Fauna and Flora of the Atlantic Islands

PROCEEDINGS OF THE 3rd SYMPOSIUM – PART A

PONTA DELGADA 21-25 SEPTEMBER 1998

III Simpósio Fauna e Flora das Ilhas Atlânticas

Ponta Delgada 21 a 25 Set 1998

Universidade dos Açores

CARLOS MEDEIROS '98

ASPECTS ON THE BIOGEOGRAPHY OF MACARONESIA FROM A BOTANICAL POINT OF VIEW

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Several Macaronesian plant species have widely disjunct distributions but some are represented by vicarious species in other parts of the world. These may be the "parents" of the Macaronesian species, which have developed into related species since Tertiary times, some of them now endemic to the island groups. A period of around 50 million years has been suggested as necessary for species differentiation, at least among bryophytes.

The Macaronesian flora includes circumboreal, Atlantic, Mediterranean, tropical/subtropical, bicentric and endemic species. Several of the tropical/subtropical species may have reached Macaronesia via the South American continent and Central America. Not all of these species managed to reach the western parts of Europe, or are nowadays extinct there. A lot of the species (e.g. *Erica arborea*) invaded via the African continent during suitable climatic periods , probably at least 10 000 years ago. Several formerly Mediterranean trees, shrubs and ferns (e.g. *Ocotea, Clethra, Ilex, Persea; Woodwardia*) now exist only in Macaronesia as Tertiary relicts. A very high number of vascular plants have been introduced to the island groups since their colonization by man, either deliberately or accidentally. Today some of these species (e.g. *Gunnera, Hedychium*) pose a threat to the native plant communities as do the recent far-reaching substitutions of native forests by plantations of alien tree species.

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INTRODUCTION

Over the last two and a half centuries, biologists and especially, botanists have visited and explored the Macaronesian island groups. Botanists became excited by the presence there of a large number of plant species which were new to science. It is mainly during this century that the Macaronesian flora has become an object for phytogeographical considerations. The ecology of species and species groups, as well as sociological work on plant communities, became features for still later investigations and are still going on today, especially in connection with suggestions on conservation.

This short paper provides some information on the phytogeographical profile of the island groups. It considers both vascular plants and bryophytes, the latter being less well known as to their distributions.

The name Macaronesia was originated by the botanist Philip Barker Webb (1860s) to include the archipelagos of the Azores, Madeira, the Canaries and the Cape Verde. In addition, parts of Morocco have some phytogeographic affinity with Macaronesia.

The main formation of the Macaronesian island groups took place during the Tertiary period but parts of the archipelagos may be even older. The islands have thus experienced the warm Tertiary climate as well as the much cooler glaciation periods during the Quaternary period. It is also important to mention that the island groups had their origin in periods when the position of the continents was quite different from today, when Eurasia and America were situated closer together.

DISPERSAL OF PLANTS

The dispersal of plants takes place by wind, water and birds but the most secure way of dispersal is a progressive migration over land. Dispersal by man must of course not be forgotten but is much more recent. The theory of long distance dispersal of diaspores by wind and water as suggested at the beginning of this century to explain the widely disjunct distributions of some plant species has become almost abandoned nowadays. Equally dispersal by birds is regarded as being less important than formerly. Instead, disjunct distributions are more often explained as relictic presences of formerly almost coherent geographic distributions.

The Macaronesian island groups are and were situated such that they could accept an invasion of diaspores from several continents. That is the main reason for the presence there of a high number of widely different phytogeographical elements, which in many cases can be considered as Tertiary relicts (cf. SÉRGIO 1984, 1989).

Among the naturally occurring species in Macaronesia are circumboreal/Nordic and Atlantic ones. Examples of circumboreal bryophytes include *Kiaeria blyttii* and *Blepharostoma trichophyllum*. Some holarctic species have even reached parts of S. America, such as the common Azorean epigeic bryophyte *Diphyscium foliosum*. So-called Atlantic species are present in westernmost Europe, including England and Ireland. Several of them occur there as outposts and are very rare (but are frequent in Macaronesia, at least on Madeira and in the Azores). Several of these species belong to the genera *Lejeunea* and *Radula*. Some of the Atlantic species also extend into Mediterranean areas.

The Mediterranean element is large, especially in the Canary Islands and has also reached the distant Azorean islands. This element has many species among bryophytes belonging to the Pottiaceae. This family is characterized by an unusually large number of calcicolous or high-pH species and many of them are concentrated in coastal habitats. The presence of the hepatic *Exormotheca pustulosa* on Madeira in the south coastal *Aeonio-Lytanthion* Sjn. 1972 community, illustrates the ecological preferences of this species. Conversely the endemic hepatic *Tylimanthus madeirensis* belongs to the Madeirensian *Clethro-Laurion* Sjögren, 1972 community, found at high altitudes.

Several mosses with southern European distributions also exist in Africa, mostly as relicts from pluvial periods of the Pleistocene. This distribution feature is also relevant for the shrub *Erica arborea*, which was able to reach Macaronesia (Madeira and the Canary Islands) via the Sahara until about 11 000 ys. ago (cf. FRAHM 1995).

The most important group of species in Macaronesia may be the Tertiary relicts. These species were formerly present in the Mediterranean area and even, according to fossil evidence, in Austria and Hungary. Among the genera represented are *Ocotea*, *Viburnum*, *Clethra*, *Laurus*, *Ilex*, *Persea*, *Picconia* and the fern *Woodwardia*. The presence today of the ferns *Woodwardia* and *Thelypteris pozoi* on the European continent is sparse and of relictic nature.

The subtropical/tropical element is composed of species also present in S. America, C. America and Africa. The Macaronesian island groups form, phytogeographically, a link between Africa, tropical America and Europe. A large number of the tropical bryophytes are hepatics and belong to families with a rich differentiation in tropical rainforests, such as the Lejeuneaceae, Radulaceae and Frullaniaceae. Some of the most "precious" hepatics of the Azores and Madeira, *Jamesoniella rubricaulis* and *Radula nudicaulis*, are otherwise tropical American species (cf. GROLLE 1969) now with only a relictual presence in Macaronesia. Localities are few and populations small, so these species are clearly endangered. Such species may formerly have reached westernmost Europe during postglacial warm periods.

Among the most interesting taxa are those which belong to the bicentric element, some represented by vicarious species. Such species occur on all the island groups and several are very old relicts with origins in the old Gondwanaland

continent. One prominent genus among the bryophytes is *Echinodium* which today has four species endemic to Macaronesia and other endemic species in Australia and in New Zealand. They occur there in the Gondwanaland forests of *Nothofagus* and *Podocarpus* but did not spread to S. America via the Antarctic connection. Another genus is *Tylimanthus*, mentioned above, which has developed two endemic hepatic species, one on Madeira and one in the Azores. Other species of this genus are African and South American. There are also disjunct Mediterranean species such as *Antitrichia californica*, which occurs in westernmost USA but in Macaronesia is only present on Madeira and in the Canary Islands. On the other hand, species such as the relictual epixylic hepatic *Telaranea nematodes* , is present in Neotropis, Paleotropis, in Macaronesia and in W. Europe. The genus *Jubula* has developed one species in Macaronesia and western Europe while the remaining species occur in C. America and in SE Asia.

Important Macaronesian tree/shrub species with affinities to species in S. Asia and even Australia include *Apollonias barbujano* (endemic to Madeira and the Canary Islands) and the two *Picconia* species (cf. IRMSCHER 1922, 1929) (*azorica* endemic to the Azores and *excelsa* to Madeira and the Canary Islands). On the other hand the large genus *Bystropogon*, with several Macaronesian endemics, is represented mainly in South America.

In general one must consider the Macaronesian flora as very old and even non-endemic species are in many cases of relictic nature.

ENDEMIC SPECIES

Naturally, one of the most important phytogeographical groups of species is the endemic species. The proportion of species endemic to an island group generally depends on the degree of isolation, and the topography, age and habitat diversity of the islands. For Macaronesia our knowledge of the endemic species becomes progressively more and more detailed. Some species have recently been found to occur also on the European and African continents, others are now known to be endemic to more than one of the Macaronesian island groups. As to endemic vascular plants there is an increase in numbers from W. to E. in Macaronesia. Most of the endemic species belong to genera well-known in other parts of the world. Several occur as shrubs, whereas their relatives in Europe are herbs or dwarf-shrubs, for example, *Hypericum* and *Vaccinium*. A few genera are also endemic, such as *Muschia* on Madeira and *Azorina* in the Azores.

The endemic species are both paleoendemics, ancient relicts, of ages when their distributions were much larger, and neoendemics. These latter evolved during long periods of isolation of fairly small populations. In areas such as Scandinavia, where time for such evolution was brief, the number of endemic species is correspondingly small and represents a very small proportion of the total flora. The time available there was only about 9000 years. It is also characteristic that several of the Macaronesian endemics such as the bryophytes *Alophosia azorica*, *Andoa berthelotiana* and *Trematodon perssoniorum*, are monotypic.

The endemic bryophytes of the Macaronesian island groups are less well-known than the vascular plants. I will therefore give more detailed information on them. One of the reasons for species remaining endemic is that their diaspores are few and poorly fitted for dispersal. Pteridophytes and bryophytes generally have numerous light spores which may disperse these species by wind over large distances. In spite of this, the number of endemic species e.g. of bryophytes amounts only to about 60 species for all Macaronesia and to some 30 species for each island group. Even among these endemic bryophytes the genera are well-known. One genus *Nobregaea*, is endemic so far to Madeira.

In the Azores it is evident that the high islands with a dissected topography like Pico, São Jorge, São Miguel and Terceira, are equipped with the highest numbers of endemic species, both among vascular plants and bryophytes. Most of these species occur preferentially within the native

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Fig. 1. *Euphrasia grandifiora* Hochst. ex Seub., a species endemic to the Azores with only a few, small populations at altitudes between 800-1000 m on the islands of Pico and São Jorge. One of the rarest and most endangered plants in Europe. - Photo David Powell, São Jorge at 1000 m in August 1998.

Fig. 2. Stem leaves of *Euphrasia grandiflora*. The specimen here grows together with *Holcus rigidus* Hochst. ex Seub. and *Tolpis azorica* (Nutt.) P. Silva, both endemic to the Azores. - Photo David Powell, São Jorge at 1000 m in August 1998.

high-altitude forests, the so called cloud-zone forests.

The endemic bryophytes are spread over a large number of families. Only Fissidentaceae, Echinodiaceae, Brachytheciaceae and Lejeuneaceae contain more than 3 endemic species each. Regarding the distribution of the endemic species, recent investigations have brought unexpectedly few new records for islands where they were not known before. Recent records of 10 endemic bryophytes in Corvo, Graciosa and Santa Maria are almost certainly due to the previously poor knowledge about the bryoflora and bryovegetation of these islands (cf. SJÖGREN 1990-1997) and not to recent colonisation of these islands by the species concerned. A few, newly described taxa from the island groups are endemic.

Even among the endemic vascular plants a, perhaps unexpected, stability of distribution has been revealed. Examples include *Marsilia azorica* which occurs in one locality on Terceira; *Euphrasia azorica* grows in a few well-known localities on Flores and Corvo; *Musschia wollastoni* nowadays occurs in only few localities on Madeira. Among bryophytes, *Neckera cephalonica* is restricted to a few localities on Pico.

There is a potent representation of endemic species of the Lamiaceae family on Madeira and in the Canary Islands with species of the genera *Bystropogon*, *Micromeria* and *Sideritis* (cf. SUNDING 1970, 1979) Only one species, *Cedronella canariensis*, has managed to reach the eastern-most Azorean island of Santa Maria, where it occurs in probably not more than a couple of localities, each with small populations. Another family, the Crassulaceae, has a huge number of endemic species in the Canary Islands, five species on Madeira and one on Santa Maria, namely *Aichryson villosum*. The species rich genus *Aeonium* is also present in Morocco and has a bicentric outpost in NE Africa.

ASPECTS ON PROTECTION

From conservation point of view the fact that some of the endemic vascular plants and bryophytes of Macaronesia are among the rarest taxa in Europe must be stressed. Today they are highly vulnerable and even in danger of becoming extinct . This applies especially to those species present in only one or a few localities and for those with small populations. One typical example is the hemiligneous *Euphrasia grandiflora*, supposed to exist on four islands including Terceira and Faial but recorded by the author only in a few localities on São Jorge and Pico, each with less than 25 specimens.

For reasons mainly linked to conservation of the endemic element of the flora it is important to establish more firmly the existence of endemic plant communities or phytocoenoses. Such endemic communities of bryophytes, for example, are richly represented in Macaronesia at the level of association and alliance (cf. SJÖGREN submitted). They should be the important foundation stones for conservation plans. They contain more or less numerous endemic species as well. For example, the epiphyllous *Cololejeuneo-Colurion* Sjn. 1978 (see also SJÖGREN 1997), can almost only reach its mature development in undisturbed native forests on Madeira and in the Azores. It contains at least 10 species of hepatics which are endemic either to individual island groups or to Macaronesia as a whole. The basis of proposals for plant communities considered most worthy of conservation must always be a profound knowledge of the autecology and synecology of the species involved.

RECENT CHANGES

The presence of relict elements in the Macaronesian flora leads naturally on to considerations of more recent changes in phytogeographical features. These are primarily connected to man's activities. The progressive opening up over more than 500 years of the comparatively dry coastal landscape for settlement and agriculture (cf. DIAS 1996) has certainly facilitated the invasion and spread of Mediterranean and cosmopolitan species. The latter are mostly anthropochorous. It has become

evident that those Azorean islands which have long been centres of communication also received the largest numbers of introduced plants. The small islands of Corvo, Graciosa and Santa Maria have always been outside the important tracks for communication with Europe and the American continents. On Madeira most anthropochorous species grow within the southern part of the island, where settlement and communication centres are located. For example, the Mediterranean hepatic *Exormotheca pustulosa*, common as an epigeic in strongly exposed habitats, is on Madeira only found in this part of the island (cf. SÉRGIO et al. 1992).

Settlement of species has recently become facilitated by man's influences. For example the common construction of cement walls has enabled rapid colonization by calcicolous bryophytes belonging mostly to the genera *Tortula* and *Barbula*. The natural presence of some species of these genera was in the Azores probably restricted to the island of Santa Maria and on Madeira to the peninsula of São Lorenço, where calcareous seashell soils are available. It is evident that wind-transported spores are always available in the atmosphere, able to colonize high-pH substrates, even of very small size and surrounded in total by acid substrates. The competitive ability of the calcicolous species is apparently very strong where they occur as primary colonizers.

It is clear that the recently ameliorated knowledge on the taxonomy and worldwide distribution of species belonging to various phytogeographical elements has supported the evaluation of the Macaronesian flora (cf. SCHUMACKER & MARTINY 1995).

INTRODUCTION OF PLANTS

The fairly recent, deliberate introduction of alien plants to Macaronesia has unfortunately meant considerable changes to the landscape during this century and in some cases also meant a threat to the very survival of native types of vegetation. Among the alien species in the Azores are the Indian lily, *Hedychium gardneranum* and the Australian *Pittosporum undulatum*. They are now integrated in both high-altitude vegetation and the more coastal *Myrica/Picconia* shrubforests. A very recent threat to native vegetation and to cultivated land has occurred on São Miguel due to the enormous spread of *Clethra arborea* and *Gunnera tinctoria*, both originally cultivated in gardens. *Clethra arborea* is a natural component of the Madeiran cloud-zone forest named as the *Clethro-Laurion* (Sj. 1972) but has never been a natural constituent of the native Azorean forests.

The escape of *Gunnera* is worthy of special mention as one example of rapid changes in recent times. In this case the escape has been facilitated by man's activities, namely the extensive collection of topsoil *Sphagnum* for pineapple cultivation. *Gunnera* is able to survive on impoverished soils because it fixes nitrogen from the atmosphere and accepted rapidly this new land provided for colonization where competition failed.

Among the introduced weeds on Madeira are *Eupatorium adenophorum* and *Erigeron karwinskianus*, which have become threats to the native flora. I suppose that in the Canary Islands *Opuntia ficus-indica* is also a very powerful invader especially of abandoned fields at low altitudes. *Erigeron* and *Eupatorium* are Mexican plants and *Opuntia* comes from tropical America.

The planting of *Cryptomeria japonica* over large areas in the Azores, to an extent not always economically justified has supported a further colonization of alien plants. They get their chance especially after the felling of ripe forest stands. Even today the planting of ornamental flowers, such as *Lantana camara*, has been followed by numerous escapes into native vegetation. *Lantana* and *Eichornia crassipes*, both from S. America, were once categorized as two of the most dangerous invasive plants in the world.

A most laboreous and even expensive fight against at least some of these exotic plants must now be planned, especially within areas considered for conservation. These areas are few and in some cases fairly small. The introduction of alien plants to isolated island groups should always be thoroughly controlled by authorities concerned with protection of the environment. For

example the recent introduction of *Myrica faya* to the Hawaian islands has had most unfortunate consequences to native vegetation.

The particular phytogeographical elements present on certain substrates and in certain vegetation types is also worth consideration. For example, the endemic, tropical and Atlantic bryophytes are concentrated in the high-altitude native forests. This is especially so with the hygrophilous hepatics and is particularly relevant for Madeira and the Azores. The endangered and rare species of Madeira have been listed and their predominant presence is within the *Clethro-Laurion*. Furthermore, most of the bryophyte groups mentioned contain species which grow preferentially epiphytically, epixylically and epiphyllously in the cloud-zone forests: they are phorophyte-bound. Their substrate preference becomes, however, progressively reduced towards altitudes around 1000 m (cf. SJÖGREN 1997). As the phytogeographically most remarkable species in the Azores and on Madeira, they strengthen considerably the preservation values of the remaining relicts of Macaronesian native forests. The epiphyllous vegetation is remarkable, being absent on the European continent and mainly a feature of the tropical rain-forests.

THE ABSENT SPECIES

Flora and vegetation investigations should include reflections on missing species also. Excursions in the field should always be an integrated part of a university education in botany. During such excursions it is very important to discuss not only what one is able to find but also why a certain species or species group expected to occur in an ecosystem has either vanished or perhaps never managed to colonize and survive.

A good knowledge of the Atlantic bryoflora of Europe provides many questions as to the Azorean and Madeirensian bryoflora. Atlantic parts of Europe are characterized e.g. by the frequent presence of *Rhytidiadelphus loreus*, *Eurhynchium striatum* and *Plagiothecium undulatum*, all large and easily recognized mosses. *R. loreus* was found in one locality in

1997 (LIFE-project) on Terceira and was previously known from only one other locality on Pico. *E. striatum* was recorded in 1996 (LIFE-project) as new to Santa Maria, in one locality, and *P. undulatum* apparently does not exist in Macaronesia. The common mire bryophyte *Aulacomnium palustre* has been recorded only in two localities on Pico. *Hyocomium armoricum* has a large population on São Jorge above 700 m but exists only there and has not managed to spread. to suitable habitats on nearby Pico. Several other examples can be provided of puzzling distribution patterns among bryophytes, indicating a rigid situation. Vascular plants also provide several examples of sparse distribution in Macaronesia. The common European pteridophyte *Botrychium lunaria* has only one locality on Pico. *Lycopodiella inundata* has been recorded on Pico (where it is probably now extinct) and São Miguel. *Juniperus phoenicia* occurs in a few localities on Madeira and Porto Santo. *Taxus baccata* is a well-known west European tree species with perhaps only one small, natural population on Pico.

The few examples given above contribute to the phytogeographical profile of the Azores,which e.g. includes both a highly frequent presence of European oceanic species, rarely found in westernmost Europe, and rare presence of species, which are common in all western Europe. The bryophytes mentioned are not new invaders. Their actual presence has remained restricted and known since more than 50 years. No formerly wide distribution has been recorded. Their initial settlements have been checked, probably due to small populations, small production of diaspores and strong competition of already firmly established species. However, such hypotheses need further investigation, following the development of the population in the field; even transplantation experiments in the field, under strict control, may provide answers to questions on distribution peculiarities.

NEW SPECIES

The discovery of new species in Macaronesia

goes on. So also does the ecosociological treatment of plants and plant communities. The structure of the flora and the effects of insularity continuously provide new objects for investigation.

The bryologically "forgotten" islands of Corvo, Graciosa and Santa Maria have recently been credited with 105, 90 and 50 species respectively which have not previously been recorded for these islands (cf. SJÖGREN 1990, 1993, 1996). CRUNDWELL et al. (1994) recorded a considerable number of species new to individual islands of the Azores, especially anthropochorous ones. HEDENÄS (1992) described five species new to science on Madeira. Several species new to the Canary Islands were listed by DIRKSE et al. (1993). Schumacker and Sérgio have during the last decades made several discoveries of species new to the Azores or to individual islands of the archipelago.

Taxonomic revisions have recently meant several reductions of taxonomic status of species. Some endemic species have been found to be identical with taxa existing in other parts of the world. Knowledge about the distribution patterns of several species, especially endemic ones, has become greatly ameliorated.

The endemic plants have become in general better known due to the creation of botanical gardens in all the Macaronesian island groups. In many cases there are differentiated races of endemic species on different islands (e.g. of *Leontodon* species). It is thus not advisable to mix material of the same species from different islands in the botanical gardens. Such a procedure may lead rapidly to an extermination of the genetic differences which have developed during long periods of insularity and small population sizes. In order to support the investigations of habitat ranges of rare plants and their competitive ability, transplantation experiments of species into native plant communities should be avoided.

There is still a lack of knowledge of the ecology of many Macaronesian plants. The importance of studies of ecological ranges of species and species groups is pronounced, especially considering their pollution-free habitats

which are nowadays very difficult to find in many parts of the world.

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DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS OF *Trichomanes speciosum* WILLD. (PTERIDOPHYTA) IN THE AZOREAN ARCHIPELAGO

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Trichomanes speciosum Willd., a globally rare and threatened pteridophyte, is most abundant in the Azorean archipelago. Even here it has undoubtedly declined through habitat destruction. The species is unique amongst European-Macaronesian ferns in that over much of its range the life-cycle is not completed. Whereas the species relies almost exclusively on asexual means of propagation throughout northern and central Europe, by gametophytic gemmae, a normal sexual alternation of generations is the predominant pattern of its reproductive biology in the Azores. Gametophyte populations existing in the absence of the sporophyte have been detected in the Azores but do not show the relative abundance witnessed in northern and central Europe. The distribution of both generations is given and their ecology discussed. Populations on man-made, i.e. recent, habitats on the island of Flores indicate colonisation, hence dispersal, at a local level. Although the species must be considered not threatened in the Azores as a whole, Azorean populations merit conservation as they provide the key to understanding the factors controlling the species reproduction. This information is vital for successful conservation elsewhere.

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INTRODUCTION

Trichomanes speciosum Willd. (syn. *Vandenboschia speciosa* (Willd.) Kunkel), the Killarney fern, is the sole native European representative of the genus *Trichomanes* (TUTIN et al. 1993), the largest of the genera of the filmy-ferns (Hymenophyllaceae). This morphologically reduced and very distinctive family achieves greatest abundance in the cloud forests of the tropics and sub-tropics, more rarely extending to constantly humid areas in the temperate zones.

Trichomanes speciosum is tetraploid (MANTON 1950), its closest affinities and possible diploid progenitors have still to be resolved. It is a Macaronesian – European endemic (TUTIN et al. 1993), that was formerly confused with *T. radicans* Sw. (see for example DANSEREAU

1961), reported from Asia, the Caribbean and South America. Morphologically similar taxa in the section *Lacosteopsis* Prantl (= *Vandenboschia* Copel.) also occur in tropical Africa, North America and Australasia.

The Killarney fern has been considered one of Europe's most vulnerable species threatened by habitat destruction and a victim of over-collection (WALTER & GILLET 1998). It has been accorded legal protection throughout its range under the Bern Convention (ANON. 1979) and the Habitats Directive (ANON. 1992).

Trichomanes speciosum is found on all of the Azorean islands with the exception of Santa Maria (HANSEN & SUNDING 1993). First reported by SEUBERT & HOCHSTETTER (1843) and later given by DROUËT (1866) as occurring on Faial and Flores, WATSON (1870) recorded its presence on five of the islands, those previously listed and

São Miguel, Terceira and Pico, with TRELEASE (1897) further adding Corvo. The presence of the species on São Jorge was noted by PALHINHA (1966) in his catalogue of the vascular plants of the Azores. Discovery on Graciosa, the least elevated and driest of the islands was comparatively recent and supported by a specimen at **AZU** (Poço do Ratinho, Guadalupe, Graciosa, alt. 60 m. 31.08.1995. F. Pereira **125**!).

SJÖGREN (1973) was the first to present maps of the species distribution within the Açores, plotting both his field records and those from localised literature and herbarium sources for the islands of S. Miguel, Pico, Terceira and Faial. Independently WILMANNS and RASBACH (1973) produced a map of the species occurrence on the first of these.

Trichomanes speciosum is unique amongst European ferns in that its gametophytic generation, the sexual or gamete-bearing phase of the life–cycle, is perennial, gemmiferous and capable of persisting and dispersing in the absence of its sporophyte. This latter ability, 'gametophytic independence', is apparently a very rare condition amongst the homosporous ferns. It has been reported from three families, all widespread as epiphytes in tropical regions, the Grammitidaceae, Vittariaceae and the Hymenophyllaceae, but is only well developed in those rare species found at the temperate extremes of these families ranges (RUMSEY & SHEFFIELD 1996). The discovery of the distinctive but easily overlooked gametophyte generation of *T. speciosum* in northern Europe (RUMSEY et al. 1990) post-dates the few floristic accounts concerned with the distribution and ecology of this (and other pteridophyte) species in the Azorean archipelago, (e.g. SJÖGREN 1973, 1979; WARD 1970; WILMANNS & RASBACH 1973). In view of the relative abundance of the gametophyte generation over much of north-western and central Europe (see RUMSEY, JERMY & SHEFFIELD 1998), where climate has been conjectured to be the prime factor effecting 'gametophytic independence', it was clearly desirable to establish the extent to which gametophytes occurred, and where, in areas with abundant sporophytic growth and a more

moderated climate, such as the Azores. Accordingly, field surveys were performed in April 1994 (Flores, Terceira, Faial, Pico), October 1996 (Flores, Terceira, Pico) and September 1998 (Corvo, Flores, Terceira, São Miguel).

DISTRIBUTION

The distribution as currently known on all of the islands for which this species is recorded, with the exception of Graciosa, is documented in Figs. 1-6. Distribution has been mapped on a 2 km grid level for all islands, based on the UTM grid. These maps have been derived from literature sources (SJÖGREN 1973, 1978, 1979, 1997; WARD 1970; WILMANS & RASBACH 1973), herbarium material (**BM, K, AZU**) and our own field surveys (1994-1998).

No comprehensive systematic account of the distribution of the pteridophyte flora of the Azorean archipelago has been published. It is thus difficult to assess the true abundance of species, the likely factors affecting their distribution and whether they are declining, or increasing in numbers and range. Those distribution maps previously given for *T. speciosum* do not cover the generally under-recorded western islands where the species is most abundant. Across the archipelago the percentage of grid cells per island in which the fern occurs rises from 0-5.7 for the eastern group, to 8.2-10.1 for the central to 42.9-63.6 for the western group. SJÖGREN (1973) lists only four localities from Flores, WARD (1970) mentions a further two but states that the species is "common in damp shaded places". This is probably somewhat of an exaggeration, although it is certainly widespread (Fig.6) and is locally very abundant. Continuous sporophyte colonies of greater than 100 m^2 in area have been seen in several locations, eg. Ribeira da Silva (fig. 7). On Flores it occurs from near sea level (15m Sta. Cruz, Gonçalves. **LISI**) to c. 820 m on the western slopes of the highest peak, Morro Alto (914 m). For those islands for which maps and/or descriptive accounts (e.g. Wilmanns and Rasbach, 1973) have been published our brief surveys have
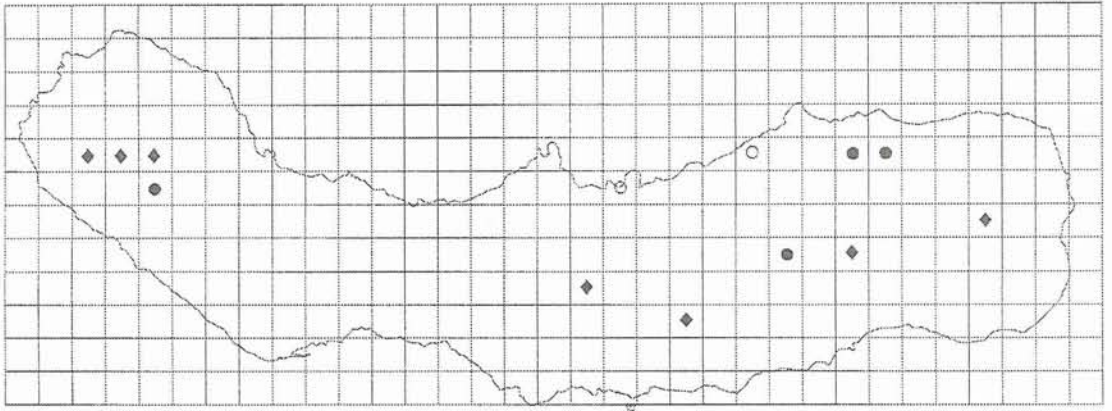
Fig. 1. Distribution of *Trichomanes speciosum* Willd. on São Miguel. Earlier records that we have confirmed are given as •, earlier unconfirmed reports as ♦. Where gametophytes alone occur in a tetrad they are represented by an open symbol, o.
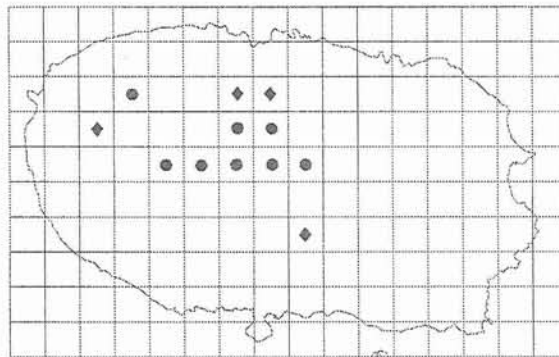
Fig. 2. Distribution of *Trichomanes speciosum* Willd. on Terceira.

increased the known distribution. The species detection from a range of apparently previously unrecorded sites is in part due to the hitherto overlooked gametophyte generation but the majority relate to new records of the sporophyte. We conclude that detailed survey would reveal the species in many more localities.

Gametophytes are not always apparent in close proximity to sporophyte colonies but in many such cases are present elsewhere within the locality. The very extensive mats of gametophyte found in sheltered caverns in northern and central Europe have only been seen in a few lowland gulley sites on Flores, Corvo and S. Miguel. In most sites gametophytes are present in small quantities (patches with an area of < 10 cm^2), although juvenile sporophytes are often produced.

Sporophytic recruitment has been noted in 19 sites distributed throughout the archipelago. Gametophytes and juvenile sporophytes are always associated with rocky substrates. Sporophyte colonies present on tree boles, humic banks, etc. we consider to have secondarily colonised such habitats via the growth of the long creeping rhizome.

Levels of sporophyte fertility fluctuate annually, presumably linked to climatic variables. The frequency with which colonies become fertile, the proportion of fertile fronds per colony and numbers of sporangia per frond varies greatly throughout the species range. At its northern limits in Great Britain the majority of colonies have never been recorded to produce spores (RATCLIFFE et al. 1993). Even within the Azores

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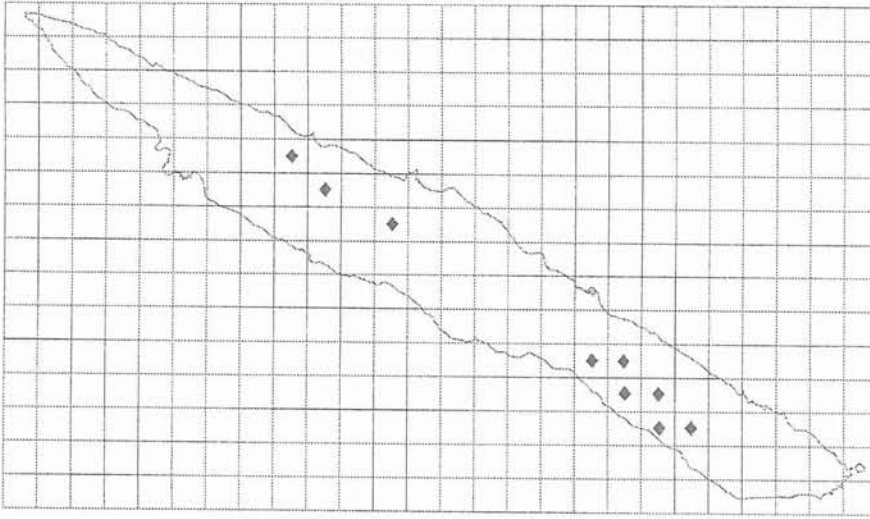
Fig. 3. Distribution of *Trichomanes speciosum* Willd. on São Jorge.
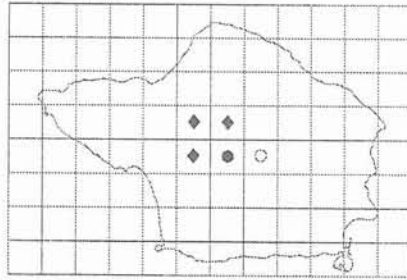
Fig. 4. Distribution of *Trichomanes speciosum* Willd. on Faial.

there exists a marked difference in fertility between the usually highly fertile western island populations and those in the central and eastern groups. The precise factors affecting fertility remain to be resolved.

ECOLOGICAL AND PHYTOSOCIOLOGICAL OBSERVATIONS

SJÖGREN (1973) considered *Trichomanes speciosum* one of the best ecological indicator species for habitats with the highest relative humidity and regarded it phytosociologically as a differential of his *Festucetum jubatae* association, a community rich in endemic taxa characterised by their low drought tolerance and need for shelter. The species occurred less regularly in the *Erico-Myrsinetum*, the most widespread natural vegetation of the islands. These associations together comprise the natural component of the *Juniperion brevifolii* alliance, the evergreen (scrub-) woodland vegetation of middle to upper altitudinal range (>500 m), i.e. the cloud-zone. Below this altitude occur the most anthropogenically affected woodlands, now often dominated by the alien *Pittosporum undulatum* Vent. These are predominantly found in the altitude range 300-600 m. and have effectively replaced the natural transitions between the coastal *Myrica* dominated scrub (SJÖGREN's (1973) *Festucion petraeae* alliance) with the species-rich mixed laurus-silva of moderate altitudes. SJÖGREN (1973) conceded that transitional zones between these communities are particularly prevalent on the damper western

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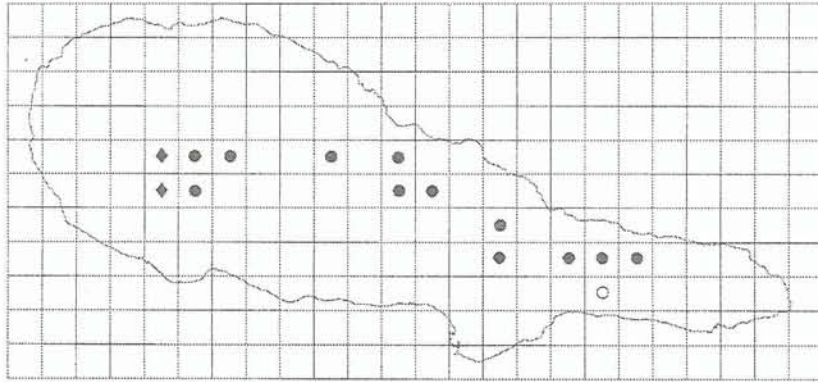
Fig. 5. Distribution of *Trichomanes speciosum* Willd. on Pico.
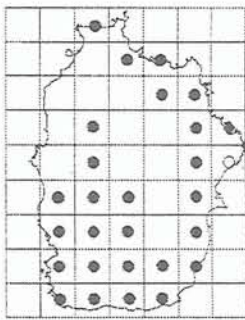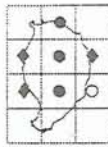
Fig. 6. Distribution of *Trichomanes speciosum* Willd. on Flores and Corvo.

islands, where the altitudinal zonation is in any case more compressed. He further suggested that by virtue of its dense canopy the spread of *Pittosporum* woodland has favoured the colonisation of a range of species associated with the *Juniperion brevifolii* below their original lower altitude limit throughout the archipelago.

SJÖGREN (1984) described *T. speciosum* as generally occurring above 500 m, although fairly frequent in the western group between 200 and 500 m, i.e. essentially restricted to the cloud zone region.

Is this categorisation of the species as non-lowland accurate and if *T. speciosum* occurs in these areas is it the result of a recent extension downwards in altitudinal range? Our survey revealed *T. speciosum* to be present in shaded, deep streambeds with waterfalls, in the lower level woodlands on all of the island groups. We have found both generations as low as 190 m on S. Miguel and at 90 m on Flores, although within the central group few localities have been found to occur below 400 m. The species and especially its gametophyte are undoubtedly under-recorded in these streambed gulley sites, which in most cases are difficult to survey. Was *T. speciosum* present at these altitudes prior to the arrival of *Pittosporum undulatum*, or is it a comparatively recent colonist? Regular associates in these situations include *Diplazium caudatum* (Cav.) Jermy and *Pteris incompleta* Cav. both of which occur as scattered individuals in sheltered cloud-zone sites but which never occur with the same abundance or luxuriance as at these lower levels. It is also noteworthy that this assemblage is found between 250 and 500 m in the Macaronesian vegetational enclave in the drier Algeciras area of southern Spain (RUMSEY & VOGEL 1998). Other pteridophytes showing habitat preferences for lowland woodland sites include *Asplenium hemionitis* L. and *A. azoricum* Lovis, Rasbach

Fig. 7. Very extensive colony of *Trichomanes speciosum*, gulley at c. 330 m alt., Ribeira da Silva, Flores

CONSERVATION STATUS

Trichomanes speciosum is adapted to life in a specialised habitat. This narrow ecological amplitude closely limits the number of potential sites, especially for the species sporophyte but such suitable sites occur very patchily over a wide geographical area. As an attractive plant, present in small numbers in many west European states, it was a prime candidate for legislative protection. Indeed, this species has taken on an almost iconic status amongst conservationists (PAGE 1997) and yet, following field and laboratory investigation of the organism throughout its life-cycle, the necessity for active conservation is being re-assessed. Until 1990 and the first report of the gametophyte generation in natural situations (RUMSEY et al. 1990) it was widely considered that this species was among the most vulnerable and threatened of Europe's plant taxa. Populations over much of its range were not only small but static, with no observed regeneration, or colonisation of novel areas (RATCLIFFE et al. 1993). This was coupled with a perceived threat through collection, a major cause of decline in Ireland in the last century. While the situation was believed to be less bleak in Macaronesia, where large populations were known to exist in northern Madeira and in the Azores, the continuing destruction of the "Laurus-silva" and the alteration of habitats by invasive aliens gave considerable cause for concern. The discovery of a widespread gametophyte distribution, akin to a vast viable seed-bank in angiosperm terms, has somewhat diminished the claim for the species to priority conservation attention (see RUMSEY et al., in press, for discussion). Within Macaronesia the gametophyte is not an obvious component of the vegetation when compared with the sporophyte, in

and Reichstein. While the presence of these fern assemblages provide support for the view that *T. speciosum* could be of natural occurrence at low altitudes, the species has certainly also colonised areas within the cloud-zone during this time-span. This is evidenced by its presence on lava fields of known age, e.g. the Misterios Negros of Terceira and various of the lava fields on Pico. Similarly, *T. speciosum* is widespread and perhaps most frequently encountered on Flores as a plant of walls, usually where shaded by the alien *Hydrangea macrophylla* (Thunb.) Ser.

contrast to the situation in northern and central Europe. It does, however, occur in sites from which the sporophyte is currently absent, particularly those at lower altitudes. The gametophyte thus extends the species distribution and may harbour genetic variation not currently present within extant sporophyte populations, if genetic diversity is maintained between, not within populations, as in northern and central Europe (RUMSEY et al. 1998). The high proportion of sites present on man-made structures within the western group in the Azores indicates the species ability to colonise novel habitats when they become available. Man-made sites are, however, also vulnerable to destruction and are less likely to support populations over the long term than larger natural rock features. Conservation actions that seek to protect a mixture of "natural" source populations and more transient but perhaps more genetically diverse man-made sites would be of benefit to the survival of the species. The ability to persist as the gametophyte generation in degraded habitats renders it less vulnerable than most species in this hygrophilous community to habitat destruction. An ability to inbreed, to produce potentially widely dispersible propagules and to propagate vegetatively may also overcome problems of habitat fragmentation (RUMSEY et al. in press). These aspects of the species biology, together with the abundance of sites on the western islands of Flores and Corvo, suggest that the species must be considered Not Threatened within the archipelago as a whole. However, if considered separately the islands would individually warrant a higher risk status. Further work is still necessary to establish extent and status on several of the islands.

For conservation action to succeed it must be grounded on a rigourous scientific basis, with a firm understanding of the biology of the species involved. The work presented here suggests that the Azores does maintain globally significant populations of *T. speciosum*. However, if conservation action is promoted on a "species" not "habitat" basis then other Azorean species must be considered more threatened and requiring more immediate action. The maintenance of the

unique vegetation within which *Trichomanes speciosum* occurs is unquestionably of paramount importance as it supports many endemic taxa whose continued survival is now of very real concern. The species itself acts as the preferred substrate for a range of epiphyllous hepatics many of which are almost exclusively confined to this habitat in Europe (SJÖGREN 1997). The presence of this species can thus be used as an indicator of a particular cryptogamic community of considerable conservation importance. The continued legal protection afforded to this fern thus by default acts to protect a wide range of less obvious but equally important taxa.

ACKNOWLEDGEMENTS

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BIOGEOGRAPHY OF AZOREAN PLANT INVADERS

L. SILVA, J. TAVARES & C. W. SMITH

Alien plants are a major component of the Azorean vascular flora. We present a general biogeographic analysis of the taxa considered as introduced in the Archipelago. This work results from the construction of a data-base of Azorean plant invaders. Of the 996 taxa recorded for the Azores, 6,6% are considered endemic, 10,2% native, 72,6% alien, and 10,5% to be of uncertain status. The percentage of alien taxa is lowest in the Pteridophyta (26,0%) and highest in the Dicotyledoneae (78,9%). Significant differences were found between islands for the proportion of invaders. The highest percentages were found in São Miguel, Terceira and Faial, and the lowest in Flores and Corvo. A quadratic model fitted a regression between percentage of invaders and human population density, and might reflect the existence of a higher propagule pressure in some of the islands. Many of the invaders are also found in mainland Portugal and in other Macaronesian islands. The invaders are largely Palearctic in origin or Subcosmopolitan, with a wide geographic distribution, and have also been introduced in other regions of the world.

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INTRODUCTION

The study of plant invaders is important not only in academic terms, but also because some of the invaders might become noxious WEEDS (CRONK & FULLER 1995; PYSEK et al. 1995). The origin of the plants invading a certain region has been extensively covered elsewhere (DRAKE et al. 1989; GROVES & DI CASTRI 1991). Today, the success of an invader in a given ecosystem is an important indicator of whether a species might become a successful invader elsewhere (WILLIAMSON 1996).

Alien plants are a major component of the Azorean vascular flora. According to PALHINHA (1949) three quarters of the Azorean vascular plant species are exotic. Although a considerable research effort was developed regarding the native vegetation (see DIAS 1996), few papers deal with plant invaders. Exceptions are those of PALHINHA (1949, 1953), REGO (1964), SJÖGREN, (1973a, 1973b) and HANSEN (1987, 1992). Since

1992, work has been carried out on the ecology and control of plant invaders, both those originating in the Azores islands (SILVA 1994, SILVA & TAVARES 1995a, SILVA & TAVARES 1995b, SILVA et al. 1995, SILVA & TAVARES 1997, SMITH et al. 1995) and those invading the archipelago from elsewhere (SILVA et al. 1996, SILVA et al. 1997). One of the aims of this study is the development of a data-base regarding the Azorean vascular flora, including an in-depth characterisation of the introduced taxa. The Azores archipelago, located in the North Atlantic Ocean, comprises nine islands divided by three island groups (Table 1): the eastern group (Santa Maria and São Miguel), the central group (Terceira, Graciosa, São Jorge, Pico and Faial), and the western group (Flores and Corvo). The islands are of volcanic origin and the climate is temperate oceanic, with a mean annual temperature of 12°C at 550 m altitude and 17°C at 70 m, and a mean rain-fall of about 2300 and 1020 mm/year, respectively (INMG 1991).

In this paper we present a general

biogeographic analysis of the vascular plant t. xa considered as introduced in the Azorean islanus. We test the hypothesis that the majority of the plant invaders in the Azores have a wide biogeographic distribution.

MATERIALS AND METHODS

A data-base of the Azorean vascular flora was compiled using FileMaker Pro 2 (Claris Corporation), and based on the checklist of Macaronesian vascular plants from HANSEN & SUNDING (1993). The data-base was complemented with information regarding the included taxa, namely, from the following sources: DROUËT (1866), TRELEASE (1897), PALHINHA (1966), SJÖGREN (1973b), Flora Europaea volumes 1-5 (TUTIN et al. 1964, 1968, 1972, 1976, 1980), FRANCO (1971, 1984), FRANCO & AFONSO (1994), PRESS & SHORT (1994), ANONYMOUS (1976).

Only the species stated to have been recorded as spontaneous (native or endemic - indigenous) or naturalised (introduced accidentally or intentionally by Man, but maintaining self-sustained populations) in the Azores have been included.

Searches of the data-base were carried out to ascertain how many taxa were assigned to the following categories: endemic, native, introduced, and of uncertain status. The latter category was used for taxa where it was not possible to decide if they were native or introduced. Although the reason for considering a species as introduced was largely based on records by previous authors, the following criteria, in different combinations, supported the decision to consider a species as introduced: i) first record during the last 100 years; ii) distribution limited to a reduced number of islands; iii) record of a recent extension (noted during the last 100 years) of the distribution in the Azores; iv) absence from other Macaronesian islands; v) disjunct distribution; vi) largely anthropochoric species - weeds, ornamental plants, medicinal plants. These criteria were applied after the exclusion of endemic species.

The percentage of invaders was calculated for the Pteridophyta, Gymnospermae, Monocotyledo-

nea and Dicotyledoneae. For each of these taxa, the biogeographic distribution of the invaders was analysed. The biogeographic regions of the world used in this work are those suggested by PIELOU (1992), namely: Antarctic, Australasian, Ethiopian, Nearctic, Neotropical, Oceanian, Oriental and Palearctic. Holarctic in this text refers to the Nearctic and Palearctic regions together. Species with a wide geographic distribution, present in more than two regions were considered as Subcosmopolitan.

Percentage of invasive taxa were calculated by island. These percentages were compared using a $\chi 2$ test (ZAR 1996), followed by a multiple comparison test. For the latter analysis, percentages were transformed in degrees using arcsine after a square root transformation.

Relationships were searched for between the number of endemic, native, indigenous and exotic taxa, and the area, maximum altitude, and human population of each Azorean island. For that purpose data were log transformed, and the statistical package SPSS for Macintosh 6.1.1. was used. Linear, logarithmic and quadratic regression models were calculated, but only those indicated as significant by ANOVA were considered.

RESULTS

For the 996 taxa considered, the percentage of plant invaders in the archipelago was found to be 72,6%. The group with the lowest percentage of invaders is the Pteridophyta, while the Dicotyledoneae present the highest proportion (Table 2). About 10% of the taxa are still of uncertain status.

For every Azorean island the percentage of introduced taxa is above 50%, with a lowest proportion of exotic taxa in the western group of islands (Corvo and Flores), and the highest proportion in São Miguel, Terceira and Faial (Table 3). A relatively high proportion of native species was thus found for the western group. Species of uncertain status accounted for between 10 and 15% of the taxa.

Significant differences were found between islands for the proportion of introduced taxa ($\chi 2 =$ 56,94; d.f.= 8; p<0,0001). Using a multiple

Table 1

Physical description of the Archipelago of the Azores.

Azorean islands	Area (km^2)	Maximum Altitude (m)	Age (MY)	Distance to mainland (km)	Human population	Density (inh./ km^2)
Santa Maria	97	587	8,120	1588	6500	66,8
São Miguel	757	1103	4,010	1584	131908	176,6
Terceira	402	1023	2,000	1764	53570	133,2
Graciosa	62	402	2,500	1844	5377	87,9
São Jorge	246	1053	0,550	1832	10361	42,2
Pico	433	2351	0,300	1860	15483	34,6
Faial	172	1043	0,730	1908	15489	89,5
Flores	142	915	2,900	2152	4352	30,7
Corvo	17	718	?	2148	370	21,6

(Adapted from BORGES 1997)

Table 2

Number and percentage of taxa from the Azorean vascular flora, divided into four categories: endemic, native, introduced, and of uncertain status.

Azorean Vascular Flora	DISTRIBUTION OF TAXA								Total
	Endemic		Native		Introduced		Uncertain		
	N	%	N	%	n	%	n	%	
Pteridophyta	9	11,7	40	51,9	20	26,0	8	10,4	77
Gymnospermae	1	20,0	1	20,0	3	60,0	0	0,0	5
Monocotyledonae	15	6,4	19	8,2	163	70,0	36	15,5	233
Dicotyledone	41	6,0	42	6,2	537	78,9	61	9,0	681
Total	66	6,6	102	10,2	723	72,6	105	10,5	996

Table 3

Distribution of the four categories of vascular plant taxa within the Azores.

Islands	VASCULAR PLANT TAXA									
	Total	Introduced		Native		Endemic		Uncertain		
		n	%	n	%	n	%	n	%	
Santa Maria	435	289	66,4	66	15,2	26	6,0	54	12,4	
São Miguel	730	503	68,9	91	12,5	50	6,8	86	11,8	
Terceira	634	427	67,4	89	14,0	48	7,6	70	11,0	
Graciosa	335	218	65,1	53	15,8	13	3,9	51	15,2	
São Jorge	464	276	59,5	77	16,6	49	10,6	62	13,4	
Pico	545	329	60,4	91	16,7	54	9,9	71	13,0	
Faial	599	403	67,3	87	14,5	47	7,8	62	10,4	
Flores	405	228	56,3	81	20,0	42	10,4	54	13,3	
Corvo	305	156	51,1	68	22,3	38	12,5	43	14,1	
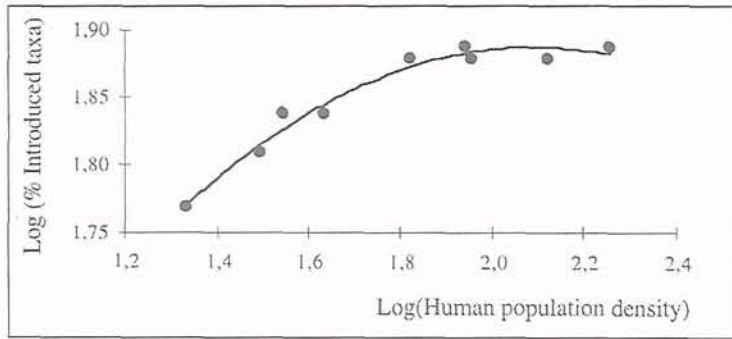
Fig.1. Relationship between human population density and percentage of introduced vascular plants in the Azorean islands. A quadratic model ($R^2=0,98$, F=69,2, and p=0,0001) with the following equation: $\log(\%$ Introduced taxa$) = -0,18 \log(\text{Density})^2 + 0,75 \log(\text{Density}) + 1,09$.
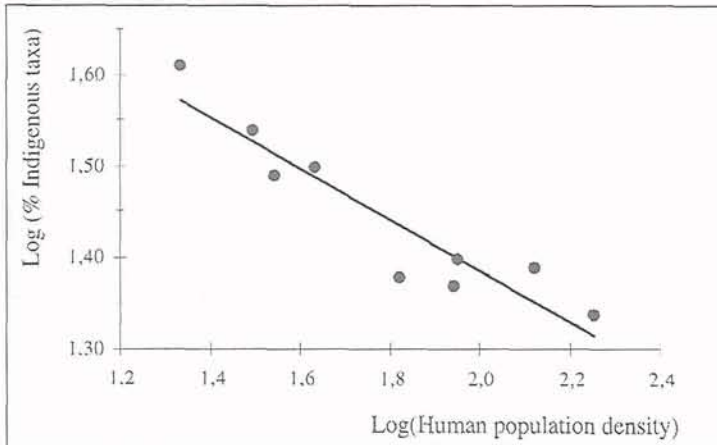
Fig. 2. Relationship between human population density and percentage of indigenous vascular plants in the Azorean islands. A linear model ($R^2=0,88$, F=51,6 and p=0,0002) with the following equation: $\log(\%$ Indigenous taxa$) = -0,28 \log(\text{Density}) + 1,94$.

comparison test significant differences were found between São Miguel and the islands of the western group (Table 4). No significant differences were found between Corvo, Flores, São Jorge and Pico, but all the remaining islands presented a proportion of invaders significantly different from that of Corvo.

A quadratic relationship was found between human population density and the percentage of introduced species (Fig. 1). A linear model was adjusted to the relationship between human population density and the percentage of indigenous species (Fig. 2).

A considerable proportion of the introduced plants found in the Azores was also present in

mainland Portugal and in other Macaronesian islands (Table 5). The Pteridophyta were an exception, with only a quarter of the introduced taxa found in mainland Portugal.

A large proportion of the introduced Pteridophyta have a Subcosmopolitan or a Palearctic distribution or are present in more than one biogeographic region (Fig. 3). The Gymnospermae has only three naturalised species: one taxa from America, one from the Mediterranean, and a third from Asia. The Monocotyledoneae also present a large proportion of Palearctic and Subcosmopolitan taxa (Fig. 4). The same was found for the Dicotyledoneae, although this group also presents a considerable

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Table 4

Percentage of introduced vascular plants in the Azores arquipelago. The percentages were re-calculated after excluding species of uncertain status. Comparison between islands (χ2 test,followed by a multiple comparison test).

Azorean Islands	Percentage of plant invaders	Comparison α=0,05		
Corvo	59,5	a		
Flores	65,0	a	b	
São Jorge	68,7	a	b	c
Pico	69,4	a	b	c
Faial	75,0		b	c
Terceira	75,7		b	c
Santa Maria	75,9		b	c
Graciosa	76,8		b	c
São Miguel	78,1			c

(Different letters = significant differences.)

proportion of introduced taxa occurring in two biogeographic regions, and some exclusively Macaronesian taxa (Fig. 5).

DISCUSSION

The percentage of invaders found in the Azores is higher than that found in other places of the world (REJMÁNEK et. al. 1991, MONTENEGRO et al. 1991, WELLS, 1991), even when compared with islands presenting a very much modified vegetation such as Hawaii and New Zealand, with 17,5-19% and 47% of introduced species, respectively (HEYWOOD 1989). Some authors suggest that isolated oceanic islands are predisposed to certain types of human-related invasions (LOOPE & MUELLER-DOMBOIS 1989), others (WILLIAMSON 1996) consider that this has yet to be proved. The Azores are considerably remote islands, and are relatively
young when compared with the other Macaronesian archipelagos. They have been intensively cultivated since the XV century. Many species have been introduced for food and fibre or as accompanying weeds, and also as ornamental and hedging plants. A large proportion of the landscape was directly changed by human activities, allowing the easy entrance of exotic species, and increasing the propagule pressure, the amount and frequency of introduction of dispersal units from an alien species.

The islands of the western group, together with São Jorge and Pico, are those presenting a lower proportion of invaders. We might thus suggest that they were under a relatively lower propagule pressure. A lower human population density allowed a lower input of alien species. São Miguel, Terceira and Faial are more heavily populated islands and also present the higher proportions of alien taxa. Furthermore, these islands have been considered as an important source of propagules from alien taxa for the other islands, during the last one hundred years (SJÖGREN 1973a). Graciosa and Santa Maria are small islands with a relatively low maximum altitude where the landscape was largely altered by human action. This might have lead to a relatively high input of alien taxa, what might explain the relatively high proportion of invaders recorded for these islands.

Differences between islands for the proportion of introduced taxa, might thus be associated with different levels of human pressure on the
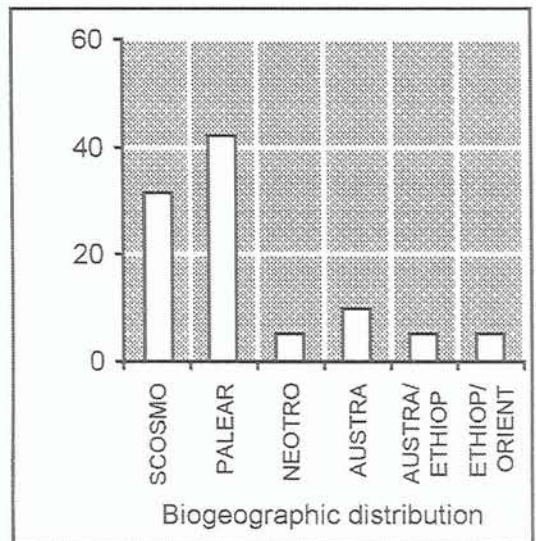
Fig. 3. Biogeographic distribution of Pteridophyta introduced to the Azores: total of 20 taxa.
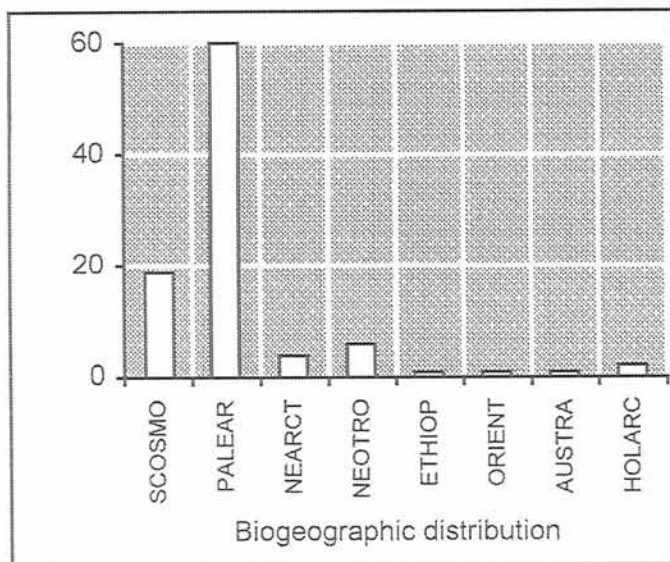
Fig. 4. Biogeographic distribution of Monocotyledoneae introduced to the Azores: total of 163 taxa.
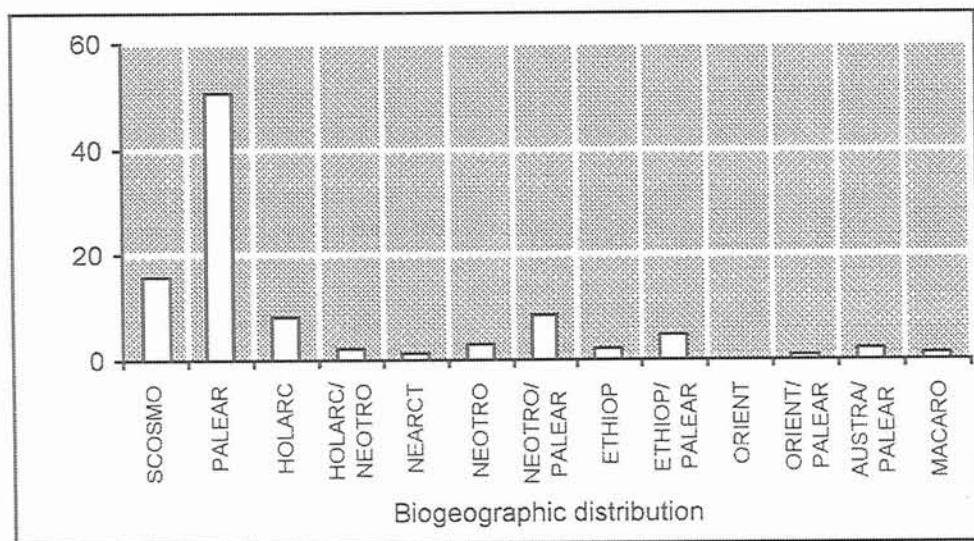
Fig. 5. Biogeographic distribution of Dicotyledoneae introduced to the Azores: total of 537 considered taxa.

environment, implying different levels of propagule pressure. The models derived from our analyses positively relating the human population density to the percentage of introduced species further support this hypothesis. WILLIAMSON (1996) reports studies where similar results were found when relating numbers of plant invaders and numbers of human visitors into nature reserves, higher numbers of visitors were associated with a higher proportion of invaders. Quarantine measures should be implemented to to avoid further introductions in the less affected islands.

A considerable proportion of Azorean plant invaders is also present in mainland Portugal or in other Macaronesian islands, what might suggest a

Table 5

Percentage of introduced taxa from the Azorean vascular flora which also occur in three regions outside Azores: mainland Portugal, Madeira island and the Macaronesia excluding the Azores. (n=number of introduced taxa)

INTRODUCED VASCULAR PLANTS	% OF TAXA			
	n	Portugal	Madeira	Macacaronesia
Pteridophyta	20	25,0	55,0	60,0
Gymnospermae	3	66,7	33,3	33,3
Monocotyledonae	163	70,6	63,2	71,2
Dicotiledonae	537	77,8	67,2	75,2

direct introduction of plants from the mainland, but also that many of those species are successful invaders elsewhere. Success as an invader in other ecosystems should be used in the future to reject a potential introduction, and also to stimulate the control of species that were already introduced but still with a limited distribution.

Many of the invaders have a Subcosmopolitan distribution, are present in two biogeographic regions or have a Palearctic distribution, i.e. always a wide distribution. This further emphasises the suggestion that success as an invader in other regions is a good indicator of the potential for similar success in the Azores. Thus, we might conclude that, as a general rule, the potentially most successful invaders in the Azores are those species with a wide biogeographic distribution which are already invaders elsewhere.

Some of the invaders present a very narrow biogeographic distribution, for example *Clethra arborea* Aiton (Clethraceae, endemic to Madeira but an invader in São Miguel), and do not followthe general scheme.

Also, some of the invaders are considered as weeds in agriculture, forestry and in nature reserves, for example *Rumex* spp. (Polygonaceae) and *Mentha suaveolens* Ehrh. (Lamiaceae) on pastureland, *Hedychium gardnerianum* Ker-Gawl (Zingiberaceae) in forestry and in nature reserves, and *Pittosporum undulatum* Vent. (Pittosporaceae) from sea level up to 600 m. Both groups deserve further study regarding their ecology and control.

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ORIGINS OF THE AZOREAN INTERTIDAL BIOTA: THE SIGNIFICANCE OF INTRODUCED SPECIES, SURVIVORS OF CHANCE EVENTS

BRIAN MORTON & JOSEPH C. BRITTON

The Azorean marine biota, with only a geologically brief opportunity for colonization, is decidedly modern. Evidence of endemism is sparse and readily apparent only with regard to the maritime vegetation. Probably no alga nor marine animal is endemic, although a few species of several phyla are currently recognized as having this status, notably representatives of the Rissoidae (Gastropoda). Rather, the majority of the Azorean marine biota seem to comprise species that have arrived, predominantly, from the Eastern Atlantic, especially the region between southern Europe and northern Africa, and the Mediterranean, but also contains taxa from other Atlantic sources. Regardless of their geographic origins, most elements of the coastal Azorean biota are chance survivors of recent chance immigrants delivered to these shores by currents, rafting or birds (phoresy), but some have received human assistance.

The majority of terrestrial plants, including many maritime species, most terrestrial mammals, reptiles, amphibians and freshwater fishes (except *Anguilla anguilla*) of the Azores were introduced by man. Feral cats and rats have adversely impacted coastally-nesting seabird populations. Unlike these well-documented introductions, there are some additional records of human-assisted marine ones and these are described and discussed. We conclude that the majority of such introductions were unintentional, either as sessile species attached to yacht hulls or as larvae in the ballast water of commercial vessels. They survive mainly in harbours and, apparently, have not, as yet, impacted the 'native' intertidal and shallow subtidal biota, either positively or negatively. The one exception to this is *Venerupis decussatus* which, following its introduction, has successfully colonized and come to dominate the lagoon at Fajã de Santo Cristo, São Jorge. Marine introduced species in the Azores are, thus, like the native biota, chance survivors of chance invasions and only in recently identified estuarine lagoon and marsh wetlands do they have the potential to adversely influence sensitive ecologies adversely.

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INTRODUCTION

Some 50 million years ago, the Mesozoic Marine Revolution placed the stamp of modernity upon global marine communities. The Azorean islands, however, are more youthful; less than one (Pico) and barely more than eight (Santa Maria) million years old (AZEVEDO et al. 1991; SERRALHEIRO & MADIERA 1993). The nine islands of the archipelago emerged at a triple junction along the mid-Atlantic Ridge at a time when continental Atlantic shorelines and the marine biota upon them resembled that which we see today. During the Azorean formative period, global events brought changes to the Atlantic Ocean. The closure of the Isthmus of Panama, beginning some four million years ago, markedly and permanently altered water circulation patterns in the Atlantic Basin (CRONIN & DOWSETT 1996). During the last two million years, moreover, a series of ice ages and interglacial warmings have alternately lowered and raised sea

levels and temperatures and produced changes in the positions and strengths of ocean currents. MORTON et al. (1998a) provide a comprehensive review of the geology of the archipelago and a discussion of currents which influence the region. The latter is explored more fully by SANTOS et al. (1995).

Although much is known about the origins of the Azorean terrestrial flora and fauna (MARTINS 1993), that of the shores and its coastal waters are less well understood. The marine algae emerge as an exception to this following the researches of HOEK (1984, 1987), PRUD'HOMME VAN REINE (1988), NETO (1994), TITTLEY & NETO (1995) and others. The origins of a few marine animal groups have also been investigated, notably sponges (BOURY-ESNAULT & LOPES 1985), hydroids (REES & WHITE 1966; CORNELIUS 1992), amphipods (LOPES et al. 1993), barnacles (SOUTHWARD 1998; YOUNG, 1998) and rissoid gastropods (GOFAS 1989, 1990), but there has been no comprehensive attempt to document systematically the origins of the some 2000 marine plant and animal species that have been recorded from the Azores. MORTON & BRITTON (2000) and BRITTON et al. (in press) are, however, addressing this deficiency.

Here, we focus on species which we conclude, often because of their 'patchy' distributions, probably have been introduced, either accidentally or deliberately, by man. We will argue that most of the marine introduced species, as currently perceived, seem to have had little or no impact on 'native' biota. Some, however, may have the potential in ecologically sensitive and rare habitats in the Azores, especially coastal wetlands, to influence adversely species occupying such habitats and, especially, attempts to conserve and preserve these otherwise unique Macaronesian wetlands.

ORIGINS OF THE AZOREAN MARINE BIOTA

A RELICT ATLANTIC COMMUNITY?

The Azores Archipelago is amongst the youngest island groups added to the central Atlantic basin. As this ocean was approaching its present configuration about eight million years ago, the first Azorean soil was being produced by volcanism and subsequent weathering near the mid-Atlantic Ridge. Most of the modern Azorean islands are no more than five million years old, some much younger. Stated another way, 95% of the present Atlantic basin had formed before the first Azorean island appeared.

Some have speculated that the Azorean marine flora and fauna had its origin as a relict community that can trace its ancestry to the narrow, primordial, Atlantic Ocean. According to this view, as the ocean basin enlarged, eastern and western littoral cognate populations persisted for more than 65 million years. In support of this, the barnacles *Tesseropora arnoldi*, endemic to the Azores (YOUNG 1998), and *T. atlanticum* endemic to Bermuda (NEWMAN & ROSS 1977), are considered Tethyan relict species, although SOUTHWARD (1998) provides compelling evidence that the former is a junior synonym of the latter. Sibling species are said to exist on the two sides of the North Atlantic, CALS (1983) giving the examples of two crustacean genera, i.e., *Derocheilocaris* and *Carcinus* represented by the American *D. typicus* and the Euro-African *D. remanei* and the Atlantic *C. maenas* and the Mediterranean *C. aesturii* (=*C. mediterraneus*). Whether these are the products of divergence brought about by sea floor spreading or more recent transportation events remains to be determined. Some species of the Azorean flora and fauna have similarly thriving populations on both sides of the Atlantic (MORTON & 2000). The sacoglossan nudibranch *Aplysiopsis formosa* is amphiatlantic (JENSEN 1995) as is the common intertidal muricid predator *Stramonita haemastoma* which has a teleplanic larva, facilitating such a pattern of wide dispersal (LAURSEN 1981). There are also some eight species of hydroids (CORNELIUS 1992), bryozoans and phoronids (HAYWARD & RYLAND 1990) which are amphiatlantic.

Leaving aside the question of relict, sibling and amphiatlantic species, however, it is known that some taxa have occupied either Eastern or Western Atlantic shores for no more than two or three centuries, introduced from one side to the other and, often, mediated by human intervention. Eastern Atlantic littorines, i.e., *Littorina littorea, L. saxatilis* and *L. obtusata*, now also typical of New England,

U.S.A., rocky shores, are good examples of such post-glacial rafting and human-mediated introductions (REID 1996). Furthermore, the current circulation of the Northern Atlantic was much different about three million years ago, prior to closure of the Isthmus of Panama (CRONIN & DOWSETT 1996). In the absence of the powerful Gulf Stream, there would be little opportunity for species from the Western Atlantic to reach eastern shores. Even if a few species in the Azores do represent an ancient relict Atlantic community, in reality, the youthfulness of the islands, in comparison to the overall age of the basin, effectively meant that these emergent shores were isolated from all population centres from which a littoral biota could be recruited, arguing overwhelmingly for an overall, very modern, pattern of gradual colonization with time.

ENDEMIC SPECIES

The Azorean coastal water and shore biota comprises a modest diversity of fauna and flora (MORTON et al. 1998a). Only a few of the coastal species are, however, restricted to the Azores. Most endemic species are numbered among the coastal flowering plants, including the Azorean bellflower *Azorina vidalii*, the Azorean spurge *Euphorbia azorica*, the small Azorean spurry *Spergularia azorica* and the Azorean heather *Erica scoparia azorica*. SJÖGREN (1993), in an examination of the bryophytes of Corvo, recognized 134 species, of which only four were endemic to the Azores. Of the 95 bryophytes recorded from São Jorge by SMOOKLER (1967), only three, *Campylopus introflexus*, *Trichostomum brachydontium* and *Trichostomum crispulum*, were collected from the supralittoral of rocky shores and, thus, as elsewhere, this phylum is here poorly adapted to the marine environment and endemism is low.

About 300 species of marine algae have been recorded from the Azores (SOUTH & TITTLEY 1986; NETO 1994; TITTLEY & NETO 1995). Only seven were identified as endemic by SCHMIDT (1931), whereas PRUD'HOMME VAN REINE (1988) recognized ten such species, a figure also identified by TITTLEY & NETO (1995), although these latter

authors also state (p. 752) that the Azores "probably support no endemic species; those suggested as being endemic are mostly members of taxonomically difficult groups and require reassessment".

Endemism among Azorean fishes has always been considered very low (BRIGGS 1974; WHITEHEAD et al. 1989; PATZNER et al. 1992). Only one of the 116 species of nearshore fishes of the Azores is regarded as endemic, a previously unrecognized species of *Centrolabrus*, i.e., *C. caeruleus* only recently being described (AZEVEDO 1999). PATZNER et al. (1992) reported the Scorpion fish, *Scorpaena azorica*, as endemic but recently it has been found in the Mediterranean (GOLANI 1996). Several deep water fishes are known, so far, only from the vicinity of the islands. Similarly for the aquatic birds, only the Azorean moorhen, *Gallinula chloropus correiana*, is considered to be an endemic subspecies and to be "somewhat intermediate between the European and the African form(s)" (BANNERMAN & BANNERMAN 1966; p.105).

The number of endemic intertidal and shallow subtidal marine invertebrate animals is equally small. BOURNY-ESNAULT & LOPES (1985) identify two species of sponges, i.e., *Hymendismia mertoni* and *Chalinula nigra*, as being only recorded from the Azores. GOSLINER (1990) described *Hypseldoris midatlantica* as an endemic Azorean nudibranch from São Miguel, but ORTEA et al. (1996) considered it a junior synonym of *H. bicolor*. Several rissoid gastropods have been considered endemic. GOFAS (1989) described two new species, *Alvania mediolittoralis* from São Miguel and Faial and *A. formicarum* from the Formigas Islands and Santa Maria, implying, but never explicitly stating, that they were endemic. He compared them with each other and Madeiran and Canary Island species, finding subtle morphometric differences distinguishing each one. GOFAS (1990) and KNUDSEN (1995) recognized *Alvania poucheti* and *A. sleursi* as Azorean endemics, with Gofas also stating that they were "distantly related to a recognizable European and or Macaronesian species" (p. 125). KNUDSEN (1995) added *Rissoa guernei*, *Manzonia unifasciata* and *Alvania angioyi* to the list of Azorean endemics but GOFAS (1990)

considered them and *Alvania mediolittoralis, A. Crisilla postrema* and *Setia subvaricosa* to be "very closely related to a recognisable European and/or Macaronesian species" (p. 125). Three other species, *Alvania cancellata, Cingula cingulus* and the related anabathrid *Pisinna punctulum*, were deemed by GOFAS (1990) to be conspecific with species occurring on European shores. Gofas also compared one other species, *Botryphallus ovummuscae*, with two closely related Canary Island species. Azorean rissoids clearly have a strong affinity with mainland Eastern Atlantic and/or Macaronesian island species. It is possible that some have speciated into endemics after rafting to the Azores on floating mats of algae, their natural habitat, although most have maintained a clear resemblance to, if not conspecificity with, the rissoids from elsewhere in the Eastern Atlantic. MARTINS (1995) recognized the rocky shore ellobiid *Ovatella vulcani* as an endemic species as did BULLOCK (1995) with respect to the chiton *Lepidochitona simrothi*, a resident among coralline algal turf.

A few other possibly endemic species could be cited, such as the ophiuroid echinoderm, *Amphiura sarsi* (PEREIRA 1997) but, clearly, with the exception of the well-recognised native coastal plants, the overwhelming preponderance of the Azorean intertidal and nearshore biota is not unique, but is common to and, thus, arrived here from other locations. MORTON & BRITTON (2000) analyse the, apparently, endemic-rich Azorean barnacles but point out that of the 13 species currently recognised as having that status, ten are deep-water species and may well also exist, for example, on other unexplored, Atlantic, seamounts.

Low marine endemism on oceanic islands suggests that initial colonisations are accomplished by teleplanic larvae (SCHELTEMA 1995), but species possessing such larvae are few in the Azores and other possible means of colonisation must be examined. With so many non-endemics constituting the majority of local species and, thereby, derived from other shores, it is reasonable to ask three questions: (1), what are the sources of the Azorean coastal biota; (2), which regions have contributed the most and least to this flora and fauna and, perhaps, most important (3), how did they get here?

MECHANISMS OF DISPERSAL AND INTRODUCTION

Broadly speaking, the present marine flora and fauna colonized Azorean shores either by: (1), natural dispersal or (2), human-assisted transport. In the first instance, a species could be transported as adults either by swimming, for example fishes, or by clinging to floating natural objects, such as driftwood, or to migrating birds and insects. Ocean currents also transport species to such remote shores as juvenile dispersive stages (animal larvae and algal propagules). In the second instance, that is, of human-assisted dispersal, colonisation could be either accidental or deliberate. Except with regard to deliberate introductions, however, and bearing in mind the vast distance of ocean to be crossed, it is clear that accidental introductions and successful colonisations must be, like natural processes, chance events.

NATURAL DISPERSAL

DISPERSAL BY PHORESY

Seabirds are capable of providing their own transportation and have probably delivered a few species to the Azores (Table 1) by phoresy, such as the Widgeon grass *Ruppia maritima* to Fajã dos Cubres (MORTON et al. 1995) and the pseudoscorpion, *Neobisium maritimum*, to Lajes do Pico (MORTON et al. 1996). RIDLEY (1930) suggested that the seeds of the seagrass *Zostera marina* can pass through the intestine of the Mallard (*Anas platyrhynchos*) and retain their viability. That this is also possible for *Ruppia maritima* is evidenced by its recent discovery in the isolated, but a decade old, quarry at Cabo do Praia, Praia da Vitória, Terceira (MORTON et al. 1997) - it can, naturally, only have been delivered there as viable drupelets in the faeces of wading birds, probably from the only other known site for this species in the Azores at Fajã dos Cubres, São Jorge, a short flight away. The quarry has also been colonised by the amphipod *Orchestia mediterranea* and by three species of assimineid gastropods, i.e., *Assiminea*

Table 1

A list of species for which there is possible evidence of migratory bird phoresy to and within the Azores.

Species	Localities	Reference
Ruppia maritima	Fajã dos Cubres, São Miguel Cabo do Praia, Terceira	MORTON et al. 1995 MORTON et al. 1997
Littorina saxtilis	São Miguel	REID 1996
Assiminea eliae	Cabo do Praia, Terceira	MORTON et al. 1997
Assiminea cf. *grayana*	Cabo do Praia, Terceira	MORTON et al. 1997
Paludinella littorina	Cabo do Praia, Terceira	MORTON et al. 1997
Orchestia mediterranea	Cabo do Praia, Terceira	MORTON et al. 1997
Neobisium maritimum	Lajes do Pico	MORTON et al. 1996

eliae, Paludinella littorina and *Assiminea* cf. *grayana*, all of which are European wetland species, but which must have been introduced very recently into the quarry, possibly by birds from elsewhere in the Azores. REID (1996) implicates seabird phoresy in the long-range dispersal of the European littorine *Littorina saxatilis*, for example, into South Africa, and the discovery of this species as isolated populations on São Miguel (MORTON et al. 1998) may also represent an introduction by this method.

RAFTING

The position of the Azores near the centre of the North Atlantic basin ensures that any mechanism of natural transport from other population centres, for example, the continental shores of either Portugal, Africa or North America or the less distant Macaronesian islands of Madeira, the Salvages and the Canaries, even if direct, will be long and arduous. Furthermore, shore organisms, at least as adults, are well-adapted for survival on coastal environments but not in the open sea. If attached opportunistically to floating substrata, however, directly-developing and brooding species, in particular, can be transported to remote areas of the world (INGOLFSSON 1995) and be assured, albeit by chance, of sufficient numbers of individuals to perpetuate the genetic diversity of the species on the newly-colonised shores.

Intertidal littorines, limpets, echinoids, isopods, amphipods, tanaids, decapods and bivalves, though not attached permanently to the shore, are usually also not equipped to survive in the open sea, but are capable of dispersal by rafting (HIGHSMITH 1985; MARTEL & CHIA 1991). All of the endemic or possibly endemic rissoids identified by GOFAS (1989; 1990) and KNUDSEN (1995) have direct development as do six other Azorean prosobranch species, i.e., *Cingula cingillus*, *C. pulcherrina*, *Omalogyra atomus*, *Ammonicera rota*, *Skeneopsis planorbis* and *Nassarius corniculus*, and all of which occur in Western Europe and/or the Mediterranean and at one or more of the Macaronesian islands, strengthening the contention that, if naturally dispersed, they reached the Azores by rafting. Also, a number of benthic species, especially molluscs, which normally live in shallow waters, have been recovered, at least as shells, from deep sea locations around the Azores, far removed from their expected distributions. DAUTZENBERG (1889) indicates many such records, including the trochid *Calliostoma exasperatus* and the triphorid *Monophorus perversus* (both from Challenger Station 112 off Pico at 1287 m),and the muricid *Ocinebra aciculata* off Faial at 914 m. Each of these may have fallen to the bottom after losing

purchase on a floating object which had carried them to sea. Alternately, they may have already colonised shallow, mid-Atlantic island shores. In this case, a few empty shells may have tumbled down the narrow, steep fringing shelves, to come to rest on the surrounding deep ocean floor. Whether sessile or errant, therefore, all coastal organisms use some means of transport to maximize and sustain their biogeographic boundaries and to colonize new lands, such as the Azores. Species of algae, hydroids, bryozoans and barnacles can ride on floating objects such as driftwood, sea turtles and algae (HOEK 1987; CORNELIUS 1992). The same is true of bivalves and HELMUTH et al. (1994) have shown that the brooding bivalve *Gaimardia trapesina* can be transported between 1300-2000 km on kelp in the South Atlantic. It is possible, even probable, although mostly undocumented, that some components of the Azorean marine biota have arrived by rafting on algae. There is, however, one striking instance spanning two centuries of research which demonstrates that rafting to the Azores is possible (SANTOS et al. 1997). CUVIER & VALENCIENNES (1836) described a blenny, *Blennius fucorum*, based on a single specimen taken from floating *Sargassum* 80 miles south of the Azores. BATH (1994) re-examined it, concluding that it was *Hypleurochilus fissicornis*, a southwestern Atlantic species normally distributed along the coasts of Brazil and Uruguay. O'FOIGHIL (1989) showed that pelagic larvae are not necessary for long range dispersal of the bivalve *Lasaea* and that species with crawl-away juveniles range more widely than those with planktotrophic larvae. In the Azores, the widely distributed *Lasaea adansoni* has crawl-away juveniles, arguing, therefore, for its initial arrival by rafting.

Perhaps the best case for rafting across long oceanic distances comes from the Hydrozoa. The unique hydroid life cycle of planula, sessile hydroid and medusa is, superficially, inappropriate for long-range dispersal, because the planula is lecithotrophic and the time spent in the plankton but a few hours or days and the medusa is similarly short-lived and, in any case, remains attached to the hydroid in over 50% of known species. The sessile hydroid is, however, particularly amenable to rafting, releasing either planulae or medusae as it

travels and when it washes ashore. Eight Azorean hydroids are virtually cosmopolitan in coastal waters within their normal latitudinal ranges. Of these four are known only from Horta Harbour, Faial, and have probably been introduced there attached to the hulls of vessels while the remaining 60 or so species have wide ranges, some amphiatlantic (CORNELIUS 1992).

LARVAL AND/OR ADULT RECRUITMENT

Species capable of rafting across the sea may also have life history stages adapted primarily for dispersal as temporary members of the meroplankton (JOKIEL 1990). Planktonic algal disseminules, either a spore or propagule, are capable of floating and surviving for days, even weeks, before they must settle to develop into the intertidal, attached, life-stage. Among marine invertebrates, the dispersive agent is usually a free-swimming larva. Such larvae, like the algal propagule, also spend a period of time floating in the sea as a member of the meroplankton before settling and metamorphosing into the adult. Larvae can be categorised into several different types, according to the amount of time they can remain in the plankton. Those capable of surviving several months in the plankton are said to be teleplanic whereas species whose larvae must settle within four to six weeks are actaeplanic. KNUDSEN (1995) showed that eight gastropod species occurring in the Azores, i.e., *Tricolia pullus*, *Alvania cancellata*, *Mitra nigra* (with actaeplanic larvae), and *Alvania crassa*, *Fossarus ambiguus*, *Cypraea lurida*, *Thais* (=*Stramonita*) *haemastoma* and *Columbella adansoni* (with teleplanic larvae) have pelagic development and broad distributions. Of these species, only *S. haemastoma* is amphiatlantic, whereas the others have broad Eastern Atlantic distributions.

Algal spores and propagules are usually more tolerant of long-duration dispersal than many animal larvae (HOEK 1987; PRUD'HOMME VAN REINE 1988), although, save for the supposed single endemic, the 41 species of shallow-water echinoderms recorded from the Azores (PEREIRA 1997) must have been recruited from far-distant

Eastern Atlantic shores because they all have planktotrophic larvae.

Larval mortality is extremely high for most planktotrophic species (NYBAKKEN 1997). Some of this loss is due to predation, even competition, within the planktonic community, but much of it occurs because such meroplankton are moved far from land by ocean currents. Only a few will reach a distant shore where they can settle, survive and reproduce again. In most cases, it is the currents that will deliver the shore colonizers, whether they be spores, propagules, larvae or floating algal mats and flotsam and jetsam bearing rafting species and it is probable that the majority of the Azorean marine biota arrived in such ways. It is, however, impossible to be certain of the number of species which have arrived in the Azores by passive larval dispersal with ocean currents. Possibly most, over time and assisted by island hopping *via* the Canaries and Madeira but, regardless of the details of their arrival, the modern constituents of the biota must represent successful chance colonists of equally chance events.

Perhaps the best known members of the Azorean marine fauna are the fishes. The fish literature is voluminous, beginning with DROUËT (1861) and continuing for a century and a half to the recent lists by ARRUDA (1997) and SANTOS et al. (1997). One might assume that fishes are capable of self-propelled delivery to the remote Azores but, in fact, few of them seem capable of making such a journey. The Atlantic seems too vast for most of the common, smaller, shallow subtidal, species to cross. For example, of the 74 species of Eastern Atlantic Gobiidae, a family mostly comprising littoral and shallow sublittoral fishes, only three, i.e., *Gobius paganellus*, *Pomatoschistus pictus* and *Thorogobius ephippiatus*, are known from the Azores (SANTOS et al. 1997). The littoral and shallow sublittoral Azorean marine ichthyofauna consists of about 116 species, or 9.8% of the Eastern Atlantic ichthyofauna as defined by WHITEHEAD et al. (1989) or 25% of the Azorean ichthyofauna listed by SANTOS et al. (1997). Only one is presently being described as endemic (AZEVEDO 1999). The majority of the 460 species of Azorean fishes listed by SANTOS et al. (1997) are either offshore pelagic (56 %) or deep sea demersal

(20 %) species. The Azorean fishes, whether including all or only shallow coastal species, have strong affinities with the central Eastern Atlantic ichthyofauna, especially that of Southern Europe, the Mediterranean, continental North Africa and the Macaronesian islands (Fig. 1). Only a few species are capable of rafting, so that most of the Azorean ichthyofauna probably colonised the archipelago by larval dispersal (SANTOS et al. 1997), also probably from these Eastern Atlantic sources. On the other hand, many of the Azorean fishes are widely distributed, either within the Altantic Ocean or throughout the world. At least one-third of them are considered cosmopolitan species (WHITEHEAD et al. 1989).

HUMAN-ASSISTED COLONISATIONS

The global transport of marine organisms has been taking place for centuries. The bivalves *Mercenaria mercenaria* and *Mya arenaria*, for example, were introduced into Europe from the United States (PETERSEN et al. 1992), probably as fresh food during transatlantic voyages. *Littorina littorea* was, conversely, introduced in to North America from Europe probably with rock ballast (CARLTON 1992). The ellobiid *Myosotella myosotis* was introduced in North America and and elsewhere in the world living on ships, in either ballast or on deck equipment and another species, *Tralia ovula*, was probably transported from the Caribbean to Principe Island, Gulf of Guinea, on ships engaged in the slave trade (MARTINS 1996). Situated on the trade route between Europe and the America's, humans have brought several species of coastal plants to the Azores, such as the Agave, *Agave americana*, the Aloe, *Aloe arborescens* and, most noticeably, the Cane *Arundo donax*. The clam, *Venerupis decussatus* (MORTON 1967; MORTON & TRISTÃO DA CUNHA 1993), probably was introduced deliberately into the lagoon at Fajã de Santo Cristo, São Jorge, from Europe. There are less obvious, more subtle, means by which humans, frequently unknowingly, have contributed to the marine flora and fauna of the Azores. Such marine interlopers, however, represent only a small percentage of the total number of species present in
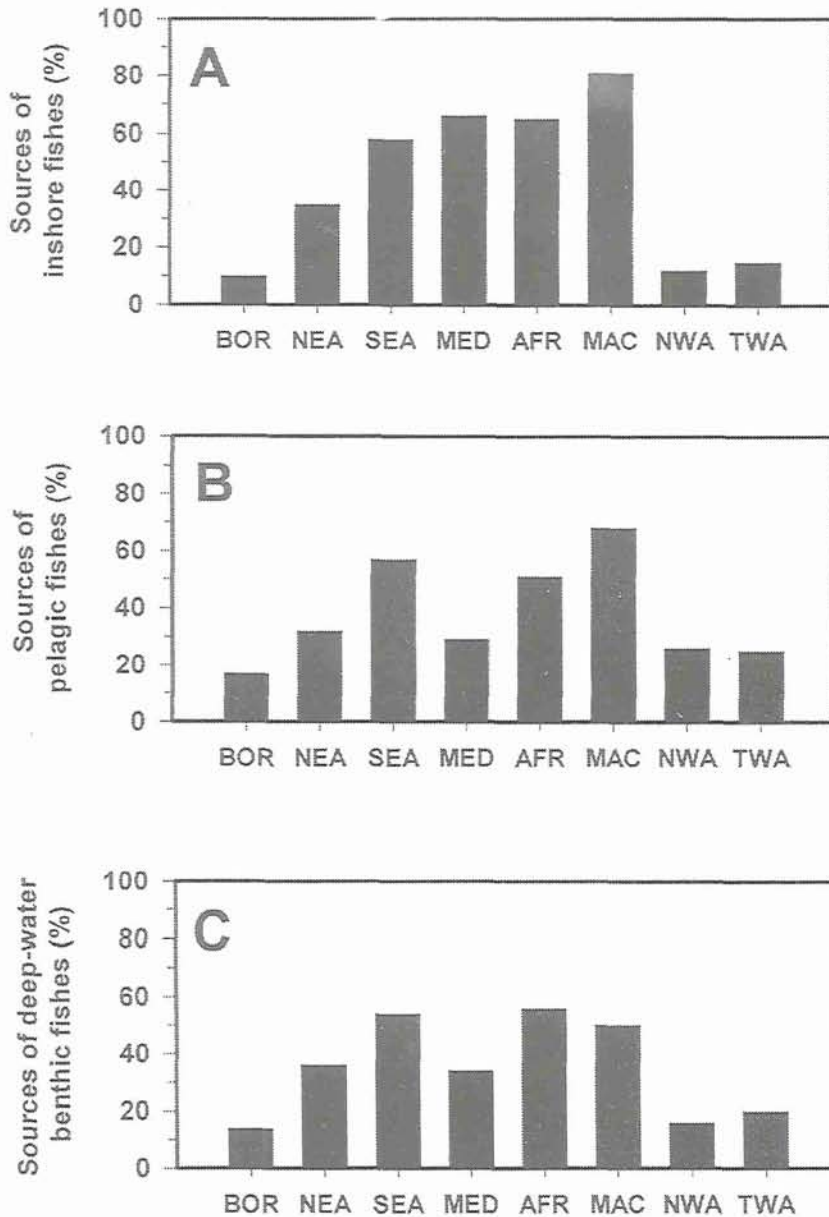
Fig.1. The fishes of the Azores and their biogeographic relationships. A, inshore fishes; B, pelagic fishes; C, deep-water fishes. The codes are: BOR, Boreal, including Greenland, Iceland and northern Scandinavia; NEA, Northeast Atlantic from southern Scandinavia and the North Sea to France, including the British Isles; SEA, Northeastern Atlantic from northern Spain to Gibraltar, including continental Portugal; MED, Mediterranean; AFR, Northwest Africa, including Morocco, Senegal and the Cape Verde Islands; MAC, Macaronesian Islands, especially the Canary Islands and Madeira; NWA, the temperate Northwestern Atlantic; TWA, the tropical and subtropical Western Atlantic, including the Caribbean basin and the Gulf of Mexico. Cumulative bars frequently exceed 100% because many species occur in two or more geographic areas. Compiled primarily from data in WHITEHEAD et al. (1989) and SANTOS et al. (1997).

the Azores and the possible routes and mechanisms by which they have arrived, and their ecological effects, if any, will be discussed in more detail later.

THE AZOREAN MARINE FLORA

There is little conclusive evidence, either historical or ecological, that the majority of Azorean marine algae arrived with human assistance but recent provocative studies raise the possibility for some species. Using DNA biochemistry analysis, KOOISTRA et al. (1992a) rejected oceanic current transport as the primary dispersal mechanism for widely separated populations of the alga *Cladophoropsis membranacea*. DNA analysis of individuals from the Caribbean, Mauritania, the Canary Islands and the Red Sea, however, supported jump dispersal rather than trans-oceanic vicariance, especially between Caribbean and Red Sea populations, implying that relatively recent human-assisted transport might be more important to algal dispersal than once supposed. In a second, more detailed, biochemical analysis of Atlantic populations of *Cladophoropsis membranacea*, however, KOOISTRA et al. (1992b) showed support for the hypothesis that long-range dispersion has occurred between the Caribbean and the tropical Eastern Atlantic. Nevertheless, human agents of transport, including shipping, aquaculture and the aquarium trade, account for a surprising number of algal species now counted among the Mediterranean marine flora (VERLAQUE 1994).

Sargassum muticum, native to Japan, appeared along the shore near Portsmouth, England, in 1973, apparently transported there among Japanese oysters which were being introduced to the region for aquaculture (FARNHAM 1980). Within eleven years it had spread from this point of introduction to the Netherlands and Norway (CRITCHLEY et al. 1983; RUENESS 1985), demonstrating an alternative and highly effective dispersal mechanism available to some algae, namely that of floating vegetative branches. The species of algae capable of drift dispersal as a result of their own buoyancy are relatively limited, but several occurring in the Azores, including *Ascophyllum nodosum*, species of *Cystoseira*, *Fucus vesiculosus* and *Fucus spiralis*

(the most commonly reported algal species in the Azores) have this capability (HOEK 1987). Considerably more species of algae, such as *Ulva rigida*, are capable of attaching to and drifting with other floating objects such as wood, cork and plastic. Floating algae can also carry other epiphytic species with them, including *Cladophora laetevirens*, *Herposiphonia* sp. and *Colpomenia sinuosa*, the latter with its capacious bladders also capable of floating without assistance (HOEK 1987). Although we cannot dismiss these mechanisms of dispersal, most components of the Azorean marine flora probably arrived on these shores as propagules delivered from remote sources by currents.

With reference to other Macaronesian islands (Madeira, the Salvages and the Canaries), algal diversity in the Azores is low, most of the representatives of the island's marine flora also being present on these islands, the cooler 'Eurafrican' continental coasts or on the shores of the Western Mediterranean (PRUD'HOMME VAN REINE 1988). Many species are present at all of these localities but the number of continental-shore species is lower in the Azores than in the other Macaronesian islands. There are also significant temperate and tropical North American elements represented in the Azorean marine flora, all of which are also common on 'Eurafrican' shores. Similarly, about 45% of the marine flora of the Canary Islands, southeast of the Azores, consists of species also present in the tropical Western Atlantic (HOEK 1987). TITTLEY & NETO (1995) point out that the Azores supports a much richer algal flora than should be expected on isolated, mid-oceanic, islands. They estimate that 24% of the North Atlantic algal flora occurs on the Azores, including mixtures of northern and southern elements together with those that show transatlantic (Mediterranean-Caribbean) links. TITTLEY et al. (1990) considered the Azorean marine algae to be affiliated with the Virginian marine flora of North America, a warm-temperate assemblage. These reports support active, vicariant, transatlantic algal dispersal. Papers by HOEK (1984) and PRUD'HOMME VAN REINE & HOEK (1988) also supported the concept of the Azorean flora possessing a strong warm-temperate component, whereas HOEK (1987) reported the flora most related to the Azores is that of southwestern

Europe and northwestern Africa. The most recent compilation of Azorean marine algae is that of NETO (1994), in which a total of 307 species is identified, of which 48 are Chlorophyta, 66 are Phaeophyta and 193 are Rhodophyta.

PRUD'HOMME VAN REINE (1988) attributed the low endemism of Azorean algae and the relatively high frequency of warm temperate and tropical Western Atlantic species to two disturbance factors -- recent, localized, extinctions and even more recent colonization *via* prevailing Atlantic currents, both facilitated by Recent surface water temperature changes. According to this view, during the last glaciation and previous Pleistocene and Pliocene episodes of global cooling, sea levels fell and surface water temperatures around the Azores were lower than at present, as evidenced in part by the presence of drifting sea ice (GROUSSET 1985), perhaps either keeping away or killing off subtropical algae. With restored warming, cool-adapted species which had colonized during the cold period were themselves displaced by either more tropical or subtropical species. To these, one might also add the closure of the Isthmus of Panama, an event that, although not considered by Prud'homme van Reine, would profoundly alter water circulation patterns in the Atlantic (CRONIN & DOWSETT 1996) and likely impact the Azores during their early colonisation. On a large scale, therefore, Azorean shores may have experienced recurrent climatic disturbances which have further served to maintain species instability and turnover among the marine algal flora. Without a prolonged period of isolation and stability for endemism to become manifest, the Azorean marine flora, it was argued, was and remains dominated by opportunistic vagrants -- "chance survivors of chance invasions by long range dispersal" (PRUD'HOMME VAN REINE 1988).

Not all algologists subscribe to the climatic disturbance hypothesis to account for the present composition of Azorean marine algae, nor even long-range dispersion by ocean currents. HOEK (1987) maintains that surface water temperature changes during Pleistocene glaciations were insufficient to rid Azorean shores of warm-temperate algal species. "The large majority, if not all, of the species now living on the Azores could

probably have survived the lowered Pleistocene temperatures." If this is true, then the low algal endemism of the Azores may be more a function of the relatively recent origins of these islands.

FRALICK & HEHRE (1990) reported upon 31 species of green algae from the Azores but indicated that two of these, cited by previous authors, probably do not occur there. Of the remaining 29 species, one, *Codium elisabethae*, is endemic (3%), 27 (93%) also occur at other Eastern Atlantic localities, 12 (41%) also occur in the temperate Western Atlantic, 18 (62%) also occur in the tropical Western Atlantic, 10 (34%) also occur in the Pacific Ocean, but only six (21%) are primarily Eastern Atlantic species. The striking feature of most Azorean chlorophytes is, therefore, how widely distributed most species are, supporting Prud'homme van Reine's concept of opportunistic vicariance.

The Azorean marine flora consists of a relatively few common algae and a large number of relatively rare species (MORTON et al. 1998a), a situation that might be expected on a remote oceanic island which receives "chance survivors of chance invasions by long range dispersal" (PRUD'HOMME VAN REINE 1988). The Azorean marine flora probably reflects the complex and locally unpredictable oceanic circulation in the vicinity of the islands and has probably also benefited both from long range dispersal by drift algae, such as *Fucus spiralis, Ascophyllum nodosum* and species of *Cystoseira,* and the occasional species introduced to the archipelago by human transport. In the latter context, NETO (1997) cited *Codium fragile* and perhaps also *C. vermilara* (Chlorophyta) as examples of algae recorded recently from the Azores which have been easily and inadvertently transported widely by several human-assisted means, including attached to ships, commercial fishery products, shellfishes or even fishing nets. *C. fragile*, with probable origins in the northwestern Pacific, has a long history of introductions throughout the world (CARLTON & SCANLON 1985). ATHANASIADIS & TITTLEY (1994) similarly suggested that three small species of Antithamniae (Rhodophyta), i.e., *Scageliopsis patens, Antithamnion diminuatum* and *A. pectinatum* were recent introductions, known in the

Table 2

A list of algae which probably have been introduced into the Azores, either unintentionally or intentionally, by human transport with a possible mechanism of transport indicated.

Species	Possible mechanism of introduction	Reference
Chlorophyta		
Codium fragile *Codium vermilara*	Unintentional, attached to boats or other transportable materials (see text)	NETO 1997
Phaeophyta		
Endarachne binghamiae *Sphaerotrichia divaricata*	Unintentional, attached to boats	TITTLEY & NETO 1994; 1995 NETO 1997
Rhodophyta		
Antithamnion diminuatum *Antithamnion pectinatum* *Scageliopsis patens* *Bonnemaisonia hamifera* (tetrasporophyte stage) *Symphyocladia marchantioides*	Unintentional, attached to boats	ANTHANASIADIS & TITTLEY 1994 TITTLEY & NETO 1994; 1995 ARDRÉ et al. 1974

Azores only from Faial but previously reported from Western Australia, Southern Australia and New Zealand, respectively. *A. pectinatum*, originally a Pacific species, was recorded from the eastern coast of North America in 1985 and the Mediterranean coast of France in 1989, prior to its discovery at Faial (TITTLEY & NETO 1995). ARDRÉ et al. (1974) identified the small *Symphyocladia marchantioides* (Rhodophyta) as a possible alien introduction and NETO (1997) speculated that the recent report of *Sphaerotrichia divaricata* (Phaeophyta) in the Azores may have been the result of a recent introduction. Another, small, Eastern Pacific alga, *Endarachne binghamiae* (Phaeophyta) reached the Azores after appearances in the Western Pacific, Indian Ocean, Brazil and St. Helena (TITTLEY & NETO 1994; 1995). Another recent discovery from Faial is the tetrasporophyte stage of *Bonnemaisonia hamifera* (Rhodophyta), a Japanese species previously widespread elsewhere in the North Atlantic (TITTLEY & NETO 1994; 1995). Table 2 identifies those algae thought to be recently introduced into the Azores and their possible means of introduction. Since most have been reported only from Faial, an important stopover port for international boat traffic, the most parsimonious explanation for their introductions is by unintentional human transport attached to the hulls of yachts, sailing ships and other watercraft, or in ballast water.

Numerous species of North American algae have reached Azorean shores, but whether they were derived from native populations, either directly or indirectly from secondary Eurafrican populations, is not known, nor whether they arrived naturally or with human assistance. The same can be said for the few tropical algae which occur on the islands, but these were probably derived from the other Macaronesian islands. The preponderance of marine algae in the Azores are warm-temperate species with the strongest connections to the flora of Western Europe and the Mediterranean (TITTLEY & NETO 1995). Many of these species could have been introduced with human assistance, but even so, their routes and origins are lost in time.

THE AZOREAN MARINE FAUNA

There is considerably more evidence of human-assisted transport for the marine fauna of the Azores, than the algal flora (Table 3). Although there is no historical record of the introduction, it seems plausible that the edible clam *Venerupis decussatus* was introduced purposely into the lagoon at Fajã de Santo Cristo, São Jorge (MORTON

1967) from Europe. Other examples of human-assisted transport are mostly inadvertent. Many sessile species, including barnacles, such as *Balanus trigonus* and *Balanus eburneus*, spirorbid polychaetes, such as *Spirorbis marioni,* and ascidians, such as *Clavelina lepadiformis, Distaplia corolla* and *Botryllus schlosseri*, can either attach to the hulls of boats and ships or survive either as larvae or juveniles within the ballast water of such vessels (MONNIOT & MONNIOT 1983; WIRTZ & MARTINS 1993). Because of the fouling propensity of these sessile species, the natural distributions of many from the Caribbean and their localised distributions in the Azores, it is possible that all have been introduced by boats.

The Pacific *Spirorbis marioni* was recorded from the Atlantic for the first time at ports in the Canaries by KNIGHT-JONES & KNIGHT-JONES (1980), presumably initially introduced as larvae in ship ballast water and has since spread, dramatically, not only to the Azores but to the Mediterranean as well (KNIGHT-JONES et al. 1991a), probably by the same mechanism. Other species which may have been introduced into the Azores by such means include *Phoronis hippocrepia, P. psammophila* and *Phoronopsis harmeri* (Phoronida), *Bugula stolonifera* and *B.simplex* (Bryozoa) and the tanaid *Tanais dulongii*, all of which have amphiatlantic and, often, near cosmopolitan distributions in ports and harbours (HAYWARD & RYLAND 1990). These and botryllid ascidians are, however, also capable of larval and post-larval rafting (WORCESTER 1994). In this context, BINGHAM & YOUNG (1991) have shown experimentally that the tadpole larva of the ascidian *Ecteinascidia turbinata* is incapable of long-distance swimming and settles preferentially near parent colonies. These authors make the point that the supposedly dispersive larval stage is, in fact, not and that long distance dispersal is *via* the adults, attached to floating objects, that is, by rafting. Conversely, tanaids lack a larval stage, so that *Tanais delongii* too probably arrived in the Azores by either adult rafting or attched to boats.

The spirorbid, *Spirorbis marioni* has been only reported from the harbours of Horta and Ponta Delgada, presumably delivered there by ships (ZIBROWIUS & BIANCHI 1981; KNIGHT-JONES et al.

1991b). Another Azorean polychaete, the serpulid *Hydroides elegans* (not *H. norvegicus* as has been often reported, *fide* H. Zibrowius, pers. comm.), is a well-known fouling species, introduced widely throughout the world (HAYWARD & RYLAND 1990), and it too could have been delivered to the islands either attached to yacht hulls or in the ballast water of ships. The large fanworm *Sabella (=Spirographis) spallanzanii* is an obvious component of the Azorean shallow sublittoral, especially in harbours (MORTON et al. 1998a). KNIGHT-JONES & PERKINS (1998), however, suggest that it too could have been introduced into the islands either attached to ship's hulls or in ballast water because its patchy distribution coincides with sailing ship routes. Furthermore, this Atlantic species recently has been introduced into Australia (ANDREW & WARD 1997).

BAKER (1967) and MORTON et al. (1998) record the barnacle *Balanus trigonus* from Fajã de Santo Cristo, São Jorge. Ships have transported this South African species throughout the world. *Balanus eburneus* is another ship-transported barnacle and an unlikely and uncommon exotic species in the Azores, usually preferring waters of reduced salinity. It has, again, been found only in Azorean harbours, usually near sources of freshwater outflow. Another barnacle, *Tesseropora arnoldi,* formerly identified from São Jorge *as Tetraclita squamosa* var. *elegans* (BAKER 1967), recently described as a new endemic species (YOUNG 1998) but considered conspecific with *T. atlanticum* from Bermuda by SOUTHWARD (1998), is a larval brooder. Such species are usually dispersed only as adults, either attached to ships or to natural floating objects such as wood, thereby rafting long distances across the sea (JOKIEL 1990).

At least three species of molluscs, the bivalves *Mytilus edulis* (CORNELIUS 1992) [MORTON 1967 recorded this species from the lagoon at Fajã de Santo Cristo in 1965, but it has not been seen there subsequently, similarly suggesting "chance" colonisation], and *Hiatella arctica* and *Pteria hirundo* have been observed washing ashore on Azorean beaches, often clinging to flotsam (MORTON et al. 1998a). Serpulid polychaetes, with short-lived planktonic larvae (TEN HOVE et al.1991), must rely upon floating objects for

Table 3

A list of coastal animals which have probably been introduced into the Azores, either unintentionally or intentionally by human transport, with a possible mechanism involved indicated.

Species	Possible mechanism(s) of introduction	References
Hydrozoa		
Silhouetta uvacarpa		
Tubularia crocea	Unintentional, attached to boats	
Tubularia indivisa		
Ventromma halecioides		CORNELIUS 1992
Bryozoa		
Bugula stolonifera	Unintentional, attached to boats	
Bugula simplex		HAYWARD & RYLAND 1990
Phoronida		
Phoronis hippocrepia	Unintentional, as larvae in ballast	
Phoronis psammophila	water	
Phoronopsis harmeri		HAYWARD & RYLAND 1990
Polychaeta		
Hydroides elegans		ZIBROWIUS & BIANCHI 1981;
Sabella (Spirographis)	Unintentional, attached to boats	HAYWARD & RYLAND 1990; KNIGHT-
spallanzanii		JONES et al. 1991b; KNIGHT-JONES &
Spirorbis marioni		PERKINS 1998
Cirripedia		
Balanus eburneus	Unintentional, either as attached	SOUTHWARD 1998;
Balanus trigonus	adults or larvae in ballast water	MORTON et al. 1998a
Tanaidacea		
Tanais dulongi	Unintentional, attached to boats	HAYWARD & RYLAND 1990
Isopoda		
Ligia italica		
Ligia oceanica	Unintentional, as shipboard	HAYWARD & RYLAND 1990;
Sphaeroma serratum	stowaways or foulers	MORTON et al. 1998a
Decapoda		
Carcinus maenas	Unintentional, either clinging	DROUËT 1861; SAMPAIO 1904;
Pilumnus spinifer	to boats or as	BOUVIER 1940; HAYWARD & RYLAND
Plagusia depressa	larvae in ballast water	1990
Gastropoda		
Engina turbinella	Unintentional, as larvae	
Murex trunculus	in ballast water	MORTON et al. 1998a
Bivalvia		
Mytilus edulis	Unintentional, attached to boats or other transportable materials, or as larvae in ballast water	MORTON 1967; CORNELIUS 1992
Venerupis decussatus	Introduced from continental Portugal	MORTON 1967; MORTON & TRISTÃO DA CUNHA 1993
Ascidiacea		
Botryllus schlosserei		
Clavelina lepadiformis	Unintentional, either attached to boats	MONNIOT & MONNIOT 1983
Clavelina oblongata	or as larvae in ballast water	WIRTZ & MARTINS 1993
Distaplia corolla		WIRTZ 1995
Cystodytes dellechiaje		

long-range dispersal and the spirorbid *Spirorbis spirorbis* which naturally attaches intertidally to algal fronds could well have been introduced into the Azores on floating algal mats. REID (1996) points out that species with non-planktotrophic larvae, such as the intertidal, ovoviviparous, gastropod *Littorina saxatilis* might have certain advantages over similar species which rely upon larvae for dispersal. In such a case, only a single brooding female rafted to a remote locality is sufficient to establish a colony (JOHANNESSON 1988), whereas, even among species which produce teleplanic larvae, at least two and, realistically, usually many more individuals must arrive upon a distant shore to establish a viable, replicating, colony.

Errant species, such as the isopod *Ligia oceanica* and the gastropods *Engina turbinella* and *Murex trunculus* are thought to have been transported to Azorean harbours as larvae in ballast water (MORTON et al. 1998a). The unique occurrence of, especially, the gastropods in these harbours argues for this means of introduction, although, significantly, *M. trunculus* is a dominant colonizer of the sea bed in Horta Harbour, Faial, (H. Martins, pers. comm.) feeding on fish carrion. Of the 51 decapod crabs recorded from shallow-waters in the Azores, three are known to be ship-borne migrants. *Plagusia depressa*, an amphiatlantic species, was introduced into the Mediterranean clinging to the hulls of ships (BOUVIER 1940). *Pilumnus spinifera* has been occasionally shipborne to other ports (HAYWARD & RYLAND 1990) while *Carcinus maenas* has been recorded from the Azores only in the old literature (DROUËT 1861; SAMPAIO 1904), but not since, although this species has been widely introduced around the world and become highly successful in its introduced range. It has, for example, been introduced into Maine, U.S.A., maritime Canada (GLUDE 1995), Australia (ZIEDLER 1978), California, U.S.A. (GROSHOLZ & RUIZ 1995) and South Africa (ROUX et al. 1990).

We have discussed previously the Azorean hydroid fauna, which provides the best case for transport by rafting (CORNELIUS 1992). Although rafting and human-assisted transport account for some of the Azorean shore fauna, some species could have arrived as teleplanic larvae. These are represented by various crustaceans, as exemplified by crab megalopa and scyllarid lobster phyllosoma larvae, both of which spend several months in the plankton (possibly as long as 18 months, explaining how these decapods may recruit to the Azores with ocean currents) and numerous prosobranch gastropods (LAURSEN 1981). Along the continental coastlines of North, Central and South America, intertidal and sublittoral prosobranch species with a planktonic larval stage have, on average, a greater geographic range than those lacking a free-drifting veliger stage. The range of species producing planktotrophic larvae, however, is unrelated to the length of time they occupy the plankton, so long as there are no major barriers to dispersal along the continental margins. Consequently, along the north-south continental coastlines of the Western Atlantic there is no significant difference in the geographic ranges between species with planktonic development times of between two to six weeks duration and those having teleplanic larvae with development times of between two to six months, or even more (SCHELTEMA et al. 1989). Transatlantic east-west dispersion is markedly different. Species with short-lived planktonic larvae seldom exhibit amphiatlantic distributions, whereas three-fourths of the prosobranchs having teleplanic veligers are known to have a range extending across the Atlantic Ocean (SCHELTEMA et al. 1989), including several species which occur in the Azores. These include the teleplanic larvae of, for example, *Stramonita haemastoma*, *Phalium granulatum*, *Cymatium parthenopeum*, *Natica canrena* and *Polinices lacteus*, all of which have been collected from the waters of the Azores and as benthic adults (LAURSEN 1981).

LEAL & BOUCHET (1991) emphasize the importance of seamounts to the dispersal of marine species with planktonic larvae and PARKER & TUNNICLIFFE (1994) demonstrate that the Cobb Seamount, 510 km west of Oregon, U.S.A., is dominated by directly-developing species and those with short-lived planktonic larvae and, further argue, that the abundance of drifting kelp near it suggests such species arrived by rafting. Despite a species' capacity for widespread dispersal, however, ecological constraints can intercede to

determine either where it can or can not survive and either restrict or expand its geographic range. For example, since the last ice age, the brachiopod *Terebratulina retusa* has re-occupied its former range near Spitsbergen, 3000 to 4000 km north of the Iberian Peninsula, where it lived at the height of the glaciation. This translocation was made possible by the progressive northward re-establishment of the North Atlantic Current, which had been deflected south during the last ice age and which represents the primary method of dispersal for short-lived pelagic brachiopod larvae (CURRY & ENDO 1991). Similarly, means of dispersal other than the drift of planktonic larvae, such as human-assisted transport, may extend species ranges beyond expectation (BHAUD 1993).

The tropical Western Atlantic has suffered significant (60-70%) molluscan extinctions since the Early Pliocene. Immigrants into this region often become common and geographically widespread. Extinction in the Eastern Atlantic has been much less, with its immigrants more often having restricted geographical distributions and, possibly, including populations that are not self-sustaining (VERMEIJ & ROSENBERG 1993). Of the 33 molluscs which have occupied the Western Atlantic from other regions, 16 are derived from the Eastern Atlantic, whereas at least 39 species dispersed eastward across the Atlantic from the tropical Americas to West Africa. Nevertheless, the limited studies presently available for relatively well known members of the Azorean marine fauna collectively suggest that most of these have strongest ties with the east, not the west.

GOFAS (1990) considered the biogeographic relationships of Azorean micromolluscs, especially members of the Rissoidae and closely related Anabathridae. Despite the overall eastward surface flow in the northern North Atlantic, Azorean rissoids are derived from Eastern rather than Western Atlantic sources. The degree of endemism among Azorean rissoids was argued to be much lower than would be expected for isolated oceanic islands, perhaps reflecting relatively recent colonizations of "young" islands. Of the 11 Azorean species treated by GOFAS (1990), two were considered endemic but distantly related to either European or Macaronesian species, six were very

closely related to such species and three were considered conspecific with others occupying different Eastern Atlantic shores. In addition to the rissoids, GOFAS (1990) cited several additional Azorean micromolluscs, including *Skeneopsis planorbis*, *Ammonicera fischeriana*, *Rissoella diaphana* and *Omalogyra atomus,* which seem conspecific with European mainland taxa. KNUDSEN (1995), however, considered five Azorean rissoids to be endemic (all with direct development) and identified six other micromolluscs with conspecifics on European shores (again all with direct development). Eight other prosobranchs had planktotrophic larvae, but six of these were teleplanic. Some of these molluscs might, therefore, have reached the Azores by long-distance larval transport but adult rafting upon drift algae, or other floating objects, is equally plausible for these species, especially those with direct development. The present southwesterly surface circulation pattern of the Northeastern Atlantic, however, would seem to preclude direct drift from the European mainland to the Azores or even from Eastern Macaronesia (GOFAS 1990). This suggests, therefore, that such species may have arrived at the Azores prior to closure of the Central American Isthmus, when the North Atlantic surface circulation pattern was radically different from the present. Alternatively, there are possibly two other, presently active, east–to-west conduits which may deliver immigrants from continental Europe or Africa to the vicinity of the Azores. One is the deep-water flow spilling into the Atlantic basin from the Mediterranean (PRICE et al. 1993) and the other brief, annual, reversals of surface or near-surface currents between the Azores and Africa and Madeira, especially in autumn and winter (SANTOS et al. 1995). There is also the possibility of either unintentional human-assisted transport or phoresy. It is likely, for example, that the three, egg-capsule producing, assimineid prosobranchs introduced within the last ten years into the quarry at Cabo do Praia, Terceira, were transported by phoresy.

We have previously addressed endemism among Azorean fishes, indicating that none of the shallow water species is presently considered endemic. The low level of endemism, combined with high conspecificity between the Azores and Eastern

Atlantic localities, suggests a relatively recent pattern of ichthyofaunal recruitment. This is difficult to explain, however, as with the micromolluscs, based upon present surface current patterns, although brief current reversals might account for the transport of some species. We have previously noted a case for rafting of the blenny *Hypleurochilus fissicornis* from the Southwestern Atlantic to the Azores.

The deep influx of Mediterranean water to the central Atlantic is a possible conduit for at least some fishes but, even this, is insufficient to explain the preponderance of Mediterranean species, considering that many shallow water forms will be restricted to depths considerably less than the intervening 900 metres. On the other hand, Mediterranean water has been implicated in the distribution of several diverse groups of invertebrates to the Azores, including certain sponges (BOURY-ESNAULT & LOPES 1985), the Mediterranean locust lobster *Scyllarides latus* (MARTINS 1985) and perhaps the hydromedusa *Zanclea costata* (BAKER 1967) and several echinoderms (MARQUES 1983).

BOURY-ESNAULT & LOPES (1985) record 83 species of sponges from the littoral waters of the Azores. Seventeen are transatlantic in distribution, but most are Eastern Atlantic with a large percentage from the Mediterranean. As with the other faunal elements discussed above, very few (four or less) are considered to be endemic.

Many members of the marine fauna of the Azores are so insufficiently documented that it is almost impossible to make accurate biogeographic inferences. For example, benthic amphipods, characterized by direct development and a reduced swimming capability, have limited dispersal abilities in comparison to those of molluscs, decapods and fishes. Accordingly, they more often display a higher degree of endemism. Early works on the Azorean marine fauna were often little more than species lists (CHEVEREUX 1888). LOPES et al. (1993) reviewed the available amphipod literature and studied several collections from the Azores, resulting in a list of 122 species from 29 families. Thirty species were identified from São Miguel and Faial collections. Of these, 15 (50%) were new records for the Azores, emphasizing an existing lack

of knowledge. Other Azorean crustaceans and the marine fauna similarly have received sporadic treatment, as indicated in the list of references compiled by MARTINS (1990).

DISCUSSION

The Azorean islands have benefited from, at first, a long history of European exploratory visits and, later, from a growing local interest in the identification of the marine life they support. The inventory of local species is growing. As knowledge of the species present grows, so does our understanding of their broader geographical and archipelago-wide distributions. This study suggests that, probably, most Azorean coastal marine species were recruited naturally from far flung shores, mostly southern European, North African and Mediterranean, either by chance propagule and larval (or adult) dispersal and by rafting with some species also recruited by phoresy on migrating birds, or insects. A few species with teleplanic larvae, for example, gastropods (LAURSEN 1981) may have been recruited from the Western Atlantic, for example *Thais* (*Stramonita*) *haemastoma*, and from the Mediterranean, for example, the locust lobster, *Scyllarides latus* (MARTINS 1985). Because of the recent geological history of the Azores, there are few endemic species and those which currently have that status, as discussed, may, eventually, as the Atlantic fauna is studied more, lose it. One exception to this generalisation are the rissoid micromolluscs, for which there is some evidence of endemism (GOFAS 1990; KNUDSEN 1995)

Few, if any, of the species identified herein as being recruited to the Azores, either attached to the hulls of yachts (Horta, Faial) or in the ballast waters of ships (Ponta Delgada, São Miguel), seem to have had any significant adverse impacts upon the 'native' marine flora and fauna and are, like them, 'chance survivors of chance immigration events'. The two species of *Ligia*, i.e., *L. oceanica* and *L.italica*, in the Azores (MORTON et al. 1998a) might have arrived on the islands by rafting but, equally possibly, also been introduced as stowaways on the earliest exploring vessels. Sea roaches such as these have been introduced world-wide by

vessels and their wide occurrence and abundance in the Azores suggests that they have had an (unknown) ecological impact. Another widely distributed isopod, *Sphaeroma serratum*, has probably been introduced into the Azores as a well-known (HAYWARD & RYLAND 1990) ship fouling species. Unlike *Ligia* and *Sphaeroma*, however, the mussel *Mytilus edulis* has been recorded but sporadically from the Azores (MORTON 1967; CORNELIUS 1992) and this 'chance immigrant' which one would expect to become highly successful and dominant, as it is elsewhere it has been introduced into, for some unknown reason, cannot survive here. Similarly, the amphiatlantic *Plagusia depressa* is a well known shipborne migrant (BOUVIER 1940) and occurs in the Azores, but not noticeably in the intertidal. *Carcinus maenas* is recorded, perhaps erroneously, in the old literature from the Azores (DROUËT 1861; SAMPAIO 1904) but, like *Mytilus edulis*, has not established itself, unlike other places in the world into which it has been introduced. The ultimate fate of the predatory gastropod, *Engina turbinella*, is unknown, although another species, *Murex trunculus*, introduced into Ponta Delgada and Horta harbours has now spread to other locations (H. Martins, pers. comm.).

Unlike many other places around the globe, the Azores has been fortunate with respect to the introduction of either terrestrial or marine pest species, but cats and rats have had profound impacts upon coastal seabird populations. Many remote islands, especially Hawaii, have suffered the continuing influx of unwanted exotics, even as measures to exclude them have been imposed. The mainland United States has some of the strictest enforcement procedures to exclude the influx of both aquatic and terrestrial unwanted pests, but new species become established there every year. Exotic invasions, such as that by the alga *Caulerpa taxifolia* in the Mediterranean (VERLAQUE & FRITAYRE 1994) or the mussel *Perna perna* in the Gulf of Mexico (HICKS & TUNNELL 1995) can have dramatic effects on the native flora or fauna.

Remarkably, few introduced, exotic, species can be demonstrated to have impacted adversely the vast majority of Azorean rocky shores. This may not, however, be true with regard to recently identified Azorean wetlands (MORTON & TRISTÃO DA CUNHA 1993; MORTON et al. 1995; 1996; 1997; 1998b). CORREIA & COSTA (1994) have described how the American Red swamp crayfish *Procambarus clarkii* has been introduced into the freshwater lake Lagoa de Peixe on São Miguel. Everywhere else this species has been introduced, it has come to almost completely dominate habitats, including marshes (CORREIA 1993). Similarly, the Northeast Atlantic Ditch shrimp, *Palaemonetes varians*, has been introduced, since 1994, into Lagoa das Furnas, São Miguel (Tristão da Cunha, pers. comm.). The significance of these two species is their colloquial names - "Swamp" crayfish and "Ditch" shrimp, for both can equally well survive and thrive in estuarine waters (SHARFSTEIN & CHAFIN 1979; ESCARAVAGE & CASTEL 1990; NEWSOM & DAVIS 1991). Should these species be introduced into the Azorean estuarine lagoons and marshes identified by MORTON & TRISTÃO DA CUNHA (1993) and MORTON et al.(1995; 1996; 1997; 1998a; b), their ecological consequences could be severe, displacing native ones and altering ecologies radically.

It is becoming increasingly clear to biologists world-wide that the rate of species introductions, usually of opportunistic pest species, is growing exponentially, causing not only severe economic problems but ecological and biogeographic ones too. Legislation and enforcement procedures are emerging in many countries to stem the tide of such immigrants. Once an alien is introduced, experience has shown, as with rats, rabbits and feral cats, that they are virtually impossible to eradicate and can have powerful adverse impacts, for example, upon coastal seabirds (BELL 1995). The conclusion drawn from this study, therefore, is that human-assisted introductions of marine organisms into the Azores are occurring but that in the majority of cases, their ecological impacts are not significant (where they have been studied).

The terrestrial and maritime flora of the Azores lost it naturalness, probably, centuries ago as species after species of plants were introduced for a variety of intentional, economic, and accidental reasons and causes and it is likely that not only will they continue to do so, but there is little chance that endemic and native naturalness can be regained.

MARTINS (1993) describes the consequences of such indiscriminate exotic planting and argues for the conservation of small surviving areas of natural vegetation. The same is true of the shore and the Azorean maritime vegetation also lost its naturalness, probably centuries ago, and a return to a pre-human settlement seascape would be impossible. Nevertheless, there exists in the Azores newly-identified coastal wetlands which, if they are to be sustained as unique Macaronesian relatively 'natural' seascapes, need to be protected from the introduction of alien exotics because it is in such places, as elsewhere, that these invaders have the profoundest ecological impacts. MORTON et al. (1998b) have argued for the conservation of these Azorean wetlands and their management for educational (in the broadest terms) and research purposes. To achieve this, they need to become, now, research foci and to be protected from alien introductions.

ACKNOWLEDGEMENTS

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NEW RECORDS OF BENTHIC MARINE RED ALGAE (CERAMIALES: RHODOPHYTA) FROM THE AZORES.

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Sixteen new records of marine red algae (Ceramiales: Rhodophyta) are reported for the Azores islands: *Aglaothamnion gallicum, A. pseudobyssoides, Anotrichium barbatum, A. furcellatum, Ceramium botryocarpum, C. flaccidum, C. secundatum, Compsothamnion decompositum, Wrangelia penicillata* (Ceramiaceae); *Haraldiophyllum bonnemaisonii, Radicilingua thysanorhizans* (Delesseriaceae); *Dasya hutchinsiae* (Dasyaceae); *Brongniartella byssoides, Chondria coerulescens, Polysiphonia foetidissima, P. furcellata* (Rhodomelaceae). Data concerning morphology, phenology, ecological conditions and geographical distribution of the species in the Atlantic are presented.

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INTRODUCTION

In contrast to the marine fauna of the Azores, which has been studied since the 18th century (ARRUDA 1998), research on the marine algae of the Azores began only in the middle of the last century when Guthnick and the two Hochstetters, father and son, visited the Azores. This expedition produced several publications on the vegetation of the Azores but the first mentioning marine algae was SEUBERT (1844), who included a list of 44 species. This work constitutes the starting point for the marine flora of these islands, although no indication of the locality on the islands where the seaweeds were collected, or their abundance, was given. Since then the taxonomic studies continued and SCHMIDT (1931) presented the first compilation of the Azorean marine algal flora. More recently, NETO (1994) brought together the existing published information on the marine plants of the Azorean islands and provided distributional records within the archipelago. Since then, TITTLEY et al. (1998) have reported 9 new records, increasing the known seaweed flora to 307 species. In the present study 16 red algal species collected from the island of São Miguel are reported as new for the Azores algal flora.

MATERIAL AND METHODS

Work was undertaken in several places of the island of São Miguel, since September 1993.

Qualitative collections were made monthly at both intertidal and subtidal levels, down to 15 m depth. Collections were made by walking, swimming or scuba-diving over the study-area.

In the laboratory, the algae were sorted into species. Whenever possible, the material was observed on the same day, otherwise the samples were refrigerated overnight. Samples that could not be examined alive were preserved in 5% buffered formaldehyde-sea water solution (NEZELOF et al. 1972).

All plants were examined microscopically, using stereo and compound microscopes, to detect the occurrence of reproductive structures. Cells and other structures were measured, using a calibrated micrometer eye piece. For the identification of some species, histological work was necessary. Transverse sections were made using a freezing microtome. While the material

was fresh, the sections were mounted in seawater and observed. With preserved material, the plants were washed and the sections were mounted in distilled or tap water.

Two kinds of permanent slides were made. In most cases the material was stained using the aniline blue method (SPARLING 1957; TSUDA & ABBOTT 1985). For a few species the glycerin method (CHEMIN 1929 *fide* TSUDA & ABBOTT 1985) was used.

Two other types of reference collections were established, one in liquid, the other on paper. In the liquid collection, specimens were preserved in 5% buffered formaldehyde-sea water solution. In the herbarium collection, the specimens were mounted on herbarium sheets, following the method described by GAYRAL & COSSON (1986). Both collections are deposited at the University of the Azores.

The systematic organization and nomenclatural synopsis of the species generally follows that adopted by SOUTH & TITTLEY (1986) with later modifications, mainly by MAGGS & PUESCHEL (1989). Spelling and abbreviations of algal authorities follow BRUMMIT & POWELL (1992). New synonyms were given by SCHNETTER et al. (1987), GUIRY & GARBARY (1990), SILVA & DECEW (1992), WYNNE & HEINE (1992), HOMMERSAND et al. (1993), NAM et al. (1994) and PRUD'DOMME VAN REINE et al. (1994). For each family, species are listed alphabetically under each genus.

ANNOTATED LIST OF SPECIES

CERAMIACEAE

Aglaothamnion gallicum (Nägeli) Halos ex Ardré

DESCRIPTION AND ICONOGRAPHY: ARDRÉ (1970, p.306); MAGGS & HOMMERSAND (1993, p.99, Fig. 33).

Azorean plants are small and delicate filaments, with a cylindrical, pyramidal or flabellate outline; the branching is alternate and distichous, in one plane; the basal cell of the lateral branch bears an abaxial branchlet, the main axis is often densely corticated and is attached by a discoid holdfast.

Tetrasporic plants were seen in April and May. A female plant was observed in April.

LOCALITIES: São Vicente (SMG-95-92; SMG-95-114; SMG-96-29; SMG-98-106), São Roque (SMG-94-329; SMG-95-422b), Pópulo (SMG-98-27; SMG-98-81; SMG-98-83), Mosteiros (SMG-98-34), Feteiras (SMG-98-47a), Caloura (SMG-98-100), Maia (SMG-98-129).

ECOLOGY: Infrequently found, this species was present at intertidal and subtidal levels.

GEOGRAPHIC DISTRIBUTION: Eastern Atlantic from the British Isles to Morocco and the Canaries, also in Mediterranean (ARDRÉ 1970; Price et al. 1986; MAGGS & HOMMERSAND 1993). The Azores represent a western extension of the known distribution range.

Aglaothamnion pseudobyssoides (P. Crouan & H. Crouan) Halos

DESCRIPTION AND ICONOGRAPHY: ARDRÉ (1970, p.305); MAGGS & HOMMERSAND (1993, p.107, Fig. 36).

Plants examined are delicate and flaccid filaments; thalli consists of erect axes growing in tufts, up to 2 cm high; the main axis is very distinct and usually naked towards the basis. This species has been regarded as synonymous with *A. byssoides* but a sterility barrier exists (MAGGS & HOMMERSAND 1993). Azorean material can be differentiated from *A. byssoides* on the main axis width (up to 150 µm wide in *A. byssoides* versus 75 µm in *A. pseudobyssoides*).

One tetrasporangial plant was found in May.

LOCALITIES: São Vicente (SMG-95-37), São Roque (SMG-95-42; SMG-95-424; SMG-95-551; SMG-97-175)

ECOLOGY: A rare species, both intertidally and subtidally.

GEOGRAPHIC DISTRIBUTION: Eastern Atlantic from the British Isles to mainland Portugal (ARDRÉ 1970; MAGGS & HOMMERSAND 1993). The Azores represent a new southern limit of distribution.

Anotrichium barbatum (C. Agardh) Nägeli

DESCRIPTION AND ICONOGRAPHY: FELDMANN-MAZOYER (1940, p.408, Figs. 159-160); TAYLOR (1967); ATHANASIADIS (1987, p.81) LITTLER et

al. (1989, p.138); MAGGS & HOMMERSAND (1993, p.179, Fig. 58).

Azorean plants form tufts of numerous fastigiate dichotomously branched filaments comprising pyriform cells, which are swollen distally; axial cells less than 200 µm in diameter; apical cell, 50µm in diameter.

No reproductive structures were seen.

LOCALITIES: São Vicente (SMG-94-18), São Roque (SMG-94-26).

ECOLOGY: This species was collected at both intertidal and subtidal levels.

GEOGRAPHIC DISTRIBUTION: Eastern and western Atlantic, and the Mediterranean (FELDMANN-MAZOYER 1940; WYNNE 1985; PRICE et al. 1986; ATHANASIADIS 1987; MAGGS & HOMMERSAND 1993).

Anotrichium furcellatum (J. Agardh) Balldock

DESCRIPTION AND ICONOGRAPHY: ATHANASIADIS (1987, p.81); MAGGS & HOMMERSAND (1993, p.181, Fig. 59).

Distinguished from *A. barbatum* by having cylindrical cells and an apical cell less than 25 µm in diameter.

Tetraspores were observed in September and a spermatangia in May.

LOCALITIES: São Vicente (SMG-93-17; SMG-94-40; SMG-95-15; SMG-95-101; SMG-95-120; SMG-95-395; SMG-95-556; SMG-95-580; SMG-96-187; SMG-96-231; SMG-96-333), São Roque (SMG-94-215; SMG-94-403; SMG-95-424), Ponta Delgada marina (SMG-94-215; SMG-94-403), Maia (SMG-98-64).

ECOLOGY: Rather more frequent than *A. barbatum*, this species was epilithic in *Centroceras* turf at intertidal and subtidal levels.

GEOGRAPHIC DISTRIBUTION: Eastern Atlantic, from the British Isles to Africa, including the Canaries. Also recorded in the Mediterranean (STEGENGA & MOL 1983; PRICE et al. 1986; MAGGS & HOMMERSAND 1993). The Azores represent a western extension of the known distribution range.

Ceramium botryocarpum Griffiths ex Harv.

DESCRIPTION AND ICONOGRAPHY: MAGGS & HOMMERSAND (1993, p.45, Fig. 13).

Plants growing in tufts with an extensive prostrate system of axes; main axis of mature thalli entirely corticated; branching irregular at intervals of 6 segments; no spines; periaxial cells typically 6.

Tetrasporic plants were seen between February and June.

LOCALITIES: São Vicente (SMG-94-22; SMG-96-59; SMG-96-63), São Roque (SMG-94-12; SMG-95-367; SMG-95-552).

ECOLOGY: Both epilithic and epiphytic this species was strictly intertidal.

GEOGRAPHIC DISTRIBUTION: Recorded in the northeast Atlantic from the British Isles to North of Spain (MAGGS & HOMMERSAND 1993). The Azores represent the new southern limit of distribution.

Ceramium flaccidum (Kützing) Ardissone

DESCRIPTION AND ICONOGRAPHY: SEOANE-CAMBA (1965, p.133, Fig. 37); ARDRÉ (1970, p.285, Pl. 15, Figs. 1-4); ATHANASIADIS (1987, p.76); MAGGS & HOMMERSAND (1993, p.59, Fig. 19).

Thalli flaccid, attached by prostrate axes and usually forming irregularly shaped tufts; main axes incompletely corticate, bearing alternate arrangements of densely branched laterals; no spines; unicellular rhizoids; apices obviously alternately branched every 5-6 segments.

No reproductive structures were seen.

LOCALITIES: São Roque (SMG-94-102; SMG-95-552; SMG-95-362; SMG-95-62), Caloura (SMG-98-96), Mosteiros (SMG-98-276).

ECOLOGY: Epilithic in the lower intertidal, both in pools and exposed rocks.

GEOGRAPHIC DISTRIBUTION: Western and eastern Atlantic and the Mediterranean (SEOANE-CAMBA 1965; WYNNE 1985; PRICE et al. 1986; ATHANASIADIS 1987; MAGGS & HOMMERSAND 1993).

Ceramium secundatum Lyngbye

DESCRIPTION AND ICONOGRAPHY: MAGGS & HOMMERSAND (1993, p. 70, Fig. 23); BOO & RUENESS (1994, p.114, Figs. 1-7).

Thalli of Azorean specimens consisting of fan-shaped or cylindrical tufts of several erect axes attached by a dense mass of multinucleate

rhizoidal filaments; main axis of mature thalli entirely corticate, branching at intervals of 10-18 segments; strongly inrolled apices; no spines; periaxial cells typically 8.

All the examined plants, except one collected in September, were tetrasporic.

LOCALITIES: São Vicente (SMG-96-314; 97-229), São Roque (SMG-94-113a; SMG-95-66; SMG-95-327; SMG-95-332), Mosteiros (SMG-98-32; SMG-98-247; SMG-98-277; SMG-98-286; SMG-98-302), Pópulo (SMG-98-25), Maia (SMG-98-122; SMG-98-137), Calhetas (SMG-98-59), Caloura (SMG-98-98).

ECOLOGY: Epilithic in intertidal pools.

GEOGRAPHIC DISTRIBUTION: Common in the British Isles (MAGGS & HOMMERSAND 1993). Because of the confusion with the former *C. rubrum* complex, the geographical distribution of this species cannot be assessed at present.

Compsothamnion decompositum (J. Agardh) Maggs & L'Hardy-Halos

DESCRIPTION AND ICONOGRAPHY: MAGGS & HOMMERSAND (1993, p.159, Fig. 52).

Filamentous and delicate plant with a monosiphonous and ecorticate thalli; main axis wider than branches, bearing laterals in an alternate arrangement in one plane; cells multinucleate.

Tetrasporangia lateral and sessile were observed in September.

LOCALITIES: São Vicente (SMG-93-30), São Roque (SMG-95-406; SMG-95-424).

ECOLOGY: Strictly subtidal, this species was epiphytic on a range of other algae.

GEOGRAPHIC DISTRIBUTION: Common in the northeast Atlantic (MAGGS & HOMMERSAND 1993). The Azores represent the new southern limit of distribution.

Wrangelia penicillata (C. Agardh) C. Agardh

DESCRIPTION AND ICONOGRAPHY: FELDMANN-MAZOYER (1940, p.425); TAYLOR (1967, p.503, Pl. 66, Figs. 5-6; Pl. 74, Fig. 5); LEVRING (1974, p.88); LAWSON & JOHN (1982, p.301, Pl. 48, Figs. 4-5); ATHANASIADIS (1987, p.84); LITTLER et al. (1989, p.148); BOUDOURESQUE et al. (1992, p.184, Fig. 200).

Plants usually solitary, stiff and erect; branching alternate and distichous, with well-developed cortication; branchlets terminating in an acute spine.

Tetrasporic plants were seen in December.

LOCALITIES: São Vicente (SMG-94-360; SMG-97-144), São Roque (SMG-95-351; SMG-95-372; SMG-97-168), Lagoa (SMG-97-193), Pópulo (SMG-98-92), Caloura (SMG-97-221).

ECOLOGY: Only seen at subtidal levels, where it was rare.

GEOGRAPHIC DISTRIBUTION: Western and eastern Atlantic and the Mediterranean (FELDMANN-MAZOYER 1940; TAYLOR 1967; LEVRING 1974; LAWSON & JOHN 1982; WYNNE 1985; ATHANASIADIS 1987; BOUDOURESQUE et al. 1992).

Haraldiophyllum bonnemaisonii (Kylin) A. Zinova

DESCRIPTION AND ICONOGRAPHY: MAGGS & HOMMERSAND (1993, p.242, Fig. 76).

Plants examined are membranous and translucent without a conspicuous midrib or microscopic veins; thalli consists of one or more blades attached by small solid holdfast with prostrate rhizoidal outgrowths; blades fan-shaped, dichotomously divided into overlapping lobes with rounded or obtuse apices and entire or dentate margins; plastids numerous, small, plate-like to bacilloid; cystocarps subspherical, with a non-protruding ostiole, tetrasporangial sori numerous, round to oval, occasionally coalescing.

Most plants were reproductive, with the tetrasporophyte generation observed in January, May and June, and a female plant observed in June.

LOCALITIES: São Vicente (SMG-93-113; SMG-93-147; SMG-94-341; SMG-94-355; SMG-94-384; SMG-95-104; SMG-96-95; SMG-96-241; SMG-96-268; SMG-97-95; SMG-97-259; SMG-97-261), São Roque (SMG-95-64; SMG-95-349), Mosteiros (SMG-98-240).

ECOLOGY: Present at intertidal and subtidal levels.

GEOGRAPHIC DISTRIBUTION: Eastern Atlantic (PRICE et al. 1992; MAGGS & HOMMERSAND 1993), the Azores represent a western extension of the known distribution range.

Radicilingua   thysanorhizans (Holmes) Papenfuss

DESCRIPTION AND ICONOGRAPHY: ARDRÉ (1970, p.316); MAGGS & HOMMERSAND (1993, p.263, Fig. 82).

Plants largely prostrate, membranous and translucent, attached by small marginal projections that develop at irregular intervals; blades monostromatic, with 40 µm in thickness; microscopic veins mostly parallel and forming a network. Although originally considered conspecific with *Acrosorium venulosum* (see WYNNE 1989), even sterile specimens can be easily separated by such features as plastid shape and attachment structures.

Only one reproductive plant with mature cystocarps was found, in September.

LOCALITIES: São Vicente (SMG-94-340; SMG-94-341; SMG-95-36; SMG-95-37; SMG-97-41), São Roque (SMG-93-64; SMG-94-15; SMG-94-46; SMG-94-246a; SMG-95-40; SMG-95-374).

ECOLOGY: Mainly epiphytic, this species was present from the intertidal to subtidal levels.

GEOGRAPHIC DISTRIBUTION: Eastern Atlantic from the British Isles to mainland Portugal and also the Mediterranean (ARDRÉ 1970; MAGGS & HOMMERSAND 1993). The Azores represent a new southern limit of distribution.

DASYACEAE

Dasya hutchinsiae Harv. in Hook.

DESCRIPTION AND ICONOGRAPHY: ARDRÉ (1970, p.321); LEVRING (1974, p.97); MAGGS & HOMMERSAND (1993, p.272, Fig. 84).

Thalli radially organized, terete and polysiphonous arising from a discoid rhizoidal holdfast; erect axes growing in tufts; spirally branched main axes, lightly to heavy corticated; pseudo-laterals branched from immersed basal cell, appearing to arise in pairs, and also from all of the next few cells; each stichidial segment containing 5 tetrasporangia.

Plants bearing stichidia with tetrasporangia were found in September, May and October.

LOCALITIES: São Vicente (SMG-94-297; SMG-94-301; SMG-94-405; SMG-95-94; SMG-95-562), São Roque (SMG-94-404; SMG-94-407;

SMG-95-559), Maia (SMG-98-136), Mosteiros (SMG-98-269; SMG-98-271).

ECOLOGY: Mainly epiphytic, this species was present in the intertidal and at subtidal levels.

GEOGRAPHIC DISTRIBUTION: The eastern Atlantic including Madeira and the Canaries (ARDRÉ 1970; LEVRING 1974; PRICE et al. 1986; MAGGS & HOMMERSAND 1993) and the Mediterranean (ATHANASIADIS 1987). The Azores represent a western extension of the known distribution range.

RHODOMELACEAE

Brongniartella byssoides (Gooden. & Woodw.)

DESCRIPTION AND ICONOGRAPHY: GAYRAL (1966, p.575, Pl. CLXXVIII); ARDRÉ (1970, p.333); ATHANASIADIS (1987, p.91); MAGGS & HOMMERSAND (1993, p.302, Fig. 92); COPPEJANS (1995, p.340, Pl. 135).

Thalli radially organized, terete and polysiphonous, composed of dense cylindrical to irregularly pyramidal tufts of erect axes attached by tangled prostrate axes. Distinguished from *Dasya* by the absence of cortication.

No reproductive structures were seen.

LOCALITIES: São Vicente (SMG-93-32).

ECOLOGY: Epiphytic on other subtidal species.

GEOGRAPHIC DISTRIBUTION: The eastern Atlantic, and the Mediterranean (GAYRAL 1966; ARDRÉ 1970; MAGGS & HOMMERSAND 1993). The Azores represent a new southern limit of distribution.

Chondria coerulescens (J. Agardh) Falkenberg.

DESCRIPTION AND ICONOGRAPHY: GAYRAL (1958, p.476, Pl. CXLII); SEOANE-CAMBA (1965, p.153); GAYRAL (1966, p.562, Pl. CLXXII); ARDRÉ (1970, p.355); LEVRING (1974, p.105); ATHANASIADIS (1987, p.91); MAGGS & HOMMERSAND (1993, p.388, Fig. 122).

Thalli flexible and cartilaginous in texture, consisting of cylindrical erect axes arising in erect or decumbent tufts from a solid lobed holdfast; erect thalli with distinct main axes, branching sparsely at irregular intervals in a spiral pattern to 1-3 orders of branching; branches curving and

reattaching by secondary holdfasts that may form stolon-like outgrowths; apices obtuse, terminating in a shallow depression, sometimes with protruding trichoblast; erect axes with 5 periaxial cells readily distinguishable from other medullary cells; young plants showing a vivid, metallic blue iridescence when alive; wart-like aborted branch initials spirally borne on the axes.

Tetrasporic plants were found in June, October and December. One cystocarpic plant was collected in July.

LOCALITIES: São Vicente (SMG-94-315; SMG-95-107; SMG-95-128), São Roque (SMG-94-89; SMG-94-326; SMG-94-399; SMG-95-60; SMG-95-342; SMG-95-423), Caloura (SMG-98-5), Feteiras (SMG-98-45), Pópulo (SMG-98-85), Calhetas (SMG-98-156), Mosteiros (SMG-98-205).

ECOLOGY: Strictly intertidal, this plant was found in pools, cervices and exposed rocks.

GEOGRAPHIC DISTRIBUTION: The eastern Atlantic, including Madeira and the Canaries (GAYRAL 1958, 1966; SEOANE-CAMBA 1965; ARDRÉ 1970; PRICE et al. 1986; MAGGS & HOMMERSAND 1993). Also recorded in the Mediterranean (ATHANASIADIS 1987). The Azores represent a western extension of the known distribution range.

Polysiphonia foetidissima Cocks ex Bornet

DESCRIPTION AND ICONOGRAPHY: TAYLOR (1967, p.581); ARDRÉ (1970, p.340); MAGGS & HOMMERSAND (1993, p.336, Fig. 103).

Plants extremely soft and flaccid in texture forming dense tufts; thalli polysiphonous, radially organized, with 7-8 pericentral cells; ecorticate main axes, less than 40 µm wide, with straight apices and spiral branching; rhizoids cut off from periaxial cells; trichoblasts numerous.

One male gametophyte was observed in December.

LOCALITIES: São Vicente (SMG-93-119).

ECOLOGY: Epiphytic on several species in the subtidal.

GEOGRAPHIC DISTRIBUTION: Western and eastern Atlantic and the Mediterranean (BATTEN 1922; TAYLOR 1967; ARDRÉ 1970; WYNNE 1985; PRICE et al. 1986; MAGGS & HOMMERSAND 1993; LAWSON et al. 1995).

Polysiphonia furcellata (C. Agardh) Harv. in Hook.

DESCRIPTION AND ICONOGRAPHY: ARDRÉ (1970, p.341); ATHANASIADIS (1987, p.100); MAGGS & HOMMERSAND (1993, p.341; Fig. 105).

Distinguished from *P. foetidissima* by having dichotomous branching and young branches with apices paired and incurved, resembling *Ceramium*.

Only sterile plants were found.

LOCALITIES: São Vicente (SMG-94-37; SMG-94-38).

ECOLOGY: Epiphytic on the algal turf in the lower intertidal.

GEOGRAPHIC DISTRIBUTION: The eastern Atlantic, and the Mediterranean (FELDMANN 1954; ARDRÉ 1970; LAURET 1970; ATHANASIADIS 1987; MAGGS & HOMMERSAND 1993; LAWSON et al. 1995). The Azores represent a western extension of the known distribution range.

DISCUSSION

Some of the new recorded species were restricted to the intertidal level, either on the exposed rocks (*Chondria coerulescens*) or lower on the shore (*Ceramium botryocarpum*, *C. flaccidum*, *C. secundatum*, *Polysiphonia furcellata*). Others were exclusively found in the subtidal zone (*Anotrichium barbatum*, *Brongniartella byssoides*, *Compsothamnion decompositum*, *Polysiphonia foetidissima*, *Wrangelia penicillata*).

Some of the studied species had a seasonal occurrence. Those occurring only in summer include *Brongniartella byssoides* and *Compsothamnion decompositum*. *Polysiphonia foetidissima* was only present in autumn and *P. furcellata* occurred only in winter. Other taxa had a larger period of occurrence: *Anotrichium barbatum* was present in autumn and winter, *Ceramium flaccidum* in winter and spring, and *Chondria coerulescens* was found throughout the year.

The absence of some species at different times of the year can be related to their life cycle, and/or to errors associated to the sampling method. In

fact, many species are small plants and occur in low densities making them easy to miss in the collections.

Most of the species reported in this work belong to the cold flora of the northeastern Atlantic. *Aglaothamnion pseudobyssoides*, *Anotrichium furcellatum*, *Ceramium botryocarpum*, *C. secundatum*, *Compsothamnion decompositum* and *Haraldiophyllum bonnemaisonii* are only known from the eastern Atlantic, most of them having their southern limit of distribution in the Azores. Other seven species (*Aglaothamnion gallicum*, *Brongniartella byssoides*, *Ceramium flaccidum*, *Chondria coerulescens*, *Dasya hutchinsiae*, *Radicilingua thysanorhizans* and *Polysiphonia furcellata*) are also only present in the eastern Atlantic, but extend into the Mediterranean. Among these, *B. byssoides* and *R. thysanorhizans* have their southern limit of distribution in the Azores. Only *Anotrichium barbatum*, *Polysiphonia foetidissima* and *Wrangelia penicillata* are amphi-Atlantic species. None of the species in the present list has a distribution range previously limited to the western Atlantic.

This is in agreement with previous biogeographical studies (SCHMIDT 1931; VAN DEN HOEK 1984, 1987; PRUD'HOMME VAN REINE 1988; PRUD'HOMME VAN REINE & VAN DEN HOEK 1990; NETO 1997), which emphasize the affinities of the Azorean flora with those from the northeastern Atlantic. In fact, few species exclusively from the western Atlantic are known to occur in the Azores. This pattern is also reflected in the present list of species.

Most of the present new records are small plants. This is probably related to the special attention that was given to the epiphytes and small plants when doing the collections and the laboratory determinations. Similar work in the future is likely to continue to expand the known algal flora of the Azores.

ACKNOWLEDGEMENTS

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STRUCTURE AND ZONATION OF ALGAL COMMUNITIES IN THE BAY OF SÃO VICENTE (SÃO MIGUEL, AZORES)

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An appraisal of the benthic marine algal communities of the bay of Sao Vicente (São Miguel island, Azores) was undertaken in July 1996 and July 1997 as part of the project "Biodiversity of the archipelago of the Azores". A permanent transect was laid down across the subtidal zone. Quadrates were sampled at pre-determined intervals along the transect from the low water level, down to 30m depth. Qualitative collections were made along the transect. The relative importance of each species was determined using a semi-quantitative scale. The transect revealed the occurrence of relatively large and frondose algae establishing the transition between the intertidal and the subtidal zones. *Pterocladiella capillacea* was the dominant species in this transition zone and extended its presence down to 12m depth. A depth-related change in the algal flora was present in both years. *Pterocladiella*, *Ulva* spp., *Stypocaulon scoparia*, *Hypnea musciformis* and *Asparagopsis armata* dominated the shallow levels; *Zonaria tournefortii*, together with *Sphaerococcus coronopifolius* and *Dictyota dichotoma* dominated the deep ones.

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INTRODUCTION

The island of São Miguel (Fig. 1), with approximately 750 km^2, is the largest of the archipelago of the Azores. The coastline, mainly of high, steep cliffs with a variety of stack, arch and gully formations, is about 155 km in length and is mostly difficult to access by land. Although seashores are generally steeply sloping, there are places where depths of less than 30m extend several hundred meters offshore. The wave action is known to be stronger on north coast and responsible for the higher erosion that occurs there (BORGES 1995). Tides are semi-diurnal and tidal range is less than 2 m, even at extreme neap tides (INSTITUTO HIDROGRÁFICO 1981).

Although the marine algal flora of the Azores has been sporadically investigated during the past century and a half (see NETO 1997 for revision), research since the late 1980s has yielded much new information. A comprehensive algal checklist (NETO 1994) brings together all existing published information and provides distributional information within the archipelago. Nonetheless, ecological investigations describing the structure and zonation of benthic marine algal communities were only recently initiated in the Azores. In São Miguel, CASTRO & VIEGAS (1987), HAWKINS et al. (1990) and NETO (1991, 1992a) studied the zonation patterns of littoral organisms at different locations around the island. NETO & AZEVEDO (1990) and more recently TITTLEY et al. (1998) studied the zonation patterns and the community structures at several sites on the island of Flores.
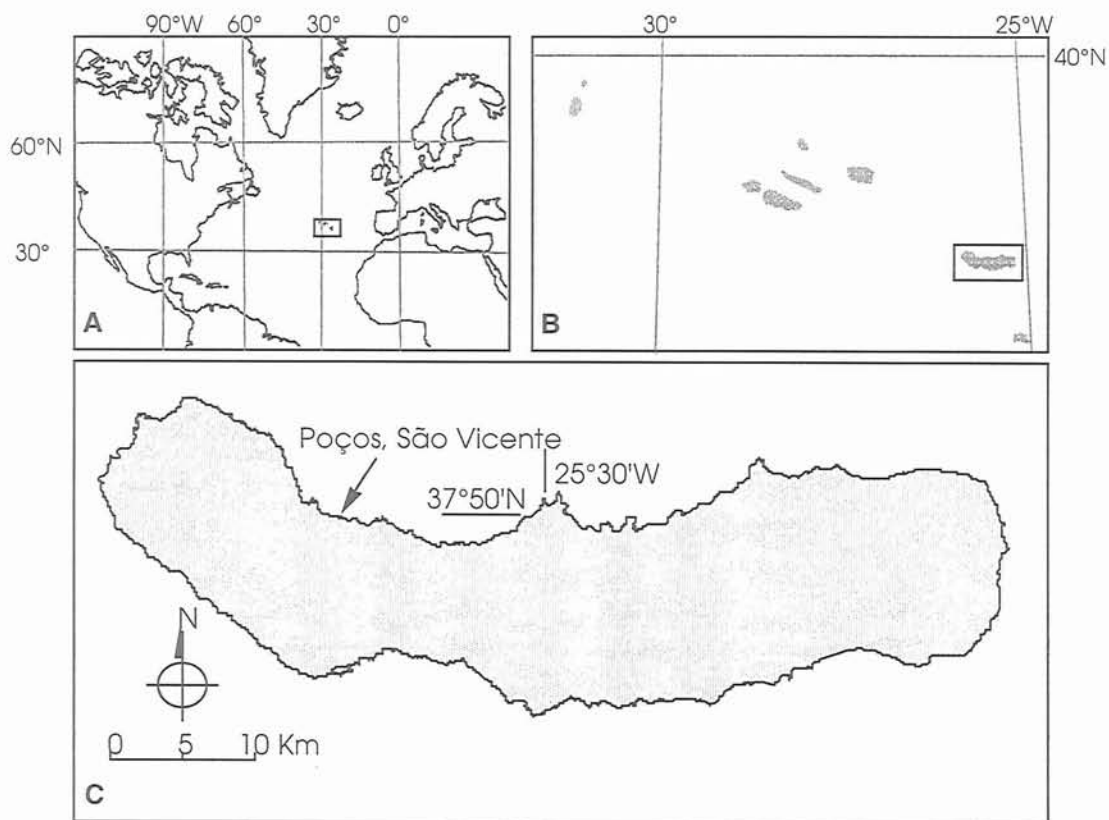
Fig. 1. The Azores (B) and its location on the North Atlantic (A). Location of the study site on the island of São Miguel (C).

TITTLEY & NETO (1994, 1995), and NETO & TITTLEY (1995) studied the algal flora and the zonation of the Monte da Guia Nature Reserve in Faial. NETO (1997), reports the results of the first detailed investigation into the marine algal communities of São Miguel, carried out over a continuous two year period, in contrast to the previous one-off expeditions discussed above.

The aim of this paper is to describe the structure of a macroalgal community on the island of São Miguel, thus contributing to the knowledge of the littoral communities of the Azores.

MATERIAL AND METHODS

Work was undertaken in São Vicente bay, in the north coast of the island of São Miguel (Fig. 1) in

July 1996 and July 1997. A permanent transect was laid down across the subtidal zone from 0 m down to 30 m depth. The bottom topography was determined by divers swimming along the transect and recording at each meter the depth and type of substrate. Depth was determined with a diving computer. The transect profile was drawn. Quantitative collections were made at pre-determined intervals along the transect (3, 8, 10, 12, 15, 20, 25, 30 meters, Fig. 2). For each level, three samples of 2500 cm^2 were collected, a sample consisting of the material obtained by carefully scraping with a chisel all the attached algae inside the quadrat into a fine mesh net bag. Qualitative collections were made by swimming around the area and collecting representative specimens into previously labelled bags. Habitat details for each species (depth, substrate, orientation and aspect of the rock, gully, crevice,
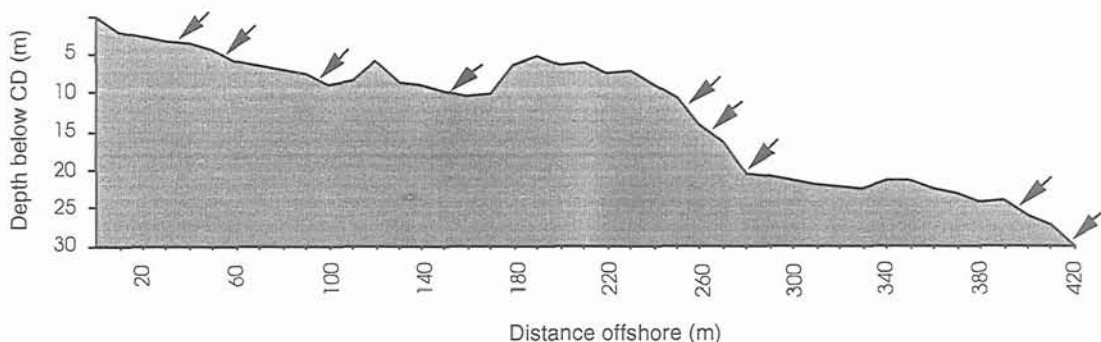
Fig. 2. Profile of the transect with indication of the collecting sites (arrows).

cave, etc.) were noted on underwater writing boards.

In the laboratory, the algae from both qualitative and quantitative collections were sorted into species. Samples that could not be examined alive were preserved in 5% buffered formaldehyde-sea water solution (NEZELOF et al., 1972). All plants were examined microscopically, using stereo and compound microscopes. Cells and other structures were measured, using a calibrated micrometer eye piece. For the identification of some species, histological work was necessary. Transverse sections were made using a freezing microtome. The relative importance of each species was determined using a semi-quantitative scale (D: dominant; A: abundant; F: frequent; O: occasional; R: rare).

Two types of reference collections were established, one in liquid, the other on paper. In the liquid collection, specimens were preserved in 5% buffered formaldehyde-sea water solution. In the herbarium collection, the specimens were mounted on herbarium sheets, following the method described by GAYRAL & COSSON (1986). Both collections are deposited at the University of the Azores.

RESULTS

A total of 201 species was identified (25 Chlorophyta, 23 Phaeophyta, 153 Rhodophyta).

In both years, variations were observed in the algal composition and abundance following the depth gradient (Fig. 3). In 1996, *Pterocladiella capillacea*, *Ulva* spp., *Stypocaulon scoparia*, *Taonia atomaria* and *Asparagopsis armata* dominated and were only present at the shallow depths. *Sphaerococcus coronopifolius* was only present below 12 m, where it was the dominant species together with *Zonaria tournefortii*. The latter and *Plocamium cartilagineum* were only present below 10-12 m. *Plocamium*, together with *Sphaerococcus*, were the abundant species at 20-25 m. *Dictyota dichotoma* and *Acrosorium* spp. were present from shallow to deep levels, with no distinct pattern. *Halopteris filicina* was a frequent species between 10 and 20 m.

In 1997 this depth-related change in the algal flora was also observed, with *Pterocladiella capillacea*, *Ulva* spp., *Stypocaulon scoparia*, *Asparagopsis armata* and *Hypnea musciformis* dominating the shallow levels and *Plocamium cartilagineum* occurring exclusively below 15 m (Fig. 3). *Pterocladiella*, *Ulva* spp. and *Hypnea* were not found below 12 m and *Stypocaulon* was not present below 15 m. *Asparagopsis*, *Halopteris* and *Dictyota* were present at all levels, the first gradually decreasing in abundance with depth, whereas *Halopteris* was more abundant below 12 m and *Dictyota dichotoma* was more abundant between 3-8 m and 15-25 m. *Zonaria tournefortii* and its epiphytes *Acrosorium* spp. were abundant species below 12 m, being the dominant ones at 25-30 m. *Sphaerococcus* was only found between 12 and 20 m.

Differences were observed on the transect between the two successive years. The major ones included, in the second year, the increased abundance of *Pterocladiella*, *Ulva* spp., *Asparagopsis* and *Halopteris*, the lack of *Taonia atomaria* and the lower abundance of *Plocamium*

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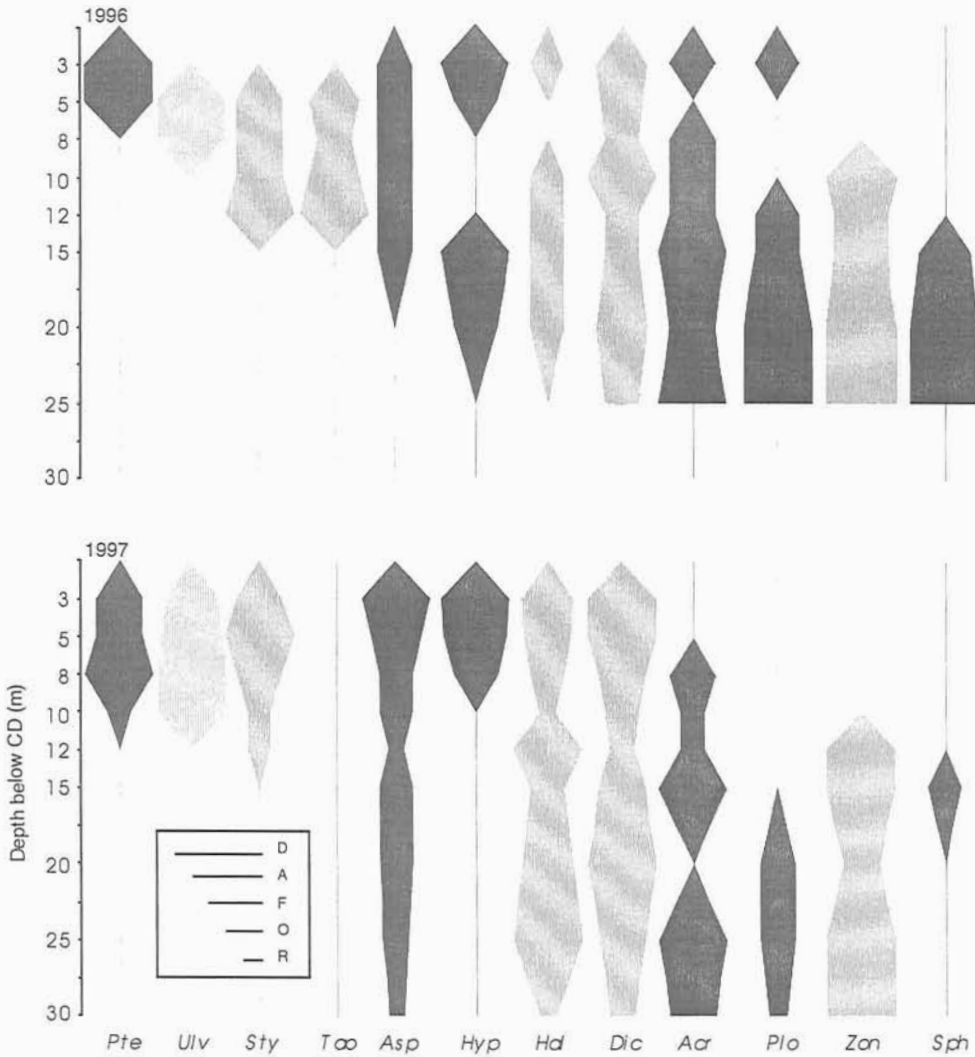
Fig. 3. Relative abundance of the more common species at each depth level in 1996 and 1997. Light grey: Chlorophyta; Medium grey: Phaeophyta; Dark grey: Rhodophyta. Pte: *Pterocladiella capillacea*; Ulv: *Ulva* spp.; Sty: *Stypocaulon scoparia*; Tao: *Taonia atomaria*; Asp: *Asparagopsis armata*; Hyp: *Hypnea musciformis*; Hal: *Halopteris filicina*; Dic: *Dictyota dichotoma*; Acr: *Acrosorium* spp.; Plo: *Plocamium cartilagineum*; Zon: *Zonaria tournefortii*; Sph: *Sphaerococcus coronopifolius*.

and *Sphaerococcus*. *Dictyota dichotoma*, *Acrosorium* spp. and *Zonaria tournefortii* had a similar abundance in both years. The species depth distribution was nevertheless not very different between the two years. In fact, the shallower levels were dominated in both years by *Pterocladiella*, *Ulva* spp., *Stypocaulon*, *Asparagopsis*, and *Hypnea*, while the lower levels were dominated by *Dictyota*, *Acrosorium* spp.

and *Zonaria*. The major differences were the abundance of *Plocamium* and *Sphaerococcus* at the lower depths in 1996 and the presence of *Asparagopsis* at all levels in 1997.

DISCUSSION

Studying the algae of the same bay in previous

years, NETO (1997) found similar results: *Pterocladiella, Stypocaulon, Asparagopsis* and *Hypnea* were the more abundant species at the shallowest level studied (5 m); *Zonaria* and *Sphaerococcus* were the dominant species at 15 m, the deepest level surveyed. A depth-related gradient in community structure was also observed. There was a gradual transition between the shallow and the deep levels. These differences between the algal associations at different depths suggests that there is a real difference in community organization as related to depth. Most descriptive studies of subtidal communities emphasize changes along such a gradient (SCHIEL & FOSTER 1986), since factors such as light and water movement (wave-exposure) are likely to be inversely related to increasing depth (ANDERSON & STEGENGA 1989). However, the fact that most species were found over a wide depth range, and that these ranges widely overlap, suggest that the vegetation changes with depth in the study areas are continuous. The same was observed by JOHN et al. (1977) in Ghana. These authors also concluded that, of all the factors analysed in their study, depth was the predominant environmental factor conditioning algal distribution.

The restriction to shallow water of certain species is probably related to changes in the quantity and quality of light, associated with increased depth (SMITH 1967; KAIN 1987). Conversely, the restriction to deeper water of many other species may be due either to intolerance to rough, turbulent water, or to an inability to compete with the abundant shallow-water macroalgae.

In the present study, the shallow levels were dominated by red algae, but below 8 m depth both brown and red algae were equally important. NETO (1997) had slightly different results but her work didn't include depths below 15 m. She found a different distribution of red and brown algae, with the first group dominating the shallower levels and the latter dominating the deeper ones. Luxuriant subtidal communities of brown algae have been found elsewhere. In Madeira, BIANCHI et al. (in press) record the dominance of *Z. tournefortii* in relatively sheltered locations, from 5 to 15 m. This species is also abundant in Mediterranean subtidal communities (GARCIA CARRASCOSA 1987),

where *Dictyopteris membranacea* is another dominant species (BALLESTEROS et al. 1984; BOISSET & GARCIA CARRASCOSA 1987; MORRI et al. 1988; BALDUZZI et al. 1994).

Zonaria and *Sphaerococcus* were the only species restricted to deep levels. NETO & TITTLEY (1995) mention *Zonaria tournefortii* as restricted to deep water (30 m) on the island of Faial. However, only the nature reserve of Monte da Guia was studied, so it is not known if this is a valid statement for all the island. On the other hand, TITTLEY et al. (1998) found this species dominating the subtidal communities of Flores Island, from shallow to deep water levels (5 to 30 m).

It is worthnoting the higher abundance of *Plocamium* at the deeper levels, confirming the status of "shade lover" given by BOUDOURESQUE (1969, 1970) merely from the evidence of its habitat. This was confirmed by KAIN (1960, 1987), SMITH (1967) and LÜNING (1970). It clearly can inhabit shallow water but is found under the laminarians and it extends into water deeper than 20 m (KAIN 1961; NORTON 1968; NORTON et al. 1969). NETO (1997) only found *P. cartilagineum* occasionally in the intertidal level, being more abundant subtidally at the deepest level surveyed at São Vicente (15 m), where it was most of the time growing in the shade of *Zonaria tournefortii*.

NETO (1997) observed stability in the communities studied. They did not exhibit major differences in species composition and abundance over the two years of investigation. The present results also suggest that, with small variations, a well established and relatively stable ecosystem is present in São Vicente bay. Surveillance over several years of rocky shores elsewhere, especially in temperate regions of the North Atlantic, indicate general stability of littoral communities, although fluctuations and cyclic changes have been observed (LEWIS 1977; HARTNOLL & HAWKINS 1985; LITTLE & KITCHING 1996). However, on those moderately exposed European shores, equivalent to the site studied on São Miguel Island, rather more variation in mosaic structure was detected (HARTNOLL & HAWKINS 1985). It would be interesting to continue the present study so as to be able to evaluate long-term fluctuations. This

should be complemented by monitoring the major environmental parameters. With the threat of a global change in climate and subsequent variations in the environmental factors, it is at present not possible to predict how the algal communities will be in the next decades.

ACKNOWLEDGEMENTS

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THE GENUS *Tesseropora* (CIRRIPEDIA:TETRACLITIDAE) FROM SÃO MIGUEL, AZORES

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The barnacle *Tesseropora* was considered as primarily an insular Indo-Pacific genus until *Tesseropora atlantica* was described from Bermuda and the Azores (S. Jorge). *T. atlantica* has also been recorded from Saint Paul's rocks (equatorial Atlantic), confirming its link with isolated oceanic islands. Recently, another *Tesseropora*, *Tesseropora arnoldi*, was described as an Azorean endemic, but as there is some doubt as to the validity of this species, we continue to refer to Azores *Tesseropora* as *T. atlantica*. Little is known of the biology of this ancient genus recorded from the Italian Oligocene. In this paper, we report on the habitat, distribution and several population parameters (relative abundance, density and size structure) of *Tesseropora atlantica* from a boulder beach at Cerco da Caloura, S. Miguel. On this shore, *Tesseropora* has a patchy distribution and is found bellow the upper limit of *Chthamalus stellatus*. Clump densities of *T. atlantica* varied between 37-66, however, nearest neighbour values indicated a rather random distribution within each patch. In addition, the morphology of external plates, examined using scanning electron microscopy, showed some differences compared with published illustrations for the two Atlantic species.

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INTRODUCTION

The genus *Tesseropora* has a long lineage being known from Italian Oligocene fossils *(T. isseli)* (NEWMAN & ROSS 1977). Primarily insular, *Tesseropora* was thought to be restricted to the Indo-Pacific region until *Tesseropora atlantica* was described from specimens collected mainly from Bermuda but also referring to Azorean material (NEWMAN & ROSS 1977). Following NEWMAN & ROSS (1977), therefore, subsequent *Tesseropora* collected from the Atlantic were assumed to be *T. atlantica*. The distribution of *T. atlantica* was extended to other Azorean islands (including S. Miguel) down to Saint Paul's Rocks in the equatorial Atlantic (EDWARDS & LUBBOCK 1983a, b). This distribution being quite remarkable for a species lacking a planktonic larval phase. Recently, YOUNG (1998) described a

new species of *Tesseropora (T. arnoldi)*, endemic to the Azores, casting doubt on the earlier records of *T. atlantica* from the Azores and St. Paul's Rocks. However, SOUTHWARD (1998), who has examined museum material from the Azores and Bermuda (including paratypes and new material), is of the opinion that most of the characters used by YOUNG (1998) to separate *T. arnoldi* are invalid and that, in particular, the differences in the labrum appear to be the result of damage to the Bermuda type used to illustrate the description by NEWMAN & ROSS (1977). Furthermore, SOUTHWARD (1998) states that the differences in the interior of the scutum are not obvious when valves of the actual type material are examined, in contrast to published drawings, as much depends on the angle of illumination used to examine them. SOUTHWARD (1998) continues to refer to the Azorean *Tesseropora* as *T. atlantica* until the

completion of a projected molecular biological study. In view of the uncertainty of the new species, we follow SOUTHWARD (1998) and refer to Azores *Tesseropora* as *T. atlantica*. Little is known of the biology of *Tesseropora*. In the current paper we report on aspects of the ecology and morphology of *T. atlantica* found on a boulder shore at Cerco da Caloura, S. Miguel.

METHODS

FIELD OBSERVATIONS

All fieldwork was carried out at Cerco da Caloura, a sheltered, gently-sloping cobble bay on the south coast of São Miguel, the largest island of the archipelago of the Azores (Fig. 1). The Azorean coastline, consisting mainly of high cliffs, rocky platforms, and boulder and cobble beaches resulting from erosion of vocanic rocks, is narrow and has limited littoral habitats (MORTON et al. 1998). The maximum tidal range for São Miguel is 1.89 m, and mean tidal ranges for neap and spring tides are 0.65 m and 1.44 m respectively (INSTITUTO HIDROGRAFICO 1981). Two transects were established (16th and 17th February 1998), each perpendicular to the sea edge, and extending from the highest point of littorinid occurrence to the lowest water level. For each transect, shore profiles were obtained using two graduated poles, each of 2 m, with an attached spirit level. These were placed at right angles at the shore position to be levelled, and the horizontal distance between the two points was read from the horizontal pole and the elevation was read from the vertical pole (EMERY 1961). The heights were related to Chart Datum (Azores) using the position of the water's edge at the time of predicted low water. Taking into account the presence of residual swell and the
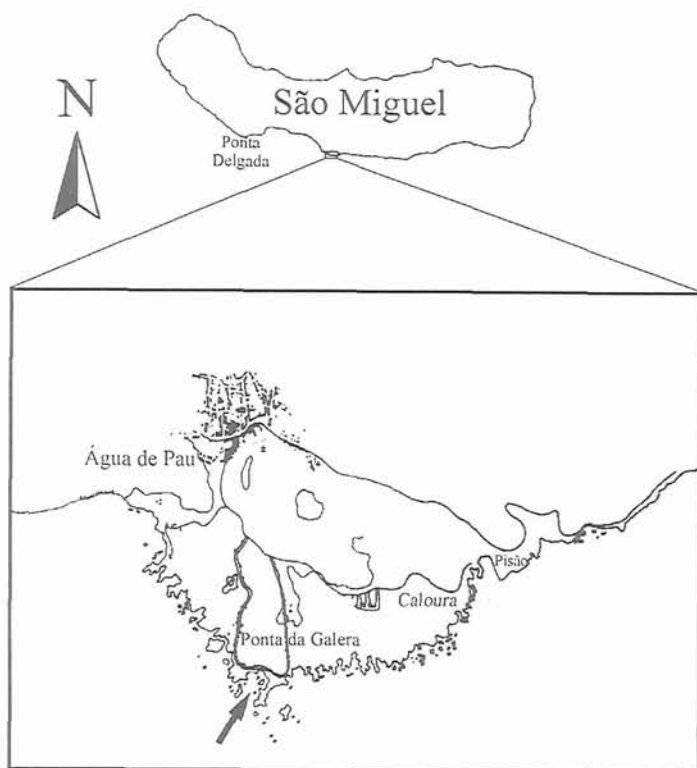
Fig. 1. Location of Cerco da Caloura in São Miguel, Azores.

methods used, shore heights are approximate ($\pm$ 0.1 m). At each sampling site along the transect (17 sites used per transect), a note was made of the macrofauna and flora, with no attempt to quantify surface cover or densities.

Having established the vertical distribution of *T. atlantica*, density and Nearest Neighbour measurements were taken. The presence of boulders made quantitative sampling very difficult and random density counts of barnacle abundance were not attempted. Instead, density counts (taken in July 1997, and February and May 1998) were based upon positioning a 10 x 10 cm quadrat on different rocks with *Tesseropora*. Hence, our density measures varied depending on the presence of other sessile animals (*Spirorbis* sp. & *Chthamalus stellatus*), and give indications of the maximum abundances for *Tesseropora*. At the same time as the densities were recorded, the lengths of all *T. atlantica* on each rock were measured using hand-held vernier calipers;

Nearest Neighbour measurements were taken in July 1997.

Barnacles, attached to their original rocks, were transported from Cerco da Caloura (July 1997) to the laboratory in seawater. In the laboratory, they were removed from the rock using a scalpel blade, fixed in 4% seawater formalin and dissected from their shells. Entire animals, together with the shell plates, were dehydrated in a series of increasing alcohol concentrations (10 min in each of 30%, 65% and two changes in 100% alcohol). Following dehydration, the shells and animals were placed (10 min in each mixture) in 50% alcohol: 50% acetone followed by two changes of 100% acetone. Finally, the shells and barnacles were placed for 20 mins in a 98% solution of hexamethyldisilane. The material was mounted on specimen stubs, coated with carbon and gold-palladium (60:40%) in a vacuum evaporator (JEE 400) and viewed with a JEOL SEM (JSM 5410).

RESULTS AND DISCUSSION

HABITAT OF *Tesseropora*

At Cerco da Caloura, the boulders tend to mask zonation patterns but three general "zones" may be distinguished. At the lowest level, the rocks are covered with a red algal turf comprising *Corallina officinalis* L. and *Gigartina acicularis* (Roth). The middle "zone" is characterised by tufts of the green alga *Ulva rigida* Agardh and the third, uppermost level, is devoid of macroalgae. On each transect, *T. atlantica* was found within the lower region of the "*Ulva* zone", generally below *Chthamalus stellatus*, although the distribution of the two species does overlap (Fig. 2). This zonation confirms the observations of SOUTHWARD (1998) who found *T. atlantica* on the outer steps of the breakwater at Ponta Delgada (São Miguel) and in the algal turf below *C. stellatus* at Porto Pim (Faial). At Cerco da Caloura and Ponta da Queimada (Água d'Alto), *T.*

atlantica is always found in crevices, on the shaded aspects of boulders and on the underside of cobbles. On these shores, individuals found towards the lower level were larger than those seen at the upper distributional limits. In the *Ulva* zone, limpets (*Patella candei*) and chitons were also found on the rocks colonized by *T. atlantica*. The underside of cobbles, where *T. atlantica* was found, was also covered with sponges and vermetid and serpulid polychaetes. In Ponta da Queimada (Água dAlto), not only could we find *T. atlantica* and *Chthamalus* on the same cobble, but also *Verruca spengleri* was frequently encountered. Interestingly, at Porto Pim, *T. atlantica* formed contiguous clusters in the holes formed by small individuals of the sea urchin *Paracentrotus lividus* (SOUTHWARD 1998). Earlier records from the Azores indicate that *Tesseropora* sp. was locally abundant at one site in Urzelina (S. Jorge) where it was found in 1 m of water (BAKER 1967). Although the data are sparse, it appears that *T. atlantica* is intolerant to water loss despite the presence of a calcareous basis, generally regarded as an adaptation to reduce desiccation stress (NEWMAN & ROSS 1977). YOUNG (1998) reported *T. arnoldi* extending from the intertidal to about 25 m depth, usually attached to *Megabalanus azoricus* and mollusc shells.

The distribution of *Tesseropora atlantica* at Cerco da Caloura was patchy and clump densities (numbers of barnacles in 10 x 10 cm quadrats) varied between 37 and 66. Nearest Neighbour values (ca. 1.6) indicated a more random than clumped distribution within each patch.

The maximum size of *Tesseropora atlantica* from Cerco da Caloura was 4.5 mm, with a mean of 2.6 mm (Fig. 3); these are the smallest sizes reported for *Tesseropora*. Although NEWMAN & ROSS (1977) do not give extensive measurements, they state that the largest basal diameter for *T. atlantica* was 10 mm (compared with maxima of 30 mm for *T. rosea* and 40 mm for *T. wireni*). SOUTHWARD (1998) gives a size range of 1.5-6.5
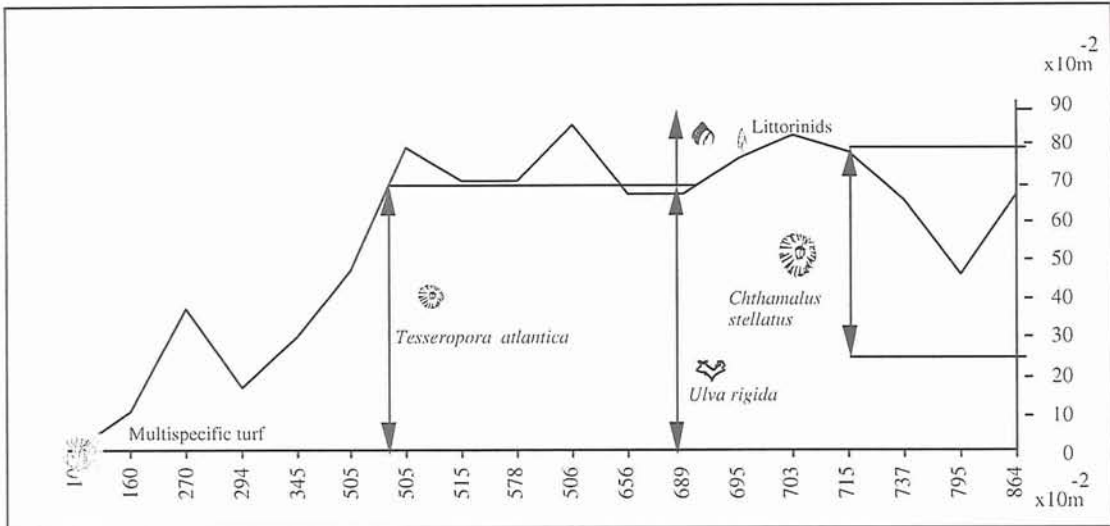
Fig. 2. Zonation of *Tesseropora atlantica* on the shore.

mm with a mode around 3.5 mm for the animals he collected in the Azores, and reported a maturity size of 4 mm shell length. YOUNG (1998) refers to a carino-rostral diameter of about 5 mm for *T. arnoldi* and only one specimen measured 7 mm.

BIOLOGY OF *Tesseropora*

Both *Tesseropora atlantica* and *T. arnoldi* have suppressed development with the nauplius being retained in the mantle cavity (SOUTHWARD 1998; YOUNG 1998). The same was reported for *T. wireni* (NEWMAN & ROSS 1877). SOUTHWARD (1998) observed that, within 24 h of release, the cyprids (carapace length of 0.63 mm) of *T. atlantica* underwent searching behaviour which continued for a further 24 h although no settlement or metamorphosis was seen. Lack of a dispersal phase in the life cycle of barnacles occupying isolated oceanic islands is intepreted as an adaptation for maintaining insular populations (NEWMAN & ROSS 1977). For example, the risk of loss of propagules from donor populations is removed. Such species will also have restricted genetic pools and it is to be anticipated that they will show high levels of endemism.
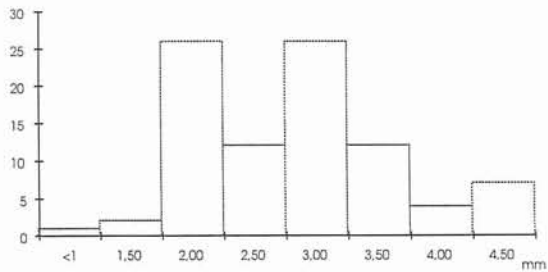
Fig. 3. Size frequency of *Tesseropora atlantica* from Cerco da Caloura.

SPECIES OF *Tesseropora*

Currently, four extant species of *Tesseropora* are described, *T. rosea*, *T. wireni*, *T. atlantica* and *T. arnoldi*. *T. rosea* is restricted to the southernhemisphere, and has been recorded from the southern tip of South Africa, New South Wales (Australia), the Kermadec Islands and New Caledonia. The other species are distributed mainly in the northern hemishere. *T.wireni* is found from Dar-es-Salaam east, and from Chagos Bank to Wake. Specimens of *T. wireni* from Hawaii do not appear to be typical for this species and may be a new species (NEWMAN & ROSS 1977). *T. atlantica*, believed to be a relict species surviving from the Sea of Tethys (NEWMAN & ROSS 1977), occurs in Bermuda (type locality),

and has been reported from the Azores (NEWMAN & ROSS 1977; SOUTHWARD 1998) and from Saint Paul's Rocks (equatorial Atlantic) (EDWARDS & LUBBOCK 1983a,b). (Since the description of *T. arnoldi*, however, there remains a question mark over these last two records.) Finally, *T. arnoldi*, endemic to the Azores, has been found on two islands (Faial and S. Miguel) (BAKER 1967; YOUNG 1998).

MORPHOLOGY OF *Tesseropora*

NEWMAN & ROSS (1977) listed the distinguishing features of extant species of *Tesseropora*, some of which are shown in Figure 4 together with the corresponding plates for the new species, *T. arnoldi* (YOUNG 1998). The most obvious difference between *T. atlantica* and the other non-Atlantic species is the differential alignment of the scutal adductor ridge with the articular ridge. In *T. atlantica*, the adductor ridge is in line, and nearly continuous, with the articular ridge whereas in the other species it overlaps the articular ridge. In *T. arnoldi*, the adductor ridge is separated from the articular ridge (YOUNG 1998). Another distinguishing feature relates to the parietal pores (Fig. 4). In *T. atlantica* and *T. arnoldi* the pores are in a single row as they are in *T. rosea*, however, the very different geographical distributions of this latter species prevents confusion. The parietal pores *of T. wireni*, on the other hand, are divided into secondary and tertiary rows leading to a dendritic pattern. All the other *Tesseropora* species have only one row of parietal pores (NEWMAN & ROSS 1977; YOUNG 1998). *T. arnoldi* can also be distinguished from Pacific *Tesseropora* (*T. rosea* and *T. wireni*) by the colour of the sheath, the development of the radii and the parietal tubes, and the structure of the cirri (NEWMAN & ROSS 1977; YOUNG 1998). Distinctions of *T. arnoldi* from *T. atlantica* reported by YOUNG (1998) include the well developed ribs from the basis to the sheath, intercalated by numerous fine ribs instead of only small numerous fine ribs; the position of the adductor ridge of the scutum in relation to the articular ridge; and the presence of conspicus teeth on the crest.

Despite the erection of *T. arnoldi* as an Azorean endemic, there are clear differences in the morphology of the opercular and lateral plates of *Tesseropora atlantica* from Cerco da Caloura (Fig. 5) and those of *T. arnoldi* described by YOUNG (1998) from the Azores (Fig. 4). More detailed descriptions of the critical distinguishing features (labrum, opercular plate, cirri) are required before concluding whether there are two species of *Tesseropora* endemic to the Azores or whether there is a high degree of polymorphism in Azorean *Tesseropora*. In the light of our findings, it is clear that a comprehensive review of the genus is required.

CONCLUSIONS

The taxonomy of genus *Tesseropora* requires careful re-appraisal in the light of the recent description of *T. arnoldi*, one of the limited number of littoral marine invertebrate Azorean endemics. Moreover, the doubts raised by SOUTHWARD (1998) and the current work, demand a very careful study of the morphology of the critical distinguishing features of these barnacles.

AKNOWLEDGEMENTS

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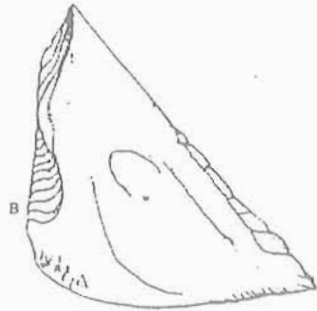
Tesseropora atlantica
(Bermuda; Newman & Ross, 1977)
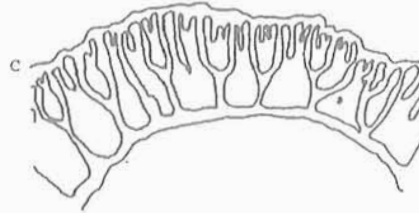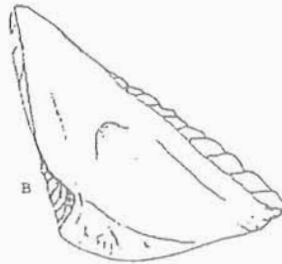
Tesseropora arnoldi
(Azores; Young, 1998)
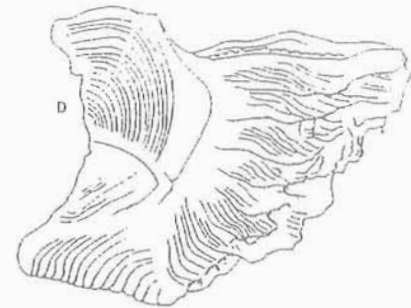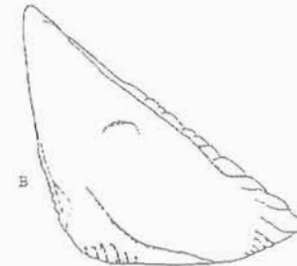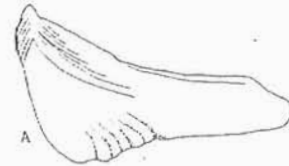
Fig. 4. Key characteristics of *Tesseropora atlantica*. Internal view of plates: A. Right tergum. B. Right scutum, D. Lateral, C. Parietal pores.
After NEWMAN & ROSS (1977) and YOUNG (1998).
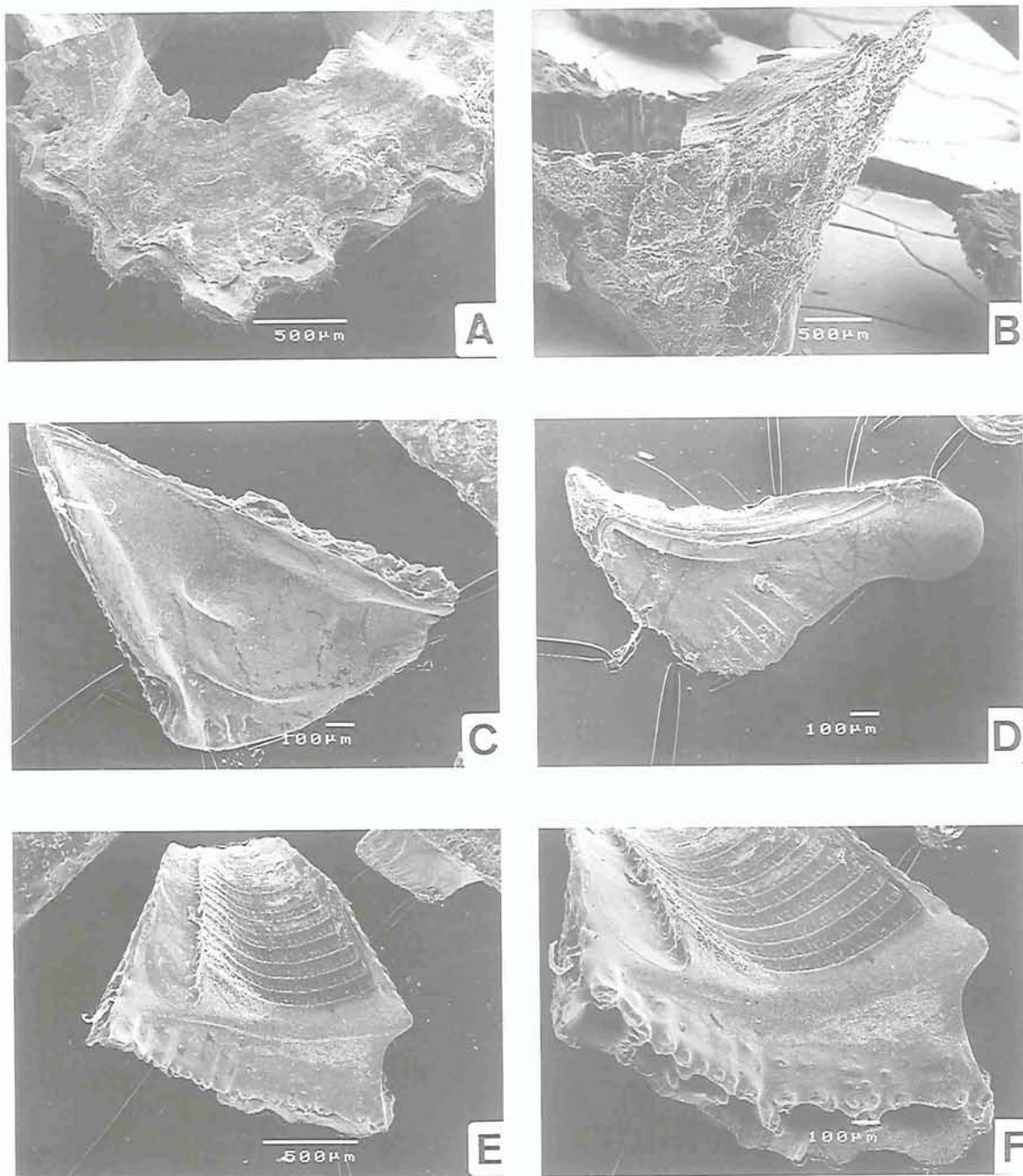
Fig. 5. Scanning Electron Microscopy (SEM) pictures of *Tesseropora atlantica* from Cerco Caloura. A, B Calcareous basis; C, D Internal view of opercular plates; E, F Internal view of lateral plate.

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ENDEMISM AND MODES OF DEVELOPMENT OF MARINE PROSOBRANCH GASTROPODS (MOLLUSCA) FROM OCEANIC ISLANDS OFF BRAZIL

JOSÉ H. LEAL

The endemism rates and the relationships between modes of development and endemism of shallow-water (<200 m) prosobranch gastropod assemblages from oceanic islands off Brazil (302 species) are assessed. Endemism rates are 5.1% (Fernando de Noronha), 8.1% (Atol das Rocas), 9.4% (Martin Vaz), and 16% (Trindade). When studied as "island groups" Rocas and Noronha (northern group) show a combined endemism rate of 19.2%, and Trindade and Martin Vaz (southern group) of 18.3%. To test the hypothesis that endemics are mostly species with non-planktotrophic development, the basic mode of development was determined for each species. Frequencies of each mode of development were analyzed for the two island groups. Non-planktotrophic species were more frequent among the insular endemics in both island groups when compared to the entire prosobranch faunas: frequencies of non-planktotrophic species at the northern and southern groups are, respectively, 84.2 and 71.4% for endemics, 60.1 and 51.7% for all species. In contrast to planktotrophic species, which have higher dispersal abilities, inception of insular endemism in non-planktotrophic species may be favored by effective reproductive isolation, offspring retention, and allopatric speciation in the absence of repeated arrivals on the islands.

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INTRODUCTION

Since DARWIN'S (1870) observations on the fauna and flora of the Galapagos and other oceanic islands, insular assemblages of animals and plants have been considered as modified and impoverished renditions of the assemblages living in the nearest continental mass. As many authors did before him, LEAL (1991a) has shown that this applies to the shallow-water (<200 m) marine gastropods from the oceanic islands off Brazil (Atol das Rocas, Fernando de Noronha, Trindade, and Martin Vaz), in the south-western Atlantic Ocean. In spite of these expected similarities to adjacent landmasses, chance arrivals on islands when followed by reproductive isolation will eventually lead to genetic divergence from the parental populations and allopatric speciation. The number of endemic species will be directly correlated with the area, age, degree of isolation

(distance from nearest source) of the islands (MACARTHUR & WILSON 1967), and other variables.

Starting with pioneer studies of THORSON (e.g., 1950, 1961), the relationship between geographic range and mode of development of marine invertebrates has been reasonably well established. Larval transport (dispersal) by ocean currents leads to increased opportunity for genetic exchange between separated populations of species with pelagic larval lives of longer duration (plankton-feeders, or planktotrophs). Planktotrophs are less prone to reproductive isolation and allopatric speciation due to enhanced probabilities for maintenance of genetic integrity via dispersal (JABLONSKI & LUTZ 1983; SCHELTEMA 1971). Species showing planktotrophic development will generally be more broadly distributed geographically. Conversely, species with planktonic larval lives of short duration (pelagic lecithotrophs) or absent

Fig. 1. Location of the study islands (names italicized) in relation to other major Atlantic volcanic islands and archipelagos.

females transported by rafting) of non-planktotrophic species will more likely provide successful founders than frequent arrivals of larvae of planktotrophic species. Due to their decreased ability for dispersal after a rare arrival (increased retention of offspring), speciation rates should be higher for newly arrived non-planktotrophs (ABBOTT 1966; HADFIELD et al. 1972; HOURIGAN & REESE 1987; JOHANNESSON 1988; REID 1996; SAFRIEL & HADFIELD 1988; SCHELTEMA 1986; STRATHMANN 1986).

If it is true that non-planktotrophs generally have narrower geographic ranges, are more apt as coloniser species, and show higher speciation rates than planktotrophs, then in any given location the subset of narrowly distributed or endemic species should show higher frequency of non-planktotrophs when compared to all prosobranchs present—assemblages of insular endemics from any oceanic island should expectedly present a higher frequency of non-planktotrophs than that computed from the entire prosobranch fauna of that island.

Since the publication of LEAL (1991a) on the prosobranchs of Brazilian islands, a number of papers dealing with or affecting the systematics and biogeography of these species have been or are being published (e.g., ABSALÃO & GOMES in press; ABSALÃO & RIOS 1995; HARASEWYCH et al. 1992; HOUART 1991; LEAL 1991b; MCLEAN in preparation; QUINN 1991; 1992a; 1992b; ROLÁN 1991; 1994; VERMEIJ & SNYDER 1998). A goal of the present study is to reassess the rates of insular endemisms based on the above mentioned new data. It also aims to evaluate and further explore the relationships between insular endemism and the two basic modes of development found in prosobranch gastropods from the Brazilian oceanic islands.

(those undergoing intracapsular metamorphosis) usually have narrower geographic distribution (HANSEN 1980; JABLONSKI & LUTZ 1983). But exceptions to this inverse relationship between length of larval life and extent of geographic range are known occur at least in the gastropod genera *Littorina* (JOHANNESSON 1988; REID 1996), *Dendropoma* (SAFRIEL & HADFIELD 1988), in the bivalve genus *Lasaea* (Ó FOIGHIL 1989), and in north temperate (VERMEIJ et al. 1990) and subantarctic (ARNAUD 1974) islands. Successful colonisation will depend not only upon chance dispersal, but also upon the establishment of viable populations; it has been suggested that rare arrivals (e.g., of gravid

An earlier listing of the material examined in this study was provided by LEAL (1991a). That earlier listing has, however, been modified to include data from the works mentioned above. An updated electronic version can be obtained from the author upon request. The material examined includes all records of shallow-water (<200 m) Brazilian insular prosobranch gastropods deposited in the collections at: American Museum of Natural History, New York (AMNH); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museu Oceanográfico, Fundação Universidade do Rio Grande, Brazil (MORG); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington (USNM). Also included are the stations made off Trindade and Martin Vaz Islands during the cruise MD55 of the French R/V *Marion-Dufresne*, in May 1987, and material collected by the author on the islands in 1982–87 and deposited in the above institutions. A commercially available relational database software was used in the assessment of endemism rates (frequencies of endemic species among all species occurring in a group of islands).

MODES OF DEVELOPMENT

Assessment of modes of development was made (1) from literature data for species with known life histories, (2) through comparisons of protoconch/larval shell between a species in this study and a close relative with known life history, (3) by complete inference from protoconch morphology. Mollusk shells are characterized by accretionary growth, which allows for retention of the embryonic and larval shell on the apical region of the adult shell. Inspection of the thus preserved sequence of embryonic and larval shells, or protoconch, allows for inference of basic modes of development (BOUCHET 1989; JABLONSKI & LUTZ 1983; LEAL 1991a; LEAL & BOUCHET 1991; SHUTO 1974; THORSON 1950). Species with
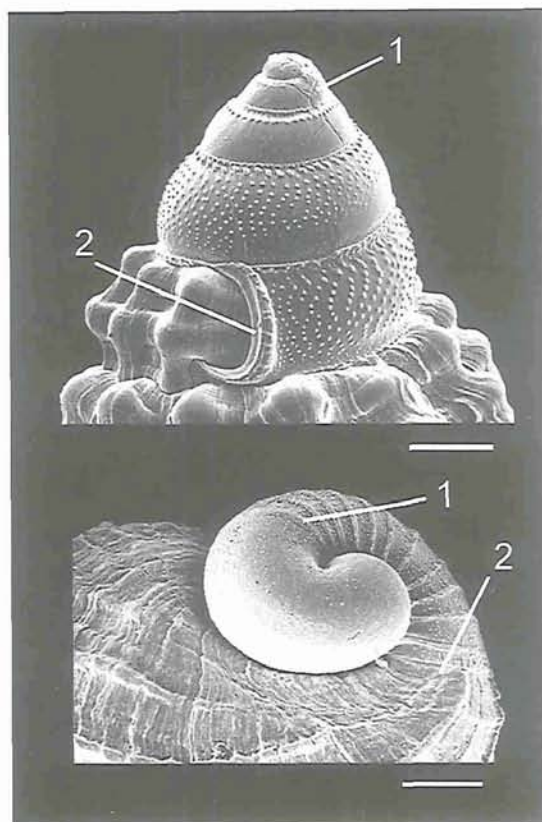
Fig. 2. Examples of the types of protoconchs representing the two basic modes of development of marine gastropods: top, *Trachypollia turricula* (von Maltzan, 1884), family Muricidae, Trindade Island, planktotrophic, with amphi-Atlantic distribution. Scale line = 200 µm; bottom, *Capulus* sp., family Capulidae, Fernando de Noronha, non-planktotrophic, restricted to SW Atlantic Ocean. Scale line = 100 µm. Lines indicate transition between (1) embryonic and larval shells and (2) larval shell and teleoconch. Note small size of embryonic shell of *T. turricula*, and its large number of whorls (4.25) when compared to number of whorls (1.5) on *Capulus* sp.

planktotrophic development have protoconchs usually elaborately sculptured and with many whorls (Fig. 2, top), usually more than 3. Planktotrophic larval shells are usually divided into a small embryonic whorl (due to the lack of a yolk sac in the embryo), followed by the true larval shell. (After settlement, the embryonic shell remains as the protoconch 1, and the true larval

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shell as the protoconch 2.) Species with lecithotrophic (intracapsular or pelagic) development, on the other hand, do not feed on external sources before metamorphosis to the bottom environment, relying instead on a reserve of yolk. The embryonic part of the shell is usually large (Figure 2, bottom) (to accommodate the yolk sac), and the shorter duration of planktonic life is reflected into a smaller number of whorls, usually not more than 2–2.5. The transition between embryonic and true larval shells in non-planktotrophs is usually blurred.

Observations of protoconchs and larval shells in this study were made under scanning electron microscope at the Rosenstiel School of Marine and Atmospheric Science, University of Miami. Number of protoconch whorls was determined following the methods of HANSEN (1980), MAES (1983), and JABLONSKI & LUTZ (1983). An annotated list of species with comments on the modes of development of each species was given by LEAL (1991a). All computations were made with using a commercially available relational database software. Computation of frequencies includes only species for which the mode of development could be determined.

STUDY SITES

The islands in this study are divided into two groups, due to geographic contiguity (Figure 1). Moreover, members of each of the two groups (see below) had similar origins as a result of the initially northwestward then westward motion of the South American tectonic plate, relative to the African plate, over two fixed hotspots (MORGAN 1983; VINK et al. 1985). For more detailed descriptions and literature of the study sites see LEAL (1991a) and LEAL & BOUCHET (1991) and the references cited below.

The Northern Group - Atol das Rocas and Fernando de Noronha.

Atol das Rocas is located at 3°52'S, 33°49'W, lying about 200 km off the coast of NE Brazil. Its bulk consists of a mixed coralline algal/vermetid reef with the ring shape characteristic of coral atolls. The atoll measures about 3.5 km in diameter, with an emerged surface at mean tide of about 7.2 km^2. It constitutes the lifted part of a much larger, relatively shallow, calcareous platform that sits on top of a submarine seamount. Sediment dredged along the bottom of the platform consists basically of calcareous sand and nodules of coralline red algae in the genus *Lithothamnium*. The age of its foundation of basaltic rock situated 80 m below sea level is unknown (OTTMANN 1963; FAIRBRIDGE & GORINI 1975).

Fernando de Noronha, located at 3°50'S, 32°25'W and about 345 km off the NE Brazilian coast, consists of a small archipelago with Fernando de Noronha Island occupying more than 95% of its emerged area, which totals 18.4 km^2. Unlike Atol das Rocas, which probably represents an older structure, situated "downstream" in their hotspot track, Fernando de Noronha is a high volcanic island. Radiometric dating has indicated that the oldest rocks in its three major volcanic formations are 8–11 million years old (Late Miocene). The bottom around Fernando de Noronha is characterized by extensive vermetid reef formation as well as *Lithothamnium* patch reefs. The prevailing soft sediment is calcareous sand. It represents the present location of the hotspot that formed the "northern" hotspot track (ALMEIDA 1958; FAIRBRIDGE & GORINI 1975; MORGAN 1983).

The Southern Group - Trindade Island and Martin Vaz Islets.

Trindade Island is located at 20°30'S, 29°20'W, lying about 1140 km off the eastern Brazilian coast. It has an area of about 8 km^2. The island is the top of a volcanic cone rising from the ocean floor at 5.5 km depth. Most of the rocks above sea level are 2.3–2.9 million years old (Pliocene). Sediments at the narrow insular shelf consist mostly of calcareous sands, conglomerates and fragments of *Lithothamnium*, and fronds and fragments of the calcareous green alga *Halimeda tuna* Lamoroux (ALMEIDA 1961; CORDANI 1970; LEAL 1988).

Martin Vaz, consisting of three small volcanic islets, is located at 20°30'S, 28°51'W. The main islet measures about 0.6 km in maximum diameter. The three islets rise from a truncated seamount that measures about 3 km in diameter. The seamount represents the present location of the hotspot that formed the "southern" hotspot track and, like Trindade, dates from the Pliocene (ALMEIDA 1961; CORDANI 1970; MORGAN 1983). Dredgings made around the islets in 1987 (LEAL 1991a) by a French-Brazilian team that included the author indicate that the prevailing soft substrate consists of calcareous sand intermixed with volcanic gravel and pebbles.

RESULTS

A total of 302 prosobranch species were considered in this study. Of these, 86 occur at Atol das Rocas, 117 at Fernando de Noronha, 94 at Trindade, and 53 at Martin Vaz. When considered as island groups, the northern group (Atol das Rocas + Fernando de Noronha) yielded a total of 145 species occurring at one or both islands. The southern group (Trindade + Martin Vaz) was represented by 120 species occurring at one or both localities. Endemisms computed for the islands separately (Figure 3, top) are: 8.1% (7 species) at Atol das Rocas, 5.1% (6 species) at Fernando de Noronha, 16% (15 species) at Trindade, and 9.4% (5 species) at Martin Vaz. Again, when examined as island groups (Figure 3, bottom), the rate of endemism was 19.2% (23 species) at the northern group and 18.3% (22 species) at the southern group.

Modes of development were assessed and quantified as numbers of species (Figure 4, top) and frequencies (Figure 4, bottom) of planktotrophs and non-planktotrophs. The computation of frequencies includes only species for which the mode of development could be determined. Of all 145 species from the northern group, 55 species (39.9%) were planktotrophs, 83 (60.1%) non-planktotrophs, and 7 species remained undetermined. Among the endemic species at the northern group, 3 species (15.8%) were planktotrophs, 16 (84.2%) non-planktotrophs, and 4 species remained

undetermined. Of all 120 species from the southern group, 57 species (48.3%) were planktotrophs, 61 (51.7%) non-planktotrophs, and 2 species remained undetermined. Among the endemic species at the northern group, 6 (28.6 %) were planktotrophs, 15 (71.4%) non-planktotrophs, and 1 species remained undetermined.

DISCUSSION

ENDEMISMS

Additions to the database since its publication (LEAL 1991a) caused the number of entries to increase from 297 to 302. These 5 additions result from the later publications by authors working on species from the Brazilian insular fauna (see listing in Introduction). Also an overall increase
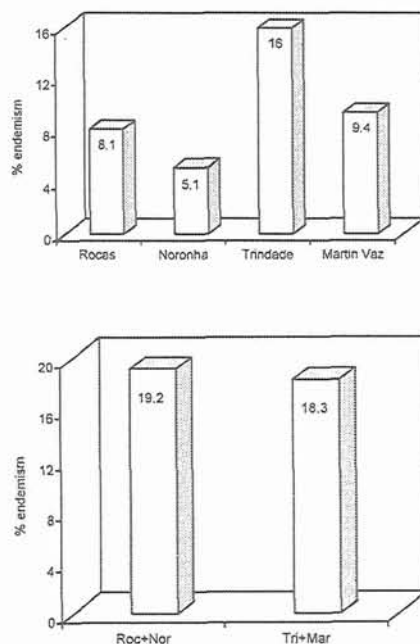
Fig. 3. Endemism rates calculated (endemic species/all species) in separate for the (top) main four study islands and (bottom) jointly for the northern (Atol das Rocas + Fernando de Noronha, **Roc+Nor**) and southern (Trindade + Martin Vaz Islets, **Tri+Mar**) island groups.
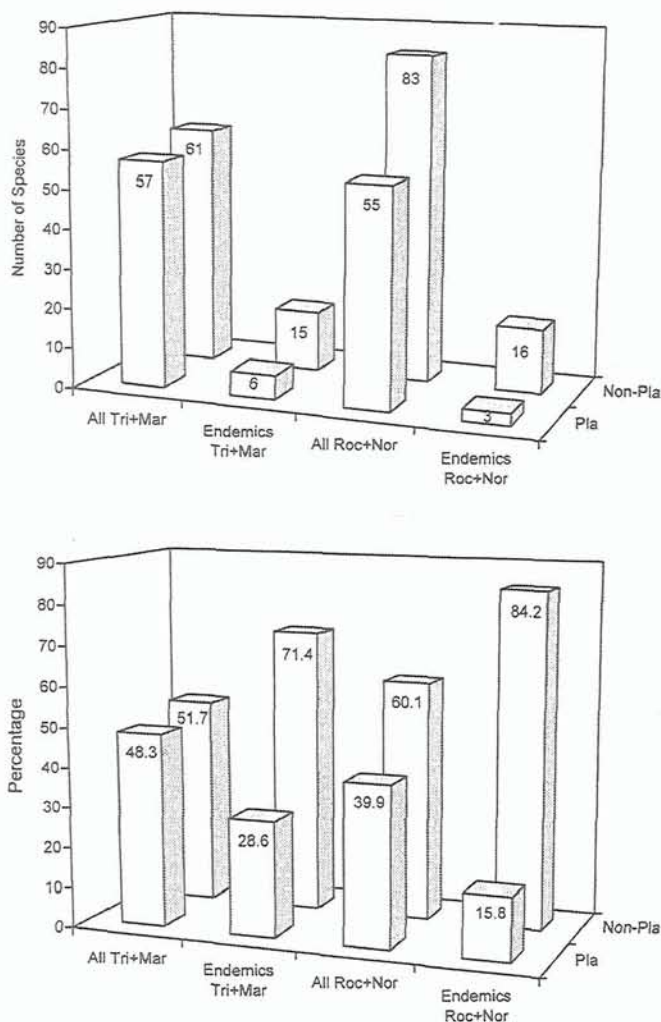
Fig. 4. Number (top) and frequencies (bottom) of basic modes of development (planktotrophic, **Pla** or non-planktotrophic, **Non-Pla**) for all species and endemics only occurring at the northern (Atol das Rocas + Fernando de Noronha, **Roc+Nor**) and southern (Trindade + Martin Vaz Islets, **Tri+Mar**) island groups.

change, remaining at 16%. LEAL (1991a) did not study the islands combined as island groups.

It is not an objective of this study to examine data under the assumptions of the classical theory of island biogeography (MACARTHUR & WILSON 1967). Nonetheless, it is possible that the slightly larger endemism rates of prosobranchs found at the southern group (when island rates are examined in separate) may have been determined by their greater distance from the closest landmass, represented by the Brazilian coast and continental shelf areas. Within a global framework, the prosobranch endemism rates at the two island groups (northern, 19.2%; southern 18.3%) are larger than at younger Ascension Island (12%, ROSEWATER 1975). But they are smaller than those of more isolated islands of the Hawaiian Archipelago (21%, KAY & PALUMBI 1987), Galapagos Islands (27%, FINET 1989), or than the molluscan endemisms of the Marquesas (20%, REHDER 1968), Kermadec (34%, DELL 1957), and Easter Island (42%, REHDER 1980).

MODES OF DEVELOPMENT AND ENDEMISMS

Frequency data in Figure 4 (bottom) show that there is a substantial increase in the ratio non-planktotrophs/planktotrophs among endemic species when compared to all prosobranch species both at northern and southern island groups. Although the type of data and sample size hamper statistical evaluation of the statistical significance of these differences, non-planktotrophs appear to be better represented within the assemblages of insular endemics. Although the overall ratio

in the taxonomic resolution of the database as it was originally established resulted from redefinition of some species, changes in knowledge about the geographic ranges of other species, and other alterations. The above mentioned alterations of the database caused the endemism rates to fall since its original publication at Martin Vaz from 15% to 9.4%, at Rocas from 14 to 8.1%, at Fernando de Noronha from 9 to 5.1%. The rate at Trindade did not

planktotrophs/non-planktotrophs in tropical oceanic islands may in some cases be higher when compared to adjacent continental areas (KAY & PALUMBI 1987; PERRON & KOHN 1985; REID 1985; SCHELTEMA & WILLIAMS 1983; TAYLOR 1971), retention of offspring, reproductive isolation, speciation and endemism rates in many groups of organisms should be higher for non-planktotrophs (ABBOTT 1966; HADFIELD ET AL. 1972; HOURIGAN & REESE 1987; JOHANNESSON 1988; REID 1996; SAFRIEL & HADFIELD 1988; SCHELTEMA 1986; STRATHMANN 1986). Increase in frequency of non-planktotrophs among endemics may be a result of rare chance arrivals followed by enhanced reproductive isolation in the absence of repeated, steady input via dispersal from external sources (which is consistent for planktotrophic, but reduced or absent in non-planktotrophic species) and repeated arrivals. Because some of the insular non-planktotrophic endemics are closely similar to non-insular planktotrophic species (sometimes differing conchologically from them only by protoconch morphology), it is also possible that these non-planktotrophic endemics derived from a planktotrophic ancestor that lost its free-feeding mode of development in conditions of enhanced isolation.

ACKNOWLEDGEMENTS

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ADDITIONS TO THE KNOWLEDGE OF THE OPISTHOBRANCH MOLLUSCS OF SELVAGENS ISLANDS, NE ATLANTIC, PORTUGAL

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MALAQUIAS, M. A. E. 2000. Additions to the knowledge of the opisthobranch molluscs of Selvagens Islands, NE Atlantic, Portugal. *Arquipélago*. Life and Marine Sciences. Supplement 2(Part A): 89-97. Ponta Delgada. ISSN 0873-4704.

During April 1996, the Museu Municipal do Funchal (História Natural) carried out an expedition ("Selvagens 96") to the Natural Reserve of Selvagens Islands. This expedition is part of a larger research program addressing the taxonomic, systematic and biogeographic issues concerning the opisthobranch molluscs of Macaronesian Archipelagos. During the "Selvagens 96" expedition, infralittoral communities of Selvagem Grande and Selvagem Pequena were sampled for opisthobranch molluscs, by SCUBA diving to a depth of 20 m. Specimens collected were examined, *in vivo*, under a stereomicroscope, and their exterior morphology was recorded in photographs and drawings; at the same time, other meaningful characters were also registered. Individuals assignable to a total of 10 species of opisthobranch molluscs from five orders were collected (2 from Cephalaspidea, 1 from Anaspidea, 2 from Notaspidea and 5 from Nudibranchia). Of these species, 4 are first records for the Selvagens Islands: *Berthellina edwardsi*, *Pleurobranchus garciagomezi*, *Chromodoris purpurea* and *Spurilla neapolitana*. The known distribution for the 10 species is given.

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INTRODUCTION

Within the framework of the research program "Opistho-Madeira" (Systematics and Biogeography of the Opisthobranch Molluscs of Macaronesian Archipelagos), the Museu Municipal do Funchal (História Natural) organised between 20 and 27 April 1996 the second expedition to Selvagens islands, nicknamed "Selvagens 96".

Selvagens islands are formed by two main islands, Selvagem Grande and Selvagem Pequena, and many islets closeby, of which we mention Ilhéu de Fora due to its larger dimensions and its biogenetical importance. This group of islands, is located 160 miles South of the Madeira archipelago, at the limit of the submarine platform of the Canary Islands, among the parallel 33° 09'N and 30° 01'N and the meridians 15° 56'W and 16° 03'W (Fig.1).

The Selvagens Islands, as well as the remaining Macaronesian archipelagos are influenced by the general circulation of the North Atlantic surface currents, being under the direct or indirect influence, of superficial currents such as the Gulf Stream, the North's Atlantic current, the Azores current, the Portugal current, the Canary current and probably of some currents that derive from the Mediterranean Sea to the Atlantic ocean (ANÓNIMO 1979; GARCÍA-TALAVERA 1983).

Macaronesian archipelagos thus have a non-negligible importance in the larval dispersal of species from various geographical origins; they may in fact act as "stepping stones" for the colonisation of new areas (GARCÍA-TALAVERA 1983). These circumstances determine the existence of faunal elements common to geographical regions as diverse as Europe, Africa and the Caribbean Sea which give these archipelagos a remarkable biogeographical importance.
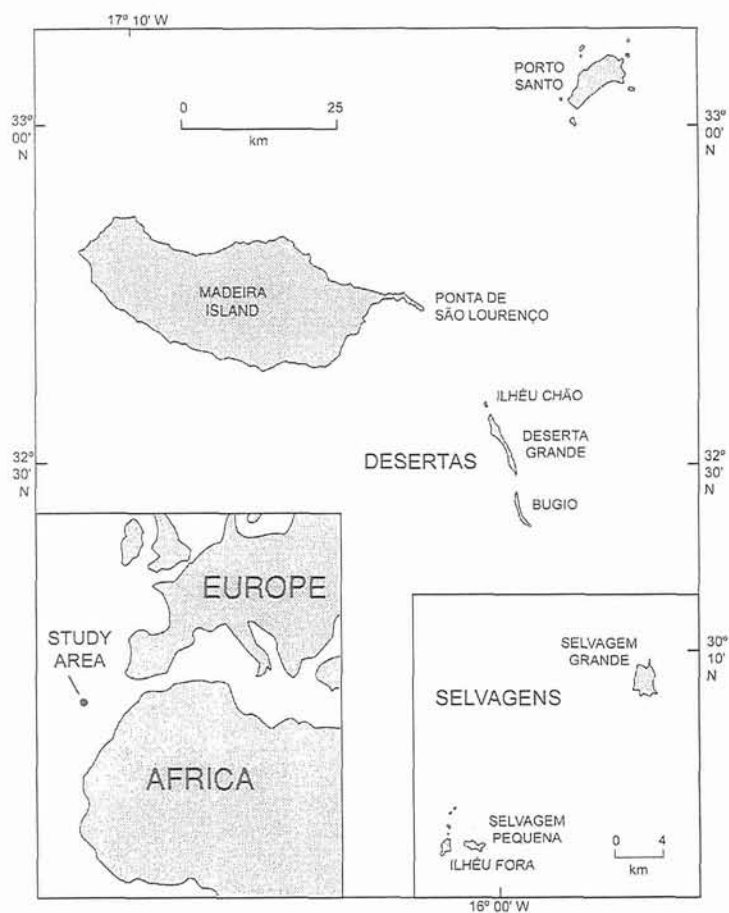
Fig. 1. Map of Selvagens Islands (adapted from ZINO and BISCOITO 1994)

MALAQUIAS & CALADO 1997), mention them for the Selvagens islands, a total of 34 species being listed.

The present paper represents an improvement in the situation and contributes to the taxonomic and zoogeographical knowledge of the opisthobranch molluscs of Macaronesia.

STUDY AREA

The study area includes one location in Selvagem Pequena and three sites in Selvagem Grande (Fig. 2), with a total of five sampling efforts.

MATERIALS AND METHODS

On the intertidal zone, small rock pools and their walls were searched. Infralittoral samplings were carried out by SCUBA diving to a depth of 20m. Whenever possible, rocky walls and surfaces of variable slope and lighting conditions were inspected and the specimens were individually collected. The underside of movable stones and small boulders, usually rich in sessile organisms, were also inspected.

Collected samples were subsequently screened at the field laboratory set up at The Natural Reserve's facilities. Opisthobranchs were identified, if possible, and their external morphology recorded, either by photography or by drawing the general appearance of the individual as well as details of meaningful external structures. In order to make this easier, specimens were anaesthetised with 7% magnesium chloride dissolved in running water. After the above procedures, specimens were preserved in 70% ethanol.

Recently, opisthobranch molluscs of these archipelagos have been receiving considerable attention and, as a consequence, numerous new species were described and several faunal inventories were published. Among these we can mention on account of their importance, ORTEA & BACALLADO (1981), SÁNCHEZ et al. (1987), CERVERA et al. (1988), ORTEA (1981; 1990), ORTEA & MARTÍNEZ (1991), MORO et al. (1995), ORTEA et al. (1996a; 1996b, 1997), MALAQUIAS & CALADO (1997) and WIRTZ (1998, 1999).

The malacological fauna of the Selvagens islands is poorly known. As far as the opisthobranch molluscs are concerned, we have found that only three works (TALAVERA 1978, NORDSIECK & TALAVERA 1979 and particularly

Fig. 2. *Selvagens Islands*: Sampling stations. A. Selvagem Grande: Portinho das Cagarras (PC - 30° 08' 17'' N; 15° 52' 11'' W); Enseada da Fonte das Galinhas (EFG - 30° 08' 12'' N; 15° 51' 56'' W); Ponta do Leste (PL - 30° 08' 09'' N; 15° 51' 16'' W). B. Selvagem Pequena: Desembarcadouro (D - 30° 01' 41'' N; 16° 01' 22'' W). (Locations corresponding to the sampling sites were named herein after the "Serviço Cartográfico do Exército, folha 15, sér. P821, Edição 1 – S.C.E.P., 1967")

RESULTS

During the expedition, specimens assignable to a total of ten species from four orders were collected (2 Cephalaspidea, 1 Anaspidea, 2 Notaspidea and 5 Nudibranchia).

All specimens were deposited in the collection of Museu Municipal do Funchal (História Natural) – MMF(HN).

Class GASTROPODA Cuvier, 1797

Subclass OPISTHOBRANCHIA Milne Edwards, 1848

Order CEPHALASPIDEA Fischer, 1883

Family RETUSIDAE Thiele, 1926

Retusa truncatula (Bruguière, 1792)

=*Bulla truncatula* Bruguière, 1792; p.377 (original description)
=*Bulla truncata* Adams J., 1800; p.1, pl.1 figs 1-2 non *Bulla truncata* Gmelin, 1791
=*Bulla retusa* Maton & Rackett, 1807
=*Bulla pellucida* Brown, 1827; non *Bulla pellucida* Sars G. O., 1878
=*Bulla smisulcata* Philippi, 1836

=*Bulla mammillata* Philippi, 1836
=*Cylichna truncatella* Locard, 1883
=*Cylichna truncata* Forbes & Hanley, 1850
=*Cylichna mammillata* Forbes & Hanley, 1850
=*Retusa canariensis* de Gregorio, 1889
=*Retusa retusa* Winckworth, 1932
=*Retusa mammillata* Pruvot-Fol, 1954
=*Utriculus truncatulus* Jeffreys, 1867
=*Utriculus mammillatus* Jeffreys, 1867
=*Tornatina truncatula* Jeffreys, 1867
=*Tornatina mammillata* Massy, 1930

LOCATION, DATE AND NUMBER OF SPECIMENS: PL - 23/4/96, one specimen (MMF(HN)29902), with a shell of 2mm (max.length).

ECOLOGICAL REMARKS: Collected on sand at a depth of 12 meters.

DISTRIBUTION: Norway, Baltic Sea, France, Canary Islands and Mediterranean Sea (DAUTZENBERG & FISCHER 1925 (as *Tornatina (Retusa) truncatula*); THOMPSON 1988); Iberian Peninsula (CERVERA et al. 1988); Azores (DAUTZENBERG 1889; MIKKELSEN 1995); Madeira (WATSON 1897; NOBRE 1937; NORDSIECK & TALAVERA 1979); Porto Santo (NOBRE 1937).

PREVIOUS RECORDS: MALAQUIAS & CALADO (1997: 153).

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Family BULLIDAE Lamarck, 1801

Bulla amygdala Dillwyn, 1817

=*Bulla mabillei* Locard, 1897; vol. 1, p.50-51; pl.2 fig. 1-2

LOCATION, DATE AND NUMBER OF SPECIMENS: PC - 24/4/96, two shells (MMF(HN)29914), 29 and 32mm long.
ECOLOGICAL REMARKS: Specimens collected on sand at a depth of 12m.
DISTRIBUTION: Cape Verde Archipelago, Canary Islands, Selvagens and Madeira (DAUTZENBERG & FISCHER 1906; DAUTZENBERG 1927; SÁNCHEZ & BATET 1991); Madeira (WATSON 1897; NOBRE 1937; NORDSIECK 1972; NORDSIECK & TALAVERA 1979), São Tomé and Gabon (SCHNIEBS 1993; BERNARD 1984).
PREVIOUS RECORDS: TALAVERA (1978: 126); NORDSIECK & TALAVERA (1979: 174, pl. XLIII, fig. 29); MALAQUIAS & CALADO (1997: 154).

Order ANASPIDEA Fischer, 1883

Family APLYSIIDAE Lamarck, 1809

Aplysia dactylomela Rang, 1828

=*Aplysia ocellata* d'Orbigny, 1839; p.44, pl.5, fig.1-4

LOCATION, DATE AND NUMBER OF SPECIMENS: EFG - 23/4/96 one specimen; PC - 24/4/96, four specimens.
ECOLOGICAL REMARKS: From the intertidal zone to a depth of 12 m.
DISTRIBUTION: It is a circumtropical species, whose geographical distribution includes Red Sea, India, Mauritius Id., South Africa, China, Japan, Philippines, Australia, New Zealand, Florida, Panama, Mexico, Brazil and Bermudas (EALES 1960); Puerto Rico, Barbados, Jamaica and Curaçao (THOMPSON 1977); Cuba (MARTÍNEZ & ORTEA 1991-92); Canary Islands (ODHNER 1931); "Cape Verde" (RANG, 1828); Senegal, Ghana (BEBBINGTON 1982) and Morocco (PRUVOT-FOL 1953); Madeira (WATSON 1897; NOBRE 1937).
PREVIOUS RECORDS: MALAQUIAS & CALADO (1997: 155).

Order NOTASPIDEA Fischer, 1883

Family PLEUROBRANCHIDAE Férussac, 1822

Pleurobranchus garciagomezi Cervera, Cattaneo-Vietti & Edmunds, 1996

LOCATION, DATE AND NUMBER OF SPECIMENS: PC – 22/4/96, two specimens (MMF(HN)29909), 18 and 25mm long.
ECOLOGICAL REMARKS: Under stones, at a depth of 10m.
DISTRIBUTION: Cape Verde, Sal Island (CERVERA et al. 1996a); Canaries (CERVERA et al. 1996b) and Madeira (MALAQUIAS pers. obs.).
PREVIOUS RECORDS: First record for Selvagens archipelago.

Berthellina edwardsi (Vayssière, 1896)

LOCATION, DATE AND NUMBER OF SPECIMENS: PC – 24/4/96, two specimens, 55 and 60mm long.
ECOLOGICAL REMARKS: Under stones, at a depth of 9m.
DISTRIBUTION: According to CERVERA (pers. com.), we must wait for the conclusion of the revision of the genus *Berthellina*, presently under way, in order to determine the geographical distribution of this species. VAYSSIÈRE (1898) mentions its presence in the Mediterranean Sea, in France and Italy, under the name *Berthella plumula* (Montagu, 1803). Also mentioned as present in South-west England (THOMPSON 1988 as *B. citrina* Rüppel & Leuckart, 1828); Mediterranean Sea, Sicily (CATTANEO-VIETTI & CHEMELLO 1987; CATTANEO-VIETTI & THOMPSON 1989 as *B. citrina* Rüppel & Leuckart, 1828); Canary Islands (SÁNCHEZ & BATET 1991 as *B. quadridens* Morch, 1863); Azores (VAYSSIÈRE 1896) and Madeira (MALAQUIAS pers. obs.)
PREVIOUS RECORDS: First record for Selvagens archipelago.

Order NUDIBRANCHIA Blainville, 1814

Suborder DORIDACEA Odhner, 1934

Family TRIOPHIDAE Odhner, 1941

Plocamopherus maderae (Lowe, 1842)

=*Peplidia maderae* Lowe, 1842; p.51-53 (original description)

LOCATION, DATE AND NUMBER OF SPECIMENS: PC – 22/4/96, one specimen (MMF(HN)29910), 23mm long; PC – 24/4/96, two specimens (MMF(HN)29892), 40mm long.

ECOLOGICAL REMARKS: Individuals of this species were collected in the subtidal zone between 8 and 12 m depth

DISTRIBUTION: Cape Verde (ELIOT, 1906) and Canary Islands (ORTEA & PÉREZ 1992; ORTEA et al. 1996a); Madeira (LOWE 1842; WATSON 1897; NOBRE 1937; NORDSIECK 1972).

PREVIOUS RECORD: MALAQUIAS & CALADO (1997: 158).

Hypselodoris picta webbi (d'Orbigny, 1839)

A detailed synonymy of this species, can be found in ORTEA et al. 1998: 43-44

LOCATION, DATE AND NUMBER OF SPECIMENS: D – 21/4/96, 4 specimens (MMF(HN)29895 / MMF(HN)29896), 80 to 90 mm long; PC – 3 specimens observed; PC – 24/4/96, 2 specimens (MMF(HN)29897 / MMF(HN)29893), 65 mm long.

ECOLOGICAL REMARKS: All were collected on rocks at 3-15 m depth.

DISTRIBUTION: From Florida to Brazil (its presence in the Caribbean Sea needing confirmation) Canary Islands to southern Spain (ORTEA et al. 1996c)

PREVIOUS RECORD: MALAQUIAS & CALADO (1997: 159)

Chromodoris purpurea (Risso in Guérin, 1831)
   =*Doris purpurea* Risso in Guérin, 1831
   =*Doris albescens* Schultz in Philippi, 1836
   =*Doris piraini* Vérany, 1846

LOCATION, DATE AND NUMBER OF SPECIMENS: D – 21/4/96, one specimen (MMF(HN)29898), 10 mm long.

ECOLOGICAL REMARKS: The specimen was collected under a stone at 3 m depth.

DISTRIBUTION: Iberian Peninsula (CERVERA et al. 1988); Algarve, Portugal (GARCÍA-GÓMEZ et al. 1991); Sicily (CATTANEO-VIETTI & CHEMELLO 1987); Ceuta (GARCÍA-GÓMEZ et al. 1989); Marocco and Canaries (ORTEA & PÉREZ 1983); Cape Verde Archipelago (ORTEA 1988); Azores (GOSLINER 1990; WIRTZ 1998).

PREVIOUS RECORD: First record for the Selvagens archipelago.

Chromodoris britoi Ortea & Perez, 1983

A detailed synonymy and discussion of this species, can be found in ORTEA et al. 1994: 243.

LOCATION, DATE AND NUMBER OF SPECIMENS: PC – 22/4/96, one specimen (MMF(HN)29912), 7mm long.

ECOLOGICAL REMARKS: The specimen was collected under a stone at 9 m depth.

DISTRIBUTION: Gibraltar (GARCÍA-GÓMEZ 1987); Catalonia (CERVERA et al. 1988); Canary Islands (ORTEA & PEREZ 1983; SÁNCHEZ et al. 1987); Madeira (ORTEA et al. 1994; WIRTZ, 1994); Azores (GOSLINER 1990 as *C. clenchi*; WIRTZ 1998).

PREVIOUS RECORDS: MALAQUIAS & CALADO (1997: 160)

Suborder AEOLIDACEA Odhner, 1934

Family TERGIPEDAE Thiele, 1931

Spurilla neapolitana (delle Chiaje, 1824)
   =*Eolis neapolitana* (delle Chiaje, 1841)
   =*Flabellina inornata* Costa A., 1866
   =*Eolis conspersa* Fischer P., 1869; non *Eolis conspersa* Dalyell, 1853
   =*Eolidina gabriellae* Vannucci, 1952
   =*Spurilla dakariensis* Pruvot-Fol, 1953
   =*Spurilla mograbina* Pruvot-Fol, 1953

LOCATION, DATE AND NUMBER OF SPECIMENS: D – 21/4/96, one specimen (MMF(HN)29900). 20 mm long.

ECOLOGICAL REMARKS: The specimen was collected under a stone, at 3 m depth.

DISTRIBUTION: Asturias (ORTEA 1977); Galiza (URGORRI & BESTEIRO 1983); Portugal (GARCÍA-GÓMEZ et al. 1991); Andaluzia (CERVERA & GARCÍA 1986); Malaga (LUQUE 1983); Barcelona (BALLESTEROS, 1977); Mediterranean Sea, Sicily, Naples (CATTANEO-VIETTI & CHEMELLO 1987; VILLANI & MARTINEZ 1993); Canary Islands (ODHNER, 1931); Cape Verde Archipelago

(SÁNCHEZ et al. 1987); Guinea (MARCUS & MARCUS 1966); Barbados, Caribbean Sea, Brazil, Mexico and Hawaii (EDMUNDS & JUST 1983); Jamaica (EDMUNDS 1964).

PREVIOUS RECORDS: First record for the Selvagens islands.

DISCUSSION

Four of the ten species found during the "Selvagens 96" expedition, are considered new records for Selvagens namely *Pleurobranchus garciagomezi*, *Berthellina edwardsi*, *Chromodoris purpurea* and *Spurilla neapolitana*. The geographical distribution of the above four species reinforces the opinion expressed by MALAQUIAS & CALADO (1997) that the opisthobranch fauna of Selvagens, although diversified from a zoogeographical viewpoint, has an Eastern Atlantic (British Isles to Senegal) affinity.

The specimens of the genus *Berthellina* found in the eastern side of the Atlantic Ocean and the Mediterranean Sea, included in the "orange chromatic group", have been assigned to distinct species such as *B. citrina*, *B. engeli* (THOMPSON 1988; CATTANEO-VIETTI & CHEMELLO 1987; CATTANEO-VIETTI & THOMPSON 1989) and *B. quadridens* (SÁNCHEZ & BATET 1991). Nevertheless, according to CERVERA (pers. com.), these names can be synonyms of *Berthellina edwardsi* or correspond in same cases to misidentifications. *Berthellina edwardsi* is a species described by VAYSSIÈRE (1896) from specimens collected at the Azores and probably also at the Cape Verde Archipelago (CERVERA et al. 1996a).

The specimens of *Pleurobranchus* collected by us agree with the description by CERVERA et al. (1996a) of *P. garciagomezi* after two specimens collected at Sal Island, Cape Verde Archipelago. Nevertheless, from the chromatic point of view there are some differences that worth to be mentioned. Our specimens have an orange mantle, while those from Cape Verde have a mantle with different shades of brown. Both ours and Cape Verde specimens have sulci, on the surface of the mantle, delimitating polygonal areas. These sulci are pale white on our specimens, whereas they are of a more intense white on the Cape Verde ones. We must say that the chromatic variation of these sulci is known within genus *Pleurobranchus*, for instance in *P. forskalii* for which the typical pattern has white sulci although this white colour may not be present in some specimens (see CERVERA et al. 1996a: 152, Pl. 1, fig. A).

ACKNOWLEDGEMENTS

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SHALLOW-WATER MARINE MOLLUSCS OF THE AZORES: BIOGEOGRAPHICAL RELATIONSHIPS

SÉRGIO PAULO ÁVILA

Shallow-water marine molluscs of the Azores were surveyed from supralittoral to a depth of 45 m which yielded an up-to-date database. The resulting list of 231 confirmed taxa of the Azores was then compared with similar lists from Scandinavia, Belgium, British Isles, Gulf of Biscay to Galiza, Portugal, Western Mediterranean, Morocco and Mauritania, Madeira, Porto Santo, Desertas and Selvagens, Canary Islands, Cape Verde, Ascension Island, Saint Helena, and the Caribbean.

A total of 18 species and 1 subspecies (*Tricolia pullus azorica*) are considered to be endemic to the Azores.

There are 20 new records to the Azores: *Metaxia abrupta* (Watson, 1880), *Monophorus erythrosoma* (Bouchet & Guillemot, 1978), *Melanella* sp., *Lamellaria latens* (O. F. Müller, 1776), *Ranella olearia* (Linnaeus, 1758), *Ocinebrina edwardsi* (Payraudeau, 1826), *Fusinus* sp., *Nassarius corniculus* (Olivi, 1792), *Crassopleura incrassata* (Dujardin, 1837), *Heliacus architae* (O. G. Costa, 1867), *Cima* cf. *minima* (Jeffreys, 1858), *Odostomia conoidea* (Brocchi, 1814), *Ondina diaphana* (Jeffreys, 1848), *Chromodoris khroni* (Verany, 1846), *Chlamys flexuosa* Poli, 1795, *Loripes lacteus* (Linnaeus, 1758), *Bornia* sp., *Parvicardium exiguum* (Gmelin, 1791), *Gastrana fragilis* (Linnaeus, 1758) and *Paphia aurea* (Gmelin, 1791).

It was possible to infer the life history of only 72 species out of the 231. Of these, 38 have a free-swimming stage and 34 have a non-planktotrophic type of development (either lecithotrophic or direct development). Thirteen endemic species were found with a non-planktotrophic type of development, all belonging to the Rissoidae.

The Mediterranean, Madeira archipelago and Portugal mainland, are the regions which share a higher number of species with the Azores, whereas Saint Helena and Ascension Island share only a small number of species with the Azores.

Some comments are made regarding the influence of the Gulf Current on the composition of the marine malacofauna of the Azores, as well on the possible routes of colonization of the Azorean islands by marine molluscs.

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INTRODUCTION

The vast majority of the works about the marine molluscs of the Azores dealt with their taxonomy and systematics (MAC ANDREW 1856; DROUËT 1858; MORELET 1860; RÖMER 1871; WATSON 1886; SIMROTH 1888; DAUTZENBERG 1889; GIRARD 1892; DAUTZENBERG & FISHER 1897; NOBRE 1924, 1930; MORTON 1967, 1990a, 1990b, 1995; MARTINS 1976, 1995; MOOLENBEEK & FABER, 1987; MOOLENBEEK & HOENSELAAR 1987; BURNAY & MARTINS 1988; GOFAS 1989a, 1989b, 1990; AZEVEDO & MARTINS 1989; AZEVEDO 1990; GOFAS 1990; GOSLINER 1990; HOUBRICK 1990; MARTINS 1990; SILVA 1990; AZEVEDO & GOFAS 1990; AZEVEDO, 1991b; GONÇALVES 1991; MENEZES

1991; VAN DER LINDEN 1993; HOEKSEMA & SEGERS 1993; LINDEN & VAN AARTSEN 1994; BIELER 1995; JENSEN 1995; MIKKELSEN 1995; REID 1996; ÁVILA & AZEVEDO 1996; ÁVILA 1997; ÁVILA & AZEVEDO 1997; WIRTZ 1998; HOENSELAAR & GOULD 1998; SALAS & GOFAS 1998; ÁVILA et al. 1998), followed by ecological studies (CHAPMAN 1955; MARTINS 1980; ARRUDA & GORDO 1984; LEMOS & VIEGAS 1987; NETO & AZEVEDO 1990; BULLOCK et al. 1990; HAWKINS et al. 1990; MORTON 1990a; AZEVEDO 1991a, 1992; GONÇALVES & MARTINS 1993; BULLOCK 1995; WIRTZ 1995; ÁVILA 1998; MORTON et al. 1998). By contrast, only two papers were published dealing with biogeography: WIRTZ & MARTINS 1993 and KNUDSEN 1995.

The strong Mediterranean component of the marine molluscs of the Azores is known since the paper of MAC ANDREW (1854), but it was never quantified, only sparse families of the Azorean shallow-water marine molluscs having been well studied. I here attempt to produce a check-list of the shallow-water Gastropoda, Bivalvia and Cephalopoda of the Azores and to infer and quantify their biogeographical relationships.

MATERIAL AND METHODS

The systematic revision was based on an extensive bibliographic compilation of the references of the shallow-water marine molluscs for the Azores. During the last four years, a survey was performed of the collections of the following institutions: DBUA – The Mollusc reference collection of the Department of Biology of the University of the Azores, Ponta Delgada; *Imag*DOP – image bank of the Department of Oceanography and Fisheries of the University of the Azores, Horta; DOP/ML – The Mollusc reference collection of the Department of Oceanography and Fisheries of the University of the Azores, Horta; MCM(HN) – Museu Carlos Machado (História Natural), Ponta Delgada and MZ/MHN-FCTUC – Museu de Zoologia/Museu de História Natural da Faculdade de Ciências e Tecnologia da Universidade de Coimbra. Taxa found were entered into a database using

Microsoft Access 97. Species were placed in synonymy according to the most recent published systematic treatment available. CLEMAM database (Check List of European Marine Mollusca), availabale through Internet (http://www.mnhn.fr/base/malaco.html) was particularly helpful and intensively used. Undescribed species (e.g. *Bittium* sp. and *Alvania* sp.) or species only identified to the genus level were also included.

The distribution of the larvae of the molluscs found near the Azores was extracted from LAURSEN (1981), SCHELTEMA (1971) and SCHELTEMA et al. (1989). The geographical distribution of the adult specimens of all the species existing in the Azores is based on POPPE & GOTO (1991; 1993) but specialized works were also used for some species (e.g. SEURAT & DIEUZEIDE 1933; GOSLING 1984; TEMPLADO 1986; BURNAY & MARTINS 1988; WARMOES et al. 1988; TAYLOR et al. 1993; HOUART & ABREU 1994; OLIVERIO 1995; ORTEA et al. 1997; HOENSELAAR & GOULD 1998; SALAS & GOFAS 1998). The Azorean marine molluscs database was compared with data from Scandinavia (HANSSON 1997), Belgium (BACKELJAU 1986), British Isles (TEBBLE 1966; GRAHAM 1988; THOMPSON 1976, 1988; THOMPSON & BROWN 1984; SMITH & HEPPELL 1991) Gulf of Biscay to Galiza (ROLAN 1984; BORJA 1987; LASTRA et al. 1988), Portugal (NOBRE 1931, 1936; NOBRE & BRAGA 1942), Western Mediterranean (RIEDL 1986; RASO et al. 1992), Morocco (POPPE & GOTO 1991, 1993; MENIOUI 1992), Madeira, Desertas and Selvagens (MAC ANDREW 1852; NOBRE 1889, 1937; NORDSIECK & TALAVERA 1979; ABREU 1991; GUERREIRO 1994; WIRTZ 1994; WIRTZ in press; ANDRADE 1995; CLARKE & LU 1995; SILVEIRA 1995; MALAQUIAS 1996; FONSECA et al. 1995), Canary Islands (MAC ANDREW 1852; NORDSIECK & TALAVERA 1979; TALAVERA, 1982; ORTEA et al. 1982), Cape Verde (NOBRE 1900; BURNAY & MONTEIRO 1977; COSEL 1982a, 1982b, 1982c; GARCIA-TALAVERA & BACALLADO 1978), Ascension and Saint Helena (ROSEWATER 1974, 1975), and the Caribbean (WARMKE & ABBOTT 1961; JONG & COOMANS 1988; ABBOTT & DANCE 1990).

A total of 701 samples of molluscs (DBUA collection) were collected in all the islands of the Azores except in São Jorge and Corvo, ranging from intertidal samples to 45 m depth (Table 1). Two dredge hauls made at 70 m depth were also performed off Vila Franca do Campo at São Miguel Island. All these samples were sorted and the molluscs identified.

A simple percentage similarity index was used to compare the shallow-water marine molluscs of the Azores with the selected regions. It was calculated as the ratio between the shared species and the 231 taxa confirmed for the Azores (Table 3). The use of indexes like those of Jaccard or Sørensen (KREBS, 1985), which take in account both the total number of species existing in each one of the compared regions, as well as the number of common species, would certainly be more accurate than the percentage similarity index. However, those "better" indexes were not used because there are no recent check-lists of some of the selected regions (e.g. Madeira, Cape Vert, Ascension islands and Saint Helena). Thus, with different degrees of knowledge of the molluscan fauna in the considered regions, I have chosen just to compare and infer on the similarity between a given region and the Azores, based on

Table 1

Samples collected at the Azores (DBUA collection).

Site	Number of samples
Flores	173
Pico	76
Faial	75
Graciosa	77
Terceira	45
Banco D. João de Castro	1
São Miguel	178
Santa Maria	43
Formigas	33
TOTAL	**701**

Table 2

Shallow water marine molluscs of the Azores. N – number of species; dr – dubious record; n. id. – species identified only to genus.

	N
Azores total	281
Azores (dr)	31
Azores (n. id.)	19
Azores (endemic species/subspecies)	19

Table 3

Number of shared species with the Azores (dubious records excluded). Sim % - percentage of similarity between the malacofauna of a given region and the Azores (231 confirmed taxa).

	Azores	Sim (%)
Scandinavia	78	33,8
Belgium	23	10,0
British Isles	112	48,5
Golf of Biscay to Galiza	125	54,1
Portugal	144	62,3
Western Mediterranean	181	78,4
Morocco	64	27,7
Madeira, Porto Santo, Desertas and Selvagens	147	63,6
Canary islands	137	59,4
Cape Verde	70	30,3
Ascension island	13	5,6
Saint Helena	12	5,2
Caribbean	22	9,5

the amount of shared molluscan species in relation to the Azorean species.

The biogeographical relationships of the shallow-water marine molluscs of the Azores were studied by comparing the Azorean species with the following selected regions (Scandinavia, British isles, Gulf of Biscay to Galiza, Western Mediterranean, Morocco, Madeira, Desertas and Selvagens, Canary islands, Cape Verde, Ascension island, Saint Helena and the Caribbean). This procedure was done for all the 231 taxa, for Gastropoda and for the Bivalvia. This procedure was repeated, with the endemic Azorean species excluded. Finally, a similar study was performed on the species grouped by biogeographical Provinces and Regions: Boreal Province (Scandinavia, Belgium and British isles); Lusitanian Province divided in Franco Iberian Region (Biscay Golf to Galiza and Portugal), Mediterranean Region, and Morocco Region (Morocco, Mauritania, Madeira, Selvagens and Desertas, and Canary islands); West-African Province, with the Senegal Region (Cape Verde), South Atlantic Province (Ascension Island and Saint Helena); and the Caribbean Province.

All dendrograms were drawn using non-transformed presence-absence data, Bray-Curtis similarity index and UPGMA method, PRIMER version 4.0 Plymouth Marine Laboratory package.

The life history of the species was also investigated, both from the literature and by inference from protoconch morphology, through SEM photos, with two possibilities considered: planktonic or non-planktonic phase (THORSON 1950; SCHELTEMA 1971; SHUTO 1974; JABLONSKI & LUTZ 1983; LEAL 1991; 1999; LEAL & BOUCHET 1991).

RESULTS

A total of 281 taxa were found to be reported for the Azores. Of these, 31 were considered dubious records, so there are 250 confirmed taxa. Twenty species were identified only to the genus level, including two of the endemic species (*Bittium* sp. and *Alvania* sp.). Although confirmed for the

Azores, *Assiminea eliae* Paladilhe, 1875 was removed from the biogeographic analysis because no reliable data were found about its geographic range. The multivariate analysis was conducted after removing *Assiminea eliae* and the 18 not identified species (*Bittium* sp. and *Alvania* sp. were included in the analysis) from the 250 confirmed taxa, thus making a total number of 231 taxa (229 confirmed species plus 2 endemic taxa identified down to the genus).

The *Columbella* species that exists in Macaronesia is *Columbella adansoni* Menke, 1853, a species reported from the Azores, Madeira, Canary Islands, Cape Verde and African coast south of Senegal. *Columbella rustica* (Linnaeus, 1758) is a different species recorded for the Mediterranean and African coast down to Senegal (OLIVERIO 1995).

Shells of *Mytilus edulis* Linnaeus, 1758 were collected inside of harbour walls (e. g. in Ponta Delgada harbour). Very recently, alive specimens were found inside Ponta Delgada harbour (Saco da Doca), ranging from 0,5 to 1 m depth. They probably arrived attached to ships (there are reports of *Mytilus* attached to tuna boats, João Brum pers. comm.). However, this very localized and small population has not so far spread out from this spot.

Spirula spirula (Linnaeus, 1758) (reported as *Spirula peronii* Lamarck, 1822 to the Azores, at shore, by MAC ANDREW 1856) as well as *Loligo forbesii* Steenstrup, 1856 (reported as *Loligo vulgaris* by DROUËT 1858), are species that usually do not live in the depths studied, but as they do sometimes occur in very shallow-waters, these molluscs were considered in this study.

There are 20 new records to the Azores: *Metaxia abrupta* (Watson, 1880), *Monophorus erythrosoma* (Bouchet & Guillemot, 1978), *Melanella* sp., *Lamellaria latens* (O F Müller, 1776), *Ranella olearia* (Linnaeus, 1758), *Ocinebrina edwardsi* (Payraudeau, 1826), *Fusinus* sp., *Nassarius corniculus* (Olivi, 1792), *Crassopleura incrassata* (Dujardin, 1837), *Heliacus architae* (O. G. Costa, 1867), *Cima* cf. *minima* (Jeffreys, 1858), *Odostomia conoidea* (Brocchi, 1814), *Ondina diaphana* (Jeffreys, 1848), *Chromodoris khroni* (Verany, 1846),

Chlamys flexuosa Poli, 1795, *Loripes lacteus* (Linnaeus, 1758), *Bornia* sp., *Parvicardium exiguum* (Gmelin, 1791), *Gastrana fragilis* (Linnaeus, 1758) and *Paphia aurea* (Gmelin, 1791).

A total of 18 species and 1 subspecies (*Tricolia pullus azorica*) (8,2%) are considered as endemic to the Azores (see Table 2).

Excluding the dubious records, a total number of 111 families and 181 genera were found. Rissoidae with 19 confirmed species (13 endemic) is the largest family, followed by Veneridae (9 species, 1 endemic), Pyramidellidae (9 species), Conidae (8 species), Muricidae, Chromodorididae and Pectinidae (all with 7 species) and Naticidae and Ellobiidae (both with 5 species). A total of 79 families are represented by a single genus and 65 families are represented by one species only (Appendix).

Janthina exigua, *Janthina janthina* and *Spirula spirula* although occurring in both sides of the Atlantic, are not considered as amphi-Atlantic, because they are pelagic species. Sixteen out of the 231 confirmed taxa (6,9%) are amphi-Atlantic species (13 gastropods and 3 bivalves): *Trivia candidula*, *Polinices lacteus*, *Phalium granulatum*, *Cymatium parthenopeum*, *Stramonita haemastoma*, *Philippia hybrida*, *Bulla striata*, *Atys macandrewii*, *Elysia ornata*, *Aplysiopsis formosa*, *Hypselodoris picta*, *Williamia gussoni*, *Myosotella myosotis*, *Pinna rudis*, *Limaria hians* and *Lasaea adansoni*.

The Mediterranean (78,4%), Madeira archipelago (63,6%) and Portugal mainland (62,3%) are the regions which share a higher number of species with the Azores, whereas Saint Helena (5,2%) and Ascension island (5,6%) share only a small number of species (Table 3).

A total of 112 species (48,5%) occurs simultaneously in the Azores, Madeira and the Canary Islands, and 53 species (22,9%) occur in all the Macaronesian Archipelagos.

Of the 231 confirmed taxa to the Azores, it was possible to determine the life history of only 72 species. Of these, 38 have a free-swimming stage and 34 have a non-planktonic type of development. The 13 endemic species with a non-planktotrophic type of development all belong to the Rissoidae, the endemic Phasianellidae subspecies *Tricolia pullus azorica* having a planktotrophic type of development.

Almost 47% of the total number of the Azorean shallow-water molluscan species, were reported since 1989 (Figure 8).

The following analysis concerns the confirmed 231 taxa.

When all species are considered (231 taxa), three groups appear, clustering the different locations at 70% similarity, all positioned in geographical order: in the first one, Scandinavia, British Isles and Biscay Golf to Galiza cluster. In the second group, two subgroups appear: the Azores and Mediterranean cluster at about 88% similarity, and then cluster to Portugal at 80%; the second subgroup contains Madeira, Porto Santo, Desertas and Selvagens, clustered with Canary Islands at 79%. Finally, in the third group, Ascension Island and Saint Helena cluster at about 72%. Morocco, Mauritania and Cape Verde cluster with the two first groups at about 52% and Belgium at only 25% similarity (Fig. 1).

When all species but the Azorean endemics (that is, a total of 212 species) are considered, three groups appear, clustering the different locations at 70% similarity: in the first one, Scandinavia, British Isles and Biscay Golf to Galiza cluster. In the second group, two subgroups appear: Azores and Mediterranean cluster at about 92% similarity, and then cluster to Portugal at 82%; the second subgroup contains Madeira, Porto Santo, Desertas and Selvagens, clustered with Canary Islands at 80%. In the third group, Ascension Island and Saint Helena cluster again at about 72%. Morocco, Mauritania and Cape Verde cluster with the two first groups at about 53% and Belgium at only 22% similarity (Fig. 2).

When the analysis is performed for the Gastropoda alone, once again, Belgium, Morocco and Mauritania, Cape Verde and the Caribbean cluster at less than 70%. Scandinavia and the British Isles cluster at 73% and this group joins the main group at about 53%. In this group, formed by 6 sites, three sub-groups exist. In the first one, Biscay and Portugal cluster at 76%. In the second sub-group, the Azores and Western

Fig. 1. Biogeographical relationships (all species). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA for all the 231 confirmed shallow-water molluscs of the Azores. AZO –Azores; SCA – Scandinavia; BEL – Belgium; BRI – British Isles; BIS – Biscay Golf; POR – Portugal; MED – Western Mediterranean; MOR – Morocco and Mauritania; MAD – Madeira, Porto Santo, Desertas and Selvagens; CAN - Canary Islands; CAP – Cape Vert; ASC – Ascension Island; STH – Saint Helena; CAR – Caribbean.

Fig. 2. Biogeographical relationships (212 species; endemic Azorean species excluded). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA. Legend as in Fig. 1.

Mediterranean cluster at 85% and in the last sub-group, Madeira Archipelago clusters with the Canary Islands at 84%. Ascension Island and Saint Helena cluster at 86% (Fig. 3).

Performing the same procedure for the Gastropoda alone (endemic Azorean species excluded), Belgium, Morocco and Mauritania, Cape Verde and the Caribbean again cluster at less than 70%. The Azores cluster with the Western Mediterranean at 90% and Portugal again clusters with the Azores/Western Mediterranean (compare with Fig. 3) (Fig. 4).

For the Bivalvia, two groups are evident at more than 70% similarity: in the smaller, Morocco and Mauritania clusters with the Canary Islands; in the second group, with 7 regions, the Azores and Western Mediterranean cluster at about 96%, and Portugal joins them at about 92% similarity. Cape Verde and Belgium cluster with these two groups at 58% and 28% similarity,

respectively. A smaller group is constituted by Ascension Island and Saint Helena, that cluster at 61% to which the Caribbean joins at 50%. This group is connected to the main one at only 13% similarity (Fig. 5).

When the endemic Azorean Bivalvia species are excluded, at more than 70% similarity, two groups appear: in the smaller, Morocco and Mauritania clusters with the Canary Islands; in the second group, with 7 regions, the Azores and Western Mediterranean cluster at about 97%, and then Portugal joins them at about 91% similarity. Cape Verde and Belgium cluster with these two groups at 58% and 27% similarity, respectively. A smaller group is constituted by Ascension Island and Saint Helena, that cluster at 60% to which the Caribbean joins at 50%. This group is connected to the main one at only 13% similarity (Fig. 6).

Comparing the three dendrograms with the endemic Azorean species included (all 231 taxa, Gastropoda and Bivalvia), there is some variation between these dendrograms, especially between the Bivalvia and the other two (see Fig.s 1, 3 and 5). Belgium, consistently clustering at low levels (ranging from 22% in the case of the Gastropoda, to 28% in the case of the Bivalvia) and the Azores

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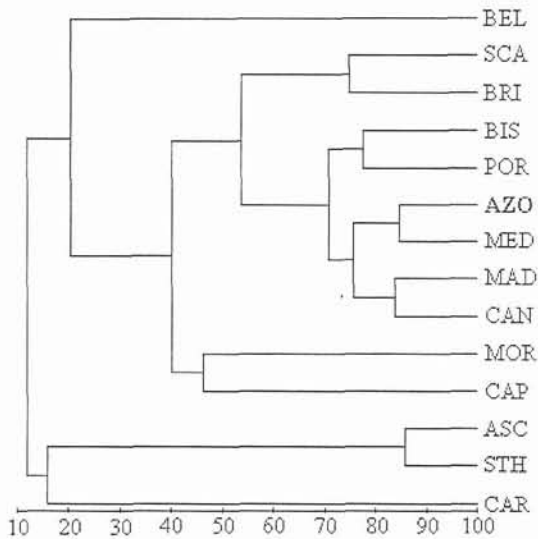
Fig. 3. Biogeographical relationships (Gastropoda only). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA. Legend as in Fig. 1.

Fig. 4. Biogeographical relationships (Gastropoda only; endemic Azorean species excluded). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA. Legend as in Fig. 1.

consistently cluster with the Western Mediterranean, and than with Portugal, the main difference occurring in the case of the Gastropoda, where Portugal cluster with Biscay.

When the endemic species are excluded, a similar pattern occurs in all dendrograms (the 212 species, Gastropoda and Bivalvia), with a consistent group formed by Ascension Island, Saint Helena and the Caribbean that cluster with the other regions at low levels of similarity. Belgium is also a region whose similarity levels are quite low, clustering always at no more than 30%. The Azores consistently cluster with Western Mediterranean in all these dendrograms (Figs 3, 5, 7).

When we look at the biogeographical provinces and regions, there is a single cluster, with Franco-Iberian and Western Mediterranean Regions clustering at about 90%, to which the Azores (87%) and Morocco Region (85%) also join. At 70%, the Boreal Province (Scandinavia, British Isles and Belgium) clusters to the latter group. West-African Province (the Senegal Region with Cape Verde) clusters with the former at 50%. The South Atlantic Province (comprising Ascension Island and Saint Helena) and the

Caribbean Province form a second group that clusters at about 28% and that joins the first group at only 15% (Fig. 7).

DISCUSSION

As early as the mid-19th century, MAC ANDREW stated that "(...) the islands of the Canaries, Madeira and the Azores possess a marine fauna closely allied to that of the old continent, notwithstanding that the prevailing set of currents is from America. Very few mollusca are common to both sides of the Atlantic, except such as are inhabitants of the Arctic Seas, and extend along the coasts radiating from that center. Out of 160 species of shells of the Canary Islands and Mediterranean, of which I sent specimens to the late Professor C. B. Adams, he informed me that he could only identify one (*Columbella cribaria*) with a West Indian species - he had probably overlooked *Neritina viridis* (= *Smaragdia viridis*) (Linnaeus, 1758), and perhaps one or two others." (MAC ANDREW 1854: 49). So, this biogeographic paradox is not new, and the question still remains: how to explain the disparity between the pattern

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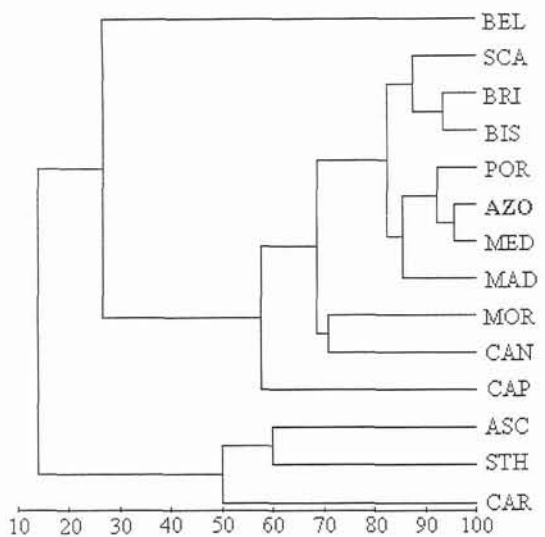
Fig. 5. Biogeographical relationships (Bivalvia only). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA. Legend as in Fig. 1.

Fig. 6. Biogeographical relationships (Bivalvia only; endemic Azorean species excluded). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA. Legend as in Fig. 1.

of sea-surface currents and the geographic range of the marine species of molluscs in the oceanic islands of the North Atlantic, in particular, in the Azores?

More recent studies on marine molluscs confirm the quoted Macaronesian/Eastern Atlantic trend: SÁNCHEZ et al. (1987) studied the biogeographic affinities of 3 suborders of Nudibranchia (Doridacea, Dendronotacea and Aeolidacea) from Canary Islands and found that 56% of the species were related to the Eastern Atlantic fauna (Mediterranean, Biscay Golf and the Channel) and 24% were species with Caribbean affinities. MALAQUIAS (1996), studied the opisthobranch fauna of Madeira, and reached the conclusion that 60,7% of the reported species were related to species inhabiting Eastern Atlantic (from Scandinavia and British Isles to Angola and Western Mediterranean), 25% were amphi-Atlantic, and 14,3% of the species were endemic to Macaronesia. WIRTZ (1998), studying the opisthobranchs of the Azores, concluded that there is a higher relation to the Eastern Atlantic (and the Western Mediterranean Sea), with almost no relation to the Western Atlantic.

A similar situation happens with fish species: BRIGGS (1974) refers to the existence of 99 species of fishes inhabiting the shores of the Azores, of which 77 (78%) were related to the Eastern Atlantic, 21 (21,2%) were considered transatlantic species and 1 (1%) species was considered endemic. The most complete check-list of the marine fishes occurring at the Azores, lists 460 species, mostly related to the Eastern Atlantic (SANTOS et al. 1997).

The same pattern was also found in the Crustacea, with the fauna of the Azores having greater affinities to the European and North-African ones, and also displaying a strong Mediterranean and insular (Madeira, Canary Islands and Cape Verde) component (COSTA 1994); LOPES et al. (1993) studied the amphipods of the Azores (only Gammaridea and Caprellidea), and recorded 122 species. Of these, 48 (39,3%) were endemic species, being the Mediterranean and the Portuguese coast the regions with more species in common with the Azores: 58 (47,5%) and 57 (46,7%) species in common, respectively.

The littoral desmosponges (Porifera) of the Azores, are also strongly related to the Eastern Atlantic, in particular to the Mediterranean, with practically no endemic species (BOURY-ESNAULT & LOPES 1985).
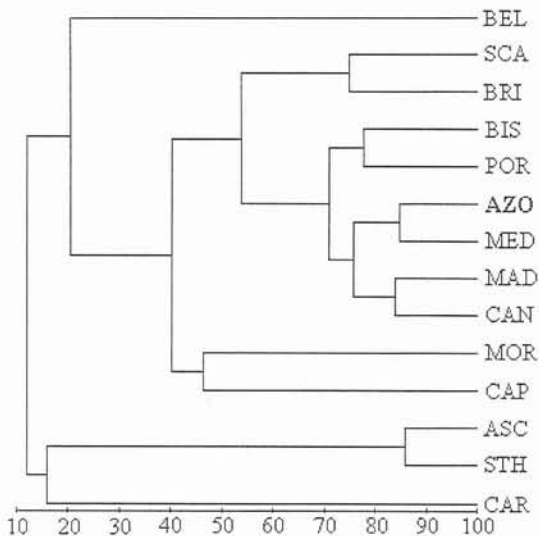
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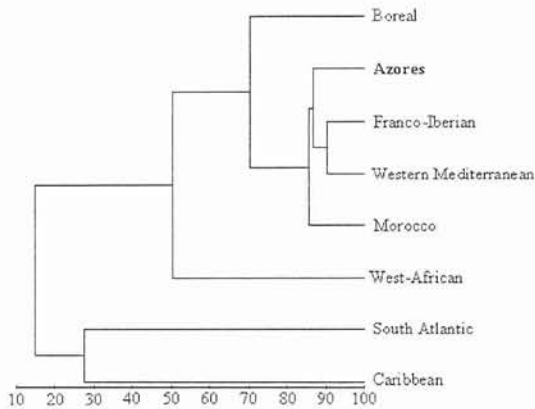
Fig. 7. Biogeographic Provinces and Regions (biogeographical relationships – all species). Bray-Curtis similarity index, non-transformed presence/absence data, UPGMA

Fig. 8. Evolution of the confirmed number of species reported to the Azores.

Around the islands of the Azores, the prosobranch larvae are more evenly dispersed throughout the water layers above 200-300 m than in the rest of the Gulf Stream (LAURSEN 1981). From the 34 larvae described by LAURSEN (1981) as leaving the Western Atlantic (Caribbean and Gulf of Mexico), 17 reach the coasts of Europe and Northwest Africa, but only 8 species are recorded as adult specimens living in the Eastern Atlantic. Around the Azores, larvae of at least 18 prosobranch species were found but, of these, only *Natica canrena, Polinices lacteus, Phalium granulatum, Cymatium parthenopeum* and *Stramonita haemastoma* are confirmed in the islands of the Azores. All these adult specimens are also found in the Eastern Atlantic (LAURSEN 1981) (Table 4). SCHELTEMA (1971) has estimated that the time required for a larvae to cross the Atlantic from Caribbean to the Europe varies from 4 to 13 months. From a conservative standpoint, the larvae may reach the Azores from 3 to 8 months, which is within the known time span of larval life of many planktonic species (for instance, the families Triphoridae, Lamellariidae, Architectonicidae, Cypraeidae, Ranellidae, Bursidae, Muricidae and Cassidae, all well known for having long lasting free-swimming stages, are represented at the Azores). However, because larvae of many species, for which there is no records of adults living in the Azores, were found

in waters surrounding the islands, we must assume that they indeed reach the Azores, but or the local conditions are not suitable for their settlement and/or further development, or the lack of adult records may be the consequence of incomplete or inadequate bottom sampling.

Some of the species that occur in the Azores were probably introduced by humans either intentionally (e.g.: *Tapes decussates*) or unintentionally (e.g.: *Truncatella subcylindrica, Hexaplex trunculus*) (MORTON et al. 1998). Ballast water of ships has been shown to be responsible for the transport of planktonic larvae and/or egg-masses over wide distances (CARLTON 1985; SCHELTEMA 1995). Some planktonic larvae may not behave as completely passive objects. If these larvae can control their vertical position, they may utilize countercurrents that run below the surface, precisely in the opposite direction (SCHELTEMA 1995); between Portugal and the Azores, this means from East to West.

In the North Atlantic, the main current is the Gulf Stream, which transports warm water of equatorial and tropical origin into the colder northern waters (KLEINE & SIEDLER 1989); Gulf Stream is also the main source of many instability processes, such as meanders and eddies, being this situation especially complicated when it leaves the North American coast, at about 40° to 45°N, toward the central zone of the North Atlantic (CREASE et al. 1985; GOULD 1985; KLEINE & SIEDLER 1989). In this zone, the Gulf Stream splits into two branches, the North Atlantic Current (NAC) and the Azores Current

Table 4

Teleplanic larvae reported to the Azores (based on Laursen, 1981)

Species	Larvae	Adults
Philippia krebsii (Mörch, 1875)	Caribbean, Sargasso Sea, Azores, Cape Verde	Both sides of the North Atlantic, Canary Islands
Cerithiopsis ? greeni (Adams, 1839)	Sargasso Sea, off the Azores	Cape Cod to Brazil, Bermuda, Gulf of Mexico
Strombus pugilis Linnaeus, 1758	Caribbean, Sargasso Sea, off the Azores	Florida to Brazil
Phalium granulatum (Born, 1778)	All the tropical and subtropical Atlantic, Mediterranean	Caribbean, Azores, Mediterranean, Madeira, Canary Islands, Cape Verde, southern Spain to Mauritania
Cymatium femorale (Linnaeus, 1758)	Caribbean, Sargasso Sea, Azores	Caribbean, Florida to Brazil, Bermuda
Cymatium pileare (Linnaeus, 1758)	Caribbean, Sargasso Sea, Azores	Caribbean, South Carolina to Brazil
Cymatium parthenopeum (von Salis, 1793)	Caribbean, Sargasso Sea, Azores, the entire North Atlantic gyre	Cape Hatteras to Brazil, Caribbean, Azores, Mediterranean, Madeira, Canary Islands, Cape Verde
Charonia variegata (Lamarck, 1816)	Caribbean, Sargasso Sea	Florida to Brazil, Caribbean, Mediterranean, Madeira, Canary Islands, Cape Verde, St. Helena
Tonna galea (Linnaeus, 1758)	Caribbean, Sargasso Sea, Azores, the entire North Atlantic Gyre	Both sides of the North Atlantic, Caribbean, Mediterranean, Madeira, Canary Islands, Cape Verde

(AC) (ISELIN 1963). Each of those branches divide also into further branches: the NAC divides in two branches, NAC1, passing north of the Azores and NAC2 passing south of the Azores. NAC2 later divides again in a branch that turns north, the Southwest European Current (SWEC) and the other towards south, the Madeira Current (MADC). Around the Canary Islands, AC1 and MADC merge originating the so called Canaries Current (CANC), which joins to AC2; the resulting current is the North Equatorial Current (NEC), which runs west, thus completing the gyre (Figure 9). This general pattern changes over the year. However, around the Azores, the general regime is from the west to the east, but there is a clear seasonal oscillation of the mean direction, with periods where NAC (coming from Northwest) has a stronger influence and periods where AC (coming from the Southwest) dominates (SANTOS et al. 1994).

ALVES (1990, 1992) has shown that even considering the means for each one of the seasons during a period of 42 years (NOAC data from 1947-1988), the complexity of the current system that surrounds the Azores is remarkable. Anomalies in the general pattern of currents were also detected in some periods, with currents moving to the northwest, that is from Africa and/or Madeira toward the Azores. During these 42 years studied, the first anomaly detected, lasted from mid-March to mid-April, with an average of 30 days, whilst the second had a duration of 25 days, beginning in October (SANTOS et al. 1995).

Within the Archipelago of the Azores, the surface currents are also complex and directly related to the submarine topography. A study by FIALHO & BARROS (1988) has shown in the Azores eddies ranging from only a few kilometers to more than 100 km occur, with cyclonic and anti-cyclonic gyres, the mean surface velocities
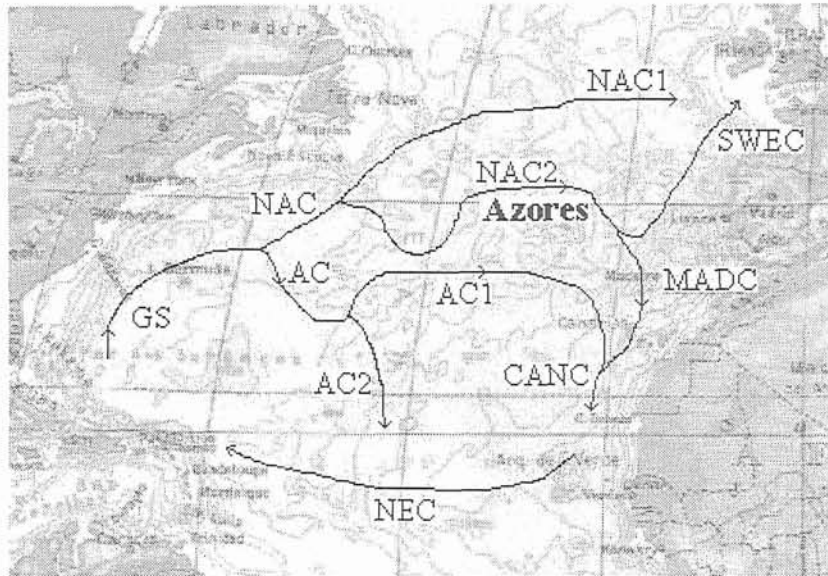
Fig. 9. Sea surface circulation in the North Atlantic: GS – Gulf Stream; NAC – North Atlantic Current; NAC1 - North Atlantic Current 1; NAC2 - North Atlantic Current 2; AC – Azores Current; AC1 - Azores Current 1; AC2 - Azores Current; SWEC – Southwest European Current; MADC – Madeira Current; CANC – Canaries Current; NEC – North Equatorial Current (adapted from ISELIN 1936; KLEINE & SIEDLER 1989)

rarely exceeding 15cm/s.

A constant pattern that emerges from the multivariate analysis (Figs. 1 to 6) is the low similarity of Belgium and of the group Ascension Island and Saint Helena plus Caribbean, which always cluster at very low values with the remaining selected regions. For Belgium, its small coast line (only a few rather uniform kilometers), may explain the small number of species. On what concerns to the South-Atlantic islands of Saint Helena and Ascension Island, their geographic position in the South Atlantic, thus quite distant from the Azores, is responsible by the small number of common species with the Azores.

Some authors suggest that the colonization of the Azores by species with European affinities must have happened under a different regime of dominant currents, thus invoking an ancient counter-clockwise gyre, which existed before the closure of the strait of Panama. The strait of Panama has closed about 3-4 MY (million years) ago (BERGGREN & HOLLISTER, 1974; RAUP, 1991), and at that time, in the region where today are the islands of the Azores, there already existed the actual islands of Santa Maria, the Formigas

Islets, part of the island of São Miguel (the Nordeste volcanic complex) and maybe other islands currently submerged (ABDEL-MONEM et al. 1975; MOORE & RUBIN 1991). The marine fossils (predominantly bivalves) that are found at Santa Maria in the Touril complex (Praia, at +2 m), are of upper Miocene to Pliocene age (5,5 to 4,5 MY) (MADEIRA 1986) and are related to the Eastern Atlantic (VERMEIJ pers. comm.).

According to authors cited below, the molluscs probably reached the Azores by means of rafts/pelagic larvae, passively transported by eddies and meanders that usually form along the Azores Front, providing westward and northward transport (GOFAS 1990; KNUDSEN 1995). Recent observations of satellite-tracked surface drifters, released between the Azores and Portugal, confirm the existence of several eddies and meanders (FIÚZA & MARTINS 1996). Taking in consideration the 63,6% of Azorean species that occur also at Madeira, a probable route of colonization with a Portugal/ Mediterranean origin towards these Archipelagos is suggested. We could even speculate that the

submarine banks of Gorringe (48m depth), Josephine (50m depth) and Ampère (18m depth), located between Portugal and Madeira, probably acted and probably still do, like stepping-stones to the marine larvae in their colonization route, especially on its way to Madeira.

Further data is needed to better define the overall picture. The recent discovery of three species of Rissoidae (*Alvania mediolittoralis*, *Alvania sleursi* and *Crisilla postrema*) formerly considered as endemic to the Azores, in the Madeira Archipelago (HOENSELAAR & GOULD 1998), suggests that more new records of small widespread species will probably be found at these latter islands, thus increasing its similarity with the Azores.

I believe that the knowledge of the molluscan fauna of the seamounts between Portugal-Madeira and Madeira-Azores, would help to clarify the role of these structures in regard to the dispersal of marine invertebrates.

ACKNOWLEDGEMENTS

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Appendix

Species of molluscs recorded from the indicated locations. St – Status (dr – dubious record; e – endemic; n.id. – not identified). Dev – type of development (p – planktotrophic; np – non-planktotrophic). AZO – Azores; SCA – Scandinavia; BEL – Belgium; BRI – British Isles; BIS – Biscay Golf to Galiza; POR – Portugal; MED – Western Mediterranean; MOR – Morocco and Mauritania; MAD – Madeira, Porto Santo, Desertas and Selvagens; CAN - Canary Islands; CAP – Cape Vert; ASC – Ascension Island; STH – Saint Helena; CAR – Caribbean.

Species	Family	St	Dev	First report	AZO	SCA	BEL	BRI	BIS	POR	MED	MOR	MAD	CAN	CAP	ASC	STH	CAR
Patella candei gomesii (Drouët, 1858)	Patellidae		p	Mac Andrew, 1856: 118, 146	1								1	1				
Patella ulyssiponensis aspera Röding, 1798	Patellidae		p	Dunker, 1853: 41 *fide* Drouët, 1858: 41	1								1	1				
Acmaea virginea (Müller, O.F., 1776)	Acmaeidae		p	Jeffreys, 1882: 671	1	1		1	1	1	1		1	1	1			
Sinezona cingulata (Costa O. G., 1861)	Scissurellidae		np	Dautzenberg, 1889: 63	1					1			1	1				
Anatoma crispata Fleming, 1828	Scissurellidae	dr	np?	Jeffreys, 1883: 88	1	1		1	1		1							1
Haliotis coccinea Reeve, 1846	Haliotidae	dr		Drouët, 1858: 38	1					1				1				
Haliotis tuberculata tuberculata Linnaeus, 1758	Haliotidae		p	Mac Andrew, 1856: 119	1			1	1	1	1		1	1	1			
Calliostoma laugieri (Payraudeau, 1826)	Trochidae	dr		Mac Andrew, 1856: 120, 147	1				1	1	1							
Calliostoma zizyphinum (Linnaeus, 1758)	Trochidae		np	Mac Andrew, 1856: 119, 147	1	1	1	1	1	1	1		1	1				
Clanculus bertheloti (d'Orbigny, 1840)	Trochidae	dr		Mac Andrew, 1856: 121, 147	1								1	1				
Gibbula magus (Linnaeus, 1758)	Trochidae		p	Dautzenberg, 1889: 63	1	1	1	1	1	1	1		1	1	1			
Jujubinus exasperatus (Pennant, 1777)	Trochidae		np	Mac Andrew, 1856: 147	1			1	1	1	1		1	1	1			
Jujubinus pseudogravinae Nordsieck, 1973	Trochidae	e		Ávila & Azevedo, 1996: 106	1													
Jujubinus striatus (Linnaeus, 1758)	Trochidae	dr	np	Mac Andrew, 1856: 120	1			1	1	1	1		1	1	1			
Bolma rugosa (Linnaeus, 1767)	Turbinidae	dr		Mac Andrew, 1856: 148	1			1	1	1			1	1	1			
Tricolia pullus azorica Dautzenberg, 1889	Tricoliidae	e	p	Mac Andrew, 1856: 121, 148	1													
Bittium sp.	Cerithiidae	e; n. id.		Mac Andrew, 1856: 124, 150	1													
Cerithium zebrum Kiener, 1842	Cerithiidae	dr		Drouët, 1858: 30	1													

Species	Family	St	Dev	First report	AZO	SCA	BEL	BRI	BIS	POR	MED	MOR	MAD	CAN	CAP	ASC	STH	CAR
Fossarus ambiguus (Linnaeus, 1758)	Fossariidae		p	Mac Andrew, 1856: 123, 149	1				1	1	1	1	1	1	1	1	1	
Litiopa melanostoma Rang, 1829 = *Litiopa grateloupeana* Drouët, 1858	Litiopidae			Drouët, 1858: 28-29	1													1
Cheirodonta pallescens (Jeffreys, 1867).	Triphoridae		p	Ávila & Azevedo, 1997: 327	1			1		1	1				1			
Marshallora adversa (Montagu, 1803)	Triphoridae		p	Mac Andrew, 1856: 150	1	1		1	1	1	1				1	1		
Metaxia abrupta (Watson, 1880)	Triphoridae		p	This work	1								1	1				
Monophorus erythrosoma (Bouchet & Guillemot, 1978)	Triphoridae		p	This work	1			1	1	1	1				1			
Monophorus perversus (Linnaeus, 1758)	Triphoridae		p	Jeffreys, 1885: 57	1				1		1	1		1				
Monophorus thiriotae Bouchet, 1984	Triphoridae		p	Bouchet, 1984	1						1				1			
Cerithiopsis barleei Jeffreys, 1867	Cerithiopsidae		p	Ávila & Azevedo, 1997: 327	1	1		1	1	1	1		1		1			
Cerithiopsis jeffreysi Watson, 1885	Cerithiopsidae			Dautzenberg, 1889: 43	1				1	1	1			1	1	1		
Cerithiopsis minima (Brusina, 1865)	Cerithiopsidae			Dautzenberg, 1889: 43	1				1	1	1			1	1	1		
Cerithiopsis tubercularis (Montagu, 1803)	Cerithiopsidae		p	Drouët, 1858: 31	1	1		1	1	1	1				1	1		
Janthina exigua Lamarck, 1816	Janthinidae		p	Mac Andrew, 1856: 119, 147	1			1		1	1			1	1	1		1
Janthina janthina (Linnaeus, 1758)	Janthinidae		p	Mac Andrew, 1856: 119, 147	1			1	1	1	1	1	1	1	1	1	1	1
Janthina pallida Harvey in Thompson, 1841	Janthinidae		p	Morton et al., 1998: 133	1			1	1	1	1		1					
Epitonium algerianum (Weinkauff, 1866)	Epitoniidae			Dautzenberg, 1889: 56	1				1	1	1	1			1			
Epitonium clathratulum (Kanmacher *in* G. Adams, 1798)	Epitoniidae			Mac Andrew, 1856: 123, 149	1	1	1	1	1	1	1			1	1			
Epitonium lamellosum (Lamarck, 1822) = *Epitonium commutatum* (Monterosato, 1877)	Epitoniidae			Drouët, 1858: 27	1			1	1	1	1			1	1			

Species	Family	St	Dev	First report	AZO	SCA	BEL	BRI	BIS	POR	MED	MOR	MAD	CAN	CAP	ASC	STH	CAR
Opalia crenata (Linnaeus, 1758)	Epitoniidae			Nobre, 1924: 81	1			1	1	1			1	1	1			
Eulima glabra (da Costa, 1778)	Eulimidae	dr	p	Jeffreys, 1884b: 365-366	1			1	1		1							
Melanella sp.	Eulimidae	n. id.		This work	1													
Parvioris sp.	Eulimidae	n. id.		Azevedo & Gofas, 1990: 85	1													
Parvioris ibizencus (Nordsieck, 1968)	Eulimidae			Dautzenberg, 1889: 58	1													
Vitreolina antiflexa Monterosato, 1844	Eulimidae	dr		Mac Andrew, 1856: 125, 150	1						1			1				
Vitreolina incurva (Bucquoy, Dautzenberg & Dollfus, 1883)	Eulimidae			Dautzenberg, 1889: 57	1					1	1			1	1			
Vitreolina sp. 1	Eulimidae	n. id.		Azevedo & Gofas, 1990: 85	1													
Vitreolina sp. 2	Eulimidae	n. id.		Azevedo & Gofas, 1990: 85	1													
Littorina nigrolineata J. E. Gray, 1839	Littorinidae	dr	np	Jeffreys, 1883: 112-113	1			1	1									
Littorina obtusata (Linnaeus, 1758)	Littorinidae	dr	p	Jeffreys, 1883: 112	1	1	1	1	1	1	1							
Littorina saxatilis (Olivi, 1792)	Littorinidae		np	Reid, 1996: 327	1	1	1	1	1	1	1	1		1				
Littorina striata King & Broderip, 1832	Littorinidae		p	Mac Andrew, 1856: 123, 149	1								1	1	1			
Melarhaphe neritoides (Linnaeus, 1758)	Littorinidae		p	Drouët, 1858: 26	1	1	1	1	1	1	1	1	1	1				
Skeneopsis planorbis (Fabricius O., 1780)	Skeneopsidae		np	Nobre, 1924: 80	1	1		1	1	1	1		1	1				
Alvania abstersa (Van der Linden & van Aartsen, 1993)	Rissoidae	e	np	Van der Linden, 1993: 80	1													
Alvania angioyi van Aartsen, 1982	Rissoidae	e	np	Dautzenberg, 1889: 51	1													
Alvania beani (Hanley in Thorpe, 1844)	Rissoidae	dr		Mac Andrew, 1856: 121	1	1		1	1		1			1				
Alvania cancellata (da Costa, 1778)	Rissoidae		p	Mac Andrew, 1856: 121, 148	1			1	1	1	1		1	1	1			
Alvania cimex (Linnaeus, 1758)	Rissoidae	dr		Mac Andrew, 1856: 121	1					1	1	1						
Alvania formicarum Gofas, 1989	Rissoidae	e	np	Gofas, 1989a: 40-41	1													
Alvania internodula Hoenselaar & Gould, 1998	Rissoidae	e	np	Hoenselaar & Gould, 1998: 83	1													

Species	Family	St	Dev	First report	AZO	SCA	BEL	BRI	BIS	POR	MED	MOR	MAD	CAN	CAP	ASC	STH	CAR
Alvania mediolittoralis Gofas, 1989	Rissoidae		np	Dautzenberg, 1889: 49	1								1					
Alvania poucheti Dautzenberg, 1889	Rissoidae	e	np	Dautzenberg, 1889: 49-50	1													
Alvania sleursi (Amati, 1987)	Rissoidae		np	Watson, 1886: 593	1									1				
Alvania tarsodes (Watson, 1886)	Rissoidae	e		Watson, 1886: 595	1													
Alvania sp.	Rissoidae	e; n. id	np	Ávila & Azevedo, 1997: 326	1													
Botryphallus ovummuscae (Gofas, 1990)	Rissoidae	e	np	Dautzenberg, 1889: 53	1													
Cingula ordinaria Smith	Rissoidae	dr		Chapman, 1955: 803	1													
Cingula trifasciata (Adams J., 1798)	Rissoidae		np	Mac Andrew, 1856: 148	1	1		1	1	1								
Crisilla postrema (Gofas, 1990)	Rissoidae		np	Dautzenberg, 1889: 52	1									1				
Manzonia crassa (Kanmacher, 1798)	Rissoidae	dr		Morton et al., 1998: 88	1			1	1	1								
Manzonia unifasciata (Dautzenberg, 1889)	Rissoidae	e	np	Dautzenberg, 1889: 51, 52	1													
Onoba moreleti Dautzenberg, 1889	Rissoidae	e	np	Dautzenberg, 1889: 52	1													
Rissoa guernei Dautzenberg, 1889	Rissoidae	e	np	Dautzenberg, 1889: 47-48	1													
Rissoa guerini Récluz, 1843	Rissoidae	dr		Chapman, 1955: 803	1			1	1		1	1			?			
Setia pulcherrima (Jeffreys, 1848)	Rissoidae	dr	np	Bullock et al., 1990: 45	1			1	1	1	1			1	1			
Setia quisquiliarum Watson, 1886	Rissoidae	e	np	Dautzenberg, 1889: 53	1													
Setia subvaricosa Gofas, 1990	Rissoidae	e	np	Dautzenberg, 1889: 52	1													
Setia sp.	Rissoidae	n. id.		Azevedo & Gofas, 1990: 85	1													
Pisinna glabatra (Von Mühlfeldt, 1824) = *Pisinna punctulum* (Philippi, 1836)	Anabathridae			Dautzenberg, 1889: 53	1							1			1			
Assiminea eliae Paladilhe, 1875	Assimineidae		p?	Ávila & Azevedo, 1996: 106	1													
Paludinella littorina (delle Chiaje, 1828)	Assimineidae		np	Morton et al., 1998: 106	1			1				1			1	1		
Caecum armoricum De Folin, 1869	Caecidae			Hoeksema & Segers, 1993: 86	1							1						
Caecum cf. *clarkii* Carpenter, 1858	Caecidae			Ávila & Azevedo, 1996: 106	1			1	1			1						

Species	Family	St	Dev	First report	AZO	SCA	BEL	BRI	BIS	POR	MED	MOR	MAD	CAN	CAP	ASC	STH	CAR
Caecum glabellum	Caecidae			Morton et al., 1998: 89	1													
Caecum vitreum Carpenter, 1858	Caecidae			Dautzenberg, 1889: 43	1				1				1	1	1			
Caecum sp.	Caecidae	n. id.		Ávila et al (1998)	1													
Truncatella subcylindrica (Linnaeus, 1767)	Truncatellidae		np	Martins, 1980: 9	1		1	1	1	1	1				1	1		
Thylaeodus cf. *rugulosus* (Monterosato, 1878)	Vermetidae		?	Bieler, 1995: 175	1						1							
Vermetus triquetrus Bivona-Bernardi, 1832	Vermetidae		?	Dautzenberg, 1889: 43	1						1	1		1	1			
Lamellaria latens (O F Müller, 1776)	Lamellariidae		p	This work	1	1		1	1									
Lamellaria perspicua (Linnaeus, 1758)	Lamellariidae		p	Dautzenberg, 1889: 54	1	1	1	1	1	1	1			1	1	1		
Trivia candidula (Gaskoin, 1835)	Triviidae		p	Watson, 1886: 696	1			1	1	1				1	1	1		1
Trivia pulex (Solander *in* Gray J.E., 1828)	Triviidae			Mac Andrew, 1856: 127	1					1	1			1	1			
Luria lurida (Linnaeus, 1758).	Cypraeidae		p	Drouët, 1858: 36	1					1	1	1	1	1	1	1	1	
Euspira pulchella (Risso, 1826) = *Lunatia alderi* (Forbes, 1838)	Naticidae			Morton et al., 1998: 144	1	1	1	1	1	1	1							
Natica adansoni de Blainville, 1825	Naticidae			Dautzenberg, 1889: 54	1							1		1	1	1		
Natica canrena (Linnaeus, 1758)	Naticidae		p	Morton et al., 1998: 194	1													1
Naticarius dillwyni (Payraudeau, 1826)	Naticidae	dr		Simroth, 1888	1						1			1	1	1		
Payraudeautia intricata (Donovan, 1804)	Naticidae			Mac Andrew, 1856: 127, 151	1						1							
Polynices lacteus (Guilding, 1834)	Naticidae		p	Morton et al., 1998: 194	1						1	1	1	1	1			1
Phalium granulatum (Born, 1778) = *Phalium undulatum* (Gmelin, 1791)	Cassidae			Drouët, 1858: 33	1				1	1	1	1	1	1	1			1
Charonia lampas lampas (Linnaeus, 1758)	Ranellidae		p	Mac Andrew, 1856: 132, 154	1		1	1	1	1	1	1	1	1	1			
Cymatium corrugatum (Lamarck, 1816)	Ranellidae			Simroth, 1888	1				1	1	1	1	1	1	1			
Cymatium muricinum (Röding, 1798) = *Triton tuberosus* Lamarck, 1822	Ranellidae	dr		Mac Andrew, 1856: 132, 154	1										1			1

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Cymatium parthenopeum (Von Salis, 1793)	Ranellidae		p	Nobre, 1924: 78	1					1	1	1	1	1	1			1
Ranella olearia (Linnaeus, 1758)	Ranellidae			This work	1		1	1			1			1				
Bursa scrobiculator (Linnaeus, 1758)	Bursidae			Mac Andrew, 1856: 132, 154	1					1	1			1	1	1		
Hexaplex trunculus (Linnaeus, 1758)	Muricidae			Nobre, 1924: 77	1					1	1			1	1			
Ocenebra erinacea (Linnaeus, 1758)	Muricidae		np	Drouët, 1858: 33	1	1	1	1	1	1	1			1	1	1		
Ocinebrina aciculata (Lamarck, 1822)	Muricidae		np	Mac Andrew, 1856: 133, 154	1			1	1	1	1			1	1			
Ocinebrina edwardsi (Payraudeau, 1826)	Muricidae			This work	1				1	1	1			1	1			
Orania fusulus (Brocchi, 1814)	Muricidae			Poppe & Goto, 1991: 140	1				1	1	1			1				
Stramonita haemastoma (Linnaeus, 1766)	Muricidae		p	Mac Andrew, 1856: 130, 153	1				1	1	1	1	1	1	1	1		1
Trophonopsis muricatus (Montagu, 1803)	Muricidae		np	Poppe & Goto, 1991: 138-139	1	1		1	1	1	1	1						
Coralliophila meyendorffi (Calcara, 1845)	Coralliophilidae			Nobre, 1924: 78	1				1	1	1	1	1	1	1	1		
Fusinus sp.	Fasciolariidae	n. id.		This work	1													
Buccinum hepaticum Montagu, 1803 = (?)	Buccinidae	dr		Adanson, 1757 *fide* Drouët, 1858	1						1							
Nassarius nitidus (Jeffreys, 1867)																		
Engina turbinella (Kiener, 1835)	Buccinidae			Morton et al., 1998: 194	1													1
Pisania striata (Gmelin, 1791)	Buccinidae	dr		Mac Andrew, 1856: 133	1						1							
Nassarius corniculus (Olivi, 1792)	Nassariidae		np	This work	1					1	1	1		1				
Nassarius cuvieri (Payraudeau, 1826)	Nassariidae			Nobre, 1924: 77	1				1		1			1	1	1		
Nassarius incrassatus (Ström, 1768)	Nassariidae		p	Mac Andrew, 1856: 131	1	1	1	1	1	1	1			1	1			
Columbella adansoni Menke, 1853	Columbellidae		p	Mac Andrew, 1856: 130	1									1	1	1		
Vexillum zebrinum (d'Orbigny, 1840)	Costellariidae	dr		Mac Andrew, 1856: 128, 152	1									1	1			
Volvarina sp.	Marginellidae	n. id.		Ávila & Azevedo, 1997: 327	1													

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Volvarina oceanica Gofas, 1989	Marginellidae	e		Gofas, 1989b: 179	1													
Gibberula sp.	Cystiscidae	n. id.		Ávila & Azevedo, 1997: 327	1													
Mitra cornea Lamarck, 1811 = *Mitra nigra* (Gmelin, 1791)	Mitridae		p	Mac Andrew, 1856: 128, 152	1			1		1		1	1	1	1			
Mitra corniculum (Linnaeus, 1758)	Mitridae			Simroth, 1888: 214	1					1	1	1	1	1	1			
Mitra zonata Marryat, 1818	Mitridae			Burnay & Martins, 1988	1					1	1	1	1	1				
Crassopleura incrassata (Dujardin, 1837) = (?) *Crassopleura maravignae* Bivona Ant. *in* Bivona And., 1838	Drilliidae			This work	1						1			1				
Haedropleura septangularis (Montagu, 1803)	Turridae		p	Mac Andrew, 1856: 129, 152	1	1		1	1	1	1			1	1			
Bela menkhorsti van Aartsen, 1988 = *Bela turgida* [(Forbes) Reeve, 1844]	Conidae			Dautzenberg, 1889: 28	1						1							
Bela nebula (Montagu, 1803)	Conidae		p	Simroth, 1888	1	1		1	1	1	1			1				
Lusitanops sp.	Conidae	n. id.		Ávila & Azevedo, 1997: 327	1													
Mitrolumna crenipicta (Dautzenberg, 1889)	Conidae			Dautzenberg, 1889: 31	1						1			1	1			
Mitrolumna olivoidea (Cantraine, 1835)	Conidae			Nobre, 1924: 77	1					1	1							
Raphitoma carnosula (Jeffreys, 1869)	Conidae			Ávila & Azevedo, 1997: 327	1		1											
Raphitoma linearis (Montagu, 1803)	Conidae		p	Dautzenberg, 1889: 29	1	1		1	1	1	1			1	1	1		
Raphitoma purpurea (Montagu, 1803)	Conidae			Dautzenberg, 1889: 28	1	1		1	1	1	1			1				
Philippia hybrida (Linnaeus, 1758)	Architectonicidae			Drouët, 1858: 30	1			1	1	1				1	1			1
Heliacus architae (O. G. Costa, 1867)	Architectonicidae			This work	1				1	1				1	1			
Rissoella diaphana (Alder, 1848)	Rissoellidae		np	Ávila & Azevedo, 1996: 106	1	1		1	1		1							
Ammonicera fischeriana (Monterosato, 1869)	Omalogyridae		np	Ávila & Azevedo, 1996: 106	1			1			1							
Ammonicera rota (Forbes & Hanley, 1850)	Omalogyridae		np	Ávila & Azevedo, 1996: 106	1	1		1	1	1	1			1	1			

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Omalogyra atomus (Philippi, 1841)	Omalogyridae		np	Dautzenberg, 1889: 46	1	1		1	1	1	1		1	1	1	1		1
Cima sp.	Cimidae	n. id.		Azevedo & Gofas, 1990: 85	1													
Cima cf. *minima* (Jeffreys, 1858)	Cimidae			This work	1				1									
Graphis sp.	Cimidae	n. id.		Azevedo & Gofas, 1990: 85	1													
Odostomella doliolum (Philippi, 1844)	Pyramidellidae			Dautzenberg, 1889: 59	1							1		1	1			
Odostomia conoidea (Brocchi, 1814)	Pyramidellidae			This work	1	1			1	1	1			1	1			
Odostomia scalaris (Macgillivray, 1843)	Pyramidellidae			Dautzenberg, 1889: 59	1	1		1		1	1			1				
Odostomia unidentata (Montagu, 1803)	Pyramidellidae			Dautzenberg, 1889: 59	1	1		1	1	1	1			1				
Odostomia sp. 1	Pyramidellidae	n. id.		Azevedo & Gofas, 1990: 86	1													
Odostomia sp. 2	Pyramidellidae	n. id.		Azevedo & Gofas, 1990: 86	1													
Odostomia sp. 3	Pyramidellidae	n. id.		Azevedo & Gofas, 1990: 86	1													
Ondina diaphana (Jeffreys, 1848)	Pyramidellidae			This work	1				1			1						
Turbonilla lactea (Linnaeus, 1758)	Pyramidellidae			Mac Andrew, 1856: 125, 150	1	1		1	1	1	1			1	1			
Ebala nitidissima (Montagu, 1803)	Ebalidae			Dautzenberg, 1889: 56	1	1		1	1	1	1			1	1			
Cephalaspidea incertae sedis = *Retusa multiquadrata* Oberling, 1970	?			Mikkelsen, 1995: 205	1							1						
Cylichnina umbilicata (Montagu, 1803)	Retusidae			Ávila & Azevedo, 1996: 106	1	1		1		1	1	1	1	1				
Retusa truncatula (Bruguière, 1792)	Retusidae			Dautzenberg, 1889: 21	1	1		1	1	1	1			1	1			
Runcina adriatica T. Thompson, 1980	Runcinidae			Gosliner, 1990: 141	1							1		1				
Runcina aurata Garcia, Lopez, Luque & Cervera, 1986	Runcinidae			Gosliner, 1990: 138	1				1									
Runcina sp.	Runcinidae	n. id.		Gosliner, 1990: 143	1													
Bulla striata Bruguière, 1792	Bullidae			Dautzenberg, 1889: 24	1		1	1							1	1		1

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Atys macandrewii E. A. Smith, 1872	Haminoeidae			Mikkelsen, 1995: 200	1								1	1				1
Haminoea hydatis (Linnaeus, 1758)	Haminoeidae			Garcia-Talavera Casañas, 1983 (1981)	1			1	1	1	1		1	1	1	1	1	
Haminoea cf. *Orteai* Talavera, Murillo & Templado, 1987	Haminoeidae			Mikkelsen, 1995: 201	1						1			1				
Philine quadrata (S. V. Wood, 1839)	Philinidae		dr	Watson, 1886: 696	1	1		1		1	1							
Cylichna cylindracea (Pennant, 1777)	Cylichnidae		dr	Pilsbry, 1895: 289-290	1	1		1	1	1	1		1	1	1			
Diacria trispinosa (Lesueur, 1821).	Cavolinidae			Ávila & Azevedo, 1997: 328	1	1		1	1	1	1		1	1	1			
Elysia ornata (Swainson, 1840)	Elysiidae			Wirtz, 1998: 2	1								1	1				1
Elysia viridis (Montagu, 1804)	Elysiidae			Azevedo, 1991a: 27	1	1		1	1	1	1	1	1	1				
Aplysiopsis formosa Pruvot-Fol, 1953	Hermaeidae			Jensen, 1995: 218	1							1		1				1
Placida verticillata Ortea, 1981	Stiligeridae			Wirtz, 1998: 2	1			1			1		?	1				
Umbraculum umbraculum (Röding, 1798)	Umbraculidae			Menezes, 1991: 101	1				1	1	↑	1	1	1	1	1	1	
Tylodina perversa (Gmelin, 1791)	Tylodinidae			Dautzenberg, 1889: 25	1			1	1	1	1	1	1	1			1	
Berthellina edwardsi (Vayssière, 1896)	Pleurobranchidae			Wirtz, 1995: 163	1			1		1	1		1					
Pleurobranchus testudinarius Cantraine, 1836	Pleurobranchidae			Wirtz & Martins, 1993: 56	1						1							
Akera bullata O F Müller, 1776	Akeridae			Nobre, 1924: 77	1	1	1	1	1	1	1		1	1				
Aplysia depilans Gmelin 1791	Aplysiidae			Wirtz, 1998: 3	1			1	1	1	1	1	1	1	1			
Aplysia fasciata Poiret, 1798	Aplysiidae			Wirtz & Martins, 1993: 56	1			1	1	1	1	1	1	1	1			
Aplysia punctata Cuvier, 1803	Aplysiidae			Simroth, 1888	1	1		1	1	1	1	1	1	1				
Diaphorodoris luteocincta (M. Sars, 1870)	Onchidorididae			Wirtz & Martins, 1993: 56	1	1		1		1	1							
Kaloplocamus ramosus (Cantraine, 1835)	Triophidae			Wirtz, 1998: 12	1			1			1			1				
Doris ocelligera (Bergh, 1881)	Dorididae			Azevedo & Gofas, 1990: 86	1				1	1	1							
Aldisa binotata Pruvot-Fol, 1953 = *Aldisa smaragdina* Ortea, Perez & Llera, 1982	Aldisidae			Wirtz, 1998: 8	1			1	1				1	1				

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Chromodoris britoi Ortea & perez, 1983	Chromodoridae			Gosliner, 1990: 148	1							1		1	1			
Chromodoris krohni (Verany, 1846)	Chromodoridae			This work	1				1	1	1							
Chromodoris purpurea (Laurillard, 1831)	Chromodoridae			Gosliner, 1990: 146-147	1				1	1	1	1	1	1	1			
Glossodoris edmundsi Cervera, García-Gómez & Ortea, 1989	Chromodoridae			Gosliner, 1990: 159	1									1	1			
Hypselodoris fontandraui (Pruvot-Fol, 1951)	Chromodoridae			Wirtz, 1995: 169	1							1			1			
Hypselodoris tricolor (Cantraine, 1835) = *Hypselodoris midatlantica* (Gosliner, 1990)	Chromodoridae			Gosliner, 1990: 152	1					1	1	1		1	1			
Hypselodoris picta (Schultz in Philippi, 1836)	Chromodoridae			Gosliner, 1990: 156	1						1	1	1	1	1	1		1
Discodoris atromaculata (Bergh, 1880)	Discodorididae			Wirtz & Martins, 1993: 56	1					1		1		1	1			
Discodoris cf. *Millegrana* (Alder and Hancock, 1854).	Discodorididae		dr	Ávila & Azevedo, 1997: 328	1			1										
Platydoris argo (Linnaeus, 1767)	Platydorididae			Wirtz & Martins, 1993: 56	1					1	1	1	1	1	1			
Limacia clavigera (O F Müller, 1776)	Polyceridae			Wirtz, 1995: 171	1	1	1	1	1	1	1							
Polycera elegans (Bergh, 1894)	Polyceridae			Wirtz & Martins, 1993: 56	1				1	1	1							
Polycera quadrilineata (O F Müller, 1776)	Polyceridae			Wirtz, 1995: 171	1	1		1	1	1	1			1				
Tambja ceutae Garcia-Gomez & Ortea, 1988	Gymnodorididae			Wirtz & Martins, 1993: 56	1							1		1	1			
Tambja sp.	Gymnodorididae	n. id.		Wirtz, 1995: 175	1									1				
Dendrodoris herytra Valdés & Ortea *in* Valdés, Ortea, Avila & Ballesteros, 1996	Dendrodorididae			Odhner, 1932	1					1	1	1	1	1	1			
Doto floridicola Simroth, 1888	Dotidae			Simroth, 1888	1						1	1						
Scyllaea pelagica Linnaeus, 1758	Scyllaeidae			Simroth, 1888	1	1		1										
Marionia blainvillea (Risso, 1818)	Tritoniidae			Wirtz, 1998: 2	1						1	1		1				
Caloria elegans (Alder & Hancock, 1845)	Facelinidae			Wirtz, 1995: 183	1	1		1		1	1			1	1			

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Fiona pinnata (Eschscholtz, 1831)	Fionidae			Wirtz, 1998: 6	1			1			1			1	1	?		
Flabellina pedata (Montagu, 1815)	Flabellinidae			Wirtz, 1998: 6	1	1		1	1	1	1							
Aeolidiella sanguinea (Norman, 1877)	Aeolidiidae			Morton et al., 1998: 171	1			1	1		1		1					
Williamia gussonii (da Costa, 1829)	Siphonariidae			Mac Andrew, 1856: 118	1						1					1	1	1
Onchidella celtica (Cuvier, 1817)	Onchidiidae			Martins, 1980: 13-14	1			1	1	1	1	1						
Auriculinella bidentata (Montagu, 1808)	Ellobiidae			Mac Andrew, 1856: 116	1	1	1	1	1	1								
Myosotella myosotis (Draparnaud, 1801)	Ellobiidae			Morelet, 1860: 206	1	1	1	1	1		1		1					1
Ovatella vulcani (Morelet, 1860)	Ellobiidae		e	Morelet, 1860: 207	1													
Pedipes pedipes (Gmelin, 1790)	Ellobiidae			Drouët, 1858: 25-26	1					1		1	1	1	1			
Pseudomelampus exiguus (Lowe, 1831)	Ellobiidae			Martins, 1976: 18	1				1									
Arca noae Linnaeus, 1758	Arcidae	dr		Jeffreys, 1879: 571	1			1	1	1	1		1	1	1	1	1	
Arca tetragona Poli, 1795	Arcidae			Jeffreys, 1879: 571	1	1		1	1	1	1		1	1	1	1		
Mytilus edulis Linnaeus, 1758	Mytilidae	dr		Morton et al., 1998: 133	1		1	1	1	1	1		1					
Trichomusculus semigranatus (Reeve, 1858)	Mytilidae			Azevedo, 1991a: 28	1						1	1	1	1	1			
Pinna rudis Linnaeus, 1758	Pinnidae			Jeffreys, 1879: 565	1						1	1		1	1	1	1	1
Pteria hirundo (Linnaeus, 1758)	Pteriidae			Jeffreys, 1879: 565	1			1	1	1	1	1	1	1	1			
Aequipecten commutatus (Monterosato, 1875)	Pectinidae			Poppe & Goto, 1993	1					1	1	1		1	1			
Aequipecten opercularis (Linnaeus, 1758)	Pectinidae			Jeffreys, 1879: 558	1	1	1	1	1	1	1			1	1			
Chlamys flexuosa Poli, 1795	Pectinidae			This work	1						1	1		1	1	1		
Crassadoma multistriata (Poli, 1795)	Pectinidae			Mac Andrew, 1856: 112	1			1	1	1	1	1	1	1	1	1	1	
Crassadoma pusio (Linnaeus, 1758) = *Hinnites distortus* (da Costa, 1778)	Pectinidae			Morton, 1967: 37	1	1		1	1	1	1	1	1	1				
Nodipecten corallinoides (d'Orbigny, 1839)	Pectinidae			Nobre, 1924: 84	1						1		1	1	1		1	
Palliolum incomparabile (Risso, 1826)	Pectinidae			Ávila & Azevedo, 1997: 328	1	1		1	1	1	1			1				

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Spondylus senegalensis Schreibers, 1793	Spondylidae			Ávila & Azevedo, 1997: 328	1							1	1	1	1	1		
Anomia ephippium Linnaeus, 1758	Anomiidae			Ávila & Azevedo, 1997: 328	1	1	1	1	1	1	1	1	1		1			
Monia aculeata (Müller, 1776) = (?) *Heteranomia squamala* (Linnaeus, 1758)	Anomiidae			Azevedo & Gofas, 1990: 86	1	1		1	1		1							
Limaria hians (Gmelin, 1791)	Limidae			Mac Andrew, 1856: 112	1	1		1	1	1	1			1	1			1
Limea loscombii (G W Sowerby I, 1823)	Limidae			Jeffreys, 1879: 564	1	1		1	1	1	1			1	1			
Limatula subauriculata (Montagu, 1808).	Limidae			Ávila & Azevedo, 1997: 328	1	1		1	1	1	1			1	1			
Neopycnodonte cochlear (Poli, 1795)	Gryphaeidae			Dautzenberg, 1889: 72	1	1		1	1	1	1	1			1			
Loripes lacteus (Linnaeus, 1758)	Lucinidae			This work	1		1	1		1	1	1	1	1				
Lucinoma borealis (Linnaeus, 1758)	Lucinidae			Dautzenberg, 1889: 59	1	1		1	1	1	1	1	1	1	1			
Myrtea spinifera (Montagu, 1803)	Lucinidae	dr		Jeffreys, 1881a: 701	1	1		1	1	1			1	1	1	1		
Thyasira flexuosa (Montagu, 1803)	Thyasiridae	dr		Jeffreys, 1881a: 701	1	1		1	1	1			1		1			
Bornia sp.	Kelliidae	n. id.		This work	1													
Lasaea adansoni (Gmelin, 1791)	Lasaeidae			Nobre, 1924: 85	1	1		1	1	1	1		1	1	1	1	1	1
Montacuta ferruginosa (Montagu, 1808)	Montacutidae			Dautzenberg, 1889: 81	1	1	1	1	1	1	1	1	1					
Mysella bidentata (Montagu, 1803)	Montacutidae			Martins, 1980: 17	1	1	1	1	1		1		1					
Neolepton cancellatum Salas & Gofas, 1998	Neoleptonidae	e		Salas & Gofas, 1998: 44-45	1													
Cardita calyculata (Linnaeus, 1758)	Carditidae			Mac Andrew, 1856: 107	1					1	1	1	1	1				
Acanthocardia aculeata (Linnaeus, 1758).	Cardiidae			Nobre, 1924: 85	1	1		1	1	1	1	1	1					
Parvicardium exiguum (Gmelin, 1791)	Cardiidae			This work	1	1		1	1	1	1		1					
Parvicardium ovale (G B Sowerby II, 1840)	Cardiidae			Jeffreys, 1881a: 708	1	1		1	1			1		1	1			
Plagiocardium papillosum (Poli, 1795)	Cardiidae			Mac Andrew, 1856: 141	1			1	1	1	1	1	1	1	1			

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Solen marginatus Pulteney, 1799	Solenidae	dr		Jeffreys, 1881b	1	1	1	1	1	1	1	1						
Gastrana fragilis (Linnaeus, 1758)	Tellinidae			This work	1	1		1	1	1	1	1			1			
Tellina donacina Linnaeus, 1758	Tellinidae			Dautzenberg, 1889: 86	1			1	1	1	1	1	1					
Tellina incarnata Linnaeus, 1758	Tellinidae			Römer, 1871: 127	1	1		1	1	1	1			1	1			
Gari costulata (Turton, 1822)	Psammobiidae			Dautzenberg & Fisher, 1897: 217	1	1		1	1	1	1	1	1	1	1	1		
Abra alba (W. Wood, 1802)	Semelidae			Morton et al., 1998: 144	1	1	1	1	1	1	1			1				
Ervilia castanea (Montagu, 1803)	Semelidae			Mac Andrew, 1856: 104	1				1		1	1		1	1			
Glossus humanus (Linnaeus, 1758)	Glossidae	dr		Jeffreys, 1881a: 710	1	1		1	1	1	1	1						
Callista chione (Linnaeus, 1758)	Veneridae			Mac Andrew, 1856: 106	1			1	1	1	1	1	1	1	1			
Dosinia cf. *lupinus* (Linnaeus, 1758)	Veneridae			Ávila & Azevedo, 1997: 329	1	1		1	1	1	1	1			1	1		
Globivenus effossa (Bivona, 1836)	Veneridae			Nobre, 1936: 257	1					1	1	1	1	1			1	
Gouldia minima (Montagu, 1803)	Veneridae			Ávila & Azevedo, 1997: 329	1	1		1	1	1	1	1	1	1	1	1		
Irus irus (Linnaeus, 1758)	Veneridae	dr		Poppe & Goto, 1993: 123	1			1	1	1	1			1	1			
Paphia aurea (Gmelin, 1791)	Veneridae			This work	1	1		1	1	1	1			1				
Pitar rudis (Poli, 1795)	Veneridae			Nobre, 1924: 85	1			1	1	1	1		1	1	1	1		
Tapes decussata (Linnaeus, 1758)	Veneridae			Morton, 1967: ADDITIONS	1			1	1	1	1	1						
Timoclea ovata (Pennant, 1777)	Veneridae			Dautzenberg, 1889: 82	1	1	1	1	1	1	1	1			1	1		
Venus casina Linnaeus, 1758	Veneridae			Jeffreys, 1884a: 145	1	1		1	1	1	1	1	1			1		
Hiatella arctica (Linnaeus, 1758)	Hiatellidae			Poppe & Goto, 1993: 131	1	1	1	1	1	1	1				1			
Nototeredo norvegica (Spengler, 1792)	Teredinidae			Dautzenberg, 1889: 85	1	1		1			1	1						
Xylophaga dorsalis (Turton, 1819)	Xylophagidae			Dautzenberg, 1889: 85	1	1		1	1	1	1			1				
Cardiomya costellata (Deshayes, 1835)	Cuspidariidae			Dautzenberg & Fischer, 1897	1	1		1	1	1	1	1	1	1				
Spirula spirula (Linnaeus, 1758)	Spirulidae			Mac Andrew, 1856: 133	1	1		1	1	1	1	1	1	1				1

Species	Family	St	Dev	First report	AZO	SCA	BEL	BRI	BIS	POR	MED	MOR	MAD	CAN	CAP	ASC	STH	CAR
Loligo forbesi Steenstrup, 1856	Loliginidae			Girard, 1892: 214	I	I	I	I	I	I	I		I	I				
Octopus macropus Risso, 1826	Octopodidae			Gonçalves, 1991: 79	I				I		I		I					
Octopus salutii Vérany, 1837	Octopodidae			Gonçalves, 1991: 78	I					I	I							
Octopus vulgaris Cuvier, 1797	Octopodidae			Drouët, 1858: 22	I	I	I	I	I	I	I			I		I		
Tremoctopus violaceus delle Chiaje, 1830	Tremoctopodidae			Gonçalves, 1991: 76	I						I				I			
Ocythoe tuberculata Rafinesque, 1814	Ocythoidae			Gonçalves, 1991: 76	I					I	I			I				
Argonauta argo Linnaeus, 1758	Argonautidae			Drouët, 1858: 21	I					I	I			I				

NOW YOU SEE ME, NOW YOU DON'T: A CASE STUDY OF THE EFFECT OF THE SAMPLING METHOD ON THE PERCEIVED STRUCTURE OF ICHTHYOLOGICAL COMMUNITIES

JOSÉ MANUEL N. AZEVEDO

The fish community of a small rocky area near Ponta Delgada, Azores, was assessed using two methods: visual census and rotenone collections. The results obtained with each method are analysed and compared. A total of 46 species was recorded for this site. The visual census recorded more species than did the rotenone collections, but each method detected species that escaped the other. The total fish diversity was found to be similar to that reported in other localized studies of littoral rocky areas of the eastern Atlantic and the Mediterranean. Each method used revealed a different spatial structure and different trophic relationships of the ichthyological community. The visual census put in evidence the pelagic/demersal component, while the rotenone collections emphasized the benthic one. Both methods agree on the importance of the benthic primary production in the trophic food web. Visual census data further suggest that the relevance of the direct consumption of algal material by omnivores and herbivores is greater than could be guessed by the species diversity in this group. Strategies are discussed for combining visual and destructive sampling methods in order to achieve a more accurate representation of a given fish community.

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INTRODUCTION

Immediately after the advent of SCUBA diving, its potential for the scientific observation of the marine environment was realized. Researchers no longer needed to rely only on blind methods such as trawling or the use of traps but could actually see their object of study in its natural environment. Censusing methods used for terrestrial organisms were quickly adapted for underwater use, BROCK (1954) being probably the first to apply them to fishes. A wide variety of underwater visual census techniques was quickly developed and has been successfully applied to various aspects of fish biology and ecology (see HARMELIN-VIVIEN et al. 1985, for a revision). Those techniques are, however, subject to bias from a variety of sources, especially when applied

to the complex field of community ecology. These biases stem from subjective factors such as the degree to which the observer is familiar with the local fauna but also include a whole range of factors such as the recording method used, the geomorphology of the place, and the peculiarities of the technique used. Because of this, and in spite of the numerous publications dedicated to comparative methodological studies (e.g. BROCK 1982; SALE & SHARP 1983; THRESHER & GUNN 1986; BORTONE et al. 1986, 1989, 1991; SANDERSON & SOLONSKY 1986; FOWLER 1987; DAVIS & ANDERSON 1989; GREENE & ALEVIZON 1989; JOHN et al. 1990), no standard technique exists for the visual qualitative and/or quantitative assessment of fish communities.

Diving also allowed the development of new capture techniques, among them the direct and selective capture of specimens using spears or
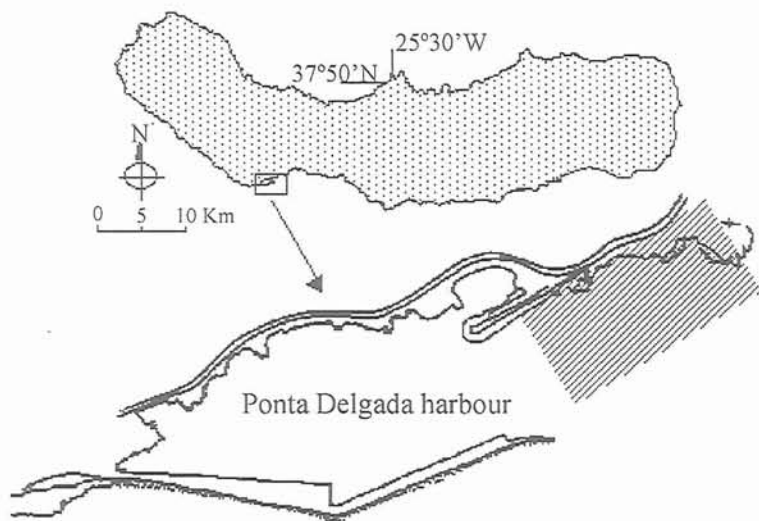
Fig. 1. São Miguel Island and location of the study area (stippled).

Miguel, Azores (Fig. 1). The substrate is mostly very irregular rock, with some areas of boulders and pockets of sand. The algal cover is abundant. Depth is approximately uniform in all the area, from 3-5 m.

Fish collections were made monthly from December 1993 to November 1995 using rotenone, in the form of a 5% liquid emulsion. The sampling method was as follows. A circular area of about 100 m² was enclosed with a 1 cm mesh net, dropped from a rigid inflatable boat at the surface with the help of two divers in the water. The net was 4 m high by 36 m long, kept straight in the water by a string of buoys on the top and one of lead beads on the bottom. The circle was closed with velcro strips attached to the lateral extremities of the net. The whole netting operation generally took less than two minutes. Immediately after the closing of the net, one diver inside the sampling area would open a hole in a plastic bag containing 1.5 L of the rotenone emulsion, previously diluted in seawater, and proceed to spread it around, close to the bottom and as uniformly as possible. After the rotenone cloud dispersed, the bottom was carefully scanned and the fish collected with hand nets. A similar technique was used by NORRIS (1985) and KULBICKI (1990), however those authors used the net to enclose a small coral reef and not, as in the present case, to delimit part of an essentially continuous area. After the capture the fish were placed in buckets with seawater and transported to the laboratory, were identification and counting took place.

Visual census were made from September 1994 to December 1995 on an irregular monthly basis. The method used was an adaptation of the "Visual Fast Count" of KIMMEL (1985). In the original method, each census takes 50 minutes, divided in 5 intervals of 10 minutes each. The diver starts to swim randomly across the area to be sampled, identifying species and counting the

hand nets, or the less selective use of ichthyocides such as quinaldine or rotenone. Ichthyocides in particular have the advantage over visual census in being non-subjective (but the disadvantage of destructiveness).

The present results were obtained during a study whose main objective was to obtain quantitative data about the spatial and trophic structure of a fish community from a marine, rocky, shallow water area of the Azores (see AZEVEDO 1997). It was decided to combine a visual census technique with rotenone collections. The present paper documents and compares the results obtained with each method. The only other instance of such a mixed approach to the ecological study of fish communities known to the author is that of PARISH et al. (1985), although KULBICKI (1990) also discussed some of the methodological problems involved. A comparison of a visual census technique and another destructive sampling technique (trawling) was made by HARMELIN-VIVIEN & FRANCOUR (1991).

METHODS

Work was carried out in a small (approx. 100x300 m) and shallow marine area near the Ponta Delgada harbour, in the island of São

respective number of individuals seen. In the present study, counts were recorded with pencil on sheets of polyester drafting film with a pre-printed species list, attached to a white acrylic board. In the following 10 minute intervals, the diver records and counts only the species not yet seen in that census. Preliminary essays with this method in the study area showed that almost all the species were sampled in the first 10 minutes, and that no species were seen in the last two or three intervals. Therefore, reducing the length of each census to 30 minutes resulted in greatly increased productivity without significantly affecting the results, either in number of species seen or in their relative abundances. It was also found that reducing the interval from 10 to 5 minutes made the counting process easier, because the diver had fewer species to look after simultaneously.

Abundance of each species is given as the number of fish counted times a coefficient related to the time interval when the species was seen. The coefficient is 1 for the first interval, 1/2 for the second, 1/3 for the third, and so on. Abundance indexes result, giving the number of fish seen per 5 minute interval. A total of 111 census was made in the area. The number of census per month ranged from 6 to 17, with an average of 11.

For the purposes of the present paper, the average number of individuals and the average biomass was computed for each species, over all the rotenone collections. The same was done for abundance indexes from the visual census. Biomass estimates were obtained from the visual census, using a Monte Carlo approach, as follows. For each observed species, an "abundance interval" and a "weight interval" was assigned. The 95% confidence interval of the mean abundance was used as the abundance interval. For the species in which enough individuals (>50) were collected, the weight interval was calculated as the 95% confidence interval of the mean weight; for the other species the interval was established in a variety of ways, including published length-weight relationships, weighing of specimens in reference collections and, in a few cases, reports from experienced fishermen. A small spreadsheet macro routine picked randomly

abundance and weight values, for each species, from within the given intervals. Species were then grouped into the spatial and trophic categories defined below, and the biomass of each category was computed. This procedure was repeated 2000 times. The result was a frequency distribution of biomass values for each category, from which averages were calculated. Given the many sources of error associated with this approach, biomass estimates thus obtained are not meant to provide more than general indications.

The spatial and trophic structure of the community was analysed after grouping the species in functional categories (Table 1). Each species was assigned to one of the spatial categories defined by HARMELIN (1987): 1 - diurnal pelagic species, usually schooling (e.g. *Boops boops*); 2 - sedentary planktonivorous (e.g. *Chromis limbata*); 3 - demersal, with vertical movements of a few meter sand important lateral movements (e.g. *Diplodus*); 4 - nectobenthic, with marked substrate affinity but important lateral movements (e.g. *Mullus surmuletus*); 5 - sedentary nectobenthic species, with little vertical or lateral mobility (like most Labridae); 6 - benthic species (like most Gobiidae and Blenniidae). The trophic categories of Azevedo (1995) were adopted, with minor modifications on the assignment of species. Species were classified as herbivorous (H), omnivorous (O), benthic carnivorous (BC) and pelagic carnivorous (PC) (including planktivores and pelagic ichthyivorous predators).

RESULTS

SPECIES RICHNESS

The list of all the species observed or collected in the study area is given on Table 1, together with the average relative abundance of each species in each of the sampling methods. Both methods combined allowed the determination of a total of 46 species. The perceived species richness was greater with the visual counts than with the rotenone collections (41 *versus* 32 species). As expected, cryptic species (the cave-dwelling

Table 1

Species composition, classification into spatial (Spt) and trophic (Tro) categories, and relative abundance of the ichthyological community at the study site, as revealed by two sampling methods: rotenone collections and visual census (VFC). Values for biomass (B) and number of individuals (N) are relative (percentual) means from all the samples.

	Category		Rotenone		Visual
	Spt	Tro	B	N	N
Seen but not captured (14 spp.):					
Balistes carolinensis	1	CB	-	-	0.03
Belone sp.	1	CP	-	-	0.00
Bothus podas	4	CB	-	-	0.12
Canthigaster rostrata	5	O	-	-	0.00
Chelon labrosus	3	CB	-	-	9.8
Dasyatis pastinaca	4	O	-	-	0.01
Kyphosus sp.	3	H	-	-	0.03
Sarpa salpa	3	CB	-	-	2.55
Serranus atricauda	5	CP	-	-	0.03
Seriola sp.	1	CP	-	-	0.10
Sparisoma cretense	3	O	-	-	0.26
Sphyraena sp.	1	CP	-	-	0.00
Syngnathus acus	3	CB	-	-	0.00
Trachinotus ovatus	1	CP	-	-	0.02
Captured but not seen (5 spp.):					
Apogon imberbis	6	CB	1.62	0.49	-
Coryphoblennius galerita	6	O	0.05	0.16	-
Diplecogaster bimaculata	6	CB	0.02	0.85	-
Gaidropsarus guttatus	6	CB	1.47	0.66	-
Hippocampus ramulosus	6	CB	0.15	0.39	-
Seen and captured (27 spp.)					
Abudefduf luridus	6	CB	1.80	0.33	0.13
Atherina presbyter	1	CP	1.45	3.27	34.12
Boops boops	1	CP	5.38	3.67	7.51
Capros aper	3	CB	0.97	0.74	0.01
Centrolabrus caeruleus	5	CB	15.27	3.31	10.88
Chromis limbata	2	CP	4.16	0.99	0.50
Coris julis	5	CB	1.46	0.22	1.51
Diplodus sargus	3	O	1.33	0.16	9.37
Gobius paganellus	6	CB	14.32	11.45	0.66
Labrus bergylta	5	CB	3.02	0.49	0.04
Macroramphosus scolopax	3	CB	2.97	2.60	0.96
Mullus surmuletus	4	CB	1,21	0.41	2.25
Muraena helena	6	CB	1.42	0.25	0.03
Ophioblennius atlanticus	6	H	9.29	1.25	0.29

(Table 1 continued)

Pagellus bogaraveo	1	CP	1.37	1.97	10.45
Pagrus pagrus	3	CB	0.78	0.27	0.86
Parablennius incognitus	6	O	1.75	14.34	0.01
Parablennius ruber	6	O	6.59	10.90	0.48
Pseudocaranx dentex	1	CB	0.12	0.16	0.25
Scorpaena maderensis	6	CB	3.75	0.59	0.03
Scorpaena notata	6	CB	3.63	0.27	0.01
Sphoeroides marmoratus	4	CB	5.33	1.35	1.44
Symphodus mediterraneus	5	CB	0.60	0.29	1.54
Thalassoma pavo	5	CB	1.78	1.13	1.83
Thorogobius ephippiatus	6	CB	0.05	0.41	0.15
Trachurus picturatus	1	CP	0.70	0.33	0.36
Tripterygion delaisi	6	CB	6.09	35.73	1.19

Apogon imberbis and the nocturnal *Gaidropsarus guttatus*) were collected but not seen. Observers nevertheless failed to see species that live in the open but that are either small (like the gobiesocid *Diplecogaster* sp.) and/or well camouflaged (*Coryphoblennius galerita* and *Hippocampus ramulosus*). Most species that were seen but not captured were fast-moving, demersal or pelagic, and medium to large-sized. Among the most frequent were *Chelon labrosus*, *Sarpa salpa*, and *Sparisoma cretense*. One exception to this rule was the flatfish *Bothus podas*. This was a small and frequently seen species that was never captured, presumably because it could escape the net by swimming below it.

SPATIAL DISTRIBUTION

Fig. 2 shows the mean relative abundance of the most common species, as determined by each method. Clearly, the visual counts were biased towards the pelagic and/or more mobile species, while the rotenone collections were dominated by benthic species. These bias are reflected in the perceived spatial structure of the community, when species are grouped into spatial categories (Fig. 3). In the rotenone collections, category 6 (benthic, sedentary species) is always dominant, either in species richness, number of individuals or total biomass. The visual counts show a different organization. The various spatial categories have less disparate species richness,

although the benthic category is still the most diverse. It is in terms of number of individuals and of total biomass that the two methods differ the most. No category is clearly dominant, but three have higher mean values: category 1 (pelagic species), predominantly the schooling *Atherina presbyter* and juveniles of *Pagellus* spp. and of *Boops boops*; category 3 (demersal), mainly *Chelon labrosus* and *Diplodus sargus*; and category 5 (nectobenthic), dominated by *Centrolabrus caeruleus*.

The visual census, therefore, reveal a spatially richer ichthyofauna than that shown by the rotenone collections. The pelagic and demersal components of the community, in particular, are seen to have an ecological importance (in both numbers and biomass) that could not be deduced from the destructive sampling or from the species lists.

TROPHIC STRUCTURE

Previous analysis of the Azorean littoral fish fauna showed that the benthic microcarnivores are the dominant trophic category, in terms of species richness (PATZNER & SANTOS 1993; AZEVEDO 1995). Most species, therefore, are dependent on the benthic primary production, which reaches them via the benthic invertebrates. A species list, however, is a poor indicator of ecological importance. To evaluate the relative dependence on a given energy pathway,
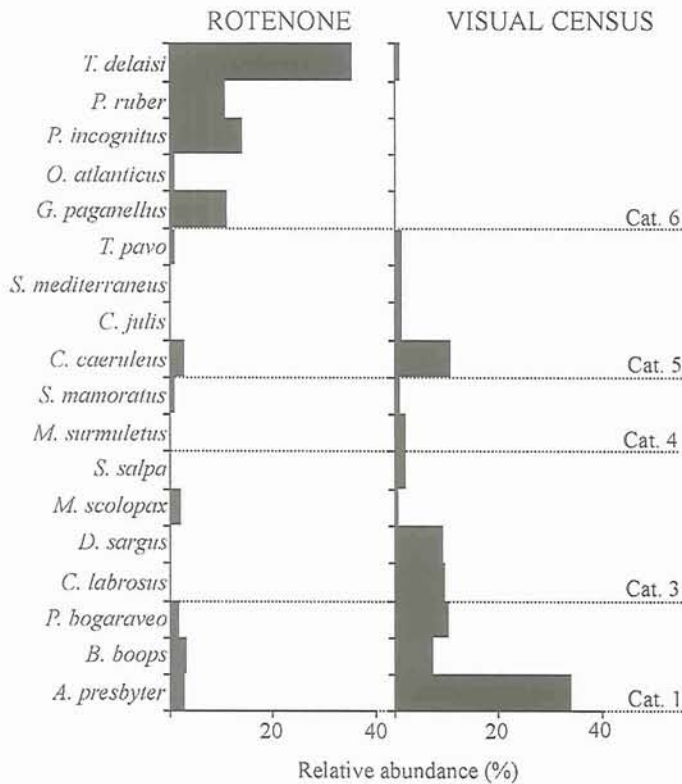
Fig. 2. Mean relative abundances (%) of the more common species, for each of the sampling methods. Species are listed by spatial category, in increasing (top to bottom) order of motility.

from this method also show that the herbivores (mainly *Sarpa salpa*) and the pelagic carnivores (*Atherina presbyter* and juveniles of *Pagellus* spp. and of *Boops boops*) are numerically important and have a non-negligible estimated biomass. This is an indication that two other energetic pathways are important to the studied fish community: benthic primary production via direct consumption of algal biomass and pelagic (planktonic) production.

DISCUSSION

The fish community perceived by the visual census was dominated in number and in biomass by mobile species, pelagic (category 1) and demersal (categories 3 and 5). On the other hand, the rotenone data show a community dominated by benthic species, with the sedentary demersal (category 5) increasing in relative importance in biomass terms. In addition, the visual census revealed a more diverse community although 2/5 of the species were invisible to one or the other methods.

quantitative data are necessary. Preferably, biomass data should be used (as in PARISH et al. 1985 or POLUNIN & KLUMPP 1992).

Fig. 4 shows the distribution of the species richness, number of individuals and fish biomass by the 4 main trophic categories, as gathered from each sampling method. The dominance of the benthic carnivores in terms of number of species is confirmed by both methods. The fish community sampled by the rotenone is dominated in biomass also by benthic carnivores. Using only this method, therefore, one could conclude that the community picture in terms of species diversity translates directly into the ecological importance of the food web pathways. The biomass evaluation based on the visual census data, however, shows a dominance of the food web by omnivorous fish. This is mainly due to *Diplodus sargus* and *Chelon labrosus*. The results

These contradictions and omissions are a direct consequence of the characteristics and the limitations of the methods used. The effect of the rotenone on an individual fish varies with the concentration and the time that it is exposed to the product (GILDERHUS 1972). The reason for closing off the sampling area with a net was to keep the fish inside it until a lethal dosage was attained. It was however seen that the more mobile species escaped even while the net was being set. The rotenone collections therefore selectively collected the less mobile species or those whose instinct made them hide instead of escaping. Its excellence in sampling this group of species is demonstrated by the capture of species that were not recorded in the visual census and would otherwise be totally missed. Two

additional factors should be kept in mind when using quantitative rotenone data, as was done in this paper. The first is the direct relationship between water temperature and rotenone efficiency (GILDERHUS 1972; MEADOWS 1973; SAMUELSEN et al. 1988; DAWSON et al. 1991): the number of fish collected is expected to be larger in summer than in winter, even if the density remains the same. The effect of the rotenone also varies across the phylogenetic scale. Different tolerances to this product between families and even species of marine fishes have in fact been documented (WINGARD & SWANSON 1992; M. LOCKETT pers. comm.), but few data exist and there is no explanation of this effect that has predictive value. Relative abundance results from rotenone collections may, then, be compounded by differences in sensitivity between the species sampled.

The visual census technique used in the present study sampled more efficiently the more visible species which, as a rule, are also the most mobile ones. Several schooling, abundant, species were consistently recorded with this method that were never captured with rotenone or were severely under represented. One of the more objectionable aspect of this technique is precisely a tendency of the observer to focus on moving objects. The relative abundance of immobile and cryptic species may thus be strongly under evaluated.

The present results establish that none of the techniques used gives a complete description of the ichthyological community, not even on qualitative terms. It is plausible to admit that a complete inventory of most ichthyological communities can only be achieved combining a variety of destructive and non-destructive sampling methods. If a quantitative description is necessary, several additional requirements must be met. Several visual census techniques produce absolute estimates of density (see revision in HARMELIN-VIVIEN et al. 1985; the distance sampling methods developed by BUCKLAND et al. 1993 are very promising in this context). It is even possible to accurately estimate the length of the fishes and, from it, their weight (as was done by, e.g., BELL et al. 1985, BELLWOOD & ALCALA 1988, JOHN et al. 1990, BORTONE et al. 1992 or MILLE & VAN TASSELL 1994). Given the multiple

spatial niches occupied by fishes, the best strategy probably involves the simultaneous use of several such methods, each directed to a given species or group of species. The choice of the methods should be preceded by preliminary work to determine its relative efficiency in each case. The best visual estimates for each species could eventually be combined with quantitative destructive collections to provide an integrated view of the community.

The species richness recorded in the present study (S=46) is equal to that given by SANTOS (1992) for another Azorean site, the Monte da Guia, Faial Island, although the species are not all the same. This diversity is low if compared with similar studies in coral reefs: 143 species in the Great Barrier Reef (SALE & DOUGLAS 1984); 158 in Hawaii (NORRIS 1985); 280 species in Moorea, French Polynesia (GALZIN & LEGENDRE 1987). Contrary to expectations based on total faunistic richness, however, the Azorean sites show a species diversity similar to that of other temperate rocky coast communities of the Atlantic and the Mediterranean: HARMELIN (1987) recorded 47 species in Port-Cros, Corse; GARCÍA-RUBIES & ZABALA (1990) observed 51 species in the island of Medes, Spain and BORTONE et al. (1991) listed 47 species in the island of El Hierro, Canaries. This apparent contradiction may be explained by taking into account the scale factor. Faunal lists are compiled over a coastline of hundreds of kilometers and a depth of several hundreds of meters, encompassing necessarily different kinds of habitat. They will therefore contain many more species than those that can be found in any single location. Nevertheless, insular biogeography theory (MACARTHUR & WILSON 1967) predicts that even when sampling area size is the same, the Azores sites should still have a lower species diversity than the above mentioned ones. Further comparative work is needed before this discrepancy can be solved.

The perceived spatial distribution of the fish community is different according to the sampling method used, the visual census emphasizing the importance of the pelagic/demersal species, the rotenone collections that of the benthic one. Better methods have therefore to be developed,
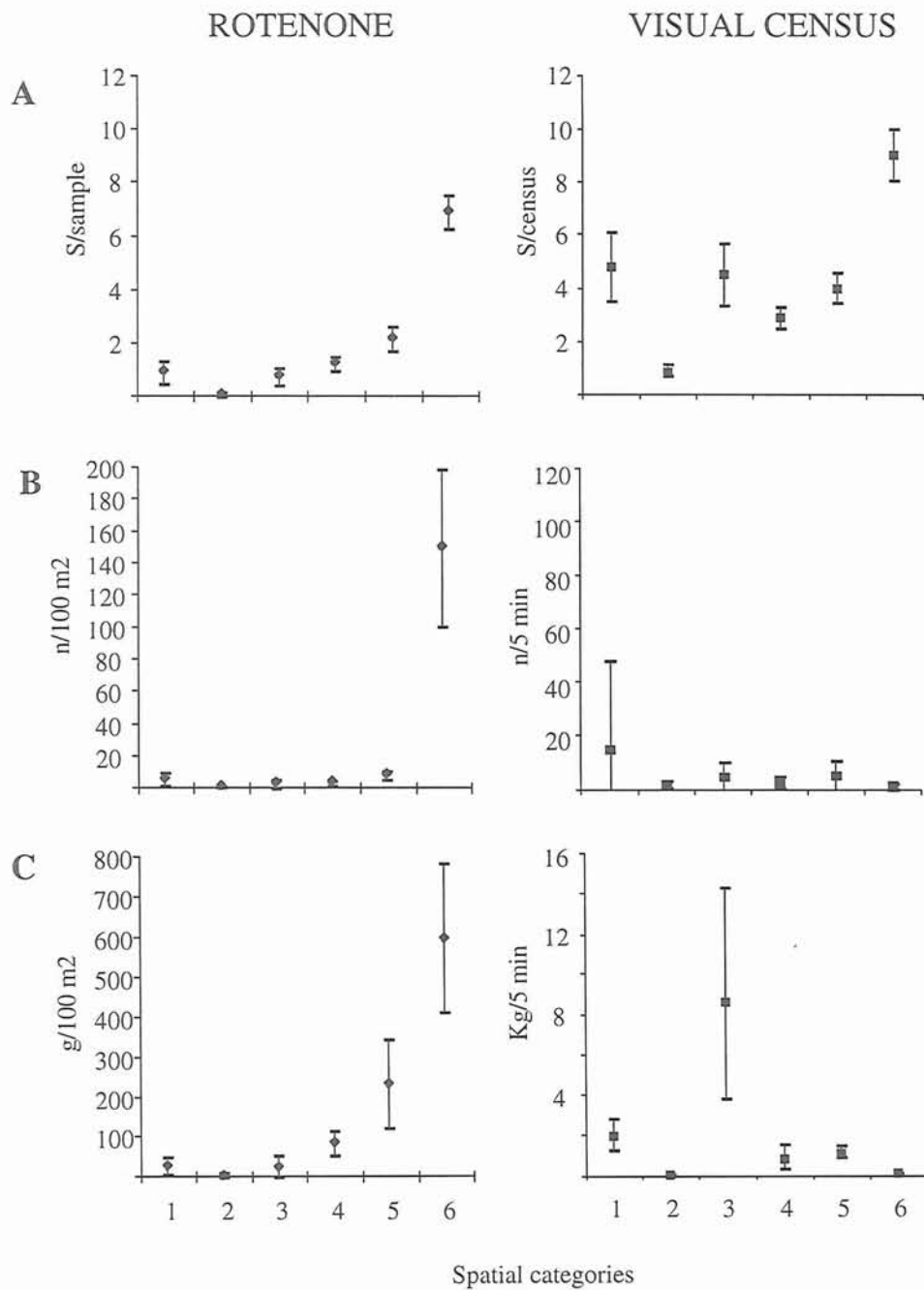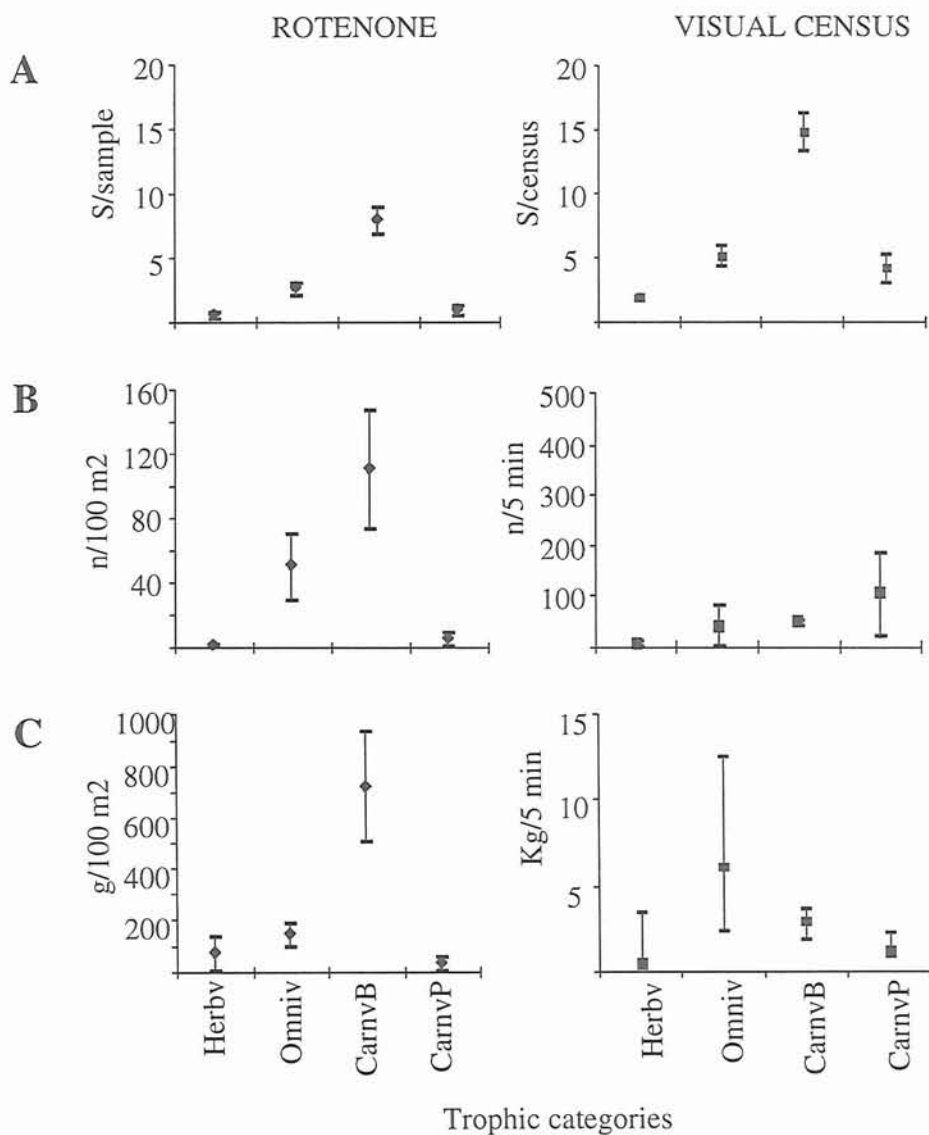
Fig. 3. Community structure: species richness, S (A), abundance (B) and biomass (C) of each spatial category, as given by the rotenone samples (left) and the visual census (right). Graphs show average ± 95% confidence interval, except for visual census biomass estimates, which show median ± 5/95 percentils.

Fig. 4. Community structure: species richness, S (A), abundance (B) and biomass (C) of each trophic category, as given by the rotenone samples (left) and the visual census (right). Conventions as in Fig. 3.

along the lines discussed above, so that a more accurate description of the spatial structure of the Azorean littoral fish community can be attained. Attention should be given to the fact that spatial categories are likely to have different weight according to factors such as depth and type of substrate. Data consistent with this statement was

obtained when geomorphologically and hydrodynamically distinct sites were compared by HARMELIN (1987) in Corse and by BORTONE et al. (1991) in the Canaries.

Little work has been done on the subject of quantification of trophic relationships within fish communities. Most studies limit themselves to

express the relative importance of trophic categories in terms of species richness. This is the current state of the knowledge in the Azores, as reported by PATZNER & SANTOS (1993) and AZEVEDO (1995). These authors note that most species feed on benthic invertebrates. The quantitative estimates obtained in the present study using the rotenone collections also show the benthic carnivores as dominant in terms of biomass and hence of ecological importance. Nevertheless, with all their associated bias, the visual census data suggest that, in this particular site, algal biomass is also an important energy pathway in the fish community. Overall, it is the benthic primary production that emerges as the main energy source of the studied community. Further work is needed to confirm these results and to verify its applicability on different geomorphological and depth settings.

The clarification and quantification of the fish trophic web has important applied aspects, as illustrated by the work of POLUNIN & KLUMPP (1992).These authors developed a trophodynamic model applied to an intensively studied area, the Davies Reef on the Great Barrier Reef, Australia. In the model the trophic chains that link the benthic and planktonic primary productions to the fish community were delineated. Data from many sources were then used to estimate the energetic input and the efficiency of transmission along the food chains. The resulting model was finally used to generate data relevant for fisheries management. This integrated approach could also be useful in the context of the littoral fisheries of the Azores which are, as in tropical areas, mainly pluriespecific.

ACKNOWLEDGEMENTS

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THE SUBTIDAL EPIBENTHIC COMMUNITIES OFF PUERTO DEL CARMEN (LANZAROTE, CANARY ISLANDS)

C. NIKE BIANCHI, RICARDO HAROUN, CARLA MORRI & PETER WIRTZ

SCUBA diving down to ca 50 m depth in February 1996 allowed the recording of 150 conspicuous species (or species groups) by visual census and photography. Five main communities were identified using cluster analysis on presence / absence data. Rock in shallow water (< 10 m) was covered by a species-rich community dominated by photophilic algae. A community characterised by several fish species inhabited sandy bottom at a depth 10 to 20 m deep. Between 20 and 50 m, a volcanic reef ran almost parallel to the coastline. A community characterised chiefly by echinoderms, encrusting invertebrates and few algae thrived on the reef head, whereas a community of sessile animals (sponges, cnidarians etc.) was recognisable on the reef wall and in caves. A further community was found on rocks at the base of the reef, and was constituted mainly by bushy cnidarians. Species composition and general physiognomy of these five epibenthic communities were similar to those already described from other sites of the Canaries and showed analogies with corresponding communities in the rest of the Atlantic-Mediterranean region.

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INTRODUCTION

The lack of a comprehensive and structured classification system of the European marine habitats, such as that developed for the terrestrial habitats (COMMISSION OF THE EUROPEAN COMMUNITIES 1991), has been highlighted by CONNOR et al. (1995). Much reference work is available for the Mediterranean Sea (AUGIER 1982; BELLAN-SANTINI et al. 1994), and PÉRÈS (1982) extended to a worldwide scale his still largely employed "Nouveau manuel de bionomie benthique de la Mer Méditerranée" (PÉRÈS & PICARD 1964). Reference is also available for the northern European seas (GLÉMAREC 1973; HISCOCK & MITCHELL 1980), whereas little exists for the Eastern Atlantic.

The Canary Islands are an important part of the Eastern Atlantic, because of their geographic position and the relationships within both the "Macaronesia" puzzle (BEYHL et al. 1995) and the Atlantic-Mediterranean region (TORTONESE 1960).

The marine flora and fauna of the Canaries are sufficiently known (BACALLADO ARÁNEGA 1984; GONZÁLES HENRÍQUEZ et al. 1986) and guides to invertebrates and fish are available (BRITO 1991; PÉREZ SÁNCHEZ & MORENO BATET 1991; WIRTZ 1994, 1995), but comparatively few studies have been undertaken on the classification of marine communities. Most of these studies deal with

algal vegetation (e. g., LAWSON & NORTON 1971; HAROUN TABRAUE et al. 1984; BALLESTEROS 1993; MEDINA et al. 1995), but HERRERA et al. (1993) and ARÍSTEGUI et al. (1987) examined whole epibenthic communities.

The aim of this paper is to characterise the main epibenthic communities and their zonation according to bottom types off Puerto del Carmen, a small town on the SE coast of the Island of Lanzarote, the easternmost of the Canaries.

METHODS

We used visual census and underwater photography by SCUBA diving down to ca 50 m depth. Four sites were investigated (Fig. 1): 1) El Agujero, 2) Bajamar, 3) Punta Tiñosa; 4) El Muelle. The first three sites were explored by SCUBA diving along depth profiles (Fig. 2). Bajamar was visited four times, to explore the deep reef in detail (Fig. 3). El Muelle (Fig. 4) is a shallow water area near the dock, and dives were conducted by simply wandering around over the bottom. Depths were measured with a diving computer, and subsequently corrected to chart datum.

In each site, 2 to 5 different stations were identified physiognomically (BIANCHI et al. 1991), i. e., a "station" was a relatively large area homogenous in aspect. In each of such stations, the "conspicuous" (HISCOCK 1987) species of flora and fauna were recorded and photographed with an underwater camera equipped with a wide-angle (15 mm) lens and an electronic strobe.

A matrix "stations × species" was produced, using presence / absence data. Similarity between stations was calculated applying Sorensen coefficient (BOUDOURESQUE 1971) and stations
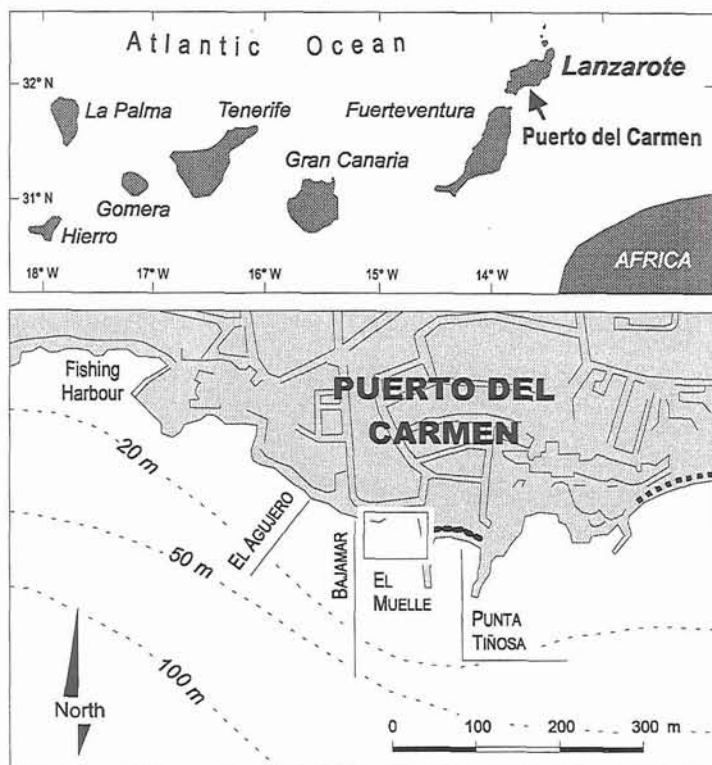
Fig. 1. Location of study area at Puerto del Carmen Lanzarote (Canary Islands), with diving sites indicated.

were subsequently clustered into a dendrogram through complete linkage.

RESULTS

A total of 152 species/species groups was observed and/or photographed in the 4 diving sites: 21 macroalgae, 11 sponges, 32 cnidarians, 10 molluscs, 6 polychaetes, 7 crustaceans, 6 lophophorates, 9 echinoderms, 4 ascidians, and 46 fishes (Table 1).

Species-groups were used in the case of organisms not easily recognised underwater or on the slides, but sharing the general aspect (HISCOCK 1987). The name "algal turf" was given to a mixture of different small-sized algal thalli, as defined by NETO (1992). A similar definition applies to hydroid mat.

Encrusting coralline algae, encrusting

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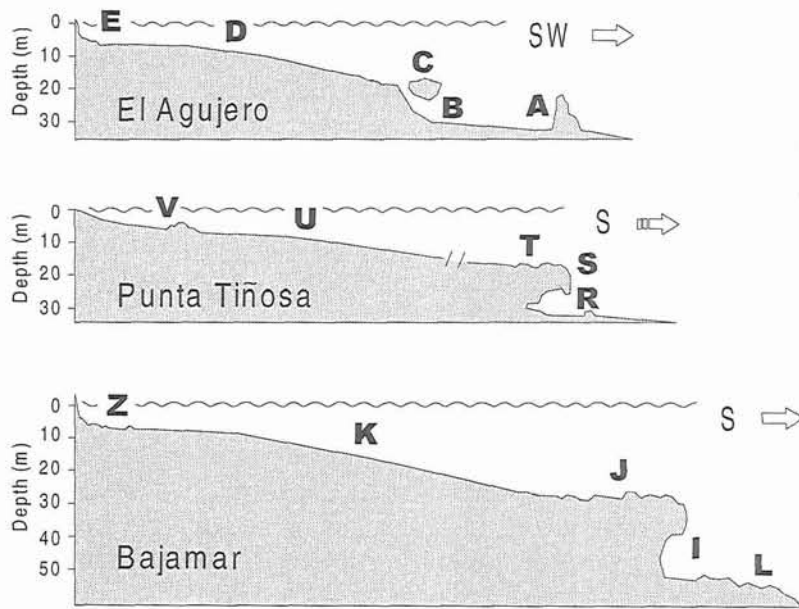
Fig. 2. Schematic sea-bottom profiles at three dive sites: El Agujero, Bajamar, Tiñosa. Horizontal distances are taken from maps and are thus simply indicative. Letters indicate stations.

bryozoans and encrusting sponges were especially abundant in sea-urchin barrens where *Baltzella inops* and *Phorbas fictitius* were the most common sponges, and *Reptadeonella violacea* and *Schizoporella longirostris* the most common bryozoans. However, similar encrusting species occurred also in other habitats, and a consistent identification down to species level was not possible.

Many different species of sponges shared a massive growth-form, but species of *Acanthella*, *Aplysina*, *Axinella*, *Ircinia* and *Spongionella* were excluded from the group and consistently recognised to at least genus level. The group "large hydroids" comprised species of *Aglaophenia*, *Eudendrium* and *Halecium*, among others. Serpulidae and Vermetidae possibly included only one species each, whereas *Ircinia* sp.p. might well correspond to different massive sponges: CRUZ SIMÓ (1984) listed five *Ircinia* species for the Canaries, all occurring in habitats such as those studied here. A similar remark applies for the alga *Hypnea* sp.p., several species being known in the region (HAROUN & PRUD'HOMME VAN REINE 1993).

Cluster analysis applied to the

presence / absence data matrix identified 5 major group of stations (Fig. 5).

The best defined cluster was composed by five stations (Q Y U D K), all located on the sand slope which, starting from the base of the littoral cliff at about 10 m, reached 25 m depth at a distance of about 150-180 m from the shore (Fig. 2). It was a rather steep slope of bare volcanic sand nearly deprived of visible flora and fauna. Thus, this cluster resulted defined primarily by a number of fish species (Table 1), among which the conger eel *Heteroconger longissimus* was noticeable for its characteristic "gardens". Swarms of the opossum shrimp *Paramysis arenosa* were also common (WITTMAN & WIRTZ 1998).

A second well-defined cluster included six stations (E G F Z H V) located on rock in shallow water (Fig. 5). These stations corresponded to the base of the littoral rocky cliff, ending generally within 7 m depth and leaving place to a boulder field (Fig. 4). The rocky substrate generally exhibited high biological cover, with the dominance of photophilic algae, such as *Dictyota dichotoma*, *Pterocladiella capillacea* and many others (Table 1). Small areas of bare rock were

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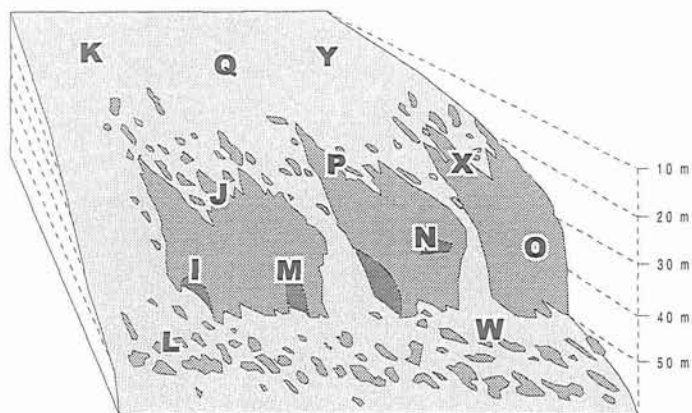
Fig. 3. A pictorial view of the submerged volcanic reef off Bajamar, running almost parallel to the coastline of Puerto del Carmen. Letters indicate stations.

nevertheless observed chiefly where sea urchins (especially *Arbacia lixula*) were abundant. The sponge *Aplysina aerophoba* and the sea anemone *Anemonia viridis* were the most important sessile invertebrates: both species are known to harbour phototrophic endosymbionts (BIANCHI et al. 1998). Many different fish species were frequent (Table 1). The boundary between rocks and sand was characterised by crowding *Arachnanthus nocturnus*, a tube anemone locally reaching the density of 200 individuals·m².

The other three clusters were less sharply separated and embraced the stations located on the impressive submerged reef that ran almost parallel to the coastline at the outer end of the sand slope, between 25 and 50 m depth (Fig. 3). The volcanic rock forming the reef was highly fissured and uneven, thus originating many different habitats, among which submarine caves and overhangs (Fig. 2).

Three stations (P J C) located on the reef head and two (X O) located on the (upper) reef wall clustered together (Fig. 5). This cluster was characterised by few algae and several sessile or sedentary animals, among which different echinoderms occurred (Table 1). Rocks at the reef head exhibited low biological cover probably because of the intense grazing by the sea-urchin *Diadema antillarum*; other common organisms were the sea-star *Narcissia canariensis*, the algae

Lobophora variegata, *Lophocladia trichoclados* and *Cottoniella filamentosa*, and the ascidian *Pycnoclavella* sp., together with encrusting sponges and bryozoans.

Another cluster was formed by height stations, five of which (B R N I M) corresponded to caves or overhangs, two (S A) to the reef wall, and only one (T) to atract of reef head near a cave (Fig. 2). A diverse sessile fauna was characteristic of this cluster (sponges, cnidarians, polychaetes etc.), whereas fish were less important (Table 1). Hydroids were abundant on the reef wall. Stations I and M, corresponding to deep overhangs characterised by the tree coral *Dendrophyllia ramea*, formed a slightly distinct subcluster (Fig. 5).

Finally, the last cluster was made up by only two stations (L W), located on the deep rocks at the base of the reef. This cluster was defined especially by its exclusive sessile biota, with the black coral *Anthipathes wollastoni* forming extensive "forests". Different gorgonian species and the epizoic zoanthid *Gerardia savaglia* were also common (Table 1).

DISCUSSION

The five station clusters may easily be interpreted as different benthic habitats, each one having its peculiar biotic community (in the sense of HISCOCK & MITCHELL 1980).

These communities fit well within the general scheme outlined for the Canaries by BACALLADO ARÁNEGA (1984) and GONZÁLES HENRÍQUEZ et al. (1986). Analogies can be found with those described by HERRERA et al. (1993) at Playa del Cabrón, Gran Canaria, and by BALLESTEROS (1993) in some stations off Fuerteventura and Lanzarote.

The main difference between the latter study and the present one, is the relatively limited extension of photophilic algal assemblages at
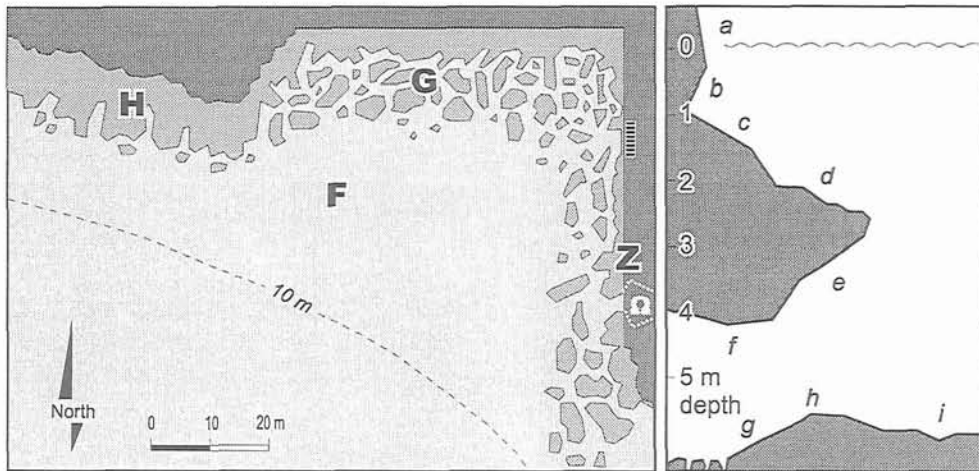
Fig. 4. Schematic map of the sea-bottom in the dive site called "El Muelle". Letters indicate stations (left). Vertical profile and zonation at station Z (right): a) *Ulva rigida* and *Actinia equina*; b) *Corynactis viridis*; c) *Corallina elongata*; d) *Arbacia lixula* and encrusting corallines; e) *Parazoanthus* sp.; f) cave with encrusting and massive sponges; g) encrusting corallines; h) *Dictyota dichotoma* and other algae.
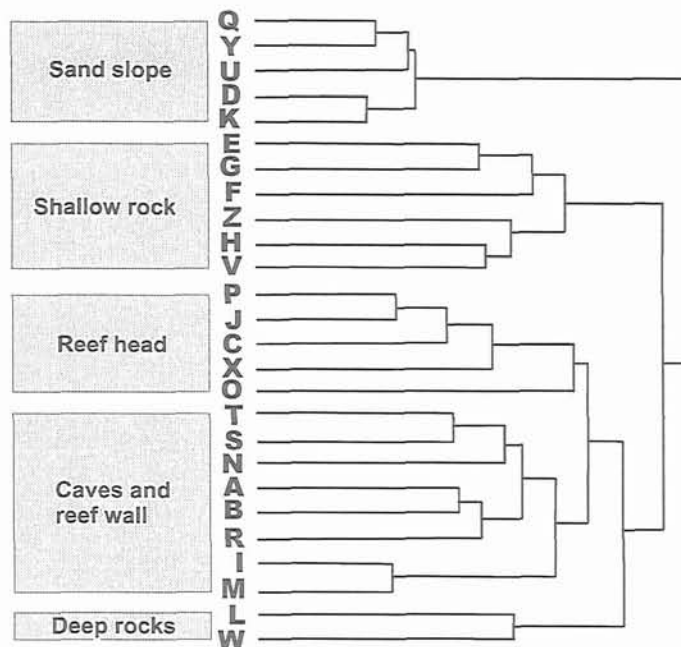

Fig. 5. Dendrogram resulting from cluster analysis (Sorensen coefficient, complete linkage). Letters indicate stations (*see text for explanation*).

Anyway, the general dominance by Dictyotales (here especially *Dictyota dichotoma*) is a common feature of such algal assemblages in the whole Atlantic-Mediterranean region (BIANCHI et al. 1998).

At Playa del Cabrón, HERRERA et al. (1993) limited their study to a depth of 30 m, whereas at Puerto del Carmen we extended investigation down to about 50 m. The community we observed in deep water is similar to that found by BALLESTEROS (1993) at 53 m depth off Punta Tiñosa and by ARÍSTEGUI et al. (1987) when dredging from 40 to 200 m depth off Tenerife. Diving allowed us to allocate *Dendrophyllia ramea* and the other bushy anthozoa (gorgonians and antipatharians) to different "sub-habitats": the former was found under overhangs, the latter on sub-horizontal rocks. Gorgonians characterise a similar depth zone on hard bottoms also in the Mediterranean Sea, but antipatharians and *Dendrophyllia ramea* live deeper (PÉRÈS & PICARD 1964). A gorgonian-

Puerto del Carmen, but this may be explained by the fact that the shallow water area investigated was rather sciophilous, under steep cliffs.

Table 1

List of the species observed or photographed during the dives at Puerto del Carmen, February 1996, 0 to 54 m depth, and their presence in the five major habitats recognised through cluster analysis and ranked according to increasing depth. Notes: [1] confused within "encrusting sponges"; [2] on shells occupied by the hermit crab *Pagurus prideaux*; [3] confused within "large hydroids"; [4] inside sponges, in very high densities (WIRTZ 1996); [5] the rich crustacean fauna associated with this species has been described by WIRTZ (1997); [6] associated with the sea-star *Astropecten aranciacus* and visible at night; [7] associated with the black coral *Antipathes wollastoni* (FRANSEN & WIRTZ 1998); [8] confused within "encrusting bryozoans".

	Shallow rock (< 10 m)	Sand slope (10-20 m)	Reef head (~ 25 m)	Caves and reef wall (30-40 m)	Deep rocks (~ 50 m)
ALGAE					
algal turf	+	.	+	+	+
Asparagopsis taxiformis	+	.	+	.	.
Carpomitra costata	.	.	.	.	+
Caulerpa racemosa	+	.	.	.	.
Caulerpa webbiana	+	.	+	+	+
Cottoniella filamentosa	.	+	+	.	+
Dictyota bartayresii	+	.	.	.	.
Dictyota dichotoma	+	.	+	+	.
encrusting corallines	+	.	+	+	+
Falkenbergia rufolanosa	+	+	+	.	+
Halopteris filicina	+	.	+	.	+
Hypnea sp. p.	+	+	+	.	.
Lobophora variegata	+	+	+	.	.
Lophocladia trichoclados	+	+	+	.	+
Mycrodictyon tenuis	.	.	.	.	+
Padina pavonica	+	+	+	.	.
Palmophyllum crassum	+	.	+	+	+
Pterocladiella capillacea	+	.	.	.	.
Stypocaulon scoparium	+	.	+	.	.
Stypopodium zonale	+	+	+	.	.
Ulva rigida	+	.	.	.	.
PORIFERA					
Acanthella acuta	.	.	.	+	.
Aplysina aerophoba	+	.	+	.	.
Axinella damicornis	.	.	+	+	+
Axinella polypoides	.	.	.	+	.
Baltzella inops [1]	+	.	+	.	.
encrusting sponges	+	.	+	+	+
Ircinia sp. p.	+	.	.	+	.
massive sponges	+	.	+	+	+
Phorbas fictitius [1]	+	.	+	.	.
Plakortis simplex	.	.	+	+	.
Spongionella pulchella	+	.	+	+	.
CNIDARIA					
Actinia equina	+	.	.	.	.
Adamsia palliata [2]	.	+	.	.	.
Aglaophenia pluma [3]	.	.	+	.	.
Aiptasia mutabilis	+	.	.	.	.
Alicia mirabilis	+	.	.	.	.
Anemonia melanaster	+	.	.	.	.

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(Table 1 continued)

Anemonia viridis	+	.	.	.	.
Antipathes wollastoni	.	.	.	+	+
Arachnanthus nocturnus	+	+	.	.	.
Balanophyllia regia	+	.	+	.	.
Caryophyllia inornata	.	.	+	+	.
Corynactis viridis	+	.	.	.	.
Dendrophyllia ramea	.	.	.	+	.
Ellisella paraplexauroides	.	.	.	.	+
Eudendrium sp. [3]	.	.	.	+	.
Eunicella verrucosa	.	.	.	.	+
Gerardia savaglia	.	.	.	.	+
Halecium sp. [3]	.	.	.	+	.
Hoplangia durotrix	.	.	.	+	.
hydroid mat	+	.	.	+	.
large hydroids	.	.	+	+	+
Leptopsammia pruvoti	.	.	+	+	+
Lophogorgia ruberrima	.	.	.	.	+
Lophogorgia viminalis	.	.	.	.	+
Madracis asperula	.	.	.	+	.
Madracis pharensis	.	.	.	+	.
Nausithoe punctata [4]	.	.	.	+	.
Pachycerianthus sp.	.	.	+	+	.
Paracyathus pulchellus	.	.	+	.	.
Parazoanthus sp.	+	.	.	+	+
Phyllangia mouchezii	.	.	+	+	.
Telmatactis cricoides [5]	+	.	+	.	.
MOLLUSCA					
Chama gryphoides	.	.	+	.	.
Coryphella pedata	.	.	+	.	.
Discodoris atromaculata	+	.	.	.	.
Hypselodoris fontandraui	+	.	.	.	.
Hypselodoris picta	.	.	.	+	.
Neopycnodonte cochlear	.	.	.	+	.
Pinna rudis	+	.	.	.	.
Spurilla neapolitana	+	.	.	.	.
Umbraculum umbraculum	+	.	.	.	.
Vermetidae gen. sp.	.	.	.	+	.
POLYCHAETA					
Acholoe squamosa [6]	.	+	.	.	.
Bispira viola	.	.	.	+	.
Hermodice carunculata	.	.	.	+	+
Protula tubularia	.	.	+	+	.
Serpulidae gen. sp.	.	.	+	+	.
Vermiliopsis sp.	.	.	.	+	.
CRUSTACEA					
Balanus trigonus	.	.	+	+	.
Eualus occultus	.	+	.	.	.
Pagurus prideaux	.	+	.	.	.
Paramysis arenosa	.	+	.	.	.
Percnon gibbesi	+	.	.	.	.
Periclimenes wirtzi [7]	.	.	.	.	+
Stenorhynchus lanceolatus	+	.	+	+	.

(Table 1 continued)

	1	2	3	4	5
LOPHOPHORATA					
Bugula plumosa	.	.	.	+	.
encrusting bryozoans	+	.	+	+	+
Phoronis hippocrepia	.	.	.	+	.
Reptadeonella violacea [8]					
Schizoporella longirostris [8]					
Smittina cervicornis	.	.	.	+	.
ECHINODERMATA					
Arbacia lixula	+	.	.	.	.
Astropecten aranciacus	.	+	.	.	.
Diadema antillarum	+	.	+	+	.
Hacelia attenuata	.	.	.	.	+
Holothuria cf. *forskali*	+	.	.	.	.
Holothuria sp.	+	+	+	.	.
Martasterias glacialis	.	.	+	.	.
Narcissa canariensis	.	.	+	+	.
Sphaerechinus granularis	+	.	+	.	.
TUNICATA					
Ascidia mentula	.	.	.	.	+
Clavelina lepadiformis	.	.	.	+	.
Didemnum sp.	+	.	.	+	+
Pycnoclavella sp.	.	.	+	+	+
PISCES					
Abudefduf luridus	+	.	+	+	.
Anthias anthias	.	.	+	.	+
Apogon imberbis	+	.	+	+	.
Bodianus scrofa	.	.	.	+	.
Boops boops	+	+	.	.	.
Bothus podas madeirensis	.	+	.	.	.
Canthigaster rostrata	+	+	+	+	.
Centrolabrus trutta	+	.	.	.	.
Chelon labrosus	+	+	.	.	.
Chromis limbata	+	.	+	.	+
Diplodus cervinus	+	.	.	.	.
Diplodus sargus cadenati	+	.	+	+	.
Diplodus vulgaris	+	.	.	.	.
Epinephelus marginatus	+	.	+	+	.
Gobius niger	.	+	.	.	.
Heteroconger longissimus	.	+	.	.	.
Lithognathus mormyrus	+	+	.	.	.
Liza aurata	+	+	.	.	.
Mullus surmuletus	+	+	.	.	.
Muraena augusti	.	.	+	.	.
Mycteroperca fusca	.	.	.	.	+
Oblada melanura	+	.	.	.	.
Ophioblennius atlanticus	+	.	.	.	.
Pagellus erythrinus	.	+	.	.	.
Parablennius parvicornis	+	.	.	.	.
Parablennius pilicornis	+	.	.	.	.
Pseudocaranx dentex juv.	.	+	.	.	.
Sardinella maderensis	+	+	.	.	.
Sarpa salpa	+	.	.	.	.
Scartella cristata	+	.	.	.	.
Scorpaena maderensis	+	.	+	+	.

(Table 1 continued)

Serranus atricauda	.	.	.	+	.
Sparisoma cretense	+	.	+	+	.
Sphoeroides marmoratus	.	.	+	.	.
Sphyraena viridensis	.	+	+	+	.
Spondyliosoma cantharus	+	.	.	.	.
Squatina squatina	.	+	.	.	.
Stephanolepis hispidus	+	.	.	.	.
Synodus saurus	+	+	.	.	.
Synodus synodus	+	.	.	.	.
Taeniura grabata	.	.	.	.	+
Thalassoma pavo	+	.	+	+	+
Trachinotus ovatus	+	.	.	.	.
Trachinus draco	.	+	.	.	.
Uranoscopus scaber	.	+	.	.	.
Xyrichthys novacula	.	+	.	.	.

antipatharian community similar to that observed at Puerto del Carmen, although composed by different species, was described from the Archipelago of Cape Verde by MORRI & BIANCHI (1995).

The discussion above suggests that an economic and "low-tech" approach, mostly based on visual census and photography, may be sufficient for the description of main epibenthic communities. Recording 150 species in a limited area with such a low "sampling" effort stands for the high marine biodiversity of the Canaries.

Clearly, a major problem is that not everything can be recognised underwater or on the photographs to the species level. This was especially true for encrusting organisms, which might well be represented by different species in the different habitats we studied, and could in some cases have dampened habitat discrimination (for example, poor sorting of reef-head and reef-wall stations in cluster analysis).

Another limit is that small species were not easily seen underwater, but might be characteristic too. In some cases, these small species lived strictly associated with other, larger organisms (see notes in Table 1). Being prevalently linked to their host rather than to the physical environment, they are species-specific not really biotope-specific (BIANCHI et al. 1989; MORRI et al. 1991). Large organisms, which monopolise or dominate the substratum on which they live, are better "indicators" (KÖNNECKER 1977) of the

environmental conditions or factors to which they are adapted and should be preferred for the description and classification of epibenthic communities.

ACKNOWLEDGEMENTS

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SHALLOW EPIBENTHIC COMMUNITIES OF ILHA DO SAL (CAPE VERDE ARCHIPELAGO, EASTERN ATLANTIC)

CARLA MORRI, RICCARDO CATTAENO-VIETTI, GIANFRANCO SARTONI & C. NIKE BANCHI

Epibenthic communities were studied by snorkelling and SCUBA diving down to 33 m depth at Sal, the island at the northeastern corner of the Cape Verde Archipelago, in the winter of 1990-1991. Apart from minor differences related to exposure, three main bionomic zones were identified: 1) the littoral, with littorinids, chthamalids and encrusting corallines; 2) the shallow sublittoral, with corals and algae; 3) the sublittoral below 20 m depth, with gorgonians and antipatharians. The first, and perhaps the third, showed a prevalent Atlantic-Mediterranean affinity, the second a pronounced tropical West Atlantic affinity. This possibly reflects the influence of distinct water layers, thus suggesting that a bionomic approach might help in the analysis of the composite biogeographic character of the Cape Verde marine biota. However, both bionomic and biogeographic studies suffer badly from a persistent lack of sufficient taxonomic knowledge.

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INTRODUCTION

The Archipelago of Cape Verde, situated at a latitude of about 15 to 17° N, is considered as at the boundary between the Atlantic-Mediterranean warm-temperate region and the Eastern Atlantic tropical (Senegalian) region by most marine biogeographers (EKMAN 1953; BRIGGS 1974).

Many scientific expeditions (see REINER 1996 for a list of the most important ones) have collected marine flora and fauna (VAN DER LAND 1993). Nevertheless, the epibenthic communities and their zonation remain little known, apart from recent studies mainly focussing on algae (OTERO-SCHMITT 1993, 1995, 1996a,b).

In the winter of 1990-1991, the Institute of Zoology of the University of Genoa organised a diving expedition to Sal, the island at the northeastern corner of the archipelago. Previous papers resulting from this expedition took into account sponges (SARÀ & BAVESTRELLO 1998), cnidarians (MORRI & BIANCHI 1995, 1996), and opistobranch molluscs (CERVERA et al. in press). The present contribution is aimed at giving a general description of the epibenthic communities as a whole, with particular attention to their depth zonation down to about 30 m.

MATERIAL AND METHODS

Epibenthic communities were studied by snorkelling and SCUBA diving along transects perpendicular to the coastline, reaching a maximum depth of 33 m. Divers annotated on a plastic board the conspicuous species (*sensu* HISCOCK 1987) of flora and fauna, together with the nature of the substrate and main topographic features (BIANCHI et al. 1991). Underwater photographs were also taken to integrate information. Observations and slides are available from the first author, while transects are illustrated in detail by MORRI & BIANCHI (1995). A total of twenty dives was conducted on the west and south coasts of Sal, in sites differing for exposure and the nature of the substrate (Fig. 1).

RESULTS

Diving sites can be grouped according to location, exposure and physiognomy of the epibenthic communities. Moderately exposed sites on the west coast will be described first, as they might be taken as exhibiting the basic pattern for community definition. Then, an exposed and a sheltered site, again on the west coast, will be described, followed by an example of a moderately exposed site on the south coast.

WEST COAST, MODERATELY EXPOSED SITES

The examples discussed here refer to the coast between Pisqueiro Ti Culão (Baía da Albacora) and Ponta do Joãsinho, to the north of Baía da Palmeira (Fig. 1). These sites are characterised by a rocky shore that continues underwater with a steep to overhanging wall ending at 8 to 10 m depth. A 10 to 50 m wide terrace of blocks,
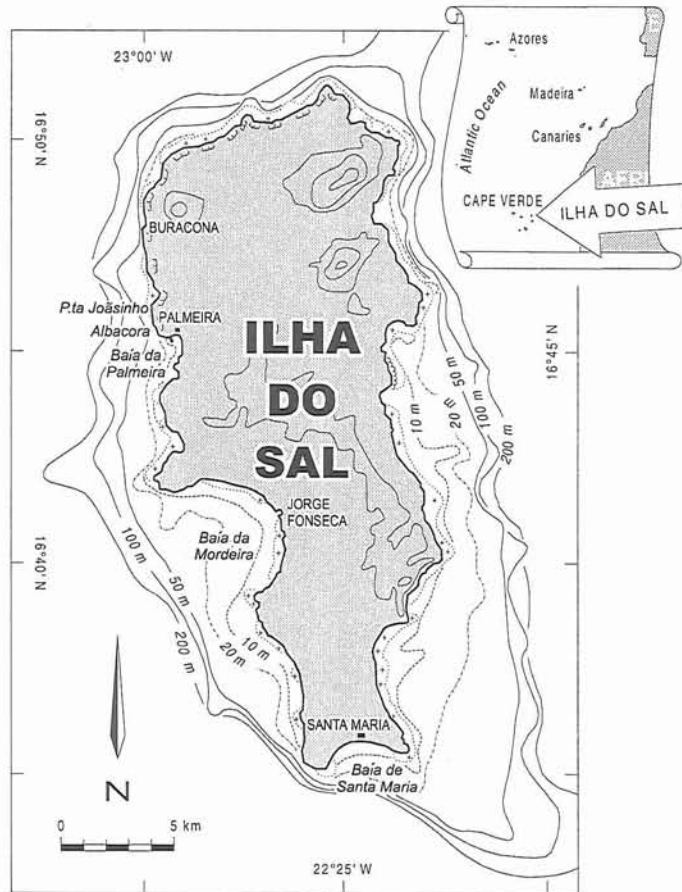
Fig. 1. Geographical setting and schematic map of Ilha do Sal, with localities mentioned in text indicated.

boulders and sand starts at the base of the wall, giving place at around 15 m to a boulder slope that reaches the sandy floor at about 30 m.

On the shore, the volcanic rock was inhabited by *Littorina punctata*, followed downward by a dense population of *Chthamalus stellatus*. Small tide pools sheltered boring sea-urchins (*Echinometra lucunter*), sea-anemones (*Actinia sali*) and molluscs (*Monodonta punctulata*), whereas algae were mainly represented by encrusting corallines and *Ulva rigida*. Encrustation by vermetids (*Vermetus adamsoni*) covered the rock to the water line, marked by discontinuous belts of *Sargassum* and *Cystoseira*.

Underwater, the hydrozoan *Millepora* sp, dominated the sessile assemblage down to 1 to

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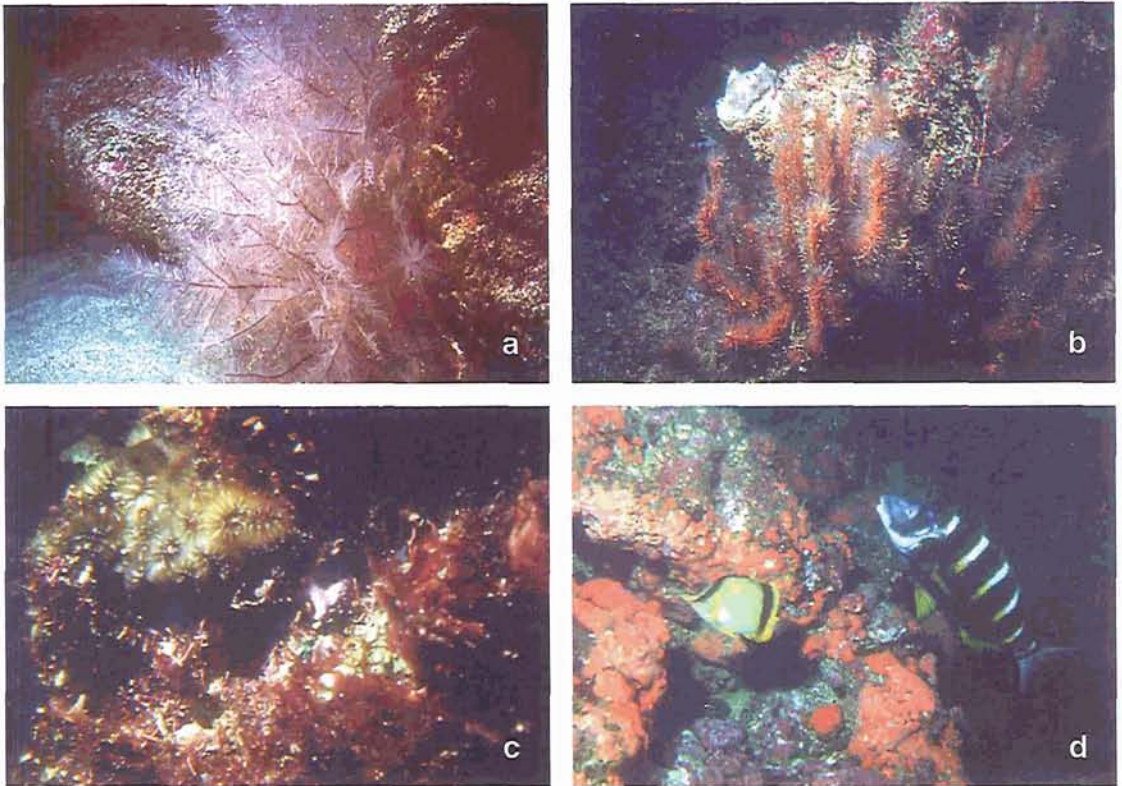
Fig. 2. Some of the problematic species observed at Sal (see text for comments): **a**) the black coral *Antipathes wollastoni*; **b**) the black coral *Antipathes spinescens*; **c**) the ahermatypic coral *Balanophyllia* sp; **d**) the butterfly-fish *Chaetodon marcellae* (left) swimming together with the sea-bream *Diplodus fasciatus* (right) at the entrance of a sea cave.

5 m depth, according to the topography of the specific site. This *Millepora* was encrusting to massive, only rarely forming stout erect branches. Another important species was *Megabalanus azoricus*, whose shells were usually covered by *Millepora*. At the lower margin of and below this *Millepora* belt, down to around 8 m depth, other species were abundant, such as the hydroid *Halocordyle disticha* and the red alga *Laurencia majuscula*. This situation was typical of the vertical wall. On some subhorizontal terraces, the zoantharian *Palythoa caribaeorum* was dominant, covering more than 50 % of the substrate, whereas on inclined areas, colonies of the coral *Porites astreoides* were also found. The only conspicuous fish in these shallow water habitats was *Ophioblennius atlanticus*.

In most cases, the underwater wall ended with an overhanging portion, the surface of which was completely covered by the azooxanthellate coral *Tubastraea aurea*. Other important organisms were crustose corallines, sponges, colonial ascidians and the red alga *Peyssonnelia*. Bare rock areas were colonised by the hydroid *Thyroscyphus marginatus* and small barnacles. Among the motile fauna, the fire-worm *Hermodice carunculata* and the sea-urchins *Diadema antillarum* and *Eucidaris tribuloides* were abundant. Fish species observed under overhangs included *Adyorix hastatus*, *Heteropriacanthus cruentatus* and *Parapristipoma humile*.

Blocks and boulders below the cliff were colonised by a mixed zooxanthellate coral

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community composed of *Millepora alcicornis*, *Porites astreoides*, *Favia fragum* and *Siderastrea radians*, the latter being especially abundant around sandy areas. Hard corals were locally replaced by *Palythoa caribaeorum*, whose encrusting colonies covered up to 3 m². Algae were also present: crustose corallines and species of *Jania*, *Peyssonnelia* and *Dictyota* were common. Other noticeable sessile organisms were hydroids (*Plumularia* sp.) and encrusting bryozoans, while a number of animals, both sessile and motile, hid among boulders. The former included the sea-anemone *Telmatactis cricoides*, the sabellid *Bispira guinensis*, and the bivalve *Pinna rudis*. The latter included the fire-worm *Hermodice carunculata*, the crabs *Stenorhynchus seticornis* and *Percnon gibbesi*, the sea-urchins *Diadema antillarum* and *Eucidaris tribuloides*, and the sea-stars *Marthasterias glacialis* and *Echinaster sepositus*. The fish fauna was extremely diverse, common species being *Bodianus speciosus*, *Cephalopholis taeniops*, *Chromis cadenati*, *C. lubbocki*, *Coris atlantica*, *Diplodus fasciatus*, *D. prayensis*, *Diodon holacanthus*, *Girella stubeli*, *Gymnothorax miliaris*, *Holacanthus africanus*, *Mulloidichthys martinicus*, *Scarus hoefleri*, *Selene dorsalis*, *Similparma hermani*, *Sparisoma cretense*, *S.* cf *strigatum*, *Stephanolepis hispidus* and *Thalassoma pavo*.

The coral-dominated community nearly disappeared after 15 m depth, the only hard coral still found at 20 m being *P. astreoides*. It was replaced by a community dominated by the antipatharians *Cirripathes* (*Stichopathes*) *leutkeni*, *Antipathes wollastoni* (Fig. 2a) and *A. spinescens* (Fig. 2b) and the gorgonians *Eunicella papillifera*, *E. granulata*, *Leptogorgia capverdensis* and *L. gaini*, the latter on the sandy floor below 30 m. On the whole, the most abundant species in this community were *L. capverdensis* and *C. leutkeni*. The sessile fauna also included encrusting sponges and the stalked colonial ascidian *Distaplia corolla*. The spiny lobster *Panulirus regius* and the sea-star *Ophidiaster ophidianus* were noticeable among the motile species, *Aulostomus strigosus*, *Chromis lubbocki*, *Epinephelus marginatus*, *Fistularia*

tabacaria and *Scorpaena laevis* among the fish.

WEST COAST, EXPOSED SITE

Further north of Palmeira, in the locality called Brocona or Buracona (Fig. 1), the coast is characterised by a high basaltic cliff which continues underwater to the maximum depth explored (27 m). One or two meters above water level, a large (about 25 m x 5 m) and deep (4 m to 1.5 m) pool opens in the rock, receiving sea water only through the highest waves. The biotic communities in the pool were different from those observed on the underwater cliff at corresponding depths. The latter will be described first, with a major emphasis on the differences as compared to the semi-exposed situation.

The littoral rock was covered by encrusting corallines (possibly *Porolithon africanum*) and the brown alga *Ralfsia expansa*. In shallow water, the most conspicuous organism was a green species of *Zoanthus*.

Tubastraea aurea, *Thyroscyphus marginatus* and the red alga *Plocamium concinnum* abounded in an overhanging portion of the cliff at about 3 m to 8 m. Below 8 m, the slope became less steep and the biotic community was composed by *Millepora* sp, *Megabalanus azoricus*, *Dictyota dichotoma* and the azooxanthellate coral *Balanophyllia* sp (Fig. 2c). *Marthasterias glacialis* was seen feeding on *Megabalanus*. This community remained similar down to about 20 m, where *P. concinnum* replaced *D. dichotoma* as the main erect alga. *Peyssonnelia*, crustose corallines and a few colonies of *Porites astreoides* were present on large boulders toward the base of the cliff. *Aulostomus strigosus*, *Cephalopholis taeniops*, *Abudefduf hoefleri*, *Chromis lubbocki*, *Similparma hermani*, *Sparisoma cretense* and *S. rubripinne* were the commonest fish.

A large cave opened at the base of the underwater cliff, between 19 m and 27 m depth. The roof was covered by *Tubastraea aurea*, the walls mostly by *Thyroscyphus marginatus*. On the floor, *Leptogorgia capverdensis* and *Antipathes spinescens* (Fig. 2b) were present amidst blocks covered by encrusting sponges. Several fish

species were observed at the entrance of the cave, including *Chaetodon marcellae* (Fig. 2d), *Diplodus fasciatus*, *Holacanthus africanus* and *Mycteroperca fusca*.

The community of the supralittoral pool was distinctly zoned according to a spatial gradient perpendicular to the sea. On the seaward wall, encrusting corallines and the sea-urchin *Arbacia lixula* were the most conspicuous organisms. The bottom of the pool, reaching 4 m at the seaward side of the pool and less than 1.5 m at the landward side, contained blocks covered with a lawn of filamentous green algae. A rich motile fauna was present among the blocks, such as the sea-star *Coscinasterias tenuispina*, the carnivorous gastropods *Purpura nodosa*, *Thais hemastoma* and *Latirus triserialis*, and many hermit crabs (probably *Calcinus talismani*) within *Littorina* and *Monodonta* shells. Two species of *Littorina* occurred at the landward side of the pool: *L. striata* above the water line, *L. punctata* at a few cm depth. Among the fish, *Lipophrys caboverdensis* and *Parablennius parvicornis* were also abundant on the bottom of the pool, whereas *Abudefduf hoefleri* and juveniles of *Thalassoma pavo* and *Oblada melanura* swam around in mid-water.

WEST COAST, SHELTERED SITE

A small inlet, named Jorge Fonseca, opens in the middle of the coast of the large Baía de Mordeira (Fig. 1). The inlet is nearly 60 m long and wide and less than 1 m deep for most of its extension. The floor is covered by shingle, with rubble and boulders.

In the inner part of the inlet, the community was dominated by zooxanthellate corals. *Siderastrea radians*, *Porites astreoides* and especially *P. porites* were the most abundant species, but *Millepora alcicornis* and *Favia fragum* were also common. Another important species was the green alga *Caulerpa sertulariodes*, especially in more sandy areas.

Near the seaward opening, where waves break into the inlet, massive construction by *Millepora* sp has formed a miniature barrier reef. Leeward of this reef, in slightly deeper water (1 to 2 m),

S. radians has formed slabs up to 1 m wide. *F. fragum* and *P. astreoides*, but no *Porites porites*, were also present. The brown alga *Dictyota* covered the vertical side of the largest blocks.

SOUTH COAST, MODERATELY EXPOSED SITE

The southern coast of Sal is sandy and a long beach borders the largely open bay called Baía de Santa Maria (Fig. 1). The sea floor is sand and gravel to about 4 m. At this depth, a line of beach rock was found nearly parallel to the coast. Another similar line occurs at about 9 m. At both depths, the beach rock was colonised by pinnacles (stout erect and branched growth forms) of *Millepora* up to 25 cm high and 50 cm wide. *Porites astreoides* and *Siderastrea radians* were also abundant. The former preferred the highest blocks, the latter formed large colonies at the base, at the boundary between rock and sand. The sandy floor was covered by a meadow of *Udotea flabellum*, whereas the most conspicuous invertebrates on sand were the sea-urchin *Rotula deciesdigitata* and the gastropod *Strombus latus*. Fish were mainly represented by *Taeniura grabata*, *Aulostomus strigosus*, *Pseudupeneus prayensis*, *Holacanthus africanus*, *Abudefduf saxatilis*, *Sparisoma cretense*, *S.* cf *strigatum* and *Acanthurus monroviae*.

DISCUSSION

Epibenthic communities at Sal exhibited a clear zonation pattern, in most cases consistent with that already described for the Cape Verde Archipelago by OTERO-SCHMITT (1993, 1995). Apart from minor differences in relation to exposure, the change of flora and fauna with depth was sharp, thus allowing recognition of at least three main bionomic zones (BOUDOURESQUE & FRESI 1976): 1) the littoral, with littorinids, chthamalids and encrusting corallines; 2) the shallow sublittoral, with corals and algae; 3) the sublittoral below 20 m depth, with gorgonians and antipatharians.

The littoral communities fitted in well with the scheme outlined for West Africa by LAWSON (1966), but the eulittoral (or midlittoral) zone showed Atlantic-Mediterranean affinities. The dominant organism was *Chthamalus stellatus*, as in most western European coasts and throughout the Mediterranean, in the Canaries (HAROUN TABRAUE *et al.* 1984), Madeira (BIANCHI *et al.* in press) and the Azores (MORTON *et al.* 1998). In truly tropical West Africa shores, *C. stellatus* is replaced by *Chthamalus dentatus* (LAWSON 1966).

In the sublittoral, analogies can be found with both warm-temperate and tropical zones. The biotic change observed at Sal around 20 m depth corresponds with the transitions from infralittoral to circalittoral in the Mediterranean (PÉRÈS 1967) and from reefal to subreefal in coral reef areas (DONE 1983).

The shallow sublittoral at Sal shares with the Mediterranean the dominance by algae, with the tropics the abundance of zooxanthellate corals. Both groups give the same biogeographic picture: Cape Verde corals are Caribbean in origin (LABOREL 1974) and algae have a distinct East American affinity (PRUD'HOMME VAN REINE & VAN DEN HOEK 1988).

Dominance by gorgonians below 20 m is a common feature in the Mediterranean Sea, but antipatharians live deeper in the circalittoral (PÉRÈS 1967). Communities dominated by co-occurring gorgonians and antipatharians are usual in subreefal habitats in tropical seas. However, the gorgonian species we found at Sal exhibit a eastern Atlantic affinity and closely related species belonging to the same genera occur in the Atlantic-Mediterranean region (GRASSHOFF 1992). The biogeographic affinity of Cape Verde antipatharians is unclear, mostly because of doubtful species identification. The two species that we call *Antipathes wollastoni* (Fig. 2a) and *A. spinescens* (Fig. 2b) in the present paper, were first tentatively referred to their west west-Atlantic relatives *A. barbadensis* and *A. tanacetum*, respectively (MORRI & BIANCHI 1995). Several different species, however, may be included under the name *Antipathes wollastoni*

Brook (= *A. subpinnata* Gray, not Ellis and Solander).

Many authors have already underlined the composite biogeographic character of the Cape Verde marine biota, and also expressed divergent views on this topic in some instances. BRIGGS (1974), who based his analysis mostly on fish, maintained that the relationships of the Cape Verde Archipelago are more tropical than warm-temperate. At Sal, we observed strictly tropical fishes, such as the butterflyfish *Chaetodon* and the angelfish *Holacanthus*, swimming together with warm-temperate breams, such as *Oblada* and *Diplodus* (Fig. 2d). Within groupers, *Cephalopholis taeniops* has a clear tropical affinity, whereas *Epinephelus marginatus* and *Mycteroperca fusca* are two Atlantic-Mediterranean species. Algae and corals give the Cape Verde Archipelago a Caribbean affinity, as mentioned above, but infaunal communities (LONGHURST 1959), sponges (VAN SOEST 1993) and, in part, brachiopods (LOGAN 1993) suggest an Atlantic-Mediterranean affinity.

VAN SOEST (1993) observed that these rival interpretations centre on the classical disagreement between dispersal and vicariance. Clearly, dispersal capabilities vary enormously among individual taxa and this may well explain the different biogeographic patterns observed in the different groups. However, the zonation seen at Sal suggests that differences might also originate according to the depth zone. In the infralittoral zone we found more pronounced tropical West Atlantic affinities, whereas in the midlittoral, and perhaps in the circalittoral, the affinity was rather Atlantic-Mediterranean.

As LONGHURST (1962) pointed out in his review of the oceanography of the Gulf of Guinea, tropical waters form only a thin surface layer in the Eastern Atlantic, whereas deeper waters are colder because of the influence of the Canary Current. According to LABOREL (1974) this warm water layer is not deeper than 20 to 30 m and this seems in perfect accord with our findings of a sharp bionomic and biogeographic change below 20 m depth. Midlittoral communities, on the other hand, may be more directly influenced by the

atmospheric climate, which in the Cape Verde Archipelago is relatively "temperate" (BÁEZ & SÁNCHEZ-PINTO 1983).

GOLIKOV & SCARLATO (1968) related biogeographic differences within bottom biocoenoses of Japan and Okhotsk seas to the heat exchange between sea and atmosphere and the position of the layers of different water masses. Our observations at Sal might lead to similar conclusions, but the alternation of tropical and warm-temperate affinities with depth derived essentially from the analysis of the sessile component of the epibenthic communities. The motile fauna gave contradictory indications: for instance, the most abundant starfish were *Marthasterias glacialis*, a temperate species, in the "tropical" infralittoral and *Ophidiaster ophidianus*, a warm-water species (TORTONESE 1985), in the colder circalittoral. For motile species, however, the zonal pattern of the reproductive stages may probably be more important than the distribution of the adults.

A major problem with both sessile and motile species is the persistent lack of sufficient knowledge on the Cape Verde marine biodiversity. Even in a study like the present one, based only on the most conspicuous and common species, species recognition turned out to be a hard task. Most invertebrate groups require extensive study. Among Cnidaria, for instance, only gorgonians (GRASSHOFF 1992) and hermatypic corals (BOEKSCHOTEN & BEST 1988) may be considered adequately known. The species we called *Balanophyllia* sp (Fig. 2c) seems to correspond with what CHEVALIER (1966) erroneously called *Balanophyllia italica* and is probably new to science (H. ZIBROWIUS *in litteris*). *Millepora* sp. is possibly a different species from or simply an ecotype of *M. alcicornis* (MORRI & BIANCHI 1995). *Actinia sali* was only recently distinguished from the common Atlantic-Mediterranean *A. equina* (MONTEIRO *et al.* 1997), and we have already mentioned difficulties with antipatharians. Fish are better known (SERET & OPIC 1986; REINER 1996; DEBELIUS 1997). Nevertheless, we met problems with several families. We tentatively used the name *Sparisoma* cf *strigatum* for a

parrotfish apparently similar to *S. strigatum* from St. Helena and Ascension, which should not occur in Cape Verde waters.

All the above discussion clearly highlights the need for further taxonomic studies on the Cape Verde marine biota. Better taxonomic knowledge may allow biogeographic analyses to be done, not only taking into account whole species lists, as is usually done, but also according to depth zones. A bionomic approach, relating species distribution to the characteristics of water masses, may help elucidate the complex biogeographic pattern of the Cape Verde marine biota.

ACKNOWLEDGEMENTS

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NEW DATA ON THE BULWER'S PETREL (*Bulweria bulwerii*) BREEDING BIOLOGY IN THE DESERTAS ISLANDS (MADEIRA ARCHIPELAGO)

MANUELA NUNES

Bulwer's Petrel *Bulweria bulwerii* colony on Desertas has been monitored from 1994 to 1997. Breeding success remained stable over the four years, from 69% to 73%, and may be considered high when compared with other Procellariiformes. The absence of heavy predation certainly contributes to this situation. In September 1997, the chicks were significantly lighter than in the previous years. This agrees with data collected in August 1997 in the Cory's Shearwater colony on Selvages which suggest that birds suffered periods of low food supply near the colonies. Data from other places would confirm the extent of this occurrence. Adult weight varied along the breeding season, reflecting the importance of the pre-laying exodus during the incubation. The males increased 20 g during the pre-laying exodus, just before the first incubation shift lasting about 10 days, while the females decreased about 9 g, after the egg production and the journey back to the colony to lay. The high synchrony of the breeding period along the four years (maximum difference < 4 days) suggests the existence of constraints on the breeding period associated with the feeding resources or the climatic conditions around the Desertas colony.

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INTRODUCTION

The Bulwer's Petrel breeds on the subtropical islands of the Pacific and Northeast Atlantic. The Madeira Archipelago, with 10,000 breeding pairs, holds more than 90% of the Atlantic population, the remainder breeding on the Canary Islands (1,000 pairs, HERNANDÉZ et al. 1990), on Cape Verde Islands (not more than 100 pairs, HAZEVOET 1995) and in the Azores (50 pairs; MONTEIRO et al. 1996a). Currently, the Madeira colonies seem stable, but numbers in the Azores and Canary Islands colonies are probably declining (TUCKER & HEATH 1994). The species has an "unfavourable" Conservation Status in Europe (TUCKER & HEATH 1994). In the Pacific, the Hawaiian Islands hold the largest breeding colony in the world, with 100000 pairs (HARRISON et al. 1984).

Data on this species are scarce and refer mainly to bird numbers and breeding chronology (see AMERSON & SHELTON 1976; BARTLE et al. 1993; HERNANDÉZ et al. 1990; JOUANIN et al. 1979; MOUGIN et al. 1992; MONTEIRO et al. 1995; MONTEIRO et al. 1996b; O'DANIEL 1993).

The colony on Desertas Islands, Madeira Archipelago, was monitored from 1994 to 1997. This study presents data on breeding success, adult and chick body mass variation along those years, adult body mass variation through the breeding season and between sexes and, finally on breeding chronology. Biometrics are compared for colonies at different latitudes.

MATERIAL AND METHODS

The Desertas Islands (33°10'N, 17°20'W) are about 40 km SE of Madeira in the Atlantic Ocean. Data were collected on Deserta Grande during the arrival, laying, hatching and fledging periods, in 1994, 1995, 1996 and 1997. Two study areas

Table 1

Breeding success in the study and control areas, from 1994 to 1997. Results of the χ^2 test applied between the years on both areas are presented (N.S. - p>0.05).

Index	Area	Year				χ^2
		1994	1995	1996	1997	g.l.=3
Hatching success	1	80\95=0.84	95\111=0.85	97\124=0.78	74/107=0.69	N.S.
	2	41/51=0.80	60/68=0.88	61/69=0.88	37/52=0.71	N.S
Fledging success	1	72\80=0.90	81\95=0.85	88\97=0.91	67/74=0.91	N.S
	2	35/41=0.85	51/60=0.85	54/61=0.88	29/37=0.78	N.S

were selected at the base of a cliff situated on the NW coast of Deserta Grande. Area 1 was visited daily throughout the sampling periods and adults and juveniles were handled. Area 2 (control) was visited on the first and last days of each sampling period. Adult body mass data were obtained from 15 April to 6 May, from 29 May to 06 June and from 13 July to 08 August and refers to all the individuals captured in the study area during those periods, including breeders and non-breeders. Chick body mass data were collected during the period 14 to 29 September. Biometrics were taken on: body weight, wing length, tarsus length, distance between foremost head feathers and bill tip (hereafter called culmen), distance between anterior edge of nostrils and bill tip (hereafter called nostrils); bill height (height at foremost head feathers); bill height at the nostrils (hereafter called nostril height) and gonys (bill height at the gonys). A Pesola spring balance of 300 g accurate to 2 g was used. Measurements were made with a Menlab calliper and a ruler - accurate to 0.05 mm and 0.5 mm respectively. Sexing of adult birds was assessed on 1997 by cloacal examination, presence of egg inside the female and by previous identification of the breeding pairs. All captured birds were ringed. Productivity indexes used were: hatching success = n° hatchlings / n° eggs laid, fledging success = n° fledglings / n° hatchlings and breeding success = n° fledglings / n° eggs laid.

Data are presented as Arithmetic Sample Mean ± SD. Statistics procedures followed ZAR (1996). Normality of adult and chick body mass variables was assessed by Kolmogorov-Smirnov goodness of fit test. Bartlett's and Box M tests were used to check variance homogeneity in One-

way and Two-way Analysis of Variance, respectively. Comparison of adult body mass variation over the years on the arrival, laying and hatching phases could not be performed due to heterogeneity of variances. In that case, it was applied one-way ANOVA or Kruskal-Wallis test accordingly to data from each breeding phase.

RESULTS

BREEDING SUCCESS

Values of hatching and fledging success each year in both study and control areas are summarised in Table 1. Characteristically, higher losses occurred at the egg stage (WARHAM 1990) and these varied from 15% in 1995 to 31% in 1997. Chick mortality is usually lower and varied from 9% in 1996 to 22% in area 2 in 1997. Although not significant, decreases occurred in 1997 in hatching success in both areas and in fledging success in area 2. The results suggest that the disturbance caused during the sampling periods did not affect breeding success (comparison of study and control areas from 1994 to 1997- χ^2 test < 0.09; all N.S.).

VARIATION IN ADULT BODY MASS

Comparison of adult body mass through the years at arrival, laying and hatching phase suggests the occurrence of differences on the adult body mass along the years (Table 2). Tukey test *a posteriori* for unequal sample size showed that, in 1997 and

Table 2

Adult body mass values in the arrival, laying and hatching phases from 1994 to 1997. Values represent average±S.D. (maximum-minimum). Results of one-way ANOVA and Kruskal- Wallis test are presented (* - p<0.001; N.S. - p>0.05).

	Arrival	Laying	Hatching
1994	90.0±6.9 (N=48) (105-74)	108.2±15.2 (N=17) (128-84)	93.4±7.9 (N=38) (110-70)
1995	94.0±7.0 (N=96) (113-78)	105.9±10.8 (N=19) (125-83)	92.1±12.9 (N=40) (122-72)
1996	95.6±6.3 (N=180) (113-79)	105.0±14.5 (N=102) (143-86)	90.7±8.5 (N=167) (112-72)
1997	97.9±7.8 (N=264) (116-82)	105.5±18.6 (N=57) (132-80)	96.9±10.2 (N=103) (120-73)
test	$F=19.5$ *	$\chi^2_3= 2.77$ N.S.	$\chi^2_3=25.7$ *

1994, the birds arrived, respectively, heavier and lighter than in the other sampling years. In the hatching phase of 1997, adults were consistently heavier than in 1996 and 1995 but no differences were found on the laying phase (Nonparametric Nemenyi test *a posteriori*). No significant correlation was observed between the adult body mass on the four years for each phase and both the hatching or fledging success (Spearman rank correlation - all variables p>0.05). Significant differences on the adult body mass occurred through the breeding season (data from 1995 - One - way ANOVA $F_{157,2} = 43,7$; p<0.001), with body mass increasing significantly by 13.2 g from the arrival to the laying phase, decreasing afterwards significantly by 19.5 g at the hatching phase (Tukey test *a posteriori* for unequal sample size).

the body mass of both males and females between the arrival and laying phases (female - $F_{65,1} = 13.2$; male - $F_{65,1} = 61.6$; p<0.001). The female weight decreased about 9.0 g from the arrival to the laying phase while the male weight increased about 20.3 g during the same period (Fig. 1). No differences were found between the male and female body mass on the arrival phase ($F_{65,1} = 1.50$; N.S.), i.e., they arrive to the colony with a similar weight (average difference - 3.12 g). Differences occurred on the laying phase ($F_{1, 65} = 164.7$; p<0.001), when the males and females differed on average 32.2 g from each other. Statistical comparison of data in the hatching phase is not possible, but observations suggest that at this phase the females had recovered to a similar weight to that observed at the arrival phase.

ADULT BODY MASS VARIATION ON 1997 – DATA SEPARATED BY THE SEX

Adult body mass was affected by the breeding phase and by the sex of the bird, being observed an effect of the breeding phase on the weight of birds of different sexes. (Fig. 1; Two – way ANOVA - breeding phase effect - $F_{65,1} = 9.24$, p<0.01; sex effect - $F_{65,1} = 97.6$, p<0.001; interaction effect - $F_{65,1} = 66.2$, p<0.001). In order to use this analysis, equal sample size was achieved by random elimination up to three values. Multiple - contrast analysis *a posteriori* showed that there were significant differences in

VARIATION OF CHICK BODY MASS AT FLEDGING

The wing growth rate is considered to be only weakly affected by short-term variations in food delivery by the adults, and may be used to age chicks (e.g. GRANADEIRO et al. 1998.; RICKLEFS 1992). Chick growth rates along the four sampling could be compared by regression of weight on wing length for each year. However, because data were collected during the final period of development, no correlation was found between weight change and wing growth. Thus, chick growth analysis was restricted to data obtained from 14 September to 29 October,
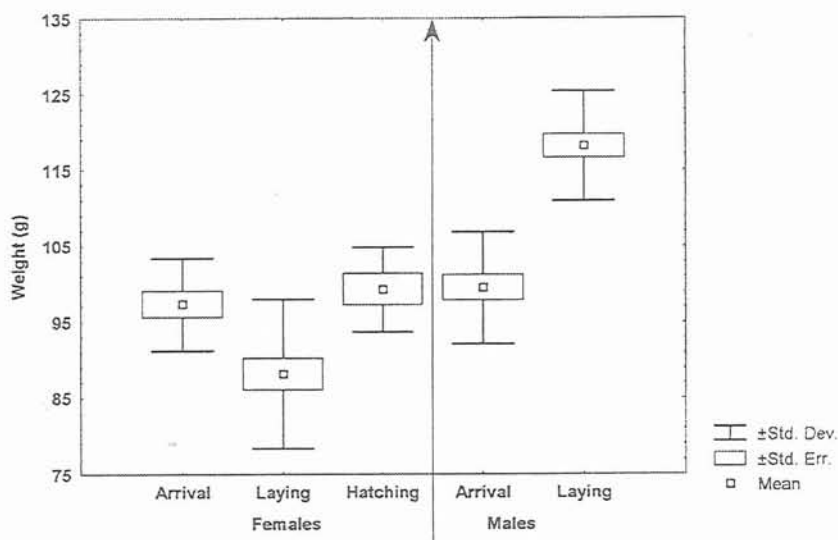
Fig. 1. Body mass of males and females on the arrival, laying and hatching phases of 1997. Number of individual per sample presented.

Table 3

Wing length and body mass values of the chicks in the period 14 to 29 of September in 1994, 1995, 1996 and 1997. Values represent average±S.D. (maximum-minimum).

Year (N)	Wing	Weight
1994 (22)	185.9±5.0 (198-180)	113.1±11.6 (135-90)
1995 (18)	189.3±4.5 (197-184)	125.0±10.7 (146-110)
1996 (21)	187.4±4.6 (196-180)	107.4±12.2 (131-93)
1997 (49)	186.9±4.6 (198-180)	97.9±7.9 (120-81)

comprising chicks with wing length greater than 180 mm. Comparison of data from the chicks under these conditions in the four years (Table 3), showed that they were in similar wing development state (ANOVA wing - $F_{105.3} = 1.84$; N.S.), but varied in weight along the years (ANOVA weight - $F_{105.3} = 35.5$; $p<0.001$). Tukey test *a posteriori* for different sample size indicated that, in 1997, the chicks were 14.9 g lighter than in 1994, 29.7 g lighter than in 1995 and 10.4 g lighter than in 1996. In 1995, the chicks were significantly higher than in the other sampling years. Chick weight did not correlate with the adult weight over the years or with the breeding success indexes (Spearman rank correlation - all variables $p>0.05$).

BREEDING CHRONOLOGY

Table 4 summarises the dates of each breeding event on Deserta Grande colony from 1994 to 1997. Median and modal values are indicated as these data are influenced by the dates spent by the researcher on the island. When laid eggs or fledged chicks were present at the beginning of the sampling period, values were estimated based on an incubation period of 45 days and fledging period of 61 days (NUNES & VICENTE 1998). One – way ANOVA was used to compare laying dates in the four years ($F_{3,193}=4.63$, $p<0.01$) and Tukey test *a posteriori* indicated differences between 1995 and 1997, although both mode and average

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Table 4

Date of the arrival, laying, hatching and fledging periods of the Bulwer's Petrel on Desertas Islands, from 1994 to 1997. Values mean: average±S.D.; sample size; range; mode, median (not given when similar to the mean).

	1994	1995	1996	1997
Arrival	At 22-Ap ~60% of the birds had arrived	27 Ap. ± 4.4 (147) 15 Ap/ 4 May; 30 Ap	27 Ap. ± 4.0 (175) 18 Ap/6 May; 29 Ap	27 Ap. ± 2.9 (159) 21 Ap \ 1 May; 1 May
Laying	3 Jun. ± 4.4 (22) 29May\16Jun; 6 Jun	2 Jun. ± 3.4 (51) 28\12 Jun; 5 Jun	3 Jun. ± 4.1 (59); 31 May\13 Jun; 3 Jun	4 Jun. ± 2.9 (65) 31-May\12-Jun; 5 Jun
Hatching	20-Jul. ± 3.7 (30) 15\28Jul; 22 Jul	18 Jul. ± 3.6 (47) 11\27Jul; 16 Jul;19 Jul	17 Jul. ± 3.9 (61) 12\25 Jul; 18 Jul	17 Jul. ± 2.4 (47) 13\22Jul; 17 Jul
Fledging	19 Sep. ± 4.9 (50) 7 Sep \2 Oct; 19 Sep	16 Sep. ± 3.0 (51) 9\21 Sep; 17 Sep	12 Sep. ± 1.9 (56) 8\17 Sep; 14 Sep	20 Sep.: 54% of the chicks had fledged; 26 Sep: 1 chick was in the nest

laying dates did not differ by more than 3 days. The results of the analysis of variance applied to the hatching dates was significant ($F_{3, 164} = 5.6$; $p < 0.01$) for the years 1997 and 1996. Again, the difference was small (<2 days) for both the mode and average hatching dates.

DISCUSSION

The results suggest that, at least under certain limits, variations in body mass of adult Bulwer's petrel did not directly affect the productivity of the colony, a fact observed on other seabird species. Birds may compensate the shortage of feeding resources by reduction of the number of breeders attending the colony, due to higher winter mortality rates, (HEUBECK et al. 1991) or by increased foraging effort (MONAGHAN et al. 1992), for example. On the other hand, inter sex variation on body weight through the breeding season is in accordance with the breeding performance of each partner. Both arrived at the colony weighing the same, but a subsequent increase of about 20 g in male weight was observed on the laying phase, after the pre-laying exodus of 29 days (NUNES & VICENTE 1998). This gives evidence on the importance of the pre-laying exodus as a strategy to store important body reserves. At this stage, the male performs the first incubation shift of 10 days, after a stay in the nest lasting up to 7 days before the female arrival to lay (NUNES & VICENTE 1998). The females, by contrast, lose about 9.0 g in the same period, after egg production and the journey back to the colony to lay. This agrees with the observed female's urgency to leave the colony on the laying night, confirming the hypothesis that they probably need to leave the nest immediately to forage (NUNES & VICENTE 1998). Although no significant relation was found between the inter annual variation and the breeding success, both the foraging capacity of breeding adults and the feeding resources available during the exodus, are expected to ultimately relate to the hatching success. In fact, although not significant, more eggs failed to hatch in 1997. In this year, the Bulwer's petrel chicks were significantly lighter than in the previous years, which may also reflect a decrease on the foraging ability of parental birds associated with a low availability of feeding resources. This agrees with data collected in August 1997 on the feeding frequency and meal size in the Cory's Shearwater colony on Selvages (GRANADEIRO et al. 1998), which suggests that birds suffered periods of low foraging resources near the colonies. Data from other places is needed to determine the extent of this occurrence.

The Bulwer's Petrel breeding chronology is similar to that observed on other sub-tropical colonies, e.g. Azores (MONTEIRO et al. 1996b), Salvages (Jouanin et al. 1979), Johnston Atoll (AMERSON & SHELTON 1976) and Sand Island (O' DANIEL 1993) in the Central Pacific Ocean. The high synchrony observed among breeding seasons (maximum difference < 4 days) was also observed by AMERSON & SHELTON (1976) on Johnston Atoll, and suggests the occurrence of ecological constraints related with the feeding resources (JOUANIN et al. 1979) or the climatic factors (MOUGIN et al. 1992) near the breeding colonies.

AKNOWLEDGEMENTS

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MADEIRAN STORM-PETREL (*Oceanodroma castro*) IN THE DESERTAS ISLANDS (MADEIRA ARCHIPELAGO): A NEW CASE OF TWO DISTINCT POPULATIONS BREEDING ANNUALLY?

MANUELA NUNES

The Madeiran Storm-Petrel (*Oceanodroma castro*) breeding cycle shows a high degree of flexibility over the breeding sites. Two distinct populations breed annually on Galapagos and Graciosa (Azores) while on Farilhão Island, off the Portuguese mainland coast, Ascension and Vila Islet (Azores), only one breeding population is known. The definition of Madeiran Storm-Petrel phenology on Desertas, Madeira Archipelago, was the objective of this study. Data from the recaptures of birds ringed from 1993 to 1997, from the brood patch and cloaca analysis and from the presence of incubating birds, females with eggs and juveniles, suggest the existence of two distinct populations breeding annually on Desertas Islands. The Hot Period population breeds from March / April to September / October and the Cool Period population from September to February / March. The Cool Period birds show bigger dimensions than the Hot Period birds, similar to the situation found on Graciosa.

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INTRODUCTION

The Madeiran Storm-Petrel is a small Procellariiform with a wide distribution throughout the tropical and sub-tropical regions of the Atlantic and Pacific Oceans (HARRIS 1969). In the Atlantic, the species breeds on the Madeira (LOCKEY 1952), Azores (MONTEIRO et al. 1996), Berlenga (TEIXEIRA & MOORE 1983), Canary (MARTÍN et al. 1984), Cape Verde (BOURNE 1955), Santa Helena and Ascension (ALLAN 1962; TUCKER & HEATH 1994) islands. There are also several colonies in the Pacific, namely in the Galapagos, Hawaii and off eastern Japan (HARRIS 1969). According to TUCKER & HEATH (1994) the European population seems stable but numbers may be declining in the Azores.

Two temporally distinct populations breed annually on Galapagos (HARRIS 1969) and Graciosa, Azores (MONTEIRO & FURNESS 1998) while on Farilhão Island, off the Portuguese mainland coast (GRANADEIRO et al. in press), Ascension (ALLAN 1962), Cape Verde (BOURNE 1955) and Vila Islet, Azores (MONTEIRO et al. 1996) only one population is known to breed annually. HARRIS (1969), in the Galapagos Islands, observed fidelity to the breeding season by both breeding and non-breeding birds. This may operate as the mechanism of isolation, resulting in biometric differentiation among both populations. MONTEIRO & FURNESS (1998) suggested that the Azores could comprise two discrete populations and may represent a case of sympatric speciation through temporal partitioning and in which case they may be better treated as sibling species. In the Madeira Archipelago, ZINO & BISCOITO (1994) referred to the existence of eggs throughout the year, with two main abundance peaks in June and October / November. However, the breeding phenology of the Madeiran Storm-Petrel is still unclear.

The definition of the species phenology on

Desertas was the main objective of this study, based on recapture of ringed birds, on brood patch analysis, on biometric comparison and on general information based on the presence of eggs, incubating birds and juveniles in the nest.

MATERIAL AND METHODS

The Desertas Islands (33°10`N, 17°20`W) are located about 40 km SE of Madeira in the Atlantic Ocean. Data were collected in a cave situated on the west coast of Deserta Grande island in four periods during 1996 – 06 to 11 June; 16 to 24 July; 06 to 24 September; 19 to 30 October - and 1997 – 24 to 28 April; 01 to 11 June; 12 to 20 July; 24 to 28 September. Birds were captured with mist-nets on the ground and on the nest. All birds were ringed and biometrics were taken of: wing length, tarsus length, distance between foremost head feathers and bill tip (hereafter called culmen), distance between anterior edge of nostrils and bill tip (hereafter called nostrils); bill height (height at foremost head feathers); gonys (bill height at the gonys) and distance between nape and bill tip (hereafter called head+bill). A Pesola spring balance of 300 g, accurate to 2 g, was used. Measurements were made with a Menlab calliper and a ruler - accurate to 0.05 mm and 0.5 mm respectively. Thirty-six adult birds were measured by the author on two different occasions to assess measurement consistency. The small dimensions of the cave and the fidelity to the breeding site observed in this petrel (HARRIS 1969), allowed a high recapture rate of birds ringed in previous sampling periods. Brood patch was classified as 0 (no brood patch), 1 (75% feathering), 2 (50% feathering), 3 (25% feathering), 4 (0% feathering) and 4+ (vascularised brood patch), the latter being used as a signal of incubation. R means re-feathering and signalled the end of incubation, i.e. the hatching phase (WARHAM 1990). Data are presented as Arithmetic Sample Mean ± SD. Data were checked for variance homogeneity and variable normality using Levene's test and Kolmogorov – Smirnov goodness of fit test respectively. Statistics procedures followed ZAR (1996).

RESULTS

RECAPTURES

The Ringing Program provided information on individual birds throughout the sampling periods, as a result of the frequent recapture of ringed birds. Ringing activities started on 1993, and the main ringing effort occurred on June, July and September (Table 1). In October 1996, only 8 birds ringed in September 96, out of the 167 individuals ringed during the previous months of

Table 1

Ringing Program Data: number of birds ringed on Furna dos Roques since first ringing on 1993 and number of recaptures on each posterior sampling period.

	June 93	June 94	Sep 95	June 96	July 96	Sep 96	Oct 96	April 97	June 97	Jul 97	Sep 97
Birds Ringed	69	36	26	36	26	74	87	36	20	46	58
BirdsHandled	(?)	36	26	55	44	99	96	47	40	104	86
June 93	-	0	0	10	10	6	0	7	2	12	0
June 94		-	0	9	7	7	0	1	2	8	2
Sep. 95			-	0	1	2	1	1	2	0	5
June 96				-	0	6	0	1	7	9	0
July 96					-	4	0	1	4	9	0
Sep. 96						-	8	0	0	4	13
Oct. 96							-	0	0	2	8
April 97								-	3	6	0
June 97									-	8	0
July 97										-	0

Table 2

Relative frequency of the brood patch scores along the sampling periods. Data from 1996 and 1997 were pooled for each month (see text).

Brood patch score	April (N=42)	June (N=90)	July (N=152)	September (N=199)	October (N=88)
0	57.2	13.3	5.9	52.8	2.3
1	7.1	3.3	2.0	12.6	0
2	7.1	1.1	1.3	6.5	0
3	9.6	4.4	0	7.5	4.6
4	7.1	17.8	6.6	17.6	10.3
4+	11.9	60.0	43.4	1.5	82.8
R	0	0	40.8	1.5	0

the year, were recaptured. Similarly, only two individuals ringed in October 1996 were caught in April, June and July of 1997. The number of birds ringed and recaptured in the same season from 1993 to 1997 (71\167 = 0.43) is significantly higher than the number of birds recaptured in a season distinct from the one in wich they were ringed (2\87 = 0.023; $\chi_1^2 = 28.4$, p<0.001). Birds caught in September were excluded from this analysis, as birds from both populations attended the colony during this month. The results suggest that the birds attending the colony from April to July are different from those present at the colony in October.

BROOD PATCH

Inter-year comparison of brood patch scores (1996 and 1997) in each month yield no significant differences (Mann-Whitney test - June - $Z_{58,40} = -0.911$, p = 0.36; July - $Z_{71, 81} = 0.28$, p = 0.78; September - $Z_{121, 124} = -0.397$, p = 0.69), suggesting that the same breeding event was occurring at each time, in both years. Pooled data from 1996 and 1997, revealed two main peaks of 4+ score, corresponding to two main incubating periods - June (60%) and October (82.8%). Data from April 1997 (Table 2) shows that the birds were arriving at the colony (score 0 = 57%) but actually some were already preparing for the incubation period (score 4+ = 11.9%). In July, most birds had brood patch 4+ and R (40,8%), the latter indicating that hatching was occurring. R score data may include breeders and non-breeders

as the latter also develop brood patch although never achieving the highly vascularised patch characteristic of incubating birds (HARRIS 1969).

EGG AND CHICK STAGE

Birds incubating the egg were found in June 1996 (n=4) and 1997 (n=3) and in October 1996 (n=4). Females with egg in the oviduct were found on 1996 (June n=3; July n=1) and 1997 (April n=1; June n=4; July n=1), but no differences were between both years (Table 2; Fisher Exact Test, June p = 0.46; July p = 0.51). Data were pooled to define the breeding chronology. In July 1996, 3 new born chicks were found and in September 1996 and 1997, fledging chicks were found in their nests (n=4 and n=1 respectively).

ADULT MORPHOLOGY

Differences between the measurements taken of 36 adult birds on two occasions, did not exceed 0.9% and were not significant (Paired t-test, N.S.), confirming measurement consistency. Based on the data presented above, the birds were assigned to two different groups: the Hot Period birds which were consistently trapped and retrapped from April to July from 1993 to 1996 but not in October 1996 and the Cold Period birds which were captured in October 1996 and never retrapped on posterior sampling periods, except September. Biometrics comparison of birds from both groups confirmed that the birds captured only in October 1996 have bigger dimensions

Table 3

Size of body structures of birds caught exclusively in October 1996 and in June and July from 1993 to 1996. Results of the t-test used to compare measurements are presented. * - one tailed t-test - p< 0.0005; ** - two-tailed t-test - p< 0.05. Values represent means ± SD, in millimetres.

	October (n=76)	June and July (n=86)	t-test (d.f.=160)
Wing length	154.7 ± 4.0	150.5 ± 3.4	7.13*
Tarsus length	23.41 ± 0.72	22.58 ± 0.67	7.63*
Head + Bill	42.05 ± 0.83	40.35 ± 0.77	13.53*
Culmen	15.20 ± 0.53	14.89 ± 0.52	3.71*
Nostril	11.42 ± 0.43	10.96 ± 0.44	6.65*
Bill height	6.23 ± 0.27	6.15 ± 0.21	2.00**
Gonys	4.99 ± 0.21	4.93 ± 0.21	1.92; N.S.

Table 4

Summary of the estimated breeding chronology on Deserta Grande (using data from the Galapagos colonies): 42 days of incubation and 70 and 78 days of fledging period for the Hot and Cool Period Populations respectively (HARRIS 1969). * - Values are estimated dates of occurrence.

	Arrival	Laying	Hatching	Fledging
Hot Period Population	April	Middle May \June	July	Middle August \ September
Cool PeriodPopulation	Early September	Middle October	Early December *	February *

than those captured from April to June / July (Table 3).

The estimated breeding chronology of the Hot and Cool Period Populations is summarised in Table 4.

DISCUSSION

Data obtained on Deserta Grande Island suggest the existence of two distinct groups of birds, breeding about four months apart and spending six to seven months on land: the Hot Period Population breeding from April to September and the Cool Period Population breeding from September to February. Score 4+ was found from as early as the end of April to July, suggesting a protracted laying period of about three to four months for the Hot Period Population. This result is similar to the laying phase of the same population in the Galapagos (HARRIS 1969). In Graciosa, Azores, MONTEIRO & FURNESS (1998) found a shorter laying period beginning in May. The Cool Period birds arrive on Desertas in September and lay during the month of October.

The estimated time of hatching and departure are December and February. In the Azores, birds with vascularised brood patch were incubating in September (MONTEIRO & FURNESS 1998), while at this stage, on Desertas, only 1.5% of the birds showed 4+ score. Further research on the Cool Period Population is needed to confirm the estimated breeding chronology presented. During late August and September, birds from both populations were present in the colony. Suggesting however, late breeding individuals of the Hot Period Population may be at disadvantage, as chicks on the nest may be dislodged by Cool Period birds sharing the same nests.

Population genetics may give evidence to support the existence of two sibling species in the Madeira Archipelago similar to the hypothesis advanced by MONTEIRO & FURNESS (1998) for the Azorean populations.

ACKNOWLEDGEMENTS

Madeira, specially to the wardens of the Desertas Natural Reserve. The Portuguese Navy is acknowledged for assuring the transportation to Desertas. I also thank two anonymous referees for their comments.

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EDITORIAL NOTES

This is the first volume (Part A) of the "Proceedings of the 3rd Symposium of the Fauna and Flora of the Atlantic Islands" that took place in Ponta Delgada, 21-25 September 1998, under the auspices of Department of Biology, University of the Azores, Ponta Delgada.

The submitted MSS have gone through the usual procedure prior to printing in the journal *Arquipélago* – Life and Marine Sciences. The papers have been peer-reviewed by at least 2 referees prior to acceptance. The papers printed in Part A were those first completed. Part B will follow shortly.

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