Hydrobiologia **216/217**: 481–487, 1991.
R. B. Williams, P. F. S. Cornelius, R. G. Hughes & E. A. Robson (eds),
Coelenterate Biology: Recent Research on Cnidaria and Ctenophora.

The benthic deep-water siphonophore *Rhodalia miranda* and other coelenterates in the south-west Atlantic: ecological and oceanographical implications

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Key words: Cnidaria, Siphonophora, *Rhodalia*, south-west Atlantic, biogeography, oceanography

Abstract

The benthic deep-water siphonophore *Rhodalia miranda* was collected for the first time in 1876 by H.M.S. 'Challenger' off the Rio de la Plata estuary beneath the Subtropical Convergence at about 1000 m depth. *Rhodalia* was reported again about 100 years later from certain distant localities in the subantarctic region of the south-west Atlantic. Hydrographic and topographic features that may be involved in creating this peculiar distribution pattern are discussed together with a likely mode of dispersal of benthic coelenterates. The disjunct distribution of *Rhodalia* and other benthos of the upper Argentine Slope suggests the subsurface oceanographic régime to be quite different from what we know of the surface layers.

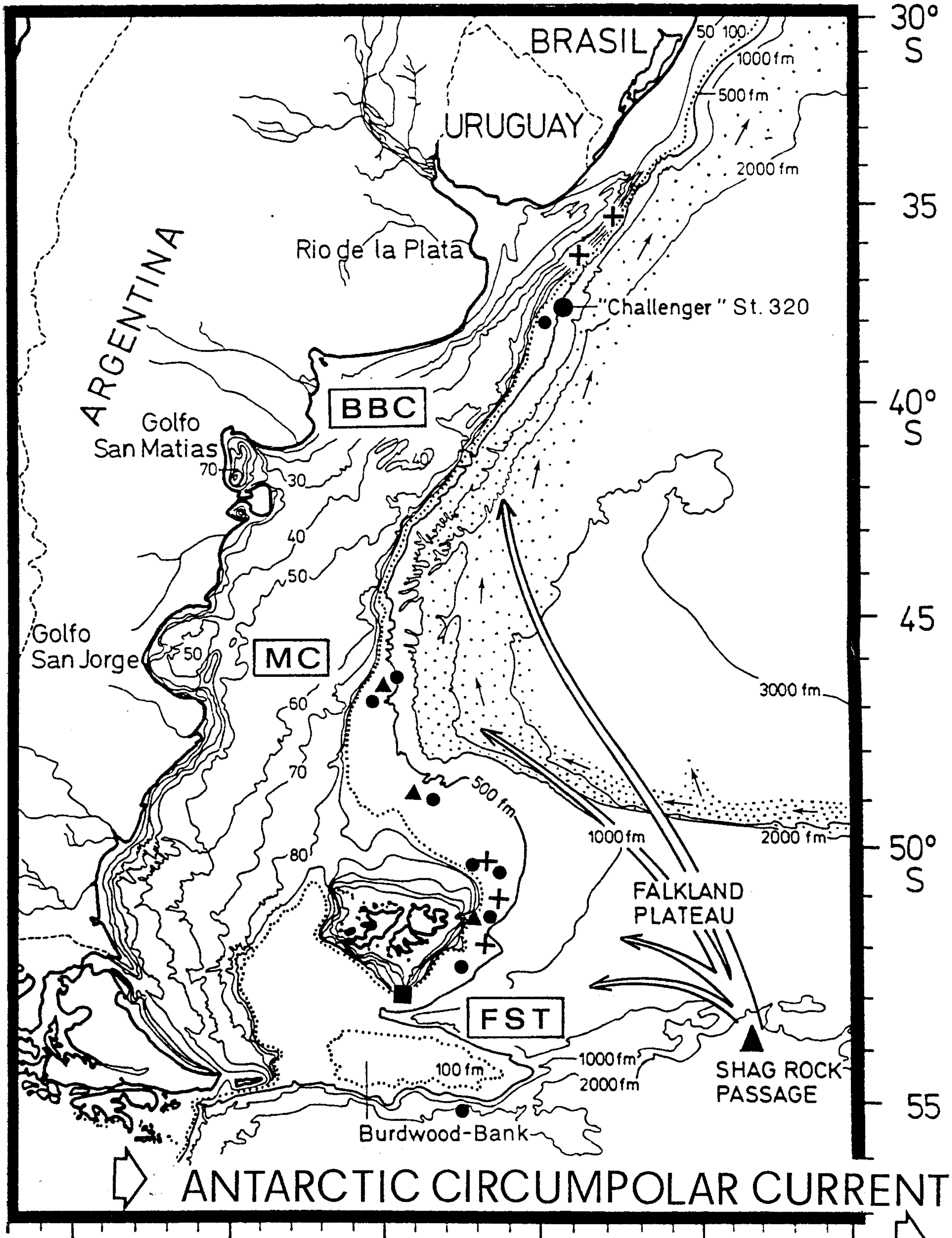
Introduction

Siphonophores of the family Rhodaliidae have come into the limelight again quite recently, when it was discovered that the so-called 'dandelions' of the Pacific deep-sea hydrothermal vents were rhodaliids (Pugh, 1983). Direct observations from submersibles revealed that these animals are positively buoyant but remain tethered by their tentacles to the bottom. These observations ended the dispute about the enigmatic way of life of rhodaliids and established that they are true benthic organisms.

The type species of its genus, *Rhodalia miranda* Haeckel, 1988, was collected in 1876 off the Rio de la Plata estuary at a depth of 1097 m by H.M.S. 'Challenger' (St. 320, 4 specimens). This station became known for having yielded one of the richest trawl hauls of the cruise, with 103 new species and 19 new genera (Murray, 1895). Curiously, many of the new species from St. 320 were not collected again until quite recently and their identity remained doubtful as the later sampling locations usually were in the subantarctic or antarctic proper, far from 'Challenger' St. 320 which lies beneath the Subtropical Convergence.

The next specimens of *Rhodalia miranda* were taken in 1962 by the American R.V. 'Eltanin' south of the Falkland Islands from 550 m depth (one specimen); in 1967 and 1974 by the Russian R.V.s 'Academician Knipovich' and 'Zoond' (11 specimens) at 3 locations along the north-eastern slope of the Falklands; and lastly from one locality on the slope facing the Golfo San Jorge off southern Argentina (Pugh, 1983) (Fig. 1).

Rhodalia miranda remains little known by deep-sea biologists, and the remarkable illustration by Haeckel (1888) is still the only satisfactory one. It was reproduced by Pugh (1983) but few provin-


BRASIL
URUGUAY
ARGENTINA
Rio de la Plata
"Challenger" St. 320
BBC
Golfo San Matias
MC
Golfo San Jorge
FST
FALKLAND PLATEAU
SHAG ROCK PASSAGE
Burdwood-Bank
50 100
1000 fm
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30 40 50 60 70 80
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ANTARCTIC CIRCUMPOLAR CURRENT
70°W
65
60°W
55
50°W

cial libraries around the world hold that publication. To promote a wider knowledge of this extraordinary life form Haeckel's figure is reproduced here (Fig. 2).

Biogeography and physiography

The pattern of occurrence of *Rhodalia miranda* might imply that this siphonophore is continuously distributed along the entire slope of the south-west Atlantic Ocean. However, extensive trawling by the German Fisheries Research Vessel 'Walther Herwig' on the Argentine Shelf and slope, in 1966 and 1970/71 (850 dredging stations, 110 of these below the shelf break), yielded another 30 specimens of *R. miranda* from 14 stations (Riemann-Zürneck, 1986) (Fig. 1). These sampling localities supported quite precisely the above disjointed pattern between 37 and 55 °S with definite locations where the siphonophore is collected regularly, usually a number of specimens, and gaps in between where it apparently does not occur.

Similarly disjunct patterns of distribution are evident in other slope-inhabiting benthic coelenterates some of which also have their type locality at 'Challenger' St. 320 (Cairns 1982, 1983): the solitary coral, *Flabellum curvatum* Moseley, and 3 species of hydrocorals (Stylasterina: *Stylaster densicaulis* Moseley, *Sporadopora dichotoma* (Moseley), and *Errina (Inferiolabiata) labiata* Moseley). All 4 species also inhabit the Antarctic Ocean to a lesser or greater extent. Among the sea anemones, *Hormathia pectinata* (Hertwig), *Epiactis georgiana* Carlgren, and *Isosicyonis alba* (Studer) are also discontinuously distributed along the Argentine shelf break (Riemann-Zürneck, 1986).

Several other slope-inhabiting invertebrates follow the same pattern of disjointed distribution. Hence it may be concluded that at upper slope depths there are benthic communities of basically similar composition that flourish only at certain sites with the northernmost location close to the Subtropical Convergence. The distribution of the constituent species shows them to be subantarctic or antarctic.

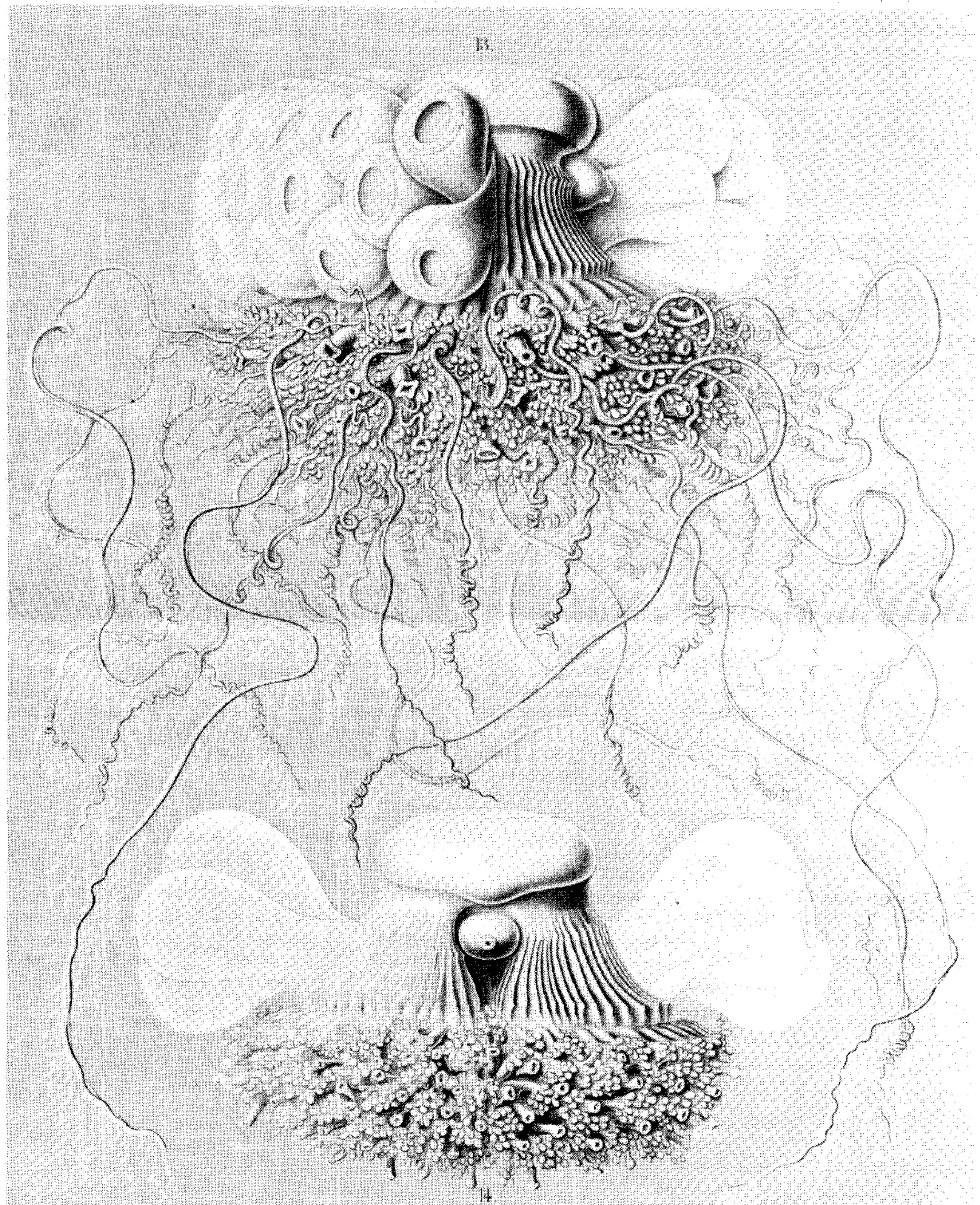
As substrate preference seems not to determine this disjunct distribution, a closer look at the topography and hydrology of the region is essential. However, this is severely hindered by the south-west Atlantic's being one of the least studied oceanic areas.

According to Lonardi & Ewing (1971) the topography of the Argentine continental slope and rise is in sharp contrast to the soft character of the shelf. There are most spectacular submarine canyons, 70 of which cut the continental margin. Two of these canyons seem to extend to the greatest depths: the Bahia Blanca Canyon with its head at 41 °S and farther south the prolongation of the canyon-like Malvinas Channel between 47 °S and 48 °S.

The slope around the Falklands is soft with a canyon-like structure only in the south and south-west which is the westward prolongation of the Falkland Southern Trough (Fig. 1).

Oceanographically, the Subtropical Convergence is a stable feature at about 38 °S over the slope down to at least 1000 m (Hubold, 1980a, 1980b; Riemann-Zürneck, 1986). At the southern border of this frontal zone a region of very cold water, known as the Falkland or Malvinas

Fig. 1. Distribution of the deep-water siphonophore *Rhodalia miranda* in the south-west Atlantic and supposed water movements that may be responsible for its discontinuous distribution pattern. ● CHALLENGER St. 320 (type locality); ■ ELTANIN cruise 6, St. 339, 3.12.1962; ▲ Collecting stations of the Russian research vessels ACADEMICIAN KNIPOVICH (1967, St. 1009 and 1021) and ZOOND (18.5.1974); WALTHER HERWIG locations 1966 (austral winter, St. 325, 330, 336, 447, 451); • WALTHER HERWIG locations 1970/71 (St. 121, 191, 221, 222, 226, 230, 242, 294, 311). The stippled area indicates the abyssal flow of the Antarctic Bottom water (AABW). The big arrows originating in Shag Rock Passage show the presumed route of Antarctic Circumpolar Water entering the south-west Atlantic. Abbreviations: BBC Bahia Blanca Canyon, FST Falkland Southern Trough, MC Malvinas Canyon. Topography according to Lonardi & Ewing (1971) with depths in fathoms (1 fathom = 1.829 m).



RHODALIA MIRANDA.

Current, parallels the shelf edge between 37° and 41 °S. Although oceanographers have long known that the lowest temperatures are invariably found in the northernmost part of the Argentine shelf edge (Klähn, 1911), and although there has never been evidence of a northward current on the slope south of 41 °S (Piola & Georgi, 1982), the entire shelf-edge water from south to north was nevertheless commonly depicted as the Falkland Current (discussion in Riemann-Zürneck, 1986) with its origin somewhere in Drake Passage branching off the Cape Horn Current.

In recent decades, however, it has become apparent that this picture has to be revised as 'it appears that the origin of the Falkland Current is quite complicated and its water may be derived from different geographical locations as depth increases' (Gordon & Goldberg, 1970). Firstly, the water rounding the southern tip of South America and turning north or north-east (sweeping over the Burdwood Bank and the Falklands shelf) is relatively warm with characteristics of eastern South Pacific water (Riemann-Zürneck, 1986: 101). It is also a relatively shallow layer of water, having nothing in common with the cold and deep-reaching slope water to the north. Secondly, the modern concept of the structure and behaviour of water masses in Drake Passage, the eastward-flowing Antarctic Circumpolar Current, is that of narrow, high-speed currents separated by broad, quiescent zones (Hofmann, 1985). Below the surface layer, the ribbons of water in the northernmost part of Drake Passage are supposed to follow the Scotia Ridge in an easterly direction (Gordon, 1966; Gordon *et al.*, 1977; Georgi, 1979). They leave the Scotia Sea presumably at 48 °W through Shag Rock Passage (Fig. 1) which is a large gap in the Scotia Ridge about 300 km wide, reaching to depths of about 3000 m.

Evidence of a strong current passing over the saddle of the Falkland Plateau is given by ripple marks and clean-swept pavement (Gordon & Greengrove, 1986). Zenk (1981) has also monitored the deepest layers within Shag Rock Passage and measured intermittent gushes of cold water (0.47° $\pm$ 0.11 °C) to the north-west. The highest speeds (65 cm s^{-1}) coincided with the lowest temperatures (0.29 °C) and the most westerly directions. The properties of the water passing through Shag Rock Passage imply a mixture of Circumpolar Deep Water (from the Ross Sea) and Weddell Sea Water. These observations show that currents originating here supply the south-west Atlantic with Subantarctic Water.

The disjunct distribution pattern of *Rhodalia miranda*, and of similarly distributed slope animals, is considered here indicative of Circumpolar Water reaching the slope of Argentina and maintaining stable environments for subantarctic invertebrates at definite sites (Fig. 1). The assemblages of subantarctic animals to the south, east and north-east of the Falkland Islands are in accordance with the westerly or north-westerly flow of part of the Shag Rock Current according to Zenk (1981). Further to the north, the next patch of subantarctic fauna is the area facing the Golfo San Jorge. This site can be related to the current traversing the saddle of the Falkland Plateau. If this current follows the topographic contours to the north-west, it is probably pushed up the slope through the Malvinas Canyon. Assuming average current velocities of about 30 cm s^{-1} (about 25 km d^{-1}) these areas could be reached within about one month.

The assemblage of subantarctic benthos near 'Challenger' St. 320 might by analogy be thought to be maintained by a strong and stable current of Circumpolar Water traversing the South Atlantic Basin. This would impinge onto the Argentine Slope at about 41 °S, and follow the upper Slope to the north. There are a few indications of such a permanent deep flow. Firstly, the lowest temperatures are invariably met close to the head of

Fig. 2. Rhodalia miranda. Reproduction of the original illustrations of the type specimen (Haeckel, 1888; pl. 3). Upper figure: lateral view of corm, semi-diagrammatic, with the majority of the nectophores removed from the trunk of the nectosome. Actual diameter of corm *ca* 6 cm. Lower figure: same, dorsal view. Further details in Haeckel (1888) and Pugh (1983).

the Bahia Blanca Canyon at 41 °S – even in summer. In this area typical antarctic species are found at depths of about 1000 m and subantarctic species are known to rise onto the shelf, whereas the common shelf species avoid this area (Riemann-Zürneck, 1986). The second argument for a permanent current through the South-west Atlantic Basin is the supposition put forward by Lonardi & Ewing (1971) that on the northern flank of the Falkland Plateau (at about 50 °S 48 °W, north of the Shag Rock Passage) part of the Antarctic Bottom Water (AABW) branches off, taking a north-westerly course through the deepest parts of the Argentine Basin (Fig. 1). According to Mantyla & Reid (1983) the AABW is composed of the same water (5/8 circumpolar, 3/8 Weddell Sea deep water) as the Shag Rock Current. Thirdly, according to Zyryanov & Severov (1979), 2 cyclonic features in the Argentine Basin could create a strong current at their westerly borders.

From a biogeographical point of view we have to ask whether it is possible for subantarctic invertebrate species to be transported successfully over distances that would take 3 or 4 months to cross. For hemi-sessile animals like *Rhodalia* this seems to be no problem since their developmental stages are most probably pelagic and the adults might also be displaced or dispersed by currents (Mackie *et al.*, 1987). In most other benthic coelenterates, such as anthozoans, pelagic larvae are usually considered the means of dispersal even over long distances (Riemann-Zürneck, 1976; Richmond, 1987). However, in antarctic and subantarctic regions production of pelagic larvae is rare, at least in sea anemones.

Brooding and releasing of postmetamorphic juveniles (*ca* 1 mm diam.) seem to play a major part in the life history and dispersal of this group. Carlgren (1903) documented the presence of such anemone 'embryos' between May and November 1898 in antarctic waters south of 70 °S at 200–450 m, and the American R.V. 'Eltanin' collected about 40 specimens of obviously similar structure in 1968 (St. 2026, Ross Sea, 801 m; see Fig. 11 in Riemann-Zürneck, 1986). Thus drifting and rafting of postmetamorphic juveniles seems to be quite common in circumantarctic waters, at least in sessile coelenterates.

In summary (Fig. 1) the discontinuous distributions of the deep-water siphonophore *Rhodalia miranda* and other subantarctic benthos in the south-west Atlantic are considered indicative of Circumpolar Water reaching the upper Argentine Slope. Currents approaching the continental margin are presumably directed by canyon topography to certain sites at different latitudes where they sustain stable subantarctic faunal assemblages. These currents may be derived entirely or partly from a strong and fast-moving current leaving the Scotia Sea through Shag Rock Passage.

Acknowledgements

The invertebrate material of the German fishery research cruises to the south-west Atlantic aboard F.R.V. 'Walther Herwig' was collected, preserved, sorted and distributed by Dr Helmut Schulz of the Bundesforschungsanstalt für Fischerei in Hamburg. It is largely through him that our knowledge of the invertebrate benthos of that region has greatly improved. This is contribution No. 280 of the Alfred-Wegener-Institute for Polar and Marine Research.

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