pleistocene glaciations, in order for a relict fauna to have survived in them.

¹¹I am indebted to K.N. Nesis for these examples.

Predominating at the Tierra del Fuegan-Falklandian faunistic centre are benthic species with a wide range of dispersion depths: sublittoral and sublittoral-upper bathyal (from 0 to 270-330 m and deeper). In terms of latitude zone affiliation these are eutemperate elements, with a major role played by the tempero-polar (South American-Antarctic), more or less widely distributed species. In general, it is evident that with movement from north to south along the coasts of South America, the number of widely dispersed species of tropical origin diminishes and the number of American-Antarctic species increases (tables 1, 2). This exchange of species is interesting not only because it reflects the natural variation in the climatic conditions with the geographic latitude, but chiefly because most of the species of tropical origin and certain of their autochthonous derivatives off the coasts of Northern and Central Chile, Northern Argentina and Uruguay are coastal-shallow water species. The predominance of these species at the Central Chilean faunistic centre is clearly indicative of pressure from the north of the tropical shallow-water fauna of the Eastern Pacific region which, presumably, has been continuously operative in recent geological epochs. This pressure is clearly evident in both the Atlantic and the Rio de Janeiro and La Plata regions (see table 3, a,b).

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As stated earlier, the biogeographic significance of each boundary (in relation to a particular sampling) is evaluated by two pairs of numerals: by the number of species and the number of co-ranges (of the syntopic elements). The difference between the

numbers of each pair is interpreted respectively as the faunistic (biotic) and species pressure at the boundary in question. Its directional orientation is determined from the sign and is indicative of the trend towards the colonisation of the species and the displacement of the faunistic elements. The boundary zone acts like a check-valve or semiconductor. The magnitude of the boundary pressure does not in itself depend at all times on the degree of significance of a particular zoogeographic boundary. We have seen that at two of the most important boundaries, at 2-5° S. in the Pacific and at 23-24° S. in the Atlantic, a very strong species- and biotic pressure is directed from north to south, from the tropics to the temperate waters, approximately two-thirds of this pressure developing on account of the littoral and upper sublittoral species (see table 3, a,b). At the third most important boundary in our region, in the vicinity of Tierra del Fuego and the Strait of Magellan, the pressure is comparatively low. With respect to the species of the shelf fauna as a whole, it is directed from the Atlantic to the Pacific, while the opposite orientation, from the Pacific to the Atlantic, is the case with species of the littoral and upper sublittoral. In both cases, the same orientation is obtained with respect to the syntopic elements (the co-ranges). It is also evident that the radiation of the species and the syntopic elements from the Central-Northern Chilean faunistic centre is in both directions, southwards and northwards, although the southward direction predominates, possibly as a result of the additional influence of the Eastern Pacific centre.

By comparing the results of our zonation, obtained by dissimilar methods, with the foregoing schemes of zonation shown in figs. 1-6, we can sometimes discern which principle of zonation was adhered to by the various investigators. Thus, the schemes shown in figs. 1 and 3 more closely correspond to the zonal-geographic approach. The schemes of T.F. Shchapova and O.G. Kusakina (fig. 5), who had very little information on warm-water fauna at their disposal, closely resemble the scheme of zonation based on species-determinants (fig. 9). The results of our zonation, which involved the use of estimates of the significance of the boundaries and of the difference between the faunas, correlate best with the zonation proposed by S.D. Boltovskoi [1964] which is based on the Foraminifera (fig. 6).

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The boundary in the Tierra del Fuego region, the importance of which was not mentioned by any of the aforementioned authors excepting Boltovskoi, separates territories of very high biogeographic rank (subregions)(podoblasti). A great disparity between the Pacific and the Atlantic South American regions is apparent with respect to the fauna and the significance of the boundary that separates them (in all, there are 238 species and 102 co-ranges, see table 3 and fig. 11). At the same time, there is currently no climatic boundary between these regions, which is conceivably an adequate explanation for the existence of such a sharply defined zoogeographic boundary. Normally, climatic boundaries separate faunas by latitudinal zones, rather than in an east-west direction. Boltovskoi [1964] suggested that the Pacific and Atlantic foraminiferal faunas evolved during a

period when, at the site of what is now Drake Passage, there existed a land isthmus which connected South America and Antarctica. In his opinion, these faunas have not succeeded in integrating since then which he attributes to the fact that bottom-dwelling Foraminifera do not have a true planktonic stage in their life cycle. But it would seem that the point at issue is not merely the absence of a continuous planktonic stage in the bottom-dwelling Foraminifera, but also the general conservatism and stability of the chorological structure of the benthos in the absence of a sharply defined "faunistic gradient" (boundary pressure). Our sampling consists of representatives of wholly different groups, the majority of which do have a planktonic larva, and the result of the zonation has a great deal in common with Boltovskoi's scheme for the southern part of South America.

Drake Passage was formed during the Upper Oligocene-Early Miocene. Although the opening of the Passage began about 29 million years ago, this process became greatly accelerated about 23.5 million years ago [Craddock and Hollister, 1976; Burkner and Burrell, 1977; Burkner et al., 1977]. The evolution of the Westerly Winds is referred to roughly the same period of time (23.5 ± 2.5 million years ago) [Burkner and Burrell, 1977]. Certain other data [Kennett, 1977 and Dott, after Craddock and Hollister, 1976] suggest that the opening of Drake Passage and the formation of the cyclical flow of the Westerlies began in the Late Eocene-Early Oligocene. A.P. Lisitsyn et al., [1980] give a less definite, more flexible dating: between 38 million and 25 million years ago (Oligocene).

Despite the absence of a land barrier throughout the last 21-25 million years at least, the Pacific and Atlantic faunas of the South American Shelf could have been separated more than once during this span of time on account of the repeated northward migrations of the climatic boundary (the Antarctic Convergence Zone) which occurred in Drake Passage during periods of climatic cooling in the Pliocene (about 5,000,000-3,500,000 years ago), and not less than four times in the Pleistocene, especially about 1,200,000 years and 56,000 years ago [Mercer, 1976; Grosval'd, 1980]. A climatic cooling, accompanied by an increase in the numbers of glaciers in the southern Andes, which has left its imprint on the marine molluscan fauna, occurred in the Holocene about 4,600-4,200 years ago (the minor "Tempanos* Glaciation") and perhaps also, about 2,700-2,000 years ago [Markov et al., 1968; Mercer, 1976].

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Ancient glaciers in the southern part of South America might similarly have had an obstructing effect on the dispersion of species in the very shallow water zone. Little is known about the positioning of these glaciers and the stages of glaciation. Flint [1963], citing Leungner, Ferulio and Auer*, draws the boundaries of glaciation on the Shelf at the Pacific side of the continent between Chiloe Island and Tierra del Fuego, and on the Atlantic side - between the Strait of Magellan and the Island de los Estados. Perhaps also contributing to the separation of faunas during periods of glaciation were

* Transliterated from the Cyrillic. Not found in any reference work consulted (Tr.).

eustatic falls in the sea level. A.S. Monin and Yu.A. Shishkov [1979] believe that during the phase of maximum glaciation in the Miocene and Pliocene, sea level was 15-45 m below what it is today; and during the period of the latest glaciation, 130 m below. Some integration of the Pacific and Atlantic faunas of South America subsequent to their isolation nevertheless did occur, chiefly in the southernmost regions of the eutemperate subzone. Thus, the Southern Chilean and Southern Argentinian regions, taken separately, and taking into consideration the Tierra del Fuego and Falklandian boundary species, are distinguished only at the level of provinces (see table 45).

The boundary effect. Earlier in this study it^{was} pointed out that the addition or subtraction of the boundary species when calculating the similarity or difference between faunas leads to substantially different results, and that these species must be taken into consideration in a faunistic zonation. The boundary species of the Tierra del Fuego and Falkland Islands region have a particularly strong masking effect on the radical differences which exist between the Pacific and Atlantic faunas of the temperate waters of South America. The existence of boundary species and endemic forms is a major problem in its own right.

In order to explain the boundary effect, two equally correct and non-mutually exclusive hypotheses can be advanced:

(1) the hypothesis of relict species and (2) the hypothesis of speciation in small populations. Both are founded on the principle of the relationship between the age of a taxon and its geographic

range [Simpson, 1948]. When it first appears, a taxon (this applies more to so-called "geographic" than to sympatric species) has a very limited range. Thereafter it takes over new regions of habitation, the range increases and becomes maximal in area during the epoch when the taxon is in its prime. As the taxon ages the range contracts and becomes discontinuous right up to the time when the taxon disappears. According to the relicts hypothesis, boundary species, known from occurrences in some small region, are disappearing, residual species, surviving under the destabilised conditions obtaining in boundary and transitional regions and especially in boundary refuges of the partially isolated basins- and marginal seas type when there is a relatively low density of ecosystem colonisation and when vacant ecological niches are present.

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The speciation in small populations hypothesis is based on the notion that discontinuous ranges form not only when a taxon is aging and the area of its habitats is contracting, but also when the range is expanding. A natural mechanism exists which can lead to spontaneous colonisation in a marine environment. It consists of the systems of currents and countercurrents which scatter the planktonic benthic larvae. At least three such systems are operative off the coasts of South America [Semenov and Berman, 1977]. The drift of benthic larvae with the currents throughout the period when they are normally present in the plankton can amount to hundreds or even thousands of nautical miles. In cases of spontaneous colonisation it would appear that a special type of range discontinuity originates.

The species has a normal, continuous range but on the periphery there are one or several micropopulations, separated from the main range by an intermediate biotope (one or several water masses), where the species in question is absent. Such ranges were noted in not less than one-tenth of the species in our sampling. They are very numerous among the American-Antarctic species, isolated populations of which live in the Tierra del Fuego and Falkland Islands region. Contributing to the emergence of isolates is the deforming effect of the environment viz. the climatic variations which are most sharply defined in the temperate waters of the temperal zone and on its periphery, where the boundary effect is also observed. According to the speciation hypothesis, in time, isolated populations even give rise to boundary species. A. Buko [1979] cites numerous findings attesting to the inverse relationship which obtains between the size of a population and the rate of evolution. The whole of his book is devoted to proving this theory. Boundary speciation probably predominates in the regions of temperate waters situated immediately adjacent to the tropical zone and right at its boundary, as evidenced by the almost 100% endemism of the boundary species (they are not found in other oceanic regions). Endemism is appreciably lower among the equally prolific boundary species of the southern part of South America (69-90%). On the one hand, this can be explained by the relicts hypothesis, and on the other, by the dispersion of part of the species by the cyclical flow of the Westerlies. A number of the American-Antarctic and South American temperal species occurring off

South Africa, New Zealand, Kerguelen Island, Prince Edward Island and other islands, and situated in the zone of influence of these winds, have been discovered on floating algae in the open sea [Smirnov, 1978]. Many of the boundary species of the Tierra del Fuego and Falkland Islands region could have been initiated by species which had evolved during the tertiary period of the Antarctic fauna and had left behind micropopulations of colonists at the time of the northward migrations of the Antarctic Convergence during the coldest epochs. 261

The Symmetry of the biological structure. In discussions about symmetry, it often happens that the following two questions are confused with each other: (1) disturbances in symmetry from the standpoint of detail: northward displacement of the equatorial plane of symmetry, and non-coincidence with respect to degrees of latitude of the boundaries of similarly named zones in the northern and southern hemispheres situated in different oceans off the west and east coasts; (2) the question of the symmetry of the biogeographic scheme in constructive plan.

The second question, in our opinion, is the more fundamental. Zenkevich [1948], in raising the question of the biological structure of the ocean, brought forward a global scheme of symmetry with three mirror planes: an equatorial and two meridional, passing through the middle of the continents and oceans. This was a tentative scheme and Zenkevich noted that symmetry is subject to major disturbances, which are due to the Earth's rotation [Zenkevich, 1948; Vinogradova, 1976].

Until now, however, the scheme with three planes, that is, the symmetry of a static, immobile body, has been passed from study to study in an unaltered form. The usual argument in favour of meridian planes is that the central regions of large oceans are occupied by special oceanic communities with a population which is greatly rarified and impoverished in terms of the species constituting it, and that to the east and west of the central zones, in the direction of the coasts, neritic concentrations of life originate, which find expression in an increase in the biomass and the number of species. On this basis, however, it would be possible to speak of an infinitely large number of mirror planes passing through the middle of the oceans (the same applies to the continents), since the concentrations of life not only increase eastwards and westwards, but in any coastward direction from the middle of the ocean. Additionally, there is the fact that, because of upwellings, the eastern margins of the Pacific and Atlantic Oceans differ greatly from the western margins in the abundance of species and the magnitude of biological yield [Gershanovich and Elizarov, 1979].

The second argument which is put forward in defence of "meridional symmetry" is the presence of species with disconnected ranges, i.e., amphioceanic, amphiboreal and amphi-American species. The point about these latter is that what was being said is related to latitudinal zonality. With an increase in divisibility of the classification of the ranges, the limitedness of the rule of the homologousness of biotopes became clear with respect to species with disconnected ranges:

although amphi-American, amphiboreal etc., ranges exist, ideally symmetrical ranges relative to the meridian plane occur among them side by side with those that are asymmetrical, in conformity with the principle of combinatorial filling of a biotopic system [Semenov, 1978]. 262

We have seen that off the east and west coasts of South America, the asymmetry of the faunistic structure of the shallow-water benthos depends wholly on an asymmetry of distribution and a non-matching of the characteristics of the water masses, even including similarly named characteristics which are parts of homologous [after Beklemishev, 1969] oceanic (subtropical, equatorial and subpolar) gyral and gyral of neutral zones. It would appear that matching of similarly named gyral and water masses with similar characteristics in the Pacific and Atlantic Oceans could only be achieved by an imaginary matching of the hydrological structures of these oceans with conventional rotation of the corresponding sectors of the Earth around the axis. From this point of view it is more correct to speak not about meridional symmetry or the absence of any symmetry other than one that is equatorial, but rather, about the symmetry of a rotating Earth (the geoid) with a second- or third-order axis of symmetry and with only one mirror plane of symmetry (m), crossing the Equator (actually slightly to the north of it) and a perpendicular axis. In the nomenclature proposed by A.V. Shubnikov and V.A. Koptsik [1972] this symmetry is of the $2/3:m$ type (it reads "two, three, colon, m "). The order of the axis of symmetry is 2 if it is viewed from the direction of the North Pole (the Pacific and Atlantic Oceans),

and 3, if it is viewed from the South Pole (the Pacific, Atlantic and Indian Oceans). The biogeographic structure of the benthos of the shelf zone (in constructive plan) has this type of symmetry.

Conclusion

In this paper we have discussed the distinctive features of the chorological structure of the benthos which become apparent as a result of a classification of the ranges of species and are directly related to the problem of biogeographic zoning. The living cover is discrete and has a well defined spatial organisation. The discreteness of the chorological plan of organisation, i.e., the macrostructure, is manifested in such a way that the entire aggregate of species breaks down into geographic or syntopic elements, that is, into groups of species with coinciding boundaries of dispersion. In a classification of ranges these elements are grouped for ease of representation into large, territorially subordinated amalgamations on the basis of the latitudinal zone principle and the degree of resemblance between the thermopathy of species (which can be judged indirectly from the confinement of species to water masses). To reveal the macrostructure of the living cover as fully as possible the biogeographic classification must be broken down to its most minute components and the syntopic elements identified on the basis of coinciding ranges (co-ranges) at a very high level of discrimination. This is only now becoming possible, in light of the present-day accuracy of data on species dispersion boundaries.

The boundaries of the geographic ranges, even of species belonging to the same syntopic element, do not coincide absolutely. Some spreading of boundaries occurs: with movement along the shore of a continent, zones of boundary thinning alternate with zones of thickening. It is on the basis of these narrow zones of thickening of the boundaries of the ranges that the zoogeographic boundaries between the units of a faunistic zonation (regions) and between the latitudinal zones and subzones are drawn.

In a marine environment the discreteness of the living cover is primarily a consequence of the physico-geographic structure of the environment, that is to say, of the global climatic zonality and the distribution of the water masses and their modifications. The syntopic elements overlap one, two or more water masses or biotopes in very diverse combinations, and the chorological structure can be described by means of the mathematical technique of combinatorial analysis. The development of combinatorial models of biological structure is still in progress and they are not discussed in the present study, nor are certain common patterns in the chorological structure and various other questions related to the combinatorial principle and the concept of the deformation (asymmetrisation) of structure [Semenov, 1977c, 1978].

The faunistic zoning and the scheme of the latitudinal zonation reflect different aspects of the natural chorological structure. In the case of a marine biota, the scheme of the latitudinal zones is constructed on the basis of the faunistic scheme, and not the other

way round. Because of this, the latitudinal-zone characteristics of species are all the more inexact and tentative, and can in no way serve as an argument to be used when ascertaining the boundaries between units of a faunistic zonation. The procedure for a chorologically based zonation is as follows: the biogeographic boundaries are drawn and the regions (regiony) and α -regions of indeterminate rank are distinguished on the basis of precisely determined and tentatively grouped syntopic (or geographic) elements. The species-determinants, the degree of significance of the boundaries and the similarity or difference of the biota form the basis for constructing the scheme of the faunistic (biotic) zonation and for determining the constructive plan of it which is most suited to a particular structure. Based on the identification of analogous faunas (and water areas) which takes the biotopical similarity into consideration, the scheme of the biological latitudinal zoning (or a different zoning for other vertical zones of the ocean) is constructed. Only after this has been done can "definitive" zoogeographic characteristics be ascribed to species. This method of successive approximations is widely used in biological systematics and is called the double-iterative method (S.V. Meien, in a lecture to the Moscow Society of Naturalists, 1979).

By using the concept of the α -region, distinguished on the basis of the type of range, an easy transition from purely chorological categories (types of ranges, co-ranges and syntopic elements) to the territorial units of a biogeographic zonation is made possible. In a faunistic zonation, the decisive argument at the species level is

the degree of similarity of the faunas (lists of species), having regard to the significance of the biogeographic boundaries. Here, the data on faunistic similarity or difference correlate better with the results of a zonation which is based on the degree of significance of boundaries than with those of a zonation which is based on species-determinants. In the interests of practicality a zonation which is based on species-determinants requires the introduction of restrictions. These may prove to be arbitrary: prohibiting the intersection of boundaries, and the principle of hierarchic integrity of large α -regions (regions) (oblasti). This type of zonation yields results that are less significant statistically, since when estimating the degree of significance of the boundaries or the species-similarity, the regions are distinguished on the basis of a larger number of species and co-ranges. Nevertheless, this method affords an opportunity of easily distinguishing regions (regiony) with a higher rank (superregion) than region (oblast') and of differentiating first- and second-order transitional zones (and α -regions). The distinguishing of transitional zones and α -regions of dissimilar order, combined with the use of the boundary pressure concept, makes it possible to arrive at a better understanding of the directional orientation and paths of dispersion of the faunistic elements and of the processes of formation of contemporary faunas.

Using estimates of the faunistic similarity or difference, the boundaries and rank of the already distinguished subdivisions are more precisely defined and the actual character of the subordination

of the biogeographic units is ascertained. It is impossible to make an à priori assumption that a suitable scheme of the hierarchic type will be correctly gradated in each specific instance, that the regions will be divided into subregions, the subregions into superprovinces, the superprovinces into provinces, etc. In reality, there will be an irregular hierarchic type of structure involving the dropping of some categories: provinces, for example, may consist of subprovinces and a separate, independent district, or they may have no further subdivisions at all. In regard to certain special purposes and special cases (for example, the benthic region of the ocean in its entirety), a scheme of a wholly different, non-hierarchic or combined constructive type, may be adopted. Often, the main advantage of a hierarchic scheme lies solely in its visual clarity and practical convenience when used.

After correlating the results of the zonation obtained by different methods, the following subdivisions are taken to hold true off the coasts of South America. There is a single South American temperate (Magellan) region, its northern boundaries lying at 5° S. in the Pacific and at 32° - $34^{\circ}30'$ S., in the Atlantic. This region is subdivided into two subregions: a Pacific (Andean) and an Atlantic (Malvinian) with the boundary between them in the vicinity of Tierra del Fuego and the Falkland Islands. The subregions are subdivided into two superprovinces: the Pacific, into a Peruvian-Northern Chilean and Southern Chilean (boundary at $41^{\circ}30'$ - 43° S.), and the Atlantic, into a Uruguayan-Northern Argentinian and Southern

Argentinian (boundary at $41^{\circ}30' - 42^{\circ}$ S). The Southern Brazilian-Uruguayan region (extending from $23-24^{\circ}$ to $32-34^{\circ}30'$ S.) is distinguished as a superprovince of the Western Atlantic tropical (Columbian) region. This superprovince is subdivided into two provinces: a Catarinan-Paulian and a Uruguayan (boundaries at $27-28^{\circ}$ S.). The Uruguayan-Northern Argentinian superprovince consists of a La Platan transitional province and a Buenos Airean (Northern Argentinian) province (boundary at $37-38^{\circ}$ S.) and is not further subdivided. The Peruvian-Northern Chilean superprovince consists of three provinces: a Northern Peruvian, a Southern Peruvian and a Northern Chilean (boundaries between them are at $12-14^{\circ}$ and $18^{\circ}30' - 20^{\circ}$ S.). The most extensive of these provinces - the Northern Chilean - is subdivided into three subprovinces: an Atacaman, a Central Chilean and an Arauco-Chiloen (boundaries at 33 and 37° S.). These subprovinces are in turn subdivided into territories of lower rank, but there is disturbance of the correct gradation. The Southern Chilean and Southern Argentinian superprovinces are not subdivided into provinces, but include only territories with the rank of superdistrict, district and subdistrict.

The hierarchic subordination of the regions of the Pacific South American subregion is more complicated than that of the Atlantic subregion. This is also reflected in the scheme of latitudinal zoning: the nototemperal zone off the west coasts of South America is subdivided into 4 subzones, and off the east coasts - into two. In the biogeographic structure of the benthos, as also in the hydrological

structure, on which it depends, there is an absence of mirror symmetry in relation to the meridian plane passing through the middle of the continent or ocean.

One of the principal results of the faunistic zonation is the radical difference between the contemporary Pacific and Atlantic faunas of the temperate waters of South America, a residual effect of their past isolation. That an amalgamation has not occurred is because, in the first place, the isolation occurred more than once - during periods of climatic cooling in the Pliocene and the Pleistocene, and not solely in the Oligocene, prior to the opening of Drake Passage, and secondly, it is a consequence of the overall stability of the chorological structure in this region. Both faunas were formed and at all times existed under similar climatic conditions and it would appear there have not been and are not now any abrupt faunistic gradients between them, such as is the case between the faunas of diverse climatic zones.

It would seem that the boundary effect is especially characteristic of transitional zones with an enhanced biotic gradient, and of regions the ecosystems of which are incompletely saturated and are in large measure subject to the destabilising influence of the climate. Such regions include the temperate waters of South America. Two non-alternative hypotheses are equally acceptable for the purpose of explaining the boundary effect: the relicts hypothesis and the hypothesis of speciation in biotopically isolated micropopulations.

In our opinion, there is at present no single universal method of biogeographic zoning. What is needed is the development and perfection of all possible methods of analysis (with subsequent synthesis), the use of which will serve to bring out more clearly the different aspects of the spatial organisation and history of the living cover.

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