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The historical reconstruction of distribution of the genus *Halecium* (Hydrozoa: Haleciidae): a biological signal of ocean warming?

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ABSTRACT

The distribution of 130 nominal species of the genus *Halecium*, based on published records, has been mapped for the first time in a comprehensive set of marine ecoregions, to analyse their distribution. Most *Halecium* species are found at mid- and high latitudes, with some overlaps in distribution ranges across regions. The species richness of *Halecium* is strongly related to the latitudinal gradient, with maximal diversity at polar and temperate latitudes. Previous detailed studies in the Mediterranean Sea show that large *Halecium* species of coldwater affinity have regressed or disappeared in recent years, probably due to global warming. Worldwide, however, the overall species richness of *Halecium* has not changed along the latitudinal gradient over recent decades, with some changes in species composition at temperate-tropical latitudes in both hemispheres, even though the majority of the species that have not been recorded for more than 50 years are of coldwater affinity. The genus can be considered an indicator for biological responses to climate changes for the Mediterranean Sea, but the available distribution data do not allow extending this possibility to the rest of the world. A focused evaluation on the distribution of *Halecium* species with the addition of new field data might reinforce the picture stemming from the present analysis.

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Introduction

Overwhelming evidence shows that climate is changing, both due to natural causes and to anthropogenic activities (Waters et al. 2016). In recent decades, the overexploitation of marine resources has impacted ecosystems, leading to habitat and species loss (McCauley et al. 2015), with a pressing demand for sustainability (Thiede et al. 2016 and references therein). If local impacts can be extremely severe, global impacts are of paramount importance: Laffoley & Baxter (2016) extensively reviewed the impact of ocean warming on marine biota, revealing alarming changes in the structure and function of ecosystems.

Changes in biodiversity composition as a response to global impacts should be assessed by periodic updates of species inventories. It is reasonable, in fact, to hypothesize that a temperature increase could result in the disappearance of cold-affinity species and the widening of distribution ranges of warm-affinity ones. Therefore, changes in regional species pools can be informative about environmental change. However, new records tend to inflate species

lists, resulting in apparent increases in biodiversity (Costello et al. 2001; Mora et al. 2011; Gravili et al. 2013): at mid-latitudes, for instance, the species added to regional check lists are often tropical, and are added to the species that were previously in the list but that, in recent times, might be unrecorded; the 'missing' species are often endemic and of coldwater affinity (Gravili et al. 2015a). The lack of long-term data is a major problem when marine community fluctuations are connected to climate change (Southward et al. 1995). Recent temperature increases caused severe mass mortalities of charismatic species of the Mediterranean Sea benthos, such as gorgonians and sponges (Rivetti et al. 2014; Parravicini et al. 2015): small changes in sea temperature can influence the biology of species and the diversity of communities (Cerrano et al. 2000; Perez et al. 2000; Garrabou et al. 2001; Moschella 2008; Torrents et al. 2008). All-species inventories are very rare and biodiversity evaluations are often restricted to thoroughly studied groups. The Hydrozoa are good candidates for such assessments; they currently comprise 3702 nominal

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species worldwide (Bouillon et al. 2006), inhabit all aquatic ecosystems, display a wide array of life-cycle strategies and many exhibit extreme sensitivity to seasonal changes that alter the seasonal patterns of species occurrence (Boero 1984; Gili & Hughes 1995; Bavestrello et al. 2006; Di Camillo et al. 2008). A recent monograph on the Hydrozoa of the Mediterranean Sea (Bouillon et al. 2004) allows for reasonably careful assessments in this basin. Burrows et al. (2011), in fact, considered that one of the few studies on the impact of ocean warming in the distribution of marine invertebrates refer to Mediterranean hydroids. The present paper focuses on the historical reconstruction of the distribution of the genus *Halecium* Oken, 1815 (Hydrozoa: Haleciidae). This speciose genus, without a medusa stage, is characterized by a broad geographic distribution and includes many species forming large and conspicuous colonies. A long history of bibliographic data on a global scale allows reconstructing long-term trends in the geographic distribution of the species of this genus. *Halecium* species are widely distributed in all oceans and their taxonomy has historically been considered difficult due to the variability of diagnostic features that led to a plethora of synonyms (Schuchert 2005). Information about this genus spans from the pioneering studies by Oken (1815), Johnston (1838), Clark (1875, 1876), Clarke (1894) and Browne (1897), to taxonomic lists (Ralph 1958; Millard 1975; Ramil-Blanco & Iglesias Diaz 1988; Park 1991; Watson 1993, 2008; El Beshbeeshy 1994; Bouillon et al. 2004); further information is included in databases such as the World Register of Marine Species (Appeltans et al. 2011) that incorporates the World Hydrozoa database (Schuchert 2015), and more taxonomic, ecological and zoogeographic studies (Cornelius 1975, 1995, 1998; Medel et al. 1998; Ramil et al. 1998; Medel & Vervoort 2000; Schuchert 2005). Vervoort & Watson (2003) made a list with 120 valid nominal species of the genus *Halecium*. Bouillon et al. (2006) updated the world list of Hydrozoa, bringing the list to 96 nominal species. Peña Cantero (2014) proposed a revision of the known Antarctic species of this genus counting 13 valid species in the Southern Ocean.

In a study covering the early 1980s, Boero & Fresi (1986) reported on the species composition and phenology of a Mediterranean hydrozoan population, covering about 100 species. Puce et al. (2009) repeated the study carried out by Boero & Fresi after more than two decades and found dramatic changes in the species composition and phenology, even if the absolute species number did not change much. The presence of species of the genus *Halecium* was strikingly different in the comparison between the data of Boero & Fresi (1986) and

Puce et al. (2009). Large species such as *Halecium halecinum* (Linnaeus, 1758), *H. labrosum* Alder, 1859 and *H. beanii* (Johnston, 1838) were abundant and often frequent in the early period (Boero & Fresi 1986), whereas they were either absent or rare in the recent period (Puce et al. 2009). Furthermore, a thorough assessment of the hydrozoan fauna of the Salento Peninsula (Gravili et al. 2015b) at the SE extreme of the Italian Peninsula, where waters are warmer than in the NW part of the Mediterranean and where Boero & Fresi (1986) carried out their study, reported large haleciids as rare and one, *H. halecinum*, was never found. Smaller species, such as *H. pusillum*, did not change their patterns of presence. Furthermore, in three research expeditions to Papua New Guinea, (Ferdinando Boero personal observations 1986, 1988, 1990) never found large *Halecium* colonies in the period 1986–1990. These observations led to the hypothesis that species of the genus *Halecium* have a marked preference for temperate and cold waters, not being well adapted to tropical conditions. In order to test this hypothesis, past and present-day information on the global geographic distribution of *Halecium* species was analysed to detect possible geographic shifts expecting that large *Halecium* disappear from tropical areas and possibly move to temperate-cold areas.

Methods

The bibliographic analysis covered more than 9000 faunal articles, published between 1815 and 2014, based on the World Hydrozoa Database, the World Register of Marine Species (Appeltans et al. 2011) and the contributions of Bouillon et al. (2006) and Schuchert (2015). A distribution map for all valid species was based on data (more than 500 articles; see Article list S1, supplementary material) extracted from the database BiblioHydro (for more details see Gravili et al. 2000). The type localities and additional confirmed records in neighbouring areas of all valid species were entered in 232 ecoregions of 12 marine realms (Marine Ecoregions of the World, MEOWs, see Spalding et al. 2007), namely: Arctic (A), Temperate Northern Atlantic (TNA), Temperate Northern Pacific (TNP), Tropical Atlantic (TAtI), Western Indo-Pacific (WIP), Central Indo-Pacific (CIP), Eastern Indo-Pacific (EIP), Tropical Eastern Pacific (TEP), Temperate South America (TSAm), Temperate Southern Africa (TSAf), Temperate Australasia (TA), Southern Ocean (SO) (Figure 1, Table I; Table SI, supplementary material).

To perform a comparative analysis of *Halecium* species distribution across spatial and temporal gradients and to avoid bias from undersampling in the past, we restricted our metadata set to the more

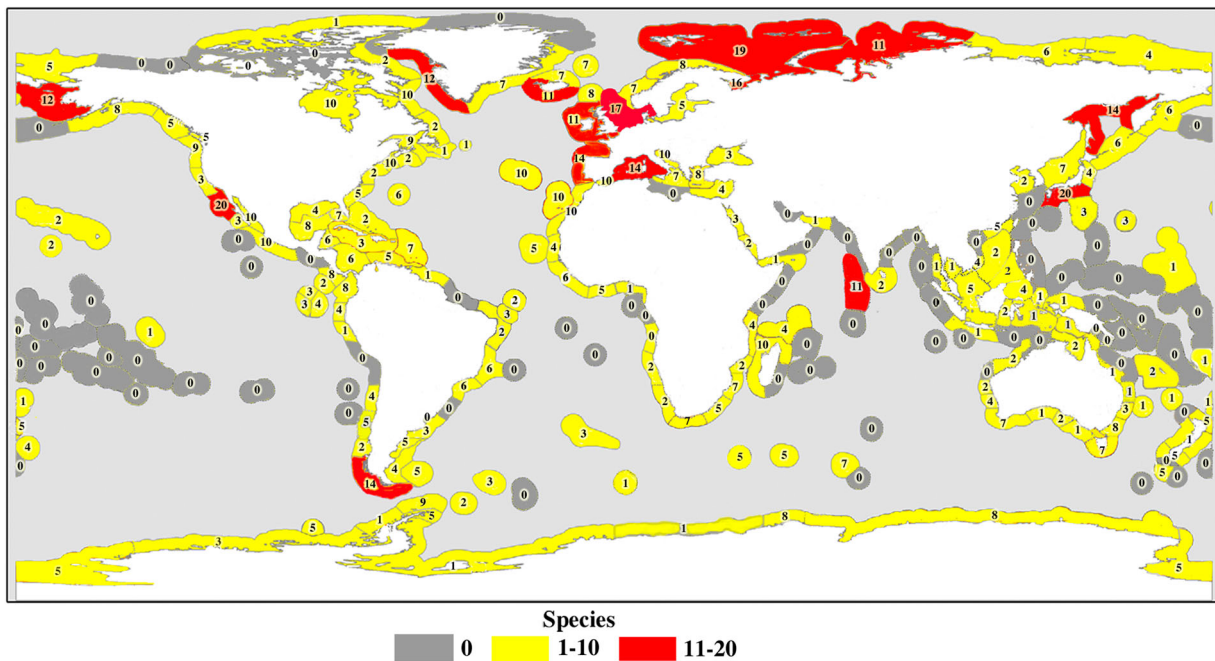


Figure 1. Current global distribution of all known valid species of the genus *Halecium*. Numbers of *Halecium* species recorded in each of 232 marine ecoregions of the world (Spalding et al. 2007) extracted from the BiblioHydro Database.

recent studies (from 1960 to 2014), covering the period in which global warming became evident, reporting on 100 species worldwide. All records were organized in a presence/absence data matrix of *Halecium* species in each Marine Ecoregion (*sensu* Spalding et al. 2007) for each decade from 1960 to 2000, and the last period from 2000 to 2014. The species number was categorized according to the marine realms where each species was observed, for two sequential time intervals (1960–1984 and 1985–2014) in order to detect the temporal shifts in *Halecium* distribution. The global relationships between number of species and number of studies per realm (log-transformed) was used to correct the data for differences in sampling effort and to compensate for the large spatial and temporal heterogeneity in the number of studies. The corrected species numbers were then investigated for latitudinal trends. Latitudinal distributions in species number before and after 1985 were compared to detect recent shifts in species distribution.

Results

The distribution of 130 nominal species of the genus *Halecium* (Table I), representing about 3% of the hydrozoan species of the world (3702 species, see Bouillon et al. 2006), were mapped in Figure 1. Valid species are found in all ecoregions, with a large heterogeneity in numbers (Figure 2).

Most species of *Halecium* occur at intermediate and high latitudes: 50 species (38% of the total) in the

Temperate North Pacific with 53 papers that cover the genus; 35 (27%) in the Temperate North Atlantic (221 papers); 24 (18%) in the Arctic (60 papers); 24 (18%) in Temperate South-America (44 papers); 22 (17%) in the Southern Ocean (43 papers); 21 (16%) in Temperate Australasia (31 papers), and 8 (6%) in Temperate Southern Africa (14 papers) (the total is higher than 100% because several species are found in more than one ecoregion). Species numbers are much lower in tropical regions: 22 species (17% of the total) occur in the Tropical Atlantic (71 papers); 18 (14%) in the Central Indo-Pacific (30 papers); 21 (16%) in the Tropical Eastern Pacific (16 papers); 12 (9%) in the Western (30 papers) and 3 (2%) in the Eastern Indo-Pacific (5 papers) (Figure 2).

Regarding the global distribution of *Halecium*, the most extensive studies were carried out in the Temperate North Atlantic realm: north-east Atlantic and Mediterranean Sea (Motz-Kossowska 1911; Stechow 1919; Peña Cantero & García Carrascosa 2002; Bouillon et al. 2004; Gravili et al. 2008); Azores, Canary Islands, Madeira, Cape Verde Islands, off Morocco and Mauritania (Medel & Vervoort 2000); Europe (Schuchert 2005), English Channel (Cornelius 1975) and Black Sea (Isinibilir et al. 2010). In the north-west Atlantic, *Halecium* species were recorded in several areas, such as the east coast of North America (Fraser 1946; Calder 2003), the Carolinian province (Fraser 1912, 1944, 1946; Calder & Hester 1978) and the Gulf of Mexico (Clarke 1879; Fraser 1946).

Table 1. Species described in the literature of the genus *Halecium* and distribution in the world realms (sensu Spalding et al. 2007).

Species	Realm distribution											Note	Synonyms	References	
	A	TNA	TNP	TAtI	WIP	CIP	EIP	TEP	TSAm	TSAf	TA				SO
<i>Halecium amphibolum</i> Watson, 1993	-	-	-	-	-	-	-	-	-	-	X	-			
<i>Halecium annulatum</i> Torrey, 1902	-	-	M	-	-	-	-	M	-	-	-	-	M*		
<i>Halecium annuliforme</i> Galea & Schories, 2012	-	-	-	-	-	-	-	-	X	-	-	-			
<i>Halecium antarcticum</i> Vanhöffen, 1910	-	-	-	-	-	-	-	-	-	-	-	X			
<i>Halecium arcticum</i> Ronowicz & Schuchert, 2007	X	-	-	-	-	-	-	-	-	-	-	-			
<i>Halecium argentum</i> Clarke, 1894	-	-	-	-	-	-	-	M	-	-	-	-	M*		
<i>Halecium articulatum</i> Clark, 1875	X	X	-	-	-	-	-	-	-	-	-	-			
<i>Halecium banyulense</i> Motz-Kossowska, 1911	-	M	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium banzare</i> Watson, 2008	-	-	-	-	-	-	-	-	-	-	-	X			
<i>Halecium beanii</i> (Johnston, 1838)	X	X	X	X	X	M	X	X	X	X	X	M			
<i>Halecium bermudense</i> Congdon, 1907	-	X	M	X	-	-	-	X	X	-	M	-			
<i>Halecium birulai</i> Spassky, 1929	M	-	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium bithecum</i> Watson, 2005	-	-	-	-	-	-	-	-	-	-	X	-			
<i>Halecium brashnikowi</i> Linko, 1911	-	-	M	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium brevithecum</i> Watson, 2008	-	-	-	-	-	-	-	-	-	-	-	X			
<i>Halecium bruniensis</i> Watson, 1975	-	-	-	-	-	-	-	-	-	-	X	-			
<i>Halecium calderi</i> Galea, 2010	-	-	-	X	-	-	-	-	-	-	-	-			
<i>Halecium conicum</i> Stechow, 1919	-	X	-	-	X	-	-	-	-	-	-	-		<i>Halecium minutum</i> Motz-Kossowska, 1911; <i>H. reflexum</i> Stechow, 1919	Schuchert (2015)
<i>Halecium corpulatum</i> Watson, 2012	-	-	-	-	-	X	-	-	-	-	-	-			
<i>Halecium corrugatissimum</i> Trebilcock, 1928	-	-	-	-	-	-	-	-	X	-	X	-			
<i>Halecium corrugatum</i> Nutting, 1899	X	X	X	-	-	-	-	-	-	-	-	-			
<i>Halecium crinis</i> Stechow, 1913	-	-	M	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium curvicaule</i> Von Lorenz, 1886	X	X	X	-	-	-	-	-	-	-	-	-		<i>Halecium kuekenthali</i> von Marktanner-Turneretscher, 1895	Schuchert (2015)
<i>Halecium cymiforme</i> Allman, 1888	-	-	M	-	-	M	-	-	X	-	-	-			
<i>Halecium cymosum</i> Fraser, 1935	-	-	M	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium delicatulum</i> Coughtrey, 1876	X	X	X	X	X	X	-	M	X	X	X	X	In Antarctic waters: = in part <i>Halecium antarcticum</i> Vanhöffen, 1910, and in part <i>H. pseudodelicatulum</i> Peña Cantero, 2014	<i>Halecium flexile</i> Allman, 1888 (possibly synonym); <i>H. flexile</i> var. <i>japonica</i> Leloup, 1938; <i>H. gracile</i> Bale, 1893; <i>Halecium parvulum</i> Bale, 1888	Peña Cantero (2014); Schuchert (2015)
<i>Halecium densus</i> Calkins, 1899	-	-	X	-	-	-	-	-	-	-	-	-			
<i>Halecium dichotomum</i> Allman, 1888	-	-	-	X	X	-	-	-	X	X	-	-			
<i>Halecium diminutivum</i> Fraser, 1940	M	M	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium discoidum</i> Galea, 2013	-	-	-	X	-	-	-	-	-	-	-	-			
<i>Halecium dubium</i> Fraser, 1944	-	X	-	X	-	-	-	-	-	-	-	-			
<i>Halecium dufresneae</i> Millard, 1975	-	-	-	-	-	-	-	-	-	-	-	X			
<i>Halecium dyssymetrum</i> Billard, 1929	-	-	-	X	X	X	-	X	X	-	X	-			

(Continued)

Table I. Continued.

	Realm distribution													Note	Synonyms	References
	A	TNA	TNP	TAtI	WIP	CIP	EIP	TEP	TSAm	TSAf	TA	SO				
<i>Halecium edwardsianum</i> (d'Orbigny, 1842)	-	-	-	-	-	-	-	-	M	-	-	-		M*		
<i>Halecium elegantulum</i> Watson, 2008	-	-	-	-	-	-	-	-	-	-	-	X				
<i>Halecium erratum</i> Galea, Försterra, Häussermann & Schories, 2014	-	-	-	-	-	-	-	-	X	-	-	-				
<i>Halecium exaggeratum</i> Peña Cantero, Boero, Piraino, 2013	-	-	-	-	-	-	-	-	-	-	-	X				
<i>Halecium exiguum</i> Fraser, 1948	-	-	-	-	-	-	-	M	-	-	-	-		M*		
<i>Halecium expansum</i> Trebilcock, 1928	-	-	-	-	-	-	-	-	-	-	M	-		M*		
<i>Halecium fasciculatum</i> Fraser, 1938	-	-	M	-	-	-	-	M	-	-	-	-		M*		
<i>Halecium filicula</i> Allman, 1877	-	M	-	-	-	-	M	-	-	-	-	-		M*		
<i>Halecium fjordlandicum</i> Galea, 2007	-	-	-	-	-	-	-	-	X	-	-	-				
<i>Halecium flabellatum</i> Fraser, 1935	-	-	M	-	-	-	-	M	-	-	-	-		M*		
<i>Halecium flexile</i> Allman, 1888	-	-	-	-	-	-	-	-	X	-	M	X				
<i>Halecium flexum</i> Fraser, 1948	-	-	M	-	-	-	-	M	-	-	-	-		M*		
<i>Halecium fragile</i> Hodgson, 1950	-	-	-	-	-	X	-	-	-	-	X	-				
<i>Halecium fraseri</i> Ralph, 1958	-	-	M	-	-	-	-	-	X	-	-	-				
<i>Halecium frigidum</i> Peña Cantero, 2010	-	-	-	-	-	-	-	-	-	-	-	X				
<i>Halecium galeatum</i> Billard, 1937	-	-	-	-	-	M	-	-	-	-	-	-		M*		
<i>Halecium groenlandicum</i> Kramp, 1911	X	-	M	-	-	-	-	-	-	-	-	-				
<i>Halecium halecinum</i> (Linnaeus, 1758)	X	X	M	X	X	M	-	X	-	X	-	-			<i>Halecium halecium</i> (Linnaeus, 1758)	Schuchert (2015)
<i>Halecium harrimani</i> Nutting, 1901	-	-	M	-	-	-	-	-	-	-	-	-		M*	<i>Halecium robustum</i> Nutting, 1901	Schuchert (2015)
<i>Halecium humeriformis</i> Galea & Schories, 2014	-	-	-	-	-	-	-	-	X	-	-	-				
<i>Halecium humile</i> Pictet, 1893	-	-	-	-	-	M	-	-	-	-	-	-		M*		
<i>Halecium incertus</i> Naumov & Stepanjants, 1962	-	-	-	-	-	-	-	-	-	-	-	X			<i>Halecium macrocaulus</i> Watson, 2008	Peña Cantero (2014)
<i>Halecium inhacae</i> Millard, 1958	-	-	-	-	X	-	-	-	-	-	X	-				
<i>Halecium insolens</i> Fraser, 1938	-	-	M	-	-	-	-	M	-	-	-	-		M*		
<i>Halecium interpolatum</i> Ritchie, 1907	-	-	-	-	-	-	-	-	-	-	-	X			<i>Halecium ovatum</i> Totton, 1930	Peña Cantero (2014)
<i>Halecium irregulare</i> Bonnevie, 1899	-	M	-	-	-	-	-	-	-	-	-	-		M*		
<i>Halecium jaederholmi</i> Vervoort, 1972	-	-	X	-	-	-	-	-	X	-	-	X				
<i>Halecium kofoidi</i> Torrey, 1902	-	-	M	-	-	-	-	-	-	-	-	-		M*		
<i>Halecium labiatum</i> Billard, 1933	-	-	-	-	X	-	-	-	-	-	-	-				
<i>Halecium labrosum</i> Alder, 1859	X	X	X	-	-	-	-	-	-	-	-	-				
<i>Halecium laeve</i> Kramp, 1932	M	-	-	-	-	-	-	-	-	-	-	-		M*		
<i>Halecium lamourouxianum</i> (d'Orbigny, 1842)	-	-	-	-	-	-	-	-	M	-	-	-		M*		
<i>Halecium lankesteri</i> (Bourne, 1890)	-	X	-	X	X	-	-	-	-	X	X	-				
<i>Halecium lenticulare</i> Trebilcock, 1928	-	-	-	-	-	-	-	-	-	-	M	-		M*		
<i>Halecium lightbourni</i> Calder, 1991	-	-	-	X	-	-	-	-	X	-	-	-				
<i>Halecium linkoi</i> Antsulevich, 1980	-	-	X	-	-	-	-	-	-	-	-	-				

(Continued)

Table I. Continued.

	Realm distribution													Note	Synonyms	References
	A	TNA	TNP	TAtI	WIP	CIP	EIP	TEP	TSAm	TSAf	TA	SO				
<i>Halecium liouvillei</i> Billard, 1934	-	X	-	X	-	-	-	-	-	-	-	-	-			
<i>Halecium lucium</i> Antsulevich, 1979	-	-	X	-	-	-	-	-	-	-	-	-	-			
<i>Halecium luteum</i> Watson, 1975	-	-	-	-	-	-	-	-	-	-	X	-	-			
<i>Halecium macrocephalum</i> Allman, 1877	-	X	M	X	-	-	-	-	-	-	-	X	-			
<i>Halecium marsupiale</i> Bergh, 1887	M	-	M	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium maximum</i> Galea & Schories, 2014	-	-	-	-	-	-	-	-	X	-	-	-	-			
<i>Halecium mediterraneum</i> Weismann, 1883	-	X	-	-	-	-	-	-	-	-	-	-	-			
<i>Halecium minutum</i> Broch, 1903	X	M	-	-	M	-	-	-	-	-	-	-	-			
<i>Halecium mirabile</i> Schydrowsky, 1902	M	M	M	-	-	M	-	-	-	-	-	-	-	M*	<i>Halecium pygmaeum</i> Fraser, 1912	Schuchert (2015)
<i>Halecium mirandus</i> Antsulevich & Regel, 1986	-	-	X	-	-	-	-	-	-	-	-	-	-			
<i>Halecium modestum</i> Galea & Schories, 2014	-	-	-	-	-	-	-	-	X	-	-	-	-			
<i>Halecium muricatum</i> (Ellis & Solander, 1786)	X	X	M	-	-	-	-	X	-	X	-	-	-			
<i>Halecium nanum</i> Alder, 1859	-	X	M	X	-	-	-	M	-	-	X	-	-			
<i>Halecium nullinodum</i> Fraser, 1935	-	-	M	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium ochotense</i> Linko, 1911	-	-	M	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium ornatum</i> Nutting, 1901	M	-	M	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium pallens</i> Jäderholm, 1905	-	-	-	-	-	-	-	-	X	-	-	X	-			
<i>Halecium paucinodum</i> (Fraser, 1947)	-	-	-	M	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium pearsonense</i> Watson, 1997	-	-	-	-	-	-	-	-	-	-	X	-	-			
<i>Halecium perexiguum</i> Hirohito, 1995	-	-	X	-	-	-	-	-	-	-	-	-	-			
<i>Halecium petrosom</i> Stechow, 1919	-	X	-	-	-	-	-	-	-	-	-	-	-			
<i>Halecium planum</i> Bonnevie, 1901	-	M	-	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium platythecum</i> Galea, Försterra & Häussermann, 2014	-	-	-	-	-	-	-	-	X	-	-	-	-			
<i>Halecium plicatocarpum</i> Vervoort & Watson, 2003	-	-	-	-	-	X	-	-	-	-	-	-	-			
<i>Halecium plumosum</i> Hincks, 1868	-	M	-	-	-	-	-	-	-	-	-	-	-	M*		
<i>Halecium profundum</i> Calder & Vervoort, 1998	-	-	-	X	-	-	-	-	-	-	-	-	-			
<i>Halecium pseudodelicatulum</i> Peña Cantero, 2014	-	-	-	-	-	-	-	-	-	-	-	X	-			
<i>Halecium pseudoincertus</i> Peña Cantero, 2014	-	-	-	-	-	-	-	-	-	-	-	X	-			
<i>Halecium pusillum</i> (M. Sars, 1857)	-	X	X	M	-	M	-	X	-	-	-	-	-		<i>Halecium schneideri</i> Bonnevie, 1898	
<i>Halecium pyriforme</i> Hirohito, 1995	-	-	X	-	-	-	-	-	-	-	-	-	-			
<i>Halecium ralphae</i> Watson & Vervoort, 2001	-	-	X	-	-	-	-	-	-	-	X	X	-			
<i>Halecium reduplicatum</i> (Fraser, 1935)	-	-	M	-	-	-	-	-	-	-	-	-	-	M*	<i>Sagamihydra reduplicata</i> Hirohito, 1995	Hirohito (1995)
<i>Halecium regulare</i> Fraser, 1938	-	-	M	-	-	-	-	M	-	-	-	-	-	M*		

(Continued)

Table I. Continued.

	Realm distribution												Note	Synonyms	References
	A	TNA	TNP	TAtl	WIP	CIP	EIP	TEP	TSAm	TSAf	TA	SO			
<i>Halecium repens</i> Jäderholm, 1908	M	–	M	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium reversum</i> Nutting, 1901	M	–	M	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium scalariformis</i> Billard, 1929	–	–	–	–	–	M	–	–	–	–	–	–	M*		
<i>Halecium scandens</i> Nutting, 1906	–	–	–	–	–	–	M	–	–	–	–	–	M*		
<i>Halecium scutum</i> Clark, 1877	X	X	X	–	–	–	–	–	–	–	–	–		<i>Halecium beringi</i> Naumov, 1960	Schuchert (2005)
<i>Halecium secundum</i> Jäderholm, 1905	–	–	–	–	–	–	–	–	–	–	–	X			
<i>Halecium sessile</i> Norman, 1867	M	X	X	X	X	X	–	–	–	X	X	–			
<i>Halecium sibogae</i> Billard, 1929	–	X	–	X	–	X	–	–	–	–	–	–			
<i>Halecium singulare</i> (Billard, 1929)	–	–	–	–	–	M	–	–	–	–	–	–	M*		
<i>Halecium spatulum</i> Watson, 2000	–	–	–	–	–	X	–	–	–	–	–	–			
<i>Halecium speciosum</i> Nutting, 1901	X	–	M	X	–	–	–	–	–	–	–	–			
<i>Halecium tabulatum</i> Watson, 2005	–	–	–	–	–	–	–	–	–	–	X	–			
<i>Halecium tehuelcum</i> (d'Orbigny, 1842)	–	–	–	–	–	–	–	–	X	–	–	–			
<i>Halecium telescopicum</i> Allman, 1888	–	–	M	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium tenellum</i> Hincks, 1861	X	X	X	X	X	X	–	X	X	X	X	X		In Antarctic waters: = ? <i>Halecium exaggeratum</i> Peña Cantero et al., 2013	Peña Cantero (2014)
<i>Halecium tensus</i> Fraser, 1941	–	M	–	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium tenue</i> Fraser, 1938	–	–	M	–	–	–	–	M	–	–	–	–	M*		
<i>Halecium textum</i> Kramp, 1911	X	X	–	–	–	–	–	–	–	–	–	–			
<i>Halecium tortile</i> Bonnevie, 1898	–	M	–	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium tortum</i> Fraser, 1938	–	–	–	–	–	–	–	M	–	–	–	–	M*		
<i>Halecium tristaniensis</i> Galea, 2014	–	–	–	–	–	–	–	–	X	–	–	–			
<i>Halecium tubatum</i> Watson, 2008	–	–	–	–	–	–	–	–	–	–	–	X			Peña Cantero (2014)
<i>Halecium undulatum</i> Billard, 1921	–	X	–	–	–	–	–	–	–	–	–	X			
<i>Halecium vagans</i> Fraser, 1938	–	–	M	–	–	–	–	M	–	–	–	–	M*		
<i>Halecium vasiforme</i> Fraser, 1935	–	–	M	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium washingtoni</i> Nutting, 1901	–	M	–	–	–	–	–	M	–	–	–	–	M*		
<i>Halecium wilsoni</i> Calkins, 1899	–	–	M	–	–	–	–	–	–	–	–	–	M*		
<i>Halecium xanthellatum</i> Galea, 2013	–	–	–	X	–	–	–	–	–	–	–	–			

A = Arctic; TNA = Temperate Northern Atlantic; TNP = Temperate Northern Pacific; TAtl = Tropical Atlantic; WIP = Western Indo-Pacific; CIP = Central Indo-Pacific; EIP = Eastern Indo-Pacific; TEP = Tropical Eastern Pacific; TSAm = Temperate South America; TSAf = Temperate Southern Africa; TA = Temperate Australasia; SO = Southern Ocean. – (absent); X (present); M (recorded only over 54 years ago); M* (missing in all realms where the species was present).

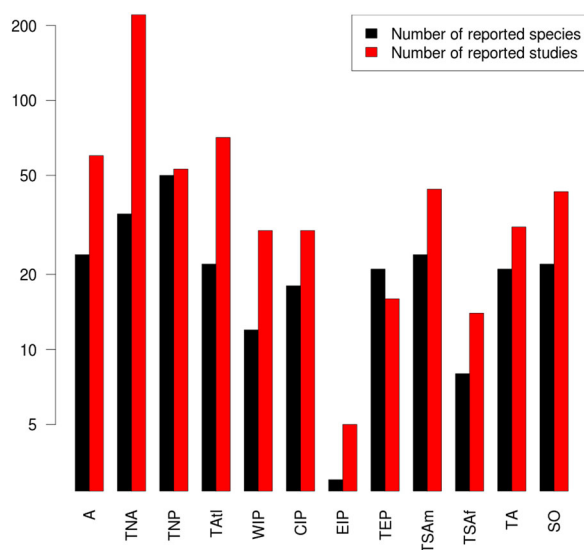


Figure 2. Number of currently valid *Halcium* species (black) and number of articles that include the genus *Halcium* from 1815 to 2014 (red) for each marine realm (*sensu* Spalding et al. 2007) (for abbreviations of the realms see Table I).

The first studies on *Halcium* species in the Arctic were carried out at the end of the 1800s (Von Lorenz 1886, Barents Sea; Holm 1889; Hartlaub 1899, West Greenland Shelf), followed by Broch (1905, White Sea), Jäderholm (1908, Siberian Sea), Kramp (1911, North-east Greenland), Linko (1911, Arctic Ocean), and in recent decades by Stepanjants (1989, Eurasian Arctic Seas), Ronowicz & Schuchert (2007, Spitsbergen), and Ronowicz et al. (2013, Svalbard).

In the Southern Ocean realm a few expeditions, conducted in the 1900–1910s, were milestones for the knowledge of the hydrozoan fauna of this area (Jäderholm 1905; Hickson & Gravely 1907; Vanhöffen 1910). More recently, these have been followed by zoogeographic and taxonomic revision papers of the Antarctic species (Peña Cantero & Carrascosa 1999; Peña

Cantero 2006, 2010, 2014; Watson 2008; Peña Cantero et al. 2013).

The species accumulation curve shows that about six new species per decade have been described and, therefore, the asymptotic number of species is far from being reached (Figure 3). Studies on *Halcium* species have shown several temporal discontinuities, mainly linked to world wars (Figure 3).

The widest geographic distributions are found for the species *Halcium beanii* and *H. delicatum* Coughtrey, 1876 (Table I), both considered as cosmopolitan (see also Medel & Vervoort 2000; Peña Cantero & García Carrascosa 2002; Bouillon et al. 2004; Schuchert 2005). On the other hand, large species such as *Halcium halecinum* and *H. labrosum* are regressing in temperate areas, e.g. the Mediterranean Sea, and are restricted to temperate-cold ecoregions (Table I) (see also Naumov 1960, 1969; Calder 1970; Stepanjants 1989; Bouillon et al. 2004). Small species, such as *Halcium dyssymetrum* Billard, 1929, *H. lightbourni* Calder, 1991, *H. pusillum* (M. Sars, 1857), *H. spatulum* Watson, 2000 and *H. tenellum* Hincks, 1861 are mostly recorded in warm-temperate ecoregions (Table I) (see also Vervoort 1959; Leloup 1960; Park 1990, 1993; Calder 1991a, 1991b, 2000; Hirohito 1995).

To restrict our analysis to *Halcium* responses to recent climate changes, we focused further analysis on recent studies from 1960 to 2014 (878 records).

It is expected that more intensive research will lead to a better appreciation of biodiversity, yielding increasingly higher species numbers approaching the actual species pool of a given region. Together with this expectation, we observed that species numbers were significantly increasing as the number of studies increased (Figure 4). Undersampling in some ecoregions such as the Tropical Eastern Pacific (Fraser 1938, 1939, 1946,

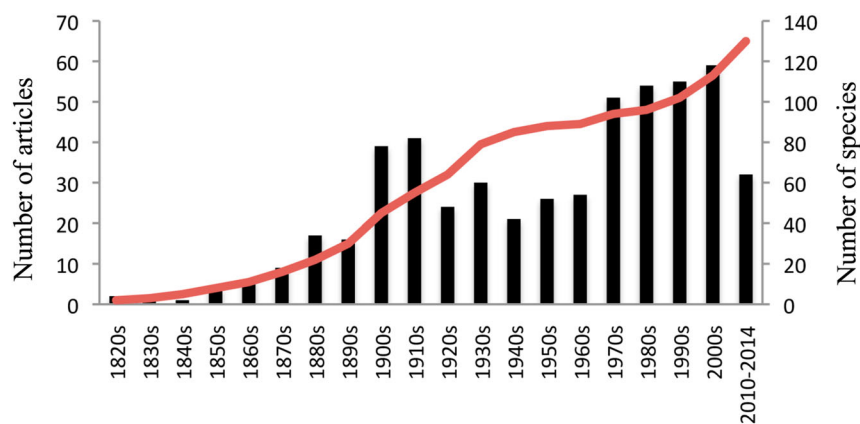


Figure 3. Cumulative number of species described from 1815 to 2014 and number of articles that include the genus *Halcium* since 1815, by decade. The line indicates the cumulative number of species and the bars indicate the number of articles.

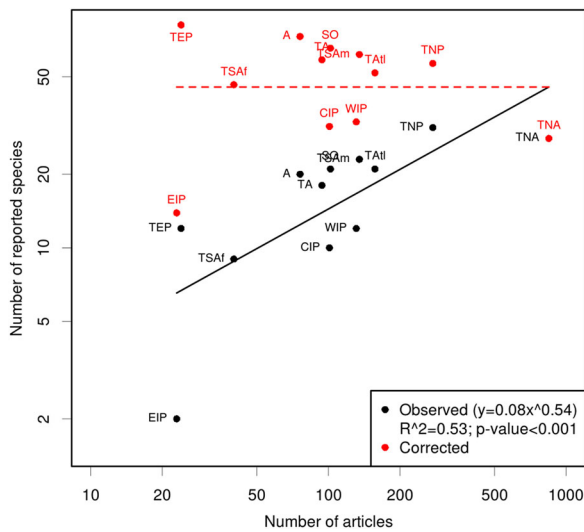


Figure 4. Relationship between number of faunal articles about Hydrozoa (from 1960 to 2014) and number of reported *Halecium* species (black) for each marine realm. Detrended values (i.e. if all the realms were sampled as much as the Temperate Northern Atlantic, red) have been used for further analysis (see Figures 5 and 6).

1948; Arai 1977), the Eastern Indo-Pacific and Temperate Southern Africa most likely led to strongly underestimated species numbers in these areas (Table II). Before proceeding with further analysis, we attempted to remove this bias from the dataset as explained below.

In the two most investigated realms (Temperate North Atlantic and Temperate North Pacific), the number of species detected in the period 1960–1984 is 81% and 77% respectively of the species detected for the whole period considered (1960–2014). In the period 1985–2014, in fact, the number of studies was nearly identical to that of the first period but it yielded an increase of species numbers of just 19% in the Atlantic and 23% in the Pacific (Table II).

Table II. Numbers of faunal articles about Hydrozoa (Articles), observed species number (Observed) and expected species number corrected for the heterogeneity in number of articles across realms (Corrected) in the following time intervals: overall (1960–2014), 1960–1984, 1985–2014.

Realm	Overall			1960–1984			1985–2014		
	Articles	Observed	Corrected	Articles	Observed	Corrected	Articles	Observed	Corrected
Arctic	76	19	72	44	18	68	32	11	46
Temperate Northern Pacific	275	30	56	122	23	43	153	16	30
Temperate Northern Atlantic	846	27	27	522	22	22	324	23	23
Tropical Eastern Pacific	24	11	80	9	7	53	15	6	47
Tropical Atlantic	157	20	51	63	7	19	94	18	46
Western Indo-Pacific	131	11	32	86	11	32	45	3	10
Central Indo-Pacific	101	9	30	43	4	15	58	9	30
Eastern Indo-Pacific	23	1	13	14	1	13	9	0	0
Temperate Southern Africa	40	8	45	27	8	45	13	3	20
Temperate Australasia	94	17	58	53	5	19	41	15	51
Temperate South America	135	22	61	52	5	15	83	22	61
Southern Ocean	102	20	64	40	9	30	62	18	58

The sum of the observed species in the two time intervals (1960–1984, 1985–2014) is higher than the total number of the observed species in the overall time period (1960–2014) due to the turnover of the species.

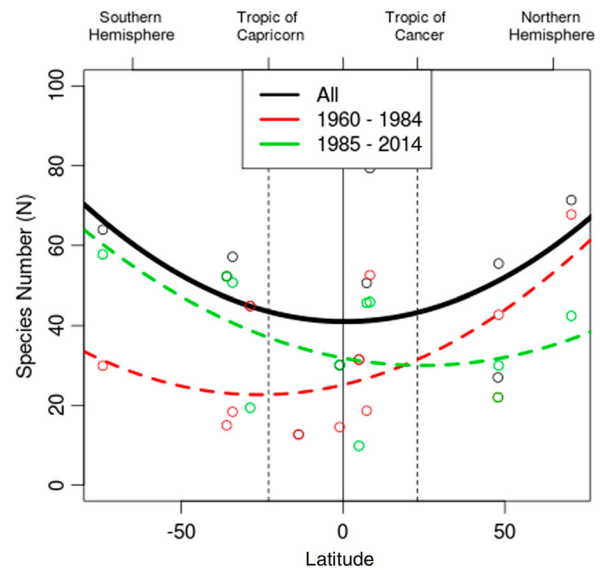


Figure 5. Relationships between the marine realms' centroid latitude and the study-effort detrended number of reported *Halecium* species, for three time intervals: from 1960 to 2014 (black), from 1960 to 1984 (red) and from 1985 to 2014 (green).

The global trend between number of detected species and number of studies (black items in Figure 4) can be used to correct the number of reported species with respect to the performed research effort, i.e. to represent (with some approximation) the global distribution of *Halecium* richness as if all realms were investigated as much in the Temperate North Atlantic (red items in Figure 4).

From the analysis of the corrected values, it appears even more clearly that the genus *Halecium* has a higher diversity at high latitudes, while it is less diverse in tropical regions (Figures 5 and 6; Table II). We did not detect significant differences in the distribution of *Halecium* species before and after the year 1985, either as absolute values or as latitudinal distribution

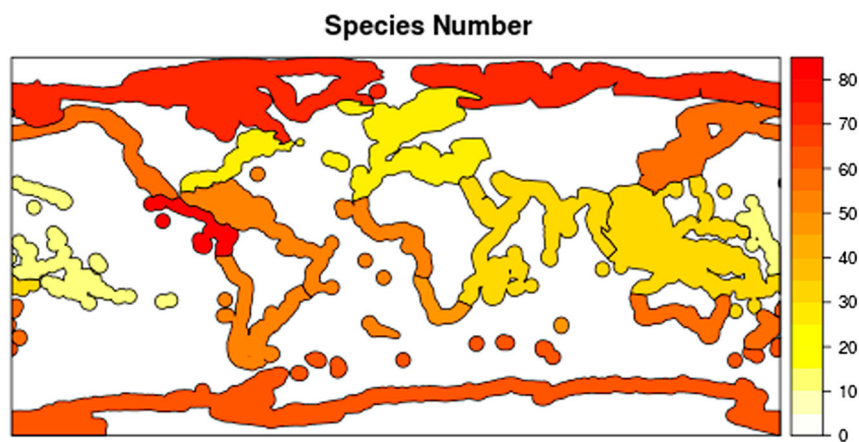


Figure 6. Global distribution of study-effort (as articles number) detrended number of reported *Halecium* species.

Table III. For each realm, number of extinct (i.e. recorded during 1960–1984 and not recorded during 1985–2014) and newly found (i.e. recorded during 1985–2014 and not recorded during 1960–1984) species, including the absolute (Delta Articles) and relative (Delta Articles %) differences in published articles between the two time periods (e.g. number of articles in the period 1985–2014 minus/ratio number of articles in the period 1960–1984).

Realms	Extinct	New found	Delta articles	Delta articles %
Arctic	7	1	–12	–27
Temperate Northern Pacific	14	7	31	25
Temperate Northern Atlantic	4	5	–198	–38
Tropical Eastern Pacific	5	4	6	67
Tropical Atlantic	2	13	31	49
Western Indo-Pacific	8	0	–41	–48
Central Indo-Pacific	0	5	15	35
Eastern Indo-Pacific	1	0	–5	–36
Temperate Southern Africa	5	0	–14	–52
Temperate Australasia	2	12	–12	–23
Temperate South America	0	17	31	60
Southern Ocean	2	11	22	55

(Figure 5; Table II), or in terms of species turnover across time periods (Table III). However, comparing species recorded in the last 54 years vs. older records, we observed higher putative extinction rates (*sensu* Gravili et al. 2015a) in the realms characterized by cold-temperate waters (73% of the missing species, 27% of the total) rather than in the tropical realms (27% of missing species, 10% of the total) (Table I).

Discussion

Species lists and distribution records are the starting point for both the study and the management of biodiversity.

The current distributions of marine animals are the result of historical aspects that must be matched with recent environmental features. Today, the combination of both human impacts and global change are causing a rapid alteration of biodiversity, affecting species' distributions with population and species loss (Boero & Gravili 2013; Templado 2014), specifically including hydrozoans (Benović et al. 2000; Benović & Lučić 2003; Boero & Gravili 2013; Gravili & Boero 2013). Anthropogenic-induced global warming can play a major role in 'shaping' the distribution of organisms (Parmesan 1996; Hughes 2000; Laffoley & Baxter 2016), although it is difficult to distinguish between the impact of warming and the impact of non-climatic factors, or simple natural variability. Clear evidence from long-term monitoring studies suggests that the climate of recent decades is anomalous when compared with past climate alterations, and species are expected to move towards higher latitudes in response to a shift in isotherms (Hughes 2000). Besides escaping by moving towards higher latitudes, organisms that live near the surface shift to deeper levels to escape from too warm waters during extreme temperature rises (Rivetti et al. 2014). Several studies showed the responses of marine life to climate change across ocean regions, recording changes in distribution, demography, abundance and phenology of marine species (see Walther et al. 2002; Perry et al. 2005; Parmesan 2006; Rijnsdorp et al. 2009; Poloczanska et al. 2016). Studies encompassing the entire range of a species or a genus are scant and focused, for example, on mammals (Beever et al. 2003), amphibians (Pounds et al. 1999, 2006) and butterflies (Parmesan 1996; Parmesan et al. 1999). The scarcity of whole-range studies probably derives from the difficulties of recording distribution data on widely distributed taxa (Parmesan 2006). In the case of *Halecium* spp., due to

lack of information, a possible reaction to global warming with alteration of depth ranges is mostly unknown, since most records are based on single observations and did not consider changes in depth distribution over time.

The hypothesis that the genus *Halecium* can be used as a sentinel taxon (a form of health indicator taxon that serves as a non-human proxy for ecosystem health – see Caro & O’Doherty 1999; Tabor & Aguirre 2004) of global warming is supported by the studies carried out in the Mediterranean Sea (Boero & Fresi 1986; Puce et al. 2009; Gravili et al. 2015b) (marked preference for temperate and cold waters, not being well adapted to tropical conditions) and by the apparent disappearance of species of cold-water affinity worldwide.

The clear trend observed in the Mediterranean Sea was supported by the biogeographic affinity of the species not recorded in the last 54 years, but was not clearly detected worldwide by our analysis of the distributions of the species that were actually recorded. The available data, in fact, show that the overall species richness of *Halecium* has not changed along the latitudinal gradient during recent decades, even though species composition has changed at temperate-tropical latitudes in both hemispheres with large species of *Halecium* that are regressing in temperate areas and are restricted to temperate-cold ecoregions, whereas small *Halecium* species are mostly recorded in warm-temperate ecoregions.

In our analysis we compensated the global heterogeneity in sampling effort by correcting the number of reported species per realm with respect to the number of published studies, but we were still not able to detect statistically significant distributional shifts on a global scale. We have to conclude, therefore, that the available data, while it represents a step ahead in organizing the existing knowledge on global *Halecium* distribution, does not fulfil the requirements to test the hypothesis that global *Halecium* distributions show responses (i.e. from 1985 onwards) to global warming as observed in the Mediterranean Sea. However, as partial confirmation of this hypothesis, we observed higher rates of putative extinction in the temperate, Arctic and sub-Arctic realms expanding the time-span of our analysis to the last 54 years.

The analysis of the available literature, thus, only partly supports the value of what has been observed in the Mediterranean Sea (i.e. large *Halecium* species of cold-water affinity are regressing at intermediate latitude) compared with the rest of the world oceans. According to Puce et al. (2009), the large *Halecium* species in the Mediterranean Sea (*Halecium beanii*,

H. halecinum and *H. labrosum*) are regressing as compared with smaller ones (*Halecium petrosom* Stechow, 1919, *H. pusillum* and *H. tenellum*). Moreover, the discrepancy between the thoroughly studied Mediterranean fauna and the rest of the world might be due to insufficient sampling efforts in several areas. In fact, the available data on the distribution of *Halecium* species were not collected to test this hypothesis according to a well-planned sampling design and in most cases, were collected occasionally, during expeditions, without thought for seasonality and long-term observation, as Boero & Fresi (1986) and Puce et al. (2009) did.

The possibility that *Halecium* species are sentinels of global warming should be taken into account in new studies, especially at the margins of their distribution ranges worldwide. For the moment, however, the sentinel role is only partly valid, due to the Mediterranean Sea observation and the putative extinction of mostly cold-temperate affinity species. Some large-size *Halecium* species can be considered habitat formers because of their ability to create wide marine forests, maintaining and modifying habitats, and providing food and refuge for several other associated organisms (Piraino et al. 2002; Cerrano et al. 2006; Fraschetti et al. 2008; Di Camillo et al. 2013). The disappearance of these habitat formers, therefore, might adversely affect the spatial complexity and interspecific interactions that determine the composition of biodiversity (Di Camillo et al. 2013).

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