FAUNA AND FLORA OF ATLANTIC ISLANDS

Edited by T. J. Hayden, D. A. Murray and J. P. O'Connor

Proceedings of the 5th international symposium on the fauna and flora of Atlantic islands

Dublin 24 -27 August 2004

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Preface

In August 2004, one hundred delegates convened at University College Dublin for FFAIS-5, the 5th International Symposium on the Fauna and Flora of Atlantic Islands. During this stimulating meeting, a series of interesting papers were presented on a wide variety of topics associated with the plants and animals of the islands. The Irish Biogeographical Society is delighted to publish a selection of the general contributions and the outcome of the workshop as *Occasional Publication* **Number 9**. The Irish Biogeographical Society is very grateful to Dr D. A. Murray and the Organising Committee for arranging for the material to be published by the Society. We also wish to thank Dr Murray and Professor T. J. Hayden for their editorial work.

J. P. O'Connor MRIA,
General Editor,
Irish Biogeographical Society
www.irishbiogeographicalsociety.com
1 September 2006

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INTRODUCTION

The *Fauna and Flora of Atlantic Islands Symposium* series developed from the recognition by researchers on Macronesian islands, of a need to understand and preserve the unique ecosystems of these isolated Atlantic islands. The first four symposia were held on Madeira, the Canary Islands, the Azores and Cape Verde. At the final session of the 4th International Symposium in Praia, Republic of Cape Verde in 2002, delegates voted to accept the invitation from Dr Declan Murray, University College Dublin, to host the 5th symposium in Ireland. Since this 5th symposium (FFAIS-5) is the first in the series to be held on an Atlantic island outside the four Macaronesian archipelagos, a major goal was to foster a greater exchange of findings between researchers from a broader range of Atlantic islands and countries.

One hundred delegates of 20 nationalities from 16 island nations convened in University College Dublin from 24th to 27th August, 2004, for three days of invited and offered papers, interaction and networking. Registration commenced on the afternoon of August 24th and the first function of FFAIS-5 was an informal reception that evening hosted by the UCD Division of Biosciences with the Deputy Lord Mayor of Dublin, Cllr Andrew Montague, in attendance. The opening session on the following morning was addressed by Professor Desmond Fitzgerald, Vice President for Research and Professor Tom Bolger, representing the Faculty of Science and the Division of Biosciences, University College Dublin. Dr Alan Craig, Director, National Parks and Wildlife, Department of the Environment, Heritage and Local Government, Dublin and Dr John Faulkner, Director, Environment and Heritage Service, Belfast, Northern Ireland, addressed delegates outlining policies and achievements in current important local and cross-border biodiversity issues in Ireland. On the evening of August 25th delegates attended a State Reception in Dublin Castle hosted by the Minister of State at the Department of the Environment, Heritage and Local Government, Pat the cope Gallagher, TD. Minister Gallagher emphasised the important role of researchers in providing essential scientific-based information for the development of conservation and management strategies.

The scientific programme of the symposium addressed topics and issues in seven all-embracing theme areas and considered multi-faceted aspects of the marine, terrestrial and aquatic environments of Atlantic Islands. Each theme session commenced with a lead keynote presentation: Erich Hoyt spoke on *Sustainable ecotourism on islands, with special reference to whale watching and marine protected areas and sanctuaries for cetaceans*; Richard J. Abbott on *Recent plant speciation in Britain and Ireland*; Max Wade on *Control and management of alien invasive plants*; Ingibjörg Jónsdóttir on *Terrestrial ecosystems on Svalbard*; Thomas Bolger on *Adequacy of surrogate taxa in assessing likely responses of biota to global change*; R. M. M Crawford on *Oceanic environments and their impact on plant distribution* and Samantha Hughes on *Application of the Water Framework Directive to Atlantic Islands.* The full texts of the Keynote presentations are published in a special issue of *Biology and Environment - Proceedings of the Royal Irish Academy* (**105B**, **3,** 2005) and may be viewed at www.ria.ie/publications/index.html).

Participating delegates delivered a total of 36 oral and 42 poster presentations, on topics distributed among symposium theme areas, based on their research on Atlantic islands as far apart as Svalbard, bordering the Arctic Ocean to the Falkland Islands, bordering Antarctic waters. This *Occasional Publication of the Irish Biogeographical Society* contains those papers. A half-day workshop on ecotourism highlighted the emerging cetacean tourism industry and dealt with socio-economic issues to attain a better understanding of tourism/nature interactions common to Cape Verde, the Azores, Ireland and Iceland.

During the final session on 27th August an invitation from Madeira to host the 6th Symposium on the island of Porto Santo, was accepted. Preliminary expressions of interest to host a subsequent symposium were received from the Azores (Terceira Island) and from the Faroes.

Following the symposium some delegates participated in a one-day post-symposium excursion to the Wicklow Mountains National Park while others went further afield on a two day excursion to the Burren region and Ireland's west coast.

SPONSORS

The Organising Committee of FFAIS-5 gratefully acknowledges assistance and support of the following sponsors of the event: Minister for the Environment, Heritage and Local Government; Department of Foreign Affairs, Development Co-operation Division; National Parks and Wildlife, Dublin; Environmental Protection Agency; Marine Institute / Marine RTDI Programme (NDP 2000-2006); Environment and Heritage Service, Northern Ireland; University College Dublin - President's Award and Faculty of Science; Aer Lingus; Anglo Irish Bank; Bank of Ireland; Fáilte Ireland; Shell E&P Ireland and Camp Dresser McKee, Ireland.

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DISTRIBUTION OF THE SEAWEEDS OF THE WESTERN COAST OF AFRICA AND ADJACENT ISLANDS

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ABSTRACT

A new catalogue on the taxonomy and geography of the seaweeds of West Africa and adjacent islands has been published. It covers the African mainland coastline from the northern boundary of Western Sahara southwards to the southern boundary of Namibia, the oceanic islands of Madeira and the Salvage Islands southwards to Ascension and St Helena, and all other islands off the African mainland. A total of 1195 species of seaweed (202 green algae, 200 brown algae and 793 red algae) are now recognized for which 2013 names have been used in the series *Seaweeds of the West of Tropical Africa and adjacent Islands* (published 1969-1998), or in other publications on West African marine algae. Information in the catalogue has been used to compare the seaweed flora of the different areas of the mainland coast and offshore islands. The seaweed flora of the Macaronesian Atlantic Islands is considerably more diverse than that of countries of the African mainland. Warm temperate areas of West Africa often have a more diverse seaweed flora than adjacent tropical ones. The seaweed flora of the Canary Islands is the most diverse and that of the tropical mainland coast the least diverse. Various factors account for the seaweed diversity patterns in West Africa, including the reduction in water temperature during the last glacial periods, absence of suitable attachment surfaces, reduced inshore salinity and severe wave-exposure.

KEYWORDS: biogeography, seaweeds, marine algae, West Africa, catalogue, Macaronesia.

INTRODUCTION

The first part of the critical assessment of the seaweeds of tropical West Africa was published in the 1960s and dealt with the green algae (Lawson & Price, 1969). Over the next 30 years, parts have appeared at irregular intervals (Price *et al.* 1978, 1986, 1988, 1992; John *et al.* 1979, 1994; Lawson *et al.* 1995) until 1998, when the series was completed with publication of the red algal genera (Woelkerling *et al.* 1998). Earlier numbers in the series were not revised before its completion despite the increase in our knowledge of the distribution of the West African algae and many taxonomic and nomenclatural changes. The one exception was in the last volume in the series, which included an update of the non-geniculate red algae. The whole series was updated and made more widely available with publication of a taxonomic and geographical catalogue (John *et al.* 2004). This catalogue covers the whole of the African mainland coastline from the northern boundary of Western Sahara southwards to the southern boundary of Namibia, the oceanic islands from Madeira and the Salvage Islands southwards to Ascension and St Helena, and all other islands pertaining to the African mainland coast (see fig. 1 in John *et al.* 2004). The coasts of Morocco and the Republic South Africa were not considered because it is not always possible to be certain to which coast published records refer (Atlantic, Mediterranean or Indian Ocean). There are now modern checklists of seaweeds for Morocco (Benhissoune *et al.* 2001-2003) and the west coast of South Africa (Stegenga *et al.* 1997). Other useful checklists for the Atlantic cover the northern part (South & Tittley 1986), Europe (Guiry 2001) and the tropical and subtropical western Atlantic (Wynne 1998).

The new catalogue (John *et al.* 2004) gives the currently accepted name of each taxon and only mentions as synonyms those cited in the series or in other publications dealing with West African algae. Under each entry there is a full listing of countries and islands from which a species has been recorded and a source reference (e.g. a floristic account, a recent checklist, another relevant paper and/or a publication in the series). Short comments often give earlier literature sources and further information on our taxonomic decisions. It has not been possible, so far, to obtain any reference to records of seaweeds for mainland Equatorial Guinea (= Rio Muni), Cabinda, or the Democratic Republic of Congo (Zaire). The new catalogue made use of information in the Leiden Atlantic Seaweeds Database and useful web-site sources such as 'AlgaeBase' (www.algaebase.org) and 'Index Nominum Algarum' (//ucjeps.berkeley.edu./INA.html).

The present paper (a) compares the specific and infra-specific diversity of seaweed taxa recorded from different parts of the West African coast and offshore islands, and (b) attempts to account for some of the seaweed diversity patterns observed, with special consideration given to species-rich ('hot spots') areas and those apparently very low in seaweed diversity.

MATERIALS AND METHODS

One of the problems with compiling lists of records, on which comparisons are based, relates to the quality of the data and differences in opinion amongst taxonomists. Most of those preparing the new catalogue (John *et al.* 2004) have considerable first-hand experience of West African algae and are therefore in a good position critically to evaluate all country records and to ensure that the most recent taxonomic opinion is followed.

In the lists that follow we have considered separately the numbers of species in each of the three major groups of marine macroalgae. Listed for different areas are the numbers of taxa for which the identification seems reasonably certain against a much smaller number of doubtful ones. The doubt attached to some taxa refers to differences in taxonomic opinion, the identification and/or whether records of drift specimens should be included. The numbers used in the analysis are taken from the new catalogue (John *et al.* 2004), but the totals for tropical West Africa are based on a book dealing with the marine macroalgae of this sub-region (John *et al.* 2003). We have used for Atlantic Morocco the recent checklists by Benhissoune *et al.* (2001-2003) and for the west coast of South Africa the seaweed flora by Stegenga *et al.* (1997). Data from the study of the seaweed flora of Namibia by Rull Lluch (2002) including his total for seaweed species from the Atlantic coasts of the Iberian Peninsula and France are also used.

RESULTS

Numbers of seaweed species in the tropical/subtropical West African region are shown in Table 1. This table shows the seaweed diversity of the Canary Islands and compares it with that for tropical West Africa. The number of species known from the long coastline lying between Gambia and Benin, including islands in the Gulf of Guinea (Bioko, Príncipe, São Tomé, Annobon), are after John *et al.* (2003). It is apparent that the Canary Islands are very species-diverse with more than half of the seaweeds known from West Africa present in this archipelago.

Numbers of seaweed species in different North Atlantic archipelagos (Macaronesia region) are shown in Table 2. Species-diverse areas include the warm temperate Madeira archipelago and the tropical to subtropical Cape Verde Islands. For the tiny Salvage Islands, located between Madeira and the Canary Islands (warm temperate), seaweed diversity is also high with a total 270 species recorded.

Numbers of seaweed species along the mainland coast of West Africa are shown in Table 3. The list includes countries where at least one experienced phycologist has worked for a considerable period and, therefore, such records are not based on one or a few samples collected almost by accident or by a non-phycologist. Of all the tropical West African mainland coasts, that of Ghana has been the most intensively studied and appears to have the most diverse seaweed flora. Subtropical coastal areas, such as northern Sénégal and Mauritanie, however, have still higher numbers of recorded seaweed species. Of the tropical coast of southern Sénégal there are only a few published records and these are not included in Table 3.

Numbers of seaweed species in southern West Africa are shown in Table 4. The diversity of the seaweed flora recorded from the warm temperate Namibian coast is significantly lower than that of the less extensive coasts in the northern part of West Africa. Data for the west coast of South Africa are not strictly comparable because records of non-geniculate coralline red algae are lacking.

Numbers of seaweed species north of the tropical/subtropical West African region are shown in Table 5. Of all areas, temperate Atlantic France has the most diverse seaweed flora with its total number just above that for the Canary Islands.

DISCUSSION

The seaweed species diversity of the most well sampled areas and countries of West Africa (islands and mainland) is shown in Table 6 along with that for some European Atlantic coasts. It is clear that even the most-studied tropical area of West Africa has the lowest diversity of all. This is probably also the case in south-eastern Asia, where in the Malesian region, which has a much longer coastline than Europe, fewer seaweed species are recorded than in Europe. The reverse situation occurs if the terrestrial vascular plant flora is compared with the Malesian region considered to be a major 'hotspot' of global diversity (Roos 1996). Reasons why the West African tropical algal flora is very species-poor include the absence of suitable hard surfaces for seaweed attachment (large areas of sand and mangrove), severe wave-exposure (very few wave-sheltered areas), often reduced inshore salinity (only mainland coast) and rare occurrence of Tethyan endemics. The latter is supposed to be a consequence of the non-optimal tropical character of the sub-region during the late Cenozoic Atlantic temperature crises resulting in many extinctions (de Jong 1998).

The most species-diverse seaweed flora in the West-African region is that of the Canary Islands. Why is this archipelago so species-diverse? Reasons may be related to its history, especially paleoclimatic events (Pakker 1995). At the present time there are several distinct biogeographical groups of seaweeds occupying this area. The tropical to subtropical species, reaching their northern distribution boundary at the Canary Islands, most probably disappeared from the Canary Island coast during the last glacial maximum (18,000 years ago) and have only recently (re-)colonized these islands by dispersal from Caribbean or tropical West African donor populations. Recent molecular research on some of these species lends support for some trans-Atlantic dispersal having taken place in the past (Pakker 1995). Another distribution group, *viz*. those tropical amphi-Atlantic species reaching their boundary in the Mediterranean, most probably also became extinct during the last glacial maximum and possibly the Canary Islands has subsequently become (re-)colonized from cold-adapted eastern Mediterranean populations. Other species, in broader temperature-related distribution groups (*viz*. tropical or subtropical-to-temperate distribution groups), have spread and can still migrate from warm-temperate European Atlantic coasts. In the case of the latter group, the southerly-flowing Canary Current might easily transport drift specimens from more northern coasts to the Canaries.

Many of the species of the tropical Atlantic distribution groups show an ancient Tethyan imprint in their historical biogeographic patterns. Others have followed a secondary migration pattern from the ancient (Indo-) Pacific Ocean into the lately developed Atlantic Ocean around the coast of South Africa (de Jong 1998).

Our data show that seaweed diversity in the eastern part of the Atlantic Ocean is higher in (warm-) temperate areas than in tropical areas. However on the well-studied Namibian coast, species numbers are similar to those recorded from Ghana. The paucity of the Namibian flora is probably due both to the scarce availability of colonisable substratum and low habitat diversity. Moreover, the Namibian seaweed flora can be considered to be a northerly extension of the seaweed flora of the South African west coast, with any tropical influence small and confined to its northernmost part; thus it is a transitional warm/cold-temperate zone. Most of the species recorded from Namibia also occur along the west coast of South Africa (159 species in common) and only 42 species known from Namibia (Rull Lluch 2002) are further north in tropical West Africa.

Comparisons of the algal floras of different regions are increasingly possible now that distributional and taxonomic information is becoming freely available on the worldwide web. For this reason we applaud initiatives underway to produce comprehensive and internally consistent lists or indices covering whole continents, possibly the Atlantic Ocean, and eventually the world. What needs to be ensured is that these lists are not only comprehensive but the datasets are reliable. We believe our regional catalogue, from which much of the data has been extracted for this analysis, represents just such a dataset.

ACKNOWLEDGEMENTS

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TABLE 1. Numbers of seaweed species in the tropical/subtropical West African region. Doubtful records in parentheses.

Area	Rhodo	Phaeo	Chloro	Total
Total tropical/subtropical West Africa	793	200	202	1195
Canary Islands	404 (30)	132(19)	113(4)	649(53)
Tropical W. Africa	190(8)	44	59	293(8)

TABLE 2. Numbers of seaweed species in different Atlantic archipelagos (Macaronesia). Doubtful records in parentheses.

Area	Rhodo	Phaeo	Chloro	Total
Madeira	209(7)	56(30	53	318(10)
Salvage Islands	158(11)	63 (1)	49	270(12)
Canary Islands	404(30)	132(19)	113(4)	649(53)
Cape Verde Islands	213(25)	50(3)	54(5)	317(33)

TABLE 3. Numbers of seaweed species in coastal areas in West Africa. Doubtful records in parentheses.

Area	Rhodo	Phaeo	Chloro	Total
Mauritanie	149(11)	45(4)	26(2)	220(17)
North Sénégal	189(6)	44(2)	54(10)	287(18)
Cape Verde Islands	213(25)	50(3)	54(5)	317(33)
Ghana	131(5)	30(2)	40(3)	201(10)
Tropical W. Africa	190(8)	44	59	293(8)
Namibia	152(10)	21(4)	32(3)	205(17)
Total tropical/subtropical West Africa	793	200	202	1195

TABLE 4. Numbers of seaweed species in southern West Africa. Doubtful records in parentheses.

Area	Rhodo	Phaeo	Chloro	Total
Total tropical/subtropical West Africa	793	200	202	1195
Namibia	152(10)	21(4)	32(3)	205(17)
West coast of South Africa*	257	49	51	357

* Not strictly comparable because records of non-geniculate coralline red algae (Stegenga *et al.* 1997) are lacking.

TABLE 5. Numbers of seaweed species north of the tropical/subtropical West African region. Doubtful records in parentheses.

Area	Rhodo	Phaeo	Chloro	Total
Atlantic France	335	191	137	663
Iberian Peninsula	328	139	104	571
Atlantic Morocco	255(15)	104(3)	71(12)	430(30)

TABLE 6. Numbers of seaweed species in selected West African countries and offshore islands (including some European Atlantic coasts).

Atlantic France	663	Tropical West Africa	293
Canary Islands	649	North Sénégal	287
Atlantic Iberian	571	Salvage Islands	270
Atlantic Morocco	430	Mauritanie	220
South Africa (west coast)	357	Namibia	205
Madeira	318	Ghana	201
Cape Verde Islands	317		

SPATIAL DISTRIBUTION PATTERNS OF LIMPETS POPULATIONS (*PATELLA* SPP.) THROUGHOUT THE CANARIAN ARCHIPELAGO, SPAIN (CENTRAL EAST ATLANTIC)

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INTRODUCTION

Nowadays, pressures on the Canary Islands intertidal communities have increased due to the rise of human population and to the gradual destruction of shoreline habitats by alterations to the coast. Among these perturbations, the harvest and collection of gastropods ("shell-fishing") is one of the main human impacts on the littoral environment (Thompson *et al.* 2002). Aside from these human-induced processes, we must consider the great spatial variability inherent to the systems and natural processes. The goal of this work is to evaluate the present status of limpets (*Patella candei* Orbigny, 1838; *Patella tenuis crenata* (Orbigny, 1840); *Patella piperata* Gould, 1846; and *Patella ulyssiponensis* Gmelin, 1791) on rocky coasts throughout the Canarian Archipelago by means of a hierarchical experimental design incorporating five orders of magnitude of spatial variability (from tens of meters to hundreds of kilometres).

MATERIALS AND METHODS

Our hierarchical sampling strategy tested the null hypothesis of no differences in the structure of limpets among the eight islands of the Canary Islands and the three zones (high, intermediate and low intertidal) in which the rocky intertidal environment can be divided along the Canarian Archipelago, following classical zonation patterns (Stephenson & Stephenson 1949). We selected three locations per island and three sites within each location as spatial replicates of our treatments. We randomly placed $n = 10$ squares of 50 x 50 cm within each band at each site and proceeded to count and measure the size of all limpets.

Differences were statistically tested by a mixed and partially nested four-way ANOVA for each species, while one-way ANOVA was used to check differences in mean sizes among the species for the overall archipelago (Underwood 1997).

RESULTS

Patella piperata Gould, 1846

Patella piperata was the most frequent species, with a presence on 64% of all sampled locations. The registered average abundance was 0.07 ± 0.16 individuals/$0.25m^{-2}$ (mean ± SD). This species did not show any significant difference in abundance among islands ($F= 10.18$, $P= 0.0004$), being more abundant in the intermediate intertidal (73.81%) (Figure 1). This species showed an average size of 18.1 ± 7.94mm (mean ± SD).

Patella tenuis crenata (Orbigny, 1840)

Patella tenuis crenata was observed in 44% of the surveyed locations. It is the least abundant limpet, with an average abundance of 0.015 ± 0.041 individuals/$0.25m^{-2}$, and showed significant differences at the smaller sampling scale (sites within locations, $F= 1.86$, $P< 0.00001$). This species demonstrated the same frequency of occurrence in the intermediate (50.07 %) band as in the lower band (49.93 %) (Figure 2). The average size was 26.8 ± 11.08 mm. It showed a higher mean size than the other species across the Canaries ($F=6.68$, $P=0.02$).

Patella ulyssiponensis Gmelin, 1791

Patella ulyssiponensis was observed in 40% of the locations. The average abundance was 0.082 ± 0.37 individuals/0.25m^{-2}. This species has shown clear differences among the three intertidal bands. Most of the recorded specimens (79.2%) were observed in the low intertidal band (Figure 3). We have not detected differences among islands ($F= 1.90$, $P > 0.01$). The average size of *P. ulyssiponensis* was 21.0 ± 9.21mm.

Patella candei Orbigny, 1838

We did not observe any *Patella candei* specimens at any of the locations. This result corroborates the serious situation of this species on the coasts of Canary Islands.

DISCUSSION

Vertical variability (differences among intertidal bands)

Our study has shown an important degree of vertical zonation, persistent among the different spatial scales across the Canary Islands. The population structure of limpets is therefore homogenous among the studied islands in similar band types.

Horizontal variability (differences among islands, locations and sites)

There is an important degree of horizontal variability at small spatial-scales (sites separated by tens of meters), in contrast to variability among islands (tens to hundreds of kilometres). This fact is attributable to the absence and/or extremely low abundance of limpets across the overall archipelago, as a result of overexploitation of this resource. Management policies for intertidal shell-fishing resources of the Canary Archipelago, backed by a solid and effective legal framework, are strongly encouraged.

Patella candei

The absence of *P. candei* from all sampled locations, including Fuerteventura Island, reflects the near extinction risk of this gastropod in the Canarian shoreline. In accordance with this result, the species is considered an endangered marine species under regional and national legislation.

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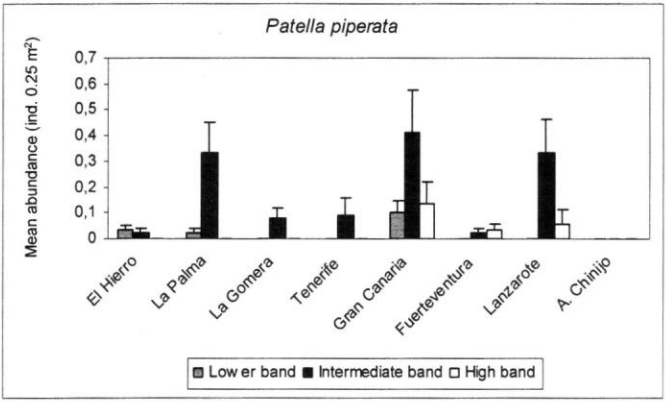

FIGURE 1. Abundance of *Patella piperata* at selected sites.

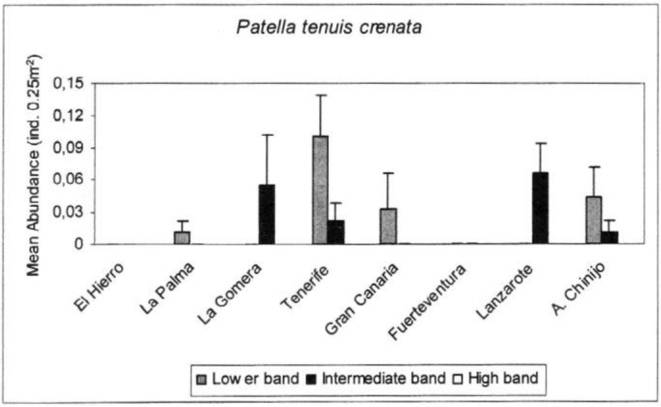

FIGURE 2. Abundance of *Patella tenuis crenata* at selected sites.

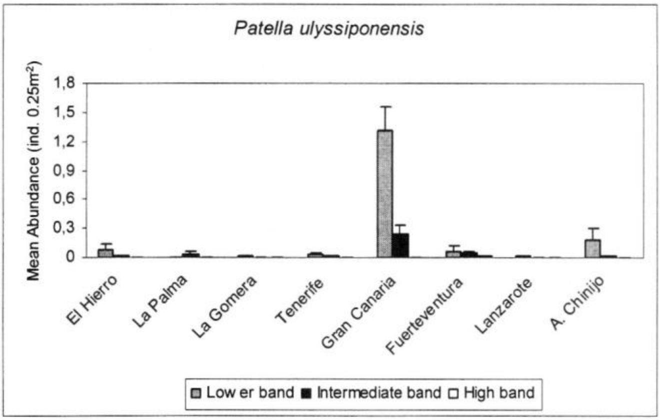

FIGURE 3. Abundance of *Patella ulyssiponensis* at selected sites.

OCEANIC ISLANDS, RAFTING, GEOGRAPHICAL RANGE AND BATHYMETRY: A NEGLECTED RELATIONSHIP?

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ABSTRACT

The dispersal of shallow-water benthic prosobranch gastropod species with non-planktotrophic development poses several problems. In this study, rafting is suggested as an important method of dispersal for many epibenthic intertidal and shallow-sublittoral species with such development. Three hypotheses are tested by means of the zonation established for the most common Azorean shallow-water species and a database of the shallow Atlantic/Mediterranean Rissoidae: (1) insular species usually living in the intertidal zone or at shallow depths should be more prone to rafting than species living at deeper levels, (2) as a consequence, there should be a direct relationship between bathymetry and the geographical range of a given species - that is, intertidal species should generally have a wider geographical range than sublittoral species and these should also have a wider geographical range than deeper ones, (3) if adults are the rafting stage, then small species would have a wider geographical distribution than medium-sized or large-sized species.

The geographical range of the most abundant Azorean species was narrower with increasing depth. Shallow species (down to 5-6m depth) have a narrower geographical distribution than intertidal species. *Alvania sleursi*, the only abundant Azorean deep-littoral species (10 to 30m depth) is restricted to the

Azores and Madeira. On the other hand, three out of the eight Azorean prosobranch species with the widest ranges and possessing a non-planktotrophic type of development, share common characteristics: all of them are small-sized and are most abundant in the intertidal (*Skeneopsis planorbis* and *Omalogyra atomus*) or higher on shores (*Truncatella subcylindrica*). This agrees well with the working hypothesis, which states that benthic, small-sized non-planktotrophic species living in the intertidal are more prone to rafting than species living in deeper levels and, as a consequence of this, they have in general wider geographical ranges.

KEYWORDS: rafting, non-planktotrophic larvae, dispersal, bathymetry, prosobranch gastropods.

INTRODUCTION

Oceanic islands arise at the boundaries between tectonic plates by accretion from convection of magma in the earth's mantle. Such islands do not possess the geotectonic characteristics of a continent and have never been connected with a continental land mass (Nunn 1994). Because of their location, in some cases very far from the nearest source of possible colonizers (a continent or another island) as is the case of the Azores, Ascension Island and Tristan da Cunha in the Atlantic Ocean, Kerguelen Island in the Indian Ocean and Easter Island in the Pacific Ocean, their fauna is usually depauperate, sometimes even disharmonic (Williamson 1981), but may be rich in endemics. One of the most interesting biogeographic problems is to study how species have reached, colonized and (at least in some cases) speciated in these islands. The subsequent dispersal of these neo-endemics (Cronk 1992) is another problem that poses many still unanswered questions.

Many benthic marine invertebrates disperse by means of pelagic larvae (Strathman 1974). Other plausible means of dispersal are by (1) foresy, that is, transported by attachment to bird feathers, a common feature in the case of some intertidal molluscs and probably *Assiminea* sp. from Terceira Island, Azores

(Ávila 2000), (2) by rafts of egg-masses, juveniles or adults of small-sized species attached to seaweeds (Vallentin 1895, Arnaud *et al.* 1976, Highsmith 1985), to carapaces of marine turtles (Frazier *et al.* 1985), pumice (Jokiel 1984), logs, or other suitable floating materials (Jokiel 1990b).

Two types of larval development can be considered in marine gastropods: planktotrophic (with a free-swimming feeding stage) and non-planktotrophic (either lecithotrophic or direct development, both without a free-swimming feeding stage) (Jablonski & Lutz 1980; Ávila & Malaquias 2003). In general, species with a non-planktotrophic type of development usually have reduced dispersal abilities and, as a consequence, have a narrower geographical distribution (Mileikovsky 1971, Scheltema 1989). However, some species lacking a planktotrophic larval stage have a wide geographical range, e.g. the brooder bivalve *Lasaea adansoni* (O'Foighil 1989) or the brooder gastropod *Littorina saxatilis* (Johannesson 1988, Reid 1996, Carlton & Cohen 1998).

Species with teleplanic larvae, that is, possessing a pelagic larvae with a prolonged free-swimming stage, have no difficulties in reaching far away islands (Scheltema 1971b, Scheltema & Williams 1983, Scheltema et al. 1996). They may even reach these islands so regularly that speciation does not occur, because of repeated episodes of gene flow between mainland and insular populations. Such species are even capable of maintaining populations on both sides of the Atlantic, without subsequent allopatric speciation (Scheltema 1971a, García-Talavera 1981, Scheltema 1989, Fernandes & Rolán 1994).

How can the existence on far away islands of benthic shallow-water species with non-planktotrophic development be explained? A possible explanation would be to postulate a planktotrophic ancestor that later speciated and acquired a non-planktotrophic type of development. This does not explain the simultaneous existence of a species with a non-planktotrophic type of development in two nearby archipelagos (e.g. Azores/Madeira, Selvagens/Canary Islands). An explanation would be that this particular species has speciated in one of the archipelagos and has later dispersed, reached and successfully established, on the other.

Some gastropod species with non-planktotrophic development are capable of dispersal by rafting (Highsmith 1985, Johannesson 1988; Parker & Tunnicliffe, 1994). A large number of rissoid species exhibit such development (Ávila unpublished data). Species of this family possess a posterior pedal gland that secretes threads of mucus on which they can suspend themselves from the surface film (Ponder & Keyzer 1998), hence providing a plausible means for dispersal, yet not very effective for large distances. Most probably, these small-sized species, usually living amongst algae, raft in patches of drifting algae dragged from the littoral zone by wave action.

In oceanic islands, shallow benthic insular species of Rissoidae are located far from other islands or continents, usually separated by deep waters that constitute an effective barrier to adult migration. This is not the case in continents, where the physical continuity of the land mass can provide an effective means for dispersal by stepwise adult migration of species with non-planktotrophic development along coastlines, over many generations (Scheltema 1989).

Dispersal depends on chance events so, the more abundant the species, the higher its chances of being rafted. Also, species usually associated with hard substrata or rocky shores covered by algae are, in general, more likely to be rafted in comparison to infaunal benthic species (Scheltema 1986b). Thus, if it is accepted that rafting is an important method of dispersal for many epibenthic intertidal and shallow-sublittoral species with non-planktotrophic development, with some achieving the colonization of insular habitats, then the following hypotheses arise: (1) insular species usually living in the intertidal zone or at shallow depths should be more prone to be rafted than species living at deeper levels; (2) as a consequence, there should be a direct relationship between bathymetry and the geographical range of a given species - that is, intertidal species should generally have a wider geographical range than sublittoral species and, in turn, these should have a wider geographical range than deeper species; (3) if the adults are the rafting stage, then small species should have a wider geographical distribution than medium-sized or large-sized species.

The Azores archipelago was chosen to address the previous questions and hypotheses, due to its geographical location in the middle of the North Atlantic Ocean, well-known geological history and low-degree of anthropogenic disturbances in the environment.

MATERIALS AND METHODS

The zonation of the most abundant algae-associated molluscan species of the Azores was established (Ávila 2003, Ávila *et al.*, submitted) and their geographical distribution tabulated. Species were separated according to their bathymetrical zonation: intertidal, shallow sublittoral (down to 5-6m depth) and deeper littoral species (usually found at depths greater than 10m). A table containing these species and their type of development, body size and geographical range, was compiled (Table 1).

As no other quantitative studies on the zonation of the most abundant algae-associated molluscan species are known for the other Atlantic archipelagos, a family of small-sized gastropods widely represented in the Atlantic was chosen (Rissoidae), its geographical distribution, zonation and type of development was compared and analysed. The Rissoidae were selected because of their high number of genera and species (many possessing non-planktotrophic development), their wide distribution in the Atlantic Ocean, being especially common in the Atlantic islands, and because of their small size and their association with algae and, therefore, potential rafting capability (Vallentin 1895, Arnaud *et al.* 1976, Highsmith 1985). Shallow water rissoid species with non-planktotrophic development and restricted to two Atlantic archipelagos were selected from Ávila (2005) (Table 2).

Rissoids lay benthic egg-capsules, which give rise to larvae with different degrees of development. The extension of the larval phase influences the dispersal ability of the species and this has evolutionary and biogeographic implications. Whether or not one species has an extended planktonic larva can be inferred from protoconch morphology. Since direct observations of larval development are lacking for most species, protoconch inspection is the only way to estimate the duration of the larval phase (Jablonski & Lutz, 1980).

RESULTS

Four out of the five most abundant intertidal Azorean species are small gastropods (up to 2.7mm), and they all possess non-planktotrophic development. Notwithstanding this, some species have a wide geographical distribution, ranging from Scandinavia south to the Mediterranean, also occurring in most of the Atlantic archipelagos e.g. *Omalogyra atomus* and *Skeneopsis planorbis*; the latter species also has an amphi-Atlantic distribution, occurring in the Caribbean (Table 1). The intertidal brooding bivalve *Lasaea adansoni* has an even wider geographical distribution, including both sides of the Atlantic, Scandinavia south to the Mediterranean and occurring in all the Atlantic archipelagos. Analysis of distributions (Table 1) shows that the geographical range of the most abundant Azorean species decreases with increasing depth. Shallow water abundant species have a narrower geographical distribution than intertidal species, and *Alvania sleursi*, the only abundant Azorean deeper littoral species, is restricted to the Azores and Madeira.

A total of 306 shallow-water Rissoidae species are reported from the Atlantic and Mediterranean. Of these, 214 have non-planktotrophic development, 59 possess planktotrophic development, and the type of development of the remaining 33 is unknown; 77 species are endemic to one of the oceanic archipelagos. In this study, only 15 species (Table 2) are relevant, *i.e.* the shallow non-planktotrophic species that are present simultaneously in only two archipelagos and that are not present on continental shores. The Cape Verde archipelago, and the islands of Saint Helena and Tristan da Cunha do not possess such rissoid species, whereas Azores and Madeira have three species, Azores/Selvagens share one species, Selvagens/Canary Islands share five species, and six species occur simultaneously on Madeira and the Canary Islands (Table 2). Of the three Azores/Madeira rissoids, one is an abundant intertidal species (*Alvania mediolittoralis*) and two are shallow-water species (the common

Rissoa guernei and *Crisilla postrema*). The other Azorean rissoid species that also occurs at Selvagens (*Alvania sleursi*) is especially abundant at 20m depth on the Azorean rocky shores covered by algae.

DISCUSSION

Although rafting has been considered by several authors as a good explanation for the dispersal of benthic species without planktotrophic development (Vallentin 1895, Arnaud *et al.* 1976, Highsmith 1985, Jokiel 1984, 1989, 1990a, 1990b), this is the first study to suggest a link between depth, where epibenthic non-planktotrophic organisms usually live, and rafting as a plausible means for dispersal, and thereby explaining geographical range distribution.

Scheltema (1977, 1986a, 1986b, 1989, 1992) has pointed out that the duration of the larval phase determines the dispersal ability of the species (but see also Bhaud 1993), and this is evident for Azorean gastropods. From 322 benthic shallow-water molluscan taxa reported from the Azores, 157 species are Caenogastropods, for which the life history is known for only 91 species. Of these, 49 are planktotrophic developers and 42 are non-planktotrophic species (Ávila 2000, 2005). Table 3 summarizes the Azorean benthic shallow-water molluscan species with wide geographical ranges and a known life history. Most of the Azorean species that are amphi-Atlantic have planktotrophic larvae, with the exceptions of the brooding bivalve *Lasaea adansoni* and the small gastropods *Skeneopsis planorbis* and *Omalogyra atomus*. In general, the Azorean caenogastropod species with planktotrophic larvae have wider geographical ranges than species with non-planktotrophic larvae, as shown by other studies (Scheltema 1989, 1995). However, some species without planktotrophic larvae also have wide geographical ranges (e.g. *Ammonicera rota*, *Ocenebra erin*acea and *Haedropleura septangularis*) (Table 3). A discussion of the possible explanatory causes for this, such as higher environmental tolerances in non-planktotrophs as suggested by Jablonski & Lutz (1980) or by Bhaud (1993), is beyond the scope of this paper.

So, how do non-planktotrophic shallow-water epibenthic species disperse between islands or even between archipelagos? Table 3 shows that three out of the eight Azorean caenogastropod species with the widest ranges and possessing non-planktotrophic development, share common characteristics: all of them are small-sized and are most abundant in the intertidal zone (*Skeneopsis planorbis* and *Omalogyra atomus*) or high up on shores (*Truncatella subcylindrica*). This supports the hypothesis that intertidal species are more prone to be rafted than those from deeper levels and have wider geographical ranges.

Further evidence of the relationship of rafting and depth occurrence in the dispersal of shallow benthic marine gastropods is provided by the analysis of the geographic distribution of the family Rissoidae in the Macaronesian archipelagos. This family is rich in endemic insular species (Table 4). Cape Verde is the archipelago with the highest number of endemic shallow-water rissoids, with a large number of *Schwartziella* species (20) (Rolán & Luque 2000). Although possessing a smaller number of shallow-water rissoids than Madeira or Canary Islands, the Azores possess a higher number of endemic species. This is because Madeira and Canary Islands share a high number of rissoid species (28, of which only three are non-planktotrophic species) (Ávila, 2005), providing evidence that rafting is the means for dispersal of species lacking a planktotrophic larva. There are three non-planktotrophic shallow-water species that occur simultaneously only in the Azores and Madeira. Of these, two are sufficiently common to have their depth zonation well established in the Azores: *Alvania mediolittoralis* is an intertidal species that may attain densities around 5,200 ind/m2 (Ávila *et al.* submitted) and *Rissoa guernei* is a common sublittoral species between 3 to 5-6m depth and with densities that may reach around 200 ind/m2. *Crisilla postrema*, another rissoid present on both Azores and Madeira is usually an uncommon species, but is locally very abundantly in the intertidal zone of Ilhéu de Vila Franca, a small islet on the south coast of São Miguel Island (Azores). Here it may reach densities higher than 10,000 ind/m2 (Bullock 1995). It is more common between 0 and 10m depth (Ávila 2003). *Alvania sleursi* is a species that occurs in the Azores and Selvagens. It is present from 3m down to 27m but it is more common around 20m depth, with maximum densities around 500 ind/m2 at 22m depth (Ávila 2003). Thus, the bathymetric-geographical range hypothesis is also supported by the Azorean rissoids: there is a higher chance of being rafted for species with non-planktotrophic development if they are common, of small size, and live in the intertidal or shallow waters. Further zonation studies are required to test these hypotheses elsewhere, particularly in other Atlantic archipelagos.

CONCLUSIONS

In contrast to the Atlantic tropical waters, where rafting plays only a secondary role in the dispersal of molluscs (Scheltema 1995), in temperate Atlantic waters, rafting seems to be an important means of dispersal for shallow-water epibenthic molluscs that are of small size, are reasonably common, exhibit non-planktotrophic development, and usually live on rocky shores covered by algae. There is a relationship between geographical range and bathymetry: species usually living in the intertidal zone or at shallow depths, are more prone to be rafted than species at deeper levels and, as a consequence, intertidal species have a wider geographical range than sublittoral ones, and these in turn also have a wider geographical range than deeper species.

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TABLE 1. Most abundant shallow-water species in the Azores. Type of development: np – non planktotrophic; p – planktotrophic; br – brooding. AZO – Azores; MAD – Madeira; CAN – Canary Islands; CAP – Cape Verde; SCA – Scandinavia; BRI – British Isles; POR – Portugal; MED – Mediterranean; ASC – Ascension Island; STH – St. Helena Island; CAR – Caribbean. Data extracted from Ávila (2000) and Ávila (2005).

	Most abundant species	Type of development	Body size (mm) height x diameter	Geographical range										
				AZO	MAD	CAN	CAP	SCA	BRI	POR	MED	ASC	STH	CAR
Intertidal	*Alvania mediolittoralis* Gofas, 1989	np	2.7 x 1.5	1	1									
	Omalogyra atomus (Philippi, 1841)	np	0.8 x 0.8	1	1	1	1	1	1	1	1	1		
	Skeneopsis planorbis (Fabricius O., 1780)	np	1.2 x 1.0	1	1	1		1	1	1	1			1
	Pisinna glabatra (Von Mühlfeldt, 1824)	np	1.5 x 0.8	1		1					1			
	Lasaea adansoni (Gmelin, 1791)	br	3.5 x 3.0	1	1	1	1	1	1	1	1	1	1	1
Shallow (3-6m)	*Anachis avaroides* Nordsieck, 1975	np	3.5 x 1.5	1	1	1								
	Parvicardium vroomi van Aartsen, Menkhorst and Gittenberger, 1984	p	3.5 x 2.6	1	?	?				1				
	Alvania angioyi van Aartsen, 1982	np	1.8 x 1.1	1										
	Manzonia unifasciata (Dautzenberg, 1889)	np	2.5 x 1.2	1										
	Rissoa guernei Dautzenberg, 1889	np	2.3 x 1.3	1										
	Gibbula delgadensis Nordsieck, 1982	np	2.0 x 2.0	1										
Deep (10-30m)	*Alvania sleursi* (Amati, 1987)	np	2.5 x 1.6	1	1									

TABLE 2. Shallow non-planktotrophic Rissoidae restricted to two contiguous oceanic archipelagos. AZO – Azores; MAD – Madeira; SEL – Selvagens; CAN – Canary Islands (Ávila, 2005).

Species	AZO	MAD	SEL	CAN
Alvania mediolittoralis Gofas, 1989	1	1		
Crisilla postrema (Gofas, 1990)	1	1		
Rissoa guernei Dautzenberg, 1889	1	1		
Alvania sleursi (Amati, 1987)	1		1	
Alvania johannae Moolenbeek & Hoenselaar, 1998			1	1
Alvania subcalathus Dautzenberg & Fischer, 1906			1	1
Manzonia castanea Moolenbeek & Faber, 1987			1	1
Manzonia guitiani Rolán, 1987 = M. pelorum Moolenbeek & Faber, 1987			1	1
Zebina paivensis (Watson, 1873)			1	1
Alvania aurantiaca (Watson, 1873)		1		1
Alvania euchila (Watson, 1886)		1		1
Alvania macandrewi (Manzoni, 1868)		1		1
Manzonia boogi Moolenbeek & Faber, 1987		1		1
Manzonia dionisi Rolán, 1987 = M. darwini Moolenbeek & Faber, 1987		1		1
Manzonia overdiepi van Aartsen, 1983c		1		1

TABLE 3. Geographical distribution of the Azorean shallow-water marine molluscs with the widest geographical ranges (Ávila 2000). Legends as in Table 1.

Species	Family	Dev	SCA	BRI	POR	MED	AZO	MAD	CAN	CAP	ASC	STH	CAR
Lasaea adansoni (Gmelin, 1791)	Lasaeidae	br	1	1	1	1	1	1	1	1	1	1	1
Lamellaria perspicua (Linnaeus, 1758)	Lamellariidae	p	1	1	1	1	1	1	1	1			1
Skeneopsis planorbis (Fabricius O., 1780)	Skeneopsidae	np	1	1	1	1	1	1	1				1
Omalogyra atomus (Philippi, 1841)	Omalogyridae	np	1	1	1	1	1	1	1	1	1		
Fossarus ambiguus (Linnaeus, 1758)	Fossariidae	p			1	1	1	1	1	1	1	1	
Raphitoma linearis (Montagu, 1803)	Conidae	p	1	1	1	1	1	1	1	1			
Luria lurida (Linnaeus, 1758)	Cypraeidae	p			1	1	1	1	1	1	1	1	
Ammonicera rota (Forbes & Hanley, 1850)	Omalogyridae	np	1	1	1	1	1	1	1				
Ocenebra erinacea (Linnaeus, 1758)	Muricidae	np	1	1	1	1	1	1	1				
Haedropleura septangularis (Montagu, 1803)	Turridae	np	1	1	1	1	1	1	1				
Phalium granulatum (Born, 1778)	Cassidae	p			1	1	1	1	1	1			1
Cymatium parthenopeum (Von Salis, 1793)	Ranellidae	p			1	1	1	1	1	1			1
Epitonium lamellosum (Lamarck, 1822)	Epitoniidae	p		1	1	1	1	1	1				1
Charonia tritonis variegata (Lamarck, 1816)	Ranellidae	p				1	1	1	1	1		1	1
Charonia lampas lampas (Linnaeus, 1758)	Ranellidae	p		1	1	1	1	1	1	1			

TABLE 3 (continued). Geographical distribution of the Azorean shallow-water marine molluscs with the widest geographical ranges (Ávila 2000). Legends as in Table 1.

Species	Family	Dev	SCA	BRI	POR	MED	AZO	MAD	CAN	CAP	ASC	STH	CAR
Nassarius incrassatus (Ström, 1768)	Nassariidae	p	1	1	1	1	1	1	1				
Acmaea virginea (Müller, O.F., 1776)	Acmaeidae	p	1	1	1	1	1	1	1				
Gibbula magus (Linnaeus, 1758)	Trochidae	p	1	1	1	1	1	1	1				
Cerithiopsis tubercularis (Montagu, 1803)	Cerithiopsidae	p	1	1	1	1	1		1	1			
Melarhaphe neritoides (Linnaeus, 1758)	Littorinidae	p	1	1	1	1	1	1	1				
Alvania cancellata (da Costa, 1778)	Rissoidae	p		1	1	1	1	1	1	1			
Ocinebrina aciculata (Lamarck, 1822)	Muricidae	np		1	1	1	1	1	1				
Littorina saxatilis (Olivi, 1792)	Littorinidae	br	1	1	1	1	1		1				
Truncatella subcylindrica (Linnaeus, 1767)	Truncatellidae	np		1	1	1	1	1	1				
Sinezona cingulata (Costa O. G., 1861)	Scissurellidae	p				1	1	1	1	1			1
Ranella olearia (Linnaeus, 1758)	Ranellidae	p		1		1	1		1	1			1

TABLE 4. Number of endemic shallow-water species of Rissoidae in each of the Atlantic archipelagos. (Ávila unpubl. data). Legends as in Table 1.

Archipelagos	Shallow-water species*	Non-planktonic development	Planktotrophic development	Unknown
AZO	12	11	0	1
MAD	3	3	0	0
SEL	1	1	0	0
CAN	11	7	0	4
CAP	43	41	2	0
STH	7	0	1	6
TRS	2	0	0	2

* depth less than 50m

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

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ABSTRACT

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

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

INTRODUCTION

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

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

The biogeographical affinities of the marine algal flora of this isolated archipelago have previously been investigated on several occasions. Schmidt (1931) suggested an affinity with Macaronesia and southern Spain. Prud'homme van Reine (1988) and Prud'homme van Reine and Van den Hoek (1988, 1990) using a numerical clustering method showed the marine algal flora to be associated with floras of the western Mediterranean Sea and the temperate Atlantic Ocean and noted fewer Azorean algae in common with east America than with the western Mediterranean Sea. Tittley *et al.* (1990) analysed the North Atlantic distributional data in South and Tittley (1986) using various numerical methods and showed affinities of the Azores brown and red algal floras with those of southern Spain and Portugal. Tittley and Neto (1995) reassessed floristic relationships with revised data for the Azores and the North Atlantic; ordination of the brown and red algae were similar to those of Tittley *et al.* (1990); the green algae showed a wider spread of floras but with the Azores remaining apart from the main group.

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

MATERIALS AND METHODS

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

The ordination method DECORANA (Detrended Correspondence Analysis) from the VESPAN computer package (Malloch 1997) was used to analyse presence and absence data for North Atlantic algae. Ideally biogeographic patterns should be determined by the abundance of species assemblages rather than by presence and absence (Adey & Steneck 2001) but at present such data are largely unavailable. North Atlantic algal distributional data was based on the 33 floristic areas in South and Tittley (1986) with the caveat that such sample areas are not ideal (Adey & Steneck 2001, Tittley *et al.* 1990).

RESULTS

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

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

Ordination of green algal data (Figure 3) showed discernable American and European series of floras. Southern floras were separated from the main cluster with the North Carolina, South Carolina and Macaronesian floras at high values on axis 1. The Azores flora was positioned closest to that of Madeira.

DISCUSSION

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

Comparison of the ordinations of red algal data in Tittley *et al.* (1990) and Tittley and Neto (1995) with that of this study shows that despite new records for the Azores and revision of the North Atlantic flora generally, the overall pattern of floristic relationships remains similar with the American and European series of floras arising from a common Arctic group. In all three sets of ordination analyses (Tittley *et al.* 1990, Tittley & Neto 1995, this study), the Azores flora was the last in the European series of floras. Axis 1 in these ordinations indicated a north to south gradient of increased sea temperature (see Morton *et al.* 1998, Figs1-16). Axis 2 represented an east – west separation of temperate Atlantic floras. The addition of data for the floras of Madeira, the Canary Islands, and North and South Carolina in the present analysis resulted in the Azorean flora placed closer to those of central Macaronesia and indicated a warm water floristic affinity. The position in the ordination of the North Carolina and South Carolina floras apart from others in America indicated a major floristic discontinuity with the floras to the north of Cape Hatteras and a transatlantic affinity with the warmer water floras of Macaronesia.

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

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

The closer affinity between the Azores flora with those of Madeira and the Canaries than with Atlantic Europe as suggested by Prud'homme van Reine and Van den Hoek (1988) is supported ecologically with the large canopy-forming fucoids and kelps common in northern Europe and in Atlantic Spain and Portugal, but largely absent in the Azores. Algal assemblages are in general characterised by turf-forming species (Neto & Tittley 1995, Tittley & Neto 2000), as occur elsewhere in Macaronesia. Adey and Steneck (2001) suggested that species assemblages that have adapted to similar conditions better define biogeographic regions.

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

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

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

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

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

The probable east Atlantic origin of Azorean marine fauna was discussed by Cornelius (1982); although the Azores hydroid fauna was amphi-Atlantic, its 18 Echinoderm species were of eastern Atlantic and Mediterranean origin, as were 77 species of fish. Only 21 fish species were amphi-Atlantic in distribution. The Azores shares 181 species of benthic marine algae with Madeira, 254 with the Canary Islands, 215 species with Portugal and southern Spain but only 87 species with North Carolina. Sources for the dispersal of algae to the Azores are probably varied as North Atlantic, Western Mediterranean, central Macaronesian, and warm-water American species are present on the Azores.

CONCLUSIONS

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

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

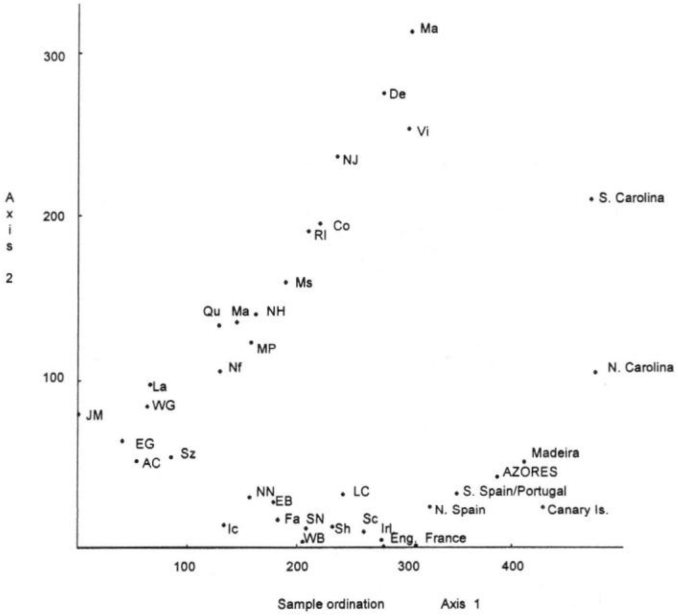


FIGURE 2. Ordination of brown algal floras in the North Atlantic Ocean.

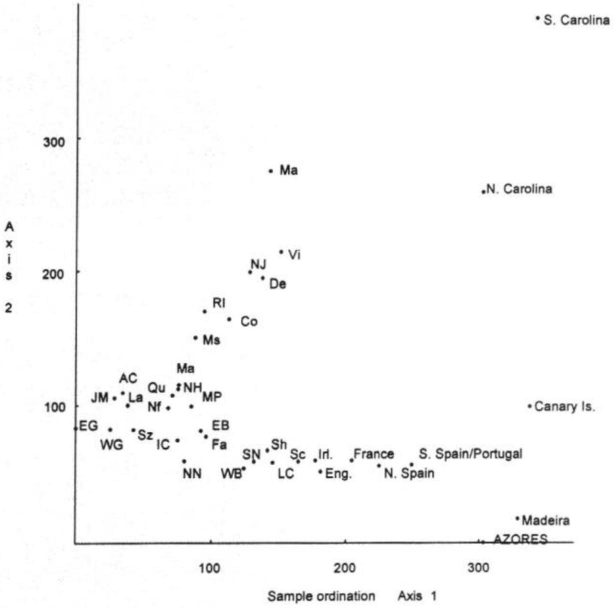
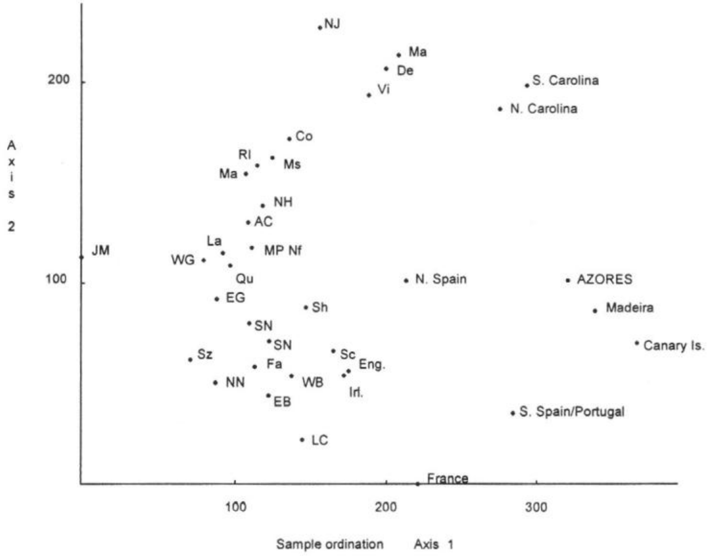


FIGURE 3. Ordination of green algal floras in the North Atlantic Ocean.



SHIPS' SEA-CHESTS – A TRANSPORT MECHANISM FOR THE INTRODUCTION OF NON-INDIGENOUS SPECIES TO ISOLATED MARINE ECOSYSTEMS

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ABSTRACT

The immigrant solitary ascidian *Styela clava* is native to the northwest Pacific. It was first recorded in British waters in 1954, and has since spread along the west coast of Europe and the neighbouring islands. This paper discusses how such sessile organisms can reach islands in sufficient numbers to form stable populations. *Styela clava* is used as a model to examine four suggested dispersal methods, two natural and two man-aided. Natural dispersal involves drifting of larvae and adults; man-aided methods involve transport of juveniles and adults, either attached to oyster shells or to ships' hulls. The problems associated with these proposed dispersal methods are examined and three additional man-aided routes are suggested - as eggs and larvae carried in ballast water, as adults attached inside ballast-water tanks, and as adults attached to the internal surfaces of sea-chests.

KEYWORDS: ships' sea-chests, non-indigenous species, man-aided dispersal, islands, *Styela clava*.

INTRODUCTION

The larvae of aquatic organisms may be transported in ships' ballast water, and this vector has often been used to explain the heterogeneous distribution of organisms. But the larvae of many sessile organisms are short lived and would not survive long voyages, so adults must have been transported to the new ecosystems. This raises the question of how sessile organisms could reach islands, and other isolated ecosystems, in sufficient numbers to form stable populations. We used the solitary ascidian *Styela clava* as a model to examine suggested methods.

The solitary ascidian *Styela clava* (Plate 1) is native to the northwest Pacific. It was first found in British waters in 1953 in the estuary of the Lynher River, near Plymouth (Carlisle 1954)[1]. It is probable that it was introduced into Plymouth Sound by military craft returning from the northwest Pacific after the Korean War in 1952. *S. clava* rapidly became established along the south coast, probably because the water temperature regime in the English Channel is similar to that of the northwest Pacific. It is intolerant of wave exposure; in sheltered environments it can be found on walls and piles from about mid-tidal level down to at least 10m below low water in the UK (Barnes *et al.* 1973), and individuals have been dredged from up to 40m depth off the French coast (Dauvin *et al.* 1991). It is also intolerant of low salinity; although it is reported to be able to survive exposure to salinity of 10 (Kelly 1974), no specimens have been found in the present study in water with salinity consistently lower than 20, which is consistent with the observation that larvae can metamorphose only at salinities between 20 and 32 (Kashenko 1996).

This paper attempts to explain the heterogeneous distribution of *S. clava* in terms of the potential dispersal methods, particularly man-aided methods, and discusses the importance of these methods for the invasion of island ecosystems.

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[1] These specimens were originally designated *Styela mammiculata* sp. nov. by Carlisle, but Millar (1960) demonstrated that this "new species" was synonymous with *Styela clava* Herdman, 1882.

Description of the adult, eggs and larvae

Only the relevant attributes of each stage of the life-cycle will be described here. *S. clava* is a large solitary ascidian; mature individuals range from 70mm to 160mm total length. The firm body is elongated and club-shaped. It is attached to the substratum by a short narrow stem-like stolon, which usually represents about one third of its total length. The base of the stolon forms an expanded membranous plate that adheres the organism to the substratum. Adults protrude from the surface and are rheophobic. They are tolerant of brief exposure; specimens have been found at low water spring tides attached to pebbles on the open beach tens and to jetty supports tens-of-centimetres above the water level.

S. clava is hermaphroditic and oviparous; a mature adult produces approximately 5000 eggs. The spherical eggs are negatively buoyant but slight agitation of the water maintains them in the water column. The eggs hatch after 12 to 15 hours at temperatures of 16 to 20°C (Davis 1997).

The pelagic lecithotrophic larvae are tadpole shaped, ranging from 0.83 to 0.87mm in length. They are negatively buoyant; however, they are also negatively geotactic and positively phototactic, particularly when exposed to hydrostatic pressure (high barokinesis), so a large proportion of the population maintain station close to the water surface (Davis 1997). They swim by flexing muscles in the tail. They may travel up to ten body lengths per second during short bursts of this 'twitching' motion, but rarely travel more than a few centimetres in sustained swimming activity. The larvae are active for approximately 12 hours.

The distribution of S. clava

The distribution of *S. clava* can best be described as patchy. In general, a sheltered high salinity site appears to be necessary for the initial development in any area but, with the exception of harbours in the Solent, it rarely spreads any distance to neighbouring suitable habitats. The following description of the distribution is not exhaustive; it merely indicates the spread of *S. clava* by highlighting its presence in continental and island harbours. Since its initial discovery in Plymouth, it spread east to Brixham and Weymouth (Davis & Davis 2004); Poole, Southampton and Shoreham Harbours (Holmes 1968); Portsmouth Harbour (Davis & Davis 2004); Langstone Harbour (Houghton & Millar 1960); Chichester Harbour (Stubbings & Houghton 1964); and Bembridge (Wells 1987), Cowes, Yarmouth and Wooten Creek on the Isle of White. We have recently found populations of *S. clava* in Brighton, Dover, Ramsgate, Sheerness, West Mersea, Harwich, Lowestoft and Grimsby (Davis & Davis 2004). To the west of Plymouth, *S. clava* has been recorded in Falmouth (Davis & Davis 2004); Milford Haven (Coughlan 1969); Holyhead (on the island of Anglesey) and Fleetwood (Davis & Davis 2004); Heysham Harbour (Coughlan 1985), and Cairnryan (Stranraer) and Ardrossan (Davis & Davis 2004). In Ireland, it has been recorded in Cork Harbour (Guiry & Guiry 1973), Fenit (Davis & Davis 2004) and Dun Laoghaire (new record, August 2004). To the south, populations have recently been found in the Channel Islands of Jersey and Guernsey (Davis & Davis 2004).

It was first recorded in North France (Dieppe) in the late 1960s (Monniot 1970) and spread up the channel to Ambleteuse (Buizer 1980) and the port of Dunkerque (Davoult *et al.* 1993). It spread further up the North Sea coast of Europe, being recorded in the harbours Zeebruge (d'Udekem d'Acoz 1986) and Ostend (Eneman 1995), Belgium; in Den Helder Harbour (Huwae 1974), the island of Texel (Huwae & Lavaleye 1975) and in the Oosterschelde (Westerweel 1975), The Netherlands; in Wilhelmshaven and the harbour of List on the Island of Sylt, Germany (Lützen 1999); and in the Limfjord (Christiansen & Thomsen 1981; Lützen & Sørensen 1993) and Kattegat (Lützen 1999), Denmark. To the south of Dieppe, it spread to the port of Le Havre (Breton & Dupont 1978), Roscoff and Brest (Minchin & Duggan 1988), Pornichet, Pornic and La Rochelle (Davis & Davis 2004); Arcachon (Bachelet *et al.* 1980); Santander and Gijon in northeast Spain (Davis & Davis 2004);

Cambados, Ría de Arosa, and Figueras, Ría del Eo (Ortea & Vizcaino 1981) and Ría de Ferrol, Galicia (Vázques & Urgorri, 1992) in northwest Spain; and Leixões (Porto), Cascais and Lisboa in Portugal (Davis & Davis, *in press*).

The majority of the sites where *S. clava* has been recorded are commercial ports and harbours, many of which have neighbouring small fishing harbours and marinas where we were unable to find any specimens of *S. clava*. This heterogeneous distribution was difficult to explain and prompted an examination of the potential methods of dispersal. However, it should be remembered that the inability to find specimens at a site does not necessarily mean that there are no colonies present in the area.

Methods of dispersal

Four methods of dispersal have been suggested for the spread of *S. clava*, two natural and two man-aided (Lützen 1999):

i) as planktonic eggs and larvae, carried by tidal currents;

ii) as sessile adults attached to drifting flotsam, e.g. the weed *Sargassum muticum*;

iii) as settled juveniles attached to oysters that have been transported and re-laid;

iv) as established adult animals attached to the hulls of ships.

In addition, we would propose:

v) transport of planktonic eggs and larvae in ships' ballast water,

vi) transport of juveniles and adults attached to the interior surfaces of ballast tanks,

vii) transport of juveniles and adults attached to the interior surfaces of sea-chests.

NATURAL DISPERSAL

The total time spent as planktonic egg and larva is approximately 24-28 hours. At the end of this period the larva must find a settlement site. A larva is capable of swimming several millimetres per second, but rarely travels more than a few centimetres in sustained swimming activity. Thus larval dispersion is mainly dependent on water movement, which in an estuary or harbour has a maximum range of the tidal excursion. This method of dispersion may account for the colonisation of adjacent inlets and harbours, for example within the Solent (southern England) where the majority of suitable harbours support *S. clava* populations, but cannot explain the long-distance spread to isolated islands.

Similarly, although dispersion as settled animals attached to floating wood or drifting weed should cover a wider area, since wind could enhance the displacement due to tidal movement, it would still probably be limited to neighbouring suitable sites. Since the animals are attached juveniles or adults, the time spent drifting is not critical. Lützen (1999) thought that this dispersion method could be of local importance. However, much flotsam washes up on the strand line (high tide mark) on beaches, where it may remain drying for several days before re-immersion. So the spread of organisms by this method would be opportunistic

As natural dispersal appears to be unpredictable and has a very limited range, the spread of *S. clava* has generally been attributed to the inadvertent introduction by man.

MAN-AIDED DISPERSAL

It has been suggested that large distance dispersion of *S. clava* could occur if juvenile animals attached to oyster shells were transported with the oysters when they were re-laid. This dispersion method, favoured by Minchin & Duggan (1988), would account for the appearance of *S. clava* in oyster culturing areas such as West Mersea in the UK, and the small harbours of

Brittany, France. However, this would only account for a few of the isolated populations.

An alternative hypothesis is that settled animals may be moved from one harbour to another attached to the hulls of ships. Transportation on slow moving wooden-hulled ships has been proposed as the method by which many of our apparently indigenous (cryptogenic) species were introduced over the last few thousand years (Carlton & Hodder 1995; Carlton 1999); but the hulls of modern operational ships are coated with anti-fouling agent to inhibit the attachment of organisms. Nevertheless, recent studies suggest that attachment to ships' hulls, particularly in areas of reduced flow, continues to be an important dispersal method for immigrant species (Gollasch 2002). However, mature specimens of *S. clava* are rheophobic; their firm bodies protrude from the surface to which they are attached, so they are unlikely to survive sustained high-velocity movement through water when the ship is in service. It has been suggested that settled organisms could be transported more slowly between harbours or marinas by pleasure craft; but most boat owners take their boats out of the water in the winter for storage and maintenance, which would stop juveniles reaching maturity and spawning. In fact, the only record of *S. clava* observed attached to a ship's hull is for a ship that had been moored for almost a year in Cork Harbour (Minchin & Duggan 1988); settlement and growth could have occurred during this time, without any ship movement. Thus, it would appear that this method of dispersal is most likely to occur when a ship is in a colonised port for sufficient time to allow breakdown of the antifouling coating and larval settlement, is then moved at low speed to a new port and remains there long enough for the animals to reach maturity and spawn. Such a series of events is unusual, but may account for the appearance of *S. clava* in the late 1980s in Loch Ryan (S. Smith, *pers. comm.*), which was far from the then closest recorded population at Heysham Harbour.

A survey of the Loch in May 2003 revealed that there was a small population in Stranraer Harbour and a few individuals around the ferry terminal (Cairnryan), but *S. clava* was very abundant on and around the derelict jetty further down the loch. This jetty had been the site of the breakers yard at Cairnryan; ships were moored to the jetty during dismantling. Holme (1997) documented the history of the port and its ship-breaking activities. Warships that had been paid off and de-equipped in Plymouth and Portsmouth were of particular interest to the present study, since these harbours supported populations of *S. clava* from the 1960s. The ships usually spent several years deteriorating in their final port, were towed slowly to Cairnryan, and then spent several years moored to the jetty whilst being dismantled - ideal conditions for the transfer of *S. clava*. A few examples will suffice to illustrate how transfer could have occurred. HMS Eagle was de-equipped over eighteen months in Portsmouth, laid up in the Hamoaze (Plymouth) for six years, then towed slowly to Cairnryan over four days; demolition took over two years. HMS Ark Royal was de-equipped over two years at Devonport, then towed slowly to Cairnryan over six days; demolition of the Ark Royal took over three years. HMS Bulwark was de-equipped over three years at Portsmouth, towed slowly to Cairnryan over seven days; demolition took over two years. However, there is no reliable evidence that any of the ships dismantled at Cairnryan were fouled with *S. clava*, so this method of distribution must remain an intriguing hypothesis.

MAN-AIDED DISPERSAL BY COMMERCIAL SHIPPING

We propose three additional man-aided routes to explain the spread of *S. clava* - as planktonic eggs and larvae carried in ships' ballast water, as established mature adults attached to the interior surfaces of ballast tanks, and as established mature adults attached to the interior surfaces of sea-chests.

TRANSPORT OF EGGS AND LARVAE

During August and September, the water in any harbour that that has a population of *S. clava* will contain eggs and larvae of this ascidian. Any ship taking on ballast water in such a port will inevitably take up some eggs and larvae with the water. If the ship discharges the ballast water in another port while the eggs or larvae are still viable, a new population may develop in that port, provided that the conditions are suitable for growth and reproduction.

Transport in ballast water has been proposed as the main modern-day transfer method for introduced species (see, for example, Carlton 1985). However, this method of dispersal would be possible for *S. clava* only for voyages of less than 24 hours duration, such as the continental car ferry routes. Using this dispersal mechanism, the original population in Plymouth could have initiated settlement in Roscoff; then, once established there, *S. clava* could have spread to Cork Harbour. Similarly, larvae from the Portsmouth and Southampton populations could have colonised Cherbourg, St. Malo and Le Havre, and larvae from the Cherboug population could have settled in Poole or *vice versa*.

Ferries are often exchanged between Portsmouth and Dover, allowing a population of *S. clava* to become established in the Port of Dover. Larvae form the Dover colony could have been carried to Calais, Dunkerque and Ostend. From Dunkerque, a population could be established in Ramsgate, which is too far from Dover to be colonised by larval drift and has no local oyster beds. A well-established population exists in the Dutch Naval Base of Den Helder, close to the Hook of Holland ferry port, which connects with Harwich where a thriving population has recently been recorded.

It is difficult to prove that larvae are transported in ballast water other than by filtering the contents of the ballast tanks, which would not be permitted since it has safety implications for the vessel; moreover, it is not easy to obtain access to the ballast tanks of operating ships. Furthermore, the presence of larvae in ballast water today provides only circumstantial evidence for the source of established populations that may have arrived many years earlier. In addition, large commercial ships also use many of the harbours, so it is difficult to exclude adult transport on these ships as the means of introduction. Nevertheless, to test the feasibility of the hypothesis of larval transport in ferry ballast water transport, a harbour was sought that was isolated from known populations, had no oyster fishery, had a regular car ferry service of less than 24 hours duration from a colonised port, and limited commercial shipping. St Helier harbour (Jersey), which has ferry links with Portsmouth, Poole, Weymouth and St Malo, was selected and the adjacent marinas were surveyed for populations of *S. clava*. Well-established populations were found in the St Helier and Elizabeth marinas on Jersey. The discovery of these populations was encouraging, but did not vindicate the hypothesis.

TRANSPORT OF ADULTS

Populations of *S. clava* have been found in most of the commercial ports surveyed although since access to the dockside in ports is normally difficult, the search has usually been restricted to adjacent marinas. Examples include Shoreham, Sheerness and Liverpool Docks in the UK; the French ports of Le Havre, Calais, Cherbourg and La Rochelle and the Spanish port of Santander. Many of these ports are served by ferries or are close to other populations of *S. clava*, so the presence of *S. clava* may be explained by either natural or man-aided larval transport.

However, populations of *S. clava* have also been found in isolated commercial harbours that are not served by ferries and have no commercial oyster fishery, for example Fenit (on the west coast of Ireland), Gijon (on the northwest coast of Spain), and Porto and Lisboa (Portugal). In fact, the only population found on the west coast of Ireland was in Fenit, an isolated harbour visited by commercial ships that transport locally manufactured cranes to other European ports. The Portuguese specimens of *S. clava* were found in the marinas at Leixões, Cascais and Bom Sucesso (Davis & Davis, *in press*); the marina at Leixões is adjacent to the commercial port of Porto, and the marinas at Cascais and Bom Sucesso are close to the commercial port of Lisboa. All these commercial ports are too far from the nearest *S. clava* populations for planktonic larvae to be carried there, and any larvae transported in ballast water would probably metamorphose into sedentary juveniles long before the water was discharged.

Since larval dispersal is unrealistic, sessile adults must have established the populations of *S. clava*. There are no oyster fisheries close to Fenit, Porto and Lisboa, and no *S. clava* populations that could provide flotsam with attached adults. In fact, there are four marinas (Vila Nova, Figueira da Foz, Nazaré and Peniche) with suitable conditions for *S. clava* colonisation in the 300km between Porto and Lisboa; but, despite exhaustive searches, no specimens of the ascidian were found in these intervening marinas, as might be expected if flotsam were a vector for adult dispersal.

There are, however, two related man-aided methods of adult dispersal that could explain the observed distribution. The first is a natural extension of larval transport in ballast water. If eggs and larvae are taken into the ballast tank when ballast water is pumped aboard, the larvae could settle on the walls of the tank and metamorphose into juveniles. Provided that they have sufficient resources to grow to maturity, they could spawn the following year. Discharge of the ballast water within 24 hours of the captive individuals spawning, would permit *S. clava* larvae to colonise a new site. This dispersion method would provide a mobile population capable of travelling long distances and spawning when the water temperature was suitable, usually in the shallow water of ports and harbours. The main limitation of this dispersal method is the availability of food and dissolved oxygen in the ballast water to sustain the maturing adults; it is extremely unlikely that they would survive a year in a ballast tank.

The other method by which adults may be transported on ships occurs when larvae settle on the internal surfaces of the ship's sea-chests (Carlton *et al.* 1995; Gollasch 2002). This method allows free access to food and dissolved oxygen. A sea-chest is a void built into the hull below the waterline

(Plate 2), with direct connection to the surrounding seawater; it is the source of the cooling-water, fire-fighting water and ballast-water pumped aboard, and is therefore covered with a grill (typically 13-25 mm mesh) to protect the pump from damage by large organisms and flotsam. Furthermore, since maintaining anti-fouling protection on the internal surfaces of sea-chests is an awkward process, it is often neglected; thus larvae have a greater chance of settling in sea-chests than on the external hull.

The number and size of sea-chests is in proportion to the size of the ship, vessels examined to date have provided 50-200m^2 of surface area for settlement (Plates 3 & 4). A recent study by Coutts *et al.* (2003) reported numerous species living in the sea-chests of a ferry that travelled between Tasmania and Australia. As yet, we have found only hydroids, barnacles, tube worms and mussels in sea-chests (Plate 5); but this indicates that they are a suitable vector for sessile organisms. In addition, sea-chests contain ledges, pipe-work and side-chambers (Plates 4 & 6) that would permit the transport of some mobile organisms.

Sea-chests therefore provide an artificial substrate in a sheltered environment that can readily be located by negatively geotactic larvae or organisms that are small enough to pass through the grill. The continuous low-flow water exchange in the sea-chests provides good conditions for growth and development. Since the substrate is mobile, populations of mature adults may be transported long distances to spawn when suitable conditions are encountered. If the ship travels through cold deep water into the warm shallow water of a harbour, the temperature shock may trigger synchronised spawning which would provide the high-density inoculum necessary to give a high probability of successful establishment of a colony in a new habitat. The presence of a population of organisms in the sea-chests of commercial ships that visit islands could explain the presence of non-indigenous species in isolated island ecosystems.

CONCLUSIONS

Since the immigrant ascidian *S. clava* was first recorded in British waters in 1954, it has spread along the coasts of the UK and western Europe. The distribution is patchy.

Natural dispersion of planktonic eggs and larvae, or settled adults attached to drifting weed will only account for local dispersal. Man-aided dispersion by transport of settled juveniles attached to oysters that have been re-laid, and adults attached to the hulls of ships, is feasible. Indeed, some *S. clava* populations have been found near commercial oyster fisheries and, although anti-fouling paint should inhibit the attachment of fouling organisms on operational ships, one instance of possible hull transport on decommissioned ships has been identified. Nevertheless, these dispersal vectors only accounts for a few populations of *S. clava*; they cannot readily explain the presence of the isolated island populations. So three additional man-aided routes have been proposed to explain the spread of *S. clava*. - as planktonic eggs and larvae carried in ships' ballast water, as juveniles attached to the interior surfaces of the ballast tanks, and as established adults attached to the interior surfaces of ships' sea-chests.

Dispersal as planktonic eggs and larvae carried in ships' ballast water is only possible for voyages of less than 24 hours; otherwise the larvae will settle and metamorphose. On longer voyages, the larvae could settle on the interior surfaces of the ballast tank, metamorphose and grow. However, the transport of the subsequent juveniles attached to the ballast tanks is not a likely dispersal mechanism, since they would die from lack of dissolved oxygen and nutrition before they could spawn.

The most realistic man-aided dispersal method for *S. clava* is as established adults attached to the interior surfaces of ships' sea-chests. The development of a population of sessile organisms attached to such a mobile substrate, transported long distances and spawning when suitable water conditions are encountered, could explain the heterogeneous distribution of

S. clava and other non-indigenous species, particularly on isolated islands. Furthermore, the sudden increase in water temperature when the ship enters a shallow port could initiate synchronised spawning of the mobile population, producing the high-density inoculum necessary to successfully initiate establishment in a new population in the receiving habitat.

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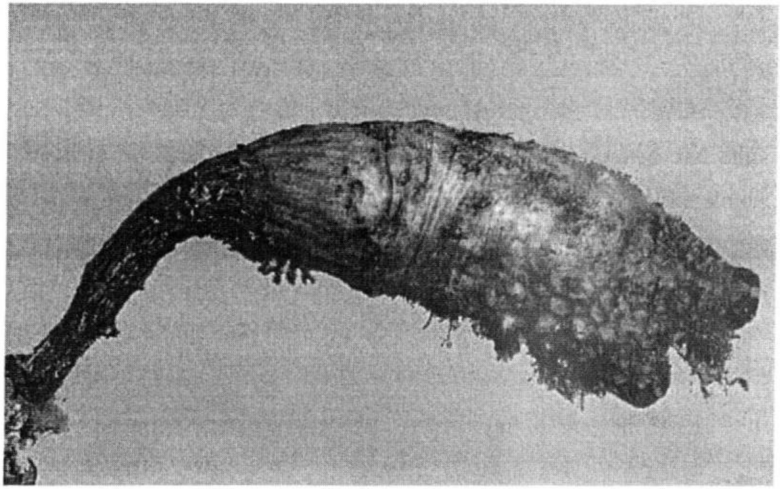

PLATE 1. *Styela clava* Herdman, 1882.

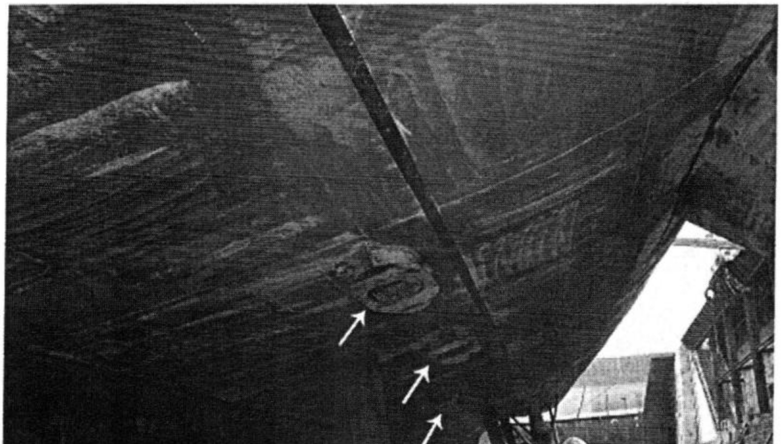

PLATE 2. Sea-chest intakes.

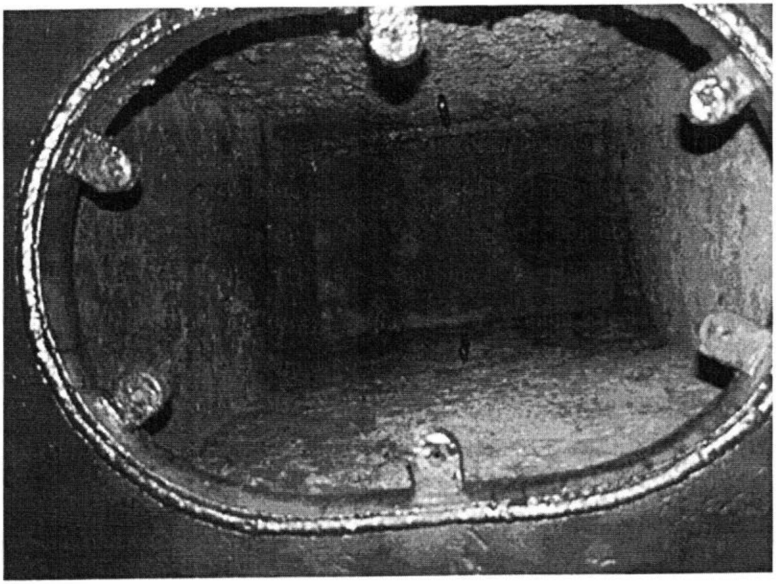

PLATE 3. Vertical sea-chest.

PLATE 4. Horizontal sea-chest.

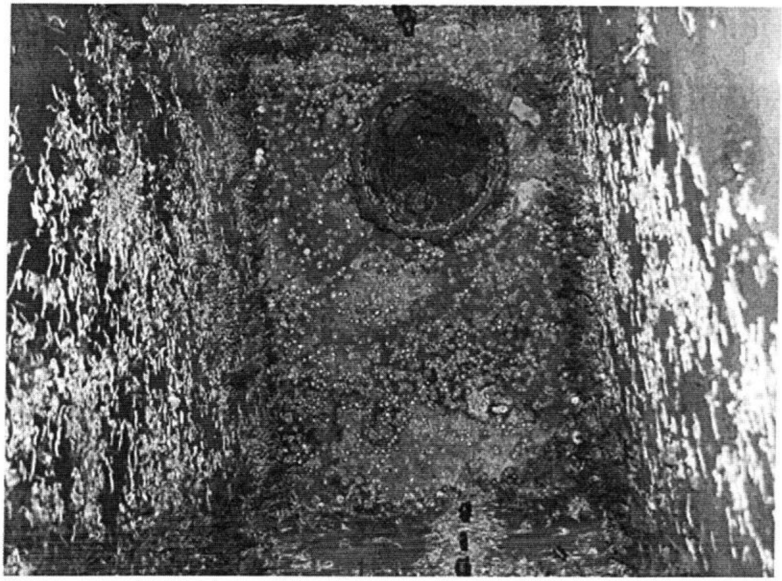

PLATE 5. Sea-chest with hydroids, barnacles and tube worms.

PLATE 6. Sheltered internal ledge of a sea-chest.

AN ANALYSIS OF GENETIC VARIATION OF POPULATIONS OF *GLYCERIA FLUITANS* (FLOATING SWEETGRASS) FROM THE ISLANDS OF BRITAIN AND IRELAND, USING AFLP ANALYSIS

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ABSTRACT

As part of a study investigating constitutional metal tolerance in wetland plants, amplified fragment length polymorphism (AFLP) was used to study the genetic diversity of the wetland grass *Glyceria fluitans* (floating sweetgrass) from six populations from the Atlantic Islands of Britain and Ireland. These six populations were compared with four populations from mainland Europe, one from Denmark and three from Poland. Six different primer combinations were used on five to nine plants from each of the ten populations, which generated a total of 796 bands, of which 670 were polymorphic to give a total of 84% polymorphism. These data were then used to calculate a dendrogram by agglomerative clustering using the unweighed pair group method with average linkage (UPGMA). The support values for the degree of confidence at the nodes of the dendrogram were evaluated by bootstrap analysis. The dendrogram contained two distinct clusters, with little overlap between populations. The first cluster contained three Irish populations, one of the British populations and the Danish population. The second cluster contained one Irish, one British and the three Polish populations. Genetic diversity between populations of *G. fluitans* did not always correlate with geographical distances, but in some instances, geographical origin was significant.

INTRODUCTION

Glyceria fluitans (L.) R. Br. (floating sweetgrass) is a wetland grass, found in habitats such as ponds, canals, streams and marshes. It is found throughout Europe and extends into West Asia and North Africa. *G. fluitans* possesses constitutional tolerance to zinc (Matthews *et al.* 2004a). Constitutional tolerance to metals such as zinc has been found in several other species of wetland plants, including *Eriophorum angustifolium* and *Carex rostrata* (Matthews *et al.* 2004b, 2005). Previous work on zinc tolerance in *G. fluitans* from six locations from across Europe (England, Ireland, Denmark and Poland), collected from both metal-contaminated and non metal-contaminated sites found that plants were equally tolerant to elevated levels of zinc, regardless of prior exposure (Matthews *et al.* 2004a). Amplified Fragment Length Polymorphism (AFLP) was used to study these six populations of *G. fluitans* from the Atlantic Islands of Ireland and Britain. These six populations were compared with four populations from mainland Europe (Denmark and Poland).

MATERIALS AND METHODS

G. fluitans genotypes were collected from ten locations in 2002 (Figure 1). DNA was extracted from leaves of individual plants using a method based on that of Pich and Schubert (1993), using approximately 0.2g of leaf material. The AFPL protocol was carried out essentially as described by Vos *et al.* (1995). Pre-amplification was performed using six primer combinations; (*Eco*R1-AAG and *Mse*1-CAC, *Eco*R1-AAG and *Mse*1-CAC, *Eco*R1-AAG and *Mse*1-CTC, *Eco*R1-ACC and *Mse*1-CAC, *Eco*R1-ACC and *Mse*1-CAC, *Eco*R1-ACC and *Mse*1-CTC), with *Eco* R1 primers ^{33}P-labelled. The ^{33}P-labelled products were then separated by electrophoresis on a 6% polyacrymide gel and developed. The resulting autoradiograms were scanned and processed using GelCompare II software (Applied Maths, Sint-Martens-Latem, Belgium). Bands on the gel were scored as present (1) or absent (0). Gels were normalised by the alignment of 25 bp molecular weight markers. A matrix of genetic distances between genotypes, based on the number of shared amplification products was calculated using the metric of Nei and Li (1979). This data were then used to calculate a dendrogram by agglomerative clustering, using the unweighed pair group method with average linkage (UPGMA), with support values evaluated by bootstrap.

RESULTS

Sixty-five individuals from the ten locations were assayed using six selective primer combinations. In total, 796 bands (mean 132 bands per primer combination) were generated across all the *G. fluitans* genotypes. In total, 670 polymoprhic bands were scored, which gave a total of 84% polymorphism. Cluster analysis divided the sixty-five genotypes into two large groups (Figure 2). Cluster A contained the three Polish genotypes, the genotypes from Sommerset (UK) and Navan (Ireland). Cluster B contained the remaining Irish genotypes (Glendalough, Lough Dan and Djouce), and the genotypes from Thisted (Denmark) and Camborne (UK). The cluster analysis shows that genotypes from any given location are more closely related to themselves than to genotypes from other locations. In each case, genotypes from a particular location form distinct clusters. There were two exceptions; the first is an individual from Radostowo that is located at the top of cluster A. The second is an individual from Lough Dan, which is grouped with the Glendalough genotypes. This indicates greater variation between genotypes from different locations than within the genotypes from a single location. The dendrogram constructed with all individuals was generally supported by high bootstrap values.

DISCUSSION

The findings indicated that genetic distance was not solely dependent on geographical distance, although in some cases clustering reflects geographical relationships (Figure 2). For example, the cluster formed by the Glendalough and Lough Dan genotypes consisted of genotypes that are located in the Wicklow Mountains and are only about 20km distant from each other. They form a structured cluster, with some overlap between them. Two genotypes from Poland, from Bartniki and Chromotowo are in their own minor cluster. There are also other genotypes that did not group based on geographical proximity. For example, cluster A contains genotypes from the three Polish sites as well as genotypes from Navan, Ireland and Sommerset, UK. *G. fluitans* is an aquatic plant and as its seeds float, they could be dispersed by water. This could account for the similarities between the Glendalough and Lough Dan genotypes from Wicklow, which are geographically close together. A possible reason for the unexpected similarities between geographically distant genotypes may be the role of birds, which can spread seeds across wide distances. In a study on herbicide resistance in *Solanum nigrum,* it was found that resistant genotypes from Poland were more closely related to resistant genotypes from France than to other Polish genotypes (Stankiewicz *et al.* 2001). Migratory birds, such as *Turdus pilaris* and *Sturnus vulgaris* were found to be responsible for spreading seed across Europe. It is possible that birds could eat seeds of *G. fluitans* and spread them afterwards. This may explain similarities between genotypes from distant sites.

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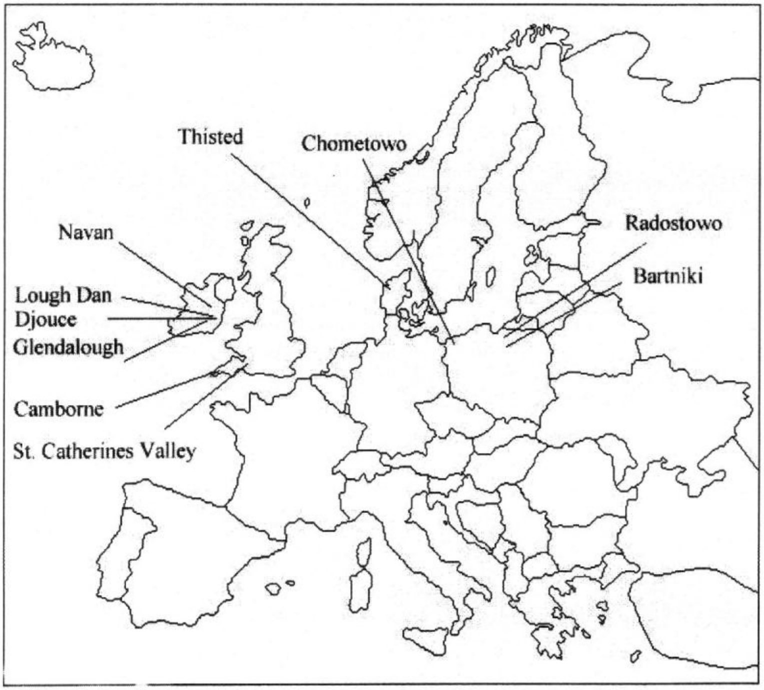

FIGURE 1. Map showing the different sites, where *G. fluitans* genotypes originated.

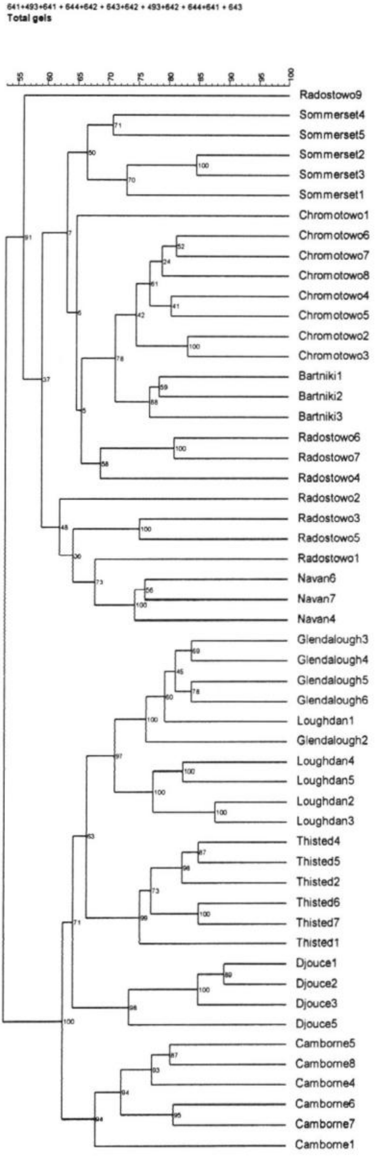

FIGURE 2. UPGMA dendrogram of the different individuals of *G. fluitans*.

FIELD COMPARISON OF TRANSECT, STATIONARY POINT COUNT AND VISUAL FAST COUNT METHODS FOR VISUAL ASSESSMENT OF FISH ASSEMBLAGES OF ROCKY HABITATS IN MADEIRA

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ABSTRACT

Fish assemblages of rocky boulder reefs of Madeira Island were assessed using a combination of visual survey techniques, including transect (T), stationary diver point count (PC) and visual fast count (VFC). The combination of the three methods provided a more complete list of species than each method alone. However, at most stations, the visual fast count method recorded an overall species list similar to that obtained by the combination of methods. Species composition, sighting frequency and relative abundance of all fishes observed were collected using the three methods. The VFC method was most efficient in terms of time spent relative to data collected; it recorded the greatest number of total species, and did so in fewer surveys. The use of PC and T methods should also be considered, since they provided density estimates and they also recorded some species missed by other methods, at most of the stations. Nonetheless, the use of both methods simultaneously was time consuming and

deemed unnecessary because of the paucity of additional data collected relative to time spent. PC or T (but not both) should be used to complement the VFC.

INTRODUCTION

Most studies of reef fish assemblages and population structure have focused on coral reefs (Alevizon & Brooks 1975, Brock 1979, Colton & Alevizon, 1981, Brock 1982, Bohnsack & Bannerot 1986). More recent studies started to address temperate reef fish assemblages (Jessee *et al.* 1985, Lindquist *et al.* 1985, Bell 1983, Harmelin 1987, Harmelin *et al.* 1995, Harmelin 1999) and fish communities on North Atlantic islands like the Canaries (Bortone *et al.* 1991b, Falcon *et al.* 1993), Azores (Azevedo 1997, Tempera 1998) and Madeira Island (Andrade & Albuquerque 1995, Delgado 1998). In fact, in the last decade, increased attention has been paid to shallow rocky habitats in temperate regions (Guidetti & Bussotti 2000).

Reef fish assemblages are difficult to sample due to the diversity, cryptic or nocturnal behavior and mobility of the fishes and the variety of microhabitats within complex reef substrates (Russel *et al.* 1978). Thus different methods have been used (Bortone *et al.* 1986, Bortone *et al.* 1991a) relying on either destructive or non-destructive inventory techniques. The applicability and limitations of the various techniques have been reviewed by several authors (Russel *et al.* 1978, Sale & Douglas 1981, Sale & Sharp 1983, Brock 1982, DeMartini & Roberts 1983, Kimmel 1985, Sanderson & Solonsky 1986). There are advantages and disadvantages to each technique, depending on the objectives of the survey. The choice of a technique is often a compromise between the biases of each method, the available time, the manpower, and the information being sought. Thus, a census method for a long-term monitoring program requires repeatability, accuracy, effective use of time, and provision of valid and comparable data to studies in other areas (Pattengill 1998).

SCUBA diving has greatly facilitated the collection and sampling of reef fishes, using the visual census techniques (VCTs). This development enhanced the research carried out on reefs, but is practically limited to depths less than 45 m (Gladfelter *et al.* 1980). The VCT was first used by Brock (1954) to count Hawaiian reef fishes and has subsequently been adopted by a number of workers. VCTs are the most frequently used non-destructive techniques for estimating reef (Sale 1980, Harmelin 1987) and seagrass fish communities (Barans & Bortone 1983), and have been widely adopted in shallow nearshore habitats with heterogeneous substratum such as coral, rock or artificial reefs (De Girolamo & Mazzoldi 2001). Although there have been numerous attempts to compare some methods (DeMartini & Roberts, 1983, Kimmel, 1985, Bortone *et al.* 1986, Sanderson & Solonsky 1986), there remains no clear consensus as to what method is the best for all or any specific set of conditions (Bortone *et al.* 1989).

The purpose of this study was to identify among three often used methods, which VCT best evaluates the structure of fish assemblages in inshore rocky habitats of Madeira Island. The results should be useful in the establishment of a suitable visual census method to use in monitoring such habitats.

METHODS

Study area

Surveys were conducted on rocky-boulder bottoms at three different areas of the South coast of Madeira Island (Figure1):

1 - Garajau Marine Reserve (**GMR**) - located between Cais do Lazareto and Ponta da Oliveira, GMR extends from the high-tide line to the 50m isobath and encompasses 376km^2.

2 - Artificial habitat of airport riprap (**AHAR**) – located in South coast (Santa Cruz), the airport construction led to the disappearance of an existing bay by the deployment of a riprap runway foundation made of rocky boulders that drop rapidly to a sand bottom at 14 –16m.

3 - Unprotected area of Caniçal (**UAC**) – is the far southeastern part of Madeira Island, with a coast formed by lava flows and the seafloor a typical rocky substrate such as that found around the island (rocky boulders, walls and platforms).

In each area visual counts were performed over rocky boulders within two similar depth strata (0-10m and 10-20m).

Survey methods

Three VCTs were used: the stationary diver technique (also referred as Point Count - **PC**) (Bohnsack & Bannerot 1986), a modification of the Kimmel method (1985) (referred as Visual Fast Count - **VFC**) and the Transect method (**T**) (Brock 1954, Brock, 1982, DeMartini & Roberts 1983, Davis & Anderson 1989) (Figure 2). Each dive consisted of three counts per method resulting in three dives per season in each area. A team of two divers performed the surveys, recording the observed species on a slate. The two same divers performed the counts, reducing estimates variability. Fish identification was done to the lowest recognizable taxon. After a complete survey, divers swam to the next sampling site and repeated the process.

Time-of-day

All data were collected during daylight (10:00 – 17:00 Local time) avoiding crepuscular periods when changes in population and community structure often occur (Colton & Alevizon 1981).

Data analysis

Data (number of species, H' diversity) generated by the three methods were compared. Analyses of variance (ANOVA), a multivariate approach, and two-way nested "Analysis of similarities" (ANOSIM) (Clarke & Warwick 2001) was used to determine if census methods were giving similar patterns in species composition. Presence/absence and fourth-root transformation on the raw data was used, before calculating a Bray-Curtis similarities matrix. The Sorensen similarity index, using presence-absence data, was calculated to compare the qualitative results of the VCTs. This index is identical to the Bray-Curtis index when the latter is calculated on presence/absence data (Clarke & Warwick 2001).

The utility of each method was also compared by examining how rapidly the cumulative number of species recorded reached an asymptote. Methods producing data that stabilized with less sampling effort were considered superior to other methods (Kimmel 1985, Bohnsack & Bannerot 1986).

The structure or relative importance of species within communities can be defined by measurements such as frequency of occurrence and numerical abundance. They provide distinct and useful characterizations of the fish assemblages, however we should note that they are complementary and not equivalent (DeMartini & Roberts 1983). So abundance of species was described by a measure of relative abundance (RA = pooled number of individuals of the i^{th} species from all surveys/the total number of all individuals in all surveys) x 100) and sighting frequency (SF = number of times a species was observed/total number of surveys) x 100). According to SF, species were classified into three categories (Schmitt & Sullivan 1996): frequent ($\geq$ 70%), common (70%<x>20%) and uncommon ($\leq$20%).

RESULTS

With the three methods a total of 45, 45 and 39 species was cumulated for GMR, UAC and AHAR respectively over the 2 year course of the study (Table 1). At all sites and in both depth strata, the VFC method accounted for significantly higher species richness than PC and T methods. There were significant differences between the VFC and the other two methods (one-way ANOVA, $p<0.001$) (Figure 3) but none between the latter two, for both average species overall and for each survey. The ANOSIM indicated differences in the observed fish assemblages between VFC and the PC and T. Comparison of densities estimates from PC and T revealed no significant differences.

Similarities in species composition were smaller at the shallow UAC (73%) and the maximum (93%) was found at the deep stratum of the airport riprap site (Table 2). This similarity range suggests a consistent level of faunal similarity for the assemblages sampled, regardless of the method used.

Unique species occurrences were mostly obtained by the VFC method. Actually 12-22% of the total species list was exclusively recorded by this method (Table 3), indicating that the VFC records a large number of species that would otherwise not be recorded. In the shallow stratum, the VFC recorded 15.8 % of the species that were not observed in the other two methods, while PC and T recorded 5.3% not observed in the VFC. For deep strata, 16.3% of the species recorded using the VFC were unique to that method, while the PC only recorded 2.3% of the species as unique to that method and the TM method recorded no unique species. This reveals the pronounced tendency of the VFC method to exclusively record some species, mainly cryptic species (e.g. *Apogon imberbis*, *Aulostomus strigosus*, *Scorpaena* sp., *Trigloporus lastoviza*), some sedentary species (e.g. *Epinephelus marginatus*, *Mycteroperca fusca* and *Parapristoma octolineatum*) and a few pelagic species like Mugillidae, *Bellone* sp., *Kyphosus sectator*, *Sarpa salpa*.

Among all species observed, frequency of sightings varied widely (Table 4). Only species like *Abudefduf luridus*, *Thalassoma pavo*, *Chromis limbata*, *Canthigaster capistrata*, had similar frequency of occurrence for the three methods. Species recorded as least common by one method, were not recorded at all by the two other methods (e.g. *A. imberbis*, *A. strigosus*, *Bellone* sp., *Sarda sarda*, *Scorpaena scrofa*). In other cases, species recorded as least common by one of the methods were actually more common according to another method and usually those species were more common according to the VFC method, even if they had been recorded as least common with PC and T methods (e.g. *Sphoroides marmoratus*, *Tripterigion delaisi* and *Scorpaena maderensis*). Generally species presented higher values of %SF with the VFC method, however correlations between %SF from each method were high (lowest $r= 0.81$, $n= 33$; $p>0.05$).

Frequently seen species were also usually more abundant while uncommon species tended to have lower abundance. However, frequency was not a good predictor of abundance because some pelagic schooling species were infrequently observed in large schools (e.g. *Atherina presbyter*, *Boops boops*). Uncommon species included rare, cryptic (e.g. *A. imberbis*, *A. strigosus*, *Myliobatis aquila* etc.) and pelagic transient reef visitors (e.g. *Balistes capriscus*, *Pseudocaranx dentex, Seriola* sp.). The present study revealed that the frequency observed depended on the sampling method used (Table 4).

The cumulative curves for the three techniques reached the asymptotic levels with few additional species being added as the number of observations reached 10 (Figure 4). The VFC method accumulated more species in fewer samples than PC and T, with 5 VFC surveys accumulating more than 50% of the total species list. PC and T showed a much slower but similar rise in the number of species recorded. Likewise VFC, the PC and T methods seemed to stabilize around the same number of surveys (10 to 14 surveys). The VFC method registered a higher number of species in all areas, ranging between 86-100% of the total species list observed in the rocky reefs after two years surveying. However this does not mean that the fishes censused account for 86-100% of the total fish fauna present on the sampling areas. PC and T tend to record similar number of species, censusing between 63 to 86% of the species.

DISCUSSION

The VCTs used in this study (PC, T and VFC) were complementary in characterizing the reef fish assemblages of rocky habitats of the south coast of Madeira island. The VFC method was better able to record the fish species present in a given area by free swimming over a large area. This allowed the observer to find a greater number of species in a shorter amount of time. The roving nature of the method also allowed surveys of a variety of habitats within a site (Schmitt & Sullivan 1996). Besides the restriction to a predefined area, PC and T method also have the disadvantage that species seen outside the corridor or outside the circle cannot be included. Those species are generally of three types: (1) solitary species that avoid diver's presence, staying away from the predefined area of a transect or point count (such as *A. imberbis*, *E. marginatus*; (2) species present in low numbers, less likely to be detected (e.g. *A. strigosus*, *G. thompsoni*, *M. aquila*) and (3) schooling species that may be abundant and never enter in the sampling area of the transect or point count (i.e. *Bellone* sp., Mugillidae, *P. dentex*, *S. salpa*).

The frequent species (such as *A. luridus*, *C. capistrata*, *C. limbata* and *T. pavo*) presented similar %RA and %SF for the three methods, whilst more rare and gregarious species (e.g. *M. fusca*, *S. maderensis*, *A. imberbis*, *A. strigosus*) had some differences. Actually %SF was greater with the VFC method and thus some uncommon species (e.g. *A. strigosus*, *A. imberbis*, *E. marginatus*, *G. thompsoni*, *Muraena augusti*) were better sampled by this method. Some researchers suggest that rare and uncommon species could be considered less important than common and abundant species. Nevertheless, when the goal is to characterize a biotope or compare biotopes, the rare species are the best to illustrate differences (Kimmel 1985) and also are important for ecological and conservation-related reasons (Goldsmith 1991).

The plots of cumulative species suggest that 10-14 surveys were necessary to provide an adequate species list. The VFC method was more efficient in accumulating species (higher number of species/survey) and therefore, was less time consuming. The three VCTs combined had costs in terms of time if all are conducted, but give more realistic fish counts. As noted by Kimmel (1985), the VFC method is more time-efficient than T and the present results showed the same in comparison to the PC. Also in agreement with the Kimmel (1985) results, the relative abundance obtained with the VFC were not different from that obtained by T and PC, thus the VFC had an efficient quantitative nature and represented an alternative to the combined visual methods. As also pointed out by the same author the reduction of the number and length of census interval on the VFC method is appropriate in areas with lower species richness such as the rocky coast of Madeira, relative to the Caribbean reef censused by Kimmel (1985). A measure or estimate of the area or volume of substrate surveyed, to produce absolute densities estimates, could improve the method. The VFC count method can easily be modified to meet this or other study objectives.

Through this survey study, the three visual census methods were used simultaneously to record species composition, abundance and length of fishes in the study areas. These aspects of the fish assemblages of the coastal rocky reefs of Madeira Island can continue to be compared over time but the results obtained indicate that the use of the three methods simultaneously is unnecessary. A combination of two would be appropriate to assess fish communities in rocky reefs of Madeira Island. The best combination includes the VFC method and one of the two density methods used (T or PC). The choice between T or PC depends on researcher preferences, familiarity with methods and specific study objectives.

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TABLE 1. Summary of the survey effort performed on the study areas between Spring 2002 and Winter 2004.

	shallow			deep		
N° of surveys	PC	T	VFC	PC	T	VFC
Caniçal unprotected area	34	33	34	32	33	33
Garajau marine reserve	35	35	35	35	35	35
Artificial habitat of Airport riprap	34	35	35	35	35	35
Area/survey (m2)						
Caniçal unprotected area	201.1	150	-	201.1	150	-
Garajau marine reserve	201.1	150	-	201.1	150	-
Artificial habitat of Airport riprap	201.1	150	-	201.1	150	-
Total area (m2)						
Caniçal unprotected area	6837	4950	-	6435	4950	-
Garajau marine reserve	7039	5250	-	7039	5250	-
Artificial habitat of Airport riprap	6837	5250	-	7039	5250	-
Time/survey (minute)						
Caniçal unprotected area	7.4	5.8	15	7.5	6.3	15
Garajau marine reserve	7.4	5.7	15	7.8	6.2	15
Artificial habitat of Airport riprap	7.3	5.7	15	8	6.7	15
Total time (minute)						
Caniçal unprotected area	248,2	98,6	510	125,8	108,8	255
Garajau marine reserve	248,5	98,6	525	132,6	105,4	255
Artificial habitat of Airport riprap	248,2	98,6	525	139,4	119	255
mean species /survey						
Caniçal unprotected area	7.3	7.4	11.1	8.3	8.5	13.6
Garajau marine reserve	7.5	6.2	11.5	8.8	8.7	15.8
Artificial habitat of Airport riprap	7.6	6.1	9.9	10.2	10.5	15.1
Total number of species						
Caniçal unprotected area	22	26	31	29	29	38
Garajau marine reserve	22	20	31	32	28	37
Artificial habitat of Airport riprap	25	23	33	32	28	37

FIGURE 1. – Fish surveys areas in the south coast of Madeira island (GMR – Garajau Marine Reserve, AHAR – Artificial habitat of airport riprap, UAC – unprotected area of Caniçal).

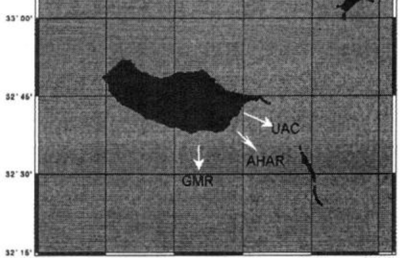


TABLE 2. Qualitative similarities (Sorensen index) among methods in the study areas.

Sampling stations	Methods	PC	T	VFC	
Artificial habitat of Airport riprap (AHAR)	Shallow	PC	1		
		T	0.92	1	
		VFC	0.84	0.84	1
	Deep	PC	1		
		T	0.93	1	
		VFC	0.93	0.86	1
Unprotected area of Caniçal (UAC)	Shallow	PC	1		
		T	0.79	1	
		VFC	0.83	0.73	1
	Deep	PC	1		
		T	0.89	1	
		VFC	0.87	0.81	1
Garajau Marine Reserve (GMR)	Shallow	PC	1		
		T	0.76	1	
		VFC	0.83	0.74	1
	Deep	PC	1		
		T	0.8	1	
		VFC	0.84	0.83	1

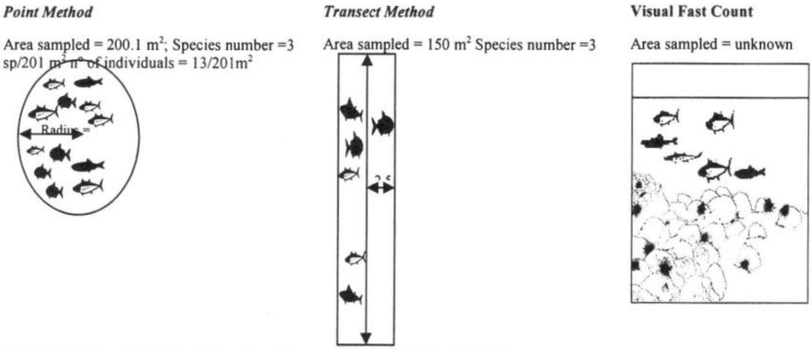


FIGURE 2. Schematic representation of the VCTs.

TABLE 3. Percentage of species that were exclusively recorded by each method on the reefs sampled.

% Exclusive records	Shallow			Deep		
	PC	T	VFC	PC	T	VFC
Artificial habitat of airport riprap	3	-	15	-	-	13.5
Unprotected area of Caniçal	-	14	22	-	5	20
Garajau marine reserve	-	3	15	-	2	12

Artificial Habitat of Airport Riprap

Family	Species	PC				T				VFC			
		Shallow		Deep		Shallow		Deep		Shallow		Deep	
		RA	SF	RA	SF	RA	SF	RA	SF	RA	SF	RA	SF
Aulostumidae	*Aulostomus strigosus* Wheeler, 1955	0.01	3	-	-	0.01	3	-	-	0.01	6	0.01	9
Apogonidae	*Apogon imberbis* (Linnaeus, 1758)	-	-	0.01	3	-	-	-	-	-	-	0.01	6
Atheriniidae	*Atherina presbyter* Cuvier, 1829	38.5	53	15.52	9	45.7	46	12.36	6	33.09	43	7	6
Ballistidae	*Ballistes carolinensis* Gmelin, 1788	0.06	18	0.11	14	0.12	9	0.12	17	0.04	11	0.08	29
Belonidae	*Belone* sp	-	-	0.3	3	-	-	-	-	0.02	3	0.01	3
Blennidae	*Indetermined*[b]	0.01	3			-							
	Ophioblennius atlanticus (Valenciennes, 1836)	2.44	94	0.03	6	2.97	91	0.09	17	2.53	94	0.14	57
Carangidae	*Pseudocaranx dentex* (Bloch & Schneider, 1801)	0.03	6	0.01	3	0.06	9	0.01	3	0.07	14	0.008	9
	Seriola sp	-	-	0.01	3	-	-	-	-	0.01	3	0.01	6
	Thachinotus ovatus (Linnaeus, 1758)	0.19	6	0.32	9	0.07	3	-	-	0.62	9	0.07	14
Haemulidae	*Pomadasis incisus* (Bowdich, 1825)	-	-	0.06	11	-	-	0.37	11	-	-	0.24	34
	Parapristoma octolineatum (Valenciennes, 1833)[a]	-	-	-	-	-	-	-	-	-	-	0.004	3
Labridae	*Thalassoma pavo* Linnaeus, 1758	16.45	100	9.03	97	29.1	100	12.21	97	22.09	97	9.84	100
Mugillidae	*Indetermined*	0.62	6	0.01	3	0.14	3	0.02	3	1.67	20	0.07	9
Mullidae	*Mullus surmuletus* Linnaeus, 1758	-	-	1.53	60	-	-	2.54	69	0.008	3	1.15	86
Muraenidae	*Muraena helena* Linnaeus, 1758	-	-	0.03	6	-	-	0.01	3	-	-	0.01	6
Pomacentridae	*Abudefduf luridus* (Cuvier, 1830)	7.9	100	7.1	100	12.8	97	9.3	100	11.9	100	7.4	100
	Chromis limbata (Valenciennes, 1830)	0.07	9	3.8	80	0.03	6	4.5	91	1.06	54	5.9	94
Priacanthidae	*Heteropriacantus cruentatus* (Lacepède, 1801)	-	-	0.01	3	-	-	0.01	3		-	0.006	6
Scaridae	*Sparisoma cretense* (Linnaeus,1758)	0.3	53	0.28	31	0.59	49	0.37	40	0.67	83	0.31	69
Scombridae	*Sarda sarda* (Bloch, 1793)	-	-	-	-	-	-	-	-		-	-	
Scorpaenidae	*Scorpaena maderensis* Valenciennes, 1833	0.03	3	0.08	14	0.04	9	0.06	11	0.04	6	0.09	46
Serranidae	*Mycteroperca fusca* (Lowe, 1836)	-	-	-	-	0.01	3	-	-	0.008	3	0..004	3
	Serranus atricauda Gunther, 1874	0.05	12	0.25	43	0.13	23	0.28	49	0.14	31	0.23	60
Sparidae	*Boops boops* (Linnaeus, 1758)	25.03	26	38.3	57	0.42	11	36.38	51	14.68	51	45.51	88
	Dentex gibbosus (Rafinesque, 1810)	-	-	0.38	31	-	-	0.34	37	0.002	3	0.33	57
	Diplodus cervinus (Lowe, 1810)	0.01	3	-	-	-	-	-	-	0.02	6	0.02	9
	Diplodus sargus (Linnaeus, 1758)	0.81	56	0.32	31	0.37	37	0.52	34	1.11	63	0.57	57
	Diplodus vulgaris (E. Geoffroy St.-Hilaire, 1817)	0.17	21	2.23	83	0.11	11	1.78	83	0.08	14	1.45	94
	Oblada melanura (Linnaeus, 1758)	6.35	68	17.09	60	5.83	51	15.52	60	7.48	89	16.46	86
	Pagellus acarne (Risso, 1827)	0.19	6			0.42	9			0.29	14		
	Pagellus erythrinus (Linnaeus, 1758)	-	-	0.01	3	-	-	0.01	3	-	-	0.05	20
	Pagrus pagrus (Linnaeus, 1758)	-	-	0.03	3	-	-	0.02	3	-	-	0.02	11
	Spondyliosoma cantharus (Linnaeus, 1758)	-	-	0.03	6	-	-	0.09	6	0.004	3	0.05	9
	Sarpa salpa (Linaneus, 1758)[a]	-	-	-	-	-	-	-	-	0.9	6	0.003	3
Synodontidae	*Synodus* sp	0.01	3	0.14	20	0.06	9	0.22	34	0.04	17	0.3	80
Sphyraenidae	*Sphyraena viridensis* (Cuvier, 1829)	0.03	3	0.06	3	-	-	0.01	3	0.05	17	0.005	3
Tetraodontidae	*Canthigaster capistrata* (Lowe, 1839)	0.16	24	1.04	94	0.1	17	1	77	0.3	57	0.9	94
	Sphoroides marmoratus (Lowe, 1839)	0.41	41	1.71	80	0.76	46	1.73	86	0.86	74	1.60	97
Trypterygiidae	*Tripterigion delaisi* Cadenat et Blache, 1971	0.05	12	0.11	20	0.13	20	0.11	23	0.14	34	0.06	26
	CUMULATIVE N° SPECIES		**25**		**32**		**23**		**28**		**31**		**37**

TABLE 4A. Total species list of reef fishes of Artificial Habitat of Airport Riprap. The list is in alphabetical order by family. Relative Abundance (RA) and Sighting frequency (SF) (%) values are given according each method in both stations sampled. Cases where the species was not recorded is indicated by (-), values of SF were colored for frequent species (dark grey - SF≥70%) and uncommon species (light grey - SF≤20%) and values not colored were the common species.

[a] - Species exclusively recorded by VFC method.

[b] – Species exclusively recorded by transect.

[c] – Species exclusively recorded by point count method.

Unprotected Area of Caniçal

Family	Species	PC				T				VFC			
		Shallow		Deep		Shallow		Deep		Shallow		Deep	
		RA	SF	RA	SF	RA	SF	RA	SF	RA	SF	RA	SF
Aulostumidae	*Aulostomus strigosus* Wheeler, 1955 [a]	-	-	-	-	-	-	-	-		-	0.01	3
Apogonidae	*Apogon imberbis* (Linnaeus, 1758)		-	0.04	9	-	-	0.02	6	0.003	3	0.12	33
Atheriniidae	*Atherina presbyter* Cuvier, 1829	3.34	3	21.9	6	3.9	3	23.9	6	6.7	6	0.01	3
Ballistidae	*Ballistes carolinensis* Gmelin, 1788	-	-	0.01	3	-	-	-	-	0.005	3	0.03	12
Belonidae	*Belone* sp[a]	-	-	-	-	-	-	-	-	0.007	3	0.13	3
Blennidae	*Ophioblennius atlanticus* (Valenciennes, 1836)	0.03	6	-	-	0.04	6	-	-	0.05	15	0.005	3
Carangidae	*Pseudocaranx dentex* (Bloch & Schneider, 1801)	-	-	0.11	9	0.5	3	0.96	3	0.006	3	0.43	6
	Thachinotus ovatus (Linnaeus, 1758)	-	-	0.04	13	-	-	-	-	-	-	1.1	6
Clupeidae	*Indetermined*[a]	-	-	-	-	-	-	-	-	3.36	6	-	-
Gobiidae	*Gnatholepis thompsoni* Jordan, 1904	0.07	12	0.02	6	0.07	12	0.02	6	0.1	44	0.09	30
	Indetermined[b]	-	-	-	-	-	-	0.01	3	-	-	-	-
Haemulidae	*Pomadasis incisus* (Bowdich, 1825) [a]	-	-	-	-	-	-	-	-	-	-	0.04	12
	Parapristoma octolineatum (Valenciennes, 1833)[b]	-	-	-	-	0.01	3	-	-	-	-	-	-
Labridae	*Coris julis* (Linnaeus, 1758)	0.02	3	-	-	-	-	0.05	9	0.02	6	0.03	12
	Centrolabrus trutta (Lowe, 1833)[b]	-	-	-	-	0.01	3						
	Pseudolepidaplois scrofa (Valenciennes, 1839)	-	-	0.03	9	0.01	3	0.05	12	0.004	3	0.06	27
	Thalassoma pavo Linnaeus, 1758	6.43	[illegible]	1.59	78	6.36	[illegible]	2.17	[illegible]	10.35	[illegible]	5.79	[illegible]
Myliobatidae	*Myliobatis aquila* (Linnaeus, 1758)[b]	-	-	-	-	0.03	3	-	-	-	-	-	-
Mugillidae	*Indetermined*	0.1	3	-		-	-	-	-	0.01	3	-	-
Mullidae	*Mullus surmuletus* Linnaeus, 1758	0.08	12	0.27	22	0.1	22	1.12	67	0.26	[illegible]	1.64	[illegible]
Muraenidae	*Muraena helena* Linnaeus, 1758[b]	-	-	-	-	0.01	3	-	-	-	-	-	-
Pomacentridae	*Abudefduf luridus* (Cuvier, 1830)	15.97	[illegible]	6.76	[illegible]	18.23	[illegible]	9.14	[illegible]	17.51	[illegible]	10.11	[illegible]
	Chromis limbata (Valenciennes, 1830)	19.1	[illegible]	26.89	[illegible]	16.46	[illegible]	39.35	[illegible]	22.61	[illegible]	34.4	[illegible]
Scaridae	*Sparisoma cretense* (Linnaeus, 1758)	0.4	38	0.5	53	0.37	42	0.66	[illegible]	0.59	[illegible]	1.35	[illegible]
Scombridae	*Sarda sarda* (Bloch, 1793)	-		0.02	3	-	-	-	-	-		0.01	3
Scorpaenidae	*Scorpaena maderensis* Valenciennes, 1833	0.08	15	0.2	41	0.05	12	0.24	33	0.15	50	0.14	42
	Scorpaena scrofa Linnaeus, 1758[a]	-	-	-	-	-	-	-	-	-	-	0.004	3
Serranidae	*Mycteroperca fusca* (Lowe, 1836)	-	-	0.16	25	-	-	0.11	18	0.01	3	0.19	48
	Serranus atricauda Gunther, 1874	0.03	6	0.25	25	-	-	0.05	12	0.04	15	0.09	24
Sparidae	*Boops boops* (Linnaeus, 1758)	43.56	29	26.1	50	47.23	33	7.1	30	28.87	29	20.19	64
	Dentex gibbosus (Rafinesque, 1810)	-	-	0.04	13	0.03	6	0.14	15	-	-	0.08	18
	Diplodus cervinus (Lowe, 1810)	0.05	9	0.01	3	0.03	6	0.17	6	0.04	12	0.06	18
	Diplodus sargus (Linnaeus, 1758)	0.75	32	0.58	25	0.62	39	0.75	15	1.31	50	1.36	49
	Diplodus vulgaris (E. Geoffroy St.-Hilaire, 1817)	0.17	15	6.51	[illegible]	0.59	27	6.82	[illegible]	0.71	56	10.33	[illegible]
	Oblada melanura (Linnaeus, 1758)	6.08	21	6.12	22	3.17	36	4.99	24	1.78	41	8.18	51
	Pagellus erythrinus (Linnaeus, 1758)	-	-	0.02	3	-	-	0.01	3	0.02	6	0.06	21
	Pagrus pagrus (Linnaeus, 1758)	-	-	0.01	3	-	-	0.04	6	-	-	0.005	3
	Spondyliosoma cantharus (Linnaeus, 1758)	0.07	3	0.05	6	0.2	3	0.13	12	0.21	3	0.15	15
Synodontidae	*Synodus* sp	0.18	32	0.33	41	0.17	27	0.1	24	0.54	[illegible]	0.36	[illegible]
Sphyraenidae	*Sphyraena viridensis* (Cuvier, 1829) [a]	-	-	-	-	-	-	-	-	-	-	0.03	6
Tetraodontidae	*Canthigaster capistrata* (Lowe, 1839)	1.85	[illegible]	1.19	[illegible]	1.21	[illegible]	1.54	[illegible]	2.21	[illegible]	2.14	[illegible]
	Sphoroides marmoratus (Lowe, 1839)	0.72	61	0.15	31	0.55	61	0.26	36	1.34	[illegible]	0.62	[illegible]
Triglidae	*Trigloporus lastoviza* (Brunnich, 1768) [a]	-	-	-	-	-	-	-	-	0.006	3	0.01	6
Trypterygiidae	*Tripterigion delaisi* Cadenat et Blache, 1971	0.9	59	0.07	19	0.43	42	0.12	24	1.11	[illegible]	0.58	[illegible]
Uranoscopidae	*Uranoscopus scaber* Linnaeus, 1758 [a]	-	-	-	-	-	-	-	-	-	-	0.007	3
CUMULATIVE N° SPECIES			**22**		**29**		**26**		**28**		**31**		**37**

TABLE 4B. Total species list of reef fishes of Unprotected Area of Caniçal. The list is in alphabetical order by family. Relative Abundance (RA) and Sighting frequency (SF) (%) values are given according each method and in both stations sampled. Cases where the species was not recorded is indicated by (-), values of SF were colored for frequent species (dark grey - SF≥70%) and uncommon species (light grey - SF≤20%) and values not colored were the common species. [a] - Species exclusively recorded by VFC method. [b] – Species exclusively recorded by transect. [c] – Species exclusively recorded by point count method.

Garajau Marine reserve

Family	Species	PC Shallow RA	PC Shallow SF	PC Deep RA	PC Deep SF	T Shallow RA	T Shallow SF	T Deep RA	T Deep SF	VFC Shallow RA	VFC Shallow SF	VFC Deep RA	VFC Deep SF
Aulostumidae	*Aulostomus strigosus* Wheeler, 1955 [a]	-	-	-	-	-	-	-	-		-	0.005	3
Apogonidae	*Apogon imberbis* (Linnaeus, 1758)[a]	-	-	-	-	-	-	-	-		-	0.003	3
Ballistidae	*Ballistes carolinensis* Gmelin, 1788	0.02	3	0.03	6	-	-	0.02	6	0.03	11	0.05	17
Belonidae	*Belone* sp[a]	-	-	-	-	-	-	-	-	0.11	3		-
Blennidae	*Ophioblennius atlanticus* (Valenciennes, 1836)	0.75	51	-	-	0.37	31	-	-	0.52	66	0.006	6
Bothidae	*Bothus podas* (Delaroche, 1809) [a]	-	-	-	-	-	-	-	-	0.004	3		-
Carangidae	*Pseudocaranx dentex* (Bloch & Schneider, 1801)	0.94	3	-	-	-	-	-	-	0.02	3	0.009	3
	Seriola sp[c]	-	-	0.01	3	-	-	-	-		-		-
	Thachinotus ovatus (Linnaeus, 1758)[c]	-	-	0.01	3	-	-	-	-		-		-
Gobiidae	*Gnatholepis thompsoni* Jordan, 1904	-	-	0.01	3	-	-	0.01	3		-	0.03	14
	Mauligobius maderensis (Valenciennes, 1837)[c]	0.06	6	-	-	-	-	-	-		-		-
Haemulidae	*Pomadasis incisus* (Bowdich, 1825)	-	-	0.06	9	0.02	3	0.16	11		-	0.22	46
Kyphosidae	*Kyphosus sectator* (Linnaeus, 1766)[a]	-	-	-	-	-	-	-	-	0.01	3		-
Labridae	*Coris julis* (Linnaeus, 1758)	0.02	3	0.06	6	-	-	0.05	9	0.02	6	0.1	37
	Pseudolepidaplois scrofa (Valenciennes, 1839)	0.02	3	0.13	26	-	-	0.1	23	0.006	3	0.09	31
	Thalassoma pavo Linnaeus, 1758	21.33	[illegible]	5.48	89	21.20	97	5.6	94	25.6	97	9.65	100
Myliobatidae	*Myliobatis aquila* (Linnaeus, 1758)	-	-	-	-	0.02	3	-	-	0.02	6		
Mugillidae	*Indetermined*[a]	-	-	-	-	-	-	-	-			0.004	3
Mullidae	*Mullus surmuletus* Linnaeus, 1758	-	-	1.05	20	0.02	3	1.2	26	0.05	20	0.48	46
Muraenidae	*Enchelycore anatina*(Lowe, 1837)	0.02	3	-	-	-	-	-	-	0.01	3	0.003	3
	Gymnothorax unicolor (Delaroche, 1809)[b]	-	-	-	-	-	-	0.01	3		-		-
	Muraena Augusti (Kaup, 1856)[a]	-	-	-	-	0.04	6	0.01	3	0.01	6	0.004	3
Pomacentridae	*Abudefduf luridus* (Cuvier, 1830)	34.67	100	10.69	100	42.88	100	14.26	100	31.89	100	12.5	100
	Chromis limbata (Valenciennes, 1830)	31.69	[illegible]	56.27	94	25.63	74	61.31	100	25.35	97	52.71	100
Priacanthidae	*Heteropriacantus cruentatus* (Lacepède, 1801)	-		-	-	-	-	0.01	3			0.08	23
Scaridae	*Sparisoma cretense* (Linnaeus, 1758)	2.9	[illegible]	0.42	51	3.16	71	0.53	51	4.3	94	1.06	97
Scombridae	*Sarda sarda* (Bloch, 1793)[c]	-	-	0.08	3	-	-	-	-				
Scorpaenidae	*Scorpaena maderensis* Valenciennes, 1833	0.33	31	0.18	23	0.12	14	0.17	26	0.21	46	0.21	60
Serranidae	*Epinephelus marginatus* (Lowe, 1834)[a]	-	-	-	-	-	-	-	-		-	0.004	3
	Mycteroperca fusca (Lowe, 1836)	-	-	0.04	9	-	-	0.08	17	0.01	3	0.06	29
	Serranus atricauda Gunther, 1874	0.75	66	0.84	80	0.41	40	0.74	74	0.92	86	1.1	86
Sparidae	*Boops boops* (Linnaeus, 1758)	2.35	3	16.96	20	0.21	9	9.58	17	1.06	9	11.3	34
	Dentex gibbosus(Rafinesque, 1810)	0.09	9	0.18	14	-	-	0.11	14	0.02	9	0.13	40
	Diplodus cervinus(Lowe, 1810)	-	-	0.22	23	-	-	0.08	17	0.05	14	0.18	37
	Diplodus sargus (Linnaeus, 1758)	0.05	6	0.07	14	0.08	6	0.13	11	0.85	29	0.22	40
	Diplodus vulgaris (E. Geoffroy St.-Hilaire, 1817)	0.66	20	3.19	54	2.34	37	2.87	51	3.13	[illegible]	3.73	89
	Oblada melanura (Linnaeus, 1758)	0.14	6	1.36	11	1.05	6	1.04	11	0.52	31	2.43	37
	Pagellus erythrinus(Linnaeus, 1758)	-	-	-	-	-	-	0.01	3		-	0.05	14
	Pagrus pagrus (Linnaeus, 1758)	0.28	34	0.22	23	0.1	14	0.24	23	0.12	34	0.36	71
	Spondyliosoma cantharus (Linnaeus, 1758)	-	-	0.51	6	-	-	-	-		-	0.13	3
	Sarpa salpa (Linaneus, 1758)[a]	-	-	-	-	-	-	-	-	0.96	14	0.31	11
Synodontidae	*Synodus* sp	0.05	6	0.04	9	0.05	9	0.08	20	0.55	60	0.2	69
Sphyraenidae	*Sphyraena viridensis* (Cuvier, 1829)	-	-	0.03	6	-	-	-	-		-	0.09	11
Tetraodontidae	*Canthigaster capistrata* (Lowe, 1839)	1.64	[illegible]	1.53	[illegible]	1.54	[illegible]	1.37	[illegible]	2.29	[illegible]	1.96	100
	Sphoroides marmoratus (Lowe, 1839)	0.54	34	0.08	11	0.33	29	0.21	26	0.93	[illegible]	0.28	[illegible]
Trypterygiidae	*Tripterigion delaisi* Cadenat et Blache, 1971	0.75	40	0.21	34	0.43	37	0.11	11	0.47	57	0.18	54
CUMULATIVE N° SPECIES			**23**		**29**		**20**		**28**		**31**		**37**

TABLE 4C. Total species list of reef fishes of Garajau Marine Reserve. Legend continued on next page.

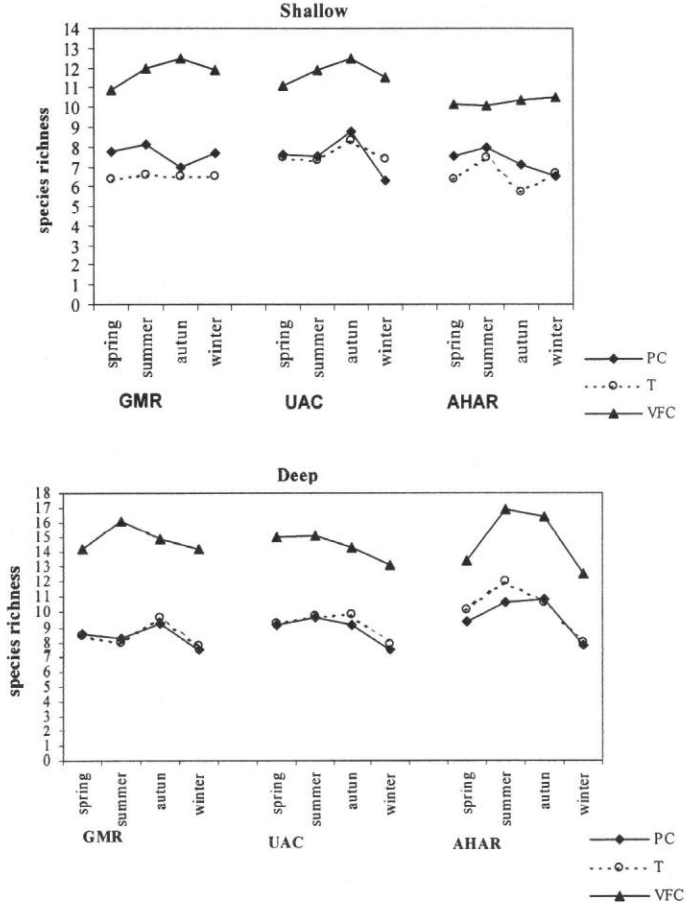
TABLE 4C (continued). Total species list of reef fishes of Garajau Marine Reserve. The list is in alphabetical order by family. Relative abundance (RA) and Sighting frequency (SF) (%) values are given according each method and in both stations sampled. Cases where the species was not recorded is indicated by (-), values of SF were colored for frequent species (dark grey - SF≥70%) and uncommon species (light grey - SF≤20%) and values not colored were the common species.

[a] - Species exclusively recorded by VFC method.

[b] – Species exclusively recorded by transect.

[c] – Species exclusively recorded by point count method.

FIGURE 3. Mean species richness at shallow and deep sites in the three study areas in each season according to the VCT used.



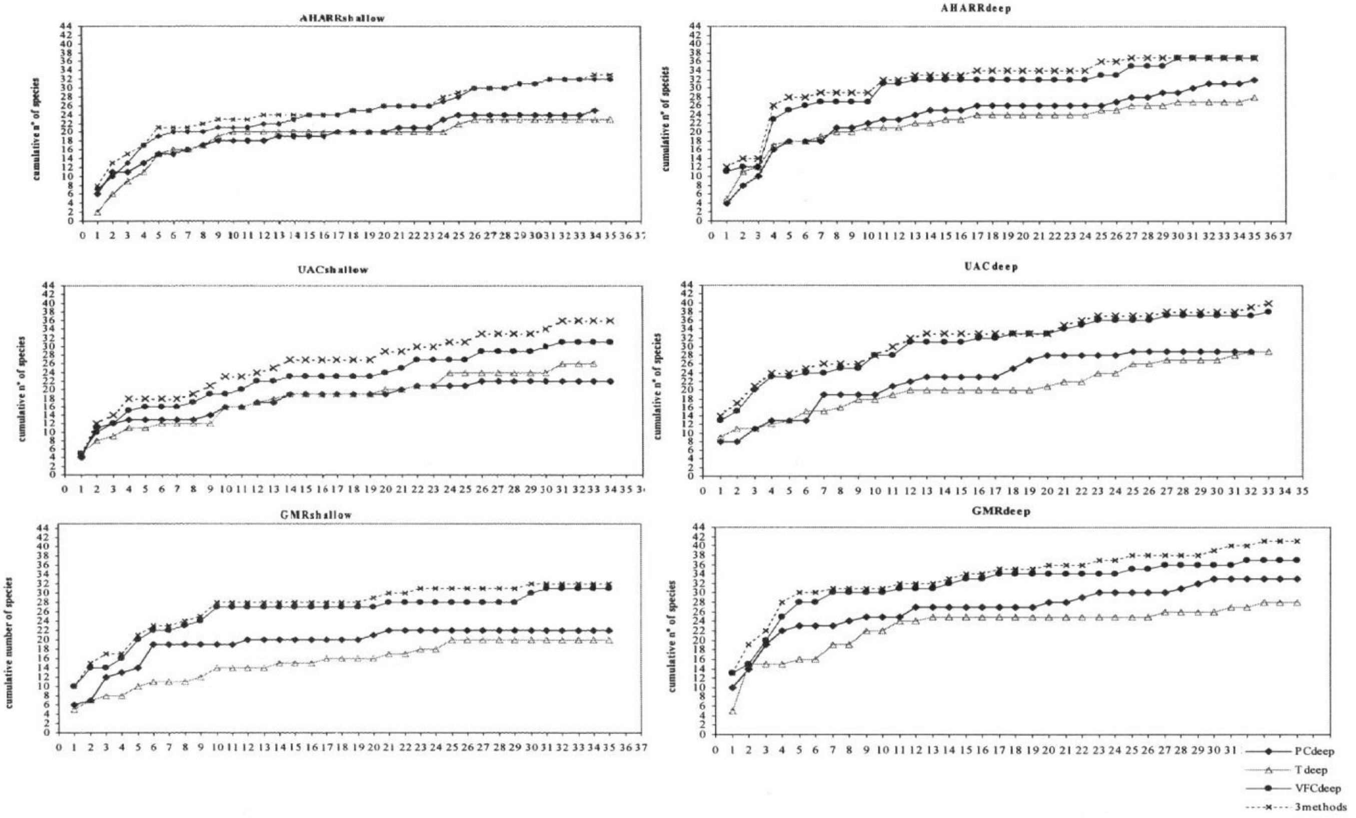


FIGURE 4. Species observation curves for the three methods in both shallow and deep water.

INTRODUCED PLANTS AND THE REDUCTION OF INDIGENOUS PLANT POPULATIONS IN THE AZORES ISLANDS

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ABSTRACT

The nine Azorean islands have today an estimated flora of 1000 vascular plant species and 430 bryophytes. One third of the fanerogams are native species; 65 species are endemic to the Azores or to the Macaronesian island groups. Several of these precious species are now more or less endangered. This is also the case for several of the endemic bryophytes. The survival of the Azorean native plants depends on available ecosystems, where suitable environmental conditions prevail. Their survival also depends on the numbers and sites of populations. Few and small populations become susceptible to loss of genetic variation and consequently the environmental range of such species will decrease.

INTRODUCTION

The number and size of Azorean sites with native plant communities have progressively decreased since the colonization of the islands by man. However, the decrease has become considerably more pronounced during the last century. Large areas on the islands have become transformed into grazing land and for the cultivation of alien tree species, such as *Cryptomeria japonica* and *Eucalyptus globulus*. All remote islands and island groups are very much susceptible to introduction of non-native plants and animals. Some species are not able to compete with native species and do not become incorporated into the native plant communities; but unfortunately several species may develop to become an imminent threat.

A few examples of the most successful introduced species in the Azores are given below. They were all deliberately introduced to the islands and have become favoured by different sorts of land use.

INVASIVE PLANTS IN THE AZORES

The fast-growing Australian *Pittosporum undulatum* was introduced to the Azores in the beginning of the twentieth century, principally to be used for plantation of hedges to protect crops from salty winds. *P. undulatum* has escaped and is now firmly established on all the Azorean islands, especially on lava flows up to about 500m of altitude. This species has successfully invaded the native coastal *Myrica faya - Picconia azorica* shrub community and is still expanding its range e.g. on abandoned fields. The former cutting of *P. undulatum* for fuel decreased when gas was introduced as stove fuel. Most of the Azorean islands have lost their typical native coastal plant communities, now occupied by the invasive *P. undulatum*.

A still more invasive plant has been *Hedychium gardnerianum* (Zingiberaceae) originating in the Himalayas. This plant was introduced, also about 100 years ago, but as an ornamental species. It is a rhizomatous perennial herb with stems up to 2m high. Where *H. gardnerianum* has invaded e.g. in open grassland and in ravines, it has no competitors. It occurs over large areas on all nine of the Azorean islands and is especially a threat to the native *Juniperus brevifolia - Laurus azorica* forest. Thinning and cutting of these slow-growing forests is generally followed by an irreversible colonization by *H. gardnerianum*. The so-called Ginger Lily is also a fast invader of newly cut *Cryptomeria* stands, making recuperation by native forest species impossible.

Such an invasion also renders new plantation of *Cryptomeria* difficult and costly.

The Brazilian *Lantana camara*, nowadays present in all tropical regions and looked upon as one of the most dangerous invasive species in the world, has unfortunately become an appreciated ornamental plant, deliberately spread along roads. *L. camara* has locally invaded surrounding vegetation over a wide altitudinal range. This invasion continues today.

A comparatively recent invasion of the South American *Gunnera tinctoria* has occured on the island of Sao Miguel. This peculiar species of the family Haloragaceae can grow to at least 1m tall. It was originally cultivated in a botanical garden, from where it suddenly escaped and spread vigorously over large grassland areas. It is now also invading ravines and sites with native forests. The plant is a nitrogen-fixer and is consequently able to invade very poor soil where *Sphagnum* bryophytes are dominant. *G. tinctoria* creates thousands of sticky seeds on every infloresence. Preventing this plant from spreading to other Azorean islands should be a priority.

A far-reaching transformation of the Azorean landscape and its native vegetation began a little more than 100 years ago when the Southeast Asian conifer tree *Cryptomeria japonica* was introduced, mainly for timber production. This conifer has optimal growing conditions in the Azores, from the coast at sea-level up to about 700m of altitude. It was planted in dense stands, generally after cutting of native forests. The growth is exceptionally fast and the trees become ready for harvest in many sites after only 15 years. *Cryptomeria* became a favoured alternative to cultivation of slowly growing *Pinus* species.

New plant species that spontaneously arrive among native vegetation on remote islands face several obstacles in order to become established. Competition from environmentally well-adapted native plant species is difficult to overcome. However, the deliberate import of new species may in some cases be successful, especially if accompanied by changes of land use. In the Azores, cultivation of *C. japonioca* became possible after cutting of native forests. *H. gardnerianum* readily became a pest on the islands in newly created grazing land and where native forests were cut for fuel and timber. Some deliberately planted plants in gardens and along roads unfortunately also became successful invaders in native plant communities. This happened where new successional stages were created with not very strong competition from native species. The harvest of topsoil from grasslands on the island of Sao Miguel for cultivation of pineapple in greenhouses, provided space for the invasion of *G. tinctoria*. The decline in the use of *P. undulatum* as a fuel considerably favoured the spread of this species in coastal areas in the Azores.

BRYOPHYTES

Bryophytes are important components on all substrates in the native Azorean plant communities. Highly diversified moss-carpets on soil and on living and dead trunks provide substrates for colonization by herbs and ferns in later successional stages. It should be stressed that studies of the bryoflora and bryovegetation of the Azores are exceptionally valuable due to presence of endemic species and the richness of different plant geographical components (Sjoegren 2001). Some of the Azorean species occur as European relicts only in Ireland and sporadically in England (Stewart 1995). Some species are outposts forming links between Macaronesia and S. America (Sunding 1979). The progressive changes in land-use and the introduction of alien plant species to the Azores naturally influence indirectly the survival of numerous bryophyte species, making several endangered. Several might even face extinction.

Only the Azores in Europe has got epiphyllous bryo-communities. Hepatics with very narrow ecological ranges predominate as epiphytes. They disappear from cleared sites in native forests, where introduced vascular plants now hinder the recolonisation of native tree species. Epiphyllous hepatics need stable environmental conditions, particularly high relative humidity and efficient shelter. Their presence also depends on available preferred substrates, namely fronds of ferns and leaves of evergreen trees such as *Laurus* and *Ilex*. Ferns such as *Trichomanes*, *Hymenophyllum*, *Elaphoglossum* and *Phyllitis* are most frequently colonized. They occur preferentially in dark, moist sites in the cloud-zone forests. Stands of these *Juniperus-Laurus* forests at 600-800m have now been found to require a minimum area of one hectare in order to provide suitable environmental conditions and phorophytes for epiphyllous bryophyte communities.

Studies of the bryoflora and bryovegetation of the Azores islands reveal an unusual stability and resistance to invasive bryophyte species. For example, there are several species that have been restricted for many years to only a few of the islands, although suitable habitat conditions prevail over large areas on nearby islands. Furthermore, there are several oceanic species, common on the European continent, which are still extremely rare or even absent in the Azores (or at least still not recorded).

A rise of the bryophyte diversity in the Azores has only taken place in ruderal sites and the species responsible are generally more or less cosmopolitan ones. Only the calcicolous species of the Pottiaceae family are frequent and rapid invaders, such as on newly constructed cement walls. They occur on calcareous soil and stone mainly on the island of Santa Maria.

Long-distance dispersal by wind of diaspores of bryophytes and establishment on the remote islands of the Azores is currently unlikely. A supply of diaspores to the Azores does probably occur continuously but the main problem is the inability of new species to become established and to compete with already firmly established taxa. At least an intrusion into the native forest communities, on various substrates, is unlikely. However, the creation of new ecosystems, where highly-invasive introduced vascular plants dominate, may create environmental conditions not formerly available which may be susceptible to a spontaneous invasion of alien bryophytes.

Observations on invasive plants between 1995-2004 in the Azores give the following information. The occupation of sites by *H. gardnerianum* and *P. undulatum* is almost stabilized, with hardly any possibility for recuperation of native forest communities. Areas planted with *C. japonica* have not increased very much after the laborious new plantations in the 1970s. *G. tinctoria* is still spreading and *L. camara* is still being planted and is locally spreading into the native vegetation.

A few recently spreading plants that do not originally belong to the Azorean native flora have been observed. The coastal endemic *Festuca petraea* community suffers from spontaneous invasion by *Carpobrotus edulis* (Aizoaceae) and *Cyrtomium falcatum* (Dryopteridaceae). Both species were originally introduced for ornamental purposes. *Polygonum capitatum* from the Himalayas is vigorously spreading in strongly exposed sites along roads and on lavaflows. *Clethra arborea* (Clethraceae) is spreading rapidly in the eastern part of Sao Miguel, where it was originally introduced into gardens. The spread started spontaneously in the 1960s and the author made a few records in the Pico da Vara region at that time. The "Lily Tree" is probably a very old member of the laurel forests of Madeira. *Hydrangea macrophylla* (Hydrangeaceae), with its origin in Japan, was used for creation of hedges around grazing land. This plant is strongly invasive in abandoned fields and in river-ravines. Altogether, those plants that in the Azores of today primarily form the view of the landscape and are attractive as beautiful flowers do not belong to the native flora of the islands (Sjoegren 2000). They were imported from widely separated parts of the world, as Japan, India, China, Australia, South America and South Africa.

ACTION

1) There is an urgent need for the creation of an immigrant office for control of all introduced alien plants. This is to reduce the probability of introduction of diaspores in the soil accompanying ornamental flowers.
2) Abolition of plantation of alien tree species at altitudes above 600m is recommended in order to save the few relicts of native forests.
3) Rapid replantation of harvested stands of alien tree species with native species in order to check the invasion of invasive alien species, especially *H. gardnerianum*.

4) Translocation of native plants from one island to another should be discouraged in order to prevent loss of between-island genetic variation.
5) Stands of cloud-zone forest however small, and particularly in river ravines and caldeiras, should be protected. These offer suitable habitats for the survival of endemic plants.

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ANTHROPOGENIC SUCCESSION IN *JUNIPERUS BREVIFOLIA* FORESTS ON TERCEIRA ISLAND (AZORES)

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ABSTRACT

We addressed the following questions regarding anthropogenic succession on *Juniperus brevifolia* forests in Terceira Island. Do successional pathways depend on substrate features, namely geology? Do tree species differ in abilities to establish and persist in the recovering vegetation? Are there irreversible thresholds that prevent disturbed vegetation from spontaneously returning to the original state? Ten 25m^2 plots were implemented in areas subjected to different degrees of disturbance by livestock. Data on floristic composition, vegetation biovolume, structure and demography were collected. Two successional pathways were identified: in areas with pumice downfall deposits, *Calluna vulgaris* is the main colonist; on younger lava substrates, without pumice deposits, the main colonist is *Erica azorica*. *Juniperus brevifolia* is a good gap colonizer and establishes early in the succession, becoming successively the dominant shrub and canopy species. *Laurus azorica* and *Ilex perado* ssp. *azorica* seedlings appear mostly when there is already a *Juniperus brevifolia* canopy present. Spontaneous return to the original vegetation seems possible even in those areas where trees were completely removed.

KEYWORDS: secondary succession, geology, disturbance, regeneration, ecological restoration.

INTRODUCTION

Livestock rearing is one of the most important economic activities of the Azores Islands. The consequence of this fact is a growing pressure on natural areas, which suffer different levels of anthropogenic disturbance. Some of these disturbed areas are close to natural areas and became part of protected sites, namely Sites of Community Importance for the NATURA 2000 Network (Dias *et al.* 2004). Information about human-induced vegetation changes is essential to understand invasion of exotics, changes in natural regeneration and for application in management practices (González-Espinosa *et al.* 1991; Miles 1987). In the Azores, the knowledge of secondary successions for conservation purposes is even more important since these islands have unique ecological processes, some of them related to vegetation dynamics (Elias & Dias 2004).

MATERIALS AND METHODS

The Azores are composed of nine Islands, divided in 3 groups: Western (with two islands), Central (five islands) and Eastern (two islands). The study area is located in the centre of Terceira (one of the central islands) (38°44'N; 27°12'W), in one of the largest natural vegetation sites of the Azores, which is part of the Site of Community Importance of Santa Bárbara and Pico Alto (NATURA 2000 Network). Several lava domes and coulées dominate the landscape and the emission from these volcanic structures (which are often preceded by explosive events) has produced two main geologic substrates: young rocky (trachyte) substrates and older substrates with pumice downfall deposits (Self 1976). Endemic *Juniperus brevifolia* (Seub.) Antoine (Cupressaceae) forests (Elias & Dias 2004) occupy most of the area but their distribution has been reduced in recent years due to cutting by local farmers. These forests are now protected but ecological restoration will be needed in order to repair the disturbed areas.

Areas subjected to different degrees of disturbance by livestock were selected. Ten 25m^2 plots were implemented in two different substrate types: PPL (I, II, III, IV) and F, in rocky substrates, PS (I, II, III, IV) and PMO in pumice downfall deposits. The height and width of every adult plant, and number of seedlings and saplings of the tree species, were measured. Plant biovolume (volume occupied by plant species in the plots) was determined by assuming that the canopy shape is similar to a cylinder, and calculating the volume of that cylinder. The height distribution of the biovolume was analysed in order to determine the vertical structure of the vegetation. A PCA analysis, using the CANOCO program (ter Braak & Šmilauer 1998), was conducted in order to determine the position of the plots along the succession gradient.

RESULTS

The eigenvalues of the two axes in the PCA ordination were 0.497 and 0.213, for axis one and two, respectively. Together the two axes explained 71.1% of variance in the data (Figure 1). The positive extreme of axis 1 was associated with late succession tree species: e.g. *Ilex perado* Ait. ssp. *azorica* (Loes.) Tutin (Aquifoliaceae), *Laurus azorica* (Seub.) Franco (Lauraceae) and *Juniperus brevifolia*. The negative side of that axis was defined by *Calluna vulgaris* (L.) Hull (Ericaceae) and several species of grasses e.g. *Holcus lanatus* L. (Poaceae), *Agrostis castellana* Boiss. et Reut. (Poaceae) and *Danthonia decumbens* (L.) DC. (Poaceae).

These results indicate that axis 1 is associated with the level of disturbance, with the less disturbed plots on the positive side. Axis 2 is probably associated with soil water accumulation since *Erica azorica* Hochst. ex. Seub. (Ericaceae), a typical species of drier areas, is situated in the positive extreme, and *Sphagnum palustre* L. (Sphagnaceae) and *Eleocharis multicaulis* (Sm.) Desv. (Cyperaceae) (dominant species in peat bogs) appear on the opposite side.

With the exceptions of PPLI, PSI, PMO and F, there was a separation along axis 2 of the plots according to the geologic substrate. Thus, it seems clear that pumice downfall deposits are associated with wetter conditions where *Calluna vulgaris* is the dominant species in the more disturbed plots, whereas rocky substrates are associated with drier conditions where *Erica azorica* is the dominant species in early succession plots. Structural analysis is in accordance with the PCA. Structural complexity increases from PSI to PMO and from PPLI to F (Figure 2). In both successional pathways the vegetation evolves from an open scrub, to close scrub and to forest. *Juniperus brevifolia* becomes increasingly dominant along the succession gradient; at the same time the biovolume of *Calluna vulgaris* and *Erica azorica* decreases in late succession plots.

Erica azorica seedlings and saplings appear only in the first and intermediate stages of succession, in open spaces (Figure 3). *Ilex perado* ssp. *azorica* and *Frangula azorica* Grubow (Rhamnaceae) seedlings and saplings are mainly associated with the final succession stages. *Juniperus brevifolia* seedlings appear throughout the succession but saplings appear mostly in the first and intermediate stages. The presence of seedlings and saplings of *Laurus azorica* seems to be associated with the presence of a canopy layer.

DISCUSSION

The PCA and vegetation structure analysis enable us to describe two successional pathways, which differ in the geologic substrate and dominant colonizing species. The beginning and end of the succession are somewhat similar but the intermediate stages are clearly different. In younger rocky substrates, *Erica azorica* plays the dominant role among the colonizing species. *Erica azorica* Hochst. ex. Seub. (Ericaceae) is a typical species of drier areas (Dias 1996). In older substrates with pumice downfall deposits and associated with wetter conditions, the early dominant species is *Calluna vulgaris*. The succession culminates, in both cases, in *Juniperus*-dominated forests, but in pumice downfall deposits this domination is more evident.

Juniperus brevifolia is a good gap colonizer and establishes early in the succession, becoming, successively, the dominant shrub and canopy species as succession develops. *Laurus azorica* and *Ilex perado* ssp. *azorica* seedlings appear mostly when there is already a *J. brevifolia* canopy present.

The presence of *J. brevifolia* throughout the succession was also found in primary successions on lava domes, and is probably associated with the low number of natural species in the Azores (Elias & Dias 2004). This fact is very important for the ecological restoration of disturbed areas, since the spontaneous return to the original vegetation seems possible even in those areas where tree species were completely removed. In those areas the dominant late succession tree species is present in the form of seedlings and saplings, and the other tree species establish and persist as soon as *J. brevifolia* creates a under-canopy environment. The elimination of grazing and cutting, and the control of alien species should enable the recovery of the original vegetation.

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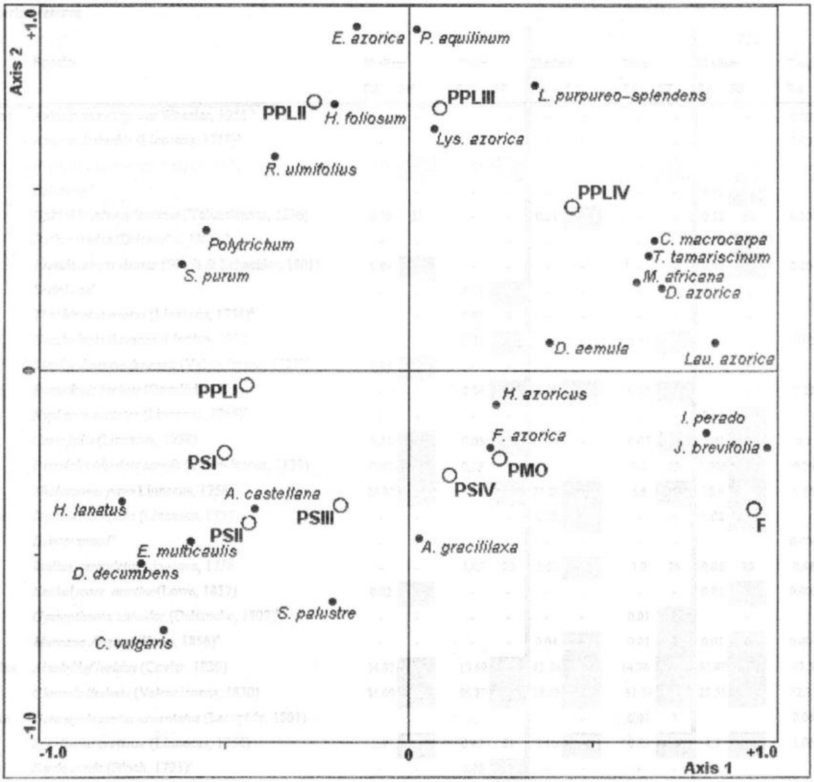

FIGURE 1. Species and plots ordination obtained with Principal Component Analysis (PCA). Abbreviations: *Agrostis castellana (A. castellana); Agrostis gracililaxa (A. gracililaxa); Calluna vulgaris (C. vulgaris); Culcita macrocarpa (C. macrocarpa); Danthonia decumbens (D. decumbens); Dryopteris aemula (D. aemula); Dryopteris azorica (D. azorica); Eleocharis multicaulis (E. multicaulis); Erica azorica (E. azorica); Frangula azorica (F. azorica); Herbertus azoricus (H. azoricus); Holcus lanatus (H. lanatus); Hypericum foliosum (H. foliosum); Ilex perado* ssp. *azorica (I. perado); Juniperus brevifolia (J. brevifolia); Laurus azorica (Lau. azorica); Luzula purpureo-splendens (L. purpureo-splendens); Lysimachia azorica (Lys. azorica); Myrsine africana (M. africana); Polytrichum* sp. *(Polytrichum); Pteridium aquilinum (P. aquilinum); Rubus ulmifolius (R. ulmifolius); Scleropodium purum (S. purum); Sphagnum palustre (S. palustre); Thuidium tamariscinum (T. tamariscinum).*

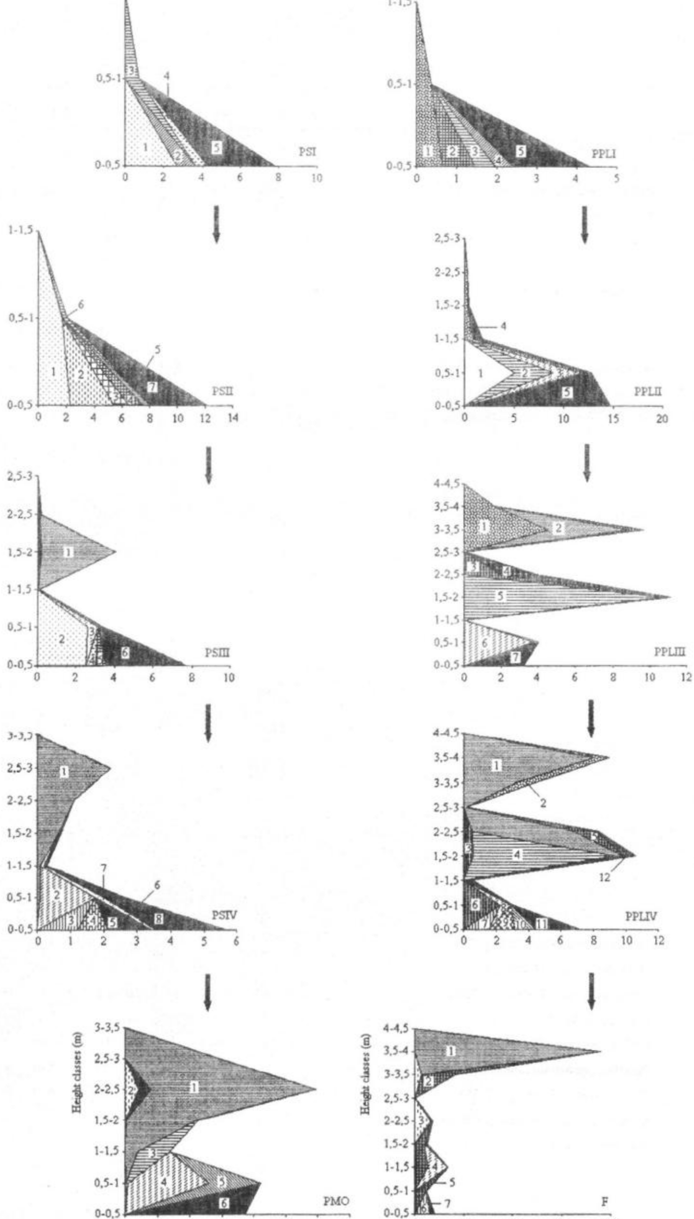
PSI
PPLI
PSII
PPLII
PSIII
PPLIII
PSIV
PPLIV
PMO
F
Height classes (m)
Biovolume (m³/25m²)
0-0,5
0,5-1
1-1,5
1,5-2
2-2,5
2,5-3
3-3,5
3,5-4
4-4,5

FIGURE 2. Anthropogenic succession on *Juniperus brevifolia* forests: each step (PSI, PPLI, etc.) shows the vertical structure of the vegetation. PSI to PMO: succession in pumice downfall deposits. PPLI to F: succession in rocky substrates (plots are ordered according to the PCA). Legend: PSI: 1- *Calluna vulgaris*; 2- *Blechnum spicant*; 3- *Pteridium aquilinum*; 4- *Holcus lanatus*; 5- Other species. PSII: 1- *Calluna vulgaris*; 2- *Agrostis castellana*; 3- *Agrostis* sp.; 4- *Danthonia decumbens*; 5- *Juniperus brevifolia*; 6- *Pteridium aquilinum*; 7- Other species. PSIII: 1- *Juniperus brevifolia*; 2- *Calluna vulgaris*; 3- *Culcita macrocarpa*; 4- *Agrostis gracililaxa*; 5- *Danthonia decumbens*; 6- Other species. PSIV: 1- *Juniperus brevifolia*; 2- *Culcita macrocarpa*; 3- *Thuidium tamariscinum*; 4- *Blechnum spicant*; 5- *Sphagnum palustre*; 6- *Lysimachia azorica*; 7- *Calluna vulgaris*; 8- Other species. PMO: 1- *Juniperus brevifolia*; 2- *Ilex perado* ssp. *azorica*; 3- *Myrsine africana*; 4- *Culcita macrocarpa*; 5- *Dryopteris aemula*; 6- Other species. PPLI: 1- *Erica azorica*; 2- *Danthonia decumbens*; 3- *Pteridium aquilinum*; 4- *Blechnum spicant*; 5- Other species. PPLII: 1- *Rubus ulmifolius*; 2- *Pteridium aquilinum*; 3- *Culcita macrocarpa*; 4- *Erica azorica*; 5- Other species. PPLIII: 1- *Erica azorica*; 2- *Juniperus brevifolia*; 3- *Laurus azorica*; 4- *Vaccinium cylindraceum*; 5- *Pteridium aquilinum*; 6- *Culcita macrocarpa*; 7- Other species. PPLIV: 1- *Juniperus brevifolia*; 2- *Erica azorica*; 3- *Vaccinium cylindraceum*; 4- *Pteridium aquilinum*; 5- *Laurus azorica*; 6- *Dryopteris azorica*; 7- *Thuidium tamariscinum*; 8- *Culcita macrocarpa*; 9- *Luzula purpureo-splendens*; 10- *Dryopteris aemula*; 11- Other species. F: 1- *Juniperus brevifolia*; 2- *Laurus azorica*; 3- *Ilex perado* ssp. *azorica*; 4- *Culcita macrocarpa*; 5- *Dryopteris azorica*; 6- *Thuidium tamariscinum*; 7- Other species.

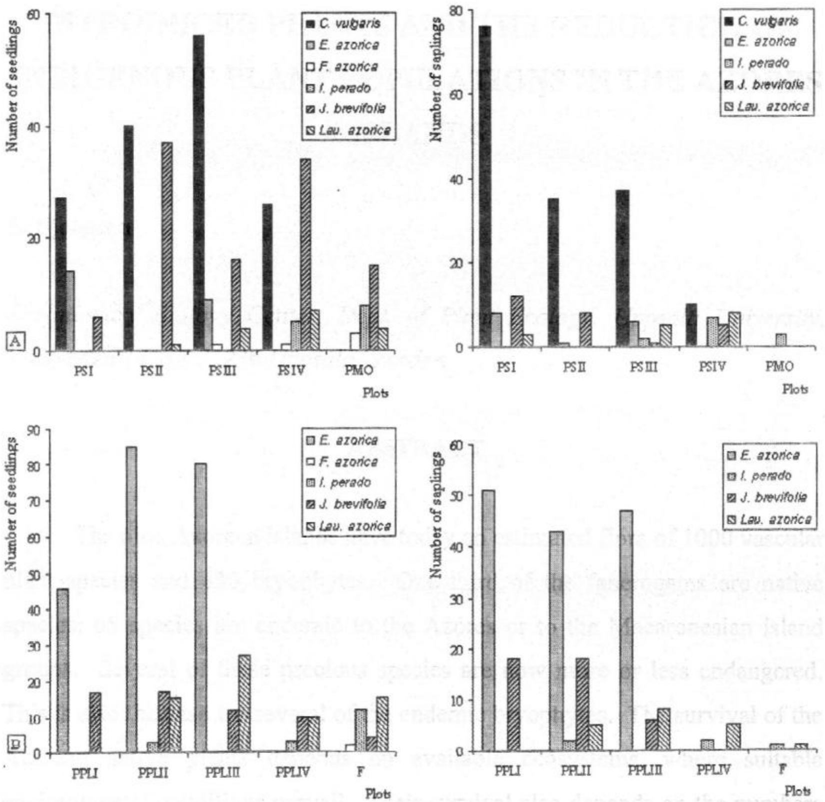

FIGURE 3. Number of seedlings and saplings in the plots located on pumice deposits (A) and rocky substrates (B). Abbreviations: see legend of Figure 1.

THE ECOLOGY OF THE BANK VOLE *CLETHRIONOMYS GLAREOLUS*, AN INTRODUCED SPECIES, IN IRELAND

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ABSTRACT

The bank vole was first discovered in south-western Ireland in 1964. It is now spreading at a rate of between about 2-4 km per year. Back-projecting the current rate of spread suggests the range expansion began around the 1930s or 1940s. The species is spreading through and is mainly restricted to hedgerows, woodland and scrub and shows no signs of competitive release into grasslands. It forms an important addition to the prey of a range of carnivorous mammals and birds, but causes localised losses in commercial forests.

INTRODUCTION

The bank vole *Clethrionomys glareolus* is one of the most widespread and abundant small mammals in Europe. It ranges across most of the continent, from the Mediterranean to northern Fennoscandia, and from the British Isles to central Russia (Alibhai & Gipps 1991). It is a woodland rodent that has adapted well to the modern landscape, inhabiting hedgerows, scrub and young forest plantations. Its main habitat specialisation is a requirement for heavy ground vegetation that, as a mainly crepuscular species but can be active at any time of the day or night, protects it from diurnal predators and eases access to its primary food sources of forbs and leaves (Gurnell 1985, King 1985).

IRELAND'S MAMMALS

Although considered native to Britain, the bank vole never colonised Ireland during the period between the retreat of the ice sheets 13,000 years ago and its subsequent isolation by rising sea levels. It was only discovered in Ireland in 1964 (Claasens & O'Gorman 1965), and judging by its restricted range and rate of spread, it is probably a recent introduction. Although it was introduced to Ireland, it would be incorrect to call the bank vole an alien species, as its former absence was probably more a result of Ireland's post-glacial isolation than any ecological unsuitability. It is not alone among the Irish mammalian fauna in this regard. Species such as the hedgehog *Erinaceus europaeus*, rabbit *Oryctolagus cuniculus* and pygmy shrew *Sorex minutus* have wide European and British distributions, but were absent from Ireland prior to their introduction by man (Fairley 2001, Hayden 2002, Mascheretti *et al.* 2003). The successful introductions of such "missing" species have led to mammals introduced to continental islands such as Ireland and Newfoundland being classed as exceptions to the "Tens Rule" (Williamson 1996, Williamson & Fitter 1996). Because Ireland was isolated by rising sea levels so soon after the end of the Ice Age, many species that would otherwise inhabit the island never got the opportunity to colonise, resulting in an impoverished flora and fauna compared to Britain and Europe. Vacant niches and ecological matching meant that the subsequent introductions of such missing species were generally successful (Williamson 1996).

Of a total of 22 extant terrestrial mammal species in Ireland (excluding bats and seals), at least 13 were introduced by man (Hayden 2002) (see table 1). The influence of man is especially evident in the species composition of rodents, insectivores and carnivores. All of the carnivores except for the mink *Mustela vison* may be native. However, of the two insectivores and six rodents, only the wood mouse *Apodemus sylvaticus* (whose populations have been augmented by introductions) and red squirrel *Sciurus vulgaris* (which went extinct in the 18th century before being reintroduced) are considered native (Hayden 2002).

THE SPREAD OF THE BANK VOLE IN IRELAND

The bank vole was first discovered in Ireland in County Kerry in 1964 (Claasens & O'Gorman 1965). Subsequent surveys showed that the species had a restricted, but ever-expanding range in the southwest of the country, increasing from 6,000km^2 to 12,500km^2 between 1971 and 1982 (Fairley 1971, Fairley & O'Donnell 1970, Smal & Fairley 1984). Spread proceeded at a rate of up to 4.5km per year and varied according to the nature of the landscape. A recent survey by the authors found that the bank vole had doubled its range size once more to almost 26,000km^2 by 2001 (Meehan 2004). A mean rate of spread of 1.9km per year was observed along the northern/eastern section of the range front where expansion is continuing. Back-projecting the current rate of spread suggests the range expansion began around the 1930s or 1940s, but the exact date and mode of the introduction is impossible to determine. The pattern of spread and records of introduced, but localized, fleas associated with bank voles suggest that the point of entry was probably somewhere along the south side of the Shannon Estuary (Fairley 1979, 1997).

THE IMPACT OF THE BANK VOLE IN IRELAND

The number of small mammals (excluding bats and carnivores) inhabiting forested regions of western Europe ranges from 3 to 11 species, depending on location and stage of succession (Gurnell 1985). Of the species commonly found in British and other European forests, only the wood mouse, pygmy shrew and red and grey squirrels *Sciurus carolinensis* are found in Ireland. Species such as field voles *Microtus agrestis* and grey-sided voles *Clethrionomys rufocanus,* with which bank voles compete in Europe, are not found in Ireland. Because only the nocturnal wood mouse and the insectivorous pygmy shrew in Ireland occupy the normal habitats of bank voles, it is unlikely that bank voles have a serious impact on any native species in terms of space or diet.

The ecology of the bank vole in Ireland is consistent with that in Britain and Continental Europe. Dietary analyses by Smal & Fairley (1980) showed a broad overlap in the different classes of food items consumed by bank voles and wood mice, but great differences in the relative importance of these classes to each species, as is the case in Britain and Continental Europe (e.g. Gurnell 1985, Hansson 1985). Wood mice are mainly granivorous, but turn to other types of food, mainly invertebrates, when seed and fruit supplies decline in spring. Bank voles are classed as folivore-granivores, and live mainly on the green parts of herbs and leaves. Seeds are also important, but invertebrates feature much less in their diet than in that of wood mice.

Both species inhabit woodland, hedgerows, field and road verges, and scrub. However, wood mice are more generalized in their habitat requirements than bank voles. While bank voles require thick ground vegetation, wood mice are very variable in their cover requirements and have even been observed inhabiting ploughed fields, although they are commonly associated with high level shrub and canopy cover that protects them from nocturnal predators such as owls (e.g. Kikkawa 1964, Pollard & Relton 1970, Geuse 1985, Gurnell 1985, Flowerdew 1993, Fitzgibbon 1997, Kotzageorgis & Mason 1997). Irish studies have confirmed these findings (Fairley & Jones 1976, Smal & Fairley 1982, Rooney 1999, Meehan 2004). In Irish agricultural land, both species are mainly restricted to hedgerows, woodland and scrub (Rooney 1999, Meehan 2004). Meehan (2004) found that both species were most common in woodland and hedgerows, and scarce (wood mice) or absent (bank voles) in farmland and parkland where ground cover was absent or composed of monospecific grass or arable crops. Both species occurred in lower densities in young plantations where grasses dominated the field layer. Bank voles were positively associated with structural habitat features such as the height, density and horizontal cover of ground vegetation. Wood mice were positively associated with the density of trees, shrubs and canopy. Both species were positively associated with scattered logs and branches, which can provide cover for small mammals when on the move (Ucitel *et al.* 2003). Smal & Fairley (1982) found a positive association between the abundance of both species and the amount of cover provided by fissures in limestone pavement.

In other countries, both species are excluded from grassland when *Microtus* spp. densities are high (Myllymaki 1977, Hentonnen *et al.* 1977, Gurnell 1985), but despite the absence of *Microtus* spp. from Ireland offering an opportunity for competitive release, the densities of bank voles and wood mice in grass-dominated habitats such as farmland, parkland, forest rides and young coniferous plantations was always much lower than in adjacent woodland and hedgerows.

Although Ireland lacks species such as the weasel and tawny owl that specialize in voles and mice elsewhere (Southern & Lowe 1968, 1982, King 1985) the absence of species such as the field vole and common shrew mean that the bank vole is a valuable addition to the prey base of species such as the barn owl. Studies have confirmed that the barn owl *Tyto alba* (Smal 1987, Fairley & Smal 1989, Cooke *et al.* 1996, Farnsworth *et al.* 2002), and to a lesser extent the short-eared owl *Asio flammeus* (Jones 1979, Smal 1989) and stoat *Mustela erminea hibernica* (Sleeman 1992) have incorporated the bank vole into their diets. Although Irish studies are lacking, the bank vole is an important prey species for the pine marten *Martes martes* in Europe (Zalewski *et al.* 1995, Lanszki 2002), while its diurnal habits means that it is probably preyed upon by the kestrel *Falco tinnunculus*, a predator of bank voles and field voles in Britain and Continental Europe (Village 1982, Korpiamaki & Norrdahl 1991). The hen harrier *Circus cyaneus* feeds heavily upon field voles in Britain (Redpath *et al.* 2002), so it is possible that the bank vole may become an important prey species for it in Ireland, especially in young, second rotation coniferous plantations which are an important habitat for the harrier. A comparison of the hen harrier's patchy Irish range (Norriss *et al.* 2002) with the range of the bank vole reveals a very large overlap, which may be significant.

Species such as the barn owl, hen harrier and pine marten are of conservation concern, so the introduction of the bank vole is positive in this respect. Other species that may prey on bank voles include foxes *Vulpes vulpes*, American mink *Mustela vision*, badgers *Meles meles* and buzzards *Buteo buteo*.

As well as their ecological effects, introduced species often have economic impacts. Over much of Europe, especially in northern and eastern regions where populations undergo multi-annual cycles, the bank vole is a major forestry pest, damaging seeds, buds, bark and shoots of numerous species of trees (Hansson & Zejda 1977). However, in western Europe, populations are non-cyclic, and the bank vole has much less impact as a pest, although as an important seed consumer (Hansson 2002), it has been partially blamed for the poor regeneration of beech and ash in Britain (Ashby 1967). In Ireland, the bank vole has become a pest of forestry plantations when vole densities increase locally and other food sources dwindle, mainly by ring-barking and budding young trees such as sitka spruce *Picea sitchensis*. Damage to commercial forestry was first noted in 1973, but did not increase substantially until the late 1980s when the rates of afforestation increased. Surveys in County Limerick in 1990 revealed damage to less than 1% of trees overall, but up to 15-40% on localized sites (Ward 1994). When preventative measures such as the removal of ground vegetation and woody debris are taken, the level of damage decreases significantly (Keane 1998). Other steps, such as the use of protective collars and the provision of perches to encourage avian predators, may also be useful in reducing damage (Rooney & Hayden 2002).

CONCLUSION

Apart from the commensal house mouse and brown rat, which generally occur near human settlements (Fairley & Smal 1987), the only small ground-level mammals in Ireland other than the bank vole are the wood mouse and pygmy shrew, from which bank voles are segregated by microhabitat associations and diet and temporal distribution. Thus, the bank vole is spreading through a network of woodland and hedgerows, relatively unimpeded by competition and is exploiting a niche that is vacant only because the bank vole never reached the island from Britain and Continental Europe after the Ice Age. Except for occasional losses to the forestry industry, the addition of the bank vole to the Irish fauna is probably a positive one overall as it provides an additional food source for mammalian and avian predators, some of which are of conservation concern and it does not appear to have negatively impacted other species such as wood mice.

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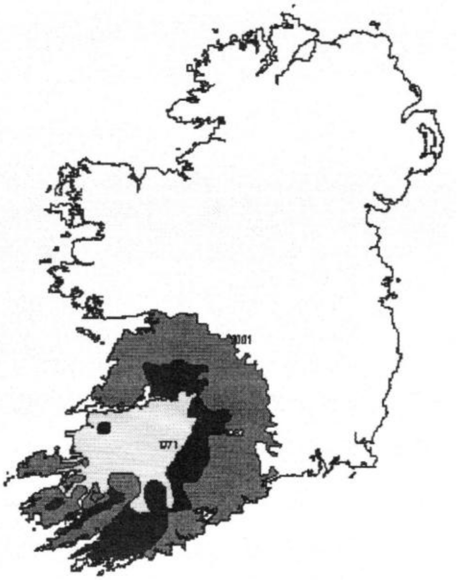
TABLE 1. Origins of the Irish terrestrial mammalian fauna (adapted from Sleeman 1997, Hayden 2002).

Status	**Species**
Native	Stoat *Mustela erminea hibernica*, Irish hare *Lepus timidus hibernicus*, red squirrel *Sciurus vulgaris*, red deer *Cervus elaphus*, fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, otter *Lutra lutra roensis*, wood mouse *Apodemus sylvaticus*
Intentionally introduced	Hedgehog *Erinaceus europaeus*, rabbit *Oryctolagus cuniculus*, brown hare *Lepus europaeus*, grey squirrel *Sciurus carolinensis*, American mink *Mustela vison*, fallow deer *Dama dama*, sika deer *Cervus nippon*, feral goat *Capra hircus*
Accidentally introduced	Bank vole, black rat *Rattus rattus*, brown rat *Rattus norvegicus*, house mouse *Mus domesticus*, pygmy shrew *Sorex minutes*

FIGURE 1. Range expansion by *C. glareolus* in Ireland between 1970 and 2001.

- ■ Location of discovery
- • 1971 range
- • 1971-82 expansion
- • 1982-2001 expansion



IN-STREAM DISTRIBUTION AND INTERACTIONS BETWEEN NATIVE *GAMMARUS DUEBENI CELTICUS* (CRUSTACEA, AMPHIPODA) POPULATIONS AND THE INTRODUCED SPECIES *GAMMARUS PULEX* (L.), IN THE UPPER REACHES OF THE RIVER LIFFEY IN CO. WICKLOW, IRELAND.

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ABSTRACT

Historically, *Gammarus pulex* has displaced populations of *Gammarus duebeni celticus* all across Europe. *G. duebeni* now remains only in Brittany in Northwest France and across the island of Ireland. Since it was introduced to the Brittas River, *G. pulex* has become the dominant species in many locations, with *G. duebeni* in some instances totally absent. This study examined the populations of both species using samples taken from 1999 to 2001. No change in relative abundance of two species was observed. *G. pulex* dominated at seven of the nine sites. There was no difference between the occurrence of gammarids in the central and marginal habitats.

INTRODUCTION

The most common brackish and freshwater amphipod species in Ireland is *Gammarus duebeni* Liljeborg (Holmes 1978). Freshwater (*G. duebeni celticus*) and brackish water (*G. duebeni duebeni*) forms are recognised (Reid 1939, Pinkster *et al.* 1970). *G. duebeni celticus* occurs throughout Ireland and in Brittany in Northwestern France. *G. duebeni duebeni* occurs in Western

Europe, North America and in parts of Britain. Another species, *Gammarus pulex* (Linneaus) spread from the mainland of Europe to Britain before the English Channel formed. It however, failed to reach the island of Ireland while a land bridge linked it to Britain (Hynes 1954; Pinkster *et al.* 1970). This alien amphipod species was however introduced to Northern Ireland from Yorkshire in Northeast England in order to enhance the food supply for fish in local angling waters (Strange and Glass 1979). Such introductions are of concern because *G. pulex* may displace the native populations of *G. duebeni*. Pinkster *et al.* (1970) wrote that *G. duebeni* is displaced by *G. pulex* and is restricted to the uppermost reaches of the stream. *G. pulex* was first discovered in the Brittas River in County Wicklow by Keatinge (1989). This introduction was also linked to local fish farms that brought young fish from hatcheries in Britain. The present study examines the gammarid species in samples taken from the Brittas River in 1999 and in 2001. Several aspects of the population structure and spatial distribution of both species are reported here.

STUDY AREA AND METHODS

The Brittas River is located in north County Wicklow and is a part of the Liffey catchment. It joins the River Liffey before it enters the Pollaphuca Reservoir. Nine sites were sampled (Figure 1) all with moderate to fast flow. Conductivity values ranged from 79 to 463μS/cm and pH from 7.05 to 8.27. The nine sites were sampled in both 1999 (mid October to mid September) and 2001 (late September), five of which were located on the Brittas River and the remaining four on adjacent streams. Three samples were taken at the margins and in the centre (mid-stream) of each site, bringing the total number of samples to fifty-four. The sampling methods varied slightly between the two years. Kick samples were taken in 1999 and surber samples (area $0.25m^2$) were collected in 2001. Gammarids were removed from each sample, and counted and identified using standard keys (Gledhill 1993). All animals were measured to the nearest 0.5mm by straightening the individual and measuring from the tip of the head to the end of the telson. Those with length of 8.5mm or greater were considered to be adults, as reproductive structures are poorly formed in smaller individuals. These mature individuals were sexed.

RESULTS

There was a positive correlation between conductivity and the total number of gammarids found at each site ($R^2 = 0.77$). No correlation was found between pH and total gammarid numbers.

When the totals were combined, no significant change was observed in the proportions of each species from 1999 to 2001 (signed rank test $p>0.5$). At three sites (Sites 1, 8 and 9), there were larger proportions of *G. duebeni* in the 2001 samples. Only one site (Site 3) showed a proportional decrease of *G. duebeni* in the 2001 samples. The proportions in the other five sites remained the same from 1999 to 2001. When the data from all sites were pooled there was no significant difference (student's t-test, $P>0.05$, $n=4779$) between the total number of gammarids (adult and juvenile combined) found in the centre and margins of the river.

When adults (both species combined) were examined, no significant difference between habitats was found (One-way ANOVA, $P>0.05$, $n=595$). There was also no significant difference between juvenile numbers (both species combined) found in the centres and at the margins for all nine sites (One-way ANOVA, $P>0.05$, $n=4184$). The same applied to within site comparisons (Paired t-test, $P>0.05$, $n=4184$). Three sites (1, 3 and 9) showed a significant ($\chi^2 > 3.84$, $P<0.05$) deviation from the expected frequencies (1:1) of males and females.

G. duebeni adults were significantly larger than those of *G. pulex* (ANOVA; $P<0.05$, $n=585$). The highest percentage of *G. pulex* adults (44%) fell within the 8.5mm to 9.4mm range. Only about 12% measured 12.5mm and above. In contrast 18% of *G. duebeni* individuals fell within the 11.5mm to

12.4mm range, with over 46% measuring 12.5mm and above. Within each species, the males were on average larger than the females (ANOVA; $P<0.05$, *G. duebeni*: 32 males 34 females, *G. pulex*: 329 males 190 females). The highest percentage of *G. pulex* males (31.3%) and females (66.3%) were within the 8.5mm to 9.4mm range. For *G. duebeni* the highest percentage of males (29.4%) were within 13.5mm to 14.4mm range with the highest percentage of females (21.8%) within the 11.5mm to 12.4mm range.

DISCUSSION

G. pulex has been reported to displace *G. duebeni* in several river systems (Dick *et al.* 1990). In the present study, *G. pulex* was numerically dominant at all sites on the Brittas River where both species existed. Hynes (1955) considered that if these two species make more or less the same demands on the habitat, *G. pulex*, having a higher biotic potential, would eventually out-compete *G. duebeni* in any habitat. Out of all the sites examined in this study, only two (Sites 4 and 7) still remained inhabited exclusively by *G. duebeni*. All others were largely dominated by *G. pulex*. However, the proportional representation of the two species did not change from 1999 to 2001. This suggests that displacement by *G. pulex* had already occurred at an earlier stage, and the species may have reached a competitive equilibrium.

The small changes noted at some sites may simply represent annual variation. In a study on similar streams (tributaries of the Vartry River in County Wicklow), it was also shown that gammarid population sizes varied greatly between years (Mellett 2001).

Possible reasons for the displacement of *G. duebeni* by *G. pulex* are discussed by a number of authors. Dick *et al.* (1993) and Dick (1995) observed that *G. duebeni celticus* was significantly more cannibalistic on moulted conspecifics than *G. pulex*. Predation by intermoult individuals on moulted congenerics in all sorts of combinations, including adults, juveniles and even those in the precopulatory mate-guarding phase was observed in both species. It was noted that *G. pulex* was the dominant predator in most combinations.

Predation between species also exceeded cannibalism within species (Dick *et al.* 1993).

G. duebeni has a breeding cycle generally starting in October and peaking in March, whereas *G. pulex* has a longer period, beginning in December and continuing through to September (Hynes 1954). The extended breeding cycle for *G. pulex* allows its numbers to increase more and may explain some of the disparity between both species. Each *G. pulex* female will produce at least two hundred to three hundred offspring in her lifecycle (Hynes 1955). *G. duebeni* produces up to one hundred offspring (Hynes 1954). This ability to produce a greater number of offspring may contribute somewhat to a greater biotic potential and might be partly responsible for its ecological dominance over *G. duebeni* (Hynes 1955).

A reproductive weakness of *G. duebeni* may be another possible reason for this displacement. Prior to her moult, the female *Gammarus* will attract a male, who will hold onto and "guard" her until she is ready to oviposit (Hynes 1955). The female is only available for mating for a short time after moulting. Successful guarding ensures a mate for the male and provides protection to the female through this vulnerable life stage. After the female moult and copulation the two individuals separate from each other. This strategy is very effective due to the short time period that encompasses moulting, copulation and the hardening of the new exoskeleton (Cowley 1992). Among *G. duebeni* precopula pairs, there is apparently a significantly larger amount of disruption to the couple when *G. pulex* males were added in comparison to *G. pulex* precopula pairs with *G. duebeni* males (Cowley 1992). The disruption of the precopula pairs prevents fertilisation and leaves vulnerable females unguarded and at risk from predation (Dick *et al.* 1990).

In the present study there was a positive correlation between gammarid numbers and conductivity. Calcium is required for building and maintaining hard calcium carbonate exoskeletons and is especially important during the moulting process. Waters with a higher conductivity and higher pH tend to contain more dissolved ions including calcium.

Although more juvenile gammarids were found within the margin, the difference was statistically insignificant. Marginal areas often tend to provide the most suitable habitat for macrophyte vegetation such as *Apium nodiflorum* (Fool's water cress) and *Rorippa nasturtium-aquaticum* (Water cress). Previous work by Kaenel (1998) has indicated macrophyte cover as an important determinant of macroinvertebrate presence. Harrod (1964) demonstrated that different macrophyte species, with their differing morphological structure, provide habitat to certain types of macroinvertebrate, with *G. pulex* favouring *Callitriche* spp. *Callitriche* spp. prefer more sheltered marginal and stream bed locations due to the slower flow. The slight excess of juveniles in these areas may be due to the lower current velocities found along the margin and the greater protection from predators offered by stands of vegetation. Numbers of *G. duebeni* however were quite low.

Males were larger than females. This agrees with previous work on *G. pulex* (Pringle 1982) and *G. duebeni* (Hynes 1954). *G. duebeni celticus* occurs in both Ireland and Brittany in Northwest France. Most of Western Europe has seen the replacement of *G. duebeni* by *G. pulex* (Dick *et al.* 1993). The isolation of the island of Ireland from the rest of the continent has delayed this replacement. Amphipod invasions and replacements are frequently accompanied by environmental degradation (Prenter *et al.* 2004). Kelly *et al.* (2003) studied interactions between both gammarid species and their environments. Stretches of river were taken, one containing only *G. pulex* and one with only *G. duebeni*. *G. pulex* dominated its reach and diversity of other macroinvertebrates was relatively low, whereas in the other stretch *G. duebeni* abundance was relatively lower but there was a greater diversity of other macroinvertebrates. A mixed site was also examined which displayed intermediate results. It seems probable that over time this country, like most of Europe, will see a total replacement of the native *G. duebeni* with the invasive *G. pulex* and this may have a detrimental affect on the overall macroinvertebrate diversity.

ACKNOWLEDGEMENT

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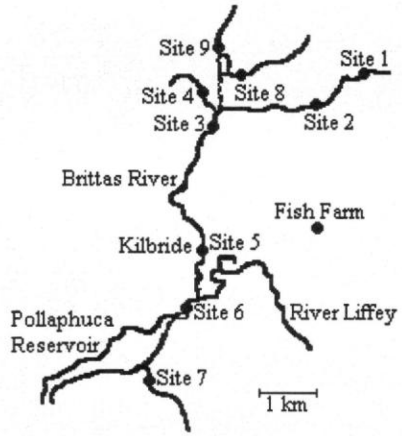

TABLE 1. Site grid references

Site	**Grid Reference**
Site 1	O069 219
Site 2	O055 212
Site 3	O030 207
Site 4	O027 216
Site 5	O026 175
Site 6	O025 162
Site 7	O013 144
Site 8	O039 221
Site 9	O033 234

FIGURE 1. Map of study area.

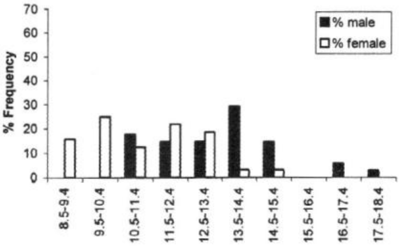

FIGURE 2. Length % frequency distribution for *G. duebeni.*

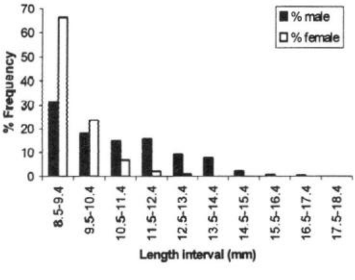

FIGURE 3. Length % frequency distribution for *G. pulex*.

THE CURRENT STATUS OF AND THREATS TO, THE FLORA OF THE FALKLAND ISLANDS, SOUTH ATLANTIC

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ABSTRACT

The Falkland Islands (51° - 53°S; 57° - 62°W) are an archipelago of over 700 islands in the South Atlantic, covering an area of 12173km^2 and approximately 500km from mainland South America. Currently, of 348 species in the vascular flora, 173 are native and 175 are non-native taxa. The juxtaposition of the islands between Antarctica, South America and other remote south Atlantic Islands gives them high biogeographic importance. Since the mid 1980's a programme of land reform and considerable inward investment has put greater pressure on the natural resources of the islands, largely through greater ease of countryside access and pressure to diversify the rural economy from the traditional land use of sheep ranching. Other threats to the flora include plant introductions, deliberate and natural fires and climate change. The flora is poorly known but recent work has greatly increased knowledge of its status and distribution. A Red Data list has highlighted the need to protect more species than are covered by the current legislation. The way ahead is seen as a mixture of education, awareness, nature reserve acquisition, legislation, sustainable farming practices and research into ecological and genetic aspects of the flora. Sustainable eco-tourism should be seen as having a positive role in the conservation of the flora.

KEYWORDS: endemic flora, sustainability, vascular flora, ecology, Falklands.

INTRODUCTION

The Falkland Islands are an archipelago of 782 islands (Woods 2001) situated in the South Atlantic between latitudes 51°S and 53°S and longitudes 57°W and 62°W. They cover an area of *circa* 12,200km^2 and are approximately 500km from the nearest point on mainland South America. The climate is cool temperate oceanic and is characterised by its lack of extremes. Temperatures are never high but are maintained at a moderate level with a mean for January of 9.4°C and a mean for July of 2.2°C, and ground frosts can occur throughout the year. Rainfall is low with a mean annual precipitation during the period 1944-1978 at Stanley of 640mm, though the mean annual rainfall received tends to decline towards the south and west. Rainfall is lowest in spring and this, combined with the strong winds, reduces plant growth (McAdam 1985; Summers & McAdam 1993). Climatic variation across the Falkland Islands archipelago is poorly understood but West Falkland tends to benefit from a milder, drier and sunnier climatic regime, particularly in the northwest.

SOILS AND VEGETATION

The topography of the Islands is not extreme with the landscape being generally hilly and the tallest mountain, Mt Usborne on East Falkland, is only 705m high. A typical Falkland soil comprises a shallow (typical no deeper than 38cm) peaty horizon overlying a compact, poorly drained silty clay subsoil. Mineral soils occur in areas wherever the underlying geology is exposed, particularly on mountaintops and in coastal areas. Falkland soils generally have a pH in the range 4.1 to 5.0 and are deficient in calcium and phosphate (Cruickshank 2001). The main vegetation types are acid grasslands dominated by *Cortaderia pilosa* (Poaceae) and dwarf shrub heathland dominated by *Empetrum rubrum* (Ericaceae), but other vegetation types of more limited extent may be locally important particularly around the coasts. Scrub communities dominated by *Chiliotrichum diffusum* (Asteraceae) or *Hebe elliptica* (Plantaginaceae) would have been much more widespread before the introduction of livestock as would a community dominated by the three metre tall grass, *Poa flabellata* (Poaceae), which today survives mainly on small offshore islands. There is no native tree cover.

LAND USE

The history of land use in the islands is one of little change since post-glacial times until man's limited presence about 160 years ago (Summers & McAdam 1993). Sheep were introduced in the 1860's, with numbers increasing up to a maximum of 800,000 in the early 1900's. Stock density remained relatively constant (at approximately one sheep per 2ha) from the late 1800's until early in the 1980's when a programme of farm-subdivision was introduced (McAdam 1984a; Summers & McAdam 1993) and since then sheep numbers have increased by approximately 20% (Summers *et al.* 1993). Some reseeding has been carried out using introduced European forage species but most of the grassland is extensively grazed. Since the late 1990's there have been moves to increase the numbers of cattle on the islands. The rural population is small (3-400 people) and most are engaged in agriculture. Farm-based tourism has steadily increased in popularity in recent years.

THE FLORA

The first botanist known to have visited the Falkland Islands was Antoine-Joseph Pernetty in 1764 (Moore 1968) and botanists have continued to visit the islands throughout their history. Over 60 botanists have made collections of Falkland Islands plants and these collections are summarised in Moore (1968). Accounts of the flora were produced at disjunct intervals interspersed with long periods of inactivity (e.g. Skottsberg 1913, Moore 1968) and it was not until the latter publication that a significant step forward was taken in the understanding of the Falkland Islands flora. Moore's work can be regarded as the first true Flora, as the keys and full species descriptions it contained allowed identification of taxa, and as a result was more than just a list of species recorded. In consequence, this text is still the definitive guide to the flora of the Falkland Islands and has provided a firm foundation for all subsequent floristic investigation in the archipelago. Recent work (Broughton & McAdam 2002a,b,c, 2003, Broughton *et al.* 2000) which included substantial field recording, has resulted in a significant increase in the number of species recognised, particularly through a substantial increase in the known alien flora (Broughton & McAdam 2002c) and in our knowledge of the status and distribution of the flora (Broughton & McAdam 2002a, 2003). Similarly, there have been changes to accepted nomenclature for those species considered endemic, and a gradual increase in knowledge of the flora as a whole.

Seventy-five families, 215 genera, and 348 species have so far been recorded growing wild in the Falkland Islands and are listed in the checklist (Broughton & McAdam 2002a). Of these, fifty-four families, 120 genera and 173 species are native. The substantial non-native flora of 175 species has been reviewed (Broughton & McAdam 2002c). There are 18 native and 3 non-native pteridophyts (Broughton & McAdam 2003).

The Falkland Islands are currently considered to have 14 endemic species. These are: *Calandrinia feltonii*, *Chevreulia Lycopodiodes*, *Erigeron incertus*, *Gamochaeta antartica*, *Hamadryas argentea*, *Leucheria suaveolens*, *Nassauvia gaudichaudii*, *Nassauvia serpens*, *Nastanthus falklandicus*, *Phlebolobium maclovianum*, *Plantago moorei*, *Senecio littoralis* and *Senecio vaginatus*. Two taxa (*Nastanthus falklandicus* and *Plantago moorei*) are of particular note, as they appear to be narrow-endemics, restricted to the southern coast of West Falkland.

As would be expected the native flora shows strong affinities with that of southern South America. Thirty-three species (19%) have a 'circum-Antarctic' distribution occurring in some part of the sub-Antarctic zone, New Zealand or southeastern Australia, and sixteen species (9%) have a bipolar distribution, being found also in the higher latitudes of North America and to a slightly lesser extent, Europe (Moore, 1968). The juxtaposition of the islands between Antarctica, South America and other remote South Atlantic Islands gives them high biogeographic importance.

THREATS TO THE FLORA

Reform of rural infrastructure

Land reform in the 1980's has resulted in farm subdivision and increased stock numbers. In many cases this has been accompanied by fencing and greater stock control but overgrazing and erosion of some of the shallow, fertile soils has occurred. Other rural development activities related to oil, fishing, aquaculture and tourism have had limited impact.

Plant introductions

The total number of non-native species is now known to be 175, nearly double that previously recognised by Moore (1968), and exceeding the total for native taxa (173 species) (Broughton & McAdam 2002c). Taxa come from 46 families of which the Asteraceae (28 species and 16% of the non-native flora) and the Poaceae (36 species and 21% of the non-native flora) are undoubtedly the most important. Most non-native species, (131 taxa and 75% of the non-native flora), show an association with human habitation and other built environments. Of these, approximately 50% are dependent upon such habitats, reflecting the requirement of many non-natives for open or disturbed ground. Other species associated with habitation are more widespread and can also be found in naturally open and disturbed habitats such as beaches and seabird colonies, or in vegetation that has been modified by domestic animals. However, the association of some species with habitation is equally a reflection of their horticultural and agricultural origins and some species, particularly the trees and shrubs, are merely relicts surviving where settlements and gardens have been abandoned. Most non-native taxa were rare or local in occurrence and so probably do not have the competitive ability to spread far in the harsh environment of the Falklands (Broughton & McAdam 2002c). As man's activities continue to expand and diversify in the Falkland Islands the non-native flora can also be expected to expand and to become more prominent. A similar trend has already been noted in Tierra del Fuego, where the increasing activity of man has undoubtedly extended the area of many non-native taxa (Moore 1983). *Cirsium vulgare,* for example, arrived in Tierra del Fuego prior to 1917 but was not common. During the 1960's, however, it became more widespread, particularly along roads.

Countryside access

Before 1985 there were virtually no roads in the Falkland Islands and building of a rural road network commenced. Now a sparse network of roads exists, giving more people from Stanley (the only town) access to the countryside. This, coupled with more leisure time and greater interest in wildlife, has put more pressure on coastal and other sensitive habitats. A road network allows weed species to expand their range and *Cirsium vulgare* may follow the same expansion pattern as on Tierra del Fuego.

Fire

As vegetation emerges from the winter it has accumulated a high proportion of dead matter that creates a fire hazard, particularly in the dry windy spring and summer (McAdam 1984b). It is common land management practice to burn pasture in spring to remove this dead material and to make the greener leaves below more available to sheep. This practice may have some detrimental effect on the flora, but this is not clearly known. Fires can also occur through carelessness and from lightening strikes.

Climate change

On a more global scale, climatic change may have a significant effect on the flora of the Falkland Islands (Wadhams 1993). There is evidence that rainfall is slowly declining on the islands (Hoppé & Mc Adam 1998) and there are occasional periods when ozone depletion is particularly strong over the islands. A combination of these processes may well have a significant impact on the flora.

CURRENT STATUS AND DISTRIBUTION

The extent and distribution of the flora were little known until work by Moore (1968, 1973) and, a more thorough and extensive study, a DEFRA-funded Darwin Institute Project. The latter resulted in the production of a checklist and atlas of the distribution of the flora. Broughton & McAdam (2002a) produced the first comprehensive assessment of the conservation status of the flora and a review of conservation measures in place (Broughton & McAdam 2002b). Detailed studies of floras of specific islands (McAdam & Woods 1995, Broughton *et al.* 2000) and groups (Broughton & McAdam 2003) highlighted the uniformity of the distribution of the flora.

The greatest increases in sheep numbers have been on vegetation types overlying drier; more fertile soils such as around pounds, in valleys and on coastal pastures. There is some evidence that soil erosion on shallow soils may have increased in extent because of overgrazing but little is understood of the response of individual communities to increased grazing pressure (Kerr, 2003).

While sheep grazing has affected the flora considerably there is no evidence to confirm loss of species arising from the practice.

PROTECTION

Under the Conservation of Wildlife and Nature Ordinance, 1999 (Anon. 1999), nineteen species of plant are protected. Broughton & McAdam (2002b) produced the first national Red Data List for the Falklands. This contained 23 species and included a further 16 species of relevance to the national conservation strategy. Internationally the conservation of endemic Falkland Islands taxa is perhaps of greatest importance, and should be the focus of priority action. Thirteen species (8% of the native flora) are endemic to the Falkland Islands archipelago. Six of these (46% of endemics) are threatened (26% of threatened plants) and one is "Near Threatened". Of the threatened endemic plants, the Felton's-flower (*Calandrinia feltonii*) is Critically Endangered, the Antarctic cudweed *Gamochaeta antartica* is Endangered, and the other four species are Vulnerable.

The only international Convention currently relevant to the Falkland Islands flora is CITES and the Convention is only applicable to the four Falkland Islands members of the Orchidaeae, only one of which is threatened. All orchids are covered by Appendix II of the Convention. The conservation of wild flora in the Falkland Islands is still in its early stages and has advanced little beyond initiatives to purchase nature reserves. However, with an increase in public awareness and interest in conservation issues, fuelled to some degree by land reform and the increased role of tourism in the economy, there are signs of a shift in focus from protecting sites of high wildlife value to direct action to address conservation problems, such as a trial reintroduction of the Felton's-flower. In particular, there is a slowly growing awareness of the need to protect and manage threatened plants outside nature reserves and protected sites. This will be vital because most of the species on the Red List are not well represented in the current framework of protected areas. Thus, landmanagers whose prime concern is other than nature conservation may have a significant responsibility in ensuring the continued survival of threatened plant species. The establishment of a national herbarium and the production of a new field guide (Woods 2000) will generate further interest and encourage conservation of the flora.

In conclusion, whilst agriculture and development have been identified as major factors in the decline of some elements of the native flora, it is also possible to implicate a general ignorance of the native Falkland Islands flora and its importance. Given the small size of the Falkland Island's human population, there is scope for halting and reversing the decline of threatened flora. However, this will be dependent on the provision of sufficient resources and increased public awareness. Regular monitoring of threatened plant populations is required along with investigations of their biology and the reasons for their decline, and all threatened taxa not currently protected need to be afforded full legal protection. Also, given the importance of conserving genetic diversity (Wigginton 1999, Lesica & Allendorf 1995), the genetic aspects of rare plant conservation require greater attention.

Most visitors to the islands (30,000+ in 2002) are cruise-ship based tourists and make little or no impact on the flora. There are a small number of special-interest tourists who visit the islands, mainly for the wildlife. Such tourists represent a considerable income potential for the islands and, provided their activities are managed in a sustainable manner, as has been recommended for e.g. Tussac grass (Hoppé & McAdam 1992), such eco-tourism should be viewed as a positive step for sustainable conservation.

ACKNOWLEDGEMENTS

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THE CLARE ISLAND SURVEY OF 1909 – 1911: A MULTIDISCIPLINARY SUCCESS

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ABSTRACT

The multidisciplinary nature of the Survey covering the flora, fauna and antiquities of the Clare Island and surrounding area of west Mayo, is detailed. The impact of the joint input from professional researchers and amateur naturalists, using the resources of government departments, with the backing of other institutions such as learned societies and amateur naturalists' field clubs, is assessed. The special place occupied by the Royal Irish Academy in fostering such research is noted. The publication of the results comprising 67 reports in a special three-section volume of the *Proceedings of the Royal Irish Academy* under the editorship of Robert Lloyd Praeger is commented on. With the publication of the final papers in 1915, a chapter of Irish natural history came to a close, with nothing on such a scale being attempted in Ireland for many decades. In 1991, the New Survey of Clare Island was formally launched by the Royal Irish Academy. To date, nearly twenty-six separate studies have been carried out, with three volumes of results so far published, a fourth in press and a further eight in preparation.

INTRODUCTION

The Clare Island survey of 1909 – 1911 was the most ambitious collective undertaking of all up to this time and was the jewel in the crown of the golden age of Irish natural history. The importance of this survey at the time and subsequently as a template for similar biological surveys elsewhere is widely accepted (Collins 1999). The results of the three-year survey, which began to appear in print in 1911 were quite startling and, to this day, are worthy of comment. In all, some 3,219 spp. of plants were collected and identified, 585 were new to Ireland (an 18% increase in the known flora), with 11 spp. new to science, mostly algae and fungi. The total fauna listed came to 5,269 spp., 1,253 were new to Ireland (a 24% increase in the known fauna), with 109 spp. new to science. These additions were, not surprisingly, among the more obscure and less-studied groups, such as mites, polychaetes, Diptera and Hymenoptera. Almost one hundred workers from Ireland, Britain, Europe and America took part in the fieldwork, with a similar number working subsequently on identifying the material collected.

BACKGROUND TO THE SURVEY

To understand how the Clare Island Survey evolved into such an organisational and scientific success, it is necessary to go back some years, looking at two particular strands in the development of island studies in Ireland. The first can be traced to the founding by the German zoologist Anton Dohrn of the world's first marine zoological station at Naples in 1873. Others soon followed in various parts of Europe, including Britain, where the Plymouth Marine Laboratory opened in 1884. By the turn of the 20th century, the Queens Colleges and Trinity College Dublin operated small coastal marine stations, where there was a guaranteed supply of living specimens to collect and study. These establishments offered research facilities and were funded by government grants and institutional research fees. They presented an opportunity for professional researchers, who could work in teams on large-scale projects, which individually they couldn't even contemplate. The only drawback was that they were not open to the public or to interested amateurs.

The second strand can be traced to the rise of the amateur naturalist in Ireland. Following the lead in Britain, the first amateur naturalists' field club in Ireland was founded in Belfast in 1863. Within a few years, similar clubs had appeared in various cities and towns across the north and east of Ireland, with the Dublin Naturalists' Field Club being founded in 1886. These clubs attracted large numbers of gifted amateurs who, in spite of the fact that it was only a part-time pursuit consisting of weekend outings or excursions in the summer months and regular public meetings during the winter, produced a significant corpus of original data based on local floral and faunal surveys.

ROBERT LLOYD PRAEGER

By the turn of the 20th century, the acknowledged leader of this nationwide grouping was Co. Down-born Robert Lloyd Praeger, who combined in one frame an unparalleled breadth of knowledge, organising skill, considerable literary gifts, a prolific output and an unwavering intellectual purpose; a rare combination. Praeger's impact on Irish natural history studies at this time can only be described as torrential. An engineer by qualification, a librarian by profession and a naturalist by inclination, Praeger was therefore classed as an amateur, but that didn't deter him from completing major work on the geology and later the botany of the north east of Ireland before departing Belfast for Dublin in 1893 on his appointment as Assistant Librarian to the National Library of Ireland. Already elected a Member of the Royal Irish Academy in 1891 for his geological and botanical work, Praeger was able to influence the collecting programmes of the Dublin Naturalists' Field Club using the assistance of the Royal Irish Academy which, along with the Royal Dublin Society, supported amateur naturalists by providing financial assistance in the form of grants, and by publishing the results of such work in the *Proceedings of the Royal Irish Academy* (Collins 1985).

For instance, from the 1880s onward the Royal Irish Academy had been providing grants to support the early deep sea dredging expeditions off the south and west coasts of Ireland on board the *Lord Bandon*, later the *Flying Falcon*. Such support was formalised in 1893, at Praeger's instigation, with the setting up of the Fauna and Flora Committee which, to this day, supports fieldwork in Ireland by providing assistance to those carrying out floral and faunal surveys.

From start to finish, the initiative for a biological survey of an offshore island was largely Praeger's. During the fieldwork associated with his major work on the flora of Ireland, *Irish topographical botany*, published by the Royal Irish Academy in 1901, he had become very interested in the flora of our offshore islands, subsequently publishing short listings of the flora of Rathlin, the Aran Islands, Inishmurray, Achill, the Inishkeas, Inishturk, Inishbofin and, of course, Clare Island. In 1903, the Hon. Cecil Baring, of the banking family, came to the National Library, seeking information from Praeger on the known flora, fauna and antiquities of Lambay, an island some six miles north east of Howth, Co. Dublin, which he had just bought. At Praeger's suggestion, a total of 20 specialists visited the island singly and in small groups during the years 1905 – 1906, noting and collecting. In the resultant report published in 1907 nearly 90 new species previously unrecorded in Ireland were noted, with five species new to science. Besides Praeger, who reported on the flora, the survey team consisted of a blend of amateur and professional, which would form the core of all later surveys; R.F. Scharff; W.F. de Vismes Kane; A.W. Stelfox and J.N. Halbert, to name but a few (Praeger 1907). The unexpected success of this intensive investigation of a specific area by a group of specialists led to the idea of carrying out a more ambitious, scaled-up survey of an island off the west coast of Ireland.

Following suggestions ranging from Tory and Arranmore in the north, to the Blaskets and Valentia in the south, from interested parties, both amateur and professional, Clare Island was the agreed choice by virtue of its manageable size and relative ease of access and accommodation. It was also chosen because it was thought to be sufficiently remote from the mainland to possess slight species differentiation from mainland populations. The fact that, over three years, groups of fieldworkers numbering up to a dozen at a time arrived by train from Westport before spending a week or more on the island and its environs without a hitch, is a testimony to Praeger's organisational abilities and powers of inspiration. The point has been made that the amazing response to Praeger's call for volunteer fieldworkers was because European naturalists, both amateur and professional, were fully aware by now of the benefits, and pleasures, of having botanists, geologists and zoologists working side by side in teams. As originally envisaged by Anton Dohrn and his colleagues thirty years before, Clare Island became, in effect, a temporary three-year marine station deliberately designed to look inland as well as seaward.

CLARE ISLAND

Clare Island lies across the entrance of Clew Bay, separated from the mainland by channels of *circa* 3 miles on the north and the south-east. Most of the cultivated land was, and still is, found towards the eastern end of the island. The western side is bare and windswept with the high crest of Knockmore dominating the northwest of the island. The island is almost totally cliff-bound, varying in height from 5m to 15m in the south and east, to an average of 35m in the west and north. The inland side of Knockmore consisted of a steep heathery slope while the seaward side plunges into the Atlantic Ocean. This scarp was found to be the home of an alpine flora and a productive collecting ground for several other groups, such as terrestrial molluscs. The shallow waters around Clare Island possess many varied habitats of mud, sand and rock. For the purposes of the marine survey, the 50 fathom line was taken as the seaward limit. As well as Clare Island, the adjoining islands of Caher, Inishturk and Inishbofin, and the adjoining mainland eastward as far as Castlebar, were also surveyed to provide comparative data.

THE CLARE ISLAND SURVEY

The fieldwork began formally with the arrival of the first group of nine workers, led by Praeger, on the island in April 1909. Professional expertise was supplied by personnel from the relevant government departments and bodies, such as the Department of Agriculture and Technical Instruction for Ireland, the Ordinance Survey, the Geological Survey, the National Museum and, of course, the National Library. Most enthusiastic, though, were the members of the amateur naturalists' field clubs, who had more experience of carrying out this kind of multidisciplinary fieldwork, gained from the many field club outings and excursions.

In the first of three progress reports, Praeger noted with some satisfaction that eight groups had visited the island between April and September 1909, while a large number visited the island and surrounding district singly right up to December (Praeger 1909). Ornithologist Charles Patten actually spent Christmas and New Year on the island studying the winter avifauna. The arrival of the newly commissioned fishery research cruiser *Helga II* in August 1909 meant that dredging under the direction of Rowland Southern commenced. Praeger was extremely fortunate in having the cooperation of the Fisheries Branch of the Dept of Agriculture and Technical Instruction for Ireland and the friendship of the specialist staff, who saw the benefits of completing such a survey to fishery development in the region.

The fieldwork commenced in earnest again in April 1910 and continued until November. Praeger himself made five lengthy visits, collecting, working on his vegetation map and assisting others, both on the shore and inland. When the *Helga II* arrived in August, he went aboard to assist with the sorting of material being dredged up. Having completed his vegetation map, Praeger also assisted A.W. Stelfox, Thomas Westropp and George Fogerty with their work on Caher Island and Inishbofin. Praeger's last visit of the year was in December, when he accompanied mycologist Carleton Rea, whose 'fungus foray' was hampered by snow, a rare occurrence on Clare Island. Bad weather was a continuing problem throughout the whole of the survey, and there are many accounts of how the various individual workers coped with the inclement conditions.

The third and final season's fieldwork followed the same pattern as previous years, commencing at Easter with parties collecting on the island and its environs, individuals arriving at all times, and the *Helga II* continuing to dredge the surrounding waters. Throughout 1911 Praeger provided assistance to others whenever he was available. In October he again accompanied Carleton Rea on his fungi collecting excursions in west Mayo while, later that same month in stormy wet weather, he helped Jane Stephens dredge for freshwater sponges in various lakes between Louisburgh and Westport. In one of the last fieldtrips of the survey, in November 1911, Praeger accompanied A.W. Stelfox, in freezing conditions, to Lakelands Lough in east Mayo, where they dredged for samples of lake bottom marls, looking for mollusc shells.

THE RESULTS

The results began to appear in print in April 1911, even as many workers were beginning their final season's collecting. Published in the *Proceedings of the Royal Irish Academy* in a special three-part volume, the speed with which they were sent to press is yet another example of Praeger's skills as an editor. Although the published papers show a remarkable biodiversity for an island flora and fauna, Praeger was not able to demonstrate any degree of species variation from mainland populations. In his 1915 paper summarizing the results of the survey he had to admit that this failure to note any variation was due to Clare Island's proximity to the mainland, to which it had been joined until recent geological times (Praeger 1915). He also reported that the time elapsed since the last Ice Age was too short to show even the beginnings of such evolutionary variation in the flora and fauna. Nevertheless, the results were extremely rewarding.

The naming of the new taxa, while following recognised rules of nomenclature, gave great scope to the naturalists who discovered them. Several of the names, not all of which are currently valid, reflect the Irish origin of the organisms to which they apply. *Chaetosoma hibernicum* (a nematode), *Macrobiotus hibernicus* (a tardigrade) and *Apseudes hibernicus* (a polychaete) as well as *Sabatiera celtica* (a nematode), *Halolaelaps celticus* (a watermite) illustrate this. Still more were closely related to the location of their original discovery, especially if it was in, or near Clare Island. *Planispirina cliarensis* (a foraminiferan), *Leucandra cliarensis* (a marine sponge) and *Lyngbya cliarensis* (a freshwater alga) are examples, as are *Chaetozone killariensis* (a polychaete) and *Closterium eboracense* var. *achillense* (a freshwater alga). Grace O'Malley, or Granuaile, the sixteenth century pirate queen of Clare Island was commemorated by Rowland Southern in the naming of a new genus and species of oligochaete worm, *Grania maricola*. Many of the naturalists who took part in the survey had new species named after them by appreciative colleagues. Praeger received frequent attention, *Discorbina praegeri* (a foraminiferan) and *Canthocamptus praegeri* (a freshwater entomostracan) being just two examples. Southern even named a new genus of polychaete worm after him, *Praegeria remota* being the first species named. Others following this pattern were *Frontipoda carpenteri* (a water mite), *Stenolaimus marioni* (a nematode) and *Ogma murrayi* (a nematode) named by Southern in memory of James Murray, who perished on the *Karluck* expedition in the Arctic in 1914 before his work on Clare Island was published. Southern's major contribution did not go unnoticed either. J.N. Halbert named a new species of mite, *Halacarus southerni*, in his honour.

And so the members of the great team of volunteers assembled by circular in 1908 and held together by Praeger's management skills over the intervening years went their separate ways as they completed the fieldwork and submitted their results for publication. The experience gained was later to stand most of them in good stead elsewhere.

Sadly, by the time the last paper, Praeger's summary, was published in 1915, such work had been superseded by global events, as World War I gained momentum. In Ireland the War of Independence followed the Easter Rising of 1916. The creation of the Irish Free State and the partition of Ireland in 1922 were followed by the Civil War. As a result it was just not possible for groups of people to pursue fieldwork in the countryside or on the seashore in safety. Research in all disciplines suffered in the 1920s and 1930s, while the 1940s brought another world war. The 1950s saw post-war depression and emigration and it was not until the 1960s that a trickle of funding resulted in the commencement of small scale ecological surveys.

CLARE ISLAND REVISITED

Like history repeating itself, work published through the 1970s and 1980s demonstrated once again the value of multidisciplinary surveys. Because there was such a wide groundswell of support from amateur and professional groups and individuals in favour of a new multidisciplinary survey of Clare Island, the Royal Irish Academy agreed to organise and supervise a new survey. The fieldwork for the New Survey of Clare Island, which commenced in 1992, has resulted in 26 separate studies being completed to date, on the flora, fauna and archaeology of the island, using the original survey results as a baseline. Three volumes of results have so far been published by the Royal Irish Academy: Volume 1 on the history of the original survey and the cultural landscape; Volume 2 detailing the geology; Volume 3 detailing the intertidal zoology. Volume 4 on the history and archaeology of the Abbey is to be published shortly, with further volumes on archaeology, flora and fauna (marine, freshwater and terrestrial) to follow. Both Clare Island and the original Clare Island Survey will continue to play a pivotal role in floral and faunal studies for many years to come.

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PLATE 1. Members of the ninth party to visit Clare Island in June 1910, posing on a pucaun in front of Granuaile's Castle: front left to right: Thomas Greer, W.F. de Vismes Kane, R.J. Ussher, P. Kuckuck, H. Wallis Kew; back left to right: Nevin Foster (inset), R.Ll. Praeger, Carl Lindner, A.D. Cotton, W.J. Lyons, R.J. Welch. (*Royal Irish Academy*)

GERMINATION AND SEEDLING DEVELOPMENT IN *TORNABENEA INSULARIS*.

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ABSTRACT

Germination and seedling development of *Tornabenea insularis* were studied. Seeds of this endemic *Apiaceae* from Cape Verde islands were picked from herborized specimens one year after harvest. Germination was carried out in a climatic chamber using a 3 ppm GA_3 solution. *T. insularis* had a normal germination pattern and persistent long cotyledons. Seedlings showed a high biomass production and anthocyanin synthesis.

KEYWORDS: *Tornabenea insularis*, *Apiaceae*, seed germination, GA_3, seedling development.

INTRODUCTION

Tornabenea Parl. ex Webb is the only endemic genus of *Apiaceae* in the Cape Verde islands. Species delimitation is controversial due to some morphological plasticity. Martins (1996) considered three species: *T. insularis* Parl. ex Webb, *T. annua* Bég. and *T. tenuissima* (A. Chev.) A. Hansen & Sunding. *T. insularis* is located on almost all the islands and local people use it to treat cough (Martins 1996). The species is not yet considered an endangered species but investigations using native exemplars are limited.

The germination pattern and seedling development in *T. insularis* are not known. Seed germination was attempted in order to obtain fresh plant material for use in our studies. Many seeds require cold stratification to break dormancy and germinate (Zeiger 1998). This treatment may need to be prolonged and is therefore inconvenient. Alternatively, a GA_3 solution can be used for a short period of time.

These are preliminary studies reporting the nature of the germination process in *T. insularis* and its reaction to treatment with a GA_3 solution. Seedling development and its demands are also presented.

MATERIAL AND METHODS

Seeds: Seeds were picked from herborized exemplars of *T. insularis* adult plants, collected in Santiago Island in the Cape Verde archipelago in October 2002. A voucher exemplar is deposited in LISC (I. Gomes, D72A).

Germination: Seeds picked from *T. insularis* D72A one year after harvest were placed in plastic beds, 20cm x 14cm x 2.5cm filled with sterilized sand, in a growth chamber under 25°C and a 16-hour photoperiod. They were watered with a GA_3 solution (3ppm) until germination occurred.

First transplantation: After germination, seedlings were transplanted into plastic pots (8cm x 5cm) filled with a mixture of sand:peat (3:1), one to three seedlings in each one. They remained in a growth chamber, under 22°C and a 16-hour photoperiod and were periodically irrigated with tap water.

Second transplantation: Young plants were transplanted into plastic pots (20 cm x 16cm) filled with a mixture of black earth:sand:peat (2:1:1) and kept in a greenhouse without any environmental control.

Phenological analysis: plant phenology was followed in 20 seedlings and their development was evaluated three times a week.

RESULTS

Treatment of seeds of *Tornabenea insularis* with a GA_3 (3ppm) solution resulted in 63% successful germination within 11 days. The time course of germination achieved with the use of GA_3 solution is shown in Figure 2.

The first seedling was transplanted by the 8th day and the overall success rate was 95% of transplants. *T. insularis* produces long cotyledons (Figure 1B) and the first leaf emergence was noted on the 10th day (Figure 1B). A new leaf was seen almost weekly, so that by the 61st day, seedlings had developed the ninth leaf. Soon, young plants exhibited a clear standing habit by the fourth and fifth leaf stages and did not show any secondary branches (Figure 1C). The presence of the first leaf hairs was clearly noticed on the petiole (Figure 1D) and on the lamina, by the 36th day and by the 52nd day anthocyanins were visible on all the plants' main stem and petioles (Figure 1E). The second transplantation, into greenhouse conditions, was carried out on the 53rd day. Plants did not seem to be affected by this second transplantation, and all were healthy and growing one week later. They remained erect?, no branches were developed and fewer anthocyanins were seen (Figure 1F). The time course of seedling development is shown in Figure 3.

DISCUSSION

T. insularis seeds have a life span of at least one year, when stored under dry conditions. They failed to germinate in the presence of water throughout a previous experimental period of 8-10 days at 25°C, becoming intumescent, indicating a dormancy state. A normal germination pattern was observed in seeds treated with a GA_3 solution. The radicle tip protrudes and grows through the seed coat preceding emergence of the cotyledons. Studies of seedlings and cotyledons in *Apiaceae* have shown that there are two categories of cotyledons to be considered, long and round (Cerceau-Larrival 1971). *T. insularis* belongs to the first category, those containing long cotyledons, where the cotyledon lamina almost imperceptibly diminishes into the petiole.

T. insularis seedlings grew and developed rapidly under our study conditions. Moreover, the young plants tolerated two transplantations in a short period of time.

The presence of leaf hairs as well as anthocyanins were already noticed on mature specimens collected in Santiago. They are typical responses of plants to stressful environmental conditions. They probably act as a light screen against radiation damage (Zeiger 1998, Mazza and Minniati 1993). It shows the adaptability of these plants and it might help to explain why this endemic is not yet considered an endangered species.

ACKNOWLEDGMENTS

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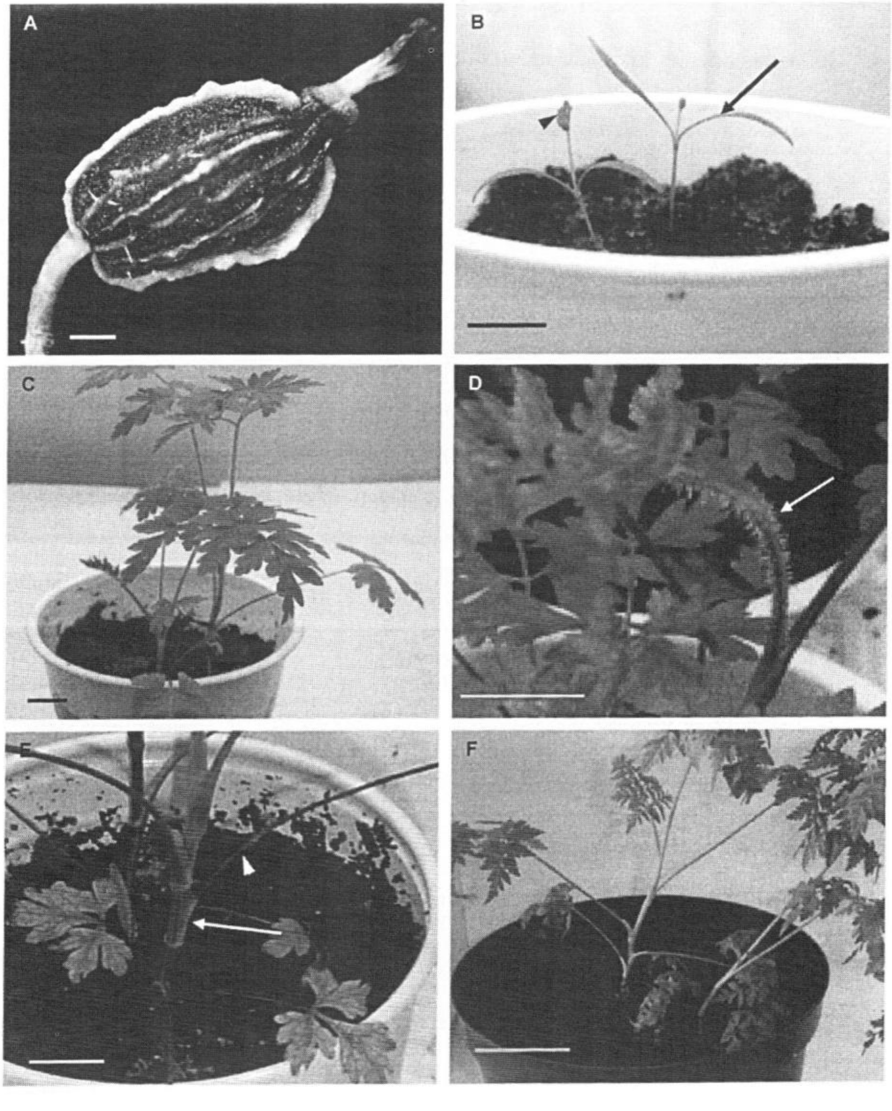

FIGURE 1. Seedling development in *T. insularis*. A – seed: dorsal view (OM, 25x, bar = 500 µm); B – long cotyledons (arrow) and first leaf emergence (arrowhead): 10th day (bar = 1 cm); C – plants with standing habit and no secondary branches at fourth and fifth leaf stages: 40th day (bar = 1 cm); D – hairs on petioles (arrow): 50th day (bar = 1 cm); E – anthocyanins in stems (arrow) and petioles (arrowhead): 52nd day (bar = 1 cm); F – plants 1 month after the second transplantation (bar = 5 cm).

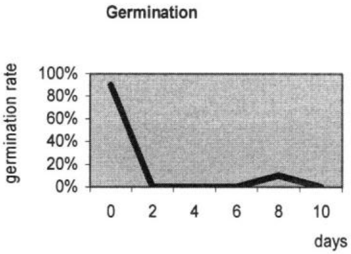

FIGURE 2. Time course of seed germination, in *T. insularis*, achieved with the use of GA_3.

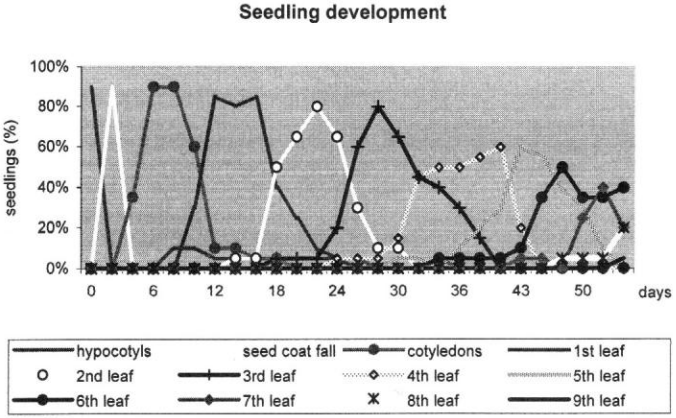

FIGURE 3. Time course of seedling development in *T. insularis*.

HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) OF THE CAPE VERDE

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ABSTRACT

The movements of individual humpback whales (*Megaptera novaeangliae*) can be tracked by matching photographs of the distinctive markings on the ventral sides of their flukes. During winter-spring research cruises conducted between 1990 and 2004, a total of 62 individual humpback whales were identified from the waters of the Cape Verde Islands. These were compared with over 5,500 individual fluke photographs taken in the North Atlantic. One photographic match was made with a whale previously photographed in the Denmark Strait off Iceland, and a second match to Bear Island, Norway. This provides the first direct evidence of a link between the

humpbacks in tropical waters of the eastern North Atlantic and high latitude feeding grounds. Ten inter-annual matches of humpback fluke photographs have demonstrated a high return rate to these waters. These findings are consistent with the mitochondrial DNA evidence of at least two distinct breeding populations of humpback whales in the North Atlantic.

INTRODUCTION

The population of humpback whales (*Megaptera novaeangliae*) in the North Atlantic Ocean is one of the best-studied populations of large whales in the world. Since the 1970's, extensive photo-identification effort has yielded information on population structure and migratory movements (Katona & Whitehead 1981, Katona & Beard 1991, Clapham & Mead 1999, Smith *et al.* 1999). Genetic tagging has also been used to determine connections between whales in different areas of the North Atlantic (Palsbøll *et al.* 1995 and 1997, Larsen *et al.* 1996, Valsecchi *et al.* 1997, Berube *et al.* 2004).

It is clear from previous studies that humpback whales feed during the summer in a number of relatively discrete grounds, including: Gulf of Maine, Newfoundland/Labrador, Gulf of St. Lawrence, Greenland, Iceland, and Norway. Fidelity to these summer feeding areas is strong and apparently maternally directed, and genetic analyses suggest that it is maintained on an evolutionary timescale (Larsen *et al.* 1996, Palsbøll *et al.* 1997). Despite the low level of movement between the various feeding grounds, photo-identification and genotyping has shown that some individuals from all of the identified high-latitude areas migrate long distances (in some instances more than 8,000km) to common winter breeding grounds in the West Indies (Martin *et al.* 1984, Stevick *et al.* 1998, 1999a and 2003) where they mix spatially and genetically. The great majority of humpback whales in the North Atlantic appear to use West Indies wintering areas, with large concentrations in the northern Antilles, especially on or near Silver Bank (Winn *et al.* 1975, Clapham & Mead 1999, Smith *et al.* 1999).

During the 19th century American open-boat whalers rarely reported taking humpbacks in the northern Antilles. Instead, their humpback whaling effort focused on portions of the southeastern Caribbean and around the Cape Verde Islands (Mitchell & Reeves 1983, Reeves *et al.* 2001 and 2002, Reeves & Smith 2002). Today, densities of humpbacks in these two historic breeding areas are comparatively low (Jann & Wenzel 2001, Swartz *et al.* 2003). A photographic match was made recently between the southeastern Caribbean and Fyllas Bank off West Greenland (Stevick *et al.* 1999b), and a genetic match was made between the southeastern Caribbean and Norway (Berube *et al.* 2004) suggesting that at least some of the whales that winter in the southern portion of the West Indies have migratory habits similar to those of the whales that winter in the northern Antilles.

Here we report the first photographic matches of individually identified humpback whales from the Cape Verde Islands to northern feeding grounds (Iceland and Bear Island, Norway), the high inter-annual return rate of individuals to the Cape Verdean waters, and discuss the implications for population structure.

METHODS AND MATERIALS

Study area

The Cape Verde Islands are situated in the eastern North Atlantic between 14° 48' - 17° 22'N and 22° 44'-25° 22'W, 460 to 830km west of Senegal, West Africa. The ten islands and several islets are of volcanic origin, with steep shores, arising from a marine bottom more than 3000m deep. Only the islands of Maio, Boavista, and Sal have a continental platform, while the north-western islands of Sao Vicente, Santa Lucia, Branco, and Raso have limited amounts of water less than 100m deep (Figure1). Most research effort since 1990 has been in the eastern sector of the archipelago around the islands of Sal, Boavista, and Maio. These Cape Verdean waters are known for strong trade winds, rough seas, and sand storms, often making navigation around the islands difficult and hazardous, and producing less than ideal conditions for mariners and whale researchers. This helps explain the low number of fluke photographs and limited amount of information on cetaceans from this region (Reiner *et al.* 1996, Hazevoet & Wenzel 2000, Jann & Wenzel 2001, Jann *et al.* 2003).

Data collection

Searches for humpback whales in the Cape Verde Islands were conducted from February to May in 1990, 1991, 1995, and 1996 aboard a 5m inflatable boat around the islands of Sal and Boavista (Reiner *et al.* 1996, Hazevoet & Wenzel 2000). The searches in 1999 (26 February – 8 April) were made from a 50m steel-hulled motor ship; in 2000 (27 – 29 February, 30 March – 4 April) and 2001 (31 March – 2 May) from a 37m schooner; and in 2002 (22 March – 2 May) from a 20m sailboat. During 2000 – 2002, a 5m inflatable boat was deployed from the larger vessels when humpbacks were observed and sea state permitted. More humpback fluke photographs were obtained in the 1999 – 2002 seasons than in previous years, presumably because of the advantages associated with using larger vessels in the types of sea-state conditions that prevail in these waters.

For each cetacean sighting, the time, GPS position, group size and composition, and behaviour were noted. Fluke photographs were taken to identify individual whales. The photographs were taken with a 35mm single lens reflex camera equipped with a 75-300mm zoom lens using 400 ASA black and white and/or color print film.

Photo comparison

There are two major projects involving individual identification of humpback whales that include geographical coverage over much of the North Atlantic Ocean: the North Atlantic Humpback Whale Catalogue (NAHWC) and the collection from the Years of the North Atlantic Humpback Whale

(YoNAH) project. Both humpback catalogues (NAHWC and YoNAH) are maintained at Allied Whale, College of the Atlantic, 105 Eden St., Bar Harbor, Maine 04609, USA.

The NAHWC is a central curatorial facility for photographs of humpback whales from throughout the North Atlantic Ocean. Photographs date from 1952 to 2004, though few are available from years prior to 1978. The NAHWC project is collaborative, and more than 350 contributors have submitted photographs. Photographs have been obtained opportunistically, so temporal and spatial coverage is highly variable. Most photographs were taken on the western North Atlantic feeding grounds (Table 1 and 2).

The YoNAH project, an extensive study of humpback whales in the North Atlantic, was conducted during 1992 and 1993. It did not include the waters of the Cape Verde Islands, the Irish Sea and other parts of the eastern North Atlantic. As part of that study, identification photographs were obtained in all of the known major feeding grounds and in the West Indies, using standardized protocols. Due to logistical considerations, sampling intensity in Icelandic and Norwegian waters, while considerably greater than during any previous effort, was less than that in the western North Atlantic feeding areas (i.e. Greenland, eastern Canada, and northeastern United States Gulf of Maine) (Smith *et al.* 1999). All identification photographs from the Cape Verde Islands were compared to both the NAHWC and the YoNAH collections (Tables 1 and 2) using methods described by Katona & Whitehead (1981), Katona & Beard (1990) and Smith *et al.* (1999).

RESULTS

Photographic match

A total of 62 individual humpback whales have been identified thus far in the Cape Verde Islands. The first Cape Verde fluke photographs were obtained in 1991 (n=2), and numbers, thereafter, were one in 1995, 22 in 1999, one in 2001, 15 in 2002, 12 in 2003 and 9 in 2004. Ten individuals have been identified in more than one year (Table 3).

An individual, NAHWC#4504, photographed on 10 March 1999 in the Bay of Sal Rei, Boavista, at 16° 02'N, 23° 02'W, had previously been photographed in the Denmark Strait west of Iceland, at 65° 66'N, 27° 30'W, in July 1982 (Fig. 2a – 2b). No other photographic identifications of this animal were recorded during the 18 years between the 1982 and 1999 sightings.

An individual NAHWC#4810, photographed on 4 April 2004, off Boa Vista had been previously photographed off Bear Island, Norway on 9 September 1984. No other photographic identifications of this animal were recorded during the 20 years between the 1984 and 2004 sightings.

DISCUSSION

Over the years, several authors have suggested the existence of two breeding stocks of humpback whales in the North Atlantic, one along the western and another along the eastern margin of the North Atlantic basin, separated roughly at Cape Farewell, Greenland (Ingebrigtsen 1929, Kellogg 1929). However, the degree of separation, overlap and limits of the two proposed stocks have often been discussed and questioned (Mitchell & Reeves 1983, Larsen *et al.* 1996, Palsboll *et al.* 1995 and 1997, Valsecchi *et al.* 1997, Smith *et al.* 1999, Stevick *et al.* 1999a).

Two spatially distinct tropical regions of the North Atlantic have been used traditionally by humpback whales during the winter calving/breeding season – one in the West Indies (assuming a continuous distribution from the Greater Antilles to Venezuela) and one in the Cape Verde Islands. The recent sightings of mothers with new-born calves, recordings of humpback songs, and observations of surface-active groups establish that the waters around the Cape Verde Islands are currently used as breeding and calving habitat during the boreal winter and spring (Hazevoet & Wenzel 2000, Jann *et al.* 2003).

The photographic matches with Iceland and Norway are the first evidence of a feeding-ground destination for humpback whales from the Cape Verde Islands. Humpbacks photo-identified and biopsied off Iceland (Martin *et al.* 1984, Smith *et al.* 1999, Stevick *et al.* 2003), and Norway (Stevick *et al.* 2003, Berube *et al.* 2004) have also been observed in the West Indies. These matches are consistent with the hypothesis that there is overlap in the feeding grounds of animals that visit the West Indies and Cape Verde Islands. Moreover, the failure to match any of the photo-identified animals from the Cape Verde Islands with those from western feeding grounds or the West Indies breeding ground is consistent with the hypothesis that humpbacks from the Cape Verde Islands constitute a distinct breeding population that feeds preferentially or exclusively in eastern feeding areas. Such a model is supported by the existence of mitochondrial DNA differences between eastern and western feeding areas (Larsen *et al.* 1996, Palsboll *et al.* 1995 and 1997, Valsecchi *et al.* 1997).

It is difficult to interpret effort for the NAHWC by region and years. The NAHWC humpback fluke catalogue has grown enormously over the last 30 years, and YoNAH was a limited two-year study (1992 and 1993). However, the low match rate (2) strongly suggests that most of the whales that winter in the Cape Verde Islands use one or more eastern North Atlantic summer feeding areas where there has been little or no recent sampling effort. When one considers how limited the photo-identification effort has been in the eastern feeding areas over the last 20 years, it is not particularly surprising that there are only two matches with a Cape Verde Islands fluke collection, or that there has been an 18 to 20 year interval between the photographs.

CONCLUSIONS

Research effort in the Cape Verde Islands has been modest in comparison to that in the West Indies and many other parts of the western North Atlantic. The first long-distance matches, reported in this paper, should stimulate increased photo-identification effort not only in the Cape Verde

Islands, but also at sites along the likely migratory route to the north (e.g. Azores, Canary Islands, Madeira) and on potential eastern North Atlantic feeding grounds (e.g. the Irish Sea). It should also give impetus to intensified efforts to obtain biopsies and fluke photographs from whales in Cape Verdean waters for comparative genetic and photo analyses. From a local perspective, it is desirable to improve understanding of habitat use patterns, residency times, and site fidelity of individual humpbacks within the Cape Verde archipelago, and to determine whether the population is increasing in this part of the species' range as they have been elsewhere in the North Atlantic (Sigurjonsson & Gunnlaugsson 1990, Smith *et al.* 1999).

The high re-sighting rate for the CVI humpback breeding ground suggests a low abundance of humpbacks return to the Cape Verde Islands for mating and calving (Table 3). However, Cape Verde Island's humpback whale research is problematic. Most effort has been in the northeastern CVI near the islands of Sal, Boa Vista and Maio. Other parts of the archipelago have little or no sampling, and the CVI archipelago extends over 250km. Reports of humpback sightings from the islands of St. Nicolau and St. Luzia, have gone unconfirmed. Does a low abundance, high re sight on this breeding area, highlight the slow recovery of the CVI humpback population? Additional research including, photo-identification and biopsy and a wider more expansive study area encompassing the entire CVI archipelago, will be required to answer these questions.

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TABLE 1. Total number of photographs and identified whales per region, including re-sightings between year and region.

Region	Total Number Photos	Total Number Whales	Number Re-sighted in More Than One Year	Number Re-sighted in More Than One Area
Virgin Islands	204	140	3	57
Puerto Rico	614	470	25	175
Dominican Republic	2,686	1,728	169	537
Bermuda	279	136	5	55
US South. of Cape Cod	191	70	4	30
Gulf of Maine	8,495	1,117	650	198
Gulf of St. Lawrence	1,259	346	161	180
Newfoundland	4,654	1,839	424	482
Greenland	1,179	411	210	85
Iceland	62	43	2	12
Eastern North Atlantic	182	118	0	14
Europe	18	10	0	0
Cape Verde Islands	109	62	10	2
Total NAHWC	19,932		1,663	

TABLE 2. Number of individual whales sampled in each region, the distribution of re sightings between regions, and the number of individuals re sighted in each region in more than one year.

Region	Total	Betw/Yr	V	P	D	B	U	M	L	N	G	I	E
Virgin Islands	140	3											
Puerto Rico	470	25	13										
Dominican Republic	1728	169	24	67									
Bermuda	136	5	4	7	22								
US So. Of Cape Cod	70	4	-	-	3	-							
Gulf of **M**aine	1117	650	7	21	120	12	23						
Gulf of St. **L**awrence	345	161	2	22	51	4	1	23					
Newfoundland	1839	425	16	83	280	17	6	24	143				
Greenland	411	210	8	7	62	3	-	1	3	13			
Iceland	43	2	-	4	3	1	-	-	-	-	0		
Eastern North Atlantic	118	-	-	3	8	-	-	-	-	-		5	
Europe	11	-	-	-	-	-	-	-	-	-		-	-
Cape Verde Islands	62	10	-	-	-	-	-	-	-	-		1	1

TABLE 3. Total number of photo-identified humpbacks by fluke photographs by year. All CVI flukes in the NAHWC (Code 3 or better quality).

Year	1991	1995	1999	2000	2001	2002	2003	2004	Total
n (New Flukes per year - CVI)	2	1	22	0	1	15	12	9	62
Resightings from previous CVI yrs.	0	0	0	0	0	0	7	3	10
Humpbacks matched to NAHWC			1					1	

FRAMEWORKS FOR DEVELOPING RESPONSIBLE WHALE-WATCHING IN IRELAND AND ON OTHER ISLANDS IN THE NORTHEAST ATLANTIC

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ABSTRACT

Whale-watching is one of the fastest growing tourism industries in the world with an estimated growth between 1991 and 1998 of 12% per annum. On Atlantic islands, whale-watching is carried out from Iceland to the Canary Islands including the Faroes, Britain, Ireland and the Azores. In Ireland, whale-watching is estimated to be already worth €7.9 million per annum but the potential is still under-developed, especially off the south coast. Whale-watching can bring economic benefits to coastal communities and can enhance the conservation status and public awareness of cetaceans. However, most cetacean species are protected and some species are declining or rare and the subject of conservation measures. Other populations are still severely depleted after decades of over-exploitation. Responsible whale-watching provides an economic benefit to operators and coastal communities but should not displace cetaceans or degrade their habitat. In order to develop and manage responsible whale-watching, a framework is necessary. In this paper, a potential framework is presented for developing or managing whale-watching on Atlantic islands.

INTRODUCTION

Whale-watching is one of the fastest growing tourism industries in the world with an estimated growth between 1991 and 1998 of 12% per annum (Hoyt 2000). On Atlantic islands, whale-watching is carried out from Iceland to the Canary Islands including the Faroes, Britain, Ireland and the Azores. However the scale ranges from over one million whale-watchers in the Canaries to only a handful in the Faroes and the Cape Verde. In Ireland, whale-watching was estimated to be already worth €7.9 million per annum in 1998 but the potential was still considered under-developed, especially off the south coast (Hoyt 2000). At least four cetacean species have been identified with good to excellent potential for supporting whale-watching. These are fin and humpback whales and common and bottlenose dolphins (Berrow, 2001). Thus the Atlantic islands offer the full spectrum of sites to assess the development and management of whale-watching.

Whale-watching can bring economic benefits to coastal communities and can enhance the conservation status and public awareness of cetaceans. However, all cetacean species are protected and populations of some species are declining or rare and the subject of conservation measures. Other populations are still severely depleted after decades of over-exploitation. In order to achieve the development of responsible and sustainable whale-watching, which brings positive benefits to people and cetaceans, a framework is required for conservation management and tourism development. This paper discusses appropriate frameworks to ensure responsible whale-watching on Atlantic islands.

WHALE-WATCHING ON ATLANTIC ISLANDS

Whale-watching on Atlantic islands is economically significant (>€0.5 million in direct revenues) for six island groups (Table 1). Only on the Faroes and Cape Verde is whale-watching still largely undeveloped. The potential in the Faroes is limited due to unfavourable weather conditions but Cape Verde, where humpback whales breed, has potential.

WHALE-WATCHING IN IRELAND

The majority of the estimated 177,600 whale-watchers in Ireland in 1998 visited the wild, solitary, bottlenose dolphin in Dingle Harbour, Co Kerry. This dolphin has been in the harbour since 1984, however this whale-watching is not sustainable as it is based on one dolphin, which will eventually die or move away. Whale-watching on bottlenose dolphins in the Shannon estuary started in 1993 and by 1995 around 2,500 people were visiting west Clare to see the dolphins. In 2000 visitor numbers increased to about 12,000 people and presently around 450-500 trips, catering for 15-20,000 people are carried out each year (Berrow 2003a). Whale-watching in 1997-98 was estimated to be worth between €108,000-241,000 to the local economy (Berrow and Holmes 1999). Since 2000, the Shannon estuary has been designated a candidate Special Area of Conservation for bottlenose dolphins under the EU Habitats Directive. Under this legislation, the operation of commercial recreational activities such as whale-watching is a notifiable activity and all persons must obtain the written consent of the Minister of Environment, Heritage and Local Government.

A dedicated whale-watching operator has recently become established off southwest Ireland, operating from Castletownshend in County Cork with a range of species being watched, including common, bottlenose and Risso's dolphins and minke, fin and humpback whales. Since 2001 this one operator has carried out around 150-200 trips per annum. In addition, a number of angling and diving boats around the country are advertising whale and dolphin watching as part of a marine wildlife trip. Land-based whale-watching is popular and widespread all around the island of Ireland. Dedicated whale-watching weekends on Cape Clear Island, County Cork and Tory Island, County Donegal have been held since 2001. To date over 300 people have attended these weekends, which can make a significant contribution to these islands' economies.

Visitor surveys have shown that the present market for whale-watching is mainly from within Ireland, accounting for around 60% of those interviewed. However whale-watching is also an important attraction for overseas visitors. For example, in a survey carried out in Dingle in 1999, 42% of overseas people interviewed said that the dolphin was the main reason for visiting the town and 5% stated that the dolphin was the main reason they decided to holiday in Ireland (Berrow and Whooley 1999). In a survey carried out in Kilrush, County Clare in 2003, 30% of those interviewed said the dolphins were a major factor for coming to County Clare and 68% a major factor in them coming to Kilrush (Berrow *et al.* 2004). Nearly 15% of those people attending whale-watching weekends on Cape Clear travelled from the UK. Thus whale-watching offers a potentially very important tourism product for attracting people into Ireland, especially if packaged with other outdoor nature-based activities.

WHAT IS RESPONSIBLE WHALE-WATCHING?

Whale-watching is well developed or expanding in many EU countries but these tourism activities can have a detrimental effect on the behaviour of whales (IFAW *et al.* 1995) and the long-term sustainability of whale-watching has not been assessed. If whale-watching, along with other forms of marine ecotourism, are to be viable long-term economic alternatives for coastal communities in Europe, it is essential that activities are sustainable. The scientific management of whale-watching and tourism is extremely limited. There are few published studies of whale-watching operations and, despite the economic importance of whale-watching, there have been few socio-economic studies on this industry.

Responsible whale-watching provides an economic benefit to operators and coastal communities but should not displace cetaceans or degrade their habitat. It should also provide information on the species and habitat being exploited and should aim to enhance the conservation status of the species.

FRAMEWORK REQUIRED FOR RESPONSIBLE WHALE-WATCHING

A number of factors must be considered to ensure whale-watching is carried out responsibly. These factors should be modified for each location and species involved but each element should be in place. This framework can also be applied to other marine wildlife tourism (see Berrow 2001). We recommend the following factors should be considered in a framework designed to develop responsible whale-watching (a full description of all these factors is available in Berrow 2003b).

Regulations and Legislation

Voluntary guidelines (e.g. Codes of Conduct) can be very effective in minimising disturbance to cetaceans but they may not always be strong enough to control potentially damaging activities (Carlson 2000). Codes of Conduct must be developed for each site independently and in consultation with operators and other stakeholders but drawing on the experience of sites elsewhere. The designation of Marine Protected Areas (MPA) for cetaceans is expanding rapidly and these can play an important role in managing whale-watching (Hoyt 2005). In Ireland, the Habitats Directive has been used to manage whale-watching in the Shannon estuary (Berrow 2003a).

Research

There is a lack of basic information on the ecology of cetaceans in Irish waters and the impact of tourism. All cetacean species in Irish waters are legally protected, but many species that could form the basis for whale-watching in Ireland are also depleted after overexploitation, and thus conservation is a priority. Research should be an essential element of whale-watching, and whale-watching vessels offer a very important platform with which to carry out research. Hypothesis testing, which can be used to assess the effectiveness of different monitoring parameter used to determine impact, is essential for the scientific management of whale-watching (IFAW *et al.* 1995). Research can enhance the tourism experience and studies have shown whale-watchers are willing to pay more if a proportion of the money funds research.

Education and awareness

Similar to research, education should be an integral part of developing responsible whale-watching. Information on the species and habitat being exploited should be available to whale-watchers and operators alike. Information on legislation and guidelines, such as any code of conduct etc., should be promoted at all opportunities together with the sensitivity and conservation value of the site.

Funding

Responsible and sustainable development of whale-watching requires a long-term funding commitment. The whale-watching industry could generate the funds necessary for monitoring of their activities through an environmental levy, which should be considered an operating overhead.

Monitoring

The effect of tourism activity on cetacean species and the habitat they exploit must be quantified and its impact assessed. This information is essential to determine carrying capacity, which is the amount of activity a species or habitat can be subjected to without affecting its long-term viability, and is the biological framework within which whale-watching should be managed. In order to develop responsible ecotourism, monitoring people and product satisfaction is also essential. Monitoring must be conducted in the long-term, which requires a regular commitment rather than through short-term, intensive studies.

SUMMARY

Whale-watching is already economically important or is expanding rapidly on most Atlantic Islands. It can make a significant contribution to the economy of these islands but in order to be sustainable and contribute to the conservation of cetaceans it should be planned and monitored. A framework for planning and/or managing whale-watching on Atlantic islands is presented. All of the elements in the framework should be considered and implemented to ensure whale-watching is managed responsibly.

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TABLE 1. Numbers of whale-watchers and their expenditure (€) on Atlantic islands (adapted from Hoyt 2000).

Country	No. of Whale-watchers	Year began	No. communities	Value Direct	Value Indirect
Azores	9,500	1989	2	652,000	3,774,000
Canaries	1,000,000	Late 1980s	5	19,902,000	69,658,000
Cape Verde	minimal	1990s	1	-	-
Faroe Islands	minimal	1996	1	-	-
Greenland	2,500	early 1990s	6	932,000	3,080,000
Iceland	30,330	1991	8	3,313,000	7,246,000
Ireland	177,600	1986	3	1,480,000	7,973,000
Britain	121,125+	mid 1980s	>10	2,110,000	9,219,000

ECOTOURISM WORKSHOP: ON THE DEVELOPMENT OF RESPONSIBLE WHALE-WATCHING ON ATLANTIC ISLANDS: CHALLENGES AND OPPORTUNITIES

University College, Dublin: 25 August, 2004

Attended by: Simon Berrow, Dorete Bloch, Margaret Duffy, Bernard Faria, Bob Firmin, Erich Hoyt, Beatrice Jann, Ana Margarida Madeira, Sonia Elsy Merino, Claudia Riberiro, Fred Slater, Amy Tibble, Dave Wall, Fred Wenzel, Faith Wilson.

OBJECTIVES

Whale-watching is one of the fastest growing tourism industries in the world but the potential in many Atlantic islands is still under-developed. Whale-watching and other forms of marine ecotourism have the potential to bring economic benefits to remote coastal communities, but are exploiting protected species. This workshop will explore some of the opportunities to develop whale-watching in the Atlantic islands, some of the constraints any development has to consider and will seek to establish guidelines for the development of responsible and sustainable marine ecotourism.

INTRODUCTION

The workshop wished to state that they thought marine ecotourism[2] was a positive development in a community and should be encouraged. Concern was expressed about the potential impact of unregulated marine ecotourism without regulation or a development framework. The background to

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[2] The definitions of ecotourism follow META (see www.tourismresearch.org/).

developing marine ecotourism and some of the problems involved were presented at the conference.

OPPORTUNITIES

The opportunities for developing marine ecotourism were discussed and what aspects should be considered if intending to promote marine ecotourism. An audit or inventory of the opportunities is recommended for marine ecotourism. This audit should be as inclusive as possible to create ownership. An audit should include:

i) Species present (all flora and fauna)
ii) Cultural heritage
iii) Seasonal distribution
iv) Present knowledge, access to databases
v) Life history of key species, e.g breeding and feeding behaviour
vi) Present ecotourism activities
vii) Identify stakeholders (including fisheries) and their responsibilities
viii) Relevant legislation

MANAGEMENT

A number of aspects, which should be considered to manage marine ecotourism, were discussed. These included:

i) Licensing: a license for carrying out marine ecotourism should be encouraged. This is the most effective way of regulating the impacts of marine ecotourism as the number of vessels can be controlled. The licensing fee could be used for monitoring and/or research. A company or operator that has applied for a license should be assessed on a number of factors including local involvement in the company (e.g. the proportion of local staff) and any educational component (e.g. use of trained guides, local knowledge etc.). An accreditation scheme for licensed operators is often very effective.

ii) Business plan: a business plan should be submitted with a license application. The plan should include; the number of trips to be carried out per annum, areas exploited, land-based facilities and operation, education programme, local employment potential, any research to be carried out and a cost-benefit analysis. A business plan should be compulsory for grant aid.

iii) Monitoring: all marine ecotourism operations should be monitored for their potential impact on the environment. Marine ecotourism should be carried out within the carrying capacity of the species/habitat and, where this is not known, should adopt the precautionary principal. A code of conduct is often very useful in promoting good practice but the effectiveness of any code should be quantified. Monitoring of the economic benefits of marine ecotourism and visitor satisfaction should also be carried out. Economic carrying capacity is also important (infrastructure, resource use etc.) and often is easier to quantify and regulate compared to biological carrying capacity.

iv) Marine Protected Areas (MPA): the effectiveness of MPA was discussed. These can be very effective once critical habitats for the species/habitat exploited have been identified. Within MPA there should be control areas, no-go zones or sanctuaries where no marine ecotourism is permitted. These may be seasonal or permanent but without control areas the impact of marine ecotourism is very difficult to determine. Where relevant MPA should be linked to the life history of the species (e.g. feeding and calving grounds).

SUMMARY

The workshop considered marine ecotourism to be a positive opportunity for coastal communities and should be encouraged. Controls, including licensing and monitoring, should be an essential part of an overall framework for promoting and managing marine ecotourism.

MARINE ECO-TOURISM IN CAPE VERDE: ITS POTENTIAL FOR SUSTAINABLE DEVELOPMENT AND CONSERVATION OF MARINE BIODIVERSITY

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ABSTRACT

The ten islands forming the Cape Verde archipelago are surrounded by 734,265km^2 of sea, which makes up the Exclusive Economic Zone. The nearest point to the African continent is Ponta Roque in Boavista, 560km to the east. With an average maximum sustainable yield (MSY) of only 40,000 tonnes and a worldwide decrease in fish landings the whole population of the Cape Verde Islands (CVI), but in particular the fishing communities, are vulnerable to reductions in fish populations. Fish is the staple diet of the CVI population and incomes among fishermen are getting lower each year. Marine eco-tourism is an alternative option for sustainable use of marine resources and further developing the economy. At least 17 cetacean species occur in the archipelago. Blue and humpback whales occur seasonally and a wide variety of dolphins are seen throughout the year in the bays and around the islands. Five species of marine turtles use the islands as feeding grounds. Loggerhead turtles nest from June to October and green turtles visit the islands high-energy zones, where they feed all year round. Marine birds and the under-researched coral reefs are also important for marine eco-tourism. Endemism in the CVI is very important. Scientific tourism has been significant in the archipelago for

many years and needs to be planned and developed in a fair manner by interested international scientists. A framework is required to develop marine eco-tourism, which will enhance conservation, increase environmental awareness and provide economic benefits to the Cape Verde.

INTRODUCTION

The Cape Verde Islands are located in the Sahel and the harsh climate is typical of the region, with drought, erosion and serious limitation in water resources. Due to these constraints, agriculture and fisheries make only a small contribution to the national growth product (NGP), of 9% and 1% respectively. This limited input is linked to food security, generation of economic activities and stabilising the national salary balance.

Due to the harsh environment and limited natural resources, a culture of survival and subsistence has endured from the time the first settlers arrived in Cape Verde in 1460. Nonetheless, the sea around the Cape Verde provides high quality protein, equivalent to 26.2 kg per capita in 2000, and fishing directly and indirectly employs an estimated 5.2% of the economically active population (PNGP 2003). The remoteness of the Cape Verde archipelago has also resulted in high biodiversity with a large proportion of endemic species, typical of oceanic islands, especially among marine ecosystems and provides breeding grounds for a diversity of migratory marine species.

BIODIVERSITY IN THE CAPE VERDE ISLANDS

The Cape Verde archipelago is surrounded by an estimated 734,265km^2 of ocean, which accounts for the islands Exclusive Economic Zone (Bravo de Laguna, 1985). Despite the occurrence of interesting regional currents and counter-currents and local upwellings caused by the island effect, oceanic and coastal primary productivity are limited. The influence of the Canary current upwelling and thus, its influence on the regions net biomass is limited (0.1-0.46

mg/m^3) (IPIMAR/INDP, 1997) due to remoteness of the Cape Verde from the African continent.

The components of the marine ecosystems are characterised by five species of marine turtles, 17 cetacean species and a wide diversity of elasmobranches (sharks and rays, including manta rays) but that are poorly known. The islands are surrounded by a limited shelf area (up to 200m deep) of only 5,394km^2 (0.7% of total EEZ) which provides shelter and nursery grounds for at least 80% of the known marine species (Ronald 1992, Van der Land 1993) and supports a coral environment that has been ranked eleventh among the eighteen richest sites for marine biodiversity in the world and eighth among the most threatened (Laborel 1974, Roberts *et al.* 2002). The diversity of coastal waters not only provides a range of excellent sites for turtles to lay their eggs but also suitable feeding areas and shelter grounds. These same coastal zones are also important to some migratory and endemic birds. Oceanic and deep-sea ecosystems in the region include a system of sea-mounts rich in fish life.

Defined as a strategic tool for the sustainable economic development of the CVI, over the last two decades the tourism industry has been favoured by incentives. Due to the Cape Verde natural environment, a high percentage of that tourism is concentrated in the coastal zone. Hotel tourism target activities include beach tourism, diving, game fishing, and a diversity of aquatic sports. In recent years uncontrolled whale watching has also been going on, while some organised turtle watching has started in Boavista Island. One very important activity is sport fishing. In the opinion of some specialists, if properly developed, the value of this fishery would greatly exceed that of the commercial and artisanal fisheries.

MARINE PROTECTED AREAS AND ECO-TOURISM

In the context of the National Environmental Action Plan (PANAII) and with technical support and advice from the Regional Programme for the

Conservation of the Marine and Coastal Zone in West Africa (PRCM) a process for creating sustainable Marine Protected Areas (MPA) has started in Cape Verde. Two main zones in the Cape Verde have been identified as especially important for conservation.

The Sal-Boavista-Maio islands zone has more than 60% of the country's total biodiversity, the gross of it primarily occurring on the shallow shelf. North Atlantic humpback whales seem to be strongly linked to these areas, which they use each year, for breeding (Jann & Wenzel 2001, Hazevoit & Wenzel 2000). These three islands also provide breeding beaches, shelter and feeding grounds to at least loggerhead, hawksbill and green sea turtles.

The second, the São Vicente-Santa Luzia islands and the Branco and Raso islets zone constitute the rest of the archipelago shelf flora and fauna. Dolphins and whales are frequently seen in this area. On Santa Luzia, a mass stranding of 162 melon-headed whales (*Peponochephala electra*) occurred in November 2003. Marine birds and endemic reptiles occur at the Branco and Raso islets and the whole zone also supports reproduction and provides feeding grounds to marine turtles.

Both zones are important centres for marine biodiversity (DGMP 1997) and thus are important for conservation and have great potential for marine eco-tourism. More importantly for Cape Verde, they are also home to the majority of the local fish resources and provide animal protein that in 2000 was equivalent to 26.5 kg per person (PANA 2003). Besides, it is well known that the waters around the archipelago provide migratory corridors for leatherback and olive ridley sea turtles (Fretey 2001).

Despite being worth an estimated €38 million in 2000 and growing at around 20% per annum (Hoyt 2001), tourism still provides little employment (0.4%) in Cape Verde among locals and does not yet contribute to the national salary balance (PND 2000). Besides, tourism suffers from insufficient regulation, deficient surveillance and enforcement and uncontrolled development within a limited legislative framework. Tourism occurs in ecologically sensitive areas and in some cases can actually compete with fishing. Furthermore, the legal framework in Cape Verde means that the tourist administration services are provided for free and the islands do not benefit from the presence of national tourism operators.

In an ideal framework, eco-tourism could be an excellent tool for the future management and planning of conservation by encouraging enjoyment and delight of nature while minimising the threat of overexploitation of natural resources and promoting local sustainable economic development (Thomas & Middleton 2003). This framework would link conservation with environmental education and development of a conservation consciousness and awareness. In such a framework, it is important to distinguish eco-tourism from nature tourism, the latter using nature to generate revenues while disregarding ecological and economic sustainability. Besides, non-consumptive use of marine resources is also important as a mean to soften the blow for fishermen when fishing rights are introduced.

In order to maintain and improve biodiversity in the ecosystem, non-consumptive use of marine resources, namely eco-tourism, needs to be carefully planned and monitored, to prevent it transforming into chaos. There is a need to study and develop guidelines for whale and turtle watching that are internationally acceptable, in harmony with accepted practices. Any planned activity must not jeopardise the life history of the animals (sharks, whales, turtles, seabirds, coral reefs, and so forth).

When integrated into a MPA system that is strategically linked to environmental education and awareness while simultaneously generating revenues for the local economy, eco-tourism can smooth the path to a participative process in the organisation and co-management of existing protected areas.

CHALLENGES

- ⇒ To drive people to the conclusion that the MPA concept is a strategic tool both for conservation and sustainable economic development and use of marine resources;
- ⇒ Change the mentality of current tourism administration and operators by integrating eco-tourism in the National Strategic Plan for Tourism (NEPT) as one more type of tourism with powerful potential for conservation and sustainable ecological and economic development;
- ⇒ Involve a wide range of interested people in the co-management process of establishing new MPA´s: local communities, governmental structures, current tourism operators; and establish political willingness so that ecotourism politics is incorporated in the tourism development national strategy;
- ⇒ Transform scientific tourism in an effective and efficient manner as a source of scientific knowledge shared internationally, producing revenues for local conservation and incomes to locals, carried out in a fair and sustainable manner;
- ⇒ An operational and effective legislation framework;
- ⇒ Conservation and ecotourism surveillance and enforcement specific actions;
- ⇒ A capacity building strategy (at various levels).

CONCLUSION

In short, such a framework needs to be planned and managed appropriately and incorporated into a participatory process for establishing MPAs in Cape Verde. In economic terms it needs to generate income for the local communities, provide revenue for the conservation of marine resources and support the co-management and enforcement of MPA´s, but has also to provide revenues for tourism operators, the tourism administration and generate new employment.

At the education and training level, a framework for MPA and eco-tourism needs to generate local environmental and conservation awareness and promote changes in attitude while generating new habits on use of the environment and natural resources. We need to identify ways for transforming the extractive mentality of users to a new conservationist mentality of use of natural resources. But we also need to prepare new conservationist and eco-tourism operators and guides.

Careful planning and responsible management are essential to achieve the above-mentioned goals and objectives, which is the gateway to eco-tourism benefits.

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SUSTAINABLE TOURISM IN SANTA MARIA, SAL, CAPE VERDE: A SWOT ANALYSIS

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INTRODUCTION

Of all the island groups of Macronesia, the Cape Verde Republic has the least well-developed tourist economy. Relative to its scale there is, however, very rapid tourism development in a few areas, particularly in the south of Sal, especially in, and in the vicinity of, Santa Maria. Because of the experience gained by similar developments in comparable places elsewhere, there is a fund of knowledge which could be used in Cape Verde to add environmental sustainability of tourist developments for the advantage of visitors and the local economy (Page & Dowling 2002). By taking Santa Maria as an example, we conducted a SWOT analysis to examine the strengths and weaknesses of the location for sustainable tourism and consider both the opportunities and threats that the future could hold.

STRENGTHS

The Cape Verde Islands, situated as they are some 16° N between the Equator and the Tropic of Cancer, have a climate well suited to beach-based tourism. Santa Maria on the island of Sal is located on the south coast some 20 minutes drive from the main international airport in the archipelago, which provides easy access for visitors and a stopping-off point for tourists to other islands. The prevailing Northeast Trade Winds that provide onshore winds to the eastern beaches conversely provide offshore winds on the southern beaches, ideal for many sea-based activities. The environs of Santa Maria provide the potential for other non-wind dependent activities such as diving, cetacean watching, turtle watching as well as several kilometres of pristine beach. Tourism is also a market for locally sourced seafood.

WEAKNESSES

The rapid spread of resort-type developments threatens the natural social and cultural ambience of the town. These developments appear to have no clear plan for sustainable development, let alone an ecotourism plan. For example, the disposal of solid and liquid wastes does not appear to be a priority and, because water on the islands is almost always supplied by desalination, the greening of hotel grounds by planting and constantly watering grass is a prime example of an unsustainable activity. Although the main southern beach at Santa Maria benefits from the offshore winds, the otherwise pristine beaches to the east of Santa Maria receive all the debris carried by the Northeast Trade Winds, a problem for which there is no easy answer (Figure 1). The history of Santa Maria is linked to the salt industry and the old salinas have been destroyed by development removing an opportunity to link the past to the present.

OPPORTUNITIES

There is an opportunity before Santa Maria gets too big, for a development plan to be implemented with sustainability in mind. Not only could some salinas be kept working as tourist attractions but others could be redeveloped as treatment areas for waste water which would encourage general biodiversity and birds in particular, in an area of the archipelago short of birding sites.

A sustainable development plan could insist that hotel developments use the concept of "signature landscapes" when greening their grounds i.e. use native drought resistant species for extensive plantings rather than water-demanding alien grass. Similarly, dune stabilisation may soon be necessary to offset recreational vehicular traffic and this can be done with suitable, non water-demanding species of plant.

To take controlled advantage of the growing demand for ecotourism, guides for visitors to turtle nesting-sites and cetacean watching need to be trained from within the local population. Some salinas could be retained in working order as a tourist attraction. There is also the potential to develop a local craft industry to provide souvenirs for visitors rather than rely on imports from the African mainland. In renewable energy terms, the key to sustainability could be wave and wind power.

THREATS

The current economic success of tourism has lead to problems such as over-fishing of some resources such as lobster and overpricing of fish to meet tourism demand to the detriment of local people. There is an unstructured eastward spread of development towards the east-coast turtle beaches combined with the increasing use of "dune buggies" and 4-wheel drive vehicles in the coastal dune areas. These have been seen cutting through turtle nesting sites, leaving deep ruts parallel to the sea into which hatchling turtles can fall to be taken by the increasing number of dogs that come with increasing human numbers. On these beaches the turtles already have their natural predators and large quantities of sea borne debris to deal with, particularly nets and rope in which animals can be come entangled.

The Cape Verdian character of the town is under threat with the loss of historical and cultural elements of the area, particularly the salinas and locally owned facilities, in the face of mainly European investment in tourist developments. However, if the salinas areas were to be used for water treatment, care should be taken to control any potential mosquito problem.

DISCUSSION

It is clear that Santa Maria has the climate, beaches and general location to be an economically successful tourist location. However, its tourist infrastructure of hotels and apartment blocks is expanding at such a rate, due largely to southern European investment, that this baby of an industry with such potential, is in danger of being thrown out with its own polluted bathwater. Certainly it is an ideal place for wind-based water sports, beach holidays and diving and has the ecotourism potential of turtles and cetaceans and a good reputation for locally caught seafood. What it lacks is the vision of where the current developments should lead, a plan for sustainable development and an understanding of the potential of the controlled utilisation of the local wildlife resources.

Sustainability need not be costly. The development of water efficient "signature landscape" plantings would save thousands of litres of water per day to some resort hotels. Centralizing waste water treatment in redeveloped salinas would avoid disposal of sewage in the sea or cess pits and would provide recycled water for non-consumptive uses such as watering and would make the treatment areas magnets for water birds. Evidence that birds would use the treatment area is already present. At the extreme western end of the beachfront developments, a 15m x 10m pool of waste water emanating from the adjacent holiday complex in July 2004 held 11 species. These were Black-winged Stilts (4), Cattle Egrets (4), Sanderling (20), Common Ringed Plover (6), Little Stint (3), Whimbrel (1) and Ibis (1), plus at least four other species of wader. In addition at least 5 pairs of Kentish Plovers were nesting (some with eggs, some with young) within 100m of the pool. This list is similar to that found by Sargent (1997) around the salinas before major development began. The potential for biodiversity development, not just birds, in a water treatment area is therefore considerable.

Turtle and whale/dolphin watching could become a lucrative trade (Hoyt 2000), but would require trained guides to be sustainable. Guides to turtle beaches drawn from local people would be ideal if not easy to provide, train and control. It is likely that whale and dolphin watching will develop and will be mainly from larger foreign-owned boats. Here the government has an opportunity to insist on licences for cetacean watching boats and that such boats should carry a trained local naturalist/guide giving local people a stake in the resource. Similarly if a working salina were kept as a tourist attraction, local people could share in its success.

The eastward spread of development seems sporadic and unstructured. However, the debris-strewn beaches of the east coast may have limited attractiveness to visitors leaving them available for nesting turtles. They are, however far from ideal. Much of the beach debris is rope, nets and floats from the fishing industry and nesting turtles and returning hatchlings have to cross this littered landscape with the ever present risk of entanglement. Ruts caused by four-wheel drive vehicles and "dune buggies" trap hatchlings. Domestic dogs already prey on nests and more development will inevitably lead to more dogs.

On a larger scale and in the longer term, wind and wave power could make Cape Verde a world leader in sustainable green-energy production. Santa Maria is the vanguard of tourist development in the Cape Verde Island, it still has the opportunity to secure sustainability for its environment, but that window of opportunity will be short-lived and within less than a decade, if nothing is done, many local people will be saying the Crioulo equivalent of "if only."

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FIGURE 1. Map of Sal showing location of Santa Maria and the direction of the Northeast Trade Winds.