

FAUNA AND FLORA OF ATLANTIC ISLANDS

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THE MARINE ALGAL FLORA OF THE AZORES: ISLAND ISOLATION OR ATLANTIC STEPPING- STONES?

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ABSTRACT

Ordination analysis was performed on the Chlorophyta, Chromophyta (Phaeophyceae) and Rhodophyta floras of 37 regions of the east and west North Atlantic Ocean from the Arctic to southern Europe, the Azores, Madeira, the Canary and Salvage Islands, and North and South Carolina. Results showed close affinities of the Azores green, brown and red marine algal floras with those of Madeira and the Canary Islands. Analyses also indicated, particularly for the red algae, trans-Atlantic affinities between the algal floras of Macaronesia and the Carolinas. Low endemicity suggests that the Azores algal flora is not an isolated one. The islands may serve as trans-Atlantic stepping-stones in the dispersal distribution of some species but the various elements in the flora suggest the islands to be an Atlantic crossroad.

KEYWORDS: marine algae; Azores; North Atlantic Ocean; biogeography; ordination analysis.

INTRODUCTION

A period of detailed study on the marine algal flora of the Azores has considerably increased the total of species recorded from the 137 listed in Schmidt's (1931) first study of the marine algae of the archipelago. The checklist and distributional index of the marine algae of the North Atlantic Ocean (South & Tittley 1986) listed 189 species for the Azores and the subsequent biogeographical analysis of Tittley and Neto (1995) reported an increased total of 274. Currently the Azores algal flora stands at 323 species (46 Chlorophyceae, 60 Phaeophyceae, 217 Rhodophyceae) with a further 41 species requiring confirmation, and a single species known only from drift material. Sixteen species listed in Neto (1994) and South and Tittley (1986) have been removed from the flora.

The Azores are located towards the mid Atlantic Ocean approximately 1000km northwest of warm-temperate Madeira, 1200km west of Lisbon, 3000 km southeast of subarctic Newfoundland and 3000km northeast of tropical Bermuda. The archipelago comprises nine main islands and the Formigas islets, and is spread over a distance of 500km from east to west. The rocky islands are of relatively recent volcanic origin (see Morton *et al.* 1998) and provide a diverse range of habitats for algal colonisation at intertidal and subtidal levels down to 100m in depth.

The biogeographical affinities of the marine algal flora of this isolated archipelago have previously been investigated on several occasions. Schmidt (1931) suggested an affinity with Macaronesia and southern Spain. Prud'homme van Reine (1988) and Prud'homme van Reine and Van den Hoek (1988, 1990) using a numerical clustering method showed the marine algal flora to be associated with floras of the western Mediterranean Sea and the temperate Atlantic Ocean and noted fewer Azorean algae in common with east America than with the western Mediterranean Sea. Tittley *et al.* (1990) analysed the North Atlantic distributional data in South and Tittley (1986) using various numerical methods and showed affinities of the Azores brown

and red algal floras with those of southern Spain and Portugal. Tittley and Neto (1995) reassessed floristic relationships with revised data for the Azores and the North Atlantic; ordination of the brown and red algae were similar to those of Tittley *et al.* (1990); the green algae showed a wider spread of floras but with the Azores remaining apart from the main group.

The aim of the present study is to reassess the relationships of the marine algal flora of the Azores in the light of (i) considerably revised data for the Azores, (ii) revised data for the northern North Atlantic Ocean with 1161 species currently listed, and (iii) additional floristic data for the Canary and Salvage Islands, the Madeiran archipelago, and North and South Carolina (1527 species in total).

MATERIALS AND METHODS

The checklist and distributional index of the northern North Atlantic Ocean (South & Tittley 1986) was revised using new taxonomic and distributional information. The taxonomy of the 1527 species and subspecies used in this study followed 'Algaebase' (July 2004). Uncertain species records were excluded from the analysis. As mentioned, to the northern North Atlantic data set was added species information for the Canary and Salvage Islands (Haroun *et al.* 2001), the Madeiran archipelago (Neto *et al.* 2002), and North and South Carolina (Schneider & Searles 1991). Revised distributional information for Great Britain and Ireland was taken from Hardy and Guiry (2003), for the Baltic Sea from Nielsen *et al.* (1995), for the northern Atlantic islands (Orkney to Iceland) from Tittley *et al.* (2004, *in press*) and for Norway from Brattegard and Holthe (1997). Low Countries (southern North Sea) floristic information was revised using Stegenga *et al.* (1997) and Bartsch and Kuhlenskamp (2000). Additional geographical information was also gleaned from 'Algaebase' (July, 2004).

The ordination method DECORANA (Detrended Correspondence Analysis) from the VESPAN computer package (Malloch 1997) was used to

analyse presence and absence data for North Atlantic algae. Ideally biogeographic patterns should be determined by the abundance of species assemblages rather than by presence and absence (Adey & Steneck 2001) but at present such data are largely unavailable. North Atlantic algal distributional data was based on the 33 floristic areas in South and Tittley (1986) with the caveat that such sample areas are not ideal (Adey & Steneck 2001, Tittley *et al.* 1990).

RESULTS

The ordination of red algal data showed two series of floras that commenced at a common origin comprising Arctic floras (below 100 on axis 1 in Figure 1). The upper series of points represented a north to south succession of American red algal floras from Newfoundland and Quebec to Virginia, Delaware and Maryland. The lower series was spread along axis 1 and comprised a north to south succession of European floras from Iceland to a Macaronesian group with the Canary Islands at the end of the series. The red algal floras of North Carolina and South Carolina were positioned at highest values on axis 1 separated from the American series with North Carolina closest to the Macaronesian group.

Ordination of brown algal data (Figure 2) produced two series of floras with a common origin in an arctic group. An American series of floras was spread along axis 2 almost perpendicular to a European series. The brown algal floras of North Carolina and South Carolina were positioned high on axis 2 separate from the American series and each other with North Carolina almost equidistant from Maryland and Virginia and the Canary islands. The European series of floras were spread linearly along axis 1 to southern Spain and Portugal with the Azores closest to Madeira near the end of this series.

Ordination of green algal data (Figure 3) showed discernable American and European series of floras. Southern floras were separated from the main cluster with the North Carolina, South Carolina and Macaronesian floras at

high values on axis 1. The Azores flora was positioned closest to that of Madeira.

DISCUSSION

Of the 1161 confirmed species records for the northern North Atlantic Ocean, 323 (365 including uncertain records) occur in the Azores representing 28% of the North Atlantic flora. New algal records recently reported for the Azores have been mainly southern warm-water species (e.g. Neto *et al.* 2002); those excluded were species mainly from northern colder waters. The total for the Azores archipelago is provisional and will increase as specimens of taxonomically difficult groups in collections are correctly identified. The Azores marine algal flora is less species-rich than that of the Canary Islands (over 600 listed), but like the floras of Madeira and the Canaries contains a greater proportion of red algae (Tittley 2003). The east Atlantic Ocean is richer in species than the west, with the Azores flora richer than that of the cold-temperate Maritime Provinces of Canada and the warm-temperate subtropical North Carolina that have the highest species totals on the American coast. The ordinations of North Atlantic algal floras indicate a closer affinity of the Azores flora with east Atlantic floras despite their isolation from Europe and Macaronesia and the prevailing currents that might be expected to facilitate dispersal from the west. Geographic isolation appears not to have contributed to the development of a distinct Azores algal flora with its low number of endemic species (see Adey & Steneck 2001).

Comparison of the ordinations of red algal data in Tittley *et al.* (1990) and Tittley and Neto (1995) with that of this study shows that despite new records for the Azores and revision of the North Atlantic flora generally, the overall pattern of floristic relationships remains similar with the American and European series of floras arising from a common Arctic group. In all three sets of ordination analyses (Tittley *et al.* 1990, Tittley & Neto 1995, this study), the Azores flora was the last in the European series of floras. Axis 1 in these ordinations indicated a north to south gradient of increased sea temperature

(see Morton *et al.* 1998, Figs 1-16). Axis 2 represented an east – west separation of temperate Atlantic floras. The addition of data for the floras of Madeira, the Canary Islands, and North and South Carolina in the present analysis resulted in the Azorean flora placed closer to those of central Macaronesia and indicated a warm water floristic affinity. The position in the ordination of the North Carolina and South Carolina floras apart from others in America indicated a major floristic discontinuity with the floras to the north of Cape Hatteras and a transatlantic affinity with the warmer water floras of Macaronesia.

The ordination of brown algal floras showed a similar pattern to that of the red algae and to the ordination of Tittley *et al.* (1990) that placed the Azores flora at the end of a European series. The addition of data for the floras of central Macaronesia and the Carolinas showed a closer floristic affinity of the Azores flora with the former while the wide separation of the Carolinas from other American floras suggested a floristic discontinuity.

The ordination of green algal data contrasted with that of Tittley *et al.* (1990) in which floras of the North Atlantic clustered together as a tight group due to many species in common but with the exception of the Azores flora. Its separation from the main group was due to warm water species present in the Azores that were absent elsewhere in the North Atlantic Ocean. The ordination of Tittley and Neto (1995, Fig. 8) also showed the floristic dissimilarity of the Azores. The present results (Figure 2) showed the American and European series of floras more clearly with the Azores flora placed nearest those of Madeira and the Canaries. As with the red and brown algae Axis 1 of the ordination indicated a north to south cold to warm water series of Chlorophyta floras. The position in the plot of the Carolinas floras towards those of Macaronesia again suggested a transatlantic floristic affinity.

The closer affinity between the Azores flora with those of Madeira and the Canaries than with Atlantic Europe as suggested by Prud'homme van Reine and Van den Hoek (1988) is supported ecologically with the large canopy-forming furoids and kelps common in northern Europe and in Atlantic Spain

and Portugal, but largely absent in the Azores. Algal assemblages are in general characterised by turf-forming species (Neto & Tittley 1995, Tittley & Neto 2000), as occur elsewhere in Macaronesia. Adey and Steneck (2001) suggested that species assemblages that have adapted to similar conditions better define biogeographic regions.

Algal occurrences and distributions are kept within their limits by the major forcing function of sea temperature (Breemen 1990). Adey and Steneck (2001) suggested that habitat types within a seasonal range of water temperatures are a prime determinant of biogeographical pattern while Pakker (1990) noted that regional biogeographical boundaries followed temperature discontinuities rather than latitude. The Azores are located near the summer 20°C isotherm in the Atlantic (Morton *et al.* 1998) with winter temperatures around 15°C, while Madeira and the Canaries lie in warmer water between the 20°C and 22°C summer isotherms. The species poor nature of the Azores flora with fewer tropical species compared to the Canaries may be due to lower sea temperatures. Periodic long-term temperature fluctuations (see Edwards & Richardson 2003) may potentially affect algal occurrence and account for the sporadic occurrence of warm-waters species such as *Phyllocladon anastomosans* (Harvey) Kraft and M.J.Wynne.

As mentioned, the results of ordination analyses also suggested a biogeographical discontinuity between Virginia and North Carolina. Cape Hatteras has been long known as a boundary (Searles & Schneider 1991) due to the cold south-flowing current to the north of the Cape and a warm northeast-flowing current (the North Atlantic Current) to the south. No such discontinuity is evident in the eastern North Atlantic. The warm waters around the Azores are due to the North Atlantic Current and its southern arm, the Azores current (Morton *et al.* 1998).

In the Carolinas there is a difference between the floras of shallow inshore and deeper offshore waters where tropical species prevail. No depth related floristic difference occurs in the Azores. Although prevailing currents from the west are responsible for the transport of a variety of biota from

America to the Azores (Morton *et al.* 1998) ordination analysis of algal floras indicated the Azores to have a greater affinity with Macaronesia and Europe to the east rather than the west. The means of dispersal to these isolated islands remains unclear. Species commonly found in the Azores as rafting material include the fucoid *Ascophyllum nodosum* (Linnaeus) Le Jolis, an amphi-North Atlantic species the source of which may be from the east or the west, and the tropical *Sargassum natans* (Linnaeus) Meyen that is probably of western Atlantic origin. However, in July 2004 *A. nodosum* was found growing attached in the Azores for the first time (P. Raposeiro, *pers. obs.*) indicating the potential of fertile rafting material to establish a population; the casual or permanent nature of these populations requires further investigation. Tittley (1986) and Bartsch and Kuhlenskamp (2000) showed the ability of *A. nodosum* to spread successfully over short distances in the southern North Sea including to the island of Helgoland 60 km from the continental mainland while Tittley *et al.* (1982) recorded *A. nodosum* in fjords on the isolated Faroe islands 350 km from Scotland and 660 km from Norway.

The deeper subtidal currents that flow from the east Atlantic and the Mediterranean Sea to the west may also play a role in dispersal. Isolated sea-mounts in the east Atlantic support algal floras that contain species typical of warm-temperate waters (R.Santos *pers comm.*) and, during glacial periods when sea-level was lower, may have provided stepping stones for marginal spread. Adey and Steneck (2001) noted scattered islands, acting as stepping stones, to be responsible for the large measure of floristic uniformity across the Indo-Pacific. The floristic comparison undertaken here suggests that this may be true for the North Atlantic, and the distance of the Azores from the nearest landfall (1000 – 1800 km) is insufficient to form an oceanic barrier (Adey & Steneck 2001).

The probable east Atlantic origin of Azorean marine fauna was discussed by Cornelius (1982); although the Azores hydroid fauna was amphi-Atlantic, its 18 Echinoderm species were of eastern Atlantic and Mediterranean origin, as were 77 species of fish. Only 21 fish species were amphi-Atlantic in

distribution. The Azores shares 181 species of benthic marine algae with Madeira, 254 with the Canary Islands, 215 species with Portugal and southern Spain but only 87 species with North Carolina. Sources for the dispersal of algae to the Azores are probably varied as North Atlantic, Western Mediterranean, central Macaronesian, and warm-water American species are present on the Azores.

CONCLUSIONS

The marine algal flora of the Azores is relatively species rich with a greater proportion of Rhodophyta typical of warm water regions. Although the Azores algal flora shares species in common with the east and west North Atlantic, the strongest relationship is with the east and with Macaronesia in particular. Low endemism and species shared with locations elsewhere in the Atlantic indicates that the marine algal flora of the Azores is not floristically isolated and may be of relatively recent origin. Although the islands may have served as stepping-stones for the spread of some species, the overall content of the Azores marine algal flora with species from the north, south, east and west suggests the islands to be an Atlantic crossroad.

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FIGURE 1. Ordination of red algal floras in the North Atlantic Ocean.

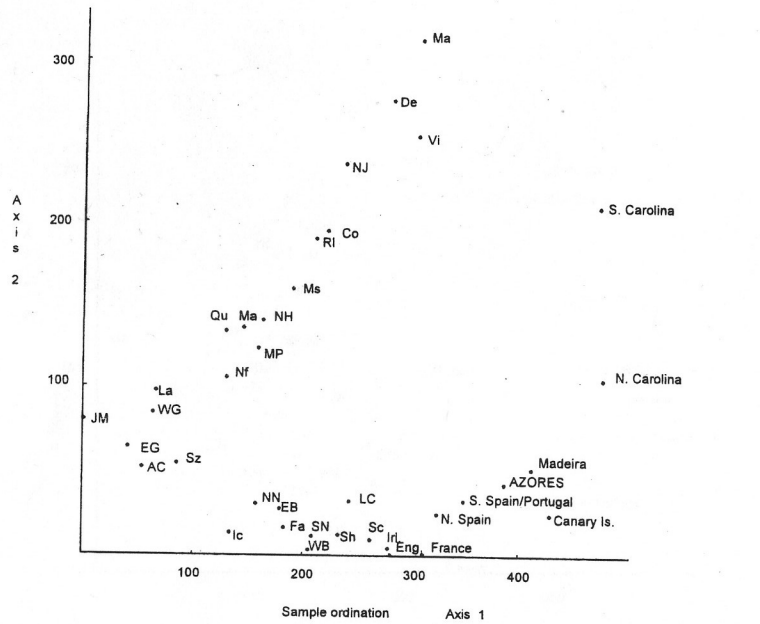


FIGURE 2. Ordination of brown algal floras in the North Atlantic Ocean.

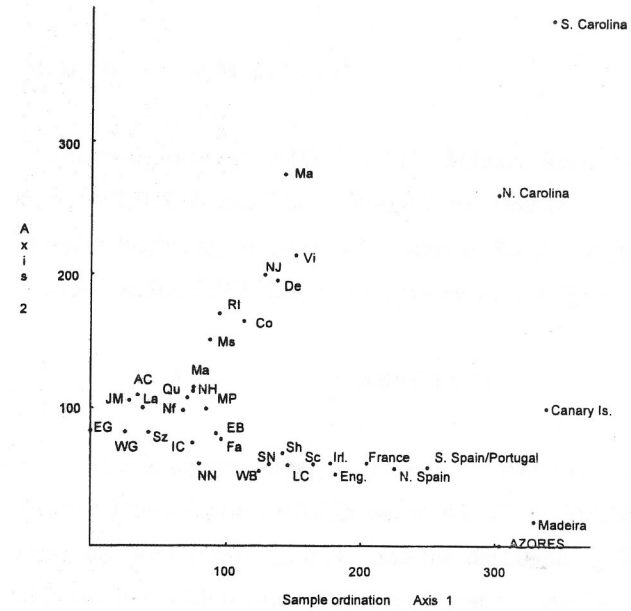
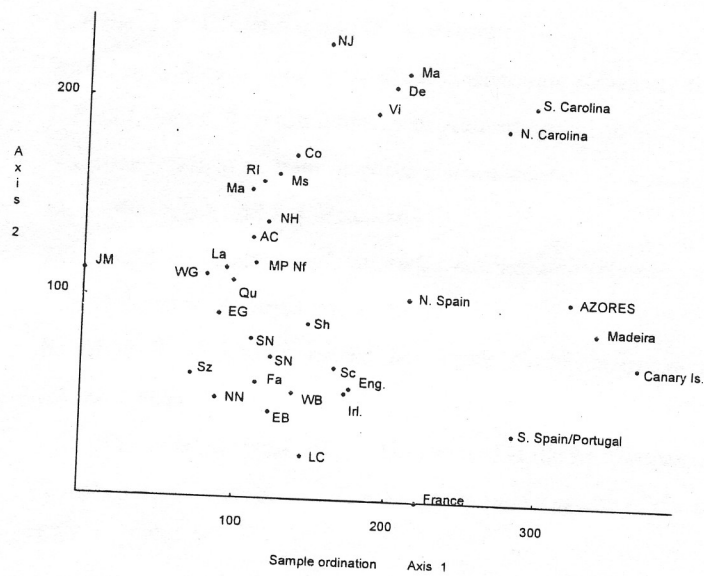


FIGURE 3. Ordination of green algal floras in the North Atlantic Ocean.



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