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Hypothesizing Marine Provincialism on the Basis of Seaweed Distribution in Malaysia

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ABSTRACT Biogeographically, Malaysia is included in the Indo-West Pacific tropical marine region, which harbours the highest diversity of coral reefs, seagrasses and mangroves. We hypothesize that the Malaysian coastline may be divided into smaller spatial units in the order of *provinces* and *districts* in order to better understand the distribution patterns of marine biota. This paper will examine how the distribution pattern of seaweeds along the Malaysian coastline is clustered geographically at different taxonomic levels (family, genus, species). Data is sourced from field sampling (1984 - 2004) and published checklists. In this analysis, the Malaysian coastline is divided into five operational geographic units (OGU): (1) West Coast Peninsular Malaysia (2) East Coast Peninsular Malaysia (3) Sarawak (4) West Coast Sabah, and (4) East Coast Sabah. Sorensen's Similarity Index was calculated for each OGU. The results of this preliminary analysis show that (i) there was no distinction between any of the OGUs at the level of the family; (ii) at the genus level, there was a marked separation between the seaweed populace of Peninsular Malaysia and North Borneo; (iii) at the species level, all the OGUs are distinctly separated. The findings of this research tell us that in the case of seaweeds, provinces may best be reflected at the generic level, and districts at the species level.

ABSTRAK Dari segi biogeografi, Malaysia terletak di kawasan tropical marin Pasifik Indo-Barat, yang megandungi diversiti batu karang, rumput laut dan paya bakau yang tertinggi. Kami menghipotesis bahawa pesisiran pantai Malaysia boleh dibahagikan kepada unit spatial yang lebih kecil iaitu *wilayah* dan *daerah* bagi pemahaman yang lebih mendalam mengenai corak penyebaran biota marin. Kertas kerja ini akan memeriksa bagaimana corak penyebaran rumpai air laut disepanjang pesisiran pantai Malaysia dikelompokkan secara geografi pada aras taksonomik (famili, genus, spesis) yang berbeza. Sumber data diperolehi daripada persampelan kerja lapangan (1984 – 2004) dan senarai yang telah diterbitkan. Dalam analisis ini, pesisiran pantai Malaysia dibahagikan kepada lima unit operasi geografi (OGU): (1) Pantai Barat Semenanjung Malaysia (2) Pantai Timur Semenanjung Malaysia (3) Sarawak (4) Pantai Barat Sabah, dan (5) Pantai Timur Sabah. Indeks Similariti Sorensen telah dikira untuk setiap OGU. Keputusan awal analisis menunjukkan bahawa (i) tidak ada perbezaan di antara mana-mana OGU pada peringkat famili; (ii) dalam peringkat genus, terdapat pengasingan yang ketara di antara populasi rumpai air laut Semenanjung Malaysia dan Borneo Utara; (iii) pada peringkat spesis, semua OGU adalah jelas diasingkan. Penemuan daripada kajian ini menunjukkan bahawa untuk kes rumpair air laut, wilayah boleh ditunjukkan pada peringkat generik, dan daerah pada peringkat spesis.

(Seaweed, provincialism, similarity, distribution, spatial unit, biodiversity, biogeography)

INTRODUCTION

Biogeography, here defined as the spatial and temporal analysis of how biological communities are distributed on the earth, has had within it the concept of provincialism as a persistent and recurring theme since the early history of the discipline. Provincialism analysis seeks to classify the biosphere into distinct spatial units on the basis of biodiversity, with taxonomic diversity as the most common criteria, followed by taxonomic endemism. However, other criteria that have been proposed are morphological diversity, functional diversity, ecological diversity, genetic diversity [1], and taxonomic abundance [2]. These spatial units are referred to as biogeographic units or regions. Other terms, such as kingdom, realm, province, and district, are names also applied to biogeographic units but at different spatial scales.

The principle underlying provincialism is presumably that each floral or faunal unit is distinctive from the rest as a result of isolation. The most famous barrier and border between adjacent biogeographic units is, of course, the Wallace Line – an imaginary boundary that separates the Australian and Oriental fauna at the regional level.

BIOGEOGRAPHY AND PROVINCIALISM

In essence, the discipline we know today as biogeography began with the study of provincialism when, in the eighteenth and nineteenth centuries, the distribution of animals and plants in the context of space became an issue of interest for naturalists who realized that living organisms were distributed neither randomly nor continuously. They began to order and rank the distribution patterns that became evident to them. The Comte de Buffon (1707-1788), who first observed in 1771 that the large mammals of the tropical regions of the Old World and the New World were distinctly different, proceeded to formulate the first law of biogeography: that distant regions with similar climate have different animal species. This law was also interpreted to mean that such animals had evolved *in situ* and had not migrated from elsewhere [3]. Buffon's law was extended by von Humboldt (1769-1859) to birds, reptiles, insects, spiders and flowering plants [4].

The recognition of formal biogeographic provincialism was first introduced in 1820 by Augustin de Candolle [5], who referred to these spatial units as *areas of endemism*. He identified 20 regions of global plant endemism, stating that each area was characterized by species whose distribution was bounded by natural barriers of ocean, desert or temperature change, or by the presence of competing plants. Later, he increased the number of areas of endemism to 40. Unfortunately, de Candolle did not provide any maps to illustrate his views.

When Darwinian evolution brought biological dialogue to a head in the second half of the nineteenth century, the historical aspect of species development became a new area of interest. Inquiry began into the why and how of species development in different spatial units. Taking off on de Candolle's areas of floral endemism, Engler was the first to trace the history of floras within each spatial unit back to the Tertiary [4]. He defined four 'Realms' – the Arcto-Tertiary, the Palaeotropical, the Neotropical and the ancient ocean Realm. These four Realms in turn contained 32 regions. Subsequently, Good [6] named the major divisions Kingdoms rather than Realms. Subsequent modifications have been made by various researchers in phyto- and zoogeography. However, the systems that are best known today are that of Sclater-Wallace for birds and mammals, and Takhtajan for plants.

The study of provincialism changed drastically in the twentieth century. Before the advent of continental drift theory by Alfred Wegener in the first quarter of the twentieth century, and plate tectonics by Harry Hess in 1960, the spatial distribution of animals and plants was always viewed as emerging from and on stationary continents. Those in this school of thought relied on explanations of the modes and processes of *dispersal* across barriers when discussing how biological distribution patterns emerge. After the emergence of ideas on plate tectonics, the options for biogeographers grew wider. Instead of formulating hypothetical cross-oceanic land bridges, sunken continents, and notions of terrestrial life dispersing across oceans by rafting to explain disjunct distributions, the new school of vicariance biogeography that emerged began to look to the geological and geographical history of continents and islands as likely explanations of how biological populations are broken up and how some are brought together. It became clear that the history of the land was intertwined with the history of the species.

Although the Sclater-Wallace and Takhtajan schemes for fauna and flora, respectively, have become standards, the revision of biogeographic provincialism schemes is on-going. In 2000, Myers *et al.* [7] identified global biodiversity hotspots. In 2001, Barry Cox [4] reviewed the progress of ideas in the development of biogeographic regions and critiqued some of the inconsistencies in commonly accepted biogeographic schemes. In 2002, Morrone [8] responded to Barry Cox's critique by proposing a new system for terrestrial flora and fauna. Morrone's scheme encompasses three kingdoms, the Holarctic, Holotropical, and Austral kingdoms, together with twelve separate regions. What distinguishes this scheme from the rest is his recognition of some of the smaller regions, namely, the Cape, Andean, and Neoguinean regions.

Some contemporary research that has shed light on the different ways of delineating spatial units at subregional level using taxon distribution include McLaughlin [9] on the flora of the Western USA, Proches [10] on the distribution of bats, Porzecanski and Cracraft [11] on avian distribution in the South American aridlands, and Haffer [12] on avian distribution in the lowland forests of South America. Olson *et al.* [13] produced a new global map of terrestrial ecoregions that reflected a huge collaborative effort between more than 1000 biogeographers, taxonomists, conservation biologists, and ecologists. In this new map, the world was subdivided into 14 biomes and eight biogeographic realms, within which were nestled 867 ecoregions.

SPATIAL UNITS

Provincialism is the classification of the biosphere into distinct and separate spatial units on the basis of biological diversity. The determination of provincialism in terrestrial or marine habitats should be the first line of inquiry in any biogeographic study above the local level because it presents us with a picture of biological distribution that allows us to determine the investigative direction.

In order of decreasing size, the common spatial units are Realms or Regions, Subregions, Provinces, and Districts. Following the terminology of Takhtajan for plants, Kingdoms/Realms are spatial units characterized by high endemism at the level of families and subfamilies; Regions at the generic or species level, and sometimes at the levels of families and orders; Provinces at the species level; and Districts are delineated mainly at the subspecies level [4]. Takhtajan's analysis, however, was mainly at the level of families, genera and species. However, these spatial units and their related taxonomic levels differ depending on the type of biota in question [9].

MARINE PROVINCIALISM

The technology for marine research has always lagged behind that of terrestrial research. As pointed out by Briggs [14], the publication of comprehensive marine surveys came a full six to ten decades behind the terrestrial appraisals of Alfred Wallace. Today, however, marine biogeography has emerged as a rigorous discipline, with the works of John Briggs, *Marine Zoogeography* [15]; Geerat Vermeij, *Marine Biogeography and Adaptation* [16] and *Evolution and Escalation* [17]; and A. Longhurst, *Ecological Geography of the* Sea [18] as notable publications.

Marine biogeographic provinces have been suggested by Forbes, Ekman, Briggs, Vermeij, and van den Hoek [4]. Edward Forbes (1815-1854) produced the first comprehensive work on marine biogeography in Johnston's *The Physical Atlas of Natural Phenomena* in 1856. He divided the ocean into 25 provinces and also recognized a series of five depth zones. However, these early delineations of regions or provinces have been mostly intuitive, with no systematic comparison of the composition of biota given by the authors, leading Longhurst to declare that the biogeography of the sea belonged "to the family of intractable scientific problems" [18].

Today, seven groups of marine biogeographical regions based on zoogeographic and phycological distributions are recognized [19]:

(1) Arctic group (one region)
(2) Cold temperate group, Northern Hemisphere (three regions)
(3) Warm temperate group, Northern Hemisphere (four regions)
(4) Tropical group (four regions)
(5) Warm temperate group, Southern Hemisphere (five regions)
(6) Cold temperate group, Southern Hemisphere (five regions)
(7) Antarctic group (one region)

This system is largely based on that of Briggs [15], who identified 24 marine regions on the basis of marine faunal distribution (Figure 1). The boundaries between these marine regions appear to follow certain surface seawater isotherms, thereby signalling the significance of water temperature as the main factor governing the geographical distribution of species. Van den Hoek [4] suggested that boundaries between regions be drawn where there is extensive overlapping of species, rather than relying on areas of species endemism alone. However, the regions revealed by this method broadly agree with the marine regions of Briggs.

More recently, Adey and Steneck [2] investigated the existence of marine provinces on the basis of the biogeography of crustose coralline red algae (Rhodophyta/Corallinales) using their newly designed thermo-geographic model, in which time was treated using the temperature/area/distributions for the present (interglacial period) integrated with that of 18,000 years before present (glacial period). They suggested the use of abundance rather than species presence/absence (Figure 2). However, the resulting thermogeographic model defined 20 regions that also largely corresponded to Briggs's marine biogeographic zones.

Following the coastal biogeographic regions of Briggs [15], and Adey and Steneck [2], Malaysia is located in the Indo-West Pacific tropical region that stretches from East Africa, past Southeast Asia, to the Polynesian archipelago in the Pacific Ocean. However, this region is a large one, covering an area of 175,020 nautical miles [2]. For the purpose of management and marine conservation, this region may be further subdivided into finer-scale spatial units such as provinces and districts. We performed a preliminary analysis on the distribution pattern of seaweeds along the Malaysian coastline to determine whether those patterns are clustered geographically (display provincialism).

METHODS

Data sets

The distribution data of seaweeds in Malaysia was obtained from checklists published by Phang [20], Masuda *et al.* [21, 22, 23, 24, 25, 26, 27, 28], Terada *et al.* [29], and Yamagishi *et al.* [30]. A large part of the specimens included in this analysis come from the collection of the Seaweeds and Seagrasses Herbarium housed at Rimba Ilmu, University of Malaya. This collection is the single largest seaweed collection in Malaysia, with over 9,000 specimens deposited since the 1984.

Spatial units

Conventionally, a georeferenced grid is used as the basic spatial unit of analysis, whereby a study area is divided into grids of appropriate sizes following the lines of latitude and longitude. This method was not employed in this study for two reasons: (i) because this would have required even sampling efforts in smaller areas than possible for this preliminary survey and, (ii) because the older data sets had not incorporated latitude and longitude readings but instead, referred to general locations such as 'West Coast Peninsular Malaysia' and 'Sarawak'. In order to incorporate these older data sets, we divided the coastline and islands of Malaysia into Operational Geographic Units (OGU) 1 – 5 that encompassed the coastline and outlying islands of West Coast Peninsular Malaysia (OGU I), East Coast Peninsular Malaysia (OGU II), Sarawak (OGU III), West Coast Sabah (OGU IV) and East Coast Sabah (OGU V) (Figure 3). These OGUs were also approximately similar in coastline length. The analysis was performed on a dataset of 372 Malaysian seaweed taxa belonging to 8 families, 17 taxa of Cyanophyta; 13 families, 101 taxa of Chlorophyta; 27 families, 182 taxa of Rhodophyta; and 8 families, 72 taxa of Phaeophyta.

Analyses

Taxon richness (number of family, genus, species) was enumerated for each OGU. The clustering of marine floristic provinces was performed with Sorensen's Index of Similarity as the resemblance function and the Unweighted Pair Group Method with Arithmetic Averages (UPGMA) as the clustering method. Sorensen's

Index of Similarity was used because binary data was used, the samples were not known to be truly representative, and joint non-occurrences of taxa were discounted. The results are displayed in dendrograms. Sorensen's Index of Similarity is calculated as follows:

$$S = 2a/2a+b+c,$$

Where,
a = number of species in sample 1 and 2
b = number of species in sample 2 but absent from sample 1
c = number of species in sample 1 but absent from sample 2

Three different data sets were used: (1) family presence/absence (2) genus absence/presence (3) species presence/absence. Complete similarity is denoted by a similarity index of 1 (100%). The limits set for each taxonomic level in the separation of possible provinces were 40% similarity at the family level, 50% similarity at the generic level, and 75% similarity at the species level. These similarity limits are arbitrary but comparable to similar studies such as in Proches [10].

RESULTS AND DISCUSSION

Taxon Richness

The number of species was highest in West Peninsular Malaysia (OGU I) and lowest in East Sabah (OGU V) (Table 1). Generic richness was highest in West Peninsular Malaysia (OGU I), and lowest in Sarawak (OGU III) and East Sabah (OGU V) (Table 2). However, sampling efforts may also have influenced the relative paucity of species counts in the waters around Sarawak and Sabah. With Sabah at the edge of the East Indies Triangle, an area with the richest marine biodiversity, one would have expected this zone to possess the greatest seaweed diversity with a gradual decrease outwards towards West Coast Peninsular Malaysia. However, from the opposite point of view, the East Indies Triangle is also an area with the greatest occurrences of hermatypic corals which compete with seaweeds for space [19]. The relationship between coral richness and seaweed richness has yet to be adequately enumerated.

Similarity

The dendrograms obtained from the cluster analysis show that the type of seaweed families, genera and species shared by the OGUs decrease with increasing distance between the OGUs (Figure 4). The clustering procedures on family presence/absence (40% similarity) did not show a separation between the OGUs (Figure 4a).

The analysis on genus presence/absence (50% similarity) resulted in four clusters: Peninsular Malaysia (combination of OGU I and II), Sarawak (OGU III), West Sabah (OGU IV) and East Sabah (OGU V) (Figure 4b). Only East Peninsular Malaysia and West Peninsular Malaysia, in sharing 65% of their seaweed diversity at the generic level, fulfilled the 50% threshold. At this taxonomic level, the seaweed biota of Peninsular Malaysia is separated from that of East Malaysia, possibly with the South China Sea acting as a boundary between the seaweed forms of Peninsular and East Malaysia.

Species presence/absence (75%) resulted in the greatest breakdown into possible provinces. West Peninsular Malaysia (OGU I) and East Peninsular Malaysia (OGU II) were separated; while Sarawak (OGU III), West Sabah (OGU IV) and East Sabah (OGU V) remained separate as individual areas (Figure 4c). At this taxonomic level, possible boundaries could have been determined by more local and recent factors such as hydrography, coastal geomorphology, substratum, and water quality. These will need to be related to the OGUs in further studies. Overall, the results of this analysis tell us that in the case of seaweeds in Malaysia, provinces may best be defined at the generic level, whilst districts are likely to be reflected at the species level.

Although this preliminary analysis was in no means a complete and definitive way of delineating marine provinces, it does, even in this cursory fashion, show a spatial separation of the seaweed flora. This serves to point us in the direction of inquiring into the significance of the South China Sea as a barrier, and how permeable a barrier it is. It makes us inquire into the relationship between local environmental factors that have forced a separation onto the seaweed populace of West Coast and East Coast Peninsular Malaysia at the species level, and even between the West Coast and East Coast of Sabah. The revealed patterns also draw us to look into the separation of seaweeds at the generic and species level in the light of eustatic sea-level fluctuations. There is also the possibility of harnessing the potential of DNA sequence divergence to test the age and permeability of these existing biogeographic boundaries [31].

A more conclusive study on marine provincialism in Malaysia will, we believe, result in the delineation of finer spatial units than revealed in this preliminary study. The identification of provinces, districts, and even subdistricts, will be useful in designing management and conservation plans that are suitable for the biological community in a particular spatial unit. Marine provincialism analysis will also make significant contributions to how marine protected areas are selected and protected. The ideal end-product of such an analysis is a series of maps delineating areas of diversity, endemism, and if possible, active zones of successful speciation, all of which are factors to be considered in the selection and management of marine protected areas. Future analysis requires the integration of at least morphological and functional diversity because these two metrics, unlike taxonomic diversity, may be able to shed light on the underlying processes of distribution patterns. The boundaries between provinces may also be better delineated by species turnover such as that proposed by Roy, Jablonksi and Valentine [1] for marine molluscs in the Northern Hemisphere.

CONCLUSION

The study of provincialism - how spatial units may be delineated according to the type of species that inhabit them – is a science that is almost 200 years old. Marine provinces need to be delineated for the sake of gaining a better understanding of how and why our marine resources are located where they are today. With this knowledge in hand, the advancement of marine conservation science would be significant. Organisms such as seaweeds, seagrasses, and corals better reflect patterns of provincialism by virtue of their sessile nature. A preliminary analysis of marine provincialism on the basis of seaweed distribution in Malaysia by using Sorensen's Similarity Index shows a separation between the West Coast Peninsular Malaysia, East Coast Peninsular Malaysia, Sarawak, East Coast Sabah, and West Coast Sabah at the species level. The South China Sea appears to be a barrier against the exchange of seaweed genera between Peninsular Malaysia and East Malaysia. A more conclusive study on marine provincialism in Malaysia is quite likely to result in the delineation of finer spatial units than revealed in this preliminary study. The identification of these spatial units will be useful for marine conservation and management, and will set the foundation for higher-level historical biogeography techniques, in particular cladistic biogeography.

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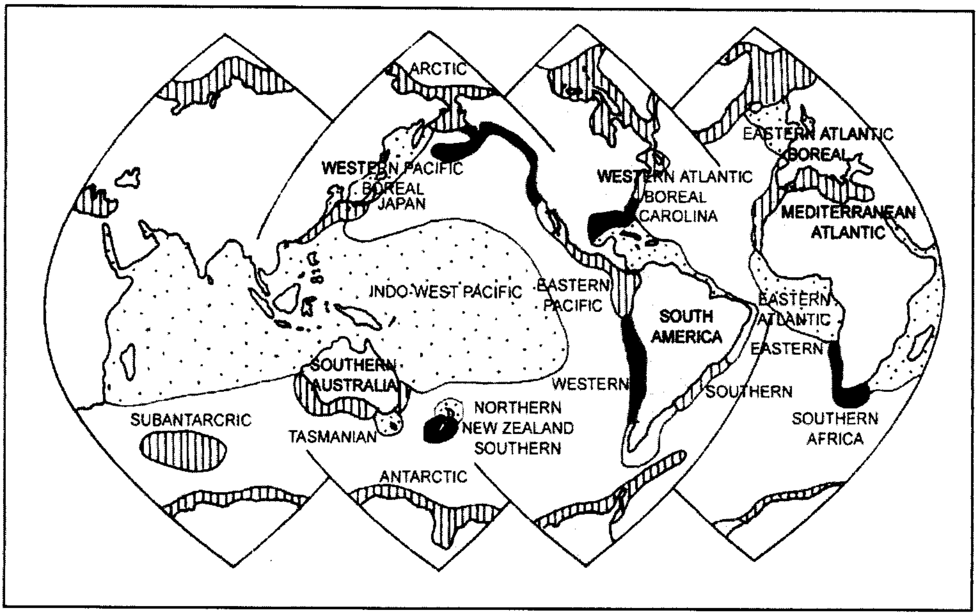

Figure 1. Classic coastal biogeographic regions of Briggs. Redrawn from Adey and Steneck [2].

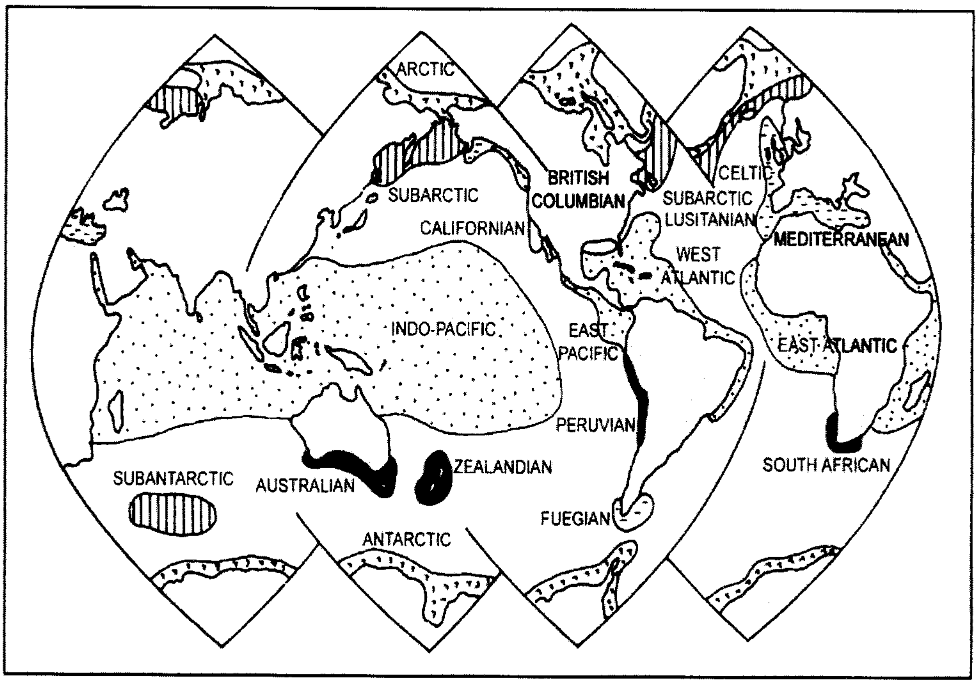

Figure 2. Thermogeographic zones derived from the distribution of crustose coralline algae by Adey and Steneck. Redrawn from Adey and Steneck [2].

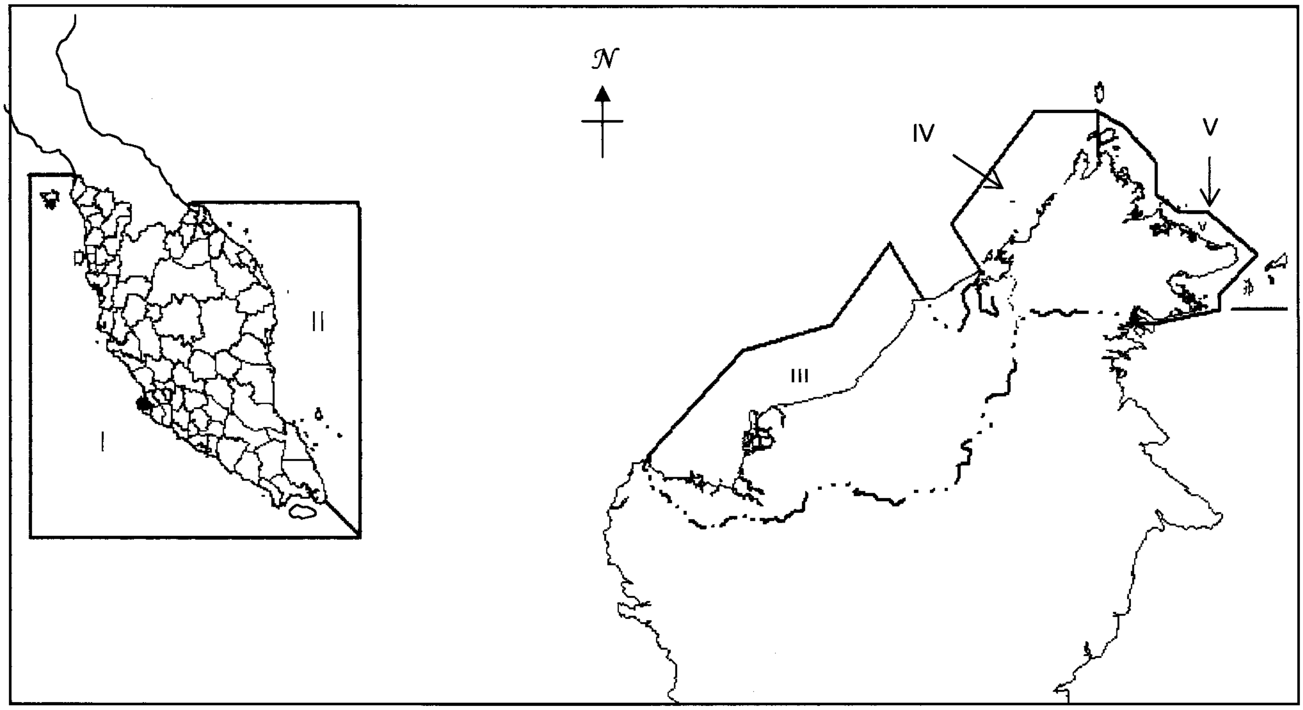

Figure 3. Map of Malaysia and the division of its coastline into operational geographic units. OGU 1 = West Peninsular Malaysia; OGU II = East Peninsular Malaysia; OGU III = Sarawak; OGU IV = West Sabah; OGU V = East Sabah.

Table 1. Number of seaweed species in Malaysia

	OGU I	OGU II	OGU III	OGU IV	OGU V
Cyanophyta	16	1	0	0	0
Chlorophyta	63	56	1	14	4
Rhodophyta	89	103	16	29	22
Phaeophyta	50	35	11	20	6
Total	218	105	28	63	32

Table 2. Number of seaweed genera in Malaysia

	OGU I	OGU II	OGU III	OGU IV	OGU V
Cyanophyta	14	1	0	0	0
Chlorophyta	22	24	2	6	2
Rhodophyta	41	47	9	15	16
Phaeophyta	15	12	8	9	1
Total	92	84	19	30	19

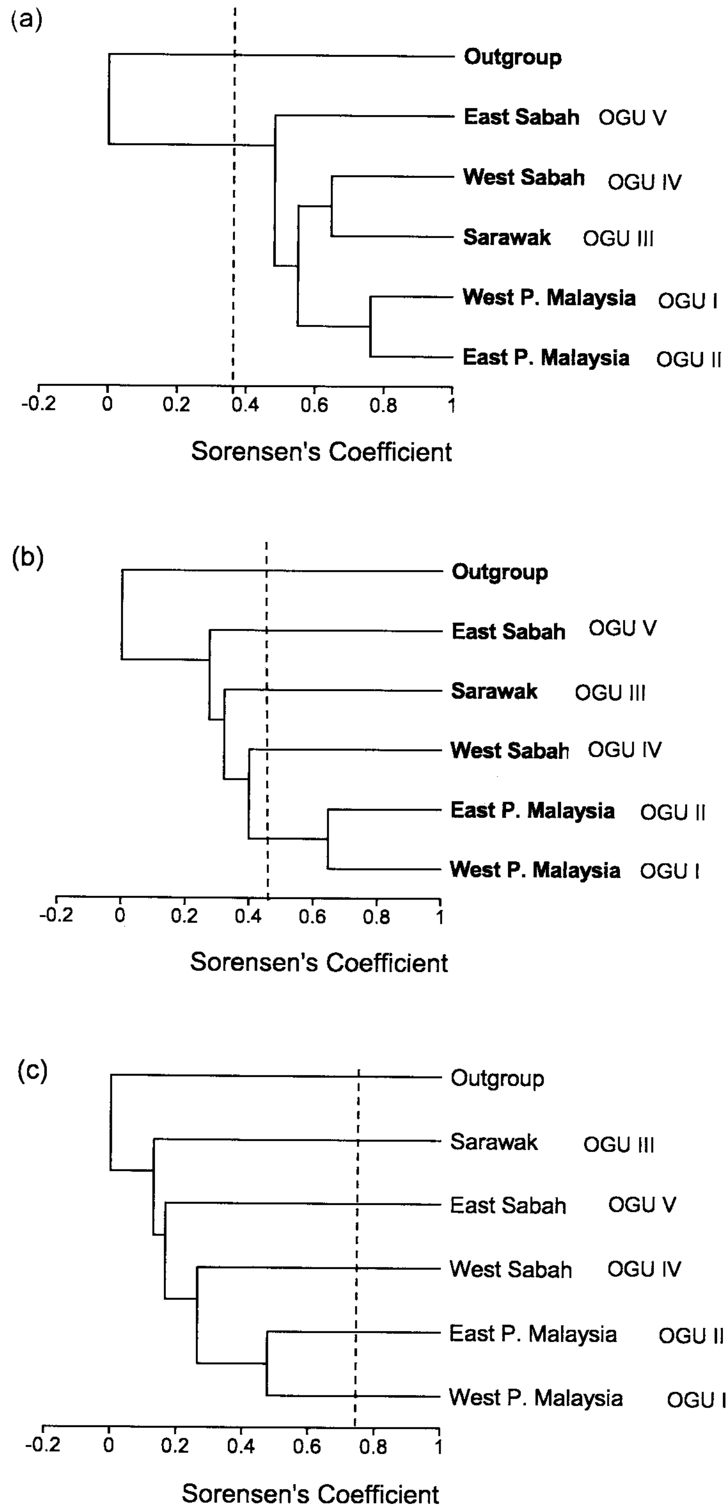

Figure 4. Results of the clustering procedures (group average linkage, Sorensen's index of similarity) based on seaweed distribution in Malaysia.
(a) Family presence/absence (40% similarity threshold),
(b) Genera presence/absence (50% similarity threshold),
(c) Species presence/absence (75% similarity threshold).
The outgroup has 0 presence.