

Bathymetric distribution patterns and biodiversity of benthic Medusozoa (Cnidaria) in the Bay of Biscay (north-eastern Atlantic)

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Bathymetric distribution data were compiled on benthic Medusozoa (Cnidaria) of the Bay of Biscay and nearby seas. The area of study extended from 42°N to 48°30'N, and westwards to 10°W. The depth range of each species was traced in a review of the literature. The number of species in each of several depth zones is summarized here: intertidal, intertidal–30 m, 30–100 m, and thereafter at 100 m depth intervals throughout the entire column (0–5000 m). Some 200 species were included (six Scyphozoa, four Staurozoa, 190 Hydrozoa). Of these, 196 could be ascribed to the Coastal Realm (0–200 m) (118 exclusives; 60% of the fauna) and Deep Benthic Realm (200+ m) (31 exclusives; 16%), with 47 species inhabiting both (24%). Eighty-eight species (45%) were present intertidally. Biodiversity was highest above the summer thermocline (30 m) (133 species, 67%), and no species have been recorded from depths greater than 4706 m. Beyond the thermocline, biodiversity dropped with increasing depth. A significant change occurred in the 30–100 m interval (123 to 78 species; Distinctiveness=51%), although all intervals down to the 300 m isobath exhibited substantial changes. Most species in the Deep Benthic Realm thrive on the upper part of the slope (200–800 m; 50 species). Biodiversity appeared homogeneous across wide bathymetric ranges in deep bathyal and abyssal regions, perhaps due to unique vertical biocenological units. Thus, 15 species are known between 1400 and 2000 m, and four between 3100 and 4300 m. Fifty-four species were considered eurybathic (34%), with some showing impressive bathymetric ranges of over 4000 m, but most species were stenobathic (106, 66%).

As with data on benthic medusozoans from South Africa, the north-western Atlantic, the Arctic, and the warm western Atlantic (Bermuda), bathymetric biodiversity was highest in the first 100 m, with a substantial drop below that in species numbers on the shelf and at the beginning of the bathyal. While numbers of species may vary widely from one geographical region to another, such variations are due to differences in biodiversity in the upper 100 m. Hydroid species richness in the deep bathyal and abyssal is similar and always low. Worldwide, benthic medusozoan biodiversity is highest at shallow depths, and these organisms normally seem to be minor components of deep benthos. Very likely, the graph of biodiversity at increasing depth is similar worldwide for the Hydrozoa.

INTRODUCTION

There is much information hidden in the faunistic and taxonomic literature that, if globally processed, may lead to interesting studies. The analysis of this literature is of great importance, since the majority of the biodiversity information is stored therein and it is hardly used as a source of information. Since the first records by Beltrémieux (1864), the benthic Medusozoa (classes Staurozoa, Scyphozoa and Hydrozoa) of the Bay of Biscay have been the direct or indirect subject of no fewer than 211 papers. Of these, 81 have dealt with taxonomy and systematics. While a similar number of works provide varied ecological data on these animals, only two (d'Hondt, 1966; Lagardère & Tardy, 1980) are strictly ecological or bionomical. Even for hydroids, with the highest number of species within the Medusozoa and an abundant group in shallow water communities, ecological information is incomplete and scattered worldwide (Boero & Fresi, 1986). Boero (1984) and Gili & Hughes (1995)

have provided meaningful reviews of their ecology. In the Bay of Biscay, hydroids are common animals that may even form facies (see Le Danois, 1948). The existing literature, while scattered, provides a good source of data for global ecological or biogeographical studies. In particular, bathymetric distribution is an especially interesting indicator of ecological tolerances of species. While a progressive increase in hydrostatic pressure may have little direct effect on medusozoans, changes in depth are associated with modifications in other physical parameters (light, temperature, hydrodynamics, food availability, siltation, etc.) that are determinants for the bathymetric distribution of the species (see García Carrascosa, 1981). Many Medusozoa are eurybathic, indicating high ecological tolerance, and bottom invertebrates with wide vertical ranges tend to have extensive horizontal ranges as well (Vinogradova, 1958, 1997; Pielou, 1992).

While depth data are commonly given in taxonomic or ecological papers, bathymetric analyses of the medusozoan fauna of a given geographical area from intertidal to

abyssal depths are scarce. Similar bathymetric distribution patterns, with highest hydroid species richness in the upper 100 m, have been reported by Millard (1978) from South Africa, by Stepanjants (1989) in Arctic seas, by Calder (1996) in the north-western Atlantic and adjacent areas, by Calder (1998) in the Bermuda region and by Schuchert (2000) from Iceland. Peña Cantero (2004) studied the bathymetric distribution of Antarctic species, and assigned them to several bathymetric groups.

Data for species of benthic Medusozoa in the Bay of Biscay are presented herein, along with an overview of the bathymetric distribution of the fauna. The vertical zonation of every species represented is documented, and the results are compared with data by authors from other parts of the world. Generalizations pertaining to depth distributions and biodiversity are advanced based on analysis of all these works.

MATERIALS AND METHODS

Literature on Medusozoa of the Bay of Biscay and nearby areas was reviewed for an area from 42° to 48°30'N, and westwards to 10°W (Figure 1). A list of valid species and reliable depth records was prepared following the catalogue by Altuna (in preparation). Data on depth distributions of species was pooled from the entire area. This procedure, as undertaken by Le Danois (1948) with several animal groups in the Bay of Biscay and nearby areas, was criticized by Menzies et al. (1973) because the region included more than one biogeographical province. However, the coastal area assessed herein from the shelf is entirely within the Lusitanian province of the Mediterranean Atlantic Region (Briggs, 1974), of the Western Temperate Coastal-margin Realm (Hayden et al., 1984). According to Hayden et al. (1984), the rest of the fauna is comprised of the Deep Benthic Realm II. The area included herein comprises the following divisions of the so-called 'Province Franco-ibérique' (Le Danois, 1948): Armorican (48°30'N–46°00'N), Aquitanian (46°00'N–Capbreton Canyon) and North-Iberian (Capbreton Canyon–43°N).

Depth records were compiled for every species, and the bathymetric range given as the interval between shallowest and deepest records. The entire bathymetric range (intertidal–5000 m) was subdivided into 100 m depth intervals into which species were assigned, except for three intervals in the first 100 m: intertidal, intertidal–30 m, and 30–100 m. This was done to discern possible faunal changes in species richness due to the influence of the summer thermocline established around the 30 m isobath, at least in the north-eastern and south-eastern sectors of the bay (see Castric-Fey, 1974; Valencia Santana et al., 1988). For each interval, overall biodiversity, species appearing, and those disappearing, were indicated. The species were then ascribed to geomorphological units: the Coastal Realm (C, 0–200 m depth), the Deep Benthic Realm (D, +200 m) or both (CD). The 200 m isobath has been largely considered the edge of the shelf and the beginning of the Deep Benthic Realm (see Briggs, 1974).

Distinctiveness between intervals was calculated following Menzies et al. (1973) by applying the formula $D\% = (T - T_c)100/T$ for the determination of faunal changes (T_c = total taxa in common between any two

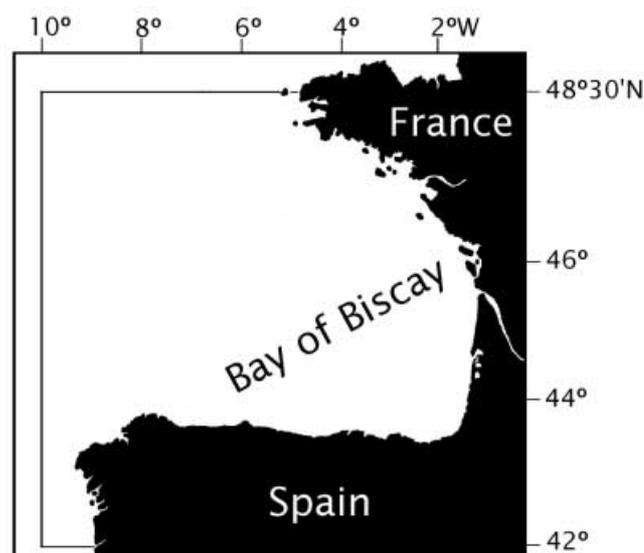


Figure 1. Study area. (Portugal border not shown).

points; T = total of species; $D\%$ = percentage of distinctiveness). Finally, the species (Scyphozoa and Staurozoa excluded to allow comparisons with other authors' results) were clustered in bathymetric groups following some modifications of the schemes proposed by García Carrascosa (1981) and Peña Cantero (2004), as follows: (A) Coastal Realm species occurring exclusively at depths above the summer thermocline (shallow fauna) (0–30 m); (B) Coastal Realm species absent over the summer thermocline (30–200 m); (C) Species distributed in the whole Coastal Realm (intertidal–200 m); (D) species ranging from below the summer thermocline to the Deep Benthic Realm (limited tolerance to seasonal changes whatever the nature) (30–200+ m); (E) species with a wide vertical distribution, and thus with a high ecological tolerance, that included both Realms (intertidal–200+ m); (F) species restricted to the Deep Benthic Realm and absent from the continental shelf (200+ m).

The most important papers the data were taken from are those of Roule (1896), Pictet & Bedot (1900), Billard (1906, 1927, 1931), Browne (1907), Leloup (1940), Fey (1969), Chas Brínquez & Rodríguez Babio (1977), García Corrales et al. (1978, 1979, 1981), Isasi Urdangarín (1985), Vervoort (1985), Ramil Blanco (1988), Álvarez-Claudio (1993) and Altuna Prados (1994). Other works give important species lists but with no depth data. In order to give an idea about how thoroughly the region has been sampled, the number of original records and of times that every species is mentioned in the Bay of Biscay literature is given in Appendix 1. Every different sampling station in a given paper is considered a new record.

RESULTS

Fauna of the geomorphological realms

Two hundred species were considered valid within the limits of the study area (Table 1; Appendix 1). For 188 of these species, detailed bathymetric data were gathered and 196 of them could be ascribed to either of the two realms. A total of 118 species was exclusive to the Coastal

Table 1. Number of species/ssp. in the area of study. *, Total number of species/ssp. including those that cannot be ascribed to a given Realm due to lack of precise bathymetric data. Numbers in parentheses, percentage referred to the total of species/ssp. from which precise bathymetric data is available.

Class	Subclass	Order	Suborder	(A) Coastal Realm	(B) Deep Benthic Realm	(C) Both Realms	Coastal Realm Fauna (A+C)	Deep Benthic Realm Fauna (B+C)	Total
Staurozoa		Stauromedusae		4 (100)	0	0	4	0	4
Scyphozoa	Discomedusae	Coronatae		2 (50)	2 (50)	0	2	2	4
		Semacostomeae		1 (100)	0	0	1	0	1
		Rhizostomeae		1 (100)	0	0	1	0	1
Hydrozoa	Trachylina Leptolina	Limnomedusae		1 (100)	0	0	1	0	1
		Actinulida		4 (100)	0	0	4	0	4
		Leptothecata	Conica	55 (50)	19 (17)	34 (32)	89	53	108/110*
			Proboscoida	13 (65)	1 (5)	6 (30)	19	7	20/21*
			Filifera	16 (55)	6 (21)	7 (24)	23	13	29/30*
			Capitata	21 (88)	3 (12)	0	21	3	24
Total				118 (60)	31 (16)	47 (24)	165	78	196/200*

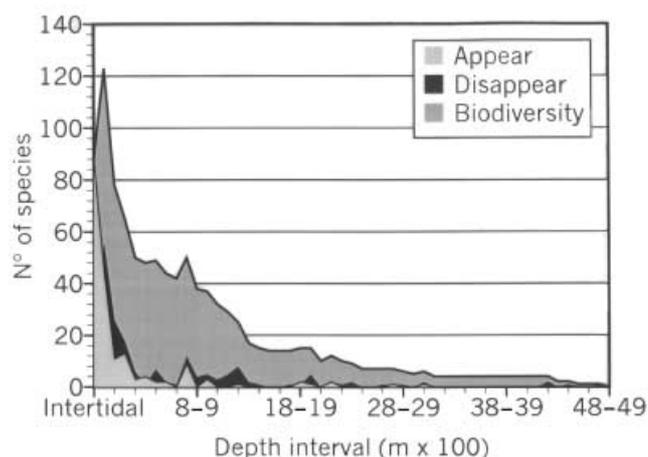


Figure 2. Changes of biodiversity in the Bay of Biscay along the entire bathymetric range, and number of species that appear or disappear in each depth interval. (Scyphozoa and Staurozoa included).

Realm (60%), and 31 to the Deep Benthic Realm (16%); 47 species inhabit both realms (24%). Thus, the coastal (shelf) fauna comprises 165 species and the deep benthic 78. Except for the order Coronatae (Scyphozoa), all orders were more diversified in the Coastal Realm. Nevertheless, as more studies become available, more species of Coronatae will likely be discovered within the Deep Benthic Realm.

Changes of biodiversity at increasing depth

Maximal depth in the Bay of Biscay is slightly over 5000 m depth (Le Danois, 1948). While Medusozoa are known to occur along virtually the entire bathymetric profile, vertical distribution of biodiversity is uneven (Figure 2). Eighty-eight species (45% of the fauna) were recorded intertidally, and biodiversity was highest over the range of the summer thermocline (30 m) (133 species; 67% of the fauna). No species are known deeper than 4706 m. Diminution in biodiversity was clearly evident below the thermocline at increasing depth, with the species numbers curve dropping markedly at first and then rather more gently. The thermocline is a significant environmental factor in the Bay of Biscay; Castric-Fey et al. (1978–1979) distinguished the 30 m isobath as a critical depth for benthos in the north of the bay and noted an important change of species there. The south-east part of the bay (Basque coast), with high summer water temperatures, has some warm-water species that thrive over the thermocline and are known only therein [*Nausithoe punctata* K lliker, 1853, *Dipurena reesi* Vannucci, 1956, *Campalecium cirratum* Millard & Bouillon, 1975, *Aglaophenia picardi* Svoboda, 1979, *Clytia linearis* (Thornely, 1899)].

All selected depth intervals in the Coastal Realm are also characterized by high biodiversity, as are those at the beginning of the bathyal. Herein, all intervals from 200 to 500 m depth have a similar biodiversity (50, 48, 49). A noteworthy change in biodiversity occurs between the thermocline interval and the zone immediately below it (123–78, D=51%), although all intervals to a depth of

300 m show important changes. Moreover, appearances of new species in the Coastal Realm between intervals are also significant (Figure 2), especially so below the tidal area (40) and the thermocline (11). At the beginning of the slope (200–300 m) there is a diminution in the appearance of new species (13 to 3) and of biodiversity as a whole (65 to 50). In the Deep Benthic Realm, appearance of new species is comparatively low (30), although the 700–800 m depth was striking with nine species added [*Garveia arborea* (Browne, 1907), '*Garveia biscayana*' (Browne, 1907), *Egmondella grimaldi* Leloup, 1940, *Egmondella* sp. 2, *Stegolaria geniculata* (Allman, 1888), *Stegopoma bathyale* Vervoort, 1966, *Acryptolaria longitheca* (Allman, 1877), *Cryptolaria abyssicola* (Allman, 1888) and *Nemertesia norvegica* (G.O. Sars, 1874)] thereby breaking the gradual drop seen from the 200–300 m interval downwards at the beginning of the continental slope. This 700–800 m depth interval was followed by another loss of species at 900–1000 m (from 50 to 38 species).

Most Deep Benthic Realm species occur on the upper part of the slope, and numbers of exclusively bathyal species are low. Thus, 50 species are known from depths of 200–800 m but only 12 at 2200 m. From a depth of 1300 m downwards, biodiversity in the various intervals was low (<17), with only seven species unknown from upper levels [*Acaulis primarius* Stimpson, 1854, *Zanlea costata* Gegenbaur, 1856, ? *Lovenella producta* (G.O. Sars, 1874), *Symplectoscyphus tricuspoidatus* (Alder, 1856), *S. bathyalis* Vervoort, 1972, *Cladocarpus corneliusi* Ramil & Vervoort, 1992, *Campanularia* cf. *agas* Cornelius, 1982], and with no additional species being beyond 3100 m. Medusozoa are minor components of the Bay of Biscay profundal benthos, as has been suggested also in other areas by works of other authors (Vervoort, 1966; Calder, 1996, 1997).

Fifteen species are known to occur between 1400 and 2000 m (D=23%) and four between 3100 and 4300 m (D=33%). This homogeneity in biodiversity across wide bathymetric ranges within the deep bathyal and abyssal may be indicative of a unique vertical province or any of its subdivisions in the sense of Menzies et al. (1973).

From curves showing disappearances of species (Figures 2 & 3), maximal loss of biodiversity takes place in the interval between the tidal zone and the thermocline 56 species, with meaningful losses also in the following intervals within the shelf. At the 200–300 m interval, a significant change occurs, from a loss of 18 (100–200 m) species to only six (D=32%). Other significant intervals of change are at 1200–1300 m (25 to 17 species, D=32%) and at 1800–2000 m and 2000–2100 m (from 15 to 10 species, D=33%) although again, the 700–800 m is particularly meaningful (12 species). Because of low abyssal biodiversity, loss of a unique species may result in 50% distinctiveness, as happens below 4000 m, but it is unclear whether this is associated with meaningful biocological changes. From the graphs of appearances and disappearances of Medusozoa (Figures 2 & 3), no meaningful change in the fauna was apparent around 3000 m that might reflect the beginning of the abyssal (see Vinogradova, 1962) in the Bay of Biscay. Even the so-called transition layer between the bathyal and the abyssal (2500–3500 m depth) was undetectable. Nevertheless, below 3000 m no additional species appeared and the

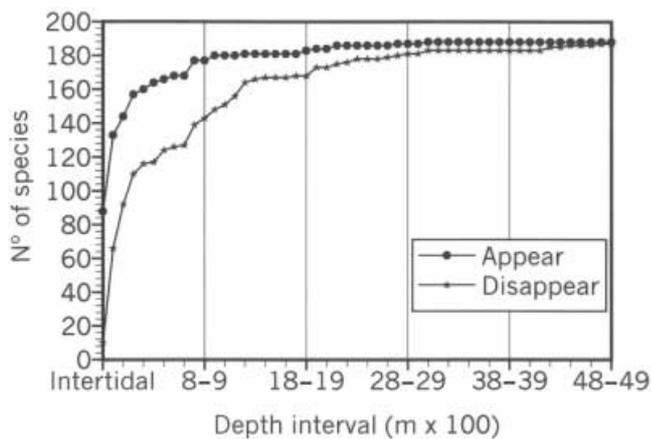


Figure 3. Accumulative curves of appearance and disappearance of species along the entire bathymetric range. (Scyphozoa and Staurozoa included).

remaining six in the bathymetric column disappeared [*Garveia arborea*, *Acaulis primarius*, *Campanulina panicula* G.O. Sars, 1874, *Cryptolarella abyssicola*, *Obelia dichotoma* (L., 1758) and *Campanularia* cf. *agas*]. Benthic Medusozoa seem to be of little value as potential indicators of zonation in deep bathyal and abyssal environments of the Bay of Biscay.

The accumulative curve of species numbers with increasing depth (Figure 3) shows that most appeared in shelf waters (0–200 m). Another noticeable increase occurred in the 700–800 m interval, where the addition of nine species brought the total to 177. From this interval to the greatest depths, additional species appeared very gradually, with only ten species appearing below 800 m (to a total of 188 species). The accumulative graph of species that disappear is similar, and most species do not penetrate to depths beyond the shelf. Again, the 700–800 m interval was notable within the bathyal, as 12 species disappeared therein. This interval shows an important turnover of species (21) in the Deep Benthic Realm.

Eurybathy and stenobathy of the species and bathymetric groups

Eurybathic or stenobathic species are ones whose depth range exceeds, or is less than, 300 m respectively (Menzies et al., 1973; Pielou, 1992), although 200 m was taken as the critical depth range in this sense by Millard (1978). Accordingly, many species in the Bay of Biscay are eurybathic and some have impressive bathymetric ranges, suggesting high ecological tolerance. Most, however, appear to be stenobathic (106 species, 66%) with 73 (46%) having a known depth range under 50 m (Figure 4). The eurybathy of many species (54, 34%) restricts their usefulness as zonation indicators, with low values of distinctiveness between intervals. Twenty-six showed depth ranges of over 1000 m (14%) and two (1%) ranged between 4000 and 4500 m (*Campanulina panicula*, 4160 m; *Obelia dichotoma*, 4210 m), although the latter depth record is doubtful (Vervoort, 1985). Forty-four of the 54 eurybathic species (81%) occurred in both realms, and 14 of them (26%) exist also in the intertidal. Just ten (18%) of the eurybathic species were strictly bathyal-abyssal. This contrasts with the Anthozoa of the Bay of Biscay, the

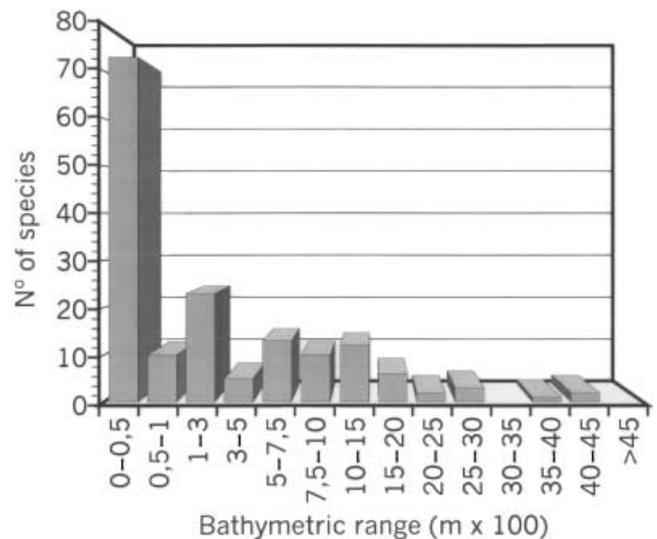


Figure 4. Eurybathy and stenobathy of all the species. Species with a depth range in excess of 300 m are considered eurybathic (eurybathial) following Menzies et al. (1973). Species with a range of less than 300 m are considered stenobathic (stenobathial). (Depth intervals do not represent isobaths, but are absolute depth ranges in metres regardless of the region of the bathymetric column where the species lives).

other class in the phylum Cnidaria having more eurybathic species than the Medusozoa that, nevertheless, are exclusives of the Deep Benthic Realm.

The deepest record of a benthic medusozoan in the Bay of Biscay is a report of a tentatively identified *Acaulis primarius* from 4706 m (Vervoort, 1985). A large number of species occur intertidally (88, 45% of the total), where they exist at the upper edge of their range. Nine species have been reported only from the intertidal, but it is unlikely that any of them are restricted to this zone in the Bay of Biscay. Some, however, may find optimal conditions there [*Coryne muscoides* (L., 1766), *Clava multicornis* (Forsskål, 1755), *Laomedea flexuosa* Alder, 1857 and *Dynamena pumila* (L., 1758)]. Worldwide, relatively few species occur only intertidally, and even fewer occur where they are exposed directly to the air (Gili & Hughes, 1995). Given the opportunistic strategy of many hydroids, infralittoral species may grow intertidally in crevices, overhangs, or pools (infralittoral enclaves in the intertidal), or occur there with reduced vitality and do not reproduce. For instance, *Hartlaubella gelatinosa* (Pallas, 1766), *Halecium nanum* Alder, 1859 and *Laomedea neglecta* Alder, 1856, have been reported only in the intertidal of the bay, but without doubt they also exist subtidally. This conclusion applies to many other geographical areas (see Millard, 1978).

Significant ecological preferences are characteristic of certain species. Some of the changes in faunal composition within the intertidal to 30 m depth zone within the bay may be due to temperature (Table 2). The submergence patterns of some species in Spanish Mediterranean fauna have been discussed in relation to North Atlantic records as well (García Carrascosa, 1981), suggesting that several factors may be involved, not only temperature.

Scyphozoa and Staurozoa apparently have very narrow ranges, although these groups, and particularly the Coronate scyphopolypae, have received little attention in

Table 2. Differences in bathymetric distribution of some species common to the British Isles, the Bay of Biscay and Galicia (only partially included in the bay). The British Isles, Galicia (SW), and Finistère (NE) are comparatively cold areas, while the Basque coast (SE) is warm, with summer temperatures exceeding those in the other areas. (Data after Fey, 1969; Cornelius, 1975, 1979; Castric-Fey et al., 1978–1979; Ramil Blanco, 1988; Sorbe, 1990; Altuna Prados, 1994).

Species	British Isles	Bay of Biscay		
		Finistère	Basque Coast	Galicia
<i>Aglaophenia tubulifera</i> (Hincks, 1861)	10+	23+	25+	8+
<i>Amphisbetia operculata</i> (L., 1758)	Intertidal+	2+	6+	4+
<i>Gymnangium montagui</i> (Billard, 1912)	'Deep water'	6+	6+	Intertidal+
<i>Halecium beanii</i> (Johnston, 1838)	5+	30+	40+	15+
<i>Halecium sessile</i> Norman, 1867	Intertidal+	5+	100	—
<i>Halopteris catharina</i> (Johnston, 1833)	Intertidal+	25+	40+	—
<i>Lafoea dumosa</i> (Fleming, 1820)	Intertidal+	6+	25+	Intertidal+
<i>Sertularella gayi</i> (Lamouroux, 1821)	Intertidal+	25+	25+	9+
<i>Sertularella polyzonias</i> (L., 1758)	Intertidal+	2+	40+	4+
<i>Tamarisca tamarisca</i> (L., 1758)	10+	—	100	—

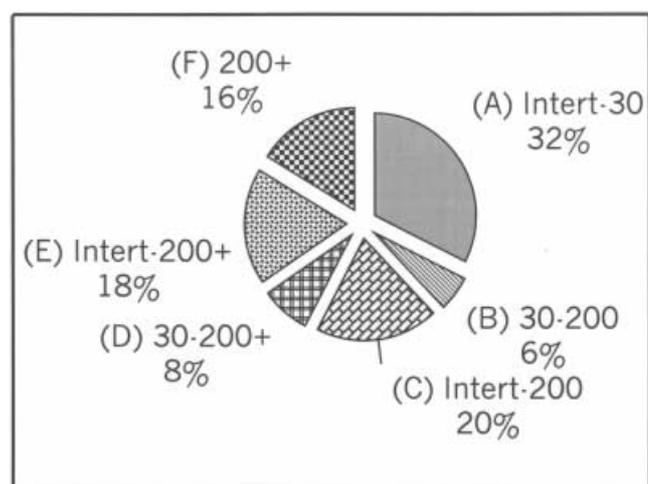


Figure 5. Bathymetric groups (Scyphozoa and Staurozoa excluded).

the literature. Their vertical distributions are undoubtedly underestimated. Some species of *Nausithoe* Kölliker, 1853 may be widely distributed in the bathyal and upper abyssal, with wide depth ranges.

Species were combined into a number of bathymetric groups (Figure 5; Appendix 1). Group A (intertidal–30 m) included the greatest number of species (58, 32%). Competition for space on marine hard-bottom communities in this zone is high, with hydroids being amongst the most abundant and characteristic sessile animals (Boero & Fresi, 1986). The apparent richness here may nevertheless be partially due to higher collecting effort in a region easily accessed for study. However, the result is in consonance with the known general vertical distribution of hydroids, with the number of species highest in shallow water communities (Gili & Hughes, 1995). Also diverse was Group C, with species exclusive to the shelf (intertidal–200, 35 species, 20%). Notable as well were those in Group E (intertidal–200+, 33 species, 18%), some having high ecological tolerances with bathymetric ranges extending from a few metres depth to at least the

beginning of the slope. A few extended even into the abyssal region [*Clytia hemisphaerica* (L., 1767) and *Obelia dichotoma* (doubtful depth records, Vervoort, 1985)]. Species exclusive of bathymetric levels beyond the shelf (200+ m) were relatively few in number (31 species, 16%). This group included some widely distributed to cosmopolitan hydroids, with two of them being anthoathecates, a taxonomic group with very few species in the bathyal (see Table 1, *Acaulis primarius*, 1894–4706 m; *Garveia arborea*, 754–3100 m; *Cryptolarella abyssicola*, 754–4425 m). As for the Antarctic hydroid fauna (Peña Cantero, 2004; 155 species), while the composition of the fauna is very different, the bathymetric groups of the shelf (0–200 m) are almost identical (first data Bay of Biscay) (A, 32: 33%; B, 6: 6%; C, 19: 18%), quite similar in the wide ranging species of the whole column (E, 18: 22%), and substantially different in Groups D and F (D, 8: 14%; F, 16: 7%).

DISCUSSION

Changes in hydroid biodiversity with depth have been studied by Millard (1978) in South Africa, by Stepanjants (1989) in the Arctic, by Calder (1996) in the north-west Atlantic, by Calder (1998) around Bermuda and by Schuchert (2000) from Iceland. Results were all quite similar with highest diversity noted in the upper 200 m. Millard concluded that there were more hydroids present in shallow waters (0–100 m) than in any other level, with only eight species at 1000 m depth. Stepanjants found that in the Arctic, the maximum number of species occurred around 50 m depth (about 45 species) and remained over 35 species until 300 m from where diminution was progressive lasting at about five down to at least 2000 m depth. Calder (1996) collated bathymetric records of 424 species of hydroids from the western North Atlantic and adjacent waters and pooled the number of species from various depths. The graph of his data was similar to those of Millard and Stepanjants, and to the Bay of Biscay results presented herein (Figure 2), although identical

expression of the results takes place at slightly different bathymetric intervals. This may be related to the recognized differences in the depths at which the boundaries of the benthic faunal zones occur at different geographical locations (see Menzies et al., 1973; Pielou, 1992). Finally, Schuchert (2000) found the highest diversity in the 100–200 m depth interval but in his study sampling started at 18 m depth. In every case, biodiversity shows a very clear and dramatic increase in the first metre depth, a maximum always located in the first 100 m depth, and a progressive diminution that is more apparent at 500 m depths in the Arctic, 900 m in the north-west Atlantic, 300 m in the Bay of Biscay, and 250 m in South Africa. In every area, after a transitory stabilization in which species richness is almost invariable, the slope of the curve is very subtle. In Calder's (1996) study area the number of species in the upper bathyal falls off rapidly with increasing depth and passed from ± 88 species at 200 m depth to 20 at 900 m. In the Bay of Biscay, 50 species are known in the 200–300 m depth interval and 38 in the 800–900 m. In both areas of the Atlantic, the loss of species richness in the same depth interval is very different—77% western North Atlantic and 24% in the Bay of Biscay—with a biodiversity surprisingly higher in the latter at the same depth despite its fauna being somewhat poorer. A parallel conclusion applies to the fauna of South Africa studied by Millard (1978). There, the fauna is more diverse (251 species), but only 45 species are known below 400 m depth, whereas some 67 species (Scyphozoa and Staurozoa excluded) occur in the same depth range from the Bay of Biscay. This could be related either to a better knowledge of the deep-sea fauna of the bay, or to the different depths at which the vertical provinces might be located and a given isobath does not correspond exactly with the same biocenological level in both areas. Compared with the fauna of the western North Atlantic, species richness was considerably lower in the Bay of Biscay (200 species—ten of them Scyphozoa and Staurozoa—against 424 for all Hydrozoa), but the number of species known below 2000 m was the same (ten species); below a depth of 3000 m numbers were almost identical (seven instead of eight) and also below 4000 m (four species). Diverse hydroid faunas in other parts of the world are due to high species richness within the first 100 m isobath of the shelf, while faunal diversity in the deep bathyal and abyssal zones is similar and always low. In this sense, only 37 species of hydroids have been reported from depths of 1000 m or greater in the western North Atlantic (Calder, 1997) and 39 are known in the same interval from the Bay of Biscay after data presented herein; nevertheless, there are only 12 species in common between both inventories. From a given depth within the bathyal downwards, the number of species is homogeneous in the North Atlantic. These curves of Medusozoa diversity disagree with one of the central paradigms of marine diversity, that species richness increases with depth to a maximum approximately 2000 m and thereafter decreases (see Gray, 2001).

Similar studies in tropical areas at low latitudes, and particularly in coral reefs areas of the Pacific and Indian Oceans are needed for comparative purposes. The results from the Bermuda area as presented by Calder (1998) fully agree with data from the Bay of Biscay, with richest

hydroid fauna at shallow waters (<100 m) and poorest in the deep sea with changes in diversity along the bathymetric gradient greatest over the upper 500 m. Further studies are needed to discern if the biodiversity graph at increasing depth as presented herein is a worldwide feature. It may prove to be so, and for instance Vervoort (1966) gave a partial list of 41 species from bottoms below 2000 m in all oceans and Millard (1978) only eight from depths below 1000 m in the well-studied southern African coasts. Calder & Vervoort (1998) found only nine species in samples from the Mid-Atlantic Ridge from depths of 500–1000 m, eight from 1001–2000 m, three from both 2001–3000 and 3001–4000 m and one from below 4000 m. Calder (1998) only collected seven species at depths exceeding 1000 m from the Bermuda area.

This general picture may be slightly modified in some areas in which Stylasteridae are particularly rich—for instance, 59 species are known from New Zealand (Cairns, 1991) and only three in the Bay of Biscay, whereas 79 is the number of the rest of Anthoathecata, medusae included (Schuchert, 1996)—as most of the approximately 200 species in the family occur at depths of 200–700 m although they are known to thrive to 2800 m (Cairns, 1985). For instance, 22 species are known from 1000–1500 m and only nine from 15–100 m in New Zealand (Cairns, 1991). Worldwide distribution of these animals is peculiar as they show a pronounced insular pattern, being found primarily on small oceanic islands, atolls, archipelagos, seamounts, and submarine ridges, and few occur close to continental land masses (Cairns, 1992).

The results presented in this study are conditioned by the differences in the sampling effort, which is greater at shallow depths, and by the sorting procedures that may underestimate in the deep-sea samples tiny soft-bodied animals, small epibionts and symbiotic species. From the 211 papers inventoried, 145 provided useful data from the Coastal Realm and 49 from the Deep Benthic Realm. Nevertheless, many of the papers dealing with the Coastal Realm fauna provide records of just a few species, frequently only one. On the other hand, when remote collection is used in the Deep Benthic Realm, a single paper with just a few species recorded may be the result of a great sampling effort during an oceanographic expedition. Thus, we think that intensive deep-sea sampling hardly could affect significantly the Bay of Biscay results as presented herein, as the hard substrata environment of the shallow waters seems to offer the highest opportunities for Medusozoa—particularly Hydrozoa—in this region. The ecological factors favouring hydroid distribution have been discussed at length in the literature (see Boero, 1984; Gili & Hughes, 1995) the most important being water movement and light, in this order. Although hard substrata may favour hydroid presence, Calder (1998) found that these animals were scarce below 500 m depth around Bermuda despite the existence of suitable substrata and suggested that his results appear due to factors other than simply the paucity of suitable substrates and could be related to the trophic habits of the hydroids. After Schuchert (2000), perhaps the scarcity of food, the hydroids sedentary mode of life, and the lack of currents that transport food may be related to their low deep-water diversity. We may conclude that, although the deep-sea biodiversity

may be underestimated by the sampling effort and the sorting methods, the deep bathyal and abyssal environments are not favourable for a great diversification of the Medusozoa if globally considered and only unsuspected biodiversity fields could modify the curve.

With a similar methodology as used herein, we could gather substrate data that tell us about the habitat, reproductive periods, distribution of the species and possible modifications of geographical boundaries in time, present and past abundance, evaluation of the sampling effort at the different depth intervals, species that may be in expansion (*Clytia linearis* see Boero et al., 2005) or regression and those that are rare or frequent. All these aspects and many others could be a further development of this work.

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Appendix 1. List of species indicating depth interval, Realm (*R*), number of papers in which the species is mentioned in the Bay of Biscay literature (*NP*), number of original records (*NR*), and bathymetric group A–F (see *Materials and Methods*). Realms: C: Coastal; D: Deep Benthic; CD: Both. Classification follows Marques & Collins (2004) and Bouillon et al. (2004). *, Doubtful depth record.

Species	Depth	R	NP	NR	A	B	C	D	E	F
Subphylum Medusozoa Petersen, 1979										
Class Staurozoa Marques & Collins, 2004										
Order Stauromedusae Haeckel, 1877										
Family Lucernariidae Johnston, 1847										
<i>Haliclystus octoradiatus</i> (Lamarck, 1816)	Intertidal–25 ?	C	6	4	▲					
<i>Lucernaria quadricornis</i> O.F. Müller, 1776	30	C	3	1	▲					
<i>Stylocoronella riedli</i> Salvini-Plawen, 1966	14	C	2	6	▲					
Family Kishinoueyidae Uchida, 1929										
<i>Lucernariopsis campanulata</i> (Lamouroux, 1815)	Intertidal–10	C	4	3	▲					
Class Scyphozoa Goette, 1887										
Order Coronatae Vanhöffen, 1892										
Family Nausithoidae Haeckel, 1880										
<i>Nausithoe punctata</i> Kölliker, 1853	4–25	C	2	12	▲					
<i>Nausithoe sorbei</i> Jarms, Tiemann & Altuna Prados, 2003	948–991	D	1	8						▲
<i>Nausithoe</i> sp.1	948–991	D	2	1						▲
? <i>Nausithoe</i> sp. 2	100	C	3	11		▲				
Subclass Discomedusae Haeckel, 1880										
Order Semaestomeae L. Agassiz, 1862										
Family Ulmaridae Haeckel, 1880										
<i>Aurelia aurita</i> (L., 1758)	Infralittoral	C	2	3	▲					
Order Rhizostomeae Cuvier, 1799										
Family Rhizostomatidae Cuvier, 1799										
<i>Rhizostoma</i> cf. <i>octopus</i> (L., 1788)	Intertidal	C	2	1	▲					
Class Hydrozoa Huxley, 1856										
Order Limnomedusae Kramp, 1938										
Family Olindiidae Haeckel, 1879										
<i>Monobrachium parasitum</i> Mereschkowsky, 1877	11–39	C	2	19			▲			
Subclass Trachylina Haeckel, 1879										
Order Actinulida Swedmark & Teissier, 1959										
Family Halammohydridae Remane, 1927										
<i>Halammohydra octopodides</i> Remane, 1927	Intertidal	C	10	8	▲					
<i>Halammohydra schulzei</i> Remane, 1927	Intertidal–14	C	3	4	▲					
<i>Halammohydra vermiformis</i> Swedmark & Teissier, 1957	Intertidal	C	6	6	▲					
Family Otohydridae Swedmark & Teissier, 1958										
<i>Otohydra vagans</i> Swedmark & Teissier, 1958	14	C	2	1	▲					
Subclass Leptolina Haeckel, 1879										
Order Leptothecata Cornelius, 1992										
Suborder Conica Broch, 1910										
Family Aglaopheniidae Broch, 1918										
<i>Aglaophenia acacia</i> Allman, 1883	12–35	C	5	5			▲			
<i>Aglaophenia kirchenpaueri</i> (Heller, 1868)	Intertidal–986	CD	33	70						▲
<i>Aglaophenia lophocarpa</i> Allman, 1877	10–702	CD	10	10						▲
<i>Aglaophenia octodonta</i> (Heller, 1868)	Intertidal–20	C	20	63	▲					
<i>Aglaophenia parvula</i> Bale, 1882	Intertidal–65	C	18	44			▲			
<i>Aglaophenia picardi</i> Svoboda, 1979	Intertidal–35	C	9	51			▲			
<i>Aglaophenia pluma</i> (L., 1758)	Intertidal–50	C	50	113			▲			
<i>Aglaophenia tubiformis</i> Marktanner, 1890	Intertidal–35	C	15	24			▲			
<i>Aglaophenia tubulifera</i> (Hincks, 1861)	Intertidal–240	CD	34	61					▲	
<i>Cladocarpus corneliusi</i> Ramil & Vervoort, 1992	2194	D	1	1						▲
<i>Cladocarpus multiseptatus</i> (Bale, 1915)	227	D	3	1						▲
<i>Cladocarpus sigma</i> (Allman, 1877) <i>folini</i> Billard, 1906	100–769	CD	18	23				▲		
<i>Gymnangium montagui</i> (Billard, 1912)	Intertidal–45	C	25	50			▲			
<i>Lytocarpia bispinosa</i> (Allman, 1877)	400	D	1	1						▲
<i>Lytocarpia myriophyllum</i> (L., 1758)	45–1347	CD	36	62				▲		

(continued)

Appendix 1. (Continued.)

Species	Depth	R	NP	NR	A	B	C	D	E	F
Family Campanulinidae Hincks, 1868										
<i>Calycella syringa</i> (L., 1767)	Intertidal–24	C	14	21	▲					
<i>Campanulina panicula</i> G.O. Sars, 1874	100–4260	CD	12	20				▲		
<i>Egmundella grimaldii</i> Leloup, 1940	748–1262	D	3	2						▲
<i>Egmundella</i> sp.1	954–1023	D	3	2						▲
<i>Egmundella</i> sp. 2	702	D	2	1						▲
<i>Lafoeina tenuis</i> G.O. Sars, 1874	Intertidal–227	CD	10	25					▲	
Family Haleciidae Hincks, 1868										
<i>Halecium beanii</i> (Johnston, 1838)	6–227	CD	21	28					▲	
<i>Halecium delicatum</i> Coughtrey, 1876	Intertidal–140	C	13	48			▲			
<i>Halecium halecinum</i> (L., 1758)	Intertidal–72	C	31	53			▲			
<i>Halecium labrosum</i> Alder, 1859	Intertidal–769	CD	16	15					▲	
<i>Halecium lankesteri</i> (Bourne, 1890)	Intertidal–72	C	20	69			▲			
<i>Halecium liouvillei</i> Billard, 1934	12–60	C	13	13			▲			
<i>Halecium muricatum</i> (Ellis & Solander, 1786)	146–769	CD	5	6				▲		
<i>Halecium nanum</i> Alder, 1859	Intertidal	C	2	2	▲					
<i>Halecium pusillum</i> (M. Sars, 1857)	Intertidal–30	C	18	48	▲					
<i>Halecium sessile</i> Norman, 1867	5–754	CD	18	56					▲	
<i>Halecium telescopicum</i> Allman, 1888	155–180	C	1	2		▲				
<i>Halecium tenellum</i> Hincks, 1861	2–117	C	15	24			▲			
<i>Hydrodendron mirabile</i> (Hincks, 1866)	Intertidal–12	C	8	19	▲					
Family Halopterididae Millard, 1962										
<i>Antennella secundaria</i> (Gmelin, 1791)	Intertidal–981	CD	30	84					▲	
<i>Antennella siliquosa</i> (Hincks, 1877)	4–10	C	7	4	▲					
<i>Halopteris catharina</i> (Johnston, 1833)	17–183	C	18	23			▲			
<i>Halopteris diaphana</i> (Heller, 1868)	Intertidal–35	C	14	38			▲			
<i>Schizotricha frutescens</i> (Ellis & Solander, 1786)	28–1262	CD	23	19					▲	
Family Hebellidae Fraser, 1912										
<i>Anthohebella parasitica</i> (Ciamician, 1880)	Intertidal–35	C	13	55			▲			
<i>Bedotella armata</i> (Pictet & Bedot, 1900)	100–893	CD	13	9				▲		
<i>Hebella scandens</i> (Bale, 1888)	Intertidal–14	C	9	55	▲					
<i>Scandia gigas</i> (Pieper, 1884)	Intertidal–6	C	7	6	▲					
Family Kirchenpaueriidae Millard, 1962										
<i>Kirchenpaueria bonneviae</i> (Billard, 1906)	300–411	D	5	2						▲
<i>Kirchenpaueria halecioides</i> (Alder, 1859)	Intertidal–10	C	13	19	▲					
<i>Kirchenpaueria pinnata</i> (L., 1758)	Intertidal–812	CD	46	156					▲	
Family Lafoeidae A. Agassiz, 1865										
<i>Acryptolaria conferta</i> (Allman, 1877)	102–2695	CD	11	15				▲		
<i>Acryptolaria longitheca</i> (Allman, 1877)	748–2175	D	5	4						▲
<i>Cryptolarella abyssicola</i> (Allman, 1888)	754–4425	D	3	9						▲
<i>Cryptolaria pectinata</i> (Allman, 1888)	300–1262	D	5	7						▲
<i>Filellum serpens</i> (Hassall, 1848)	6–1970	CD	11	29					▲	
<i>Filellum serratum</i> (Clarke, 1879)	Intertidal–1023	CD	12	19					▲	
<i>Lafoea dumosa</i> (Fleming, 1820)	Intertidal–1920	CD	33	85					▲	
<i>Zygophylax biarmata</i> Billard, 1905	227–411	D	11	3						▲
<i>Zygophylax brownei</i> Billard, 1924	134–754	CD	8	4				▲		
<i>Zygophylax levinsenii</i> (Saemundsson, 1911)	183–1700	CD	9	5				▲		
<i>Zygophylax sibogae</i> Billard, 1918	500–1120	D	4	5						▲
Family Laodiceidae Agassiz, 1862										
<i>Laodicea undulata</i> (Forbes & Goodsir, 1851)	Intertidal–137	C	9	9			▲			
<i>Staurophora mertensii</i> Brandy, 1834	20	C	1	1	▲					
Family Lovenellidae Russell, 1953										
<i>Campalecium cirratum</i> Millard & Bouillon, 1975	1–12	C	6	14	▲					
<i>Eucheilota maculata</i> Hartlaub, 1894	Intertidal–15	C	4	15	▲					
<i>Hydranthea margarica</i> (Hincks, 1862)	6–9	C	5	6	▲					
<i>Lovenella clausa</i> (Lovén, 1836)	4–161	C	6	22			▲			
? <i>Lovenella producta</i> (G.O. Sars, 1874)	2171–2360	D	2	2						▲
Family Mitrocomidae Haeckel, 1879										
<i>Cosmetira pilosella</i> (Forbes, 1848)	Intertidal–199	C	7	10			▲			
? <i>Mitrocomella polydiademata</i> (Romanes, 1876)	117–161	C	1	5		▲				
Family Phialellidae Russell, 1953										
<i>Opercularella lacerata</i> (Johnston, 1847)	Intertidal–10	C	4	16	▲					

(continued)

Appendix 1. (Continued.)

Species	Depth	R	NP	NR	A	B	C	D	E	F
<i>Phialella quadrata</i> (Forbes, 1848)	20–30	C	7	12	▲					
Family Plumulariidae Hincks, 1868										
<i>Monothecha obliqua</i> (Johnston, 1847)	Intertidal–28	C	16	39	▲					
<i>Monothecha pulchella</i> (Bale, 1882)	1–3	C	2	2	▲					
<i>Nemertesia antennina</i> (L., 1758)	Intertidal–1970	CD	45	81					▲	
<i>Nemertesia norvegica</i> (G.O. Sars, 1874)	754	D	1	1						▲
<i>Nemertesia perrieri</i> (Billard, 1901)	72–135	C	8	7		▲				
<i>Nemertesia ramosa</i> (Lamouroux, 1816)	11–769	CD	30	59					▲	
<i>Nemertesia ventriculiformis</i> (Marktanner, 1890)	23–100	C	10	10			▲			
<i>Plumularia setacea</i> (L., 1758)	Intertidal–754	CD	40	146					▲	
<i>Polyplumaria flabellata</i> G.O. Sars, 1874	60–893	CD	22	32				▲		
Family Sertulariidae Lamouroux, 1812										
<i>Abietinaria abietina</i> (L., 1758)	28–1970	CD	16	17					▲	
<i>Abietinaria filicula</i> (Ellis & Solander, 1786)	No precise data	?	1	1						
<i>Abietinaria interversa</i> (Pictet & Bedot, 1900)	240	D	1	1						▲
<i>Amphisbetia operculata</i> (L., 1758)	Intertidal–65	C	49	80			▲			
<i>Diphasia alata</i> (Hincks, 1855)	19–411	CD	19	16					▲	
<i>Diphasia attenuata</i> (Hincks, 1866)	2–32	C	12	26			▲			
<i>Diphasia delagei</i> Billard, 1912	No precise data	?	1	1						
<i>Diphasia margareta</i> (Hassall, 1841)	55–1262	CD	24	34				▲		
<i>Diphasia nigra</i> (Pallas, 1766)	137–500	CD	9	6				▲		
<i>Diphasia rosacea</i> (L., 1758)	Intertidal–40	C	19	23				▲		
<i>Dynamena disticha</i> (Bosc, 1802)	3–15	C	1	1	▲					
<i>Dynamena pumila</i> (L., 1758)	Intertidal–15	C	30	87	▲					
<i>Hydrallmania falcata</i> (L., 1758)	5–1970	CD	13	22					▲	
<i>Salacia articulata</i> (Pallas, 1766)	30–180	C	6	7		▲				
<i>Salacia desmoides</i> (Torrey, 1902)	Intertidal–24	C	21	62	▲					
<i>Sertularella ellisii</i> (Deshayes & M. Edwards, 1836)	Intertidal–60	C	37	235		▲				
<i>Sertularella gayi</i> (Lamouroux, 1821)	Intertidal–1262	CD	37	77					▲	
<i>Sertularella lagenoides</i> Stechow, 1919	6–8	C	2	2	▲					
<i>Sertularella polyzonias</i> (L., 1758)	Intertidal–439	CD	40	119					▲	
<i>Sertularella rugosa</i> (L., 1758)	No precise data	C	2	1						
<i>Sertularella tenella</i> (Alder, 1856)	25–100	C	7	3			▲			
<i>Sertularia cupressina</i> L., 1758	Intertidal–136	C	28	68			▲			
<i>Sertularia marginata</i> (Kirchenpauer, 1864)	10–20	C	1	1	▲					
<i>Sertularia tenera</i> G.O. Sars, 1874	No precise data	C	1	1						
<i>Symplectoscyphus bathyalis</i> Vervoort, 1972	1828	D	2	1						▲
<i>Symplectoscyphus tricuspidatus</i> (Alder, 1856)	1220–1410	D	1	2						▲
<i>Tamarisca tamarisca</i> (L., 1758)	100–1262	CD	14	8				▲		
<i>Thuiaria thuja</i> (L., 1758)	No precise data	C	1	1						
<i>Tridentata distans</i> (Lamouroux, 1816)	Intertidal–33	C	25	131			▲			
Family Thyroscyphidae Stechow, 1920										
<i>Sertularelloides cylindritheca</i> (Allman, 1888)	73–100	C	5	3		▲				
Family Tiarannidae Russell, 1940										
<i>Modeeria rotunda</i> (Quoy & Gaimard, 1827)	60–1262	CD	13	25				▲		
<i>Stegolaria geniculata</i> (Allman, 1888)	769–1331	D	3	4						▲
<i>Stegopoma bathyale</i> Vervoort, 1966	702–893	D	3	2						▲
Suborder Proboscoida Broch, 1910										
Family Campanulariidae Johnston, 1836										
<i>Campanularia</i> cf. <i>agas</i> Cornelius, 1982	3100*	D	1	1						▲
<i>Campanularia hincksii</i> Alder, 1856	Intertidal–1262	CD	29	72					▲	
<i>Campanularia volubilis</i> (L., 1758)	Intertidal–8	C	10	9	▲					
<i>Clytia gracilis</i> (M. Sars, 1850)	Intertidal–120	C	20	51			▲			
<i>Clytia hemisphaerica</i> (L., 1767)	Intertidal–2878*	CD	49	145					▲	
<i>Clytia linearis</i> (Thornely, 1899)	4–25	C	8	24	▲					
<i>Clytia paulensis</i> (Vanhöffen, 1910)	Intertidal–227	CD	17	53					▲	
<i>Gonothyrea loveni</i> (Allman, 1859)	Intertidal–65	C	15	20			▲			
<i>Hartlaubella gelatinosa</i> (Pallas, 1766)	Intertidal	C	7	7	▲					
<i>Laomedea angulata</i> Hincks, 1861	Infralittoral–3.5	C	13	11	▲					
<i>Laomedea calceolifera</i> (Hincks, 1871)	Intertidal–183	C	19	52			▲			
<i>Laomedea flexuosa</i> Alder, 1857	Intertidal–12	C	31	42	▲					
<i>Laomedea neglecta</i> Alder, 1856	Intertidal	C	2	2	▲					

(continued)

Appendix 1. (Continued.)

Species	Depth	R	NP	NR	A	B	C	D	E	F
<i>Laomedea pseudodichotoma</i> Vervoort, 1959	172	C	3	1		▲				
<i>Obelia bidentata</i> Clarke, 1875	Intertidal–702	CD	22	36					▲	
<i>Obelia dichotoma</i> (L., 1758)	Intertidal–4210*	CD	40	170					▲	
<i>Obelia geniculata</i> (L., 1758)	Intertidal–531	CD	52	125					▲	
<i>Obelia longissima</i> (Pallas, 1766)	Intertidal–15	C	13	14	▲					
<i>Orthopyxis crenata</i> (Hartlaub, 1901)	Intertidal–21	C	11	21	▲					
<i>Orthopyxis integra</i> (MacGillivray, 1842)	Intertidal–30	C	22	53	▲					
<i>Rhizocaulus verticillatus</i> (L., 1758)	No precise data	?	2	1						
Order Anthoathecata Cornelius, 1992										
Suborder Filifera Kühn, 1913										
Family Bougainvilliidae Lütken, 1850										
<i>Bimeria vestita</i> Wright, 1859	Intertidal–137	C	10	15			▲			
<i>Bougainvillia muscus</i> (Allman, 1863)	Intertidal–1186	CD	20	51					▲	
? <i>Bougainvillia</i> sp.	Intertidal	C	4	1	▲					
<i>Dicoryne conferta</i> (Alder, 1856)	Infralittoral–1146	CD	12	11					▲	
<i>Dicoryne conybeari</i> (Allman, 1864)	No precise data	?	2	1						
<i>Garveia arborea</i> (Browne, 1907)	754–3100	D	3	15						▲
' <i>Garveia</i> ' <i>biscayana</i> (Browne, 1907)	754	D	1	1						▲
<i>Garveia nutans</i> Wright, 1859	137	C	1	2		▲				
<i>Garveia</i> sp.	100	C	4	3		▲				
Family Clavidae McCrady, 1859										
<i>Clava multicornis</i> (Forsskål, 1755)	Intertidal–8	C	19	15	▲					
<i>Cordylophora caspia</i> (Pallas, 1766)	No precise data	C	3	4						
<i>Merona cornucopiae</i> (Norman, 1864)	4–424	CD	9	15					▲	
<i>Tubiclava lucerna</i> Allman, 1863	Infralittoral	C	1	1	▲					
Family Eudendriidae L. Agassiz, 1862										
<i>Eudendrium album</i> Nutting, 1898	Intertidal–12	C	7	15	▲					
<i>Eudendrium capillare</i> Alder, 1856	Intertidal–132	C	21	39			▲			
<i>Eudendrium glomeratum</i> Picard, 1951	5–31	C	10	13			▲			
<i>Eudendrium racemosum</i> (Cavolini, 1785)	Infralittoral	C	3	3	▲					
<i>Eudendrium rameum</i> (Pallas, 1771)	137–2360	CD	3	5				▲		
<i>Eudendrium ramosum</i> (L., 1758)	Intertidal–1098	CD	14	20					▲	
Family Hydractiniidae L. Agassiz, 1862										
<i>Hydractinia carnea</i> (M. Sars, 1846)	Intertidal–540	CD	24	55					▲	
<i>Hydractinia claviformis</i> (Bouillon, 1965)	Intertidal–10	C	3	4	▲					
<i>Hydractinia echinata</i> (Fleming, 1828)	9–66	C	19	21			▲			
<i>Hydractinia inermis</i> (Allman, 1872)	5–20	C	5	5	▲					
Family Pandeidae Haeckel, 1879										
<i>Amphinema dinema</i> (Péron & Lesueur, 1810)	Intertidal–infralittoral	C	2	2	▲					
<i>Amphinema rugosum</i> (Mayer, 1900)	4–10	C	2	6	▲					
<i>Leuckartiara octona</i> (Fleming, 1823)	Intertidal–954	CD	13	20					▲	
Family Proboscicidactylidae Hand & Hendrickson, 1950										
<i>Proboscicidactyla</i> (= <i>Lar</i>) sp.	2740	D	1	1						▲
Family Stylasteridae Gray, 1847										
<i>Pliobothrus symmetricus</i> Pourtalès, 1868	380–1115	D	1	3						▲
<i>Stenohelia maderensis</i> (Johnson, 1862)	545–1189	D	5	12						▲
<i>Stylaster ibericus</i> Zibrowius & Cairns, 1992	450–620	D	1	8						▲
Suborder Capitata Kühn, 1913										
Family Moerisiidae Poche, 1914										
<i>Odessia maeotica</i> (Ostroumoff, 1896)	No precise data	C	1	1						
Family Protohydridae Allman, 1888										
<i>Protohydra leuckarti</i> Greeff, 1869	No precise data	C	1	1						
Family Acaulidae Fraser, 1924										
<i>Acaulis primarius</i> Stimpson, 1854	1894–4706	D	1	8						▲
Family Candelabridae De Blainville, 1830										
<i>Candelabrum cocksii</i> (Cocks, 1854)	Intertidal–17	C	8	5	▲					
Family Cladonematidae Gegenbaur, 1856 (Allman, 1872)										
<i>Cladonema radiatum</i> Dujardin, 1843	Intertidal	C	9	14	▲					
<i>Eleutheria dichotoma</i> Quatrefages, 1842	Intertidal	C	6	3	▲					
Family Corymorphidae Allman, 1872										
<i>Corymorpha nutans</i> M. Sars, 1835	8–10	C	2	3	▲					

(continued)

Appendix 1. (Continued.)

Species	Depth	R	NP	NR	A	B	C	D	E	F
Family Corynidae Johnston, 1836										
<i>Coryne eximia</i> Allman, 1859	13–25	C	11	9	▲					
<i>Coryne muscoides</i> (L., 1761)	Intertidal–15	C	26	45	▲					
<i>Coryne pintneri</i> Schneider, 1897	Intertidal	C	2	2	▲					
<i>Coryne producta</i> (Wright, 1858)	Intertidal–infralittoral	C	7	2	▲					
<i>Coryne pusilla</i> Gaertner, 1774	Intertidal–10	C	12	6	▲					
<i>Dipurena reesi</i> Vannucci, 1956	No precise data	C	4	2						
<i>Sarsia tubulosa</i> (M. Sars, 1835)	Intertidal–9	C	6	6	▲					
? <i>Sarsia</i> sp.	No precise data	C	3	1						
Family Tubulariidae Fleming, 1828										
<i>Ectopleura crocea</i> (L. Agassiz, 1862)	Intertidal–infralittoral	C	4	2	▲					
<i>Ectopleura dumortieri</i> (Van Beneden, 1844)	Intertidal–35	C	10	14				▲		
<i>Ectopleura larynx</i> (Ellis & Solander, 1786)	Intertidal–35	C	24	32				▲		
<i>Tubularia indivisa</i> L., 1758	Intertidal–132	C	32	42				▲		
Family Cladocorynidae Allman, 1872										
<i>Cladocoryne floccosa</i> Rotch, 1871	4–12	C	6	5						
Family Rosalindidae Bouillon, 1985										
<i>Rosalinda williamsi</i> Totton, 1949	440	D	4	1						▲
Family Zancleidae Russell, 1953										
<i>Zanclea costata</i> Gegenbaur, 1856	1900–2300	D	1	1						▲
<i>Zanclea sessilis</i> (Gosse, 1853)	Intertidal–20	C	8	7	▲					
<i>Zanclea</i> sp.	4–6	C	2	1	▲					