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Seaweeds, latitudinal diversity patterns, and Rapoport's Rule

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Abstract. We analysed the geographic distribution of 645 species of marine benthic algae along the Atlantic coast of Europe and Pacific coast of temperate South America to test for the existence of an association between geographic range size and latitude (Rapoport's Rule) and for three key components of the explanations offered for it. We found that species in high diversity areas are characterized by small geographic ranges and by low specific growth rates as compared to species with large geographic ranges, thus supporting the Rapoport-rescue hypothesis. However, the pattern is not related to species' tolerances, to abiotic conditions or to climatic variability. Further, the inverse latitudinal diversity pattern shown by the marine algal flora of temperate Pacific South America, and the opposite patterns shown by tropical and subantarctic species within this flora, stressed that small geographic ranges are linked to high diversity areas in general, and not only in relation to the pole to tropic species diversity gradient.

Key words. Climatic variation; growth rates; latitudinal diversity patterns; Rapoport's Rule; seaweeds distribution.

INTRODUCTION

Rapoport's Rule (Rapoport, 1982) refers to the tendency for species geographical ranges to become smaller towards the tropics. This pattern is explained (Stevens, 1989, 1992) on the basis of climatic variation and tolerance ranges; high-latitude environments are expected to have a greater annual range of climatic conditions than low latitude environments, therefore favouring the evolution of eurytolerant species, with larger geographic ranges than those evolved in the less variable, tropical environments. Thus, low latitude organisms should be characterized by a broadening of climatic tolerance as compared to low-latitudes organisms. As a consequence of a small geographic range, most low latitude localities will have relatively more species near the margin of their geographic ranges than high latitude sites. Populations near the margin, although poorly adapted to local conditions, are not locally excluded because of the continuous arrival of migrants from areas where the species does well, thereby inflating species richness. This explanation emphasizes that both the Rapoport's Rule and the latitudinal diversity gradient are the result of the same phenomenon. As a corollary of this explanation it is expected that high diversity areas should exhibit lower climatic variability than low diversity areas.

Fitting distributional patterns to Rapoport's Rule has produced mixed results. Distributional data of various groups of marine and terrestrial invertebrates, vertebrates and land plants have supported the rule, allowing its extension to elevational and bathymetric gradients (Stevens, 1989, 1992; Pagel, May & Collier, 1991; France, 1992; Pineda, 1993; MacPherson & Duarte, 1994). Analysis of other animal groups (Ricklefs & Latham, 1992; Smith, May & Harvey, 1994; Rhode, Heap & Heap, 1993; Roy, Jablonski & Valentine, 1994) have failed to find the proposed pattern and suggested the rule might be an artefact derived from non-independent sampling (Rhode *et al*., 1993) or from inadequate consideration of province-scale biogeography (Roy *et al*., 1994), which influences latitudinal species range and diversity gradients.

All previous studies have worked with organisms with latitudinal patterns characterized by increasing species richness towards low latitudes. Marine benthic algae exhibit variable patterns of latitudinal species richness in different areas. In the Atlantic coast of

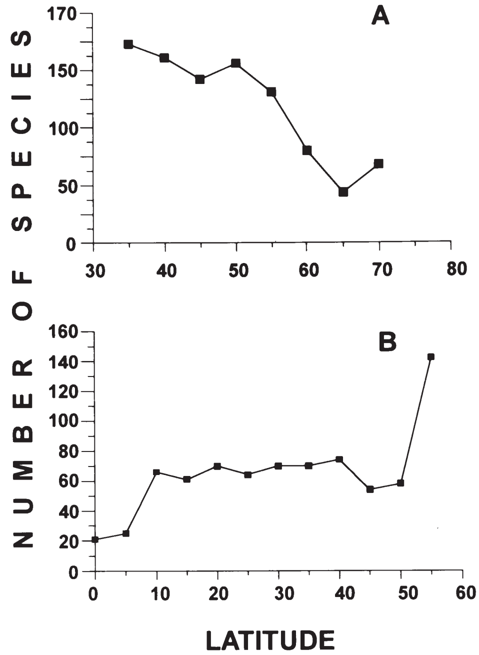

Fig. 1. Latitudinal algal species diversity gradients along the Atlantic coast of Europe (A) and the temperate Pacific coast of South America (B).

Europe (Fig. 1A), the seaweed flora shows the classical pattern with species richness increasing to the Equator (van den Hoek, 1975). However, a different pattern occurs in temperate Pacific South America (Fig. 1B), where the number of species increases between 10°S to 55°S, (Santelices, 1980). This inverted latitudinal pattern of seaweed species richness in temperate Pacific South America is the result of the interweaving of species with different geographic origins along the coastlines of Peru and Chile (Santelices, 1980). The region is characterized by high endemism (32.3% of the flora) and a very unequal contribution of tropical (3.4%) and subantarctic (34.4%) species. The number of tropical species decreases towards the south pole, while the subantarctic elements increase. The abundance of endemic species is relatively similar along most of this coastline, as is the abundance of the other two algal groups found there, namely the widely distributed (22.8% of the flora) and the bipolar species (7.1%).

Since low and high latitudes can be high diversity areas for the seaweed in different coastlines (e.g. northern Europe versus temperate Pacific South America) seaweeds can be used to test key predictions of Rapoport's Rule. Furthermore, the very different patterns of distribution of species with tropical versus subantarctic affinities determine an extra-tropical peak of species within temperate Pacific South America which allows decoupling of the climate-based explanation for Rapoport's Rule from the competition-based argument. Using the distributional patterns of these species we tested four conceptual components of Rapoport's Rule and explanation, namely (a) that species in high richness areas exhibit smaller latitudinal ranges than species in low richness areas, (b) that high richness areas are climatically more stable than low richness areas, (c) that species with larger geographic ranges have wider tolerance limits than species with smaller geographic ranges, and (d) that species with small geographic ranges are usually less capable of maintaining self-sustaining populations, and possess a lower ability for growth and reproduction as compared to widely distributed species.

MATERIALS AND METHODS

Data on the geographic distribution of seaweed species included 265 taxas reported (van den Hoek, 1975) for the Atlantic coast of Europe and 380 species reported (Santelices, 1980) for the temperate coast of Pacific South America.

Rapoport's Rule predicts a correlation between the mean latitudinal breadth of taxa occurring at any particular point along a latitudinal gradient and the latitudinal position of the point. This pattern was searched using Steven's (1989) method which is based in averaging over the latitudinal ranges of all species occurring in the same 5° latitude band after rounding ranges to the nearest 5°. We followed this method with the seaweed distributional data. However, under this method points to be plotted are not statistically independent, which preclude the use of simple correlation analysis.

Surface water temperature data for the Pacific coast of South America were obtained from Wooster & Sievers (1970). Equivalent data for the Atlantic coast of Europe were obtained from van den Hoek & Donze (1967).

Data on optimum and limiting temperature for growth and survival for species with subantarctic affinities and different mean latitudinal ranges along temperate Pacific South America were determined, under laboratory conditions by Wiencke & Tom Dieck

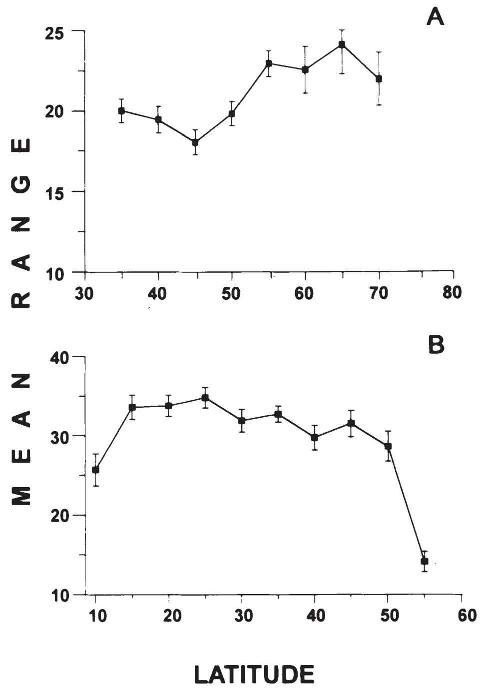

Fig. 2. Mean latitudinal range size of algal species along the Atlantic coast of Europe (A) and the temperate Pacific coast of South America (B).

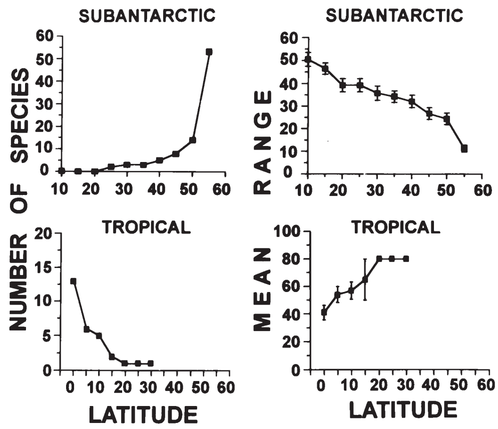

Fig. 3. Latitudinal gradient in species diversity and mean range size for subantartic and tropical species along the Pacific coast of South America.

(1990). Such data were used to correlate mean latitudinal range with temperature tolerance and growth potential.

RESULTS AND DISCUSSION

(a) Latitudinal range and species richness

The pattern of distribution of the marine algal flora of northern Europe supports Rapoport's prediction (Fig. 2A). The mean latitudinal range increases with latitude and tends to be smaller in the highest-species richness area. A similar relationship is exhibited by the marine algal flora of Peru and Chile (Fig. 2B) despite the shallow and inverted latitudinal richness gradient exhibited by this flora. The slight southwards increase in species richness between 15°S and 50°S correlates with a slight southwards decrease in mean latitudinal range; the sharp increase in species richness between 50°S and 55°S correlates with a sharp decrease in mean species range.

The inverse relationship between latitudinal species richness and mean latitudinal range also occurs in the subantarctic and tropical biogeographic components of the marine algal flora of temperate Pacific South America (Fig. 3). Species with subantarctic and with tropical affinities have well defined, opposite latitudinal gradients of species richness along this coastline. Their patterns of mean latitudinal range also are contrastingly different and, in both cases, correlated negatively with species richness.

The pattern of species richness and geographic range size described by Rapoport's Rule has up to now been applied to entire species assemblages only, focusing on the current conditions uncluttered by phylogenetic constraints. Results gathered in this study suggest application of the rule could be also extended to subsets of species within an assemblage.

(b) Climatic variation and species richness

No apparent correlation between the observed trend in surface water temperature range and mean latitudinal range was detected for the European and the South American coasts studied (Fig. 4). Areas with high species richness do not show a smaller temperature range than areas of low species richness as has been reported in support of the presently suggested explanation of Rapoport's Rule (Stevens 1989).

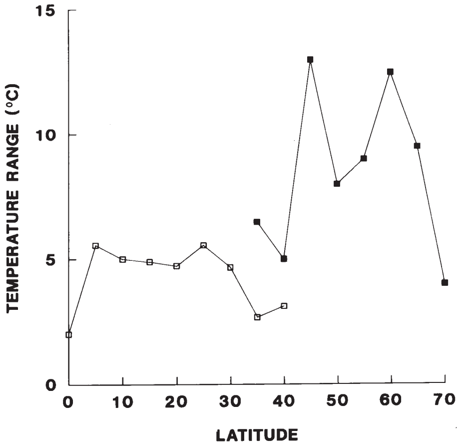

Fig. 4. Shallow water temperature range along the Atlantic coast of Europe (closed symbols) and the Pacific coast of South America (open symbols).

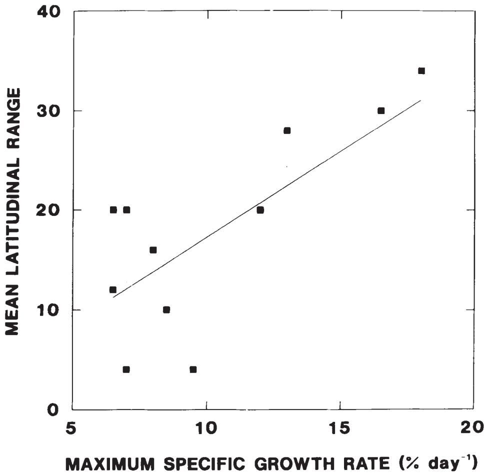

Fig. 5. Relationship between maximum growth capacity and mean latitudinal range for algal species from the Pacific coast of South America.

(c) Mean latitudinal range and temperature tolerance

Species with subantarctic affinities may reach various latitudes along temperate Pacific South America. Optimum and limiting temperature for growth and survival of a subset of these species was recently determined (Wiencke & Tom Dieck, 1990). Mean latitudinal range along this coastline shows no statistically significant relationship with temperature tolerance (Pearson's $r=0.069$; $P=0.822$; $n=13$). Species with extended (e.g. *Enteromorpha bulbosa*, *E. clathrata*) and with more reduced latitudinal distribution (e.g. *Urospora implexa*, *Prasiola crispa*) have similar temperature limits. Furthermore, the range of temperature tolerance exhibited by most species widely exceeds the field temperature ranges.

(d) Geographic range size and growth potential

Laboratory data (Wiencke & Tom Dieck, 1990) suggests a relationship between mean latitudinal range and specific maximum growth rate (Pearson's $r=0.67$; $P=0.012$; $n=13$). Species reaching high growth rates under laboratory conditions are also the ones exhibiting more extended latitudinal ranges (Fig. 5).

Laboratory conditions are obviously different from those experienced in the field and success in the laboratory may not reflect field success. However, the above results point to the importance of growth potential, an attribute scarcely considered in biogeographic studies but one which is obviously related to population survival and expansion, specially in organisms such as seaweeds, which may propagate vegetatively or exhibit a growth-dependent reproductive potential.

Stevens (1989) proposed that high diversity is observed in areas where most species have small geographic ranges because there, local diversity will be inflated through rescue effects (Brown & Kodric-Brown, 1977). A typical locality in a high diversity area will be composed mostly by sink populations unable to persist without the continuous arrival of immigrants from source populations, and whose individuals are poorly adapted to local conditions. The correlation between specific maximum growth rate and latitudinal range suggest that once a population stock has colonized a given area, a greater growth potential may allow them to reach population densities such that at least a few of them would survive adverse conditions, serving as population sources for future expansions and new growth. In turn, this capacity would allow for a more extended geographic distribution. On the contrary, species with reduced growth potential would recover more slowly from disturbances and would not be able to grow and expand fast enough under favourable environmental conditions.

The evidence we have presented for algae suggests that species in high diversity areas are characterized by small geographic ranges and by low specific growth rates as compared to species with large geographic ranges, thus supporting the Rapoport-rescue hypothesis. However, no apparent correlation was found between temperature variation and species richness or between mean latitudinal range and temperature tolerance. Furthermore, the inverse latitudinal diversity pattern shown by the marine algal flora of temperate Pacific South America, and the opposite patterns shown by tropical and subantarctic species within this flora, stressed that small geographic ranges are linked to high diversity areas in general, and not only in relation to the pole to tropic species diversity gradient. Further, our data and analysis suggests that Rapoport's Rule is not restricted to the northern landmasses, as pointed out by Rhode & Heap (1996), and might be a general biogeographic pattern.

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