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Larger scyphozoan species dwelling in temperate, shallow waters show higher blooming potential

Alfredo Fernández-Alías [*], Concepción Marcos, Angel Pérez-Ruzafa

Department of Ecology and Hydrology and Regional Campus of International Excellence "Mare Nostrum", University of Murcia, 30100, Spain

A B S T R A C T

142 scientific publications have been reviewed on the characteristics of the scyphozoans with respect to their ability to develop blooms and the most significant environmental characteristics that determine them. Special attention was paid to depth, temperature, salinity, chlorophyll concentration, and the habitat of the 39 registered blooming genera. After the review, we find that over the past decades, the number of scyphozoan blooming-species is higher than previously recorded, increasing from circa 14% to 25% of the class.

Species that inhabit depths less than 27.1 m are prone to produce blooms, particularly in semienclosed areas with low rates of water renewal and high thermal amplitudes. Temperature appears as the main environmental factor controlling blooms, but food availability is essential to sustain the proliferations. Interspecies variability in the response to environmental factors observed in this work suggest that bloom predictive models should be constructed species-habitat-specific.

1. Introduction

There is a widespread perception of an increase in the abundance of gelatinous plankton in our oceans (Arai, 2001; Brotz et al., 2012). Many of these species undergo seasonal blooms as part of their life cycle, where they are known to dominate the water column (Gershwin, 2016; Frolova and Miglietta, 2020). When blooms occur within inshore areas, they are conspicuous and cause a number of socioeconomic impacts to coastal tourism, fisheries, aquaculture or can disrupt the operations of coastal power plants (Richardson et al., 2009; Purcell et al., 2013). The negative effect of these blooms generally overwhelms the benefits obtained from them such as keeping water quality in eutrophication processes (Pérez-Ruzafa et al., 2002) or serving as food (Omori and Nakano, 2001).

The term 'jellyfish' does not have a formal definition (Brotz et al., 2012) and usually refers to gelatinous zooplankton that include the medusa-phase of specimens belonging to the phylum Cnidaria (Classes Cubozoa, Hydrozoa, Scyphozoa and Staurozoa) and some other planktonic species of the phyla Ctenophora or Chordata (Hamner and Dawson, 2009; Richardson et al., 2009; Brotz et al., 2012; Purcell et al., 2012). However, it exists a deep genetic divergence within the gelatinous plankton (Khalturin et al., 2019) and its massive occurrences are not randomly distributed within the phylum Cnidaria but concentrate mainly on those species commonly considered "true jellyfish" (class Scyphozoa) which have a metagenic life history (Hamner and Dawson, 2009). Through this review we use the term jellyfish to refer only the class Scyphozoa.

Trends that indicate an increase in jellyfish blooms have often been linked to phenomena such as climate change or anthropogenic stress: eutrophication, overfishing, species translocations or habitat modifications (Arai, 2001; Richardson et al., 2009; Brotz et al., 2012; Purcell et al., 2013). However, these appraisals could have been overamplified or taken beyond the evidence (Sanz-Martín et al., 2016; Pitt et al., 2018), being the mechanism behind the boom-and-bust jellyfish cycles and their interannual and spatial variability a topic that still needs much study. In line with the ongoing debate, it has been suggested the existence of decadal cycles affecting jellyfish abundances (Condon et al., 2013) and conditioning the relationships found in correlative studies (Pitt et al., 2018).

Moreover, many general assumptions built for the scyphozoan class are mainly based in the *Aurelia* genus (Pitt et al., 2018). These assumptions could be misleading given that different responses to environmental factors have been recorded when analyzing more than one species (Vanwalraven et al., 2015; Fernández-Alías et al., 2020). For the whole class, the differential response to environmental factors, in light of the broad physiological and ecological diversity existing for the class

Scyphozoa (Hamner and Dawson, 2009), remains unstudied.

Previous studies on the class Scyphozoa used the detection of a species bloom as a general indicator of its blooming capability and estimated the percentage of species capable of blooming ('blooming-species') to be approximately 14% of the entire class (Hamner and Dawson, 2009) without attempting to analyze the differences between blooming and non-blooming species. In addition, it should be noted that the number of papers including the term "jellyfish bloom" have increased in recent years in a very significant way (Pitt et al., 2018) and data have to be revisited. Thereby, the aims of this review are i) to update the 'blooming-species' list of the Scyphozoa class, ii) to update and analyze the known temperature frame and habitat characteristics of blooming species, and iii) to perform an initial species-specific analysis outlining differences between blooming and non-blooming species.

2. Material and methods

2.1. Blooming species list of the Scyphozoa class and bloom driving forces

The taxonomic classification for the present revision follows the current accepted families, genera and species recorded in the World Register of Marine Species (WORMS; http://www.marinespecies.org/).

For the bibliographic review, the 'Preferred Reporting Items for Systematic reviews and Meta-Analyses' (PRISMA) protocol (Moher et al., 2009) was adapted. All the Scyphozoa genera recorded in WORMS were searched individually in the categories 'Abstract', 'Keyword' and 'Title' in Scopus (www.scopus.com/) and 'Topic' in Web of Science (WoS; www.webofknowledge.com/) databases. Currently non accepted genera that are now included in an accepted one were also searched. No filters were applied in terms of citation or antiquity of the papers reviewed, and the search was conducted until December 2020. In this first step, a total of 5305 references were obtained in Scopus and 6971 in WoS. Our review tried to identify all the scyphozoan blooming species, the temperature and habitat characteristics in which blooming species dwell and to outline differences between the blooming and non-blooming groups. Thus, in a second step, duplicates were removed and abstracts selected if any of the following topics, closely related to our objectives, were discussed on them: "life history", "ecology", "commercial importance", "bloom", "human activity", "population dynamic" or "climate change". This second selection resulted in a total of 368 articles.

Works being species checklists from a given area or biotechnological applications from jellyfish molecules were excluded from this selection. After the removal of those papers that did not match with the objectives aimed in the review, the final selection for the full text revision and the statistical analyses comprised a total of 142 articles. Further details on the search are provided in Table S1.

Through this review, different events of high abundance and density of jellyfish are discussed. Following the recommendations from Graham et al. (2001) and Hamner and Dawson (2009), we use aggregation, accumulation or 'apparent-bloom' to refer to a high density of jellyfish produced by wind or tides. They also refer to entrapments in enclosed areas like harbours. Species that are present throughout the year in high but similar abundances can also be referred to by these terms since no proliferation is recorded. The term bloom is used to describe a sudden outbreak of the population when, from a total absence or little presence of the adult specimens, a blooming event leads to a high density of the same in the water column. Finally, swarm refers to a concentration of individuals not directed by the wind or currents, but by their own swimming capability. This swarm behavior may be related to reproductive strategies or defense strategies against possible predators.

The analysis of the articles was done looking for indications of aggregation, blooming or swarming events performed by the species, driving forces directing the events, and evidences given to confirm these driving forces. As the jellyfish bloom records have been collected for more than a century, we considered that the species lacking any report that point them as blooming can be considered as "non-blooming species". However, it cannot be ruled out that environmental changes might lead to a future bloom of some species that do not present this behavior right now. Following Hamner and Dawson (2009), species that are regularly fished and commercially distributed are also considered as blooming species. We are also aware that some species indicated as 'non-blooming' could be blooming, but that different past or present problems with their classification may generate a certain degree of doubt (as is the case of *Rhizostoma luteum* [Quoy & Gaymard, 1827] which has been frequently classified as *Rhizostoma pulmo* [Macri, 1778] in the Mediterranean Sea (Kienberger and Prieto, 2018)). A matrix with the taxonomical classification, list of the blooming species and their percentage within the different taxonomic levels has been constructed.

The driving forces, understood as the factor pointed as 'promoter' of the bloom, that direct the blooming events, were also recorded. Following Pitt et al. (2018), we considered as 'providers of evidence' only the studies in which a model is elaborated, a specific variable is laboratory tested as significative, or in which field measurements show a significative correlation. A table with the species, blooming, aggregating and/or swarming ability and the supporting evidences has been constructed (Table S3). A solar diagram indicating the percentage of papers that name a blooming cause versus the percentage that provide evidences for these causes has been elaborated.

2.2. Blooming species temperature frame and habitat characteristics

For blooming species, the water temperature ranges in which the species inhabit have been retrieved from the original papers when the information was available or from www.seatemperature.org when that information was not provided (see Table S4).

For a more detailed study of the temperature frame of the different stages (medusa, planula, polyp, strobila and ephyra) we selected six scyphozoan species, four of them with summer presence of the adult phase (*Aurelia* sp. 1, *Cotylorhiza tuberculata* [Macri, 1778], *Nemopilema nomurai* Kishinouye, 1922 and *Rhopilema esculentum* Kishinouye, 1891) and two with a year-round presence (*Rhizostoma pulmo* and *Cassiopea xamachana* Bigelow, 1892). The temperature frame for each stage of the selected species was retrieved from the original publications (Table S5).

We have also registered the habitats in which blooms occurred attending to the original papers, and classifying them as semienclosed (coastal lagoons, marine lakes, marshes, harbours, semienclosed bays, bights, fjords and estuaries) when there existed restrictions to the water exchange, open coastal (archipelagos, straits, open coastal areas) when the bloom occurred near a shore without impediment for water exchange, and offshore (offshore and deep-sea) when the bloom was detected far from the coast.

2.3. Blooming against non-blooming species

A matrix for statistical analysis was constructed using 13 variables: maximum length, temperature (maximum, minimum and main, here understood as the value with more recorded detections), salinity (max, min and main), depth (max, min and main) and chlorophyll *a* (max, min and mean); and 2 factors: 'Order' (3 levels, Coronatae, Semaeostomeae and Rhizostomeae) and 'Blooming ability' (2 levels, Blooming and Non-Blooming). Maximum length was retrieved from www.sealifebase.ca. Maximum, minimum and main values for temperature, salinity and depth in which the species can inhabit were retrieved from www.obis.org. Data on sea surface chlorophyll *a* were retrieved from www.earthobservatory.nasa.gov for the decade 2010–2019 for the registered bloom locations for each species (Fig. 1, Table S2). The minimum, maximum and mean values of chlorophyll *a* during this period were also calculated for the distribution area of each species indicated in Table S2. Orders were retrieved from the taxonomical classification available in WORMS while the Blooming ability was obtained from the revision. The matrix was analyzed at two different levels, using genera as samples and
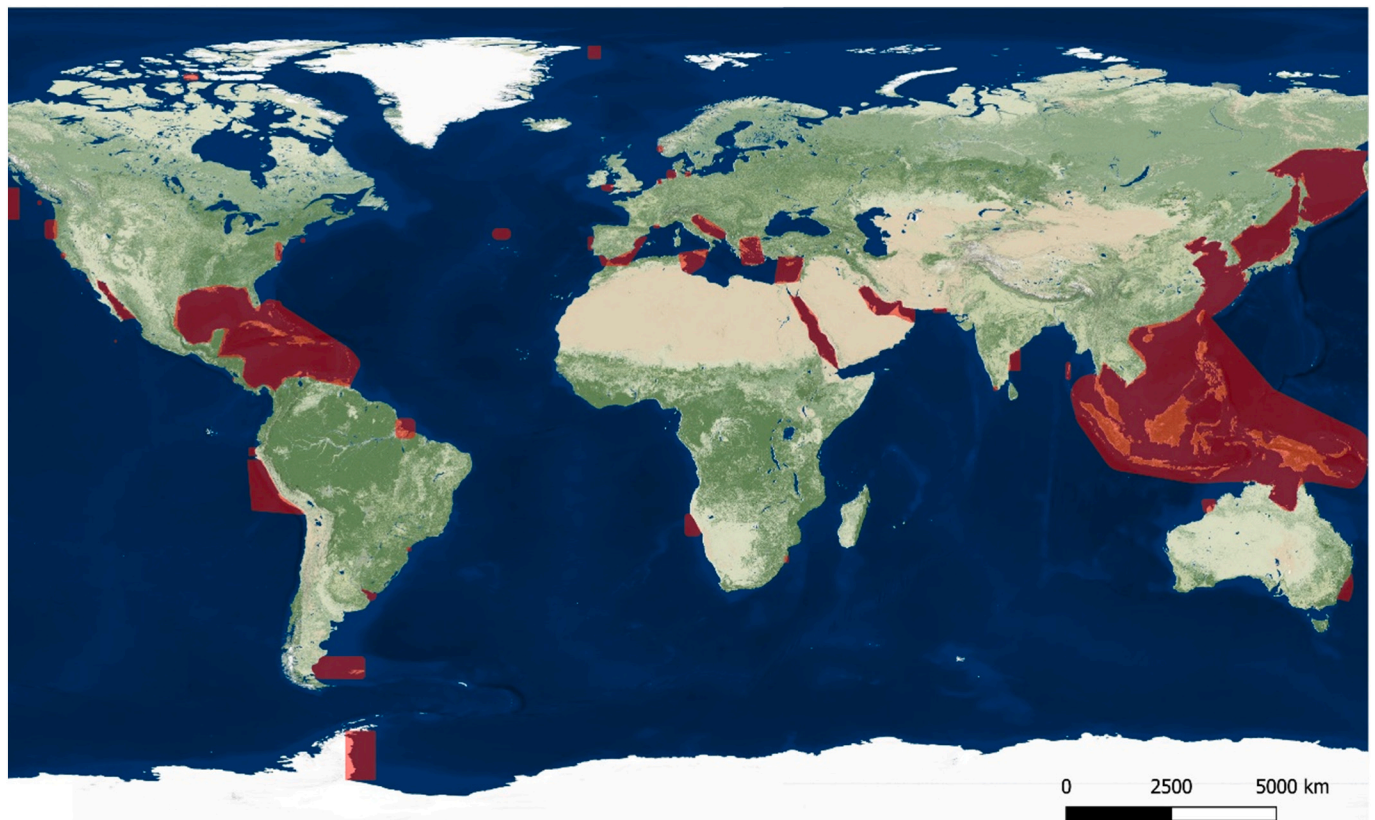
Fig. 1. Blooming locations for the class Scyphozoa recorded through the review process and used for the calculation of maximum, minimum and mean sea surface chlorophyll *a* through the 2010–2019 decade. Details of exact coordinates and species for every spot are provided in Table S2.

using species as samples. All the analysis were done in PRIMER 7 + PERMANOVA (Anderson et al., 2008).

Some of these studied variables can also represent trends or changes due to anthropic pressures, such as global warming or changes in the trophic state of marine ecosystems.

2.3.1. Genera as samples

To analyze differences between blooming and non-blooming groups in the three orders of Scyphozoa we have constructed a matrix at genera level. The values for the 13 variables analyzed were calculated as the average of the species values within each genus. We distinguish between three types of genera, those in which all the species with available information do bloom (16 genera), those without blooming species (16 genera) and those with blooming and non-blooming species (6 genera). Those genera which include blooming and non-blooming species were divided into two different samples (*e.g. Pelagia*-blooming and *Pelagia*-non-blooming). Then, a total of 44 samples (38 genera) were included for the analysis.

To visually represent the differences between the blooming and non-blooming groups as well as between the three orders of Scyphozoa, a Principal Component Analysis (PCA) has been carried out on the genera matrix after a $\log(x + 1)$ transformation has been carried out.

To test if there existed significant differences between blooming and non-blooming groups, between orders, and between the cross of both factors, a permutational multivariate analysis of variance (PERMANOVA) (Order × Bloom; 9999 permutations and Monte Carlo test) on a Euclidean resemblance matrix after a $\log(x + 1)$ transformation has been carried out.

To test if there exist significant differences between the blooming and non-blooming groups within an order, a pairwise comparison for the factor 'Bloom' on the previous PERMANOVA has been carried out (Bloom, 9999 permutations and Monte Carlo test). The contribution (%)

of each variable to the differences between the blooming and non-blooming genera for each order have been obtained through a SIMPER analysis.

2.3.2. Species as samples

To analyze differences between blooming and non-blooming groups in the three orders of Scyphozoa we have constructed a matrix at species level. When we use species as samples, the variables considered were maximum length and maximum, minimum and main temperature for the 78 analyzed species.

To test if there existed significant differences between blooming and non-blooming groups, between orders, and between the cross of both factors, a permutational multivariate analysis of variance (PERMANOVA) (Order × Bloom; 9999 permutations and Monte Carlo test) on a Euclidean resemblance matrix after a square root transformation has been carried out.

To test if there exist significant differences between the blooming and non-blooming groups within an order, a pairwise comparison for the factor 'Bloom' on the previous PERMANOVA has been carried out (Bloom, 9999 permutations and Monte Carlo test). The contribution (%) of each variable to the differences between the blooming and non-blooming species for each order have been obtained through a SIMPER analysis.

3. Results

3.1. Jellyfish blooming species and factors directing the blooms

This work provides an updated list of the 'blooming-species' from the Scyphozoa class (Table 1). It constitutes the first list published at species level and suppose an increase in the recognized percentage of the species capable of blooming within the Scyphozoa from circa 14% of the last

Table 1

Taxonomic classification of the Class Scyphozoa. Number of species, number of blooming species, list of blooming species and percentage of blooming species for each genus, family, order and the whole class and reference(s).

	Order	Family	Genus	Total number of species	Blooming species (number)	Percentage of blooming species within the total of each taxon	Blooming species (names)	Reference (s)
Class Scyphozoa				220	55	25%		
Subclass								
Coronamedusae	Coronatae			56	4	7.14%		
		Atollidae	*Atolla*	10	0	0%		1–3
		Atorellidae	*Atorella*	6	0	0%		4
		Linuchidae		4	2	50%		
			Linantha	1	0	0%		No article found
			Linuche	3	2	66.67%	*Linuche unguiculata* (Swartz, 1788) *Linuche aquila* (Haeckel, 1880)	5–8
		Nausithoidae		26	1	3.85%		
			Nausithoe	22	1	4.55%	*Nausithoe punctata* Kölliker, 1853	9,10
			Palephyra	3	0	0%		No article found
			Thecoscyphus	1	0	0%		11
		Periphyllidae	*Paraphyllina*	3	0	0%		9
		Periphyllidae		7	1	14.29%		
			Nauphanthopsis	1	0	0%		No article found
			Pericolpa	3	0	0%		No article found
			Periphylla	1	1	100%	*Periphylla periphylla* (Péron & Lesueur, 1810)	9, 12–16
			Peryphyllosis	2	0	0%		9
Discomedusae				164	50	30.49%		
	Semaeostomeae			76	22	28.94%		
		Cyaneidae		21	3	14.29%		
			Cyanea	17	3	17.65%	*Cyanea nozakii* Kishinouye, 1891 *Cyanea capillata* (Linnaeus, 1758) *Cyanea lamarckii* Perón & Lesueur, 1810	17–20
			Desmonema	4	0	0%		3
		Drymonematidae	*Drymonema*	4	1	25%	*Drymonema dalmatinum* Haeckel, 1880	21,22
		Pelagiidae		25	8	32%		
			Chrysaora	17	6	35.29%	*Chrysaora chesapeakei* (Papenfuss, 1936) *Chrysaora fuscescens* Brandt, 1835 *Chrysaora quinquecirrha* (Desor, 1848) *Chrysaora hysoscella* (Linnaeus, 1767) *Chrysaora melanaster* Brandt, 1835 *Chrysaora ploclamia* (Lesson, 1830)	3, 23–35
			Mawia	1	1	100%	*Mawia benovici* (Piraino et al., 2014)	36, 37
			Pelagia	5	1	20%	*Pelagia noctiluca* (Forsskål, 1775)	38–44
			Sanderia	2	0	0%		No article found
		Phacellophoridae	*Phacellophora*	1	0	0%		45, 46
		Ulmaridae		25	10	40%		
			*Aurelia**	9	7–9	100%	*Aurelia aurita* L. (sensu stricto) (Linnaeus, 1758) *Aurelia coerulea* von Lendenfeld, 1884	47–64

Table 1 (*continued*)

Order	Family	Genus	Total number of species	Blooming species (number)	Percentage of blooming species within the total of each taxon	Blooming species (names)	Reference (s)
						Aurelia solida Browne, 1905 *Aurelia* sp. 1 *Aurelia* sp. 8 *Aurelia* sp. 9 *Aurelia* sp. new	
		Deepstaria	2	0	0%		65
		Aurosa	1	0	0%		No article found
		Diplulmaris	2	0	0%		66
		Discomedusa	2	1	50%	*Discomedusa lobata* Claus, 1877	35, 67
		Floresca	1	0	0%		No article found
		Parumbrosa	1	0	0%		68
		Poralia	1	0	0%		69
		Stellamedusa	1	0	0%		70, 71
		Sthenonia	1	0	0%		No article found
		Stygiomedusa	1	0	0%		72, 73
		Tiburonia	1	0	0%		4, 74
		Ulmaris	2	0	0%		No article found
Rhizostomeae			88	29	32.95%		
	Cassiopeidae	*Cassiopea***	9	2	22.22%	*Cassiopea andromeda* (Forskål, 1775) *Cassiopea xamachana* Bigelow, 1892	75–80
	Catostylidae		25	9	36%		
		Acromitoides	2	0	0%		81
		Acromitus	5	1	20%	*Acromitus hardenbergi* Stiasny, 1934	82–84
		Catostylus	10	3	30%	*Catostylus mosaicus* (Quoy & Gaimard, 1824) *Catostylus perezi* Ranson, 1945 *Catostylus tagi* (Haeckel, 1869)	85–89
		Crambione	3	1	33.33%	*Crambione mastigophora* Maas, 1903	87, 90, 91
		Crambionella	4	4	100%	*Cambrionella orsisi* (Vanhöffen, 1888) *Cambrionella annandalei* Rao, 1931 *Cambrionella stuhlmanni* (Chun, 1896) *Cambrionella helmbiru* Nishikawa et al., 2015	87, 92–96
		Leptobrachia	1	0	0%		No article found
	Cepheidae		14	2	14.29%		
		Cephea	4	1	25%	*Cephea cephea* (Forskål, 1775)	97
		Cotylorhiza	4	1	25%	*Cotylorhiza tuberculata* (Macri, 1778)	98–104
		Marivagia	1	0	0%		105, 106
		Netrostoma	4	0	0%		107
		Polyrhiza	1	0	0%		No article found
	Lobonematidae		4	3	75%		
		Lobonema	1	1	100%	*Lobonema smithii* Mayer, 1910	87, 91, 108
		Lobonemoides	3	2	66.67%	*Lobonemoides gracilis* Light, 1914 *Lobomenoides*	87, 91, 109

Table 1 (*continued*)

Order	Family	Genus	Total number of species	Blooming species (number)	Percentage of blooming species within the total of each taxon	Blooming species (names)	Reference(s)
						robustus Stiasny, 1920	
	Lychnorhizidae		6	2	33.33%		
		Anomalorhiza	1	0	0%		110, 111
		Lychnorhiza	3	2	66.67%	*Lychnorhiza lucerna* Haeckel, 1880 *Lychnorhiza malayensis* Stiasny, 1920	3, 112–114
		Pseudorhiza	2	0	0%		115
	Mastigiidae		13	4	30.76%		
		*Mastigias***	8	1–3	37.5%	*Mastigias papua* (Lesson, 1830)	116–120
		Mastigietta	1	0	0%		No article found
		Phyllorhiza	3	1	33.33%	*Phyllorhiza punctata* von Lendenfeld, 1884	121, 122
		Versuriga	1	0	0%		123
	Rhizostomatidae		12	6	50%		
		Eupilema	2	0	0%		No article found
		Nemopilema	1	1	100%	*Nemopilema nomurai* Kishinouye, 1922	17, 18, 124–128
		Rhizostoma	3	2	66.66%	*Rhizostoma octopus* (Gmelin, 1791) *Rhizostoma pulmo* (Macri, 1778)	99, 101, 104, 129–133
		Rhopilema	6	3	50%	*Rhopilema esculentum* Kishinouye, 1891 *Rhopilema hispidum* (Vanhöffen, 1888) *Rhopilema nomadica* Galil et al., 1990	83, 124, 134–138
	Stomolophidae	*Stomolophus*	2	1	50%	*Stomolophus meleagris* Agassiz, 1860	139–141
	Thysanostomatidae	*Thysanostoma*	3	0	0%		142

References: 1 - Russell, 1959; 2 - Osborn et al., 2007; 3 - Schiariti et al., 2018; 4 - Gasca and Loman-Ramos, 2014; 5 - Kremer et al., 1990; 6 - Larson, 1992; 7 - Segura-Puertas et al., 2008; 8 - Guevara et al., 2017; 9 - Herring and Widder, 2004; 10 - Tseng et al., 2015; 11 - Sötje and Jarms, 2009; 12 - Fosså, 1992; 13 - Riemann et al., 2006; 14 - Sørnes et al., 2007; 15 - Ugland et al., 2014; 16 - Båmstedt et al., 2020; 17 - Dong et al., 2010; 18 - Feng et al., 2015a; 19 - Vanwalraven et al., 2015; 20 - Crawford, 2016; 21 - Larson, 1987; 22 - Williams et al., 2001; 23 - Martin et al., 1997; 24 - Masilamoni et al., 2000; 25 - Sparks et al., 2001; 26 - Brodeur et al., 2002; 27 - Lynam et al., 2006; 28 - Decker et al., 2007; 29 - Suchman et al., 2012; 30 - Marques et al., 2014; 31 - Quiñones et al., 2015; 32 - Ruzicka et al., 2016; 33 - Quiñones et al., 2018; 34 - Stone et al., 2019; 35 - Violić et al., 2019; 36 - Piraino et al., 2014; 37 - Avian et al., 2016; 38 - Zavodnik, 1987; 39 - Goy et al., 1989; 40 - Daly Yahia et al., 2010; 41 - Rosa et al., 2013; 42 - Canepa et al., 2014; 43 - Milisenda et al., 2018; 44 - Bellido et al., 2020; 45 - Il'inskii and Zavolkin, 2011; 46 - Radchenko, 2013; 47 - Möller, 1980; 48 - Hernroth and Gröndahl, 1983; 49 - Schneider and Behrends, 1994; 50 - Omori et al., 1995; 51 - Lucas, 1996; 52 - Miyake et al., 1997; 53 - Toyokawa et al., 2000; 54 - Di Camillo et al., 2010; 55 - Malej et al., 2012; 56 - Wang and Li, 2015; 57 - Wang and Sun, 2015; 58 - Wang et al., 2015; 59 - Dong et al., 2018; 60 - Chi et al., 2019; 61 - Frolova and Miglietta, 2020; 62 - Gueroun et al., 2020; 63 - Goldstein and Steiner, 2020; 64 - Marques et al., 2020; 65 - Gruber et al., 2018; 66 - Pagès, 2000; 67 - Isinibilir et al., 2015; 68 - Miyake et al., 2005; 69 - Doya et al., 2017; 70 - Raskoff and Matsumoto, 2004; 71 - Corrales-Ugalde and Morales-Ramírez, 2017; 72 - Drazen and Robison, 2004; 73 - Benfield and Graham, 2010; 74 - Matsumoto et al., 2003; 75 - Fitt and Costley, 1998; 76 - Arai, 2001; 77 - Holland et al., 2004; 78 - Bolton and Graham, 2006; 79 - Stoner et al., 2011; 80 - Deidun et al., 2018; 82 - Boco and Metillo, 2018; 82 - Hamner and Dawson, 2009; 83 - Khong et al., 2016; 84 - Syazwan et al., 2020a; 85 - Pitt and Kingsford, 2000; 86 - Pitt and Kingsford, 2003; 87 - Omori and Nakano, 2001; 88 - Waryani et al., 2015; 89 - Rodrigues et al., 2020; 90 - Keesing et al., 2016; 91 - Purcell et al., 2013; 92 - Nishikawa et al., 2015; 93 - Behera et al., 2020; 94 - Billett et al., 2006; 95 - Daryanabard and Dawson, 2008; 96 - Perissinotto et al., 2013; 97 - Cruz-Rivera and El-Regal, 2016; 98 - Kikinger, 1992; 99 - Pérez-Ruzafa et al., 2002; 100 - Prieto et al., 2010; 101 - Purcell et al., 2012; 102 - Ruiz et al., 2012; 103 - Galil et al., 2017; 104 - Fernández-Alías et al., 2020; 105 - Galil et al., 2013; 106 - Mamish and Durgham, 2016; 107 - Gul et al., 2015; 108 - Bujang and Hassan, 2017; 109 - Rizman-Idid et al., 2016; 110 - Cooke, 1984; 111 - Chuan et al., 2020; 112 - Schiariti et al., 2008; 113 - Nagata et al., 2009; 114 - Syazwan et al., 2020b; 115 - Browne et al., 2020; 116 - Hamner and Hauri, 1981; 117 - Dawson et al., 2001; 118 - Martin et al., 2006; 119 - Swift et al., 2016; 120 - De Souza and Dawson, 2018; 121 - Graham et al., 2003; 122 - Johnson et al., 2005; 123 - Sun et al., 2018; 124 - Kawahara et al., 2006; 125 - Feng et al., 2015b; 126 - Feng et al., 2018; 127 - Feng et al., 2020; 128 - Kitajima et al., 2020; 129 - Prieto et al., 2013; 130 - Kienberger and Prieto, 2018; 131 - Kienberger et al., 2018; 132 - Holst et al., 2007; 133 - Lilley et al., 2009; 134 - Dong et al., 2009; 135 - Takao and Uye, 2018; 136 - Fu et al., 2019; 137 - Sakinan, 2011; 138 - Edelist et al., 2020; 139 - Girón-Nava et al., 2015; 140 - López-Martínez et al., 2020; 141 - Banha et al., 2020; 142 - Zakai and Galil, 2001.

* Most of the literature about *Aurelia* spp. was written before the genetics of this species was solved (Scorrano et al., 2017) and therefore the data refer to *Aurelia aurita*, but, attending to the review by Lucas (2001), we do not see any reason to think that a current species of the genus Aurelia may lack the capability to bloom.

** It has been reported that *Cassiopea* spp. accumulates and increases its abundance in harbours after dredging. From literature we deduce that at least two of the species of this genus are capable of blooming.

*** *Mastigias* spp. is a special case as it undergoes continuous recruitment. However, the blooming ability within this genus should not be ruled out since very rapid recoveries have been described in the face of temperature fluctuations (Martin et al., 2006). It is considered that between 1 and 3 species can bloom since the genetics were not well understood at the time of that study.

published estimate (Hamner and Dawson, 2009) to a value of 25%. We also provide the first published table connecting each blooming species with the blooming factors it has been associated with, and the supporting evidences when they exist (Table S3).

From the 142 reviewed papers, 108 refer to blooming and 34 to non-blooming species. In the first case, eight different options were mentioned as bloom driving forces. These causes are (Fig. 2, Table S3):

- Temperature (named in 49.07% with evidences provided in 19.44% of the works). Its study has included laboratory experiments, sea temperature anomalies modelling, sea surface temperature regression analysis and literature citations.
- Food availability and overfishing (named in 21.30% and with explicit evidences in 2.78% of the publications). The study of these aspects included regressions between fish and jellyfish abundances, zooplankton and jellyfish correlations, laboratory experiments and literature citations. Those factors have been studied together as planktivorous fishes are competitors of jellyfish and complex and indirect relationships can be established between them in relation to food availability.
- Eutrophication and nutrient loads (named in 13.89% and evidences provided in 2.78% of the works) considered relations, correlations and regressions observed between upwelling, nutrient inputs, chlorophyll *a* and jellyfish as well as literature citations.
- Habitat (11.11% and 1.85%) has been considered from those papers which refer to the coastal morphology, bottom depth and water renewal rate, and, in general, water masses characteristics in which blooms occur, and relate them with jellyfish abundance.
- Invasion (9.26% and 3.70%) included those references alluding to the expansion of a species, inferences from the path undergone for the invasion and literature citations.
- Construction of submerged structures (7.41% and 0%), considered those works that provide images of polyps in underwater structures considering them as the cause of the bloom as well as those that makes inferences on the subject.
- Salinity (6.48% and 3.70%) included laboratory experiments and correlations between jellyfish distribution and salinity.
- Finally, meteorology and atmospheric indices (6.48% and 0%) included the articles that have looked for correlations or regressions between the jellyfish abundance or distribution and rainy days or atmospheric regimes.
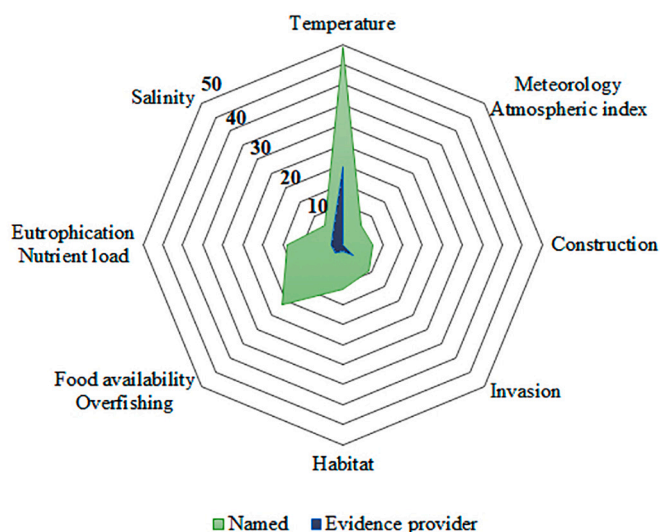

Fig. 2. Percentage of papers which name (green) or name and provide evidence (blue) for each of the eight explicative causes for the jellyfish blooms. N = 108. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

25% of the species belonging to the class Syphozoa has been detected as producing blooms. This class is divided in three orders, Coronatae, Semaeostomeae and Rhizostomeae, whose species produce blooms in 7.14%, 28.94% and 31.82%, respectively (Table 1).

Since the last revision (Hamner and Dawson, 2009), a new list of species from the genus *Linuche*, *Nausithoe*, *Cyanea*, *Mawia*, *Discomedusa*, *Cassiopea*, *Cotylorhiza*, *Mastigias* and *Lychnorhiza* have been reported to bloom (Table 1, S3).

Linuche unguiculata (Swartz, 1788) and *L. aquila* (Haeckel, 1880) were previously considered to form aggregations or 'apparent' blooms directed by currents (Larson, 1992; Hamner and Dawson, 2009), but Segura-Puertas et al. (2008) confirmed their seasonal appearance triggered by temperature confirming the formation of true blooms. A *Nausithoe punctata* Kölliker, 1853 bloom was detected in Taiwan waters after a typhoon and, although it could be argued that it could seem an 'apparent' bloom, it represented the unique event of massive appearance after studying the effect of several typhoons, indicating that we could be facing a 'true' bloom' (Tseng et al., 2015). *Cyanea nozakii* Kishinouye, 1891 blooming ability was laboratory proven (Feng et al., 2015a) while the ability of *C. capillata* (Linnaeus, 1758) and *C. lamarckii* Péron & Lesueur, 1810 was registered in a 50 years time series of daily catches (Vanwalraven et al., 2015). *Mawia benovici* (Piraino et al., 2014) was described after a bloom in North Adriatic Sea in late 2013 (Piraino et al., 2014; Avian et al., 2016). Violić et al. (2019) recorded the first known bloom of *Discomedusa lobata* Claus, 1877 in April 2014 in Southern Adriatic. *Cassiopea* spp. has been reported to produce massive appearance after its translocation to new habitats as polyps living in rocks (Bolton and Graham, 2006), being its blooming ability confirmed after the detection of 'true' blooms of *Cassiopea andromeda* (Forskål, 1775) in Maltese Islands in January 2018 (Deidun et al., 2018). Pérez-Ruzafa et al. (2002) and Fernández-Alías et al. (2020) reported seasonal blooms of *Cotylorhiza tuberculata* in a Mediterranean coastal lagoon. And, finally, *Mastigias* spp. is the most ambiguous genus to be considered as blooming since it undergoes continuous recruitment, but we opted to consider it as a blooming genus after its population disappearance and explosive recovery in Lake Palau (Dawson et al., 2001; Martin et al., 2006).

3.2. Temperature frame and habitat for blooming species

Depending on the species, medusa stages from blooming species can be present in the water column from 0 °C to 35 °C. From the blooming species recorded in Table 1, 2 inhabit cold seas (0–10 °C), 1 is temperate-cold, 14 inhabit temperate seas (10.01–25 °C), 11 are subtropical, 19 are tropical (25.01–35 °C) and 6 can survive in a temperature range from cold to tropical (Fig. 3, Table S4).

From the complete review of the biological cycles carried out in six species in particular, three different strategies can be observed regarding temperature according to the jellyfish stages (Fig. 4, Table S5). In the first one, polyps are more temperature tolerant than pelagic phases, but having a narrower temperature frame for the strobilation (Figs. 4a, c, d, f). As an example, *Aurelia* sp.1 polyp can survive from 5 to 25 °C, while the ephyra do it between 13 and 20 °C, planula between 23 and 24 °C, and medusa phase between 20 and 25 °C. The same strategy, with differences in the temperature frame, is recorded for *C. tuberculata* (polyp 14–28 °C, ephyra and strobila 20–28 °C, planula 23–24 °C and medusa 17–30 °C), *N. nomurai* (polyp 0–27.5 °C, ephyra 10–18 °C, strobila 6.4–18 °C and medusa 10–25 °C) and *R. esculentum* (polyp 10–30 °C, ephyra 16–28 °C, strobila 18–20 °C and medusa 18–28 °C). In the second strategy, adopted by *C. xamachana*, the medusa stage (13–33 °C) is the overwintering phase, while polyps, strobilation and ephyrae occur during the summer (20–33 °C) (Fig. 4b). In the last one strategy, used by *R. pulmo*, the plasticity of every stage allows the coexistence from polyps and medusae all year round (Fig. 4e; polyp and strobila 14–28 °C, ephyra 17–28 °C and medusa 13–29.4 °C).

Of the articles that refer to a jellyfish bloom, jellyfish fishery or
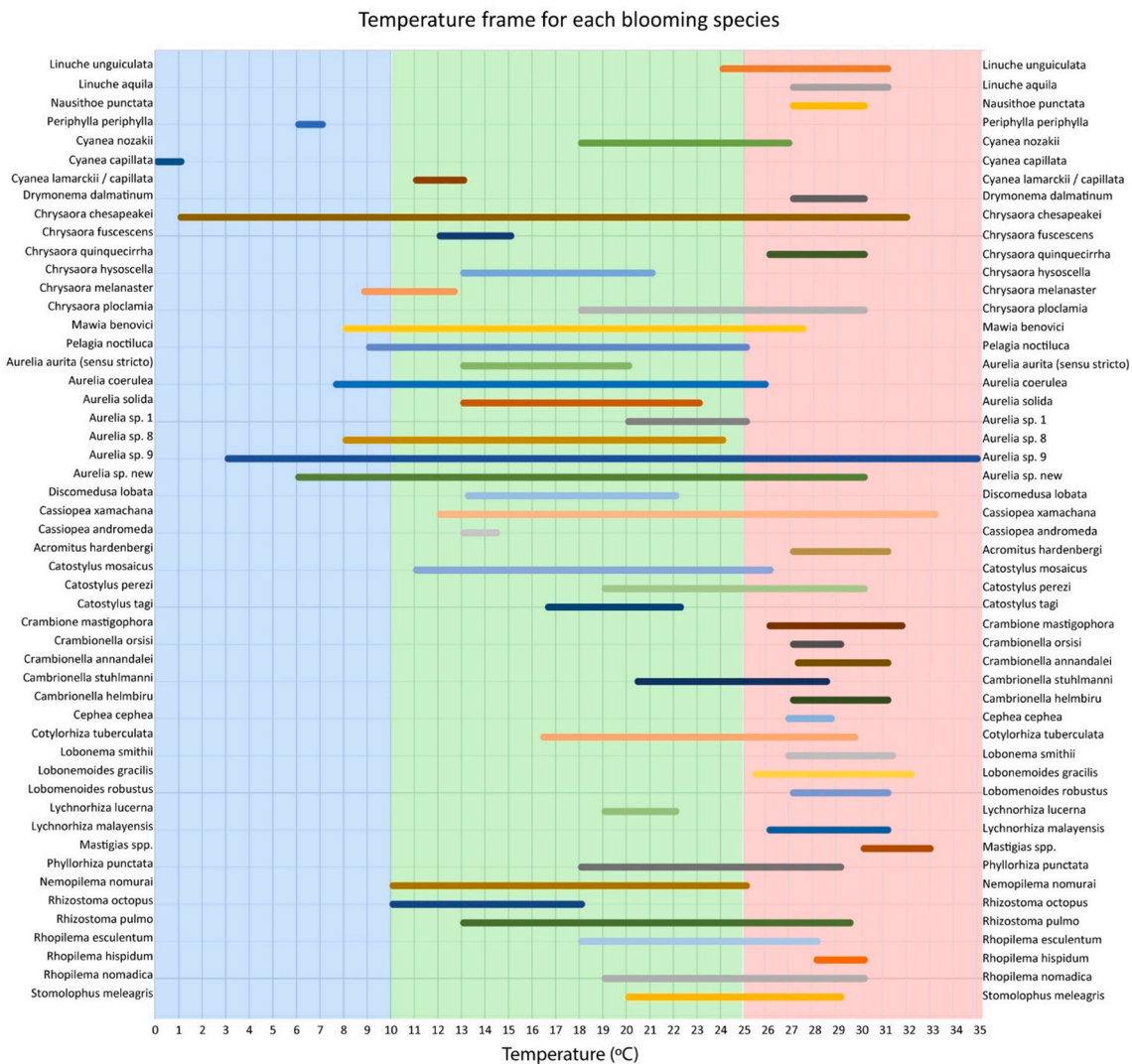
Temperature frame for each blooming species

Fig. 3. Temperature (degrees Celsius) frame in which the medusa stage from blooming species can be present in the water column. Background colours indicate the temperature frame for cold seas (light blue), temperate seas (light green) and tropical seas (light red). *Aurelia* sp. 9 and *Aurelia* sp. new temperature frames belong to the polyp stage due to the impossibility of retrieving the information for the medusa stage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

jellyfish collection of a blooming species (93 in total), we found 110 allusions to coastal zones (76 semienclosed areas and 34 open coastal areas) against 6 papers alluding to offshore environments (5 offshore and 1 deep sea) (Fig. 5).

Semienclosed areas included semienclosed bays (recorded in 30 papers), coastal lagoons (11), marine lakes (7), fjords (7), harbours (4), estuaries (12), bights (4) and marshes (1). The open coastal areas included open bays (21), islands or archipelagos (6) and straits (7). Offshore waters also included a reference to a massive deposition of jellyfish carcasses in deep sea waters (Fig. 5).

3.3. Blooming against non-blooming species

At genus level, the PERMANOVA indicated significant differences for the factor 'Order' ($p = 0.0011$) and 'Bloom' ($p = 0.0004$), but not for 'Bloom × Order' ($p = 0.4351$) (Table 2). When using species as samples, only the factor 'Order' shows significant differences ($p = 0.0007$) (Table 2).

PCA ordination in two axes is explicative for 80% of the variability. The first axis itself is explicative for 56.1% of the variation and it is directed by the maximum length of the species and the depth (Max, min

and main) acting in opposite directions, while the second axis explains an added 23.9% of the variation and is directed by the minimum and main temperature and maximum and minimum depth in which inhabit the different species (Fig. 6).

The PERMANOVAs performed for each Order also showed that there are only significant differences between blooming and non-blooming genera within orders Semaeostomeae ($p = 0.0176$) and Coronatae ($p = 0.0177$) (Table 3). SIMPER analysis showed that these differences are mainly explained by depth and temperature (80.4% and 11.37%, respectively, in Semaeostomeae, and 80.71% and 12.38% in Coronatae). In the case of Rhizostomeae, despite the absence of significant differences, SIMPER analysis reveals that blooming species live in shallower waters than non-blooming, this being in line with what was observed in the other Orders.

On the contrary, the analysis at species level only revealed significative differences within Rhizostomeae in account of the higher maximum length of its blooming species (91.29%). In the case of Coronatae and Semaeostomeae, despite the absence of significant differences, SIMPER analysis revealed that blooming species are also larger than the non-blooming ones.
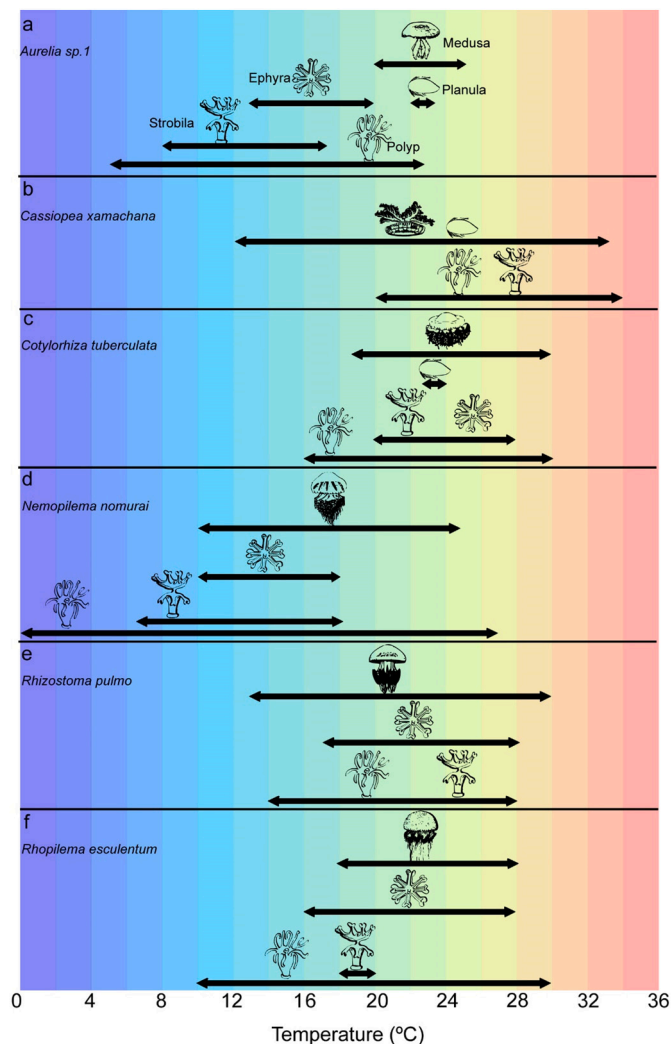
Fig. 4. Temperature (Celsius degrees) frame for the different stages of the life cycle of six scyphozoan species. a) *Aurelia* sp. 1. b) *Cassiopea xamachana*. c) *Cotylorhiza tuberculata*. d) *Nemopilema nomurai*. e) *Rhizostoma pulmo*. f) *Rhopilema esculentum*. Black arrows indicate the temperature frame for the stage above them. Two stages appear over the same arrow when the temperature frame is shared for both.

4. Discussion and conclusions

After twenty years of a growing perception that the jellyfish abundance is increasing due to natural or anthropogenic stressors, there is still a high degree of uncertainty towards this. In this sense, Pitt et al. (2018) indicated that most of the literature including the term "jellyfish bloom" refers to theoretical causes as evidences. Taking this into account, it seems necessary to reconsider and study which species has been related to one or multiple stressors in each case and their importance (Table S3).

Blooming events are not recorded for all scyphozoan species, but only for a small percentage of the class. However, it should be noted that this percentage has increased during the last decade from around 14%, registered by Hamner and Dawson (2009) in the last major review carried out on this group, to 25% calculated in the present work (55 species). This contrasts with the absence of a significant increase in the overall abundance of jellyfish between 1970 and 2011 (Condon et al., 2013), which indicates that the number of species detected that produce blooms could be increasing paired with the number of observations, publications and studies on this topic (Condon et al., 2013; Pitt et al., 2018), which would not necessarily mean a real increase in the number

of blooms. However, it could not be ruled out that the greater interest in jellyfish populations, recorded through the increase in publications (Pitt et al., 2018), might be the reason underneath the detection of new blooming species. Despite the underlying reason explaining this increase, the updated blooming species list should be considered in the jellyfish monitoring systems.

To define the environmental frame for blooming species and to compare those with non-blooming ones, three different groups of factors can be suggested as implicated in the jellyfish abundance and proliferation even if not all the species respond in the same manner: physical forcing, nourishment and biotope.

4.1. Physical forcing: temperature and salinity

Temperature is the most reported driving factor in blooming events (49.07% of the reviewed publications), and evidences are provided in 19.44% of the papers.

Our multivariate analysis indicates that the minimum and main dwelling temperature is higher for those species capable of blooming within the Coronatae order, slightly lower for the Semaeostomeae order and not significant for the Rhizostomeae (Fig. 6; Table 3). The lower effect of temperature over the separation of blooming and non-blooming species from the Semaeostomeae and Rhizostomeae orders can be explained by the higher diversity of scyphozoan species registered in warmer waters, in which those orders mainly live (Hamner and Dawson, 2009; Figs. 1, 3, 6). The Coronatae order, less capable of producing a bloom (Table 1), has differences with Rhizostomeae and Semaeostomeae (Table 2), being composed by smaller organisms and inhabitants of colder and deeper waters (Fig. 6, Table 3). It should be noted that the blooming species belonging to Coronatae order inhabit in shallower and warmer environments than the non-blooming ones, keeping consistency with the differences observed in the other orders (Table 3).

Our results suggest that the distribution of the species is limited by temperature (Figs. 3, 6). The list of genera capable of blooming in temperate seas include *Pelagia*, *Discomedusa* and *Nemopilema* (14 species in total) and those that can bloom in temperate, subtropical or tropical seas include *Linuche*, *Nausithoe*, *Cyanea*, *Chrysaora*, *Mawia*, *Aurelia*, *Cassiopea*, *Acromitus*, *Catostylus*, *Crambione*, *Crambionella*, *Cephea*, *Cotylorhiza*, *Lobonema*, *Lobonemoides*, *Lychnorhiza*, *Mastigias*, *Phyllorhiza*, *Rhizostoma*, *Rhopilema* and *Stomolophus* (39 species in total). Therefore, the global warming trend recorded in the oceans (Ramanathan and Feng, 2009) might lead to a higher proliferation of jellyfish induced by the expansion of those which inhabit or tolerate warmer waters.

Beyond the effect over the distribution, the effect of temperature over the life cycle should be considered. Long term studies usually conceal the effect of temperature as bloom promoter (Vanwalraven et al., 2015), which is probably influenced by the existence of long period (decadal) oscillations in the abundance (Condon et al., 2013). However, the experiments carried out in the laboratory under fully controlled microcosms, preventing the effect from being blurred by other factors, indicate that temperature does affect asexual reproduction, induces strobilation when fluctuations occur, and favors growth in certain species (Prieto et al., 2010; Fuentes et al., 2011; Purcell et al., 2012; Feng et al., 2015a, 2015b). These effects reported in the laboratory have also been revealed to be important cause-effects relationships in nature during short-term studies (Waryani et al., 2015; Fernández-Alías et al., 2020; Gueroun et al., 2020). In longer time series, even considering that 'absence' periods are registered, blooming of jellyfish, when present, normally shows a seasonality inside the frame of the year (Vanwalraven et al., 2015; Ruzicka et al., 2016; Guevara et al., 2017; Stone et al., 2019).

However, even if the temperature acts as a regulator, the traditionally accepted quote 'The warmer the better' (Ruiz et al., 2012) has some exceptions between blooming species. *Mastigias* spp. (Martin et al., 2006), *Aurelia aurita* (Linnaeus, 1758) (Fuchs et al., 2014), and *Aurelia*
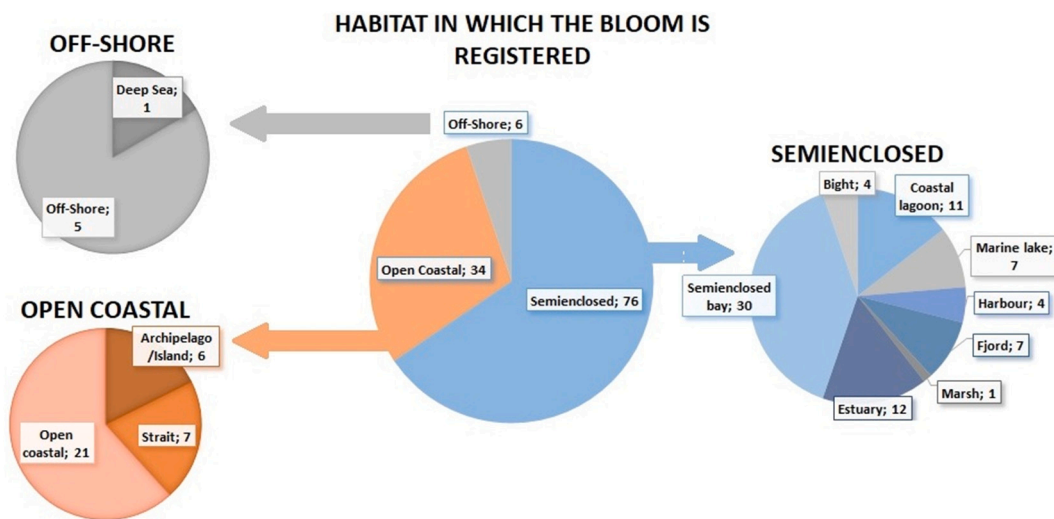
Fig. 5. Number of papers which allude to a specific habitat as host of a jellyfish bloom, jellyfish fishery or jellyfish blooming species collection.

Table 2
PERMANOVA for the scyphozoan genera and species with available information regarding maximum length of the species and minimum, maximum and main temperature, salinity and depth of detection of the species and minimum, maximum and mean chlorophyll *a* in the type location in the consulted databases (38/60 genera, 78/223 species).

Genera as samples							
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Order	2	145.93	72.966	4.5256	0.0007	9939	0.0011
Bloom	1	140.03	140.03	8.6852	0.0004	9944	0.0004
Order × Bloom	2	30.922	15.461	0.9590	0.4601	9945	0.4351

Species as samples							
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Order	2	3159.2	1576.6	5.2536	0.0016	9937	0.0007
Bloom	1	634.38	634.38	2.1099	0.1122	9956	0.1085
Order × Bloom	2	331.36	165.68	0.55104	0.7249	9942	0.7318

sp. (Fernández-Alías et al., 2020) are reported to need a period of low temperature to proliferate, and *Stomolophus meleagris* Agassiz, 1860 cannot survive in temperatures higher than 29 °C (Girón-Nava et al., 2015). This quote is normally used to refer to the adult phase since the medusa stages, in most of the blooming species, appear in summer and are inhabitants of temperate and tropical seas (Fig. 3), but generally ignores the importance of the thermal amplitude as a requirement for the species to complete their life cycle (Fig. 4). The six scyphozoan species whose life cycle has been analyzed in detail reflect that there exists more than a single strategy applied during the seasonal thermal variation (Fig. 4).

At least two different strategies are recorded for species in which the medusa stage is present throughout the year. As examples, *Cassiopea xamachana* presents asexual reproduction of the polyps and strobilation limited to the summer season (Fitt and Costley, 1998) while *Rhizostoma pulmo* exhibits multiple cohorts throughout the year, being able to strobilate in a wide temperature range, particularly when temperature changes are registered (Fuentes et al., 2011; Purcell et al., 2012; Fernández-Alías et al., 2020).

It should be pointed that even if most of the connections between blooming jellyfish life cycles and temperature are based on experiences and observations, the genetic pathways and the explanations that can underlie in this regard remain undescribed. In this line, we have found three studies in which an expression microarray was ensembled (Fuchs et al., 2014; Brekhman et al., 2015; Khalturin et al., 2019). Khalturin et al. (2019) found stage-specific gene expression, being 4.3% of the

genes from *A. aurita* specific from the medusa stage and 8.7% from polyp stage, indicating that exists a deep genetic regulation. Three genes of *A. aurita* were identified to increase its expression 35,000-fold when the temperature was reduced 8 °C (Fuchs et al., 2014). The most overexpressed gene, *CL390* or *CL390*-like, has been suggested as the strobilatory hormone that is released with temperature fluctuations, whether it decreases (Fuchs et al., 2014) or increases (Brekhman et al., 2015). This is a promising research field since an accurate description of the molecular strobilation mechanisms would suppose much improvement for the blooming predictive models.

Affecting distribution, along with temperature, it is also important to consider the water salinity. Evidences indicating the influence of salinity in the distribution of jellyfish species are given in 3.70% of the total reviewed papers. Freshwater inputs and salinity gradients are characteristics of semi-isolated environments that have been proven to affect the settlement and distribution patterns of jellyfish (Pérez-Ruzafa et al., 2002; Fu et al., 2019; Stone et al., 2019; Feng et al., 2020; Fernández-Alías et al., 2020). However, our multivariate analysis indicates that there is no difference between the salinities in which the blooming and non-blooming species dwell (Fig. 6). Thus, salinity could be a predictor of jellyfish distribution and, locally, acts as a barrier that prevents the entry or exit of species from specific hypersaline or brackish habitats, although it does not seem to modulate the intensity of a bloom.

We can conclude that temperature is the main factor that regulates the life cycles of jellyfish and drives strobilation, but, as inferred from the loss of the latter relationship in long-term studies, seasonality in
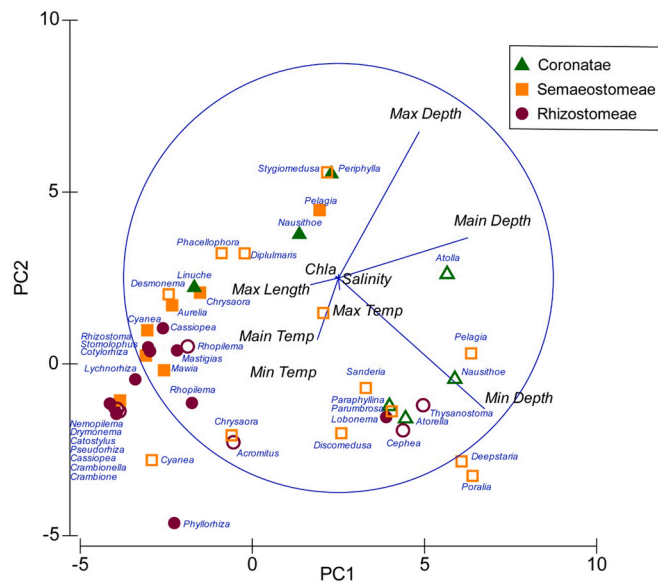
Fig. 6. Principal Component Analysis (PCA) for the scyphozoan genera which have available information regarding maximum length of the species and minimum, maximum and main temperature, salinity and depth of detection of the species, and minimum, maximum and average chlorophyll *a* in each type of location of the species (Table S2; 38/60 genus). Filled shapes indicate 'blooming species' and empty ones indicate 'non-blooming species'.

itself does not guarantee the appearance of a bloom within a certain year, this being also affected by other factors. Furthermore, as species can record different behaviors in relation to temperature and salinity, a single model cannot be constructed to predict the response of the class Scyphozoa as a whole and it is important to consider each species independently.

These two parameters also act in a coordinated way establishing the biogeographical distribution for each species, the distribution found today being an image that can be modified in a more or less close climate change scenario. On the other hand, it must be borne in mind that not all the scyphozoan species are benefiting from the global warming trend and some of them are prone to see their habitat reduced. As an example, *Periphylla periphylla* shows a distribution limited by an upper limit of 7 °C, and *Cyanea lamarckii* and *Chrysaora melanaster* Brandt, 1835 by an upper limit of 13 °C (Fig. 3).

4.2. Nourishment: food availability, overfishing, nutrient loads and eutrophication

Food availability and overfishing are recorded as bloom promoting factors in 21.30% of the reviewed papers, while eutrophication and nutrient loads are reported in 13.89% of them. In both cases, evidence is provided in 2.78% from the total of the analyzed publications. When the maximum, minimum and mean chlorophyll *a* recorded through a decade in the locations of the scyphozoan species were analyzed, we did not find an influence of this factor on the distribution of blooming and non-blooming jellyfish (Fig. 6, Table 3).

Our results indicate that blooming and non-blooming species distribution is not affected by the concentration of chlorophyll *a*, but this might be indicative of complex bottom-up and top-down interactions. On one hand, a higher nutrients or food availability generally is directly related with the abundance of the species benefiting from them, being the abundance of gelatinous plankton greater in upwelling areas (Suchman et al., 2012). This effect has also been found specifically for the Scyphozoa class. We can mention how *Rhizostoma pulmo* shows a significant relationship with the nitrate inputs in a coastal lagoon that undergoes a severe eutrophication process (Pérez-Ruzafa et al., 2002;

Table 3

Pairwise and SIMPER analysis performed for each Order of scyphozoan for the factor 'Bloom' (Blooming versus Non-Blooming group), at genus and species level, using the available information on maximum length of the species, minimum, maximum and main temperature, salinity and depth of detection of the species, and minimum, maximum and mean chlorophyll *a* in the type location in the consulted databases (38/60 genera, 78/223 species).

Genera as samples

Source	P (perm)	Unique perms	P (MC)
Rhizostomeae	0.1266	7669	0.1323
Semaeostomeae	0.0160	9056	0.0176
Coronatae	0.0302	35	0.0177

Variable	Blooming Mean	Non-blooming Mean	Contribution
Rhizostomeae			
Min depth (m)	27.1	171	45.21%
Main depth (m)	40.4	214	24.12%
Max depth (m)	112	258	20.70%
Semaeostomeae			
Min depth (m)	0	789	43.19%
Main depth (m)	260	667	23.28%
Max depth (m)	775	1600	13.93%
Min temp (°C)	10.4	12.7	6.85%
Main temp (°C)	17.4	17.5	4.52%
Coronatae			
Min depth (m)	0	328	59.40%
Main depth (m)	685	1190	16.92%
Min temp (°C)	12.8	8.46	6.45%
Main temp (°C)	18.1	15.4	5.93%
Max depth (m)	3670	2270	4.39%

Species as samples

Source	P (perm)	Unique perms	P (MC)
Rhizostomeae	0.0004	9941	0.0030
Semaeostomeae	0.7676	9903	0.5655
Coronatae	0.5691	1901	0.5450

Variable	Blooming Mean	Non-blooming Mean	Contribution
Rhizostomeae			
Max length (cm)	37.8	13.7	91.29%
Semaeostomeae			
Max length (cm)	49	30.8	57.96%
Min temp (°C)	10.4	12.7	21.01%
Main temp (°C)	17.4	17.5	12.36%
Coronatae			
Min temp (°C)	12.8	8.46	42.89%
Main temp (°C)	18.1	15.4	39.61%
Max length (cm)	6.4	5.52	12.5%

Fernández-Alías et al., 2020), *Nemopilema nomurai* polyps are reported to exhibit a higher asexual reproduction rate when there is a high plankton availability in laboratory (Sun et al., 2015), or *Stomolophus meleagris* needs rapidly available food to survive after the strobilation takes place (Girón-Nava et al., 2015). On the other hand, in the Mar Menor coastal lagoon, under a high nutrient input scenario, blooms of three scyphozoan species (*Aurelia* sp., *Cotylorhiza tuberculata* and *Rhizostoma pulmo*) segregate over time maintaining, together with ichthyoplankton, low levels of chlorophyll *a* (Pérez-Ruzafa et al., 2002; Fernández-Alías et al., 2020). This poses a scenario in which the effect of chlorophyll *a* concentration can easily be concealed as it occurs in our analysis and in long-term studies (Vanwalraven et al., 2015; Stone et al., 2019).

Even though, the importance of the bottom-up effect seems particularly important during the polyp and strobila stages, having been the

quantity and quality of the food proved to control and modulate the intensity of blooms under the appropriate temperature regime (Schiariti et al., 2014; Wang et al., 2015; Wang and Li, 2015; Goldstein and Steiner, 2020; Marques et al., 2020). Here, it should be noted that most of those observations have been made for the *Aurelia* genus, being it smaller than the average size of the blooming species from Rhizostomeae and Semaeostomeae orders (Table 3; Scorrano et al., 2017; Fernández-Alías et al., 2020; Marques et al., 2020). It can be inferred that larger species will need a higher amount of nutrients as they need to satisfy growth rates that exceed 4 mm/day (Kikinger, 1992; López-Martínez et al., 2020; Leoni et al., 2021). Considering that our results suggest that larger species are more likely to bloom (Fig. 6, Table 3), which is probably linked to an increase of the gonadosomatic index with size (Fernández-Alías et al., 2020), it seems plausible that the existence of complex bottom-up and top-down relationships within the trophic net control and modulate the intensity of a bloom (Pérez-Ruzafa et al., 2002; Stone et al., 2019; Marques et al., 2020) being them blurred in long term analysis.

The complex equilibrium between the top-down and bottom-up interactions (Boero et al., 2008) might also be fragile since, through eutrophication processes, the dominance of jellyfish blooms can eventually shift to an algae and dinoflagellate dominance (Boero, 2015; Pérez-Ruzafa et al., 2019). However, it cannot be ruled out that the decline or disappearance of jellyfish in these cases may be accelerated or caused by human interferences in the reproduction strategies and further studies are needed to elucidate these relationships.

A less studied effect that might also regulate the intensity of the blooms is the predation and mortality that may exists on non-medusa stages. There are some intrinsic difficulties to the study of those stages since, in most places and occasions, polyps have not been found in the field and early stage ephyrae and planulae cannot be seen without the aid of a microscope. Even though, nudibranchs, amphipods, pycnogonids and decapods have been reported to be the main jellyfish polyp predators (Lucas et al., 2012; Takao et al., 2014). Here it should be noted that the resistance structures formed at the pedal disc of the polyps, named podocysts, can help to survival of the polyps under food scarcity and predation periods; thus contributing to bloom formation (Arai, 2008). Ishii et al. (2004) reported that, when ephyrae are preyed upon by naturally present zooplankton, a death rate of up to 99% of newly released ephyrae can be achieved and, although there is a gap in the knowledge about predation on planulae, from an experimental study of Kuplik et al. (2015) it can be inferred that this stage can also be predated.

4.3. Biotope: habitat, invasions and construction of submerged structures

In the group 'Biotope' we have found habitat, invasions and construction of submerged structures as the main factors related to the existence and proliferation of jellyfish.

Habitat is recorded in 11.11%, and evidences indicating the influence of the habitat over population dynamics are provided in 1.85% of the reviewed papers. It is not an inducer of strobilation, but it facilitates the conditions for strobilation when it provides solid settlement and slow water renewal rate conditions. In our opinion, this category could be highly underestimated since, in the analyzed works, 110 allusions have been found to coastal areas (in which blooms were detected, are used for a jellyfish fishery or are used to collect blooming individuals) compared to 6 allusions in open or deep waters (Fig. 5). Moreover, our analysis reveals that the main difference between blooming and non-blooming genera is the depth in which they inhabit (Fig. 6, Table 3). Minimum, main and maximum depth of jellyfish detection are pointed as the most influential factors and, more specifically, genera which are able of living in the first 27.1 m of the water column are more likely to bloom (Table 3).

Most blooms are registered in semienclosed areas, semienclosed bays, coastal lagoons, marine lakes, fjords, harbours, estuaries, bights

and marshes. These habitats, considered as more suitable to host jellyfish blooms, show significant thermal oscillations, throughout the year but also daily, due to the reduced connection with the open sea and their naturally stressed system conditions (Umgiesser et al., 2014). As mentioned above, sudden temperature fluctuations coincide with strobilation events, and it has also been reported that genetic pathway is activated due to these changes (Fuchs et al., 2014; Brekhman et al., 2015; Fernández-Alías et al., 2020). So, this naturally fluctuating and heterogeneous behavior of these systems explains in part the presence of blooms mainly in semienclosed areas, followed by open coastal areas, and their absence in deep waters (Fig. 5).

It may be argued that monitoring of open waters includes additional difficulties that could limit the detection of blooming events. However, in semienclosed areas jellyfish are able of overcoming the water movement and produce swarming events (Hamner and Hauri, 1981; Pitt and Kingsford, 2000; Ugland et al., 2014; Fernández-Alías et al., 2020) while in open waters the distribution of jellyfish is mainly driven by the movement of water masses and currents (El Rahi et al., 2020; Kitajima et al., 2020). In addition, those studies that measure the distance to the coast suggest that the closer to the coast the greater the probability of finding jellyfish (Sparks et al., 2001) and insist that blooming scyphozoan species are mostly collected near shore (Schiariti et al., 2018).

Blooms of deep-sea species do not seem to occur, and different explanations for this situation can be suggested. The first would be related to the own characteristics of the species found in these environments and their inability to perform bloom events, the second would assume that there are species that can carry out blooming events in deep waters, but these have not yet been recorded due to the depth in which they occur, and, finally, the last explanation suggest that deep-sea jellyfish could only bloom when find conditions that are optimal for them, in very specific and sometimes difficult-to-detect situations, as is the case of *Periphylla periphylla*, a typically deep-water inhabitant, that is capable of blooming in semienclosed fjords, where it appears in shallow waters and even in the surface (Riemann et al., 2006). In deep-water environments, an important abundance of corpses of *Crambionella orsini* (Vanhöffen, 1888), a shallow water species, that falls along the continental shelf when it is dying, has also been recorded (Billett et al., 2006).

We are more inclined to the third explanation, as it is proven that the thermal amplitude and accumulation of nutrients, the two main drivers involved in the blooming events, are greater in semienclosed areas than in open waters and higher depths (Smith, 1994).

The relationship observed between abrupt changes in temperature and strobilation (Fernández-Alías et al., 2020) could eventually affect the distribution of jellyfish populations. Thus, blooms and populations are going to be increasing in abundance and number in the tropics and subtropics, but reduced in the polar areas, which correspond to the increase-decrease temperature standard deviation predicted for those areas (Vincze et al., 2017; Bathiany et al., 2018). This implies that not only terrestrial zones in poor countries, but also their marine ecosystems, are going to be deeply affected by climate change in this sense (Bathiany et al., 2018).

Invasions from alien species are registered in 9.26% and proved in 3.70% of all the articles that have to do with the term 'biotope'. We have no doubt that some species such as *Cassiopea* spp. and *Aurelia* spp. have increased their range of distribution, but since we have only considered 'the proven facts' in those papers in which the pathway of invasions are determined, there is a great gap between what is hypothesized and what is proven. Within this point it has only been proved that the translocation of a species into a habitat suitable to host a bloom can lead to a massive proliferation of the introduced species (Bolton and Graham, 2006).

Species translocation and alien species invasion are not strobilation inductors, but have a great influence on increasing jellyfish abundance in terms of habitat functioning (Richardson et al., 2009). There may be areas in which the conditions to promote the bloom of a certain species are optimal but reaching them is beyond its swimming capacity. That

distance can only be covered by jellyfish translocated in ballast waters, strong currents, through recently opened channels or as polyps in 'living rocks', platforms or navigational structures (Bolton and Graham, 2006; Graham et al., 2003; Johnson et al., 2005; Richardson et al., 2009; Sakinan, 2011; Galil et al., 2013).

Only one work could be found, carried out by Killi et al. (2020), that performs a risk screening of the potential invasiveness of gelatinous zooplankton, taking into account biological aspects to be able to identify "potential invaders" but leaving in the background the identification of places at risk of invasion. This work points the size of the species as an indicative feature of the invasiveness potential, being it coincident with the evolution of blooming species towards larger sizes (Fig. 6, Table 3).

Similar considerations can be made for the category 'Construction of submerged structures'. There are articles that provide images of polyps growing on submerged artificial structures (Malej et al., 2012; Wang and Sun, 2015), but they do not provide statistical analysis comparing these structures with hard natural substrates in the same environmental conditions. In this line, Duarte et al. (2013) proposed that the detection of polyps after the deployment of artificial substrate in habitats where previous surveys yielded no detection is indicative of their preference for artificial structures. Moreover, two experiments were carried out yielding that artificial substrates provide a similar or better spot for planulae settlement than the natural ones (Duarte et al., 2013). It is important to bear in mind that these structures can also facilitate and/or increase the connectivity between populations with the consequent effects on the distribution of some species and the colonization of new environments.

As final remark we can conclude that i) the percentage of blooming scyphozoan species has increased up to 25% during the last decade, which means going from a list of 31 species producing blooms to an updated list of 55 species, ii) temperature and food availability are the main factors modelling the intensity of a bloom, iii) semienclosed, shallow water environments are more likely to host a bloom, iv) larger species capable of living near surface hold a higher blooming potential and v) the interspecific variability in the response towards environmental factors suggest that the prediction model should be constructed species-habitat-specific.

CRediT authorship contribution statement

Alfredo Fernández-Alías: Conceptualization, Investigation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Validation. **Concepción Marcos:** Data curation, Writing – original draft, Writing – review & editing, Validation. **Angel Pérez-Ruzafa:** Conceptualization, Data curation, Writing – review & editing, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2021.113100.

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