

THE AZORES HYDROID FAUNA AND ITS ORIGIN, WITH DISCUSSION OF RAFTING AND MEDUSA SUPPRESSION

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ARQUIPÉLAGO



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An international study of Azorean coastal benthos, especially of that around Faial island, has added ten hydroid species to the faunal list which now totals about 70 species depending on taxonomic opinion. The species newly recorded are: *Tubularia crocea*, *T. indivisa*, *Eudendrium* sp., *Bougainvillia* sp., *Silhouetta uvacarpa*, *Laomedea calceolifera*, *Amphisbetia operculata*, *Diphasia* cf. *attenuata*, *Ventromma halecioides* and *Aglaophenia picardi*. The nature and zoogeographic origin of this limited hydroid and hydromedusa fauna are discussed in relation to ocean currents and other environmental factors.

The shallow-water fauna has a high proportion of hydroid species lacking a medusa stage. Their recruitment to the Azores is likely to have been through trans-oceanic rafting. Further, most of the locally recorded hydroids which do have a medusa stage are known to raft. Possibly no shallow-water Azorean hydroid has become established in the archipelago by means of a medusa stage liberated on a mainland continental coast.

Winter storms and browsing by subtidal fish are considered important factors in limiting Azorean hydroid populations.

A recognisable group of rafting hydroid species, some having and some lacking a medusa stage, occurs on oceanic islands around the world. The concept of "species club" is introduced to embrace this phenomenon.

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Um estudo internacional do benthos costeiro dos Açores, especialmente daquele ao redor da ilha Faial, permitiu adicionar dez novas espécies de hidróides à lista faunística, a qual totaliza agora setenta espécies dependendo da linha taxonómica adotada. As novas ocorrências regionais são: *Tubularia crocea*, *T. indivisa*, *Eudendrium* sp., *Bougainvillia* sp., *Silhouetta uvacarpa*, *Laomedea calceolifera*, *Amphisbetia operculata*, *Diphasia* cf. *attenuata*, *Ventromma halecioides* e *Aglaophenia picardi*. A natureza e a origem zoogeográfica da limitada fauna de hidróides e de hidromedusas são discutidas em relação às correntes oceânicas e a outros fatores ambientais.

A fauna de águas rasas tem uma alta proporção de espécies de hidróides nas quais a fase de medusa está ausente. É provável que o seu recrutamento para os Açores tenha ocorrido através de deriva trans-oceânica. Além disso, a maioria dos hidróides, reportados para o local, que possuem uma fase de medusa, derivam. Possivelmente, nenhum hidróide açoriano de águas rasas, se estabeleceu no Arquipélago, através de um estado de medusa proveniente da zona costeira continental.

As tempestades de Inverno e o facto de serem alimento dos peixes da região infralitoral são considerados importantes factores na limitação das populações dos hidróides açorianos.

Um grupo reconhecido de espécies de hidróides derivantes, alguns com e outros sem o estado de medusa, ocorre em ilhas oceânicas ao redor do mundo. O conceito de "species club" é introduzido para explicar este fenómeno.

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INTRODUCTION

"The marine invertebrates of the Azores are apparently quite poorly known and no reliable data could be found" (BRIGGS 1974: 208).

New records of hydroids collected during a study of Azorean coastal benthos - "Expedition Azores 1989", are presented and analyzed along with previous local records of the group. The parent investigation sought to document and describe the benthic biota to a depth of ca. 30 m. Plankton was not especially collected. The present account is based largely on material gathered during the author's secondment to this joint study. Specimens collected have been deposited either in the Department of Oceanography and Fisheries, Horta [DOPH], Faial, University of the Azores, or in the Zoology Department, The Natural History Museum, London, [BMNH; registration series 1990.5.2.1-28]. More details about "Expedition Azores 1989" can be found in MARTINS & al. (1992).

Biogeographically the Azores archipelago is interesting for several reasons. The islands are young and remote, being formed from volcanic activity connected with the Mid-Atlantic Ridge. They rise steeply from the surrounding undulating abyssal plain which is mostly 1000-2000 m deep. The relevant prevailing ocean currents mostly tend not to cross directly from the nearest land masses, considerably increasing the geographic isolation of the islands (NAVAL INTELLIGENCE DIVISION 1945; HYDROGRAPHIC DEPARTMENT e.g. 1953; summaries of various aspects in GOFAS 1990, BIGG 1990 and publications cited therein). Identification of the Azores hydroid and hydromedusa fauna is considered elsewhere (CORNELIUS in press).

The larvae of some shallow-water invertebrates can cross great oceanic widths (SCHELTEMA & WILLIAMS 1983; SCHELTEMA 1989, and literature reviewed therein). But the distances are still so great as probably to prevent the dispersive planula and/or hydromedusa stages of many hydroids, from reaching the Azores, with consequent implications for the fauna. Some hydromedusae can bud off new medusae thus bypassing a benthic stage and this might substantially increase

their dispersive capability. The necessary analysis of which species have this capability has not been done, though many that do are coastal forms which may not be adapted to open-oceanic conditions: not least plankton density. The basic hydromedusan life cycle comprises a succession of planula, hydroid and hydromedusa (often simply termed 'medusa'). But in some thirty-five per cent of the genera and perhaps half the species the medusa stage never leaves the parent hydroid colony and is not dispersive (see p. 91). The planulae of most species are considered to be lecithotrophic and hence short lived, probably settling after a matter of hours to a few days. Most hydrozoan planulae contrast with those of anthozoans many of which are said to be larger and longer lived, planktotrophy being widely recorded among planulae of the latter group (WERNER 1984: 50). Further, it seems that most coastal hydromedusae live for only a few weeks (RUSSELL 1953) and would similarly be unable to make a long oceanic crossing (RALPH 1961c; KRAMP 1968; CORNELIUS 1981, 1990b). Analysis of the remote Azorean hydroid fauna contributes to an understanding of how this group disperses across such distances.

The widely distributed pelagic *Porpita* and *Velella*, which have a conspicuous floating hydroid stage, often occur in the Azores. Although they release a typical hydromedusa the neustonic way of life of their hydroid stages is exceptional. They are not mentioned further.

Hydroids and medusae are jointly referred to as leptolids, a little-used term discussed elsewhere (CORNELIUS 1990b). The authorities for scientific names of species mentioned are given in an Appendix.

General aspects of the biology and evolution of hydroids and hydromedusae, with particular reference to remote-island forms, are considered further elsewhere (CORNELIUS 1992).

The specific aims of the present paper are to report additions to the known hydroid fauna collected during "Expedition Azores 1989" together with some previously collected specimens, to review and confirm existing records, and to assess

the biogeographical implications of the species recorded from the Azores.

THE LEPTOLID FAUNA

Records and collections of leptolids from the Azores

There are few publications treating the Azores hydroids (MARTINS 1990). The majority of records of leptolids from the Azores region are of the hydroid stage. Most of the species recorded do not have a free medusa stage in their life cycles. This bias in the records might simply have been because most of the visiting expeditions have concentrated on benthos, so that species which are predominantly medusoid might have been missed. But it seems the bias may validly reflect the composition of the fauna.

A. Records before 1965

A nearly complete summary of records and authors prior to 1965 was provided by REES & WHITE (1966). Their survey need not be repeated except to mention that several major expeditions had until that time provided virtually all the records. Among the ships were the 'Josephine' (1860s), 'Challenger' (1870s), 'Talisman' (1880s), and the Prince of Monaco's 'Hirondelle' (1890s). Certain

records missed by REES & WHITE (1966) are listed in Table 1.

The first report of hydroids from the Azores was by LAMOUROUX (in FREYCINET 1824), who recorded '*Tubularia clytoides*' (discussion in CORNELIUS 1982: 118-119).

MEYEN (1834), who was wrongly cited by REES & WHITE (1966; details in CORNELIUS 1982: 50, 118-119), recorded and described two previously unknown species. The first, *Silicularia gracilis*, based on infertile material, came from 'the Sargasso Sea, in the neighbourhood of the Azores' and was presumably found on floating weed. The species still defies accurate identification (CORNELIUS 1982: 50) but a related or identical species, *S. bilabiata*, has been redescribed recently by HARRIS (1990) from Australasian waters: it has a medusa stage. The second, *Sertularia indivisa*, may not have been evaluated by any recent reviewer of the group. Meyen stated it to be 'very similar to' the ubiquitous *Dynamena pumila* of more northerly waters. The stated substrate was 'mussels or marine plants'. This is noteworthy since mussels are rare in the Azores, only encountered sometimes on floating objects, such as buoys (H.R. Martins, pers. commn.). Meyen's figures show a sertulariid with exactly opposite, paired hydrothecae and *S. indivisa* might be referred to one of several species possibly occurring in the area. However, the elongate nature of the hydrotheca and the long internode suggest that

Table 1
Hydroid records from Terceira island additional to those of REES & WHITE (1966)

Species	Locality	Depth (m)	Date	Material	Comments
<i>Sertularella gaudichaudi</i> *	Silveira harbour	5	19.vii.59	?	Mentioned by BAKER (1967: 40, as <i>S. mediterranea</i>)
	Monte Brazil W	18-21	27.vii.59	?	"
	Frocinhas Rocks	intertidal to 27	viii.59	?	"
<i>Lafoeina tenuis</i>	S of Terceira	610	viii.59	Epizoic colony	On specimen of <i>Halecium sessile</i> recorded by REES & WHITE (1966); mentioned by CORNELIUS 1975b: 406, footnote, as <i>Lafoenia</i> sp.; only Azores record

the nominal species should be referred to *Tridentata distans* Lamouroux (as redescribed in CORNELIUS 1979, as *Sertularia*). If this is accepted MEYEN's (1834) record becomes the earliest of *T. distans* from the Azores region.

In contrast the species *Halecium nanum* ALDER 1859, also collected from floating weed, has been widely accepted. The type material was taken from its most usual substrate, *Sargassum*, a few hundred km from the Azores at 34° 48' N, 34° 25' W (CORNELIUS & GARFATH 1980; redescrptions of the species in CALDER 1991 and CORNELIUS in press). It evidently disperses widely across the North Atlantic Ocean and has recently been noted thriving on Rockall in water hitherto considered prohibitively cool (CORNELIUS in press, coll. K. Hiscock & al.). Thus the species will almost certainly occur in the Archipelago and can be admitted to the faunal list in anticipation of its discovery.

RITCHIE's (1908) record of '*Clytia geniculata*' previously stated to be from the Azores (CORNELIUS 1982: 86) was in fact from the Cape Verde Islands. The species involved was almost certainly that known today as *C. linearis* of which there are a few genuine Azores records.

More recently, and after a substantial period during which apparently no leptolid collecting took place, there were expeditions from three colleges of London University: Queen Mary College [QMC] in 1952 (CHAPMAN 1954, 1955), Imperial College [IC] in 1959 (REES & WHITE 1966), and Chelsea College [CC] in 1965 (BAKER 1967). The cnidarian collections from the IC and CC expeditions were described by these authors and are discussed below. The material from the IC expedition (mostly hydroids plus a few scyphomedusae and anthozoans, there being no hydromedusae) has BMNH registered numbers of the series 1962.1.15.1-32, 1962.2.10.1-38 and 1962.2.13.1-8, and that from the CC expedition 1986.1.2.1-22 (scyphomedusae and siphonophores) and 1986.1.3.1-20 (hydroids and hydromedusae). I have not located cnidarian material from the QMC expedition.

KRAMP (1959, 1961) provided an indication of which hydromedusae might be expected in the North Atlantic Ocean and hence which open-ocean pelagic species might occur in the Azores.

B. Records since 1965

The hydroid and medusa records of BAKER (1967) seem to have been widely overlooked, and since that publication is scarce they are summarized in Table 2. BAKER provided the first Azores, and also European, record, of *Laomedea pseudodichotoma*. The species has since been collected from SW mainland Portugal (in 'plankton', estuary of R. Mira, May & October 1984, coll. J. Paula, det. S. J. Moore, BMNH regd no. 1985.3.5.7-8) but so far not further north. Other records of it are from the coastal waters of Senegal, Ghana and Ivory Coast (CORNELIUS 1982).

A feature of BAKER's records is the high proportion of hydroid specimens collected from floating substrates (Table 2). BAKER (1967: 41) noted that '*Clytia hemisphaerica* can be replenished on *Sargassum*'. This comment on rafting was possibly stimulated by conversation with W.J. REES who helped BAKER with his identifications. REES had made a similar observation with respect to all shallow-water Azorean hydroids (REES & WHITE 1966: 281). RALPH (1961c), who had visited REES, had earlier made similar remarks in relation to the New Zealand hydroid fauna, but HINCKS (1868: 140) had recorded *Clytia* on floating *Sargassum* earlier still.

Among the nine nominal species and subspecies of hydromedusae recorded by BAKER five were oceanic, two were coastal and two further coastal species were taxonomically dubious. Of the coastal taxa the rafting of *Clytia hemisphaerica* has just been mentioned, and *Zanclea costata* s. str. was stated by BAKER to be endemic to the Mediterranean and thought to have been brought to the Azores with Mediterranean Water.

VAN SOEST (1973) gave a list of oceanic hydromedusae from the mid-Atlantic Ocean. From the Azores area he recorded *Calycopsis typa*, the narcomedusan *Cunina duplicata*, *Pandea conica*, and, *Sibogita geometrica*, the first three not having been reported from the area before.

There has been a long-running Dutch project to study biological aspects of the Macaronesian islands which has taken in the Azores, the CANCAP Project (Contributions to the Zoology, Botany and Paleontology of the CANarian-CAPE Verdean Region of the North Atlantic Ocean; DEN HARTOG 1984), organized by the Rijksmuseum van Na-

tuurlijke Historie [RMNH], Leiden. Large collections were made but those of hydroids, preserved in the RMNH, have yet to be studied.

Another Dutch expedition studied plankton, including hydromedusae (WINKLER 1982). Winkler recorded 30 species of hydromedusae, many from the general area of the Azores, and provided

Table 2

The Azores hydroid and hydromedusa records of BAKER (1967) excepting those of *Sertularella gaudichaudi* sens. CORNELIUS (1979), which are given in Table 1. All were stated to have been collected from 'the coast', and those below were from São Jorge island.

Species	Locality	Depth (m)	Date	Material	Comments
i) Hydroids					
<i>Clytia hemisphaerica</i>	Santo Cristo	'surface'	10.viii.65	'Small colonies'	One on drift wood, several on
	Urzelina	0-2	2.ix.65	" "	<i>Grateloupia filicina</i> , one each on <i>Codium adherens</i> and <i>Polysiphonia</i> sp.
<i>Orthopyxis integra</i>	Urzelina	0-2	30.vii.65	?	Recorded as <i>O. caliculata</i> ; all on <i>G. filicina</i> ; earliest Azores record
<i>Laomedea pseudodichotoma</i>	Urzelina	'surface'	3.ix.65	Large colony 'up to' 4cm high; fertile male and female	On floating polythene; see text
<i>Sertularella gaudichaudi</i> sensu CORNELIUS 1979	Santo Cristo	'surface'	10.viii.65	One unbranched colony	Recorded as <i>S. mediterranea</i> ; on floating brown alga
<i>Sertularella polyzonias</i>	Urzelina	1-10	30.vii.65	Mostly unbranched colonies	On <i>Pinna rudis</i> , sponges, and <i>G. filicina</i>
<i>Tridentata distans</i>	Santo Cristo	'surface'	9.vii.65	Many small colonies	Recorded as <i>S. distans</i> var. <i>gracilis</i> , on floating brown algae
<i>Aglaophenia pluma</i>	Urzelina	0-3	2.ix.65	Small colonies	On <i>G. filicina</i>
ii) Hydromedusae					
<i>Clytia hemisphaerica</i>	Off Urzelina	0-120	'1965'	?	
' <i>Clytia brunescens</i> '	"	"	"	'A few specimens'	'First' for the Azores of this unassessed nominal species
<i>Krampella dubia</i>	"	"	"	First ever complete specimen	Oceanic species; this specimen apparently never described
<i>Stomotoca rugosum</i>	"	"	"	?	First Azores record
<i>Zanclea costata</i> s. str.	"	"	"	One specimen	First record of nominal species outside Mediterranean Sea; thought by BAKER (1967) to be evidence of transport by Mediterranean Water
<i>Aglaura hemistoma</i>	"	"	"	Many specimens	Oceanic species
<i>Rhopalonema velatum</i>	"	"	"	?	"
<i>Solmaris corona</i>	"	"	"	?	"
<i>Lyriopoe tetraphylla</i>	"	"	"	?	"

a zoogeographical analysis related to water-mass origin. Later cruises of the same expedition provided more than 60 species from the same region including two new to science, and a detailed faunal analysis was made (BLEEKER & VAN DER SPOEL 1988). Though these accounts greatly increased the local faunal list most of the species were known to be typical oceanic forms. Probably none was a shallow water coastal species, perhaps a reflection of the sampling stations most of which were, in fact, in open-oceanic waters.

C. Hydroids identified during the 1989 joint expedition

Material came mainly from two sources. First, from snorkelling and from the expedition's SCUBA divers who worked to a depth of c. 30 m. Second, from a collection of a few dozen specimens collected previously, mainly by dredging, by Dr Helen Martins, DOPH. In addition a little information was provided by a remote underwater video camera operated by Dr Richard Nash, Port Erin Marine Laboratory [PEML], University of Liverpool, at depths down to ca. 100 m, during the expedition. The records were all from Faial and are grouped in Table 3.

Hydroids were also sought, unsuccessfully, on the north coast of São Jorge island in a coastal lagoon at Caldeira do Santo Cristo; on Faial island in an intertidal natural sea-water swimming pool at Varadouro, in the often moderately sheltered bay west of Porto Pim, and in the rock pools on the exposed rocky shore at Feteira; and on Pico island around the moderately sheltered coastal rocks and gullies to the south of Madalena, and in the extensive shallow lagoon at Lajes do Pico. The virtual absence of hydroids from these places, all except Feteira being topographically suitable for their growth, emphasizes their scarcity in the region.

FAUNAL ANALYSIS

REES & WHITE (1966) listed some 66 nominal species of hydroid recorded from the Azores. Taxonomic revision has removed about 9 of these, and 5 varieties they listed are not recognized by all authorities (Table 4). Their list includes about

58 full species currently regarded valid. Precise counting is not possible since some of the taxa are of uncertain status.

Some thirteen species of hydroids have since been added to the faunal list and a number of hydromedusae (Table 3 and elsewhere in this paper). Most were collected by the present expedition, two were recorded by BAKER (1967), one (*Laomedea calceolifera*) was collected by Dr Helen Martins in 1980 and is newly reported here, and there is a single record of *Lafoeina tenuis* (Table 1; CORNELIUS 1975b). The last-named species was from 610 m and *Laomedea calceolifera* from ca. 100 m, but the other eleven newly recorded hydroids were mostly taken within a depth range of 0-30 m. This reflects the emphasis of earlier collecting effort on the group, which before the 1950s was exclusively deeper than 100 m.

Several of the species newly recorded in the Azores came from sheltered pontoons in the now busy Horta yachting marina, a locality probably subject to recruitment from ship-borne colonies. Most of this habitat has been created since REES & WHITE (1966) wrote. The four species *Silhouetta uvacarpa*, *Tubularia crocea*, *T. indivisa* and *Ventromma halecioides* were found only at this place. The last three have been widely recorded as fouling organisms on marine structures (MORRI & BOERO 1986) supporting the view that ship transport could have occurred. The first species is discussed in more detail below (p. 88).

Several 'second records' from the Azores were collected by the present expedition (Table 3) and are as informative as the 'first records': *Pennaria disticha* (30 m), *Sarsia tubulosa* (0.5 m), *Halcium tenellum* (30 m), *Clytia linearis* (10-12 m), *Obelia bidentata* (?ca. 3 m), *Orthopyxis integra* (0.3 m), and *Kirchenpaueria similis* (2 m). Strictly, the record of *Obelia bidentata* is the third, the species having been recorded by REES & WHITE (1966) as *O. bicuspidata* (Table 4). These several species are virtually cosmopolitan in coastal waters within their normal latitudinal ranges.

None of these 'second record' species was taken in the sheltered waters of the Horta marina. They thus tend to confirm that there is a 'true' hydroid fauna in the Azores Archipelago and that the earlier records of these species need not be considered unusual. They may not have been ship-borne.

Table 3

Some new records of hydroids from the Azores, including some of species not recorded from the area before.

Species	Locality	Depth (m)	Date	Material	Habitat and other notes
TUBULARIIDAE					
*** <i>Tubularia crocea</i>	Horta marina	0.3	25.vii.89	Several fertile colonies; DOPH/BMNH; coll. PFSC	On tubes of polychaete <i>Spirographis spallanzanii</i> and on polythene floats in shade
*** <i>Tubularia indivisa</i>	Horta marina	0.3	26.vii.89	Several infertile colonies; BMNH; coll. PFSC	On moored polythene float
HALOCORDYLIDAE					
** <i>Pennaria disticha</i>	SE corner of Monte da Guia	0.5	vii.89	5 infertile colonies up to 10 cm high; DOPH/BMNH; coll. PFSC	Fully exposed coastline; previous Azores record Terceira (REES & WHITE 1966, as <i>Halocordyle tiarella</i> ; discussion in GIBBONS & RYLAND 1989); this sample and next had unusually long ramules (cf. CALDER 1988)
	Ilhéu Negro entre Montes, Horta		22.vii.89	2 colonies, up to ca. 8 cm; infertile; coll. J. Azevedo	See previous
CORYNIDAE					
** <i>Sarsia</i> sp. cf. <i>tubulosa</i>	W coast of Monte da Guia		1.viii.89	Small, fertile colony with near-release medusae; BMNH; coll. R. & A.-M. Patzner	Fully exposed coastline; see text
EUDENDRIIDAE					
*** <i>Eudendrium</i> sp.	Seamount 3km ESE of Horta	20	vii.89	Some fertile; DOPH/BMNH	
	SE corner of Monte da Guia; 20 m inside cave	10	vii.89	Small colonies; DOPH/BMNH	Fully exposed coastline; same species as above
	NE corner of Monte da Guia	3	vii.89	DOPH/BMNH	Slightly less exposed; same species as above
BOUGAINVILLIIDAE					
*** <i>Bougainvillia</i> sp.	Horta marina	0.3	26.vii.89	Infertile colonies; BMNH; coll. PFSC	On rope and polythene float; very sheltered
	Horta harbour	2	vii.89	as above	On <i>S. spallanzanii</i> on jetty; sheltered
	SE corner of Monte da Guia in cave	25-30	vii.89	as above	Fully exposed coastline; all records of one well-established species
*** <i>Silhouetta uvacarpa</i>	Horta marina	0.3	2.vii.89 onwards	Several thriving colonies, some releasing medusae; BMNH; coll. PFSC	On live and dead <i>Mytilus edulis</i>
HALECIIDAE					
** <i>Halecium tenellum</i>	SE corner of Monte da Guia at entrance to rift	30	28.vii.89	Two infertile colonies on <i>Sertularella</i> ; DOPH; coll. R. & A.-M. Patzner	Previous Azores record by PICTET & BEDOT (1900; cited in REES & WHITE 1966)

*denotes the first and ** the second Azores record of the species, and *** the first of the genus. First records from individual islands are not noted. The localities are around Faial island unless otherwise stated. Most of the material came from the ecological collections of the Expedition (see Introduction) and, where

Table 3 (cont.)

Species	Locality	Depth (m)	Date	Material	Habitat and other notes
LAFOEIDAE					
<i>Cryptolaria pectinata</i>	near Horta	ca. 30	vii.89	One colony; coll. D. Moss	On base of hydroid <i>Polyplumaria flabellata</i>
CAMPANULARIIDAE					
<i>Clytia hemisphaerica</i>	Monte da Guia, on SW coast of of inner crater	3	17.vii.89	5 unithecate pedicels on stolon; infertile; BMNH	On tunicate cf. <i>Styella</i> ; several previous Azores records
** <i>Clytia linearis</i>	Seamount 3 km ESE of Horta	10-12	31.vii.89	Several dense colonies, some releasing medusae; DOPH; coll. M. Bate	On <i>Dictyota dichotoma</i> ; two previous records, Terceira (REES & WHITE 1966)
* <i>Laomedea calceolifera</i>	Off Castelo Branco	ca. 100	1.x.80	About 20 fertile male, female and infertile shoots, up to 2.5cm; DOPH; coll. H.R. Martins	Distinctive female gonothecae present
<i>Obelia bidentata</i>	Ilhéu Negro entre Montes; Horta	?	22.vii.89	One infertile colony, ca. 4cm, with long hydrothecae; DOPH; coll. J. Azevedo	
** <i>Orthopyxis integrá</i>	W coast of Monte da Guia;	0.3	1.viii.89	Small fertile colony with fully developed 'intra-capsular sporosacs', gonads brown; BMNH; coll. R. & A.-M. Patzner	On <i>Balanus tintinnabulum</i> ; very exposed situation; one previous Azores record (Table 2)
SERTULARIIDAE					
*** <i>Amphisbetia operculata</i>	At entrance to cave off SE corner of Monte da Guia	15	18.vii.89	Dense clump ca. 5cm high; infertile; DOPH; coll. D. Moss	Open coast; some <i>Eudendrium</i> in sample
* <i>Diphasia cf. attenuata</i>	On seamount 3km ESE of Horta	20	17.vii.89	Two small infertile shoots one with tendrils; BMNH	On <i>Sertularella</i> and fucoid; poor material, identification provisional
** <i>Dynamena cornicina</i>	On seamount 3 km ESE of Horta	10-12, 20-56	17.31.vii.89	3 samples; colonies up to 6 cm, infertile; DOPH/BMNH; coll. C. R. Wood, M. Bate	Common at this location
<i>Sertularella gaudichaudi</i> sens. CORNELIUS 1979	Many places: common around Monte da Guia; on 3 km seamount ESE of Horta; off Espalamaca	5-20, 20-56, down to ca. 100	vii-viii.89	Many colonies, some fertile; DOPH/BMNH	Ubiquitous; tending to be in coralline turf in shallower localities and in more open microniches deeper; epizoid on <i>S. gayi</i> in places; previously recorded as <i>S. mediterranea</i>
<i>Sertularella gayi</i>	Off Espalamaca	ca. 100	5.iv.79	5 infertile pinnate colonies; DOPH; coll. H.R. Martins	Both this and <i>S. polyzonias</i> have been recorded before; distinctions are problematic (CORNELIUS 1979)
	On seamount 3 km ESE of Horta	ca. 20	17.vii.89	3 infertile stems up to 6cm; DOPH; coll. C.R. Wood	See above
<i>Tridentata distans</i>	SE corner of Monte da Guia	ca. 15, ca. 30	18.28.vii.89	Several infertile unbranched shoots up to ca. 2 cm; DOPH; coll. D. Moss, R. & A.-M. Patzner	At entrance to cave at 15 & 30 m; on open coastline;
PLUMULARIIDAE					
HALOPTERIINAE					
<i>Antennella secundaria</i>	1 mile off Espalamaca	100	5.iv.89	Several infertile colonies + loose fragments; DOPH; coll. H.R. Martins	On <i>Aglaophenia acacia</i> over bivalve reef; REES & WHITE (1966) cited 5 previous records, 98-1250 m

Table 3 (cont.)

Species	Locality	Depth (m)	Date	Material	Habitat and other notes
KIRCHENPAUERIIINAE					
**<i>Kirchenpaueria similis</i>	Outer side of old jetty in SW corner of Horta harbour	2	26.vii.89	Two infertile plumes; BMNH; coll. PFSC	On tubes of polychaete <i>Spirographis spallanzanii</i> ; sheltered; recorded from Terceira by REES & WHITE (1966, as <i>K. pinnata</i> var. <i>similis</i>)
PLUMULARIINAE					
<i>Nemertesia ramosa</i>	Off Castelo Branco	ca. 100	1.x.80	One 12cm colony; DOPH; coll. H.R. Martins	
	SE corner of Monte da Guia at entrance to rift	30	28.vii.89	Two 7.5cm colonies, young, simply-pinnate, fertile; plus one infertile, 2.5 cm; DOPH; coll. R. & A.-M. Patzner	
	Off Espalamarca	ca. 100	29.vii.89	Many colonies seen by remote TV; via R. Nash; det. PFSC	
<i>Plumularia setacea</i>	Off Castelo Branco	ca. 100	1.x.80	DOPH; coll. H.R. Martins	Four previous Azores records, two of var. <i>elongata</i> Bedot (REES & WHITE 1966)
	SE corner of Monte da Guia, at entrance to cave	5-10	vii.89	Several plumes, some with distinctive gonothecae; DOPH/BMNH; coll. D. Moss	
***<i>Ventromma halecioides</i>	Horta marina	0.3-2	18.25.vii.89	Abundant; infertile; DOPH; coll. PFSC	On sponge, <i>S. spallanzanii</i> & polythene float
AGLAOPHENIIDAE					
<i>Aglaophenia acacia</i>	1 mile off Espalamarca, on bivalve reef	ca. 100	5.iv.79	8 trichotomously-forked colonies; DOPH; coll. H.R. Martins	Frequent from 15m (REES & WHITE 1966) probably to hundreds of metres
	Same area		27.vii.89	Numerous colonies seen by remote TV; via R. Nash; det. PFSC	
	Off Ribeiras, Pico	120-180	5.ii.89	Two infertile plumes up to 5 cm on short stolon; DOPH; coll. H.R. Martins	On <i>Charonia lampas</i> shell occupied by pagurid
*<i>Aglaophenia picardi</i>	'Azores'			Det. A. Svoboda (pers. comm)	No further information; records and material lost; recorded from Canaries by SVOBODA & CORNELIUS (1991)
<i>Aglaophenia pluma</i>	From variety of exposed and sheltered situations inside and outside Monte da Guia; also on seamount 3 km ESE of Horta	5-20	vii.89	Numerous colonies up to 8 cm long, some fertile; DOPH/BMNH; coll. D. Moss, C.R. Wood, and others	Common where indicated; on varied substrates including stones, rock, <i>Pinna</i> shell, fucoids; possible taxonomic implications of varied substrata discussed in SVOBODA & CORNELIUS (1991)
<i>Aglaophenia tubulifera</i>	Off Castelo Branco	ca. 100	1.x.80	DOPH; coll. H.R. Martins	Epizoic on <i>Nemertesia ramosa</i>
	On seamount 3km ESE Horta;	20	17.vii.89	Infertile colonies up to 7cm; DOPH/BMNH; coll. C.R. Wood	

Table 4

Changes in taxonomy and interpretation of some earlier records since the lists of REES & WHITE (1966). Species are listed in alphabetical order as in that paper.

1. *Aglaophenia pluma*. As in many hydroid species no varieties are now recognised, the extremes of variation once given such status now being regarded as phenotypes (SVOBODA & CORNELIUS 1991).
2. *Clytia gigantea* is now referred to *C. hemisphaerica* (see CORNELIUS 1982).
3. *Clytia longicyatha* has been referred to *Obelia bidentata* (see CORNELIUS 1975a: 264) but a review of its validity would seem necessary.
4. *Clytia noliformis* sens. REES & WHITE is probably best referred to *C. hemisphaerica* (discussion in CORNELIUS 1982: 80). The main character on which it was based, the stage of medusa development on release, varies in *Clytia* (noted in HINCKS, 1868: 147; summary in CORNELIUS 1990a: 545).
5. *Clytia raridentata*. Several authors, including REES & THURSFIELD (1965), have referred this nominal species to *C. hemisphaerica* and recent studies of its type material have upheld this view (CORNELIUS & GARFATH 1980; CORNELIUS & ÖSTMAN 1986).
6. *Clytia striata*. Should probably be referred to *C. linearis* (discussion in CORNELIUS 1982: 86).
7. *Halocordyle tiarella* has been widely regarded as conspecific with *Pennaria disticha*, the generic and specific names of which must each take priority (GIBBONS & RYLAND 1989).
8. *Kirchenpaueria pinnata* var. *similis* is here considered a full species, following HINCKS (1868) among others. The nominate 'variety' has not yet been recorded from the Azores.
9. *Lafoea fruticosa* is referred to *L. dumosa* (discussion in CORNELIUS 1975b; VERVOORT in REES & VERVOORT 1987: 44).
10. *Lafoea serrata* is referred to the genus *Filellum* (following MILLARD 1975).
11. *Obelia bicuspidata* is called *O. bidentata* (discussion in CORNELIUS 1975a).
12. *Obelia hyalina* is of uncertain taxonomic status but was probably based on *O. dichotoma* which is otherwise recorded from the Azores (discussion in CORNELIUS 1982: 94, 119).
13. *Obelia kincaidi* sens. REES & WHITE has been provisionally referred to *Clytia* (by CORNELIUS 1975a: 280) and the Azores record itself has been challenged (CORNELIUS 1982: 90). Although CALDER (1971, 1991) provisionally recognized the species full evaluation is desirable.
14. *Orthopyxis clytioides* sens. REES & WHITE has been reidentified as *Obelia* sp. (by CORNELIUS 1982: 118-119) and was almost certainly based on one or other species of that genus already recorded from the Azores.
15. *Sertularella laxa* (Allman) sens. REES & WHITE is provisionally referred to *S. gaudichaudi* sens. CORNELIUS 1979. The similarly-named deep-water *Thuiaria laxa* (Allman) is a different nominal species and is probably valid (CORNELIUS 1979).
16. *Sertularella mediterranea* is provisionally referred to *S. gaudichaudi* sens. CORNELIUS 1979.
17. *Sertularia distans* var. *gracilis* was never soundly based and is no longer recognised (CORNELIUS 1979). Discussion on referral of the species to *Tridentata* has been given most recently by CALDER (1991).
18. *Thecocarpus myriophyllum* is referred to another genus, as *Lytocarpia myriophyllum* (discussion in REES & VERVOORT 1987: 177).

No analysis is attempted of the few but varied hydromedusan records for two reasons. First, the present expedition did not collect plankton; and second, as BAKER (1967) and VAN SOEST (1973) implied, the majority of hydromedusae occurring in the Azores are probably deep- to mid-water oceanic forms whose dispersal and distribution are governed by factors different from those affecting the mainly coastal-benthic species discussed here.

Remarkably, all but 3 of the 58 or so valid species listed by REES & WHITE (1966) are referred to the thecate suborder. In contrast, in the group as a whole there are roughly equal numbers of athecate and thecate genera - about 170 of each (data extracted from BOUILLON 1985). Of the 13 species since added to the faunal list 5 are athecate and 8 thecate, but the overall disproportion remains between the Azorean records of the two

suborders. It may not necessarily be due to thecate being the commoner. The typically greater colony size of thecate may have led to their more frequent detection and collection. However, present records are probably a true indication that they are the more numerous of the two groups in the Archipelago.

In the Hydroida as a whole, about 55% of the genera have species releasing a fully developed hydromedusa. The remainder have the medusa stage reduced, in most being completely suppressed from the life cycle. In the known Azores leptocephala the proportions are remarkably lower (<10%). This holds true for species both deeper and shallower than 90 m (Table 5). The disproportion between the two life-cycle groups is discussed below (p. 89).

DISCUSSION

THE NATURE AND DISTRIBUTION OF THE HYDROID FAUNA, AND THE FACTORS AFFECTING IT

Several major factors seem to influence hydroid distribution in the Azores region: the relatively young age of the islands and associated seamounts, the great depth and breadth of the surrounding abyssal plain, the heavy swell the islands experience, and the areas of origin of the prevail-

ing ocean currents. In addition the rather uniform subtidal and intertidal environments probably restrict the variety of species. Descriptions of Azorean shores and their biota have been provided by MORTON (1990) and HAWKINS & al. (1990). Around the coasts of Faial and Pico, for example, there are no eelgrass beds, no shores covered by large brown algae with the exception of a *Cystoclema* zone in some places, and no coral reefs or mangrove areas which might provide permanent habitats for many species. The diversity of habitats is much less than on comparable continental coasts less exposed to extreme wave action. Some of these factors will now be considered further.

A. Physical and geographical factors

i) **Remoteness, and depth of surrounding abyssal plain.** The Azores are a long way from both the Euro-African coast and the Americas. The least distance from the islands to land is about 1300 km, to the region of the Strait of Gibraltar. The Archipelago is about the same distance from the nearest Shelf on the American side, the Newfoundland Ridge, which extends to approximately 39° N, 45° W. The nearest extensive coastal waters on the western side are the Grand Banks off Newfoundland and the NE coast of South America, each approximately 3000 km distant. The islands are thus

Table 5

Numbers of benthic hydroid and medusa species recorded from the Azores region to show proportion releasing a fully functional hydromedusa.

	Below 90m (100m)				Above 90m (100m)			
	Totals		%		Totals		%	
Species releasing fully functional medusa	3	(3)	6	(7)	5	(4)	15	(10)
Species having ephemeral or no medusa stage	45	(41)	94	(93)	28	(36)	85	(90)

Compare the percentages, shown in *italics*. Medusa-releasing species are little recorded at any depth. An arbitrary depth of 90m separates coastal forms from deeper-water ones. The effect of a single, species-rich expedition trawl at a nominal 98m is shown by including (in parentheses) corresponding species-totals above and below 100m. Species recorded both above and below 90m (and 100m) are scored twice. Data from nearly all sources discussed in the present paper are pooled. The hydromedusan records of BAKER (1967) are not included since the depth of collection of all samples was given as 0-120m (present Table 2). Four nominal species of *Zygophylax* recorded by REES & WHITE (1966) are assumed taxonomically valid. Deep-sea and open-ocean hydromedusae each form a distinct faunal assemblage and are not included. See also Table 6.

the most remote in the North Atlantic. The main biogeographic questions to be answered are: which shallow-water species might be able to cross the intervening abyssal plain from the nearest populations likely to provide recruitment to the islands, whence might they come, and how might they travel?

ii) **Young age of the Archipelago.** The oldest recorded Azorean rocks date from about 8 my BP (ABDELMONEM & al. 1975) and 5.5 my BP (FERAUD & al. 1984). The age of the associated sub-surface seamounts is arguably more relevant to Azorean marine biota than the age of the terrestrial components of the Archipelago, but 5-8 million years is itself sufficiently long a period for much faunal recruitment to have occurred. Although marine faunal endemism is not a widely reported feature of the Archipelago (BRIGGS 1966, 1974) there has perhaps been adequate time for a natural faunal assemblage to accumulate and stabilise.

iii) **Ocean currents.** The surface-water Gulf Stream (GS) passes northwards off Florida, Georgia and South and North Carolina. About the latitude of New England it turns ENE and then E. From here it is known as the North Atlantic Drift or, in modern literature, North Atlantic Current (NAC). Part continues on towards northern Europe but a large part turns towards south-eastern Europe and North Africa and is termed the Azores Current (AC). Accounts of the surface currents relevant to the region are available in the publications cited above. HELLAND-HANSEN & NANSEN (1926: 30) were among the first to study the southward-flowing AC. In their view it left the NAC at ca. 46-49° N and this has been repeated by some later authors. The AC is unstable and produces temporary eddies and meanders which are responsible for the large variation generally observed on the superficial current-field (ALVES 1991). The surface layer (0-600 m) is mainly of local-origin North Atlantic Central Water (NACW). However, even when the GS arrives here (as the Azores Current) the water is already transformed (HARVEY & ARCHAN 1988).

Bottom- and mid-water arriving at the Azores is more varied in origin, comprising three main components: Mediterranean Water (MW; depth of 600-2000 m) leaving the Strait of Gibraltar in-

itially westwards, and North Atlantic Deep Water (NADW; below 2000 m) arriving from the north (HELLAND-HANSEN & NANSEN 1926; PICKARD & EMERY 1982; BIGG 1990; clear summary and further literature in GOFAS 1990). Labrador water has also been reported off the north-western region of the Azores mainly at depth between the NACW and NADW (HARVEY & ARCHAN 1988).

The MW was shown by HELLAND-HANSEN & NANSEN (1926: 44) to sink down over the Portuguese region of the Continental Slope. It eventually reaches the Azores and the region to the south at a depth variously reported over the range 600-1800 m (BIGG 1990; synopsis in GOFAS 1990), the range probably reflecting the varying depth of its fluctuating wedge-like intrusion. HELLAND-HANSEN & NANSEN (1926) recognized an anti-clockwise sub-surface gyre between Portugal and the Azores region of the Mid-Atlantic Ridge, and a reverse one immediately to the north (their Fig. 15). BIGG (1990) regarded variation from the normal current directions in the region as commonplace. Such gyres and current variations would facilitate dispersal from southern Europe and the Mediterranean Sea at a range of depths from perhaps 100 m to 1500 m.

iv) **Sea temperature.** Some tropical species which might be carried from the Caribbean sea to the Azores on flotsam would not survive in the cooler waters of the mid-Atlantic. The sea surface temperature around the Azores ranges from ca. 23° C in August down to ca. 15° C in February (NAVAL INTELLIGENCE DIVISION 1945) or even 14° C (H.R. Martins, pers. commn). Thus many of the leptolid species recorded from Bermuda (CALDER 1988, 1991) may be unable to survive in Azorean waters. However, a range of species more tolerant of cooler conditions, originating from slightly further north on the eastern U.S. seaboard as the Gulf Stream passes northward, might nevertheless be expected as with marine algae. Unfortunately, though many of the recorded hydroids fall into this category many of the species exist also on European coasts so that an American origin cannot be demonstrated.

v) **Ocean swell and tidal amplitude.** CHAPMAN (1954) provided a summary of the greatly exposed intertidal conditions prevailing in the Archipelago.

Even on windless days powerful waves of distant origin and long period crash on virtually all shores, refracting around promontories and into bays with much of their energy retained. On some days during most winters the wave force becomes extreme and potentially equal to that anywhere in the world. The majority of Azorean shores are Very Exposed to Extremely Exposed as defined by British standards (e.g. BALLANTINE 1961; LEWIS 1964). In such environments most hydroids incur mechanical damage and do not survive. The prevailing wind directions throughout the year are about equally from NE and SW (NAVAL INTELLIGENCE DIVISION 1945; CHAPMAN 1954), so that there are few permanently lee shores.

The shallow tidal amplitude of the region, less than 2 m at springs and a tenth of this at neaps (CHAPMAN 1955), narrows the intertidal zone. But the nearly incessant, heavy swell usually extends the vertical range of the intertidal biota considerably beyond these tidal limits (HAWKINS & al. 1990).

Two subtidal hydroid species have been found to be successful in these harsh conditions. The coastal medusa-releasing hydroid *Sarsia tubulosa* was reported by CHAPMAN (1955) in the protective coralline turf off Terceira at a density of 900 hydranths (not colonies) per m². The present expedition recorded the species only once, off Faial, but there found *Sertularella gaudichaudi* sens. CORNELIUS (1979), commonly in the coralline turf (Table 3).

At least down to 20-30 m depth in coastal situations the expedition's divers noted the hydroid fauna to be otherwise sparse. But on the seamount 3 km ESE of Horta at about the same depth a richer hydroid fauna was found including several species with tall colonies (Table 3). Thus the wave-force factor limiting hydroid survival may be the crashing of the swell, probably during winter storms, rather than wave surge which would be experienced on the seamount and subtidally along coastlines alike.

B. Biological aspects

i) **Browsing by subtidal fish.** Browsing fish are numerous subtidally in the Azores in all but the most exposed regions. This is typical of coastlines

in the tropical East Atlantic where fish have been identified as a major source of grazing and control of small algae (review in JOHN & al. 1992). Young hydroids and other small benthic organisms might also be browsed or disturbed by fish, either as a mechanical consequence of the grazing or by specific predation.

ii) **Distribution and depth.** Analysis of the distribution of the recorded hydroid fauna in relation to depth is greatly assisted by REES & WHITE's (1966) synopsis.

Valid depth-band groupings are difficult to determine. REES & WHITE pointed out that the question is complicated both by the poorly documented tendency of some (but not all!) boreal shallow-water species to 'descend' to greater depths with decreasing latitude, seemingly surviving best within certain temperature ranges; and by limitations in our knowledge of the shallow-water fauna. Some hydroids undoubtedly have narrower depth ranges than others, even within coastal waters (CORNELIUS 1979: Fig. 2). In addition, forms characteristic of the upper 30 m alone have strong swell and browsing fish to contend with (see above) and this may further influence the observed pattern.

Thus the high proportion of species recorded deeper than 90 m is the reverse of the better-studied situation in most boreal seas where the shallow fauna is the richer. The difference may partly reflect sampling effort and techniques used, a substantial portion of previous work having sampled depths below 100 m by dredging from sizable research vessels. In fact 17 species, roughly a quarter, have been recorded in the Azores only in waters shallower than 30 m, and 37, about half, only deeper than 90 m (Table 5). There are 5 from 201-300 m; 3 from 301-400 m; none from 401-500 m; two from 601-700 m; none from 701-800 m; 4 from 801-900 m; none from 901-1100 m; and perhaps an abyssal contingent of 6 species so far recorded in the area only from 1160 m and deeper (data mainly from REES & WHITE 1966). The figures are biased by chance bunching of existing records from certain fortuitously species-rich expedition dredge-hauls at nominal depths of 208 m, 599 m, and 610 m - each close to a multiple of 100 m.

iii) Medusa suppression among Azorean hydroids. The low proportion of medusa-releasing leptolid species recorded at all depths in the Azores is striking. The figures in Table 5 represent about eight species, all of which are known or probable rafters which, therefore, may have arrived in the Azores by means other than the dispersive capability of their medusae. Their likely mode of travel therefore, seems to be rafting of the hydroid stage.

Six of the eight are ubiquitous, coastal-cosmopolitan Campanulariidae of just two genera (*Clytia hemisphaerica*, *C. linearis*, *Obelia bidentata*, *O. dichotoma*, *O. geniculata*, *O. longissima*). The hydroid of *C. hemisphaerica* has been recorded on a variety of planktonic substrates including pelagic cirripedes and crustacean ectoparasites of fish (review in CORNELIUS 1982; further example, on floating material far from land, in VERVOORT 1985). *C. linearis* also habitually rafts on oceanic pteropods and so pursues both benthic and 'neritic' life-styles, making it one of the most widely distributed of marine invertebrates (CORNELIUS 1982, 1987). The *Obelia* species, and others in the family Campanulariidae, have often been recorded rafting (review in CORNELIUS 1982; further example in VADER & al. 1981, *O. longissima* attached to a pelagic isopod). All six can disperse long distances by rafting, despite their having well developed medusa stages (the medusa of *C. linearis* having been recorded for the first time recently by BOERO & SARÀ 1987).

The seventh, *Silhouetta uvacarpa*, has been recorded from the Azores just once, in Horta yachting marina (Table 3), and is so little known world-wide that zoogeographic comment is inappropriate save that almost all its recorded occurrences have been in harbours and similar places (literature reviewed by CALDER 1988). The closely related and similarly poorly known *Clavopsella navis* (literature review in MILLARD 1975) differs in having the medusa generation reduced to a sporosac and, though otherwise similar, would seem unlikely to be conspecific. Localities of *C. navis* not known to Millard include the Netherlands (W. Vervoort, pers. comm.) and Shoreham harbour, southern England (PFSC & C. Sartory, unpubl.; details recently published by SHEADER & SHEADER 1990).

The eighth species, the medusa-releasing *Sarsia tubulosa*, is not known to raft. However, its known micro-habitat in the Azores, amongst tightly-packed coralline algal fronds (CHAPMAN 1955), suggests that it may be able to survive a long journey amongst the epibiota on a well fouled ship's hull or natural floating substrate. Since it may not yet have been recorded on ships, rafting on weed seems the more likely (W. Vervoort, pers. comm.).

Lastly, and additionally, the species *Silicularia gracilis* was described from the Sargasso Sea and the Azores by MEYEN (1834) whose material was infertile. The related and perhaps identical nominal species *S. bilabiata* has a short-lived medusa stage which could not cross the Atlantic Ocean. If *S. gracilis* resembles this and several other orthopyxine species in having a reduced medusa (summaries in MILLARD 1975, CORNELIUS 1982) it too may well have rafted to the Azores on weed.

iv) Dispersal methods in remote island marine faunas. The paucity of medusa-releasing species in the Azores (Table 5) supports the hypothesis of RALPH (1961c) and KRAMP (1968) that coastal hydromedusae cannot span great oceanic distances - excepting the few medusa species capable of reproduction by vegetative fission. Two further factors will certainly hamper trans-oceanic transport of medusae. First, that medusae of both sexes, perhaps requiring two hydroid colonies, are required for the life cycle to be completed (CORNELIUS 1981; JACKSON 1986). Second, that liberated medusae will drift far from their coastal sources before releasing planulae, which will then have a reduced chance to settle close to newly established colonies. Hence colonies of medusa-releasing species that do settle in remote places will probably be less successful in sexual reproduction than species lacking a medusa stage.

Some recruitment of the few coastal hydromedusan species recorded in the Azores may result from medusae, and the planulae they give rise to, being released in mid-Atlantic from already-rafting hydroid colonies. Such *en route* release of dispersive stages has been suggested to occur often among rafted animals (JACKSON 1986: 593). But wide dispersion of the released stages must be so great as to make any resulting recruitment infrequent.

In invertebrates generally, and in hydroids too, species with non-dispersive intermediate stages will have a much better chance of settling locally and of contributing to a local population than will those with long-lived planktonic stages. Such forms predominate in the faunae of remote islands. An extreme tendency of this kind, and incidentally one of the first examples recorded, was noted by CRISP (1956) and FISHER (1956: 167) on the biogeographically isolated Rockall. FISHER (1956) made the first serious invertebrate collection from this islet. All of the half dozen 'intertidal' invertebrates recorded were either viviparous or lacked a pelagic dispersive stage. The faunal list was increased to about 17 marine invertebrates by MOORE (1977) but still none had a planktonic larva (see also JOHANNESSON 1988). Other early discussions of the tendency towards limited dispersal by island faunae were cited by SCHELTEMA & WILLIAMS (1983), HIGHSMITH (1985) and JOHANNESSON (1988). *Mytilus* spp. are evidently frequently transported to the Azores on ships but, though individuals survive, permanent populations have not become established: perhaps on account of the planktonic larval stage of this genus.

The same reduction of the dispersive stage seems to be a feature of the leptolid faunae of certain oceanic archipelagos where documentation is sufficiently detailed for sensible comparison (Table 6). Present knowledge, although fragmentary, suggests overwhelmingly that fewer remote-island hydroids release medusae than do so in continental-coastal faunae.

v) **Medusa reduction, perennation, and philopatry.** The process of medusa reduction is most marked in species having large, perennating colonies (Table 7). This may affect the faunal arguments presented here since, in the Azores as elsewhere, it is of course the larger and more conspicuous colonies which past collecting methods have most easily located. Some medusa-releasing species having small hydroid colonies may have been overlooked. However, if so, their numbers would probably not alter the overall finding that the hydroid faunae on oceanic islands tend to lack medusa-releasing species.

Regrettably, insufficient is known of the longevity of leptolid planulae to determine whether or not those of the shallow-water Azorean species

settle rapidly from the plankton and hence sustain coastal populations. It has recently been suggested, however, that species having a suppressed medusa stage also have short planula longevities (SOMMER in press), but data are few.

A tendency towards philopatry has been reported in several invertebrate groups ancestrally having a long-dispersing stage (JACKSON 1986; HUGHES 1989). But this is far from demonstrated among hydroids. The dispersive stages of the majority, whether planulae or medusae, probably remain planktonic long enough that settlement near the parent colony does not occur (CORNELIUS 1990b, 1991). Settlement near the parent is known in very few species (CORNELIUS 1990b). Apparently, too, close philopatry is rare in the group, for few hydroids grow in clumps of colonies.

C. Zoogeographic origin, currents and rafting

i) **Zoogeographic origin and currents.** Some zoogeographic analyses have demonstrated an Azorean shallow-water faunal element derived from the Afro-European shelf and others from the North American region, and these will be mentioned below. But hardly any of the leptolid species so far recorded in the Azores are endemic to one side of the Atlantic or the other. Hence it is useful to summarize something of what is known of the provenance of the other groups. However, it has to be said that most studies of the kind have simply compared the faunae or florae of the Azores with those of other regions without considering by what means of transport each species might have arrived.

Mediterranean Water is evidently important in faunal recruitment to the Azores and surrounding region, despite its relatively small volume and the fanning out that it must undergo. Certain sponges and the Mediterranean locust lobster, *Scyllarides latus*, are thought to have arrived with this current (BOURY-ESNAULT & LOPES 1985; MARTINS 1985). GRASSHOFF (1989: 201) considered that at least one gorgonian amongst a particular expedition collection, *Isidella elongata*, 'reaches the Ibero-Moroccan Gulf...by transport of larvae with the Mediterranean water outflow' whence transport to the Azores region is possible in the subsurface gyres described above. BAKER (1967;

Table 6

Comparison of percentage of leptolid species having fully developed hydromedusa and not, between continental-coastal and oceanic-island faunae.

Area	Source	a		b		c	d		e
		No. of species releasing planula or short-lived medusoid		No. of species releasing fully developed hydromedusa		No. of species releasing hydro-medusa and hav- ing hydroid known to raft	% having fully devel- oped hydro- medusa (bx100)/(a+b)		Species with un- predicted dis- persive method
i) Continental-coastal faunae									
Southern Africa	MILLARD 1975	182	(189)	90	(83)	7	33.0	(30.5)	5
U.S.S.R. former	NAUMOV 1969	223	(228)	65	(60)	5	22.5	(20.8)	2
British Isles	RUSSELL 1953, 1970; CORNELIUS (in press); CORNELIUS & RYLAND 1990; some data original	93	(103)	66	(56)	10	41.5	(35.2)	7
ii) Oceanic island faunae									
Bermuda, excepting Plumulariidae s. lat.	CALDER 1988, 1991	47	(53)	15	(9)	6	24.0	(14.5)	8
Fiji, excepting Plumulariidae s. lat.	GIBBONS & RYLAND 1989	24	(29)	6	(1)	5	20.0	(3.3)	8
Hawaii	NUTTING 1905, EDMONSON 1930, COOKE 1977	52	(54)	7	(5)	2	12.0	(8.5)	10
New Zealand	RALPH 1957, 1958, 1961a, b	110	(117)	7	(0)	7	6.0	(0)	10
Enewetak Atoll	COOKE 1975	16	(17)	1	(0)	1	5.9	(0)	0
Azores	Present paper								
above 100m		28	(34)	8	(2)	6	22.0	(5.5)	0
below 100m		41	(41)	3	(0)	0	6.8	(0)	0

Totals and percentages in parentheses score rafting species having a medusa stage (column c) as non-medusoid species (added to column a). This assumes that the medusa is not essential for long-distance dispersal in such species. Thus the percentages in parentheses in column d show best the relative fall in medusa-releasing species in oceanic-island faunae.

The analysis is limited by inconstant taxonomy and differing faunal coverage between the works cited. In most areas anthomedusan/athecate species are less well known than the typically more conspicuous leptomedusae/thecates. From Bermuda and Fiji no data were available on the speciose and non-medusoid Plumulariidae.

Species in which the main dispersive stage has not been predicted are excluded from the calculations (column e).

The data from Hawaii may be biased by the inclusion of several invalid nominal species of non-medusa releasing thecates described by NUTTING (1905) and by four nominal species of *Eleutheria*. The essentially non-dispersive medusa-releasing *Cladonema* and *Eleutheria* auct. are included in column (a).

The figures should be interpreted against the background of those for medusa suppression in all leptolids (Table 7).

Table 7

Correlation among leptolids between reduction and suppression of the medusa stage and possession of large, branching colony.

i) DISPERSIVE STAGES IN 'NORMAL' GENERA (i.e. excluding Stylasteridae, Velelloidea, Milleporida, and fossil forms)		
1) Releasing fully-developed hydromedusa	217	(56%)
2) Releasing short-lived medusoid	17	(5%)
3) Releasing planula	127	(33%)
4) Dispersive stage unknown	27	(7%)
5) Total 'normal' genera	388	
ii) DISPERSIVE STAGES IN GENERA HAVING LARGE AND/OR ARBORESCENT COLONY		
1) Releasing fully-developed hydromedusa	8	(7.5%)
2) Releasing short-lived medusoid	6	(5.5%)
3) Releasing planula	91	(86%)
4) Dispersive stage unknown	1	(1.0%)
5) Total large and/or arborescent genera	106	

The figures are numbers of genera. Since the reproductive pathways of only a minority of the species are definitely known, the table is somewhat hypothetical: but not much. Thus assumptions, for example, that all the Sertulariidae will prove to lack a medusa stage will probably be so close to reality that the overall pattern shown by information collected so far will be found broadly unchanged. (Data from BOUILLON, 1985; after CORNELIUS, 1991.)

present Table 2) considered that a taxonomically problematic hydromedusa, *Zanclus costatus* s. str., had come from the Mediterranean where he considered it endemic. A hydroid, *Laomedea pseudodichotoma*, known only from the Euro-African coast and the Azores, is mentioned here (Table 2) but the absence of Caribbean records may simply reflect its having been overlooked. Only one other study of cnidarians of the region has compared the fauna with eastern and western faunas. GRASSHOFF (1981) studied bathyal (360-2200 m depth) gorgonians and pennatulaceans and found in the region 6 east-Atlantic forms, 2 west-Atlantic, and 6 known from both east and west: on his small sample size, quite inconclusive of a tendency to originate from east or west. In addition, for bathyal fauna there is essentially no dispersal barrier from either direction and comparison with the possible origins of shallow-water faunal components is limited in value.

All of the 18 species and subspecies of echinoderms reported from the Azores by MARQUES (1983) were forms already known from the Mediterranean region and adjoining Atlantic coast-

line. Similarly, of 99 coastal species of fish then known from the Azores BRIGGS (1974) considered 77 to occur also on Euro-African coasts and none at all to be common with the Americas. He found 21 to occur across the Atlantic, and one Azorean endemic. One family of intertidal gastropods present in the Azores has been shown to have European faunal origins (GOFAS 1990).

The marine thaloid algae are better known across the North Atlantic Ocean than many animal groups. One analysis indicated that the Azorean algal flora is more similar to that of the other Macaronesian Islands (Canaries, Salvage Isles and Madeira), the Euro-African coast and especially the Mediterranean, particularly as regards warmer-water species, than to that of North America (PRUD'HOMME VAN REINE 1988). Another study, not contradictory though some have taken it as so, concluded that the greatest similarity was with the flora of the cool New England coastline and that Azorean algae were floristically distinct from all other temperate North Atlantic floras (TITTLE & al. 1990). Prud'homme van Reine's data and conclusions were not available to

Tittley when the latter submitted his paper (I. Tittley, pers. commn), and the Mediterranean algal flora was not included in Tittley's analysis. The two studies suggest that there are many algal species in the Azores common on the one hand with New England and on the other, and to a greater extent, with the Mediterranean.

The currents of western origin travel on the surface and those from the other directions, most importantly perhaps the Mediterranean Water, travel at several hundred metres depth. An interesting analysis would be to determine if species present in the Azores which were identifiable with particular areas of origin had dispersive stages able to travel at the depths of the currents which may have brought them. Thus the idea of BRIGGS (1974) that the major currents to the region may have changed over a post-glacial or slightly longer time-scale might be tested. However, some species usually regarded as surface forms can evidently disperse at depth. Thus the 'normally coastal' hydroid *Clytia gracilis* has been found attached to a structure moored in mid-water at 1443 m over the Wyville-Thompson Ridge at 60° 13' N, 9° 13' W, some 300 km NW of the Outer Hebrides (BMNH collection 1985.10.2.16). Clearly, species with narrower vertical distributions should be selected for such an analysis.

The Caribbean and United States coastlines may seem the most likely origin of the shallow water Azorean hydroid fauna, comprised as it is of many rafting species which would presumably travel mainly at the surface. But, as already noted, since there is little leptolid faunal difference between east and west Atlantic the origin of their Azorean faunal component cannot be deduced by simple comparison. The clear demonstration of faunal origins of several groups from the east must from our present knowledge leave that of the Azorean leptolid fauna an open question.

ii) **Rafting.** If the voracious, shallow-water hydromedusae are in general too short-lived to cross from the coasts of the Americas to the Azores then their lecithotrophic, non-feeding planulae must surely be unable to make the journey. But the sessile stages of many benthic invertebrates, including hydroids, are known to raft on floating debris, algae, turtles, maybe some whales, and fish (especially on their crustacean ectoparasites);

and hence paradoxically sometimes to traverse greater distances than their corresponding free-swimming stages (RALPH 1961c, CORNELIUS 1981, 1990b, 1991; reviews of rafting in all groups in HIGHSMITH 1985, JACKSON 1986, and JOKIEL 1989, 1990; discussion and review of recent dispersal literature in JOHANNESSON 1988).

Substantial amounts of flotsam cross the Atlantic carrying and dispersing non-swimming forms. GUPPY (1917: 460-462) summarised drift-bottle and other evidence suggesting that all surface flotsam arriving in the Azores came from the W and NW, never from the E, at all seasons of the year.

Some evidence is available on how long trans-atlantic transport might take. GUPPY (1917: 472) cited the case of a waterlogged and half-submerged schooner that took six months to drift from Newfoundland to the Hebrides 'covering the last 550 miles [880 km] at ten miles [16 km] a day'. The Gulf Stream current off Bermuda reaches 9 km/h, averaging a substantial 2 km/h. The time taken for pelagic larvae to drift between the Bahamas and NW Africa, implicitly passing the Azores on the way, is thought to be 200-400 days (review in JACKSON 1986: 595). Although some planktotrophic anthozoan planulae might postpone metamorphosis for this length of time (P.G. Tranter, pers. commn; WERNER 1984; PECHENIK 1990; discussion in CORNELIUS 1992) it seems unlikely that a lecithotrophic leptolid one would. For hydroids lacking a medusa stage rafting seems the only feasible way of reaching remote oceanic islands.

Even some adult bivalves and gastropods are thought to have rafted between oceanic localities (summaries in SCHELTEMA & WILLIAMS 1983: 560, JOHANNESSON 1988, and JOKIEL 1990). Regular trans-oceanic drifting of entire trees, even carrying rocks entwined in their roots, to remote oceanic islands has long been known to occur (DARWIN 1906, to the Marshall Islands; literature cited by RALPH 1961c, to New Zealand; and review by JOKIEL 1990).

Ralph considered recruitment of hydroids by rafting from Australia to New Zealand to be possible but, however, thought that from South America eastwards to the Australasian region the distance was too great. Possibly there are distance limitations even for rafters. The fauna of St Paul's

Rocks is evidently somewhat Brazilian in composition, accounted for by EDWARDS & LUBBOCK (1983a, b) by their being closer to Brazil than Africa.

Some cautionary evidence was presented by LEAL & BOUCHET (1991) who studied gastropod distributions along a chain of seamounts trailing about 1000 km eastwards from Brazil. They showed that distance of colonization tended not to be related either to dispersive ability or to lack of it. As the number of species tailed off away from the continental coast the proportions of long-dispersers and short-dispersers remained, paradoxically, broadly similar. They concluded this was due to successful rafting by all forms. However, this is certainly not paralleled by the leptolid faunas of remote island groups (Table 6; discussion below).

BRIGGS (1974), HIGHSMITH (1985), JOKIEL (1989, 1990) and others were apparently right to regard rafting as a common phenomenon accounting for many interrupted shallow-water marine distributions. The role of rafting in the dispersal of hydroids has been discussed previously (CORNELIUS 1981; also 1982, 1991). JACKSON (1986) went further in concluding that beyond dispersal of a few thousand metres rafting may be the commonest means of dispersal in both clonal and asexual invertebrates. The high incidence of rafting and non-medusoid species in the Azores coastal leptolid fauna is thus noteworthy.

D. A species club

Many of the shallow-water hydroids occurring in the Azores are typical of oceanic islands and, based on existing taxonomy, seem nearly cosmopolitan in coastal waters within their normal latitudinal ranges (cf. papers cited in part ii of Table 6). They include: *Tubularia* spp. (e.g. *T. crocea*, *Pennaria disticha*), certain *Eudendrium* spp., possibly *Sarsia tubulosa* (see p. 88), *Filellum serpens*, *F. serratum*, *Lafoea dumosa*, *Halecium tenellum*, *Lafoeina tenuis*, *Campanularia hincksii*, *Laomedea calceolifera*, *L. flexuosa*, four *Obelia* spp., possibly *Orthopyxis crenata*, *O. integra*, certain *Clytia* spp. including *C. gracilis*, *C. hemisphaerica* and *C. linearis*, *Dynamena cornicina*, possibly *D. disticha*, *Sertularella* spp. including *S.*

gaudichaudi sens. CORNELIUS 1979, *Tridentata distans*, *Antennella secundaria*, *Halopteris catharina*, *Kirchenpaueria similis* and/or *K. pinnata* (see Table 4), *Plumularia setacea*, *Ventromma halecioides*, and *Aglaophenia pluma* s. lat. A number of other species, such as the poorly known *Silhouetta uvacarpa* and *Clavopsella navis* (p. 88), might also be included. This list is not exhaustive: for example some of the species listed as near-cosmopolitan by STEPANYANTS (1980) may prove to be rafters occurring on oceanic islands. But on the remote Enewetak Atoll so much as half of the admittedly short hydroid faunal list comprised species from it (cf. COOKE 1975). Most of the species just listed have been recorded rafting, and all except *Filellum serpens* are substrate generalists. This species is epizoid on a range of other hydroids, and may be able to disperse in this way. *F. serratum* occurs on a range of substrates (CALDER 1991).

These 30 or more species form the bulk of the Azorean shallow-water hydroid fauna as they do around many warm- to cool-water oceanic islands world-wide. REES & WHITE (1966: 281) were perhaps following the conclusions of RALPH (1961c), based on her New Zealand work, when suggesting that 'many of the Azorean shallow-water species collected [before they wrote] seem to belong to a fauna dispersed by ocean currents. Thus campanulariids attach to *Sargassum* and other weeds. Only further collecting will determine whether the fauna is poor in species without means for long-range dispersal.' Present information indicates that this is so.

The few dozen rafting species involved form what might be described as a 'species club'. Its members apparently have in common the ability to cross oceanic distances too great for spanning by a relatively short-lived planktonic stage whether planula or medusa. The species seem often to disperse instead, perhaps 'accidentally' but perhaps not, by rafting on floating and swimming substrates. The concept of a 'club' parallels that of a species guild (as redefined by JAKSIC 1981) in which the members pursue a common activity such as predation on a well defined class of prey. The 'club' differs from this, perhaps slightly, in comprising a recognisable assemblage of unrelated species which co-occur in a number of isolated geographical localities. Species from

other groups may well belong to this 'club' but are not considered here. Unlike a guild, in such a 'club' there may be no advantage in or consequence of the grouping and the species do not necessarily interact.

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APPENDIX

Classification and original authorities for scientific names of leptolid species mentioned. The list is not a checklist of species recorded from the Azores region. Species mentioned only in Table 4 are not included. Works cited in this section are not necessarily included in the reference list but are as indicated in RALPH (1957), KRAMP (1961), MILLARD (1975), VERVOORT (1987), CALDER (1988, 1991), PETERSEN (1990), CORNELIUS (1975a, 1979, 1982) and SVOBODA & CORNELIUS (1991).

i) Hydroids

TUBULARIIDAE

Tubularia crocea (L. Agassiz, 1862)

Tubularia indivisa Linnaeus, 1758

HALOCORDYLIDAE

Pennaria disticha Goldfuss, 1820

CORYNIDAE

Sarsia sp. cf. *tubulosa* (M. Sars, 1835)

EUDENDRIIDAE

Eudendrium sp.

BOUGAINVILLIIDAE

Bougainvillia sp.

Clavopsella navis (Millard, 1959)

Silhouetta uvacarpa Millard & Bouillon, 1973

HALECIIDAE

Halecium nanum Alder, 1859

Halecium tenellum Hincks, 1861

LAFOEIDAE

Cryptolaria pectinata (Allman, 1888)

Filellum serpens (Hassall, 1848)

Filellum serratum (Clarke, 1879)

Lafoea dumosa (Fleming, 1820)

'CAMPANULINIDAE'

Lafoeina tenuis G. O. Sars, 1874

CAMPANULARIIDAE

Silicularia gracilis Meyen, 1834

S. bilabiata (Coughtrey, 1875)

Campanularia hincksi Alder, 1856

Clytia gracilis (M. Sars, 1850)

Clytia hemisphaerica (Linnaeus, 1767)

Clytia linearis (Thomely, 1899)

Laomedea angulata Hincks, 1861

Laomedea calceolifera (Hincks, 1871)

Laomedea flexuosa Alder, 1857

Laomedea pseudodichotoma Vervoort, 1959

Obelia bidentata (Clarke, 1875)

Obelia dichotoma (Linnaeus, 1758)

Obelia geniculata (Linnaeus, 1758)

Obelia longissima (Pallas, 1766)

'*Tubularia clytoides* Freycinet, 1824' (?=*Obelia* sp., discussion in CORNELIUS 1982: 118-119)

Orthopyxis crenata (Hartlaub, 1901)

Orthopyxis integra Macgillivray, 1842

SERTULARIIDAE

Amphisbetia operculata (Linnaeus, 1758)

Diphasia cf. attenuata (Hincks, 1866)
Dynamena cornicina McCrady, 1859
Dynamena disticha (Bosc, 1802)
Dynamena pumila (Linnaeus, 1758)
Sertularella gaudichaudi (Lamouroux, 1824)
 [see CORNELIUS 1979: 321]
Sertularella gayi (Lamouroux, 1821)
Sertularella polyzonias (Linnaeus, 1758)
Sertularia indivisa Meyen, 1834 (see present p. 77)
Tridentata distans (Lamouroux, 1816)
 PLUMULARIIDAE
 HALOPTERIINAE
Antennella secundaria (Gmelin, 1791)
Halopteris catharina (Johnston, 1833)
 KIRCHENPAUERIIDAE
Kirchenpaueria pinnata (Linnaeus, 1758)
Kirchenpaueria similis (Hincks, 1861)
 PLUMULARIIDAE
Nemertesia ramosa Lamouroux, 1816
Plumularia setacea (Linnaeus, 1758)
Ventromma halecioides (Alder, 1859)
 AGLAOPHENIIDAE
Aglaophenia acacia Allman, 1883
Aglaophenia picardi Svoboda, 1979
Aglaophenia pluma (Linnaeus, 1758)
Aglaophenia tubulifera (Hincks, 1861)

ii) Hydromedusae

CALYCOPSIDAE

Calycopsis typa Fewkes, 1882
Sibogita geometrica Maas, 1905
Stomotoca rugosa Mayer, 1900 (= *Amphinema*)

PANDEIDAE

Pandea conica (Quoy & Gaimard, 1827)

ZANCLEIDAE

Zanclea costata s. str. Gegenbaur, 1856

LAODICEIDAE

Krampella dubia Russell, 1957

CAMPANULARIIDAE

Clytia hemisphaerica (Linnaeus, 1767)

CUNINIDAE

Cunina duplicata Maas, 1893

SOLMARISIDAE

Solmaris corona (Keferstein & Ehlers, 1861)

GERYONIIDAE

Liriope tetraphylla (Chamisso & Eysenhardt, 1821)

RHOPALONEMATIDAE

Aglaura hemistoma Péron & Lesueur, 1810

Rhopalonema velatum Gegenbaur, 1856

