Bijdragen tot de Dierkunde, 52 (2): 191-199 — 1982

AMSTERDAM EXPEDITIONS TO THE WEST INDIAN ISLANDS, REPORT 18 *)

STYGOBIONT CRUSTACEA MALACOSTRACA FROM GEOLOGICALLY OLDER AND YOUNGER ANTILLEAN ISLANDS: A BIOGEOGRAPHIC ANALYSIS

by

JAN H. STOCK

Institute of Taxonomic Zoology, University of Amsterdam,
P.O. Box 20125, 1000 HC Amsterdam, The Netherlands

SUMMARY

Area-species graphs for stygobiont Crustacea Malacostraca of seven islands in the southern Caribbean have been compared. It appears that the "constants" C and z of these graphs are influenced by the geological time elapsed since the island's emergence. In older islands the values for C and z are higher than in younger islands. The values for z of younger and older islands are much higher (0.79-0.97) than usually obtained in literature for terrestrial animals (0.20-0.40). This may be explained by the very limited dispersal faculties of K-strategists, such as stygobiont Malacostraca.

RÉSUMÉ

On compare des graphiques aréal-espèces pour des Crustacés Malacostracés stygobiontes provenant de sept îles de la Mer des Caraïbes. Les «constantes» C et z dans ces graphiques semblent être influencées par le temps géologique écoulé depuis l'émergence de l'île respective. Dans le cas des îles plus anciennes les valeurs sont plus élevées, aussi bien pour C que pour z, que dans le cas des îles récentes. Les valeurs trouvées pour z des îles, anciennes ou récentes, sont de beaucoup plus élevées (0,79-0,97) en comparaison avec celles mentionnées dans la littérature pour des animaux terrestres (0,20-0,40). Ceci s'explique probablement par les facultés de dispersion très limitées des stratégistes-K, tels que les Malacostracés stygobiontes.

INTRODUCTION

During the past 10 years (1973-1982) a team of biologists of the University of Amsterdam, occasionally assisted by scientists of other universities, have studied the fauna of groundwater biotas (cave waters, wells, springs, hyporheic and interstitial environments) in the West Indies. Over 50 islands have been sampled in a more or less systematic and uniformous way.

The project aims at an analysis of the validity of a number of biogeographic models, explaining the origin of the West Indian nonmarine fauna, in close coherence with geological and palaeogeographic data.

In the present paper an attempt is made to evaluate the impact of age of certain islands on stygofaunal diversity (the "age" being the time that elapsed since the island's emergence above sea level). To this end, seven islands of similar morphology and with similar climates in the southern Caribbean have been compared.

METHODS

Stygofaunal samples have been taken in three ways:

(1) The Karaman-Chappuis method. A hole is dug in loose alluvia. The inflowing groundwater is ladled out and passed through a fine net (mesh 0.05 mm).

(2) The Bou-Rouch method. A hollow iron probe is driven in the substrate until it reaches the groundwater table and the groundwater is then pumped up by means of a Norton hand-pump.

(3) The Cvetkov method. A vertical plankton net (mesh 0.05 mm) provided with a back-stroke piston is lowered and lifted in drill holes, shafts, and wells.

Methods (2) and (3) have been described in more detail by Bou (1975).

The samples are preserved in 4% neutralized formalin, sorted later in the laboratory, and transferred to 70% ethanol.

Taxonomic analyses of the animal groups encountered in the samples taken have been, and will be, published in the present series of Reports on the Amsterdam Expeditions to the West Indian islands.

---

*) Report 17 appeared in Bijdr. Dierk., 52 (1): 13-42 (1982).

INTRODUCTION TO THE REGRESSION MODEL

In a number of previous papers, I have advanced the theory that sea-level fluctuations have been of great significance for the evolutionary scenario of many members of groundwater biotas (the so-called stygobionts) of the West Indian islands (Stock, 1977b, 1980a). In particular negative relative changes of the sea level, either due to local geological uplifting, or to eustatic drops of the water level, caused stranding of intertidal or shallow-water communities. For many faunal elements, such strandings will have been catastrophic, in particular of course for sessile organisms, such as reef corals. A testimony of catastrophic events by negative sea-level movements can be found on many islands of the Calcareous Antilles **) and of the Leeward group ***), in terraces of fossil coral reefs above the actual sea level. Other organisms were kind of pre-adapted to stand a chance of surviving during sea-level regressions. In particular those animals that (a) have a burrowing or interstitial life, and (b) lack pelagic stages, but have instead brood care or pass the greater part of their larval life inside the eggshell, belong to this group. During the slow process of regressive movements of the sea level, these animals could survive in the humid macro- and micro-interstitia of coral rubble, gravel or coarse sand, and evolve through vicariant processes into groundwater inhabitants. In the interstitial biotope, a very gradual shift in salinity can be observed, from fully marine near the waterline, through brackish higher up the shore, to almost fresh more inland. In many of the Antillean islands, having (nowadays) an arid climate, the salinity — even of the most inland groundwaters — stays at oligo- or mesohaline levels, so that real fresh groundwaters do not exist. The scenario in which vicariant evolution of stranded (uplifted) populations plays an important role in the colonization of groundwaters, is called the regression model (for references, see Stock, 1980a).

Many islands in the West Indies have developed endemic taxa (subspecies, species, and even genera) of stygobionts. In several cases, marine relatives (not necessarily ancestors) are still in existence. Elsewhere (Stock, 1981a) I have called attention to the fact that such stygobionts are restricted to islands in which regression of the relative sea level predominated over transgressive movements. Most islands of the Leeward group, of the Windward group and of the Greater Antilles belong to this category. In the Bahamas, including the Turks and Caicos islands, transgression has been much more important than regression. These islands strikingly lack regression model elements, but may be invaded, presumably at a rather recent (post-Pleistocene) geological epoch, by marine species, penetrating karst features that drowned during a marine transgression.

In the West Indies, for instance, regression evolution is demonstrated by an abundance of taxa of hadziid Gammaridae (Amphipoda) on many islands of the Antillean arc, whereas no hadziids have been found in the Bahamian archipelago, where stygobionts are much more rare anyway than in the Antilles.

Limiting ourselves to rising islands, it would be interesting to compare the diversity of their stygofauna with palaeogeographic data. If the major factor influencing the evolution of stygobionts in the Antilles would be the repeated trans- and regressions of the sea level during the Pleistocene, one would expect a comparable number of taxa in islands of different geological age.

If on the other hand the Plio-Miocene regressions are the most important factor in the evolution of the West Indian stygofauna, the older islands must have a significantly more diverse groundwater biota than the younger islands.

THE ISLANDS

For testing the two alternatives brought forward in the last lines of the preceding paragraph, we have selected 7 islands (6 in the Leeward group plus Barbados) from a total of some 50 islands sampled during our fieldwork program in 1973-1982. The islands selected agree with each other in that they have been subject to tectonic uplift and have important calcareous deposits. More-

---

**) Used in the sense of Weyl, 1966.

***) Used in the sense of Wagenaar Hummelinck, 1981: 8.

over, the islands are comparable by their geographic position, altitude, area of the same magnitude, and semi-arid climate.

The six islands of the Leeward group, north of the South American mainland, are Aruba, Curaçao, Bonaire, the Los Roques group, La Tortuga, and La Blanquilla. The seventh island, Barbados, is selected because it is the southernmost calcareous island of the north-south branch of the Antillean arc (this branch consists mainly of volcanic, non-calcareous, islands). The position of the seven islands compared in this paper, and certain other localities mentioned in the text, is shown in fig. 1.

Every single island, or group of coherent keys, is isolated from the next group and from the continent by deep water (400 fms and more), with the exception of Aruba (vide infra).

A number of islands of the Leeward group are excluded from our analysis because they do not fulfill all requirements: Margarita is not mainly calcareous and is not separated by deep water from the South American continent; Los Testigos are not calcareous; the Aves group and La Orchila have not been sampled by our team.

In general, and in relation to the size of the island (cf. table I), 10 to 100 samples per island have been considered sufficient for a more detailed zoogeographic analysis; only from La Tortuga a smaller number of samples (7) was available.

TABLE I

Island size.

	area (km^2)	maximum altitude (m)
Aruba	190[1]	189[1]
Curaçao	472[1]	375[1]
Bonaire	281[1]	241[1]
Los Roques	≈1000[2]	116[3]
La Blanquilla	52.5[4]	≈60[5]
La Tortuga	171[4]	30[6]-40[4]
Barbados	430[7]	340[8]

[1] Hoetink, 1969.

[2] Méndez, 1978.

[3] U.S. Defence Mapping Agency, Hydrographic Center, Washington, Chart 24444, revised ed., 1974.

[4] Williams, 1980.

[5] Hummelinck, 1940.

[6] U.S. Defence Mapping Agency, Hydrographic Center, Washington, Chart 24441, revised ed., 1973.

[7] Weyl, 1966.

[8] Directorate of Colonial Surveys (D.C.S.), 955, London, map Barbados 5, 2nd ed., 1965.

THE AGE OF THE ISLANDS

The Netherlands Leeward islands (Aruba, Bonaire, Curaçao, often called the A-B-C islands) emerged as shallow shoals on a volcanic basement during the late Miocene (De Buisonjé, 1974). Geotectonic uplifts in the post-Miocene periods are evidenced by raised abrasion terraces, excavated surf lines, and raised coral reefs, presently found at altitudes up to 150 m above sea level. The islands are separated from each other by very deep water (700 to 900 fms). Deep waters occur also between Curaçao and Bonaire and the mainland. Aruba, however, is separated from the South American Paraguana peninsula by a much shallower straits (slightly over 100 fms).

To the A-B-C islands of the Netherlands Leeward group belong, in addition to the three larger islands, two very small ones, Klein Curaçao, to the east of Curaçao, and Klein Bonaire, to the west of Bonaire. Of these, Klein Bonaire is separated by a very shallow and narrow straits from Bonaire, and forms a biogeographical unit with it. On the other hand, Klein Curaçao is surrounded by deep waters (300-800 fms), and constitutes a separate unit. We have not sampled Klein Curaçao, so its stygofauna remains unknown. Thus, for practical purposes, our data pertain to three of the five islands only: Aruba, Curaçao, and Bonaire. The fact that Aruba lies on the South American continental shelf, does not seem to have influenced its stygofauna, which has close relationships to that of Curaçao and lacks South American elements.

According to Weyl (1966: 273) the A-B-C islands form with the Venezuelan islands (Aves, Los Roques, La Orchila, La Tortuga, La Blanquilla and Los Hermanos) an "independent part of the Antillean orogenesis" (in translation).

The igneous-metamorphic basement of La Blanquilla is often compared with similar rocks in the A-B-C islands (Rutten, 1931, 1940; Schubert & Moticska, 1972, 1973). The igneous-metamorphic complex, consisting of a trondhjemite batholith, is nowadays exposed at the island's western part. It is possibly of upper-Cretaceous age (Schubert & Moticska, 1972, 1973). Mainly in the eastern part of the island, two uplifted coral terraces are

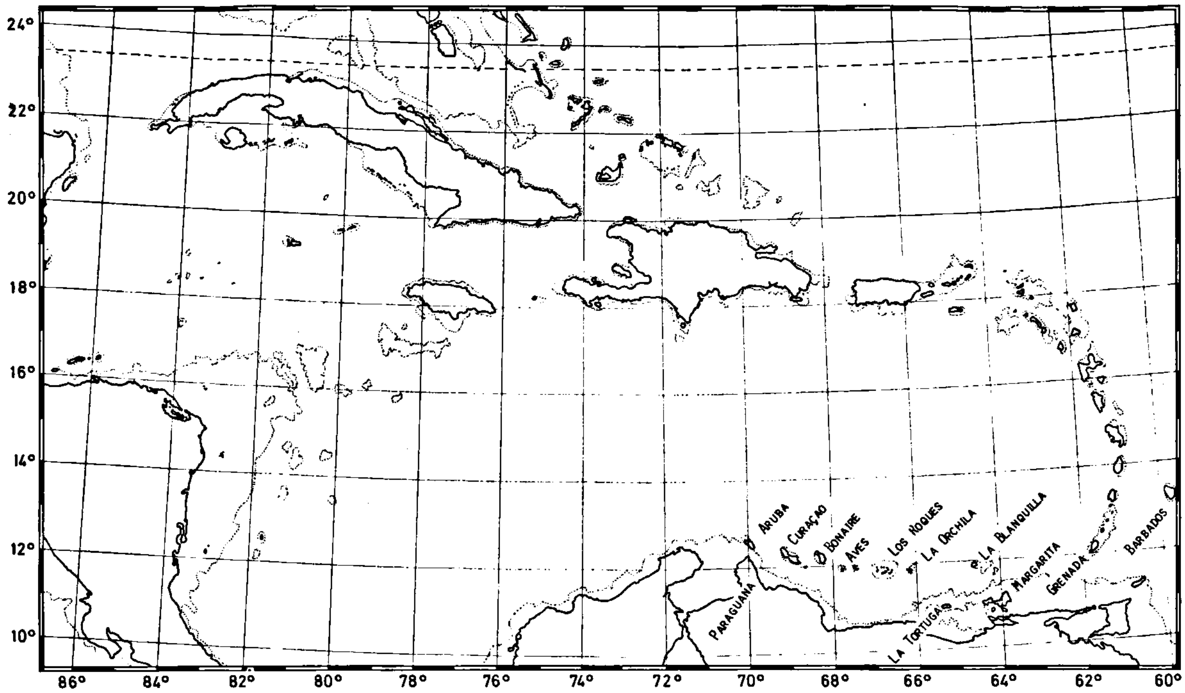

Fig. 1. The West Indies, with the names of the localities mentioned in the text.

exposed (7 and 30 m above actual sea level; Maloney, 1971), of Pleistocene-Recent age (Zuloanga, 1950). Although the geological history of La Blanquilla is less completely known than that of the A-B-C islands, my interpretation is that the extent and altitudinal uplift of the fossil terraces shows that a small portion of the island, comprising the highest top (ca. 60 m above sea level), remained emerged during the Pleistocene-Recent sea-level rise.

La Blanquilla is separated by very deep waters (100 to >2000 fms) from La Orchila in the west, and Grenada in the east, and by deep waters (>800 fms) from Margarita in the south. It must therefore be considered an oceanic island.

The Roques archipelago is much younger. It probably emerged as late as the early Quaternary (viz., the igneous-metamorphic rocks of Gran Roque), whereas the rest of the archipelago, more than 40 islands and keys, emerged even later (Méndez, 1978: 41-46). This makes the A-B-C islands, and possibly also La Blanquilla, some $14 \cdot 10^6$ years older than the Roques archipelago.

Although the archipelago consists of over 40 islands and keys, these are situated on a single common, very shallow submerged platform (water depths of at most 20 fms, usually much less), separated from the next islands (the Aves group in the west and La Orchila in the east) by waters of over 500 fms in depth. Similar depths are found between the Roques and the South American continent. So, for the purpose of this study the entire Roques group is considered a single isolated, oceanic island, without internal geographical barriers.

La Tortuga is "geologically new; it belongs to the Quaternary period" (Williams, 1980: 117, in translation). It has undergone a double uplift, resulting in two elevated coral terraces (Ernst, 1886, as quoted by Williams, 1980).

Barbados is one of the islands with actually the greatest tectonic uplift (4.3 cm · 10^{-3} years, see Matthews, 1973). In the Pleistocene, it was still covered by the sea (Weyl, 1966: 270), thus its age is comparable to that of the Roques group and La Tortuga.

THE STYGOFAUNAL MALACOSTRACA

The composition of the malacostracan stygofauna of the seven islands under consideration is enumerated in table II. These records are based on the papers of Stock (1976a, 1976b, 1977a, 1977b, 1977c, 1979, 1980b, and 1981b) on the Gammaridae, Ingolfiellidae, Microparasellidae, Bogidiellidae, and Thermosbaenacea, of Kensley (1981) on the Paranthuridae, of Botosaneanu & Stock (1979, 1982) on the Cirolanidae and cyathurids, and on unpublished data. The latter category comprises data on the occurrence in Barbados of a blind, undescribed species of *Quadrivisio* (Amphipoda, Gammaridae). Oculate, epigean species of this genus occur on several islands (including Aruba, Bonaire, and Barbados), but do not need to be considered in the present context.

The Roques islands have a limited number of stygiobiont Malacostraca (4 species), of which at least 3 belong to genera that contain both marine and limnic species. So far, no taxonomic descriptions of the Roques stygofauna have been published.

From the island La Tortuga, a single undescribed species of Gammaridae has been collected, which is locally quite abundant.

The stygofauna of Aruba, as mentioned before, is devoid of South American elements (such as Bathynellacea or limnic Bogidiellidae), notwithstanding the fact that Aruba has been connected with Paraguana (Venezuela) during the Pleistocene.

RESULTS AND DISCUSSION

The samples that have been examined from the seven islands in question are enumerated in table III.

Although the number of samples from certain islands is smaller than that from others, the less diverse stygofaunal composition of the Roques, La Tortuga, and Barbados does not seem to be accidental.

The very high incidence of stygobiont Malacostraca in Curaçao is also striking, and may be the consequence of the rather complex paleogeography of the island, which is composed of two nuclei melted into one island during the Pleisto-Holocene (Stock, 1977b). In general, the incidence of occurrence is high on the A-B-C islands and La Tortuga, low on the Roques and Barbados, and intermediate on La Blanquilla. The reason for these obvious differences remains uncertain.

TABLE II

Stygofaunal Crustacea Malacostraca in the Leeward group and Barbados.
(A = Amphipoda; I = Isopoda; T = Thermosbaenacea; D = Decapoda).

	taxa with "continental" species only			taxa in which also marine species are known											
	Metaniphargus (A)	*Arubolana* (I)	*Typhlatya* (D)	*Psammogammarus* (A)	*Saliweckelia* group (A)	blind *Quadrivisio* (A)	*Actogidiella* (A)	*Ingolfiella* (A)	Anthuridae (I)	*Curassanthura* (I)	Microparasellidae (I)	*Microcerberus* (I)	*Halosbaena* (T)	*Alpheopsis* (D)	Total
Aruba	1	1	1	0	0	0	0	1	1	0	0	0	0	0	5
Curaçao	3	0	1	1	1	0	1	2	1	1	0	1	1	0	13
Bonaire	0	0	1	0	1	0	0	2	0	0	2	1	0	0	7
Los Roques	0	0	0	1	0	0	0	0	1	0	1	0	0	1	4
La Blanquilla	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2
La Tortuga	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Barbados	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2

TABLE III

Number of samples per island, and number of samples containing stygobiont Crustacea Malacostraca.

	No. of samples	No. of samples containing Malacostraca	% of samples with Malacostraca
Aruba	56	27	48
Curaçao	111	75	68
Bonaire	93	28	30
Los Roques	24	2	8
La Blanquilla	10	2	20
La Tortuga	7	3	43
Barbados	32	3	9

As to the number of taxa on specific and subspecific level on each of the islands (table II) we reach the following conclusions:

For Aruba, Curaçao, Bonaire and La Blanquilla, the total number of taxa proves to be directly related to the size of each island. The number of taxa on Barbados, La Tortuga, and the Roques is lower than expected (fig. 2). Of the first group, the smallest island (La Blanquilla, 52.5 km^2) has the lowest number of taxa (2), followed by the next smallest island (Aruba, 190 km^2, 5 taxa), and Bonaire (281 km^2, 7 taxa), whereas the largest, Curaçao (472 km^2) has the highest number of taxa (13). Thus, a good correlation exists between the area of La Blanquilla, Aruba, Bonaire, and Curaçao (1.4 : 5 : 12.4 : 7.4) and the number of stygobiont malacostracan taxa (2 : 5 : 13 : 7).

Although the Roques group consists of many more islands and keys than the Netherlands Leeward group (>40 versus 5), and is about 1½ times larger (1500 km^2) than the A-B-C islands together (943 km^2), its stygobiont Crustacean fauna is clearly less diverse. The figures for the Roques compare well with the low diversity observed in the stygofauna of Barbados, with its 430 km^2 and 336 m of elevation of about the same size as Curaçao (472 km^2 and 372 m), but with only 2 stygobiont species of Crustacea, versus 13 in Curaçao.

One may plot, in accordance to the method elaborated by Darlington (1957) and later by MacArthur & Wilson (1967), A against S on a logarithmic scale (in which A is the area in km^2 of each island and S the number of stygobiont species or subspecies). This power function model usually is significantly better than other alternatives (Sugihara, 1981). The resulting plots lie approximately on a straight line, according to the equation $S = CA^z$. In fact, two lines (1 and 2 in fig. 2) emerge, one for La Blanquilla-Aruba-Bonaire-Curaçao, another for La Tortuga-Barbados-Los Roques. The first line slopes slightly steeper (has a higher value for z) and runs at a higher level (has a higher value for C) than the second line.

The area-species graphs confirm in general the results obtained by previous authors, for other groups of animals, and on other islands, in that the plots lie approximately on a straight line. Although the meaning of differences in value of the parameters C and z is still highly controversial (see Connor & McCoy, 1979, for an elegant review), a couple of points may deserve further consideration, or speculation if one wishes.

(1) $C_1 \approx -30$, and $C_2 \approx -58$ are both negative. As well known, the value for C, a constant, varies greatly among taxa and according to the unit of area measurement. The fact that the values

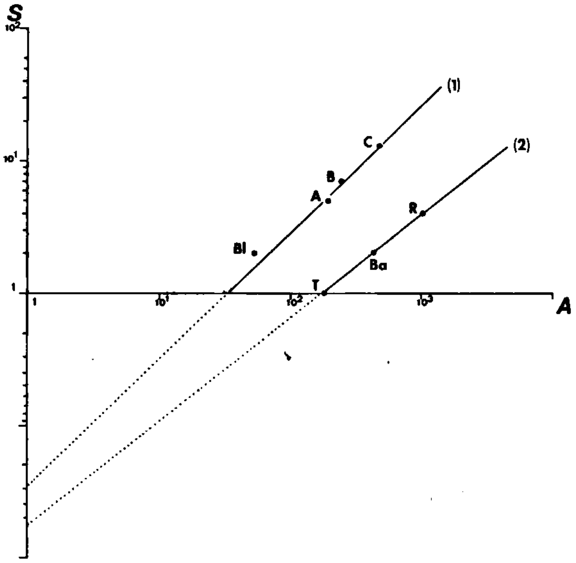

Fig. 2. The area-species curves (logarithmic scale) for stygobiont Crustacea Malacostraca of seven West Indian islands: Bl = La Blanquilla; A = Aruba; B = Bonaire; C = Curaçao; T = La Tortuga; Ba = Barbados; R = Los Roques.

for C_1 and C_2 are lower than in most cases recorded in Anglo-Saxon literature, depends partly on the use of km^2 instead of mi^2. The use of km^2 causes a shift of the graphs towards the abscissa ($C_{mi} = C_{km} + 2 \log 1.609$), but no change in z. However, C is not merely smaller, it is negative in our two graphs. In general, negative values do not tell us very much in curves on a logarithmic scale, but the negative values for C seem to permit at least one supposition: inland waters of isolated (non-continental) islands can develop a stygofauna only when the island has a certain minimum size. If below the supposed critical size, no inland stygofauna comes to development. Based on the data in fig. 2, the critical size (A at $S = 1$) is approximately 34 km^2 for graph 1, and 180 km^2 for graph 2.

(2) The value for C for graph 2 is lower than for graph 1. According to MacArthur & Wilson (1967: 17) C depends largely on the population density as well as on the innate species diversity in a given taxon, whereas its value decreases in those regions where the quality of the environment is poorer. When these broad generalizations are adapted to the situation for the West Indian islands under consideration, one might put that the lower the number of niches or habitats on an island ("monotonous islands") the lower C will be. At least the climate and the elevation of the islands cannot be of great influence, since these are largely comparable. It seems feasible however, that geologically spoken older islands have developed a finer web of ecological niches, than relatively recent islands, giving rise to a higher value of C in the older islands.

Still another factor influencing C is the degree of isolation of each island. This factor — amongst others related to the distance to the nearest centre of dispersal or source population — may be important for, say, terrestrial animals that have to be transported (dispersed) to emerging islands. For the Antillean stygofauna, this factor is considered of no importance, since it is assumed that this fauna has evolved predominantly from marine ancestors that have lived in the surrounding sea, in accordance with the regression model. The distance to the source (i.e. the sea) is zero, and the striking-chance is very large. The potential of being colonized by marine invaders is equal for each island, irrespective of the distance to the next landmass, and thereby the major part of the aquatic colonizers differs from terrestrial animal invaders.

The different values of C for the La Blanquilla-Curaçao line and the La Tortuga-Los Roques line can, in my opinion, be explained only by a different striking-chance, not related to distance to the source, but to the time of existence of the islands: geologically older islands have had a greater (longer) striking-chance, and — once hit — a longer time for adaptation to subterranean conditions, resulting in a higher diversity, than islands of a younger age.

(3) For both the La Blanquilla-Curaçao line (line 1 in fig. 2) and the La Tortuga-Los Roques line (line 2), the value for z is much larger than usual [$z_1 \approx 0.97$, $z_2 \approx 0.79$, calculated as $(\log S + \log C) \cdot \log A^{-1}$]. Empirically determined values for z often range from 0.20-0.40 (generalized to $z \simeq 0.25$). Darlington (1957) obtained arithmetically a z value of 0.301, while Preston (1962) showed that the z value resulting from a lognormal distribution should be 0.26. According to MacArthur & Wilson (1967: 18), an increase of z above 0.26 "can be explained as the outcome of the breaking up of biotas of large islands into semi-isolated communities due to the increase in topographic barriers and environmental variation on such islands". This formulation appears to apply only marginally to the situation in the seven Antillean islands studied in the present paper. First of all, none of the islands studied can be called "large islands". Secondly, "environmental variation" is expected to be low for groundwater inhabitants, one of the characteristics of groundwaters being its stability. Of course, it must be added that at least the factor salinity in the groundwaters of the islands may widely fluctuate. The presence, on certain islands such as Curaçao of "semi-isolated communities" has been demonstrated by Stock, 1977b, in a microgeographic distribution analysis of hadziid Gammaridae (Amphipoda).

The fact that z is so very much higher for both line 1 and line 2 in the present analysis, than in most previous studies, must be related to biological peculiarities of most stygofaunal Malacostraca. These animals are typically *K*-strategists, having very limited means of dispersal (a low number of large eggs, absence of pelagic stages). As repeatedly shown by various authors, a high degree of endemism, or formation of isolated and morphologically distinct populations in limited geographical areas, is very pronounced in this group of animals. I have no doubt that this factor is chiefly responsible for the high value of z for the stygobiont Malacostraca on the southern Caribbean islands.

(4) Finally we have to consider the lower value for z in the La Tortuga-Barbados-Los Roques line. In general, the value for z conforms to the rule "The better the geographic isolation, the higher z". This rule, typically formulated from a dispersionalist's viewpoint, can be modified, I think, to include also historical factors into this formulation: "The older the island (and, in consequence, the more niches or ecological subregions are developed), the higher z".

This is in agreement with the data obtained from our present analysis. Line 1 in fig. 2, representing the older islands La Blanquilla-Aruba-Bonaire-Curaçao, has a higher value for z (0.97), than line 2 (La Tortuga-Barbados-Los Roques; $z \approx 0.79$).

CONCLUSION

The difference in the value for C in the two groups of islands represented by lines 1 and 2 in fig. 2, as well as the higher value for z of line 1, both point in the direction that area-species curves give a good indication for the relative geological age (the time elapsed since the island emerged above sea level) of Caribbean islands. The emergence of the Netherlands Leeward islands is placed in the late-Miocene ($\approx 15 \cdot 10^6$ years B.P.), that of Los Roques, La Tortuga, and Barbados in Pleisto-Holocene times ($\leqslant 10^6$ years B.P.). The data for La Blanquilla are scarce, but seem to indicate a palaeogeographical history not unsimilar to that of the A-B-C islands. The area-species plot for La Blanquilla fits the A-B-C line, and thus confirms this idea.

ACKNOWLEDGEMENTS

The fieldwork on which the present study is based has been financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), The Hague; the Treub Maatschappij, Utrecht; the Beijerinck-Popping Fonds, Amsterdam; the Amsterdamse Universiteits Vereniging, Amsterdam; and the Fonds Landbouw Hogeschool, Wageningen.

The sampling program has been carried out with the assistance of the following members of our team: Dr. Lazare Botosaneanu, Drs. Nico Broodbakker, Mrs. Sylvia van Lieshout, Mr. Jos Notenboom, Dr. Steven Weinberg, and Mrs. Francisca Weinberg.

The organization of the fieldwork in Venezuela has greatly benefited from support rendered by H.M. Embassy of The Netherlands, Caracas, in particular by Dr. Ir. Th. P. M. de Wit, Agricultural Attaché.

The hospitality and support of the Fundación Cientifica Los Roques, Caracas (Drs. Roger Laughlin and Ernesto Weil), and of the Fundación La Salle de Ciencias Naturales, Campus de Margarita (Drs. J. J. Bocaranda, J. Otaola, H. Villegas), is gratefully acknowledged. The captain and crew of R.V. Dona Teresa (Punta de Piedras, Margarita) have been of great assistance on the out-islands.

The fieldwork on the A-B-C islands has been made possible through the kind cooperation of the Caribbean Marine Biological Institute, Curaçao (Dr. Ingvar Kristensen), and on Barbados, of the Bellairs Research Institute of McGill University (Dr. Finn Sander).

REFERENCES

BOTOSANEANU, L. & J. H. STOCK, 1979. Amsterdam Expeditions to the West Indian Islands, Report 6. Arubolana imula n. gen., n. sp., the first hypogean cirolanid isopod crustacean found in the Lesser Antilles. Bijdr. Dierk., **49** (2): 227-233.

—— & ——, 1982. Amsterdam Expeditions to the West Indian Islands, Report 17. Les Cyathura stygobies (Isopoda, Anthuridea) et surtout celles des Grandes et des Petites Antilles. Bijdr. Dierk., **52** (1): 13-42.

BOU, C., 1975. Les méthodes de récolte dans les eaux souterraines interstitielles. Annls. Spéléol., **29** (4): 611-619.

BUISONJÉ, P. H. DE, 1974. Neogene and Quaternary geology of Aruba, Curaçao and Bonaire. Uitg. natuurwet. Studiekring Suriname Ned. Ant., **78**: 1-293, maps 1-4.

CONNOR, E. F. & E. D. MCCOY, 1979. The statistics and biology of the species-area relationship. Am. Nat., **113** (6): 791-833.

DARLINGTON, P. J., 1957. Zoogeography: the geographical distribution of animals: i-xi, 1-675 (Wiley, New York).

ERNST, A., 1886. La exposicion nacional de Venezuela en 1883, **1** (Caracas). (Not seen, teste Williams, 1980).

HOETINK, H. (ed.), 1969. Encyclopedie van de Nederlandse Antillen: 1-708 (Elsevier, Amsterdam, Brussel).

HUMMELINCK, P. WAGENAAR, 1940. General information. Stud. Fauna Curaçao, **1**: 1-57.

——, 1981. Land and fresh-water localities. Stud. Fauna Curaçao, **63** (192): 1-133, pls. I-IL.

KENSLEY, B., 1981. Amsterdam Expeditions to the West Indian Islands, Report 10. Curassanthura halma, a new genus and species of interstitial isopod from Curaçao, West Indies (Crustacea: Isopoda: Paranthuridae). Bijdr. Dierk., **51** (1): 131-134.

MacArthur, R. H. & E. O. Wilson, 1967. The theory of island biogeography: i-xi, 1-203 (Princeton Univ. Press, Princeton, N.J.).

Maloney, N. J., 1971. Geología de la isla de La Blanquilla, y notas sobre el archipiélago de Los Hermanos, Venezuela Oriental. Acta cient. Venezol., **22**: 6-10.

Matthews, R. K., 1973. Relative elevation of Late Pliocene high sea level stands: Barbados uplift rates and their implications. J. Quat. Res., **3**: 147-153.

Méndez Baamonde, J., 1978. Archipiélago Los Roques / Islas de Aves. Cuadernos Lagoven, Ecología, **1978**: 1-48.

Preston, F. W., 1962. The canonical distribution of commonness and rarity. Ecology, **43**: 185-215 and 410-432.

Rutten, L., 1931. On rocks of the Venezuelan islands between Bonaire and Trinidad and on some rocks from northwestern Venezuela. Proc. kon. Ned. Akad. Wet., (Sci.) **34** (8): 1101-1110.

——, 1940. New data on the smaller islands north of Venezuela. Proc. kon. Ned. Akad. Wet., (Sci.) **43** (7): 820-827.

Schubert, C. & P. Moticska, 1972. Geological reconnaissance of the Venezuelan islands in the Caribbean sea between Los Roques and Los Testigos. Memorias VI Conf. geol. Caribe (Margarita): 81-82.

—— & ——, 1973. Reconocimiento geológico de las islas Venezolanas en el Mar Caribe, entre Los Roques y Los Testigos (Dependencias Federales). Acta cient. Venezol., **24**: 19-31.

Stock, J. H., 1976a. A new genus and two new species of the crustacean order Thermosbaenacea from the West Indies. Bijdr. Dierk., **46** (1): 47-70.

——, 1976b. A new member of the crustacean suborder Ingolfiellidea from Bonaire. Stud. Fauna Curaçao, **50** (164): 56-75.

——, 1977a. Microparasellidae (Isopoda, Asellota) from Bonaire — with notes on the origin of the family. Stud. Fauna Curaçao, **51** (168): 69-91.

——, 1977b. The taxonomy and zoogeography of the hadziid Amphipoda, with emphasis on the West Indian taxa. Stud. Fauna Curaçao, **55** (177): 1-130.

——, 1977c. The taxonomy and zoogeography of the crustacean suborder Ingolfiellidea, with descriptions of new West Indian taxa. Stud. Fauna Curaçao, **55** (178): 131-146.

——, 1979. Amsterdam Expeditions to the West Indian Islands, Report 2. New data on taxonomy and zoogeography of ingolfiellid Crustacea. Bijdr. Dierk., **49** (1): 81-96.

——, 1980a. Regression model evolution as exemplified by the genus Pseudoniphargus (Amphipoda). Bijdr. Dierk., **50** (1): 105-144.

——, 1980b. Amsterdam Expeditions to the West Indian Islands, Report 8. A new cave amphipod (Crustacea) from Curaçao: Psammogammarus caesicolus n. sp. Bijdr. Dierk., **50** (2): 375-386.

——, 1981a. L'origine géologique des îles des Indes Occidentales en relation avec la dispersion de quelques Malacostracés stygobiontes. Géobios (Lyon), **14** (2): 219-227.

——, 1981b. Amsterdam Expeditions to the West Indian Islands, Report 14. The taxonomy and zoogeography of the family Bogidiellidae (Crustacea, Amphipoda), with emphasis on the West Indian taxa. Bijdr. Dierk., **51** (2): 345-374.

Sugihara, G., 1981. $S = CA^z$, $z \simeq \frac{1}{4}$: a reply to Connor and McCoy. Am. Nat., **117** (4): 790-793.

Weyl, R., 1966. Geologie der Antillen. Beitr. region. Geol. Erde, **4**: i-viii, 1-410 (Borntraeger, Berlin).

Williams Trujillo, W., 1980. Las maravillosas islas Venezolanas: 1-203 (Publicaciones Seleven, Caracas).

Zuloanga, G., 1950. Isla de Pajaros, Los Hermanos y La Blanquilla. El Farol, **129**: 1-15.

Received: 30 June 1982