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Research Article

Synopsis on the knowledge and distribution of the family Bougainvilliidae (Hydrozoa, Hydroidolina)

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ABSTRACT. The family Bougainvilliidae comprises a group of anthoathecate hydrozoans that is biologically, ecologically and biogeographically poorly understood, and consequently, poorly taxonomically organized. Here, our goal is to synthesize knowledge of the family from an historical perspective, and to analyze their potential distribution based on their ecology. We analyzed all the available information on the family (based on 303 articles and databases), comprising 15 genera and 97 valid species in five oceans. Two temporal peaks (1900 and 2000) in publications are dominated by records of meroplanktonic species. The coastal zone has the most frequently reported occurrences. The widest latitudinal ranges are found in the genera *Bimeria* and *Bougainvillia*. Ecological niche modeling of 25 species (MaxEnt algorithm) finds that chlorophyll is the most important variable that influences the distribution of the family. Five possible latitudinal distributional patterns are derived from the model, dominated by the subtropical-polar distribution.

Keywords: Filifera, Anthoathecata, Bougainvilliidae, niche, taxonomy, biogeography.

Sinopsis sobre el conocimiento y distribución de la familia Bougainvilliidae (Hydrozoa, Hydroidolina)

RESUMEN. La familia Bougainvilliidae comprende un grupo de hidrozoos antoatecados, taxonómicamente mal estructurado y biológica, ecológica y biogeográficamente poco conocidos. En este caso, el objetivo de este estudio es sintetizar el conocimiento actual de la familia, desde una perspectiva histórica, y analizar su potencial de distribución en función de su ecología. Se analizó toda la información disponible sobre la familia (en 303 artículos publicados y bases de datos), que comprende un total de 15 géneros y 97 especies válidas en cinco océanos. Históricamente las publicaciones presentaron dos máximos importantes (1900 y 2000), dominadas por registros de especies meroplanctónicas. La zona costera presenta las ocurrencias más frecuentes. Los géneros *Bimeria* y *Bougainvillia* son los que presentan la mayor distribución latitudinal. El modelaje de nicho ecológico de 25 especies, realizado con el algoritmo MaxEnt, reveló que la clorofila es la variable más importante que influye en la distribución de la familia. Cinco posibles patrones de distribución latitudinales se derivan del modelo, dominado por la distribución subtropical-polar" por " Cinco posibles patrones de distribución latitudinal fueron reflejados en los modelos, siendo dominante la distribución subtropical-polar.

Palabras clave: Filifera, Anthoathecata, Bougainvilliidae, nicho, taxonomía, biogeografía.

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INTRODUCTION

The "hydroid" family Bougainvilliidae Lütken, 1850 pertains to a group of historically and conveniently (*i.e.*, not monophyletically) described of cnidarians in the orders Leptothecata and "Anthoathecata" (the latter, also not monophyletic, Cartwright *et al*., 2008) in the class Hydrozoa. As with other anthoathecates, the family Bougainvilliidae has two phases in its life cycle: fixed to a substrate as a polyp and as free-swimming medusae (which may also have a reduced form that remains with the polyp, Russell, 1953). The pseudohydrotheca characterizes this family and it is defined as an external, glycosaminoglycan covering, with or without detrital incrustations, that envelops the hydrants and which can be reduced in some genera (cf., Calder, 1988; Schuchert, 2007).

The taxonomy of the family remains poorly structured, most likely as a consequence of the few studies of its biology, ecology and geographical distribution. Despite the 200 years since the description of the first species in the family (*Koellikerina fasciculata* Péron & Lesueur, 1810), there are no compilations or syntheses of the family, its distribution or genera. Today, information is fragmented, from pioneer studies beginning *ca*. 150 years ago (Allman, 1871; Haeckel, 1879; Mayer, 1910; Kramp, 1961) to taxonomic lists in secondary sources (*i.e*., compilations) of Medusozoan species (Bouillon & Boero, 2000; Bouillon *et al*., 2006), or in data bases such as the World Register of Marine Species (WoRMS; Appeltans *et al*., 2011) and the relatively few ecological (Ballard & Myers, 1996; Frost *et al.,* 2010; Genzano, 1994) and taxonomic studies (Segura-Puertas, 1991; Xu & Huang, 2004, 2006; Xu *et al*., 2007a, 2007b, 2009, Nogueira Jr. *et al*., 2013).

Here, we will summarize the deficiencies of understanding the Bougainvilliidae, so that we may then proceed to build a context in which we can better understand the group and suggest avenues for their future study in biogeography, ecology and taxonomy. More specifically, we will synthesize current knowledge of the family based on historical and distribution perspectives, with which we will carry out an ecological analysis to predict potential occurrence of this interesting and diverse family.

MATERIALS AND METHODS

Basic taxonomy of the Bougainvilliidae and its place within the Hydrozoa follow Marques & Collins (2004), Bouillon *et al.* (2006); Schuchert (2007) and Cartwright *et al.* (2008). To determine historical series and distributions, we gathered 303 articles about the family published between 1890 and 2013. With this information, and databases, such as Genetic Sequence (GenBank) and WoRMS, we developed a data base for each genus and species, with a total of 1290 records having the following information: author, life-cycle phase, reproductive state, sex, location (body of water, country, state, region, latitude and longitude), date of collection, water depth (minimum, maximum), substrate type, salinity, temperature, synonymy and references cited. We then examined the historical and geographical information compiled.

To generate potential distribution models for valid species, we used the information from the data base described above, separating by life-cycle phase (polyp and medusa). Species were plotted using ArcGIS vers. 10 (ESRI, 2010). Environmental descriptive variables were: average surface water temperature, average surface salinity, and average concentration of nitrates, phosphates, oxygen and chlorophyll, from the BioOracle database (Tyberghein *et al*., 2011). We modeled using the Maxent algorithm (maximum entropy approach; Phillips *et al*., 2006). We used a threshold-independent measure, the area under the curve (AUC), to evaluate models and a Jackknife method (Sokal & Rohlf, 1995; Phillips *et al*., 2006) was used to examine the importance of each variable to the final model. The results of this evaluation are expressed as a measure known as gain, which shows the ecological requirements of each species, and probably determine their potential distribution. Classification of AUC values followed Metz (1986), as excellent (0.90-1.0), good (0.80-0.90), average (0.70-0.80), bad (0.60-0.70) and very bad (0.50-0.60).

RESULTS

The Bougainvilliidae comprise a total of 19 genera and 170 named species, of which 54 species were synonymized. Most of these are the cosmopolitan species *Bougainvillia muscus* (Allman, 1863). Another 19 species were doubtful. Thus, a total of 15 genera and 97 species are valid (Table 1) representing about 3% of the Hydrozoa species in the world (3,140 species, cf. Bouillon *et al*., 2006).

Species in the Bougainvilliidae tend to be meroplanktonic genera (*e.g*., *Bougainvillia, Koellikerina* and *Nubiella*, Table 2), and are not the most studied. About 65% of publications are about the genera *Bimeria* (which is benthic) and *Bougainvillia*. While reports of new species has been continuous, the species accumulation curve shows that about six new species per decade are being described, and therefore the asymptotic number of species is far from being reached (Fig. 1).

Historically, studies of the Bougainvilliidae have had several temporal hiatuses. Beginning in 1900, with very few studies from 1920-1950, increasing in the 1950s and still doing so (Fig. 1), with most of these studies (3-10 papers each) being by Calder, Galea, Genzano, Marques, Pagés, Palma, Schuchert, Segura-Puertas and Xu. Most of these were studies in tropical and southern Atlantic, northeast and northwest Atlantic, southwestern and central eastern Pacific oceans, in contrast with previous studies, which were mostly in European and North American waters.

Geographically, valid species are found in all oceans, within a range of 155° of latitude, from 76.93°N to 78.49°S, and 360° of longitude (Fig. 2). Most species occur in the Pacific (73%), with 48% in the Atlantic, 26% in the Indian Ocean, 4% in the Arctic, and 5% in the Southern Ocean (Fig. 3). The Atlantic Ocean is the best studied, with 60% of all publications on the family, while the least studied are the Indian and Southern oceans. Latitudinally, most valid species were described between 30-40°N (44 species, Fig. 4).

Table 1. Species described in the literature of the family Bougainvilliidae with life-cycle phase indicated and distribution. P: polyp, M: medusa.

Species	Phase	Distribution				
		Pacific	Atlantic	Indian	Arctic	Southern
Genus *Bimeria* Wright, 1859						
Bimeria australis Blackburn 1937	P	x	x			
Bimeria belgicae (Vanhöffen, 1910)	P					x
Bimeria corynopsis Vanhöffen, 1910	P					x
Bimeria currumbinensis Pennycuik, 1959	P	x				
Bimeria fluminalis Annandale, 1915	P			x		
Bimeria pygmaea Fraser, 1938	P	x				
Bimeria rigida Warren, 1919	P			x		
Bimeria vestita Wright, 1859	P	x	x	x		
Genus *Bougainvillia* Lesson, 1830						
Bougainvillia aberrans Calder, 1993	P/M		x			
Bougainvillia aurantiaca Bouillon, 1980	M	x	x			
Bougainvillia bitentaculata Uchida, 1925	M	x		x		
Bougainvillia britannica (Forbes, 1841)	P/M	x	x			
Bougainvillia carolinensis (Mccrady, 1859)	P/M		x			
Bougainvillia chenyapingii Xu, Huang & Guo, 2007	M	x				
Bougainvillia crassa Fraser, 1938	P	x				
Bougainvillia dimorpha Schuchert, 1996	P/M	x				
Bougainvillia frondosa Mayer, 1900	M	x	x			
Bougainvillia fulva Agassiz & Mayer, 1899	M	x		x		
Bougainvillia inaequalis Fraser, 1944	P	x	x			
Bougainvillia involuta Uchida, 1947	M	x				
Bougainvillia lamellata Xu, Huang & Liu, 2007	M	x				
Bougainvillia longistyla Xu & Huang, 2004	M	x				
Bougainvillia macloviana Lesson, 1836	P/M	x	x	x		
Bougainvillia meinertiae Jäderholm, 1923	P			x		
Bougainvillia multitentaculata Förster, 1923	M	x				
Bougainvillia muscoides (M. Sars, 1846)	P/M	x	x	x		
Bougainvillia muscus (Allman, 1863)	P/M	x	x	x		
Bougainvillia nana Hartlaub, 1911	M		x			
Bougainvillia niobe Mayer, 1894	M	x	x			
Bougainvillia pagesi Nogueira *et al.,* 2013	M		x			
Bougainvillia paraplatygaster Xu, Huang & Chen, 1991	M	x				
Bougainvillia platygaster (Haeckel, 1879)	M	x	x	x		
Bougainvillia principis (Steenstrup, 1850)	P/M	x	x		x	
Bougainvillia pyramidata (Forbes & Goodsir, 1853)	P/M	x	x			
Bougainvillia reticulata Xu & Huang, 2006	M	x				
Bougainvillia rugosa Clarke, 1882	P/M		x			
Bougainvillia superciliaris (L. Agassiz, 1849)	P/M	x	x		x	
Bougainvillia vervoorti Bouillon, 1995	P/M	x				
Genus *Chiarella* Maas, 1897						
Chiarella centripetalis Maas, 1897	M	x				
Genus *Dicoryne* Allman, 1859						
Dicoryne conferta (Alder, 1856)	P		x	x	x	
Dicoryne conybearei (Allman, 1864)	P	x	x			
Genus *Garveia* Wright, 1859						
Garveia annulata Nutting, 1901	P	x				
Garveia arborea (Browne, 1907)	P	x	x			
Garveia cerulea (Clarke, 1882)	P		x			
Garveia clevelandensis Pennycuik, 1959	P	x		x		
Garveia crassa Stechow, 1923	P			x		
Garveia franciscana (Torrey, 1902)	P	x	x	x		

Continuation

Species	Phase	Distribution				
		Pacific	Atlantic	Indian	Arctic	Southern
Garveia gracilis (Clark, 1876)	P	x	x			
Garveia grisea (Motz-Kossowska, 1905)	P		x			
Garveia nutans Wright, 1859	P	x	x			
Genus *Koellikerina* Kramp, 1939						
Koellikerina bouilloni Kawamura & Kubota, 2005	M	x				
Koellikerina constricta (Menon, 1932)	M	x		x		
Koellikerina diforficulata (Xu & Zhang, 1978)	M	x				
Koellikerina elegans (Mayer, 1900)	M		x	x		
Koellikerina fasciculata (Péron & Lesueur, 1810)	P/M	x	x			
Koellikerina heteronemalis Xu, Huang & Chen, 1991	M	x				
Koellikerina maasi (Browne, 1910)	M	x	x	x		x
Koellikerina multicirrata (Kramp, 1928)	M	x		x		
Koellikerina octonemalis (Maas, 1905)	M	x		x		
Koellikerina ornata Kramp, 1959	M	x		x		
Koellikerina staurogaster Xu & Huang, 2004	M	x				
Koellikerina taiwanensis Xu, Huang & Chen, 1991	M	x				
Genus *Millardiana* Wedler & Larson, 1986						
Millardiana logitentaculata Wedler & Larson, 1986	P		x			
Genus *Nemopsis* Agassiz, 1849						
Nemopsis bachei L. Agassiz, 1849	P/M	x	x			
Nemopsis dofleini Maas, 1909	M	x				
Nemopsis hexacanalis Huang & Xu, 1994	M	x				
Genus *Nubiella* Bouillon, 1980						
Nubiella alvarinoae (Segura-Puertas, 1980)	M	x	x			
Nubiella atentaculata Xu & Huang, 2004	M	x				
Nubiella claviformis Xu, Huang & Lin, 2009	M	x				
Nubiella intergona Xu, Huang & Lin, 2009	M	x				
Nubiella macrogastera Xu, Huang & Lin, 2009	M	x				
Nubiella macrogona Xu, Huang & Guo, 2009	M	x				
Nubiella mitra Bouillon, 1980	M	x	x			
Nubiella oralospinella Xu, Huang & Guo, 2009	M	x				
Nubiella papillaris Xu, Huang & Guo, 2009	M	x				
Nubiella paramitra Xu, Huang & Guo, 2007	M	x				
Nubiella sinica Huang, Xu, Liu & Chen, 2009	M	x				
Nubiella tubularis Xu, Huang & Guo, 2007	M	x				
Genus *Pachycordyle* Weismann, 1883						
Pachycordyle kubotai Stepanjants, Timoshkin, Anokhin & Napara, 2000	P	x				
Pachycordyle mashikoi (Itô, 1952)	P	x				
Pachycordyle michaeli (Berrill, 1948)	P		x			
Pachycordyle napolitana Weismann, 1883	P		x			
Pachycordyle navis (Millard, 1959)	P		x	x		
Pachycordyle pusilla (Motz-Kossowska, 1905)	P		x			
Genus *Parawrightia* Warren, 1907						
Parawrightia robusta Warren, 1907	P		x	x		
Genus *Rhizorhagium* M. Sars, 1874						
*Rhizorhagium antarcticum (*Hickson & Gravely, 1907)	P	x				x
Rhizorhagium arenosum (Alder, 1862)	P	x	x			
Rhizorhagium formosum (Fewkes, 1889)	P	x				
Rhizorhagium palori Mammen, 1963	P			x		
Rhizorhagium roseum Sars, 1874	P	x	x		x	
Rhizorhagium sagamiense Hirohito, 1988	P	x				
Genus *Silhouetta* Millard & Bouillon, 1973						
Silhouetta uvacarpa Millard & Bouillon, 1973	P	x	x	x		
Genus *Thamnostoma* Haeckel, 1879						

Continuation

Species	Phase	Distribution				
		Pacific	Atlantic	Indian	Arctic	Southern
Thamnostoma dibalium (Busch, 1851)	M		x			
Thamnostoma eilatensis Schmidt, 1972	M		x			
Thamnostoma macrostomum Haeckel, 1879	M			x		
Thamnostoma tetrellum (Haeckel, 1879)	M		x			
Genus *Velkovrhia* Matjasic & Sket, 1971						
Velkovrhia enigmatica Matjasic & Sket, 1971	P		x			

Table 2. List of valid species in the genera of Bougainvilliidae, 1809 to 2013. M: medusa, P: polyp.

Genus (phase)	Time interval (each column is since the year of the previous column)										
	1809-1830	1850	1870	1890	1910	1930	1950	1970	1990	2013	Total
Bimeria (P)			1		2	2	2	1			8
Bougainvillia (P/M)		5	3	2	3	4	3		1	9	30
Chiarella (M)					1						1
Dicoryne (P)			2								2
Garveia (P)			1	2	4	1		1			9
Koellikerina (P/M)	1				3	1	1	1	1	4	12
Millardiana (P)									1		1
Nemopsis (P/M)		1			1					1	3
Nubiella (M)									2	10	12
Pachycordyle (P)				1	1		1	2		1	6
Parawrightia (P)					1						1
Rhizorhagium (P)			1	2	1			1	1		6
Silhouetta (P)									1		1
Thamnostoma (M)			1	2					1		4
Velkovrhia (P)									1		1
Total	1	6	9	9	17	8	7	6	9	25	

The widest latitudinal distributions are found in the genera *Bimeria* and *Bougainvillia*. *Bimeria* is found from 56.1ºN to 76.1ºS (Fig. 5), mostly due to the species *Bimeria vestita*. The remaining species are more localized and usually in sublitoral waters (15-569 m, Vanhöffen, 1910; Fraser, 1938). *Bimeria vestita* is considered to be cosmopolitan (Ramil & Vervoort, 1992), although without records from the Arctic and Southern oceans (but see Marques *et al.*, 2000), is eurythermic (16-31^{o}C), euryhaline (salinity 29.0-36.5; Calder, 1993; Migotto, 1996), and in shallow (<25 m) to deep waters (358 m) (Vanhöffen, 1910, Wedler & Larson, 1986; Marques & Migotto, 2004; Genzano *et al.*, 2009). The *Bougainvillia* are found between 76.86^{o}N and 54.0^{o}S (Fig. 5), in water temperatures of 0.8º to 20.7ºC (Vannucci, 1957; Calder, 1990; Petrova *et al.*, 2011), and the greatest depth record was 7000 m (Kramp, 1965).

Species in the remaining genera have fragmented distributions (Fig. 5):

- *Chiarella* is in the Gulf of California (Brinton *et al.*, 1986), and subequatorial zone of the Pacific Ocean;
- *Dicoryne* is antitropical at depths of 1-400 m (Hirohito, 1988; Schuchert, 1996);
- *Garveia* is most commonly reported from subequatorial and tropical regions in the northern hemisphere in the Atlantic, Indian and Pacific oceans and in deeper waters (2100 m, Ramil & Vervoort, 1992);
- *Koellikerina* has a tropical or subtropical distribution, with the exception of *K. massi*, whose

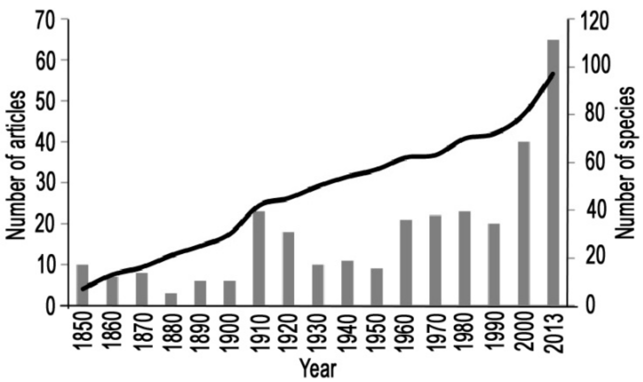

Figure 1. Cumulative number of species described since 1809 to date (2013) and number of studies that include the family Bougainvilliidae since 1809, by decade. The line indicates the cumulative number of species and the bars indicate of number the articles.

type locality is the McMurdo Strait, in Antarctica, and apparently prefers cold waters (-0.4ºC to -1.5ºC; Browne, 1910; Moteki *et al.*, 2010). The genus occurs in depths up to 100 m (*e.g.* Petersen & Vannucci, 1960; Kawamura & Kubota, 2005; Schuchert, 2007);

- *Millardiana* is restricted to Neotropical surface waters (<25 m; Calder, 1988) of the Caribbean Atlantic Ocean and ocean salinity (*ca.* 36.5, Calder, 1993);
- *Nemopsis* is found in subtropical and cold temperate waters of the north Atlantic and Pacific oceans (Calder, 1971; Schuchert, 2007; Mendoza-Becerril *et al*., 2009);
- *Nubiella* is intertropical in the Atlantic, Pacific and Indian oceans, usually less than 100 m depth (Segura-Puertas, 1980; Xu *et al.*, 2009);

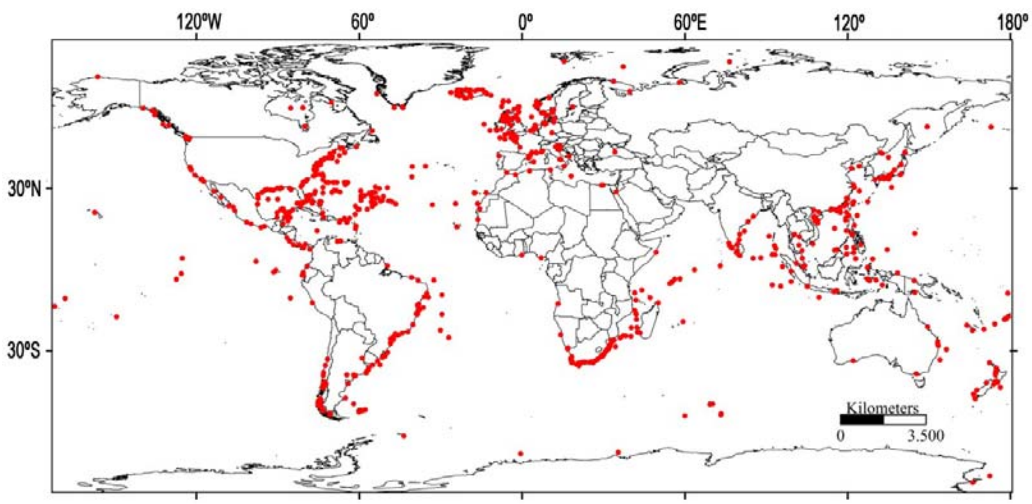

Figure 2. Current global distribution of all known valid species in the family Bougainvilliidae.

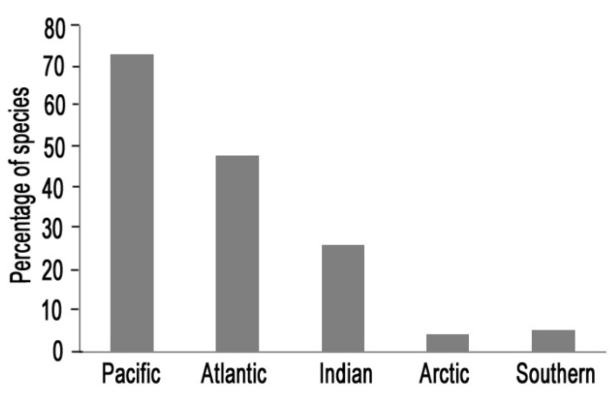

Figure 3. Percent of the total number of currently valid species in the family Bougainvilliidae found in each ocean. The total adds to greater than 100% because several species are found in more than one ocean.

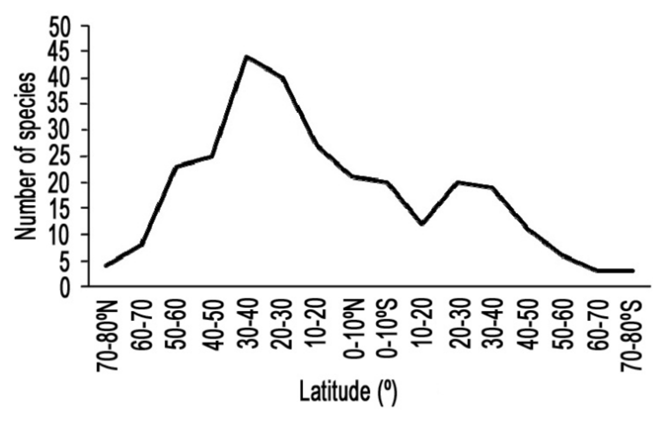

Figure 4. Frequency distribution over latitude of the number of currently valid species in the family Bougainvilliidae.

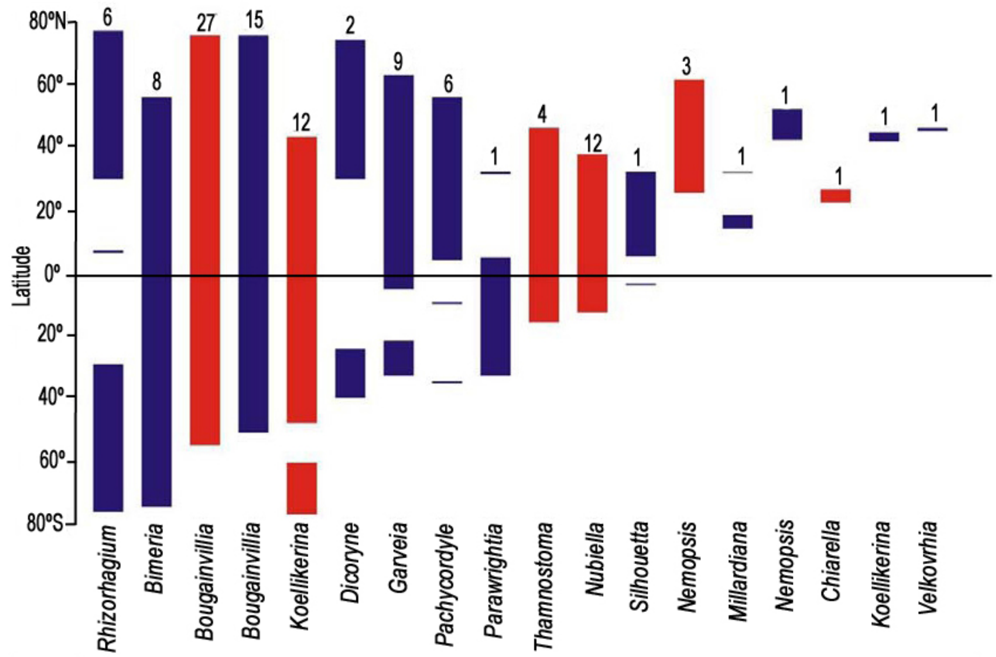

Figure 5. Latitudinal range for genera in the family Bougainvilliidae. ■ indicates genera in polyp phase, ■ indicates genera in medusa phase. The number above the bars is the number of valid species for each genus. Fragmented bars indicate that the latitudinal distribution is not continuous.

- *Pachycordyle* is found in the north Atlantic and Pacific oceans, except for *P. navis* found in the Indian Ocean near South Africa, at depths between the surface and 30 m (Calder, 1991; Kramp, 1959b);
- *Parawrightia* is found in northern and southern tropical waters of the western Atlantic and sub equatorially in the eastern Indian Ocean, at depths of 0-12 m (Kelmo & Santa-Isabel, 1998; Grohmann *et al.*, 2003), and salinity of 36.5 (Calder, 1993);
- *Rhizorhagium* has a wide latitudinal distribution in all oceans, with the majority of records from sub polar regions, at depths to 890 m (Schuchert, 2007);
- *Silhouetta* is tropical in the Atlantic, Pacific and Indian oceans, and also in the Caribbean Sea, at a maximum depth of 30 m (Millard & Bouillon, 1973), and salinity of 36.5 (Calder, 1993);
- *Thamnostoma* is common in warm tropical waters, including reefs in the Atlantic, Pacific and Indian Oceans, at depths of up to 100 m (Goy, 1979; Riera *et al.*, 1986; Segura-Puertas, 1991);
- *Velkovrhia* is the only genus restricted to fresh waters and caverns at up to 1830 m altitude (Tvrtković & Veen, 2006) near the Adriatic Sea.

Modeling of ecological niche for a total of 25 species (with a minimum of 10 location records) resulted in AUC values >0.81, which indicates that classifications were good to excellent. In general, chlorophyll is the most important variable in 69% of the models, with phosphates important in 17%, temperature in 10% and salinity in 3%. The Jackknife test indicated that chlorophyll (implicating high primary productivity) is the greatest contributor (gain) to the models (Table 3).

These models suggest five possible patterns to describe potential latitudinal and longitudinal limits for species distributions: equatorial-tropical, tropical-subtropical, subtropical-subpolar, subtropical-polar and widespread (from the equator to subpolar waters; Table 3, Figs. 6-10). The subtropical-polar category dominates, with 31% of the species and includes peaks in species richness. Coastal species are also more abundant, with 90% of the species (Table 3). Predictions of distributions from the models concur with those observed in most life-phases in the Bougainvilliidae. However, for the species *B. vestita, B. carolinensis* (polyp), *B. fulva, B. muscus* (polyp), *B. rugosa*, *G. franciscana*, *N. alvarinoae* and *R. roseum* some occurrence points do not correspond to those predicted as most adequate.

DISCUSSION

Considerations on global knowledge of the Bougainvilliidae

In the Atlantic Ocean, the most extensive studies were carried out in the northeast Atlantic and found a

Table 3. Modeled classification for distribution of the 25 valid species with >10 records.

Species	AUC	Most important variable	Life phase	Potential distribution from model	
				Latitudinal	Longitudinal
Bougainvillia platygaster	0.95	Phosphate	M	Equatorial	Oceanic
Bougainvillia niobe	0.99	Phosphate	M	Equatorial	Oceanic
Koellikerina multicirrata	0.9	Temperature	M	Equatorial	Coastal, Oceanic
Nubiella alvarinoae	0.93	Temperature	M	Equatorial	Coastal, Oceanic
Parawrightia robusta	0.98	Chlorophyll	P	Equatorial	Coastal
Bougainvillia fulva	0.93	Chlorophyll	M	Equatorial	Coastal, Oceanic
Bougainvillia muscus	0.97	Chlorophyll	M	Tropical, Subtropical	Coastal, Oceanic
Bougainvillia muscus	0.98	Chlorophyll	P	Tropical, Subtropical	Coastal, Oceanic
Nemopsis bachei	0.99	Chlorophyll	M	Tropical, Subtropical	Coastal
Bougainvillia principis	0.99	Chlorophyll	M	Subtropical, Subpolar	Coastal
Bougainvillia pyramidata	0.99	Chlorophyll	P	Subtropical, Subpolar	Coastal
Bougainvillia macloviana	0.98	Chlorophyll	M	Subtropical, Subpolar	Coastal, Oceanic
Bougainvillia carolinensis	0.95	Chlorophyll	M	Subtropical, Subpolar	Coastal, Oceanic
Bougainvillia carolinensis	0.98	Chlorophyll	P	Subtropical, Subpolar	Coastal
Bougainvillia muscoides	0.86	Chlorophyll	M	Subtropical, Polar	Coastal, Oceanic
Bougainvillia muscoides	0.99	Chlorophyll	P	Subtropical, Polar	Coastal, Oceanic
Bougainvillia britannica	0.91	Chlorophyll	M	Subtropical, Polar	Coastal, Oceanic
Bougainvillia superciliaris	0.98	Chlorophyll	M	Subtropical, Polar	Coastal
Bougainvillia superciliaris	0.93	Temperature	P	Subtropical, Polar	Coastal, Oceanic
Dicoryne conferta	0.99	Chlorophyll	P	Subtropical, Polar	Coastal
Dicoryne conybearei	0.97	Phosphate	P	Subtropical, Polar	Coastal, Oceanic
Garveia nutans	0.89	Chlorophyll	P	Subtropical, Polar	Coastal, Oceanic
Rhizorhagium roseum	0.97	Phosphate	P	Subtropical, Polar	Coastal, Oceanic
Bimeria vestita	0.97	Chlorophyll	P	Equatorial to Subpolar	Coastal, Oceanic
Bougainvillia rugosa	0.98	Chlorophyll	P	Equatorial to Subpolar	Coastal, Oceanic
Garveia franciscana	0.99	Chlorophyll	P	Equatorial to Subpolar	Coastal
Garveia gracilis	0.91	Chlorophyll	P	Equatorial to Subpolar	Coastal, Oceanic
Koellikerina fasciculata	0.82	Salinity	M	Equatorial to Subpolar	Coastal, Oceanic
Pachycordyle napolitana	0.96	Phosphate	P	Equatorial to Subpolar	Oceanic

total of 28 species when including the Mediterranean (Motz-Kossowska, 1905; Stechow, 1919; Bouillon *et al.*, 2004); Helgoland (Hartlaub, 1911), western Sweden (Rees & Rowe, 1969), Macaronesia, Mauritania, Morocco (Vervoort, 2006), Europe in general (Schuchert, 2007) and France, adjacent to the English Channel (Le Mao, 2009). In the northwest Atlantic, a total of 30 species were recorded in specific places, such as Canada (Fraser, 1944), the United States and Bermuda (Calder, 1971, 1988, 1993), the Bahamas (Bigelow, 1918), Puerto Rico (Wedler & Larson, 1986), Mexico (Segura-Puertas, 1992). It is evident, that this ocean has the greatest number of publications on this family, which is a reflection of the greater number of specialists in the region (*e.g.*, Bigelow, Bouillon, Calder, Kramp, Mayer, Russell). The Bougainvilliidae are less well known in the southern Atlantic. Three species are reported from southwest Africa (Pagès *et al.*, 1992). Comparatively, the southwestern Atlantic has been better studied, with inventories of hydromedusae (Ramírez & Zamponi, 1981; Bouillon, 1999; Migotto *et al.*, 2002; Genzano *et al.*, 2008, Nogueira Jr. *et al.*, 2013) carried out from the primary literature (*e.g.*, Haeckel, 1879; Vannucci, 1951, 1957; Vannucci & Tundisi, 1962; Kramp, 1957, 1959a; Alvariño, 1968) and by examining plankton samples, with a total of 12 species being reported.

Despite the fewer studies in the Pacific Ocean, the number of species (82) is larger than any other area. There are 11 species in the Bismarck Sea (Bouillon, 1980), 12 in New Zealand (Schuchert, 1996) and 17 along the coast of China (Xu & Huang, 2004). In China, during the last decade, many more species have been identified, mostly in the genus *Nubiella*, as a consequence of which the diversity of Bougainvilliidae is increasing in a latitudinal band of 30-40°N. The best-studied regions of the Pacific are Canada (*e.g.*,

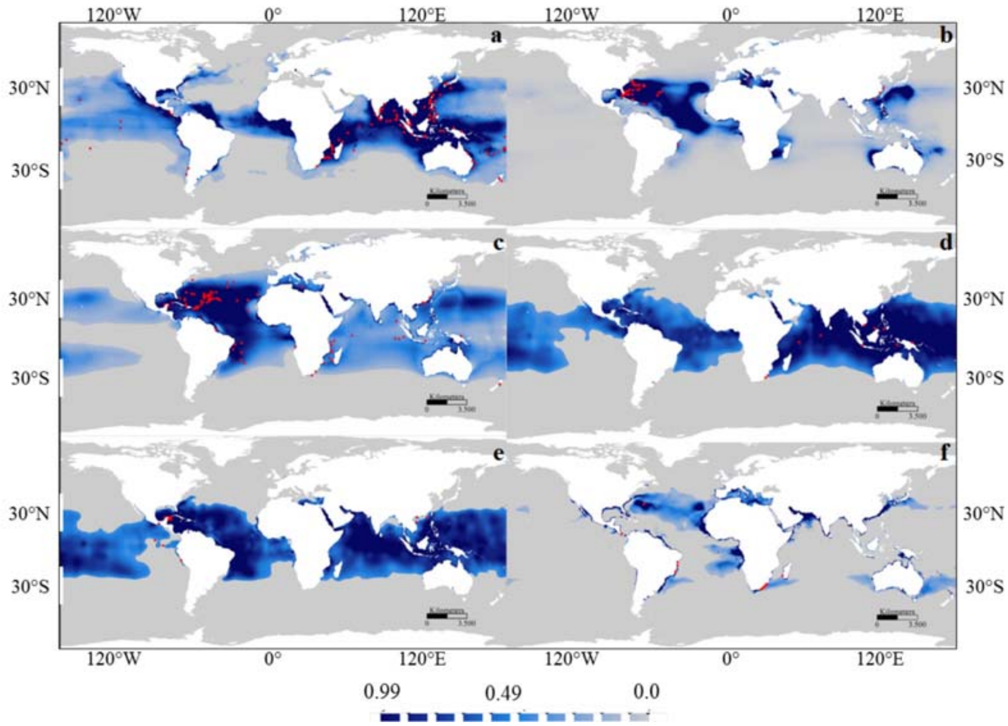

Figure 6. Potential distributions (as shades of blue indicating probabilities) from the model for equatorial-tropical species: a) *Bougainvillia fulva*-medusa, b) *Bougainvillia niobe*-medusa, c) *Bougainvillia platygaster*-medusa, d) *Nubiella alvarinoae*-medusa, e) *Koellikerina multicirrata*-medusa and f) *Parawrightia robusta*-polyp. Sampling locations are indicated by red dots.

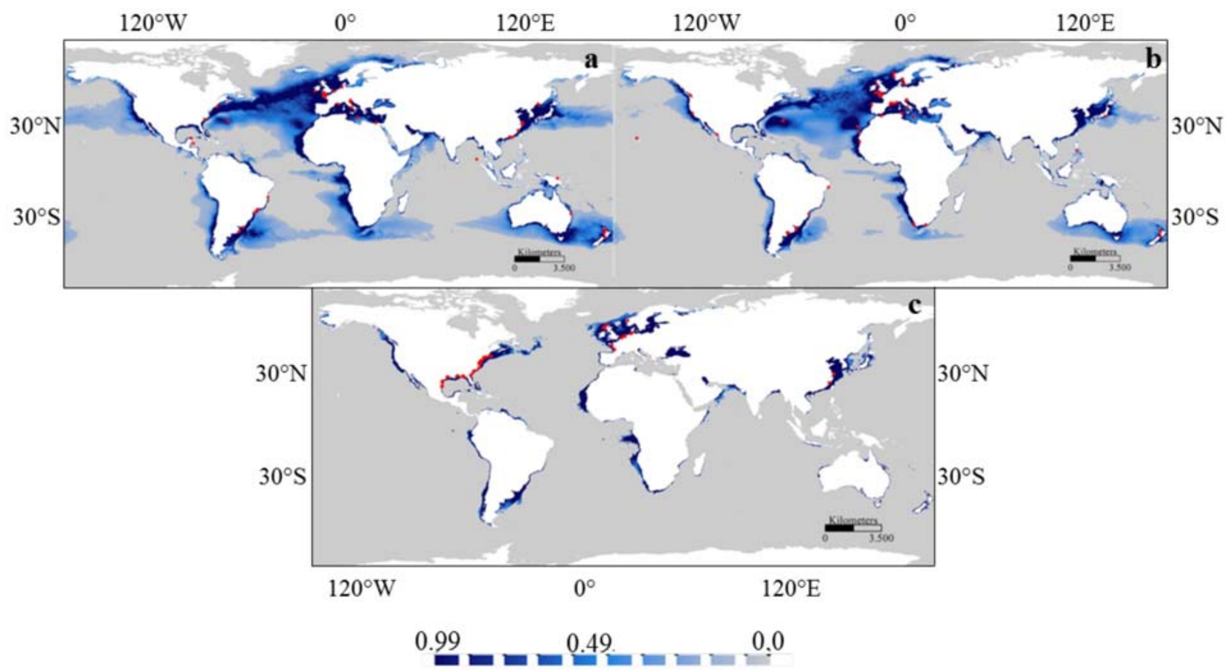

Figure 7. Potential distributions (as shades of blue indicating probabilities) from the model for tropical-subtropical species: a) *Bougainvillia muscus*-medusa, b) *Bougainvillia muscus*-polyp and c) *Nemopsis bachei*-medusa. Sampling locations are indicated by red dots.

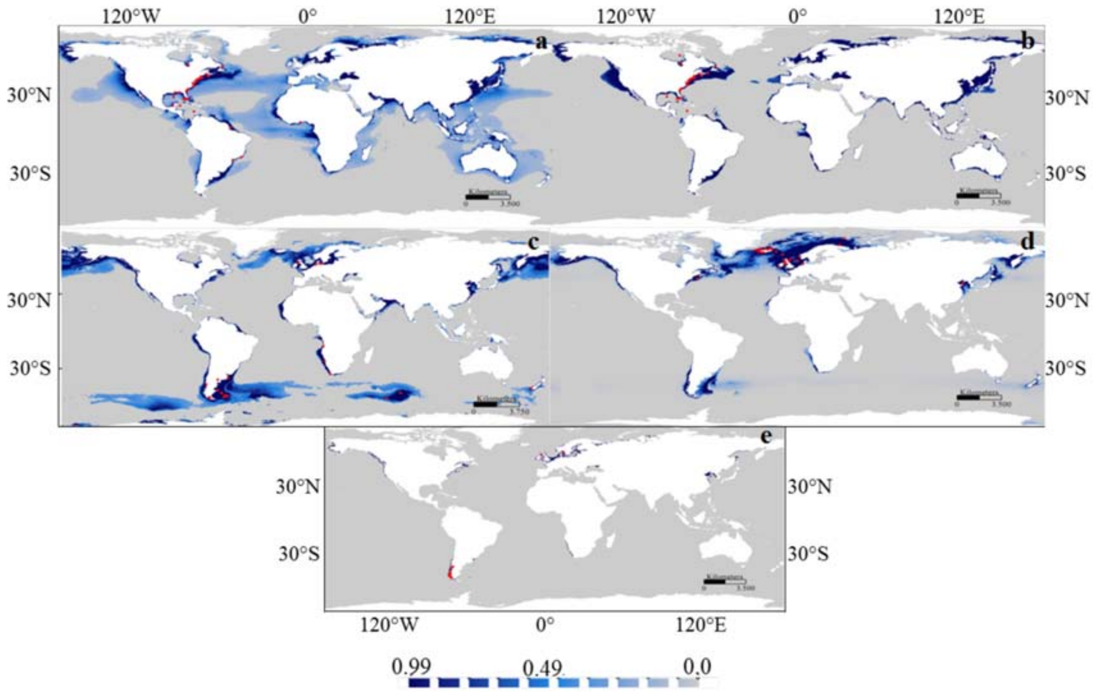

Figure 8. Potential distributions (as shades of blue indicating probabilities) from the model for subtropical-subpolar species: a) *Bougainvillia carolinensis*-medusa, b) *Bougainvillia carolinensis*-polyp, c) *Bougainvillia macloviana*-medusa, d) *Bougainvillia principis*-medusa and e) *Bougainvillia pyramidata*-polyp. Sampling locations are indicated by red dots.

Foerster, 1923; Brinckmann-Voss, 1996), United States (*e.g*., Clarke, 1876; Nutting, 1901; Torrey, 1902; Calder, 2010), Ecuador (*e.g*., Fraser, 1938) and Chile (*e.g*., Galea, 2007; Palma *et al*., 2007a, 2007b; Villenas *et al*., 2009; Bravo *et al.,* 2011; Palma *et al*., 2011).

In the Indian Ocean, two studies had the greatest sampled areas (Kramp, 1965; Millard 1975), in which 56% of the total, currently known fauna were reported. In the Arctic Ocean, the first studies were in the 1960s (Hand & Kan, 1961, EUA-Alaska; Naumov, 1969, Russia), followed by Zelickman (1972, Russia) and Ronowicz (2007, Norway). And finally, in the Southern, the expeditions of the 1900-1910's were most important (*e.g*., Hickson & Gravely, 1907; Browne, 1910; Vanhöffen, 1910).

Considerations about the distribution of the Bougainvilliidae

For a comprehensive analysis of aquatic species distributions, one must consider the three dimensions: latitude, longitude and depth (Miranda & Marques, 2011; Bentlage *et al.,* 2013). In the case of the Bougainvilliidae, due to lack of information, those three dimensions are not always known, as most studies have focused on the epipelagic zone (0-200 m), as it is typical for Medusozoa (Marques *et al*., 2003; Segura-Puertas *et al*., 2003). The epipelagic is the zone in which we expect to find most species because it is known to be most diverse for zooplankton (Angel, 1994) as well as benthic organisms (Genzano *et al.,* 2009).

Despite the lack of data, we carried out a distributional analysis in two dimensions. In latitude, the first dimension, the number of species declines (from 44 to 3) with increasing latitude, as is the case with respect to other groups of planktonic (Boltovskoy *et al.,* 1999; Genzano *et al.,* 2008) and benthic (Fautin *et al*., 2013) invertebrates. Longitudinally, the second dimension, we find that the majority of species are coastal, which shows the importance of substrates for development during the polyp phase, even for those species in which only the medusa phase is known. This suggests that the ancestral niche that was for species with both polyp and medusa phases has been maintained, despite subsequent evolutionary modifications with respect to dispersal and development.

As mentioned, models were somewhat limited by the sparse available information, both about species distribution and environmental variables. Also, alternating generations (found in some genera during their life cycles) are a problem for this type of analysis, because there are no methods that consider

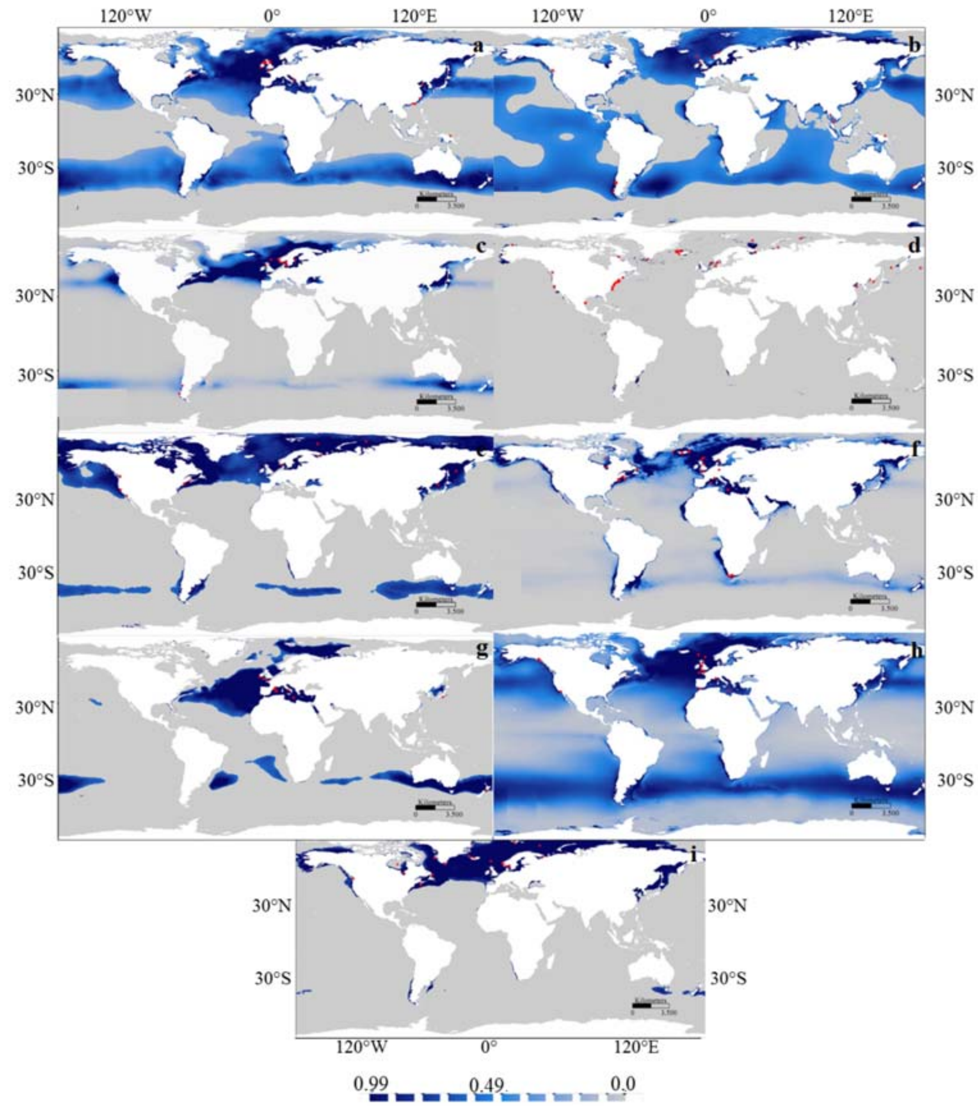

Figure 9. Potential distributions (as shades of blue indicating probabilities) from the model for subtropical-polar species: a) *Bougainvillia britannica*-medusa, b) *Bougainvillia muscoides*-medusa, c) *Bougainvillia muscoides*-polyp, d) *Bougainvillia superciliaris*-medusa, e) *Bougainvillia superciliaris*-polyp, f) *Dicoryne conferta*-polyp, g) *Dicoryne conybearei*-polyp, h) *Garveia nutans*-polyp and i) *Rhizorhagium roseum*-polyp. Sampling locations are indicated by red dots.

the influence of dispersal along with biotic and abiotic factors on each developmental phase (Pearson & Dawson, 2003). Regardless of these potential problems, the distributions generated by the models appear to be robust, in that the predicted distributions are very similar to those observed today. In the few cases with apparent incongruence's between observed and predicted distributions, these may not be errors but they rather may represent samples from sink populations of Bougainvilliidae (as in the cubomedusa *Chironex fleckeri*, Bentlage *et al*., 2009). These kinds of populations tend to exist temporarily in marginal habitats where they may often disappear if dispersal does not supply more individuals, such as when mortality exceeds natality (Dias, 1996; Palmer *et al*., 1996).

Hydrozoans distribution are known to be influenced by a variety of environmental factors (Arai, 1992), yet most models suggest that chlorophyll is the most important. Chlorophyll plays an important role and is a proxy of high primary productivity and nutrient-rich waters for some regions, hence indicating abundance of food resources for pelagic and benthic communities (Acha *et al*., 2004). It is also evident that

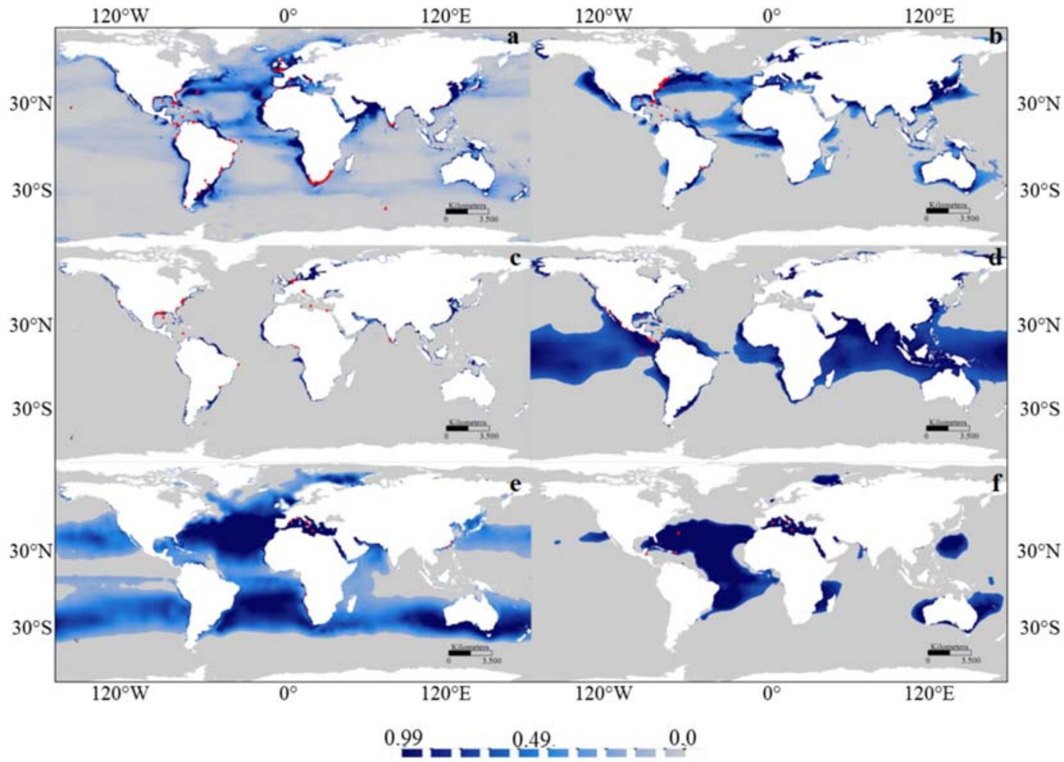

Figure 10. Potential distributions (as shades of blue indicating probabilities) from the model for widely distributed species: a) *Bimeria vestita*-polyp, b) *Bougainvillia rugosa*-polyp, c) *Garveia franciscana*-polyp, d) *Garveia gracilis*-polyp, e) *Koellikerina fasciculata*-medusa and f) *Pachycordyle napolitana*-polyp. Sampling locations are indicated by red dots.

other biotic factors can be important, yet they were not considered in the analysis, such as epibiosis (*e.g.*, Oliveira & Marques, 2007, 2011), and those associated with human activities (*e.g.*, Rocha *et al.*, 2013).

Temperature is important for the distribution of some species in the genera *Dicoryne* and *Garveia*. *Dicoryne* occurs where temperatures oscillate between 2.7-23.6ºC (Okolodkov, 2010), such as <20^{o}C for *D. conferta* (Broch, 1916), while *Garveia* is found in waters with temperatures >25ºC (Okolodkov, 2010). Temperature is often considered a key factor in determining the distribution of benthic (Boltovskoy & Wright, 1976) and planktonic (Beaugrand *et al.*, 2013) organisms. Of course, local and historical factors are considered to be important as well.

The potential distribution for some species includes regions in which important studies were carried out without noting the presence of those species. This may be due to the fact that modeling does not include biological interactions, geographic barriers and history, which clearly are also important and may explain why species seldom occupy all favorable environments (Anderson & Martínez-Meyer, 2004). An example in point is found in the latitudinal distribution of *B. superciliaris* and *Nemopsis bachei*. Both have been found in the northern hemisphere and their potential distribution due to modeling includes both hemispheres, which suggests dispersal limitation. Specifically, *N. bachei* is considered to be euryhaline (Calder, 1971) (salinity 3-35, Denayer, 1973; Mendoza-Becerril *et al.*, 2009) and usually present at temperatures <26°C (Cronin *et al.*, 1962; Denayer, 1973; Marshalonis & Pinckney, 2007).

Of the species with sufficient information for polyp and medusa phases, models can be particular to the life phase. In two species (*B. carolinensis* and *B. muscus*) patterns are similar for both phases, and in others, one phase generally has a larger predicted distribution. In *B. muscus* the medusa phase has the greatest predicted distribution while in *B. superciliaris* it is the polyp phase. Similarly, in at least *B. superciliaris*, temperature is most important for the polyp phase, while chlorophyll is most important for the medusa phase. This reinforces the idea that the influence of the environment can vary by life phase and so coupling of phases is not trivial. As a consequence, modelling without respect to life phase, for organisms with distinct phases, may overlook very important and complex patterns. Adding to uncertainty is the dispersal potential of each phase, with some considering the medusa phase as the principal dispersal agent, which is reflected by a widespread distribution, including pelagic (Bouillon, 1981; Leclère *et al.*, 2009). This is exemplified in *B. muscoides*. On the other hand, some researchers suggest the contrary (Cornelius, 1992), as seen in *B. superciliaris*. Most likely is that while some patterns predominate, there will always be exceptions.

The lack of information from a variety of regions is also clear in this analysis, especially in the south-eastern Atlantic, southern Gulf of Mexico, Central America, southwest Pacific and northeastern Indian Ocean. These regions also have relatively high AUC values (0.65-0.99) for several species and would be interesting places to increase sampling effort. However, the number of studies seems to be declining with respect to the polyp phase (Table 2). This trend and the species accumulation curves illustrate that more studies are needed, especially of benthic and planktonic faunas and at a variety of depths and aquatic environments, in addition to revisions based on morphological, reproductive and molecular characters to respond questions of evolutionary and geographic patterns.

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