

SEAWEEDS AND BIOGEOGRAPHY IN THE MACARONESIAN REGION

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With 4 tables and 3 figures

ABSTRACT. Seaweeds are marvellous target organisms for biogeography. These marine plant-like organisms are generally attached to the substrate and thrive in the border between the land and the sea, which is a relatively narrow and more or less homogenous strip. They occur only in the shallow parts, because they all need light for photosynthesis.

During a research trip made in autumn 1991 with the German research vessel "Heincke" (HEINCKE 1991 Expedition), 278 species of marine macroalgae were collected, of which at least 49 were new records for the Canary Islands, with many additional new records for the separate islands.

The finding of so many new records for a relatively well-known area like the Canary Islands proved both that records are much too scarce and that proof of absence for many species has wrongly been accepted.

The results of the expedition are discussed in connection with recent results of studies in The Netherlands on marine phycogeography.

The pattern approach in biogeographic research is mainly based on databases of known presence of species in different geographical territories. However, new information and new methods necessitate repetition of the process after a number of years. Nevertheless, results of these studies help to suggest that Macaronesia encompasses a rich seaweed biodiversity and that most of the strictly tropical species in the Atlantic Ocean are restricted to the western Atlantic, whereas tropical-to-warm temperate species have a predominantly amphi-Atlantic distribution. Many species of this tropical-to-warm temperate distribution group have a strictly tropical distribution in the western Atlantic, whereas they extend into the warm-temperate zone in the eastern Atlantic.

The above observations were recently studied in The Netherlands by using two different approaches: a genetical approach and an ecological approach. For the genetical approach at first a single target organism was studied: *Cladophoropsis membranacea*. This species shows a strong Tethyan vicariance imprint with additional, probably semi-recent dispersal events. Research using the ecological approach was on 86 isolates, belonging to 22 different species. Temperature responses of seaweeds can be expressed in curves on temperatures

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versus, respectively, growth, survival ranges and growth yields in situ. The Caribbean tropical species are optimally adapted to tropical conditions and have rather extreme stenothermal tolerance rates. Caribbean isolates of amphi-Atlantic species are significantly more tolerant to low temperatures than species restricted to the western Atlantic. For tropical-to-subtropical species, conditions at the Canary Islands are marginal: they only reach a low percentage of their potential yearly growth yield and could not have survived the pleistocene glaciations in situ. It is likely that all these seaweeds with a tropical-to-subtropical recent distribution have become extinct during the last glacial maximum and have recolonized the Canary Islands by dispersal. In species with an amphi-Atlantic tropical-to warm-temperate distribution distinct ecotypic differentiation occurs, leading to the theory that for these species the Canary Islands may have been recolonized by cold-adapted populations that have survived the glaciations in a warm-water pocket in the eastern Mediterranean.

A general picture emerges of an originally occurring tropical seaweed flora from which cold-water seaweeds developed by ecotypic differentiation caused by cold spells, occurrence and loss of geographical and ecological barriers, and extinctions. The application of molecular methods in these studies gives very interesting results, but methods to define direction and rooting of the resulting cladograms are not always satisfactory.

Historical phycogeography is another approach. Main problems are sparseness of records and problems with proofs of absence. Especially the lack of uniformity of taxonomic criteria proves to be a bottleneck, above all things because of lack of critical world monographs on seaweeds. Better tools are needed for the fascinating chess-like play of marine biogeography.

INTRODUCTION

Originally the waters of the earth were quite warm (VAN OPPEN 1995, p. 20). Global seawater temperature cooling events were most pronounced at the Eocene/Oligocene boundary (about 38 My) and in the middle Miocene (that was about 10 My). From these times on cold water biota are developing, helped by the establishment of a circum-Antarctic current, closure of the circum-global warm (or tropical) Tethys Sea, opening and later again closing of the Bering Strait and the rise of the Isthmus of Panama. That leaves us with an Atlantic Ocean in which the marine flora and fauna have inherited historical trails, while the distribution of all these organisms is also influenced by ecological and genetical factors, which play and have played their roles both nowadays and in history. And in the centre of this Ocean one finds the islands of Macaronesia.

Why should one choose seaweeds as target organisms? These plant-like organisms that occur in the seas are generally attached to the substrate and thrive in a relatively narrow and more or less homogenous strip, the border between the land and the sea. They occur only in the shallow parts, because they all need light for photosynthesis. The systematic

position and the evolutionary history of the main groups of seaweeds, thus the green, red, and brown algae, are very different and in fact these algal groups are less related to each other than extremes in the Animal Kingdom are mutually related. Nevertheless, seaweeds have several characters in common and for that reason one can compare seaweed groups in many respects in biogeography.

Biogeography seeks causal explanations for the spatial distribution of organisms. SILVA (1962) stated already: "The field of phytogeography is vast, the literature is inexhaustible, its data capable of a variety of interpretation, extraordinary manipulation, and distortion. It has the fascination of a chess game. It is a valid, though treacherous, field of investigation". Notwithstanding new developments in supporting disciplines like taxonomy, molecular genetics, eco-physiology, palaeoclimatology and palaeobotany, the SILVA statements still form an appropriate evaluation of our present understanding of phycogeography. And the four main problems contributing to this state of affairs are still:

- 1) Sparseness of records.- documented surveys are generally lacking;
- 2) Proof of absence.- not to be confused with absence of proof;
- 3) Uniformity of taxonomic criteria. - It takes many years before new criteria are accepted by all users (even if this general acceptance should ever be the case). There is also lack of information on the relationship between geographically distant seaweed populations and concepts on seaweed species. Critical world-wide revisions (monographs) of marine algae are generally lacking;
- 4) Cause and effect relation. - Are the prevailing environmental conditions really the causes of the recent distributions or are organisms still adjusting to environmental changes that occurred during the last glaciations?

MATERIALS AND METHODS

A research trip made in autumn 1991 with the German research vessel "Heincke" (HAROUN et al., 1993) made us realize that several of the earlier mentioned problems certainly still count for marine macroalgae. During that trip we had the chance to work with a group of marine phycologists, of which several taxonomists, who managed to identify on board the majority of the collected specimens. We did not only use handpicking in the intertidal as collecting method, but also snorkeling, SCUBA diving and dredging. The latter was much helped by an underwater video device, to be used to check the presence of macroalgae as well as the structure of the bottom surface. During the trip we had only one dredge, but we managed to sample very frequently till depths of about 100 meters (Table 1).

RESULTS

During the HEINCKE 1991 Expedition we collected 278 species of marine macroalgae,

of which at least 49 were new records for the Canary Islands (Table 2). For the separate islands we had in total 185 new records, that is about 15% of the total of 1247 voucher specimens from 63 collecting stations (Table 3).

DISCUSSION

In several papers phycologists from the Canary islands have added a considerable number of new records, see AFONSO-CARRILLO et al., 1992; BALLESTEROS et al., 1992; ELEJABEITIA et al., 1992; GIL-RODRIGUEZ & HAROUN, 1992, 1993; GONZALEZ-RUIZ et al., 1995; HAROUN & PRUD'HOMME VAN REINE, 1993; KVATERNIK & AFONSO-CARRILLO, 1995; REYES & AFONSO-CARRILLO, 1995; REYES & SANSON, 1991; REYES et al., 1993; ROJAS-GONZALEZ et al. 1994; SANSON, 1994; SANSON & GIL-RODRIGUEZ, 1993; SANSON et al., 1991; SANSON & REYES, 1995, and several of their new records now have priority over supposed new records observed during the HEINCKE 1991 Expedition. That does not invalidate, however, the observation that during the HEINCKE 1991 Expedition, many species were found that were then not yet known from the relatively well-studied area of the Canary Islands. This proved both that 1) records are much too sparse and that 2) proof of absence for many species has wrongly been accepted. The third problem in biogeographic research, viz. lack of uniformity of taxonomic criteria, concerns seaweeds as much as other organisms. For example the new volume on Rhodophytes in the British Seaweed Flora (MAGGS & HOMMERSAND, 1993) adds many problems in comparisons of checklists for these algal groups.

In the present paper the results of the HEINCKE 1991 Expedition will be discussed in connection with recent results of studies in The Netherlands on marine (often Macaronesian) phycogeography.

The four factors or biogeographic processes that influence distribution all have their impact on Macaronesian seaweeds:

1) Migration (Fig. 1) - All seaweeds from southwestern Europe have the possibility to migrate to Macaronesia, following the prevailing ocean currents. They will stay if they can survive.

2) Dispersal (Fig. 2) - The physical continuity of the water of the ocean allows for a potential dispersal over long distances, either actively or passively. So far, for seaweeds, however, all experimental studies on spore, gamete, or zygote viability in the water column have shown short survival periods and only small migration distances. Floating algae, or algae attached to floating or swimming objects create an important (long-range) dispersal mechanism (VAN DEN HOEK, 1987, see also ROJAS-GONZALEZ et al., 1994).

3) Vicariance (Fig. 3) - Shared patterns of distribution among evolutionarily unrelated taxa (viz. multiple, individual phylogenies all sharing a common topology), thus indicating common underlying geographical processes are emphasized in vicariance.

4) Extinction - To make it possible for a seaweed to settle, many biotic and abiotic environmental factors have to be just right (Table 4). If these factors are not satisfactory, the seaweed will not settle at all and if that occurs for a complete geographic area the seaweed will sooner or later become extinct in that area. This immediately poses a proof of absence problem. Extinction can be very local or may regard large areas, thus individuals as well as whole marine basins like the Mediterranean.

As stated before, biogeography can use many approaches, of which the four main ones are (VAN DEN HOEK, 1984):

1) Pattern approach - Whole seaweed floras are studied in relation to geographical areas.

2) Ecological approach - Species or species groups are studied on basis of their ecological capacities in boundary situations.

3) Genetical approach - Conspecific populations and related species are studied, using genetical and molecular methods like crossing experiments as well as research on enzymes, RAPDs, sequence analysis etc.

4) Historical approach - The distribution of species and populations is explained by their distribution in the geological past.

These approaches, however, are consistently related to each other and are usually combined. The present author mainly used the pattern approach (PRUD'HOMME VAN REINE, 1988; PRUD'HOMME VAN REINE & VAN DEN HOEK, 1988, 1990) in research that was mainly based on databases of known presence of species in different geographical territories. For that reason Macaronesia and surroundings were divided into different geographic areas, of which the boundaries were chosen in agreement with suggested boundaries between earlier described phytogeographic seaweed regions and climatic distribution groups of seaweeds. Thus in Tropical Africa one can expect seaweeds with a strictly tropical distribution, other seaweeds that occur in subtropical waters as well (tropical-to-subtropical distribution group), but certainly not seaweeds that belong to a strictly temperate distribution group. The great amount of new information, both on new records (as shown before in the HEINCKE 1991 results), on new taxonomic ideas (see also PRUD'HOMME VAN REINE et al., 1994) and on new species, as well as availability of fast computer methods necessitate regular repetition of that kind of studies. Nevertheless, results of the pattern approach studies mentioned above, which were in fact already a combination with the ecological approach, helped to suggest not only that Macaronesia encompasses a rich seaweed biodiversity, but also that most strictly tropical species in the Atlantic Ocean are restricted to the western Atlantic, whereas tropical-to-warm temperate species have a predominantly amphi-Atlantic distribution. This even though eastern and western populations are separated by several thousands of miles of oceanic waters. The results of these studies also suggest that many species of the tropical-to-warm temperate distribution group have a strictly tropical distribution in the western Atlantic, whereas they extend into the warm-temperate

zone in the eastern Atlantic. If these observations are correct, it can be questioned what can be the reasons for such a distribution. About the correctness: the results of the Heincke 1991 Expedition have shown that many of the Amphi-Atlantic deep-water seaweeds occur in the western Atlantic in temperate waters as well as in the tropical Caribbean (HAROUN et al. 1993). For species occurring in surface waters, however, the earlier observations are not tempted. It was tried to study the above suggestions using two main approaches: the genetical approach and the ecological approach.

For the genetical approach KOOISTRA (1993) used molecular biological methods to study the distribution of a number of taxa of the tropical-to-warm temperate distribution group. The most promising method at the start of the project was single-copy DNA-DNA hybridization, a laborious method that had nevertheless been successful during earlier studies on biogeography of the genus *Cladophora* (BOT, 1992). During the period in which the study was executed by KOOISTRA, however, also methods like allozyme variation and sequence analysis of internal transcribed spacer (=ITS) regions of the nuclear ribosomal DNA cistron were tested and proved to be usable. As a result the researcher has to stick mainly to one target organism, *Cladophoropsis membranacea* (C. Agardh) Boergesen and some related Cladophoralean taxa (KOOISTRA, 1993). Central conclusions of his research reflect a strong Tethyan vicariance imprint with at least two additional and probably semi-recent dispersal events. Greatest differences were found to occur between a Pacific group and a tropical western Atlantic group, while there is also a cluster in the eastern Mediterranean together with the Red Sea and a fourth cluster in the tropical and subtropical eastern Atlantic. This supports an original circumtropical distribution in the former Tethys sea as well as dispersal between the Canary Islands and the Cape Verde Islands within the one cluster, and even trans-Atlantic dispersal shown by two isolates from the Cape Verde Islands and one from Mauritania which were distinctly closely related to all isolates originating from the Caribbean. That all is for the tropical-to-warm temperate green alga *Cladophoropsis membranacea* only.

The ecological approach was used by PAKKER (1995), who studied 86 isolates, belonging to 22 different species. His work is based on temperature responses of seaweeds expressed in curves on temperatures versus, respectively, growth, survival ranges and growth yields in situ. Temperature responses may set biogeographic boundaries in three ways:

- 1) Lethal or tolerance limits: set by the upper and lower temperature extremes which are tolerated by the alga, may also be called "survival limits".
- 2) Growth limits: set by the temperature range in which an alga can grow sufficiently.
- 3) Reproduction limits: set by the temperature range in which the alga is able to reproduce.

On the basis of experimentally determined temperature limits and known geographical ranges it is possible to determine which responses are likely to be responsible for delimiting the distribution range, while ecotypic differentiation in temperature responses is explained

as an acceptable indication for geographic isolation. For Macaronesia mainly seaweeds of the following three different distribution groups are of interest:

- 1) West Atlantic (Caribbean) tropical species.
- 2) Amphi-Atlantic tropical-to-subtropical species, with a northern distribution limit just reaching the Canary Islands.
- 3) Amphi-Atlantic tropical-to-warm-temperate species, with a northern distribution limit reaching the Mediterranean.

The Caribbean tropical species are optimally adapted to tropical conditions and have rather extreme stenothermal tolerance rates (between 18-20°C and 30-33°C, PAKKER et al., 1995). Growth optimum and reproduction ranges are both between 25 and 30°C in these species. Caribbean isolates of amphi-Atlantic species are significantly more tolerant to low temperatures than species restricted to the western Atlantic (PAKKER et al., 1996a). That means, nevertheless, that for these species conditions at the Canary Islands are marginal: they only reach a low percentage (often about 30%) of their potential yearly growth yield and could not have survived the pleistocene glaciations in situ. The eastern and western Atlantic coast regions have been separate since about 36 My, which means that considerable genetic differentiation can be expected between eastern and western populations. However, semi-recent dispersal events complicate the picture (KOOISTRA, 1993). It is likely that all seaweeds with a tropical-to-subtropical recent distribution have become extinct in the Canary Islands during the last glacial maximum (PAKKER et al., 1996a). After that glaciation, the Canary Islands must have been recolonized by dispersal from eastern (Cape Verdean) or western (Caribbean) tropical donor populations. For the many cases where populations of deep-water species are only known from Atlantic North America and the Canary Islands (HAROUN et al., 1993) this pattern of recolonization is not very probable, however. Maybe in these cases survival of the pleistocene glaciations in situ is still to be used as an explanation.

PAKKER et al. (1996a) not only used facets of both the ecological approach and the historical approach to suggest regular gene flow and/or subrecent trans-Atlantic dispersal for several of these seaweeds with a tropical-to-subtropical distribution, but also executed crossing experiments for the red alga *Lophocladia trichoclados* (C. Agardh) Schmitz and included results of research with molecular methods to strengthen that suggestion. In that amphi-Atlantic tropical-to-subtropical distribution group PAKKER et al. (1996a) never observed any ecotypic differentiation. That was quite different for the species with an amphi-Atlantic tropical-to-warm temperate distribution. For those algae in the isolates of populations from the Mediterranean as well as in those of populations from the Canary Islands, tolerance limits were found which are significantly different from tolerance limits of isolates originating from Caribbean or Cape Verde populations (PAKKER & BREEMAN, 1996). Thus here distinct ecotypic differentiation occurs, leading to the theory that for these species the Canary Islands may have been recolonized by cold-adapted populations that have survived the glaciations

in a warm-water pocket in the eastern Mediterranean. This suggestion is endorsed by the results of crossing experiments and molecular research (RAPD analysis) of the pantropical to warm-temperate red alga *Digenea simplex* (Wulfen) C. Agardh (PAKKER et al., 1996b). Vicariance in this species is very clear between Indo-West Pacific isolates and Atlantic isolates, and rather clear between a Caribbean/Cape Verde group and a Canary Islands group. It is a pity, however, that gametophytes of the Canary Islands isolates failed to reproduce in culture, because crossing experiments in the Caribbean/Cape Verde group suggest reduced levels of interfertility between the two geographical groups of isolates in this cluster (PAKKER et al., 1996b). None of the new records collected during the HEINCKE 1991 Expedition are in contradiction with the biogeographic conclusions of PAKKER (1995).

Studies on new molecular methods to be used in biogeographical research (BAKKER, 1995; BOT, 1992; VAN OPPEN, 1995) are mainly on cold-water algae and provide indications of rather frequent occurrence of long-range dispersal. BOT (1992) observed that dispersal in *Cladophora* species occurs much more frequent in temperate areas in the Atlantic Ocean than in tropical areas, while BAKKER et al. (1995) could not decide in what direction the possible migration or long-distance dispersal of these *Cladophora* species was on the trans-arctic route between the Pacific Ocean and the Atlantic Ocean via the intermittently opened Bering Strait and the Arctic Ocean. VAN OPPEN (1995), however, found two striking events: most probably a regular semi-recent gene-flow exists between Arctic and (sub)Antarctic populations of the bipolar disjunct green seaweed species *Acrosiphonia arcta* (Dillwyn) J. Agardh and *Urospora penicilliformis* (Roth) Areschoug as well as of the brown seaweed *Desmarestia viridis* (O.F. MÜLLER) Lamouroux. It is hypothesized (VAN OPPEN et al., 1993) that small microstadia of these algae may even nowadays pass the tropical belt. For another dispersal route, the earlier mentioned trans-Arctic route, two separate invasions from Pacific Ocean species to the Atlantic Ocean are demonstrated (VAN OPPEN, 1995). Especially for the red alga *Phycodryis rubens* indications are quite convincing.

From all these studies emerges a picture of an originally occurring tropical seaweed flora from which cold-water seaweeds developed by ecotypic differentiation caused by cold spells (thus glaciations), occurrence and loss of geographical and ecological barriers, and extinctions. The application of molecular methods in these studies give very interesting results, but methods to define direction and rooting of the resulting cladograms are not always satisfactory. That is one of the reasons for the plea for "total evidence" analyses, in which molecules and morphology are used simultaneously as a single data set. Thus morphological datasets of suitable groups are also needed.

For a historical biogeographic study of the Atlantic Ocean seaweeds, both phylogenetic analyses and rather complete surveys of the distribution of the studied taxa are needed. Preparing quick (although possibly dirty) revisions of selected seaweed groups was suggested, to be followed by using the data-bases of characters for phylogenetic analyses and, together with all known records, to prepare area cladograms. Later area cladograms of

several unrelated taxa would be combined to prepare a general area cladogram depicting the biogeographic history and if possible even the geological history of biota and landmasses in and around the Atlantic Ocean. During such a study the main problems in phycogeography were met again. Sparseness of records and problems with proofs of absence are still prominent obstacles, but especially the lack of uniformity of taxonomic criteria proved to be a bottleneck, above all things because of lack of critical world monographs on seaweeds. In the brown algal genus *Nemacystus* hard work on minute morphological differences resulted in acceptable and promising results (DE JONG & PRUD'HOMME VAN REINE, 1997). In the Canary Islands we found three different *Nemacystus* species, which have reached the islands via different routes. Work on the red algal genus *Dasyopsis* (= *Eupogopon*) gives other, mainly taxonomic, problems. DE JONG et al. (1997) found that the latter genus is not well separated from the large genus *Dasya* and potentially informative species (supposed endemics) were found to be synonymous with species occurring in the Mediterranean. We have concluded so far that, although the historical approach is promising, especially in relation to "total evidence" analyses, it is not possible for a single researcher to collect enough taxonomic high-quality revisions in order to use these as the bases for phylogenetic research. Quick revisions are usually too dirty to be used to prepare databases for acceptable cladograms. What is needed are well-prepared taxonomic world monographs of seaweed genera. On the other hand surveys of distribution of taxa have to be intensified. The author was too pessimistic. Studies by DE JONG (1998) have proven that well resolved general area cladograms can be obtained by historical biogeographic analysis of pantropical benthic seaweed genera. Expeditions like the HEINCKE 1991 Expedition provide excellent possibilities to add important data, especially in undercollected areas or in undercollected habitats. Time and money are necessary and they will be well-spent to provide better tools for the fascinating chess-like play of marine biogeography.

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TABLE 1 - Station list Heincke 1991 Expedition 26 September- 14 October.

Station	Locality	Island	Depth till (in metres)
1	Punta Jandia	Fuerteventura	8
2	Punta Jandia	Fuerteventura	14
3	Punta Jandia	Fuerteventura	20
4	Playa Blanca	Lanzarote	40
5	Isla de Lobos	Ferteventura	7
6	Isla de Lobos	Ferteventura	1
7	Isla de Lobos	Ferteventura	3
8	Isla de Lobos	Ferteventura	30
9	Alegranza	Lanzarote	18
10	Alegranza	Lanzarote	1
11	Alegranza	Lanzarote	1
12	Roque del Oeste	Lanzarote	18
13	La Graciosa	Lanzarote	15
14	La Bocaina	Lanzarote	70
15	La Bocaina	Lanzarote	80
16	La Bocaina	Lanzarote	96
17	La Bocaina	Lanzarote	40
18	Isla de Lobos	Fuerteventura	21
19	Mogan	Gran Canaria	60
20	Mogan	Gran Canaria	90
21	Mogan	Gran Canaria	1
22	Mogan	Gran Canaria	15
23	Faro de Orchilla	Hierro	1
24	Faro de Orchilla	Hierro	12
25	Faro de Orchilla	Hierro	18
26	Faro de Orchilla	Hierro	17
27	Roques de Salmor	Hierro	3
28	Roques de Salmor	Hierro	23
29	Faro de Orchilla	Hierro	27
30	Faro de Orchilla	Hierro	5
31	Faro de Orchilla	Hierro	1
32	Puerto Naos	Hierro	27
33	Punta Los Frailes	Hierro	11
34	Puerto Naos	Hierro	1
35	Punta Malpique	La Palma	10

36	Punta Blanca	La Palma	27
37	Punta Larga	La Palma	1
38	Puerto Alcalá	Tenerife	90
39	Los Cristianos	Tenerife	110
40	Los Abrigos	Tenerife	30
41	El Medano	Tenerife	1
42	Bahía de S. Agueda	Gran Canaria	20
43	Bahía de S. Agueda	Gran Canaria	60
44	Faro de Maspalomas	Gran Canaria	15
45	Sardina del Norte	Gran Canaria	15
46	Sardina del Norte	Gran Canaria	40
47	Los Gigantes	Tenerife	87
48	Las Americas	Tenerife	60
49	Las Americas	Tenerife	100
50	Los Cristianos	Tenerife	50
51	Punta de Antequera	Tenerife	1
52	Punta de Antequera	Tenerife	44
53	Banco Amanay	Fuerteventura	50
54	Banco Amanay	Fuerteventura	80
55	Banco Amanay	Fuerteventura	90
56	Punta Barlovento	Fuerteventura	64
57	Punta Jandía	Fuerteventura	25
58	Punta Jandía	Fuerteventura	60
59	La Puntilla	Gran Canaria	18
60	Playa del Cabrón	Gran Canaria	1
61	Arinaga	Gran Canaria	50
62	Arinaga	Gran Canaria	70
63	Arinaga	Gran Canaria	90

TABLE 2 - New records of marine macroalgae for the Canary Islands area obtained during the Heincke 1991 Expedition.

Chlorophyta

Acetabularia calyculus Quoit et Gaimard

Cladophora dalmatica Kützting

Halimeda discoidea Decaisne

Palmophyllum crassum (Naccari) Rabenhorst

Ulva olivascens P. Dangeard

Phaeophyta

- Arthrocladia villosa* (Hudson) Duby
Carpomitra costata (Stackhouse) Batters
Discosporangium mesarthrocarpum (Meneghini) Hauck
Distromium spec.
Elachista stellaris Areschoug
Hinckesia conifera (Boergesen) Silva
Nemacystus hispanicus (Sauvageau) Kylin
Rosenvingea intricata (J. Agardh) Boergesen
Sargassum furcatum Kützing
Spatoglossum schroederi (Mertens) Kützing
Spatoglossum solieri (Chauvin) Kützing
Sphacella subtilissima Reinke
Stilophora rhizodes (Turner) J. Agardh
Syringoderma floridana Henry

Rhodophyta

- Amphiroa rigida* Lamouroux
Botryocladia boergesenii J. Feldmann
Botryocladia wynnei Ballantine
Branchioglossum prostratum C.W. Schneider
Calonitophyllum spec.
Cryptonemia seminervis (C. Agardh) C. Agardh
Gelidiocolax microsphaerica Gardner
Gloiocladia atlantica (Searles) R.E. Norris
Gloiocladia blomquistii (Searles) R.E. Norris
Halichrysis peltata (W.R. Taylor) Huvé
Halymenia elongata C. Agardh
Halymenia rosea Howe et W.R. Taylor
Halymenia vinacea Howe et W.R. Taylor
Hypnea arbuscula P. Dangeard
?Itonoa marginifera (J. Agardh) Masuda et Guiry
Kallymenia feldmannii Codomier
Kallymenia reniformis (Turner) J. Agardh
Kallymenia requeenii J. Agardh
Laurencia brongniartii J. Agardh
Laurencia corallopsis (Montagne) Howe
Laurencia intricata Lamouroux
Laurencia microcladia Kützing

Laurencia poitei (Lamouroux) Howe
Laurencia viridis Gil-Rodríguez et Haroun
Leptofauchea brasiliensis Joly
Lomentaria linearis Zanardini
Myriogramme spec.
Peyssonnelia harveyana Crouan ex J. Agardh
Predaea masonii (Setchell et Gardner) DeToni
Rhodymenia ardissoni J. Feldmann
Rhodymenia caespitosa P. Dangeard
Sarcodiotheca divaricata W.R. Taylor

TABLE 3 - List of new records of marine macroalgae for the separate Canary Islands as obtained during the HEINCKE 1991 Expedition.

FUERTEVENTURA

Chlorophyta

Bryopsidella neglecta (Berthold) Rietema
Caulerpa webbiana Montagne
Cladophora laetevirens (Dillwyn) Kützing
Derbesia furcellata (Zanardini) Ardissoni
Halimeda discoidea Decaisne
Microdictyon boergesenii Setchell
Microdictyon calodictyon (Montagne) Kützing
Phaeophila dendroides (Crouan) Batters
Polyphysa parvula (Solms-Laubach) Schnetter et Bula Meyer
Udotea petiolata Turra
Ulva olivascens P. Dangeard

Phaeophyta

Arthrocladia villosa (Hudson) Duby
Carpomitra costata (Stackhouse) Batters
Dictyota menstrualis (Hoyt) Schnetter et al.
Feldmannia irregularis (Kützing) Hamel
Hinckesia conifera (Boergesen) Silva
Nereia filiformis (J. Agardh) Zanardini
Rosenvingea intricata (J. Agardh) Boergesen
Rosenvingea sanctae-crucis Boergesen

Sargassum desfontainesii (Turner) C. Agardh
Sargassum furcatum Kützing
Spatoglossum solieri (Chauvin) Kützing
Sphacella subtilissima Reinke
Sporochmus pedunculatus (Hudson) C. Agardh
Stilophora rhizodes (Turner) J. Agardh
Syringoderma floridana Henry

Rhodophyta

Acrosymphyton purpuriferum (J. Agardh) Sjoestedt
Anotrichium furcellatum (J. Agardh) Baldock
Antithamnion plumula (Ellis) Thuret
Apoglossum ruscifolium (Turner) J. Agardh
Bangia atropurpurea (Roth) C. Agardh
Bonnemaisonia hamifera Hariot (Trailliella phase)
Botryocladia boergesenii J. Feldmann
Botryocladia chiajeana (Meneghini) Kylin
Botryocladia wynnei Ballantine
Branchioglossum prostratum C.W. Schneider
Calonitophyllum spec.
Callithamniella tingitana (Schousboe ex Bornet) G. Feldmann
Ceramium codii (Richards) Mazoyer
Ceramium flaccidum (Kützing) Ardissonne
Chondria coerulescens (J. Agardh) Falkenberg
Crouania attenuata (C. Agardh) J. Agardh
Cryptonemia crenulata (J. Agardh) J. Agardh
Cryptonemia lomation (Berthold) J. Agardh
Cryptonemia seminervis (C. Agardh) C. Agardh
Cryptopleura ramosa (Hudson) Kylin ex Newton
Gloiocladia blomquistii (Searles) R.E. Norris
Gracilaria cf. gracilis (Stackhouse) Steentoft et al.
Halichrysis peltata (W.R. Taylor) Huvé
Halurus equisetifolius (Lightfoot) Kützing
Halymenia elongata C. Agardh
Halymenia floridana J. Agardh
Halymenia rosea Howe et W.R. Taylor
Halymenia vinacea Howe et W.R. Taylor
Hypnea arbuscula P. Dangeard
?Itonoa marginifera (J. Agardh) Masuda et Guiry

Kallymenia feldmannii Codomier
Kallymenia reniformis (Turner) J. Agardh
Kallymenia requenii J. Agardh
Laurencia corallopsis (Montagne) Howe
Laurencia microcladia Kützing
Laurencia poitei (Lamouroux) Howe
Lithothamnion corallioides P. & H. Crouan
Lomentaria articulata (Hudson) Lyngbye
Lomentaria linearis Zanardini
Meredithia microphylla (J. Agardh) J. Agardh
Myriogramme spec.
Peyssonnelia harveyana Crouan ex J. Agardh
Platysiphonia miniata (C. Agardh) Boergesen
Polysiphonia elongata (Hudson) Sprengel
Rhodymenia ardissoni J. Feldmann
Rhodymenia caespitosa P. Dangeard
Sarcodiotheca divaricata W.R. Taylor
Scinaia complanata (Collins) Cotton
Sphondylothamnion multifidum (Hudson) Nägeli
Stenogramme interrupta (C. Agardh) Montagne ex Harvey
Tiffaniella capitata (Bornet) Doty et Meñez
Wrangelia argus (Montagne) Montagne

GRAN CANARIA

Chlorophyta

Struvea anastomosans (Harvey) Piccone

Phaeophyta

Dictyota liturata J. Agardh
Hincksia conifera (Boergesen) Silva
Sargassum filipendula C. Agardh
Sargassum furcatum Kützing
Sporochmus pedunculatus (Hudson) C. Agardh

Rhodophyta

Amphiroa rigida Lamouroux
Dasya corymbifera J. Agardh
Gloiocladia atlantica (Searles) R.E. Norris

Laurencia microcladia Kützing
Laurencia pinnatifida (Hudson) Lamouroux
Laurencia viridis Gil-Rodríguez et Haroun
Lomentaria linearis Zanardini
Peyssonnelia inamoena Pilger
Polysiphonia urceolata (Lightfoot) Greville
Rhodymenia caespitosa P. Dangeard

HIERRO

Chlorophyta

Cladophora coelothrix Kützing
Cladophora pellucida (Hudson) Kützing
Cladophoropsis membranacea (C. Agardh) Boergesen
Codium decorticatum (Woodward) Howe

Phaeophyta

Dictyota cervicornis Kützing
Dictyota fasciola (Roth) Lamouroux
Dictyota ligulata J. Agardh
Ectocarpus rhodoortonoides Boergesen
Feldmannia irregularis (Kützing) Hamel

Rhodophyta

Bonnemaisonia hamifera Hariot (Trailliella phase)
Ceramium circinatum (Kützing) J. Agardh
Ceratodictyon intricatum (C. Agardh) R.E. Norris
Champia parvula (C. Agardh) Harvey
Crouania attenuata (C. Agardh) J. Agardh
Dasya corymbifera J. Agardh
Gelidiocolax microsphaerica Gardner
Gelidium latifolium (Greville) Bornet et Thuret
Gymnogongrus griffithsiae (Turner) Martius
Halodictyon mirabile Zanardini
Jania pumila Lamouroux
Laurencia brongniartii J. Agardh
Laurencia corallopsis (Montagne) Howe
Laurencia microcladia Kützing
Laurencia viridis Gil-Rodríguez et Haroun

Lophocladia trichocladus (C. Agardh) Schmitz
Lophosiphonia obscura (C. Agardh) Falkenberg
Polysiphonia atlantica Kapraun et J. Norris
Stenogramme interrupta (C. Agardh) Montagne ex Harvey

LANZAROTE

Chlorophyta

Acetabularia calyculus Quoit et Gaimard
Bryopsidella neglecta (Berthold) Rietema
Bryopsis plumosa (Hudson) J. Agardh
Cladophora dalmatica Kützing
Cladophora laetevirens (Dillwyn) Kützing
Microdictyon calodictyon (Montagne) Kützing
Polyphysa polyphysoides (Crouan) Schnetter

Phacophyta

Arthrocladia villosa (Hudson) Duby
Carpomitra costata (Stackhouse) Batters
Cutleria multifida (Smith) Greville
Dictyota cervicornis Kützing
Elachista stellaris Areschoug
Halopteris filicina (Grateloup) Kützing
Rosenvingea intricata (J. Agardh) Boergesen
Rosenvingea sanctae-crucis Boergesen
Sphacelaria rigidula Kützing
Sphacelaria tribuloides Zanardini
Syringoderma floridana Henry

Rhodophyta

Anotrichium furcellatum (J. Agardh) Baldock
Antithamnion plumula (Ellis) Thuret
Bangia atropurpurea (Roth) C. Agardh
Bonnemaisonia hamifera Hariot (Trailliella phase)
Callithamniella tingitana (Schousboe ex Bornet) G. Feldmann
Ceramium codii (Richards) Mazoyer
Cryptonemia crenulata (J. Agardh) J. Agardh
Cryptonemia lomation (Berthold) J. Agardh
Cryptonemia seminervis (C. Agardh) C. Agardh

Cryptopleura ramosa (Hudson) Kylin ex Newton
Gracilaria cf. gracilis (Stackhouse) Steentoft et al.
Gymnothamnion elegans (Schousboe) J. Agardh
Halymenia floresii (Clemente) C. Agardh
Halymenia rosea Howe et W.R. Taylor
Halymenia vinacea Howe et W.R. Taylor
?Itonoa marginifera (J. Agardh) Masuda et Guiry
Kallymenia feldmannii Codomier
Kallymenia reniformis (Turner) J. Agardh
Kallymenia requeenii J. Agardh
Lomentaria linearis Zanardini
Lophosiphonia obscura (C. Agardh) Falkenberg
Meredithia microphylla (J. Agardh) J. Agardh
Platysiphonia miniata (C. Agardh) Boergesen
Polysiphonia atlantica Kapraun et J. Norris
Rhodymenia ardissoni J. Feldmann
Rhodymenia caespitosa P. Dangeard

LA PALMA

Chlorophyta

Bryopsidella neglecta (Berthold) Rietema (Derbesia stage)
Bryopsis corymbosa J. Agardh
Chaetomorpha antennina (Bory) Kützing
Cladophora liebetruthii Grunow
Cladophora sericea (Hudson) Kützing
Codium effusum (Rafinesque) Delle Chiaje
Microdictyon boergesenii Setchell
Struvea anastomosans (Harvey) Piccone

Phaeophyta

Dictyota cervicornis Kützing
Nemacystus hispanicus (Sauvageau) Kylin
Sargassum desfontainesii (Turner) C. Agardh

Rhodophyta

Botryocladia botryoides (Wulfen) J. Feldmann
Centroceras clavulatum (C. Agardh) Montagne
Griffithsia opuntiioides J. Agardh

Halymenia vinacea Howe et W.R. Taylor
Herposiphonia secunda (C. Agardh) Falkenberg
Heterosiphonia crispella (C. Agardh) Wynne
Jania capillacea Harvey
Jania pumila Lamouroux
Laurencia viridis Gil-Rodríguez et Haroun
Liagora canariensis Boergesen
Polysiphonia atlantica Kapraun et J. Norris

TENERIFE

Chlorophyta

Acetabularia calyculus Quoit et Gaimard
Cladophora albida (Hudson) Kützing
Cladophora sericea (Hudson) Kützing
Palmophyllum crassum (Naccari) Rabenhorst

Phaeophyta

Dictyota menstrualis (Hoyt) Schnetter et al.
Rosenvingea intricata (J. Agardh) Boergesen
Spatoglossum schroederi (Mertens) Kützing
Syringoderma floridana Henry

Rhodophyta

Bonnemaisonia hamifera Hariot (Trailliella phase)
Botryocladia boergesenii J. Feldmann
Cryptonemia lomation (Berthold) J. Agardh
Gracilaria cf. gracilis (Stackhouse) Steentoft et al.
Halarachnion ligulatum (Woodward) Kützing
Halodictyon mirabile Zanardini
Halymenia vinacea Howe et W.R. Taylor
Kallymenia requeenii J. Agardh
Laurencia intricata Lamouroux
Leptofaucha brasiliensis Joly
Lophocladia trichoclados (C. Agardh) Schmitz
Lophosiphonia obscura (C. Agardh) Falkenberg
Peyssonnelia inamoena Pilger
Predaea masonii (Setchell et Gardner) DeToni
Rhodymenia ardissoni J. Feldmann
Taenioma perpusillum (J. Agardh) J. Agardh

TABLE 4 - Factors to be favourable for settling of benthic seaweeds.

For settling of a benthic seaweed the following factors have to be favourable for the species:

- substratum
- temperature
- light
- salinity
- exposition
- water quality
- clearness of the water
- tidal cycle;

also are important:

- competition for space
- epiphytes
- predation (grazing)
- parasites:

and last but not least:

- the possibility for the seaweed to reach the locality.

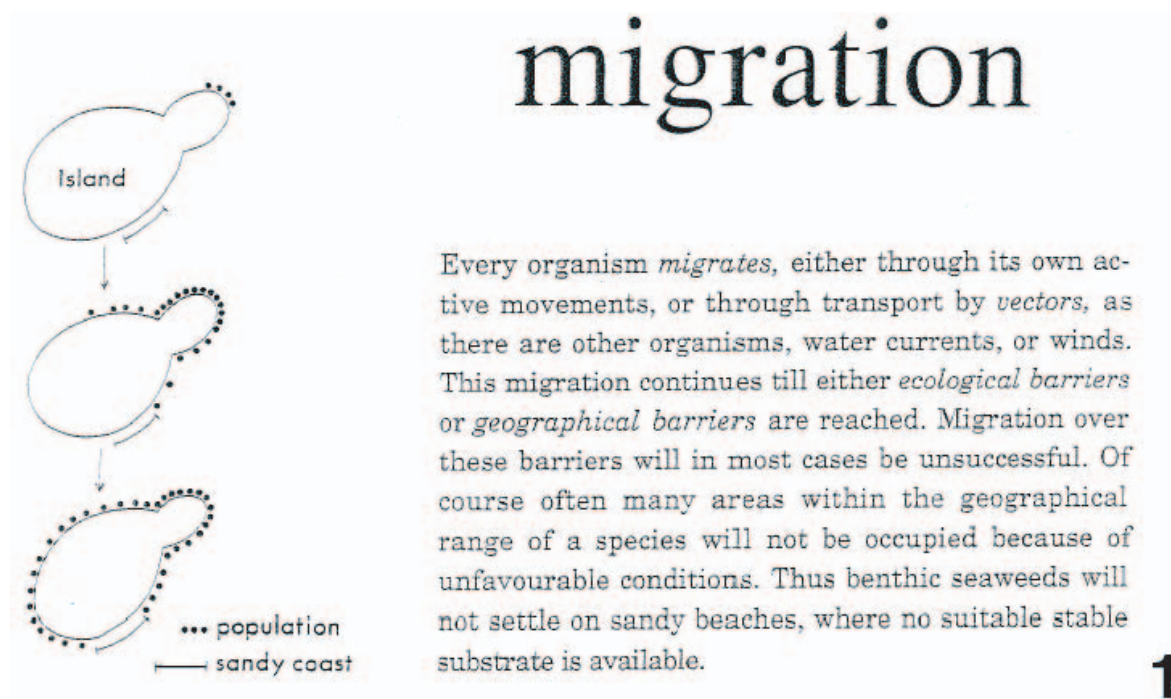


Fig. 1 - Diagram to explain migration.

dispersal

Dispersal is migration over a barrier. For seaweeds a land barrier is absolute. A wide expanse of deep sea, devoid of islands and thus of stable substrate, is also quite effective, but in this case the barrier is more like a set of filters: most specimens will not succeed in crossing that deep sea, but occasionally (perhaps only once in a million years) it nevertheless may happen. In some cases man will help (whether on purpose or not) to transport. At the newly reached coasts after *settling* again *migration* will occur, until new *barriers* have met. Genetic changes in the populations of effectively separated localities may result in formation of separate species.

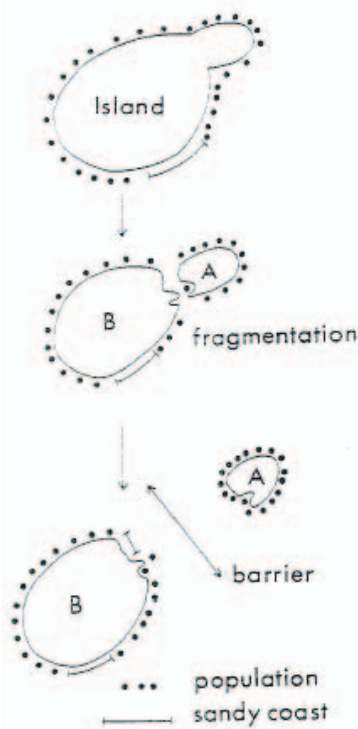


Fig. 2 - Diagram to explain dispersal.

vicariance

In *vicariance* there is always an original geographic range that becomes *fragmented* by the formation of *barriers*. These barriers may be geological-geographical (viz. fragmentation of islands or development of extensive sandy beaches) or ecological (changes in climate, changes in water quality, a disease, over-grazing).

Specimens in the newly formed smaller areas form populations which will *migrate* until new *barriers* are met. Genetic changes in the separate smaller areas may result in formation of separate species.



3

Fig. 3 - Diagram to explain vicariance.

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