Remarks on Marine and Continental Biogeography: An Areographical Viewpoint

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Remarks on marine and continental biogeography: an areographical viewpoint

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SUMMARY

Differences and similarities in the way marine and continental organisms occupy space are briefly reviewed. Among them, the 'peninsula effect' (the decline of species richness with distance from the source) is compared with the 'bay effect'. Two cases, corals in Mochima Bay, Venezuela and fishes in the Baltic Sea, are presented as examples.

The facts that the world's oceans are larger, continuous and three-dimensional, with fewer evident geographical barriers than there are on land, explain why marine biogeographical regions are less well-defined and geographical ranges of marine taxa more wide-spread. This generalization has, however, been questioned following recent findings of extremely rich and highly endemic benthic faunas. This problem is discussed using an index of cosmopolitanism to compare terrestrial and marine biotas.

1. COSMOPOLITANISM

The geographical status of a species can be estimated directly by the size of its geographical range. This yields rather superficial information on how successful or threatened by extinction that species is. However, this is not sufficient: a species may have a small area but with numerous patches distributed in two or more regions, as for some phytopathogens mapped by the Commonwealth Mycological Institute, or well-known examples of bipolar species. These cases show that although the summed total area of occupied patches may be small, the probability of extinction may be low. Some populations may become extinct but not the species. On the basis of geographical range, using the criterion of quartiles, species can be described as microareals ($< Q_1$), mesoareals ($Q_2 - Q_3$) or macroareals ($> Q_3$). Depending on the number of biogeographical regions they occupy, species may be endemic (one region), characteristic (two regions), semicosmopolitan (three to four regions) or cosmopolitan (five or more regions). Rapoport *et al.* (1976) proposed a quantitative measure of cosmopolitanism of entire taxa by means of an index (C):

$$C = \frac{\left\{\sum_{r=1}^{r_{\max}} r\, Y_r/n\right\} - 1}{r_{\max} - 1}$$

where r is the number of regions occupied by each species, Y_r the total number of species that occupy r regions, n the total number of species, and $r_{\max}$ the number of regions considered. The index ranges between 0, when all the species of a given taxon are endemic, and 1 when all the species inhabit all the regions or continents. This does not mean that all of them are occupied. It would be enough if they were present with one single population, at least, in each region. To allow comparisons between taxa, identical biogeographical divisions must be used, especially with regard to the number of regions considered ($r_{\max}$).

The world's oceans occupy 71 per cent of the planet's surface. Its biogeographical divisions are different from terrestrial ones, although some coincidences exist. As the index of cosmopolitanism does not take into consideration either the sizes of the biogeographical regions or the degree of occupancy by the species considered, but the number of biogeographical regions shared by each species (presence–absence data), it seems reasonable to make comparisons between marine and terrestrial biotas provided we use an identical number of 'natural' divisions. Biogeographical divisions of the sea, however, are not as clearly defined as terrestrial divisions. Moreover, physical conditions of coastal, pelagic and bathyal environments are extremely different. There is some agreement among authors on biogeographical divisions of the oceans. The map of figure 1 shows six proposed oceanic divisions allowing comparison with terrestrial biotic cosmopolitanism. This map is a concensus between divisions proposed by de Lattin (1967), Belyayeva (1968), Baird (1971), Shuntov (1972) and Bé (1977). The procedure used merged the most similar provinces and established a median line between the most concordant lines.

(*a*) *Chiroptera*

I consider first cosmopolitanism in terrestrial mammals. Bats constitute a relatively highly diversified group, with more than 900 species globally. Although one speciose family are fruit, nectar and pollen feeders

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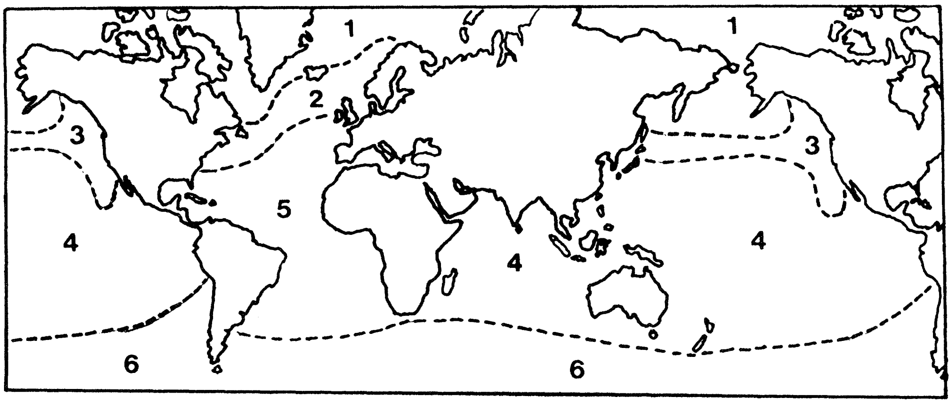

Figure 1. Six world oceanic regions used to calculate marine cosmopolitanism. See text for more explanations.

(Pteropodidae), and another family is fundamentally omnivorous (Phyllostomidae), most bats are insect-feeders. Two other dietary groups are fish-feeders (Noctilionidae) and blood-feeders (Desmodontinae), and one genus specializes in feeding on small vertebrates (*Lavia*, Megadermatidae).

North and Central American bats rank fourth in mean geographical range, after carnivores, artiodactyles and rabbits (Rapoport 1982). If North America is considered only above 30°N, bats rank third (Pagel *et al.* 1991). This is because this area excludes a high number of Central American microareal species. In South America, however, bats are relatively more widespread than their North American relatives. According to Ruggiero (1993), the order Carnivora ranks first. Their species occupy 30.3% of the continental area, on average, and Chiroptera rank second, with a mean of almost the same value, 29.1%. South American Artiodactyla rank third, with 19.9%. Table 1 summarizes values obtained from the data given by Honacki *et al.* (1982). Indices of cosmopolitanism were calculated only for families with more than ten species. The most cosmopolitan family is Vespertilionidae, showing 270 species restricted to a single biogeographical region, 50 species shared by two regions and two species sharing three regions. Of course, there are other families that seem to have a high level of cosmopolitanism, such as the Rhinopomatidae, but they cannot be compared because of their low species number. It may be stated that world bats ($C = 0.026$) are somewhat less cosmopolitan than world carnivores ($C = 0.037$). The latitudinal effect is remarkable in Chiroptera, as can be appreciated from table 1; tropical regions are more speciose: Oriental > Neotropical > Ethiopic. The latter is the region at the south of the Sahara, including Madagascar and neighbouring islands. It is surprising that the Holarctic Region (Palearctic and Nearctic), despite its enormous area, only contains 138 species in comparison to the Australian region with 147 species. Apparently, the geography of bats is greatly affected by temperature, food availability and, perhaps, because of their relatively low thermoregulatory capacity. It should be stressed that there are six species shared among three regions, and 106 species shared between two regions, but this pattern always occurs between Ethiopic–Palearctic; Palearctic–Oriental; Oriental–Australian; and Nearctic–Neotropical

Table 1. *Comparative data of chiropteran families*

family	number of genera	number of species	species per genus	number of species sharing regions			cosmopol. (C)
				1 reg	2 reg	3 reg	
Craseonycteridae	1	1	—	1	0	0	—
Emballonuridae	12	48	4.0	43	3	2	0.029
Furipteridae	2	2	—	2	0	0	—
Megadermatidae	4	5	—	5	0	0	—
Molossidae	12	86	7.2	78	8	0	0.019
Mormoopidae	2	8	—	6	2	0	—
Mystacinidae	1	1	—	1	0	0	
Myzopodidae	1	1	—	1	0	0	—
Natalidae	1	4	—	3	1	0	
Noctilionidae	1	2	—	2	0	0	
Nycteridae	1	14	—	13	1	0	0.014
Phyllostomidae	47	132	2.8	117	15	0	0.023
Pteropodidae	41	160	3.9	150	10	0	0.013
Rhinolophidae	10	128	12.8	115	13	0	0.020
Rhinopomatidae	1	3	—	1	0	2	—
Thyropteridae	1	2	—	0	2	0	—
Vespertilionidae	36	322	8.9	270	50	2	0.034
Chiroptera (total)	174	919	5.3	807	106	6	0.026

Table 2. *Comparative data on marine and terrestrial taxa*
(Chiropterans appear in table 1.)

taxon	no. spp sharing 1–6 regions 1	2	3	4	5	6	n	cosmo-politanism (C)	min/max geogr. range (km$^2 \times 10^6$)	mean geogr. range (km$^2 \times 10^6$)	s.d.	source
MARINE												
algae	10	11	3	0	0	0	24	0.233	—	—	—	Akatsuka (1987); Cambridge *et al.*(1984); Yarish *et al.* (1984)
Foraminifera[a]	2	0	5	5	3	1	16	0.525	8–250	166.7	68.2	Bé (1977)
Mollusca												
Cephalopoda	59	26	13	3	0	0	101	0.121	0.25–62.8	6.5	12.7	Boyle (1983); Sweeney *et al.* (1992)
Polychaeta												
Arenicolidae	4	6	1	0	1	0	12	0.200	—	—	—	Wells (1963)
Crustacea[b]	35	18	4	1	1	0	59	0.112	—	—	—	Chapman & Carlton (1991); Efford (1972); Bruce (1972)
Euphausiacea	6	3	1	0	0	0	10	0.100	1–167	59.3	56.6	Ayala & Valentine (1979); Gopalakrishnan (1974)
Pisces	126	95	21	9	3	1	255	0.142	0.1–289	23.9	28.9	Baird (1971); Briggs (1987); Mukhacheva (1954); Greenfield (1971); Muus & Dahlström (1971); Gibbs (1969)
Pinnipedia (totals)	15	12	6	0	0	0	33	0.146				Honacki *et al.* (1982)
Otariidae	5	6	3	0	0	0	18	0.171				Honacki *et al.* (1982)
Phocidae	10	6	2	0	0	0	33	0.100				Honacki *et al.* (1982)
Cetacea	21	25	12	10	2	4	74	0.289				Honacki *et al.* (1982)
Delphinidae	15	8	4	5	0	1	33	0.218				Honacki *et al.* (1982)
Ziphiidae	4	10	3	2	0	0	19	0.232				Honacki *et al.* (1982)
Balaenopteridae + Balaenidae	0	1	0	3	1	3	8	0.725				Honacki *et al.* (1982)
CONTINENTAL												
phytopathogens[c]	45	31	38	41	67	0	222	0.449				Rapoport *et al.* (1976)
plants (weeds)[c]	130	45	21	18	15	1	230	0.152				Rapoport (unpubl.)
plants (non-weeds)	462	15	6	5	3	0	491	0.022				Rapoport *et al.* (1976)
Insecta	944	17	10	5	3	1	980	0.014				Rapoport (unpubl.)
pests[c]	74	43	24	28	51	0	220	0.344				Rapoport *et al.* (1976)
Collembola	165	12	5	4	1	1	188	0.046				Rapoport *et al.* (1976)
Hem. Reduviidae	744	4	5	1	1	0	755	0.006				Rapoport *et al.* (1976)
Lep. & Coleopt.	35	1	0	0	1	0	37	0.040				de Lattin (1976)
Aves	204	45	25	12	8	0	294	0.111				Rapoport *et al.* (1976)
Carnivora												
Fissipedia (totals)	195	35	4	0	0	0	234	0.037				Honacki *et al.* (1982)
Canidae	28	6	1	0	0	0	35	0.046				Honacki *et al.* (1982)
Ursidae	7	1	0	0	0	0	8	0.025				Honacki *et al.* (1982)
Procyonidae	15	4	0	0	0	0	19	0.042				Honacki *et al.* (1982)
Mustelidae	50	13	0	0	0	0	63	0.041				Honacki *et al.* (1982)
Viverridae	34	0	0	0	0	0	34	0.0				Honacki *et al.* (1982)
Herpestidae	33	1	0	0	0	0	34	0.01				Honacki *et al.* (1982)
Felidae	25	10	2	0	0	0	37	0.076				Honacki *et al.* (1982)

[a] Planktonic species.
[b] Including Amphipoda + Isopoda + Decapoda + Euphausiacea.
[c] Man-assisted dispersal.

regions. No case exists of a species shared between Ethiopic–Neotropical or between Neotropical–Australian regions, despite the strong bonds shown by other taxa, especially invertebrates (Brundin 1966; Rapoport 1968, 1971) and plants (Szafer 1975). The most significant result, however, is the total absence of species shared between the Nearctic and Palearctic regions. In the tropical regions, the main apparent reason for lack of overlap seems to be the early fragmentation of the Pangea and later of Gondwana. In the Palearctic and Nearctic it seems that the Bering Strait, in spite of the proximity between Siberia and Alaska, is not only a geographical barrier for bats but also a climatic one. The Bering Land Bridge was a two-way passageway for plants and animals throughout the Cenozoic and during the Pleistocene (Brown & Gibson 1983), although if there were any exchanges of Chiropterans, these surely disappeared by extinction or by a rapid differentiation and speciation of the shared species on both sides of the Bering Strait.

The reason why I concentrate on the issue of the Chiroptera is because, in spite of their very remote phylogenetic relation with whales, the way in which both groups capture or collect food has certain similar aspects. The insectivorous bats, as well as whales, find their food in passing. This habit could manifest in similar characterists at macrogeographical level. In addition, bats and whales have a remarkable vagility and dispersal abilities, and there are migratory species in both groups. These similarities however, are not reflected in biogeographical analogies. Whales (Balaenopteridae and Balaenidae) present a cosmopolitanism 28 times higher ($C = 0.725$) than bats ($C = 0.026$). Therefore, other ecological, physiological and anatomical factors come into play and determine the geographical distribution of the above-mentioned groups.

(*b*) *Carnivora*

A second comparison is that between terrestrial and marine carnivores, i.e. between Fissipedia and Pinnipedia. As seen in table 2, the Felidae show greatest cosmopolitanism among the terrestrial families, whereas the Viverridae show the lowest, because all species are restricted to the same biogeographical region. Two species-poor families, the Protelidae and Hyanidae which do not appear in table 2, were added. Among the Hyanidae there is one of the rare species that shares three biogeographical regions (*Hyaena hyanea*). Fissipedian cosmpolitanism, however, only reaches $C = 0.037$. The Pinnipedia show a $C = 0.146$, i.e. four times higher than the former. By means of a 3 × 2 contingency table, the null hypothesis (H_o) that both groups are equal is rejected for a level of $p < 0.001$ (d.f. $= 2$, $\chi^2 = 90.77$).

(*c*) *Comparative cosmopolitanism*

Although table 2 has only an exploratory purpose, due to low availability of data, some interesting relationships appear. Although there is inadequate evidence for a general rule, in Cetaceans there is a positive correlation between body size and cosmopolitanism. The correlation coefficient between maximum body size, measured in metres, and number of regions occupied per species, reaches $r = 0.533$ ($p < 0.01$) for $n = 35$ species. This is not a totally obvious conclusion in the sense that the larger the species' geographical range, the greater the number of natural regions occupied. This is inferred from the definition of cosmopolitanism which takes no account of the quantity of area occupied by a species within a region. A species with a small total area, partitioned between regions, has equal cosmopolitanism as a species occupying large areas over the same regions. Although the total geographic range may correlate positively with body size, there is no reason to expect cosmopolitanism to correlate with body size. Species with patchy distributions in two or more continents, are rather common in collembolan insects, fungi and several other taxa. In fact a weak but significant correlation between body size and geographical range is shown by marine fishes, after processing the data compiled by Muus & Dahlström (1971) ($r = 0.281$, $p < 0.05$, $n = 70$) but there is no significant correlation between body size and number of regions occupied ($r = -0.080$). This result runs directly counter to Gaston & Lawton's (1988) findings in terrestrial arthropods but supports the observations on birds compiled by Brown & Maurer (1987).

Making a pool with all the data from tables 1 and 2, and leaving aside the cases of cosmopolitanism caused by man (agricultural phytopathogens, insect pests and weeds) but adding some taxa not included in the tables, such as Coccolithophorida, marine Plathelmintha, Chaetognatha, Priapulata, Pteropoda, Gastropoda and Pelecypoda, the general cosmopolitanism is $C = 0.125$ ($n = 1015$ species) for marine organisms, and $C = 0.031$ ($n = 2918$ species) for continental organisms. Gastropoda seem to be much more endemic than other mollusc classes ($C = 0.004$, $n = 282$ species).

2. BAYS AND PENINSULAS

Bays, for the aquatic biota, are the equivalent of peninsulas for the terrestrial biota. In peninsulas, a negative correlation between species richness and distance to the continent has been observed in several taxa. In Baja California, this pattern is valid for taxa such as mammals (Simpson 1964) and butterflies (Brown 1987), but not for reptiles (Seib 1980). The explanation of the 'peninsula effect' is based mainly on an immigration–extinction process, but other physical factors can complicate the distributional patterns as demonstrated by Feoli & Lagonegro (1982) and Milne & Forman (1986) for the peninsular floras of Italy and Maine, respectively.

Some marine groups also show what might be called the 'bay effect', i.e. a decreasing diversity with distance from epicontinental sea. For example, such would be the case for the fish fauna in the Baltic Sea. Taking intervals of 50 km from the mouth of the Skagerrak to the North Sea, and penetrating towards the northern and eastern extremes of the Baltic Sea (the Gulf of Bothnia and Gulf of Finland), I processed the data of Muus & Dahlström (1971). For each of the

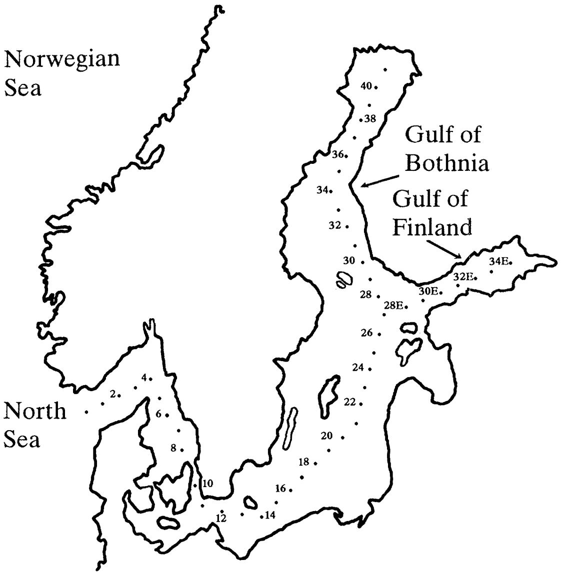

Figure 2. Sampling the number of North Sea fish species penetrating the Baltic Sea. See figure 3 for quantitative data.

122 fish species that live in the Skagerrak mouth I marked the maximum penetration in the Baltic Sea. As can be seen in figures 2 and 3, there is a general decrease in number of species with distance.

A steep fall in the species richness can be observed between the Skagerrak mouth up to the southern tip of Sweden, followed by an evident corridor about 800 km long by 300 km wide up to the entrance of the Gulfs of Finland and Bothnia. Apparently, the narrowness of the latter gulfs, together with their seasonal freezing and low salinity, produce a second strong reduction in fish species. The 'bay effect' can also be observed at mesogeographic level. The Bay of Mochima, Venezuela (figures 4 and 5) is 7.7 km long and contains a total of 21 coral species that shows a decrease in richness indicated by census data (48 censuses of approximately 100 m each, varying in richness from 0 to 17 species). The decrease of species number (Y), as a function of the distance to the Caribbean Sea (X) may be described by an exponential regression model $Y = \exp(2.46 - 0.23X)$, showing a correlation coefficient $r = -0.660$, $p < 0.001$.

The raw data were provided by M.O. Olivares, Escuela de Ciencias, Cumaná, Venezuela (unpublished, 1970) containing 17 points, 20 secondary bays and 11 beaches and islands. This inverse relation between species richness and distance to the source (open sea) obviously leads to the question of whether secondary bays, such as in the Baltic Sea, contain a depauperated fauna in comparison to nearer points or neighbouring areas in the main bay. In nine cases, points were richer than secondary bays, in thirteen cases the inverse occurred, and in one case there was an equal number of coral species. The rule of signs shows no significant differences between the two sub-samples. Apparently, the variables that take part in the determination of coral richness in Mochima Bay act differently at a smaller scale (hundreds of metres) in secondary bays than at a medium scale (kilometres).

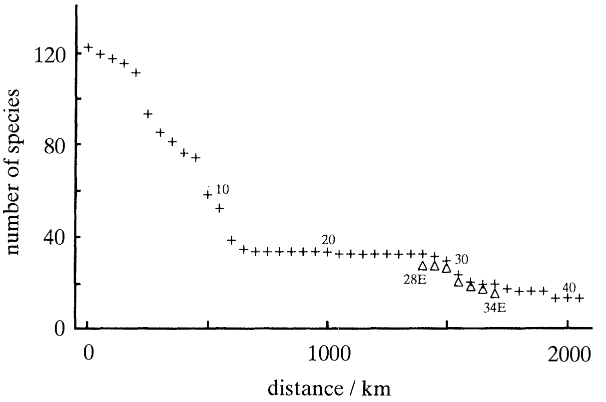

Figure 3. Fish species richness in the Baltic Sea, at different distances from the Atlantic–Skagerrak mouth. Crosses are distanced 50 km. Triangles correspond to the Gulf of Finland (data from Muus & Dahlström 1971).

At a small scale, it seems that a balance exists between immigration and extinction, but at a larger scale immigration appears deficient relative to extinction.

It is predictable that both the peninsula effect and the bay effect may be modified if the conditions prevailing at the tip or bottom, respectively, were more favourable than those of the source area. This could happen, for example, in bays and peninsulas oriented north–south, where the latitudinal effects may reinforce or counteract the peninsular effects, such as in the Scandinavian Peninsula, connected to the continent on 66°N and extending towards the south close to the 55°30′N. This would be the strict concept of peninsula but, in reality, the peninsula starts in middle Finland, say, between Oulu (Gulf of Bothnia) and Kem, White Sea, Russia, along parallel 65°N. Considering this region as a peninsula that goes from there to the north and turns south towards Sweden and Norway, it would be possible to differentiate the peninsula effect from the latitudinal effect. By 'latitude' I consider the set of factors that determine the environmental 'favourability'. Another two peninsulas that could be added, for comparison, are the peninsular portion of Italy, going in the NW–SE direction from 44°N to 38°N and the Kolskiy Poluostrov Peninsula, that goes from Murmansk towards the East in the Barents Sea.

Based on the work of Jalas & Suominen (1973–83) where the geographical distribution of European plants is depicted on 50 × 50 km square-hatched maps, I processed a sample. It is composed of the families Pinaceae to Ephedraceae (vol. 2), Salicaceae to Balanophoraceae (vol. 3), and Caryophyllaceae (vol. 6), i.e. 20 families of vascular plants. The Scandinavian and Italian peninsulas were divided into 36 and 16 bands respectively, following 50 km wide parallels. The Kol'skiy Polyostrov peninsula was divided into eight columns, 50 km wide, along meridians. In each division, the total number of registered species was computed. A superficial analysis of the results shows that in none of the three peninsulas was a decrease of species richness from the base to the tip observed; the maximum values appeared in the centre. This pattern is similar to the one observed by Brown (1987) in the

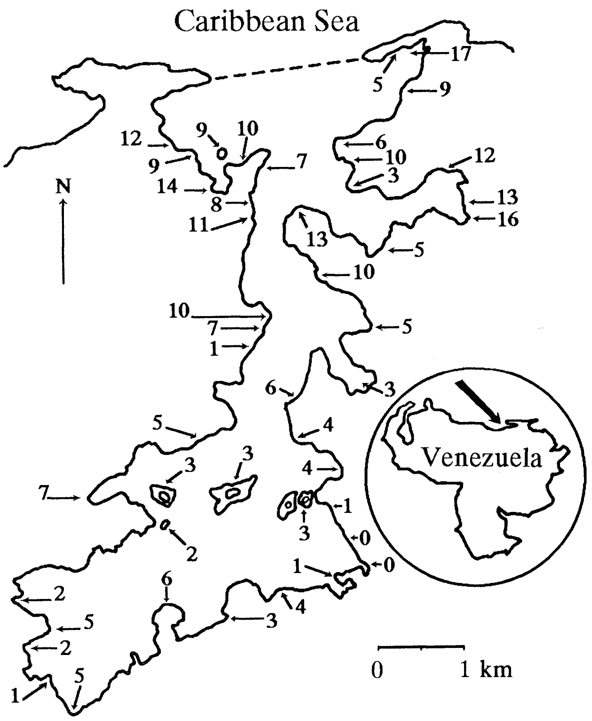

Figure 4. Number of coral species registered in Mochima Bay, at different distances from the Caribbean Sea. See figure 5 for quantitative results. Unpublished data from M. O. Olivares.

Peninsula of Baja California. This author concluded that this pattern originated from a double migratory current, one of Nearctic elements that would have migrated to the south, and another of Neotropical elements to the north. In the peninsular centre, the two currents overlap producing a maximum species richness. This same process could have occurred with the floras of the three peninsulas mentioned above.

3. CONCLUSIONS

Since the symposium held in 1990 on 'Biodiversity in marine and terrestrial environments' by the American Association for the Advancement of Science some points of view expressed there merit greater attention. The idea that keystone species play a more important role in marine than in terrestrial ecosystems, in the sense that top carnivores and grazers have been shown to have consequences on ecosystems disproportionate to their low abundance (e.g. the starfishes *Pisaster* and *Acanthaster*, or the sea urchin *Diadema*) (Ray & Grassle 1991), is no longer sustainable. Long-term monitoring experiments showed the crucial influence that herbivores may exert on plant communities (Shupe & Brotherson 1985; Samson *et al.* 1992). In addition, it no longer can be said that species introductions have more drastic consequences for marine than for terrestrial ecosystems.

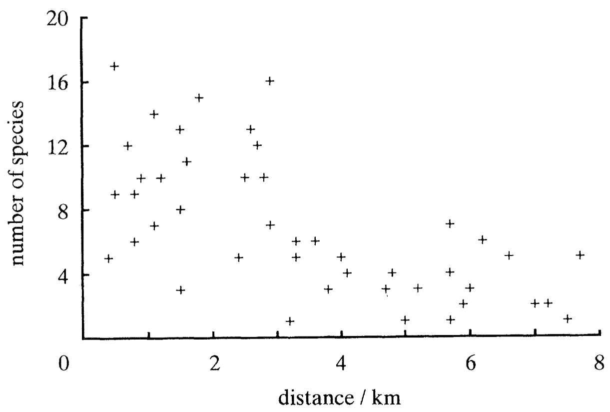

Figure 5. Coral species richness in Mochima Bay, Venezuela. An exponential regression model $Y = \exp(2.46 - 0.23X)$ shows a correlation coefficient $r = -0.660$.

Ray & Grassle (1991), based on the fact that the sea shelters 28 phyla, whereas freshwaters have 14 and continents only 11, concluded that extinctions are less likely to occur in marine than in terrestrial systems. However, because the world's oceans are four times more extensive in area and their biotas at least four times older than terrestrial environments, greater richness in higher taxa is to be predicted. What is surprising, however, is that inland waters maintain an intermediate number of phyla between seas and continents. Freshwaters and soils were an intermediate environment during conquest of the continents (Croghan 1959; Ghilarov 1956), although this appears a significant but insufficient explanation of this phenomenon. The sea has been the cradle of life and, therefore, has had more time to diversify, but only a few phyla have conquered freshwaters, and fewer still, the emerged lands. In the latter, explosive adaptative radiations were verified that gave origin to a very rich diversity at genera and species level. But the fact that freshwaters possess more phyla than terrestrial environments generates interesting questions. Is this due to the fact that these environments are geologically older and more constant, despite the climatic changes and catastrophic events of the past? Because of their smaller volume, rivers and lakes should be more vulnerable to extinction than seas and continents, due to their greater 'insularity'. If mass extinctions affected freshwater biotas more in the past, but shelter a greater number of superiour taxa than emerged lands, then we must conclude that these systems were repeatedly recolonized from marine stocks. In other words, it is easier to recolonize rivers and lakes than continents. Otherwise, we should accept that inland waters are more ancient, stable, and resilient systems than suspected.

Minimum–maximum geographical range and its corresponding mean and standard deviation (in parentheses) expressed in $\text{km}^2 \times 10^6$ is 8–250 (166.7, s.d. 68.2) for planktonic foraminiferans; 1–167 (59.3, s.d. 56.6) for Crustacea Euphausiaceae; 0.25–62.8 (6.5, s.d. 12.7) for Cephalopoda; 0.28–94 (25.8, s.d. 29.3) for Gastropoda, and 0.1–289 (23.9, s.d. 28.9) for marine fishes.

These data confirm what many authors have stated before: that the geographical range of marine species is clearly bigger than the data of terrestrial species appearing in Rapoport (1982). In the same way, cosmopolitanism is also greater. This is possibly due to a greater stability and lesser environmental stress of marine environments, to the fact that the ocean is continuous or interconnected, and that barriers are more porous than continental ones. The general marine cosmopolitanism is four times greater ($C = 0.125$) than continental values ($C = 0.031$). Considering these preliminary results, the question arises of what things would be like if continents had among them the same continuity that oceans have nowadays. Thus, barriers on continents may be a strong combination between geographical or geological (landscape), climatic and biological factors. In the seas those factors seem to be weaker in the differentiation and integration of the biotas. For example, both in seas as in continents, temperature is an important factor, but in continents precipitation or, more stricly, rainfall is an additional variable, which has, as a barrier, a weaker influence on the seas. This play between temperature and rainfall, and its resultant, evapotranspiration, conditions the various types of vegetation (Holdridge 1947; Walter 1973; Currie & Paquin 1987). The latter, on the other hand, determine the different faunistic associations. Moreover, there are strong interactions between climate, vegetation and soil types. This synergism is less apparent in marine environments.

Thermal barriers exist both in continents and oceans. In the latter, for example, a tropical belt exists between temperate and cold seas of both hemispheres. Orographic effects are also common to both environments, as well as the island effect. But, in this case, the indices of cosmopolitanism show that islands are generally more isolating for continental than for marine coastal species. Because the mean geographical range of species depends on the continental or island size (Rapoport 1982), it is not perhaps too risky to infer that the Pangean terrestrial biota should have been more widespread than the present ones.

Of a total of 523 North American non-aquatic mammals, Pagel *et al.* (1991) concluded that the mean range of species occupies 7.8% of the continent. The average increases to 12.6% if mammals whose ranges reach south of 30°N are excluded ($n = 224$). In a similar study of South American mammals ($n = 536$), Ruggiero (1993) obtained a higher value of mean occupancy, 18.6%. Eurasian birds occupy 24.4% of this continent and Australian birds 35.2% (Rapoport 1982).

Considering all five continents, except Antarctica, the only estimate available is 16 810 000 km^2 ($n = 181$ species of birds) obtained from Rapoport (1982), that is, 12.7% of occupancy. For comparison, in table 2, marine taxa range from 1.8% occupancy in Cephalopoda to 16.4% in Euphausiacea, to 21.2% in fishes and up to 46.2% in planktonic foraminiferans. The latter, however, do not represent all the class Foraminifera as the number of planktonic species is extremely low in comparison to the benthic foraminiferans, which proved to be more endemic than the former (Buzas & Culver 1991). The figures here compiled do not show appreciable differences between continental and marine taxa with respect to relative mean geographical range. This is a topic which merits a more profound analysis through a larger number of data. In answer to the question posed above on the areography of Pangea, assuming that this continent had an area equivalent to the sum of the present emerged lands (148.8 million km^2), other things being equal, the average geographical range of terrestrial species should have been of 18.7 to 52.4 million km^2. Applying the criterion of 1/4 mean occupancy revealed by birds in five continents (Rapoport 1982), the average geographic range of Pangean species must have been around around 37.2 million km^2. And this, perhaps, may help to explain why the Early Mesozoic fossil registers are so widespread.

Man-mediated dispersal increases not only the geographical range but also the cosmopolitanism of species. Weed cosmopolitanism is seven times greater than that of native plants, and agricultural insect pests are 25 times more cosmopolitan than native insects. Barriers separating natural terrestrial and marine regions have been broken by human commerce and transportation thus putting nature in a status perhaps similar to that of the Pangea, but with the singularity of having physically disconnected continents. The economic losses due to the mixing of biotas have been comparatively well-studied, but the impacts on the natural communities and the future of biogeography are not so well documented.

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