The occurrence of the jellyfish *Aequorea* cf. *forskalea* in the Adriatic Sea: comparison of historical and recent data

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Jellyfish are becoming an increasingly important component of studies of the global marine environment, as their frequent mass phenomena affect ecosystem performance and have economic and health consequences. Recent research has focused primarily on mass occurrences of scyphozoans and ctenophores, while less attention has been paid to hydromedusae blooms, which can also have significant impacts on the marine ecosystem with economic consequences. Like many members of the Scyphozoa and Ctenophora, Aequorea *species can be numerous and form blooms. Based on surveys from 2000 to 2020 and information provided by marine professionals, we examine the (multiannual) variability, seasonality, and spatial distribution patterns of the poorly studied temperate species* Aequorea cf. forskalea *(Hydrozoa: Leptothecata). We hypothesized that this macrogelatinous jellyfish with a bipartite life cycle (benthic polyps and planktonic medusae) is sensitive to seasonal and long-term temperature fluctuations, particularly because temperature has been shown to play a critical role in mediating transitions in the life cycle of cnidarians. The cold-water affinity of* A. cf. forskalea *was confirmed by a significant negative correlation with temperature and the most frequent occurrence during the winter-spring period. For the northern Adriatic (Gulf of Trieste), sea temperature data and semi-quantitative plankton data are available for the first decade of the 20th century, allowing comparison of the historical data (1900-1911) with our current data set. Compared to historical records, the current occurrence of* A. cf. forskalea *differs significantly. With the warming of the northern Adriatic Sea since the beginning of the 20th century, the current phenology of* A. cf. forskalea *has changed, probably related to the delayed production of medusae by hydroids in autumn, the absence of medusae in this season and their less frequent occurrence in winter.*

Key words: hydromedusae; blooms; long-term monitoring; multiannual variability; Mediterranean Sea

INTRODUCTION

Jellyfish are becoming an increasingly important research component of the global marine environment as their frequent mass phenomena affect ecosystem performance and have economic and health consequences (PURCELL et al., 2007; NASTAV et al., 2013; GRAHAM et al., 2014; LUCAS et al., 2014; DE DONNO et al., 2014; BOSCH-BELMAR et al., 2020). Seemingly unpredictable "boom and bust" dynamics are characteristic of bloom-forming jellyfish species (SCHNEDLER-MEYER et al., 2018), although regional and local populations may exhibit long-term oscillations (GOY et al., 1989; KOGOVŠEK et al., 2010). However, it is difficult to assess whether population dynamics are part of the fluctuation cycle because available data sets are often too short (CONDON et al., 2013).

Most research on these organisms has focused on mass occurrences of scyphozoans and ctenophores. Less attention has been paid to hydromedusae, which can also cause significant damage to the marine ecosystem, with economic consequences (BAXTER et al., 2011). These tiny medusae are generally overlooked in plankton ecology because they elude direct observation, and their blooms often cannot be detected by standard plankton sampling (BOERO et al., 2008). An exception to this is some hydromedusae, such as species of the genus *Aequorea*, primarily because of their large umbrellas (100-200 mm), unusual for most members of this cnidarian class (BOUILLON et al., 2004).

Like many members of Scyphozoa and Ctenophora, *Aequorea* species can be numerous and form blooms (PURCELL, 2018). They can negatively impact ecosystem services by feeding on various groups of mesozooplankton, including fish eggs and larvae (PURCELL, 1989, 2018; PURCELL & ARAI, 2001; COSTELLO & COLIN, 2002; RIISGÅRD, 2007), particularly because they feed more when prey density increases (PUR-CELL, 1997). Stable isotopes showed considerable overlap in the food sources of fish and jellyfish, including *Aequorea* sp. which were generally enriched in ^{13}C and depleted in ^{15}N compared to fish (NAMAN et al., 2016). In addition, *Aequorea*

specimens may directly threaten fisheries and the aquaculture sector (BOSCH-BELMAR et al., 2021) or indirectly transmit endoparasites to fish (DIAZ BRIZ et al., 2012). The most comprehensive data on the biology, ecology, and impacts of the genus *Aequorea* on marine ecosystems can be found in PURCELL (2018).

Of the 27 recognised species of *Aequorea* known worldwide (SCHUCHERT, 2022), *A. for-skalea* Peron & Lesueur, 1810 is the most frequent species in the Mediterranean Sea, according to BOUILLON et al. (2004). It is also well known in Atlantic and Indo-Pacific coastal ecosystems (KRAMP, 1961; RUSSEL, 1953; PAGÈS et al., 1992). Nevertheless, BOUILLON et al. (2004) listed three *Aequorea* species (*A. conica, A. forskalea, A. pensilis*) in their monograph of Mediterranean hydrozoans. While they doubted the occurrence of *A. pensilis* in the Mediterranean Sea, ONMUŞ et al. (2016) reported the observation of an unusual *Aequorea* from the Aegean Sea and determined that it was *A. pensilis*. In the waters off Lebanon, *A. conica* was mentioned by GOY et al. (1991), who stated that it was new to the Mediterranean. TURAN et al. (2011) reported the first occurrence of non-native *A. globosa* in Iskenderun Bay (Turkey). Another report of *A. globosa* from the coastal waters of Syria was based on a single adult specimen (MAMISH et al., 2012). However, DEIDUN & PIRAINO (2021) suggested that it should be referred to as *A. australis*, a common species of the Red Sea. *A. macrodactyla* was also known from the Red Sea and adjacent areas (GRAVILI et al., 2013). The discovery of this species near the Israeli coast was confirmed by traditional morphology and molecular phylogenetics (MIZRAHI et al., 2015) and was considered by the authors as part of the changes in the biota of the eastern Mediterranean. The list of non-native *Aequorea* species was recently completed by the detection of *A. vitrina* in the Sea of Marmara (YILMAZ et al., 2017).

There are few data on the phenology and abundance of *A. forskalea* in the Mediterranean. Historically, mass occurrence has been described from only two areas: the Gulf of Trieste and Villefranche (MAAS, 1904). In the Gulf of Trieste, they were abundant in winter and spring, and

rarely also in late autumn (CLAUS, 1880; GRA-EFFE, 1884; CORI & STEUER, 1901; STEUER, 1902, 1903; STIASNY, 1908, 1909, 1910, 1911, 1912; NEPPI & STIASNY, 1912). Recently, bloom of *A. forskalea* was recorded in April 2016 in the coastal area off Salento, Ionian Sea (MICARONI *et al*., 2022).

With the exception of the Gulf of Trieste, data for other regions of the Adriatic are very sparse: a few individuals have been recorded for the coastal section of the eastern central Adriatic (SZÜTS, 1915; PELL, 1918; BABNIK, 1948; HOENIGMAN, 1958) and the open northern Adriatic (BENOVIĆ & LUČIĆ, 1996). Along the western (Italian) coast, *Aequorea* was also found in the northern and central regions (MIZZAN, 1994; GRAVILI *et al.,* 2008), but there are no data on its abundance.

Apart from historical data from the early 20th century from the Gulf of Trieste, data on the seasonal distribution and abundance of *Aequorea* in the Mediterranean Sea are scarce. Therefore, the objectives of the present work are: (I) to collect and systematise all available data on the occurrence of *Aequorea* in the Adriatic Sea; (II) to compare the occurrence, phenology and mass phenomena of this jellyfish in the different subregions of the Adriatic Sea; (III) to compare recent data on sea temperature and medusae phenology with historical information. Since the Mediterranean is one of the hotspots of climate change (TUEL & ELTAHIR, 2020) and the Adriatic Sea is increasingly warming (BOICOURT *et al.,* 2021), we hypothesised that the seasonal occurrence of these organisms would change in response.

MATERIAL AND METHODS

Study area

The Adriatic Sea is a semi-enclosed sea basin with an orientation of SE-NW (Fig. 1) and extends approximately between 40°N (Strait of Otranto) and 46°N (Gulf of Trieste). It is relatively shallow (average depth of 252 m) and reaches a maximum depth of 1270 m in the southern part. The inflow of freshwater from the mainland, especially from the west coast, mete-
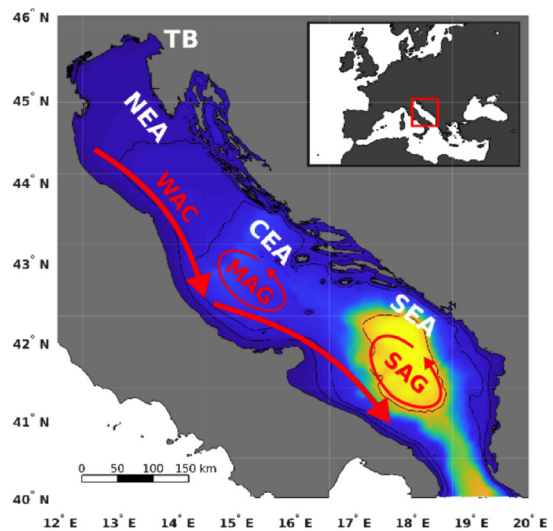

Fig. 1. Map of the Adriatic Sea divided into four subregions: TB (Gulf of Trieste), NEA (north-eastern Adriatic), CEA (central-eastern Adriatic) and SEA (southern-eastern Adriatic). Major circulation features are drawn in red colour: WAC (Western Adriatic Current), MAG (Mid Adriatic Gyre), SAG (South Adriatic Gyre). The isobaths are plotted at 50, 100 and 1000 m depths

orological conditions, water circulation and the intrusion of Mediterranean water along the east coast, and the variable anthropogenic pressures are the main factors that determine the physical, biogeochemical properties and biological processes in the water column (CIVITARESE *et al.,* 2010; FURLAN *et al.,* 2019).

According to the ecological characteristics, we divided the area of our study into four regions (Fig. 1): the shallow and productive Gulf of Trieste (TB) and the north-eastern Adriatic (NEA), the oligotrophic central-eastern Adriatic (CEA) and the south-eastern Adriatic (SEA). TB is the northernmost point of the Mediterranean Sea. Due to its location and shallow water depth (<30 m), seasonal variations in hydrographic features are large and significantly affect all biological processes (BOICOURT *et al.,* 2021). NEA continues south of TB and includes the western waters of Istria with depths up to 50 meters. The influence of freshwater and nutrients from the Po River has a strong impact on production in this area (BRUSH *et al.*, 2021), as does the influence of oligotrophic waters from

the central and southern Adriatic Sea (FUKS *et al.*, 2012). The CEA region is characterized by a well-indented area with numerous islands and bays. The waters of the CEA are oligotrophic, while mesotrophic conditions prevail in more enclosed bays and near larger cities and ports (ŠANTIĆ *et al.,* 2014). SEA is a highly oligotrophic area with a strong influence of the open deep Adriatic on all hydrographic and biological factors. In general, production is comparable to low productivity areas in the eastern Mediterranean (GAČIĆ *et al.*, 2002; SIOKOU-FRANGOU *et al.,* 2010).

Aequorea cf. forskalea data

Data on the occurrence and abundance of *A. cf. forskalea* along the eastern Adriatic coast were collected during research cruises and surveys from 2000 to 2020 by scientists from various oceanographic institutions on the Adriatic (Marine Biology Station, Piran, NIB, University of Dubrovnik, Center for Marine Research in Rovinj, IRB, Juraj Dobrila University of

Pula, Institute of Oceanography and Fisheries, Split). Additional information came from marine professionals such as autonomous divers and aquarium staff who provided accurate data with photos. The taxonomy of *Aequorea* and the characteristics of the Adriatic specimens notified in our article as *A. cf. forskalea* (Fig. 2) are briefly described below.

Due to the lack of clear morphological distinguishing characters and remarkable individual variability, the correct taxonomic identification of medusae is a significant problem (MAYER, 1910). This, together with the lack of molecular and ecological data, still makes the taxonomy of this genus (and the entire family Aequoreideae) a major challenge. Based on the relative number of radial canals compared to the number of tentacles and their position, HAECKEL (1879) established three subgenera, but CLAUS (1880) already criticized Haekel's system. NEPPY & STIASNY (1912) noted that morphological identification of *Aequorea* species is difficult due to phenotypic variability. Nowadays, morphological taxonomy
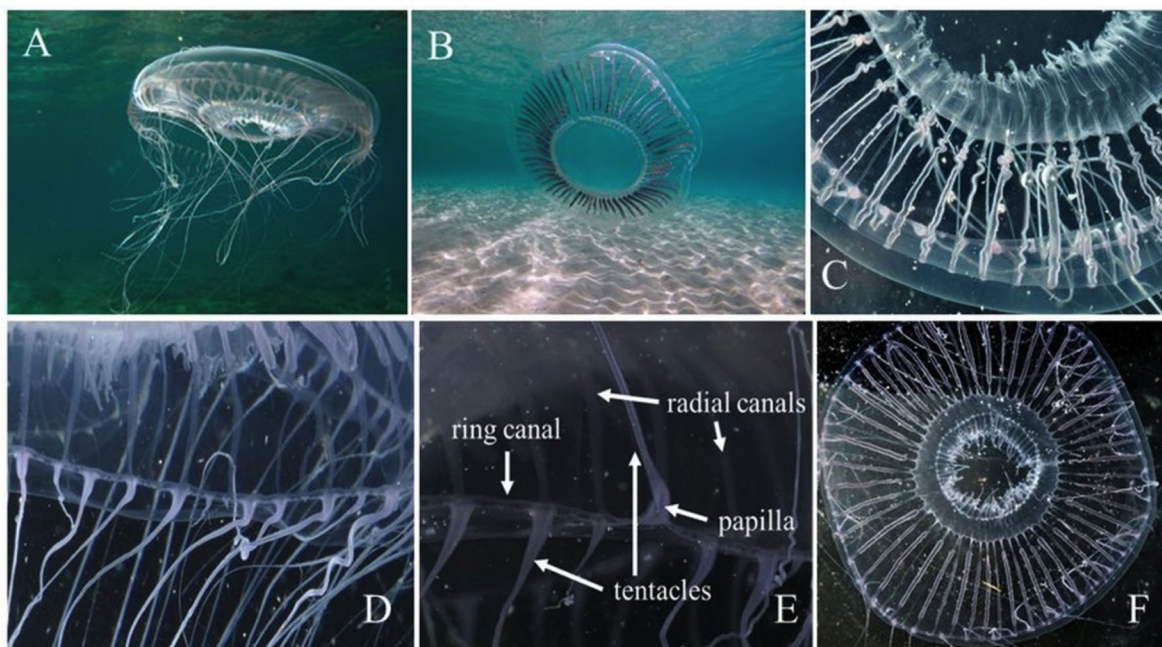

Fig. 2. Aequorea cf. forskalea *from the Adriatic Sea: (A) transparent and saucer-shaped umbrella with marginal tentacles, the number of which is approximately equal to the number of radial canals; (B) pale purple linear gonads extending along straight and narrow radial canals; (C) oral view of medusa showing mouth with curtain-like lips and transparent lines radiating from the ends of the radial canals to the lips; (D) part of umbrella margin with elongated conical tentacular bulbs; (E) subumbrella view and location of excretory pore located on short papilla at the base of a tentacle; (F) gonads extend almost entire length from bell margin to mouth. (Photos A, C-F: Tihomir Makovec, Piran; photo B: Marinko Babić, Pula)*

is based on the shape of the umbrella, the width of the stomach in relation to the diameter of the umbrella, the number of radial canals and tentacles, the presence/absence of excretory papillae, the number of statocysts between successive radial canals, the position of gonads, their shape and length along the radial canals (BOUILLON *et al.,* 2004). Fig. 2 shows characteristics of adult *A. cf. forskalea* from the Adriatic Sea. Since a taxonomic determination of the species was not made in all observations, it cannot be completely excluded that a species other than *A. cf. forskalea* was present. However, in earlier publications for the Mediterranean the occurrence of other species is mentioned only exceptionally, so that we use throughout the article only *A. cf. forskalea*.

Our recent dataset (2000 – 2020) consists of 1240 observations, of which slightly more than 10% were positive (*Aequorea* medusae were present) in the Gulf of Trieste, as well in for NEA. In the CEA and SEA their percentages were lower i.e. 4 and 2 %, respectively.

Observations of *A. cf. forskalea* were assembled on a monthly basis to create a multi-year semi-quantitative dataset for four Adriatic subregions: the northernmost Gulf of Trieste (TB), the north-eastern Adriatic (NEA), the central-eastern Adriatic (CEA) and the south-eastern Adriatic (SEA) (Fig. 1). The method used to create the monthly semi-quantitative data sets was as follows. We assigned a value between 0 and 3 to each month of the year according to the following criteria: category 0 – jellyfish were not seen at all; category 1 – sporadic occurrence of individual organisms; category 2 – occurrence of individual jellyfish and/or small aggregations; and category 3 – occurrence of large aggregations. Monthly values represent the highest category of jellyfish occurrence in a given month, regardless of the number of observations. Several authors have already used similar or the same methods to present the results of macrozooplankton research (GILI *et al.,* 2008; FUENTES *et al.,* 2009; VIOLIĆ *et al.,* 2019; LEONI *et al.,* 2021; PESTORIĆ *et al.,* 2021).

Multi-year, semi-quantitative data on historical observations (1900-1911) of *A. cf. forskalea*

exist only for the Gulf of Trieste and were taken from the following publications: CORI & STEUER (1901), STEUER (1902, 1903), STIASNY (1908, 1909, 1910, 1911, 1912). Overall 117 published observations were included in our 10 years (1900-1911) analysis of which range of positive observations was 11-33% (i.e. *Aequorea* were present). These authors reported semi-quantitative monthly observations of *A. forskalea* using notifications 0, absent; r, rare; +, non-common neither rare; c and cc, common/very common. These symbols were applied to our semi-quantitative data in the following way: absent, corresponds to our category 0; rare, corresponds to our category 1; +, corresponds to our category 2; and c, cc corresponds to our category 3.

Temperature data

Recent data (2003-2020) on sea surface temperature (SST) in the Gulf of Trieste come from *in situ* measurements from the oceanographic buoy Vida operated by the National Institute of Biology (NIB). The data are transmitted in real time via an Ethernet link to the NIB server and are publicly available via a link https://www.nib.si/mbp/en/buoy/. Historical temperature data were retrieved from RAICHICH & COLUCCCI (2021).

Statistical analyses

To evaluate the degree of correlation between the semi-quantitative abundance dataset of *A. cf. forskalea* and temperature, a biserial correlation was performed (Addinsoft 2022, XLSTAT statistical and data analysis solution. New York, USA. https://xlstat.com). The biserial correlation requires a binary variable, which in our case are the categories of the semi-quantitative abundance data set, and a continuous variable, i.e. temperature. The p-value was calculated using Monte Carlo simulations.

In order to extract distribution patterns and detect possible changes in the seasonal distribution of *A. cf. forskalea*, the data were grouped according to the factors of year and/or season. In terms of years, data from 1900-1911

were recorded as a historical period (H), while recent data (R) refer to the period from 2000 to 2020. Seasons were grouped as winter (January-March), spring (April-June), summer (July-September), and autumn (October-December).

The one-way ANOSIM test was used to analyse the temporal distribution of temperature and abundance categories of *A. cf. forskalea* during the period/season. Hierarchical clustering (HC) and multidimensional scaling (MDS) were used to describe (dis)similarity patterns between periods and seasons (CLARKE & GORLEY, 2015). As a pre-treatment, the Grower method was used to standardize semiquantitative species abundance data, with nominal variables (categories from 0 to 3) expressed as binary. The next step is to standardize the data and multiply by a correction factor due to the binary coding of the variables (GOWER, 1971). The distance (non-similarity) between periods/seasons was calculated using Euclidean distance. Clustering was performed using the group average method, applying the permutation test "similarity profile" (SIMPROF) to test the significance of the internal structure within the constructed cluster.

An MDS plot was created to illustrate the closeness, with the superimposed clusters coming from a SIMPROF similarity level cluster dendrogram. All statistical analyses were performed using PRIMER 7 software (version 7.1.21 from PRIMER-E) (CLARKE & GORLEY, 2015).

RESULTS

Aequorea cf. forskalea spatial and temporal distribution during 2000-2020

The timing of the first appearance of *A. cf. forskalea*, the duration of medusa occurrence, and the abundance varied throughout the study period. Fig. 3 shows the time series of *A. cf. forskalea* data in four Adriatic subregions during the period 2000-2020. In most years, *A. cf. forskalea* first appeared in February, although it was sometimes observed as early as January; in some years it first appeared in March and exceptionally in April or May. March was the most common month with the peak abundance and there was no clear shift to an earlier seasonal peak during the study period. Throughout the
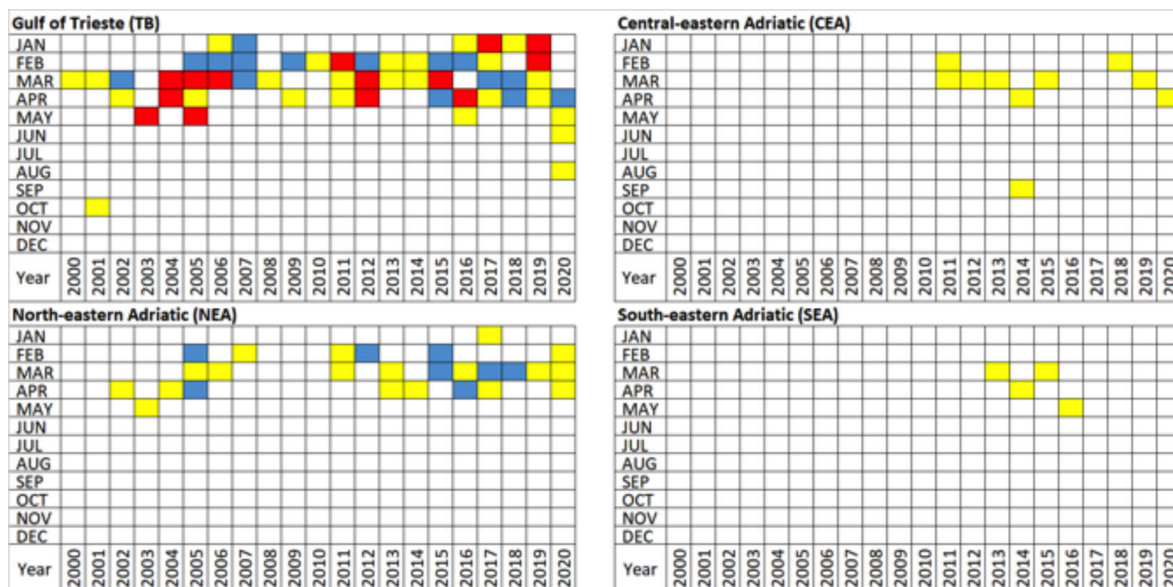

Fig. 3. Temporal variability (month/year) of semi-quantitative abundance of Aequorea cf. forskalea *in four Adriatic subregions (see Fig. 1): Gulf of Trieste (TB, top left), north-eastern Adriatic (NEA, bottom left); central-eastern Adriatic (CEA, top right); south-eastern Adriatic (SEA, bottom right). Categories of semi-quantitative abundance: empty (0, medusae not seen at all); yellow (1, sporadic occurrence of single medusae); blue (2, frequent occurrence of single medusae and/or small aggregations); red (3, regular occurrence of large aggregations/blooms)*

time series, medusae disappeared by the end of May, except in June 2020. The only observations outside the winter-spring period were in October 2001 (TB), September 2014 (CEA), and August 2020 (TB).

The highest abundance levels (category 3) were regularly found only in TB subregion. In 2004, 2012, and 2019, high densities in this subregion persisted for up to two months, and *A. cf. forskalea* was also quite abundant in 2005-2007 and 2015-2018. Medusae were least numerous in 2001 and 2008, when few individuals were noted only in March. (Fig. 3, top left). In NEA, *A. cf. forskalea* was found mainly between February and April (Fig. 3, bottom left). It was observed in all years except 2008-2010, but rarely formed large aggregations. Sighting surveys of this jellyfish in the CEA showed that *A. cf. forskalea* was not present in this subregion until 2011. Since then, it was rarely observed from February to April (Fig. 3, top right). On one occasion, it was also observed in September (2014). In SEA, few individuals were only sporadically detected during 2013-2016 (Fig. 3, bottom right).

Relationship between the occurrence of *Aequorea cf. forskalea* and temperature in the period 2003-2020

The analysis of the relationship between *A. cf. forskalea* and temperature was possible only for the Gulf of Trieste, since we have continuous sea surface temperature data for this subregion since 2003. Sea surface temperature (SST) in the Gulf of Trieste showed a typical seasonal cycle with minima around 8-10°C in February – early March and maxima around 25-27°C in July-August. The lowest monthly average was reached in February 2012 (7.44±0.95°C) and the highest monthly average in August 2018 (27.03±1.25°C).

Since 2003, *A. cf. forskalea* medusae have been observed in the water column of the Gulf of Trieste at temperatures ranging from 8.12°C to 17.87°C and only twice in 2020 at SST above 20°C. Fig. 4 shows that *A. cf. forskalea* formed blooms (abundance category 3) mainly at temperatures
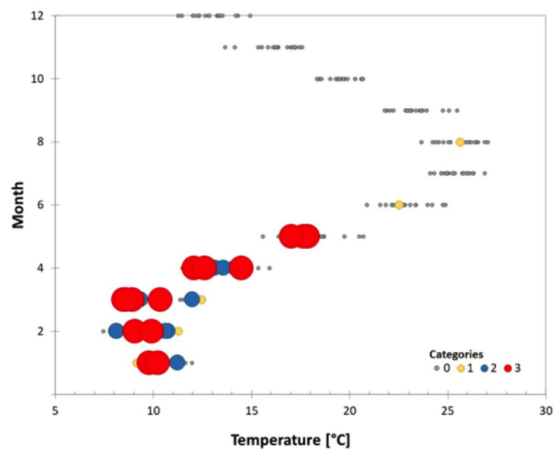

Fig. 4. Temporal variability of semi-quantitative data on recent abundance of Aequorea cf. forskalea *in the Gulf of Trieste in relation to temperature. Red bubbles indicate category 3 abundance, blue category 2 and yellow category 1; grey dots indicate that medusae were not observed*

around 10°C in January-March. Cold-water affinity of *A. cf. forskalea* was confirmed by significant negative correlation (r=-0.485, p=0.001) with temperature. Based on the frequency of occurrence of aggregations, we estimated the average temperature optimum of *A. cf. forskalea* medusae to be 11.33±2.81°C.

Historical occurrence of *A. cf. forskalea* in the Gulf of Trieste

The time series of *A. cf. forskalea* data in the Gulf of Trieste in the period 1900-1911 are shown in Fig. 5, with the gaps (no data) in 1905 and 1906, and in the autumn of 1910 (October-December).

In most years, *A. cf. forskalea* appeared as early as January, was present until April-May, and was not observed from June to September. In contrast to recent period, specimens were regularly recorded in late autumn (Fig. 5). Blooms were noted in 1900, 1903 and 1907 in winter and early spring. In 1908, medusae were abundant in the autumn and a mass occurrence was observed in December. However, the longest mass occurrence of jellyfish was recorded from January to April 1909.
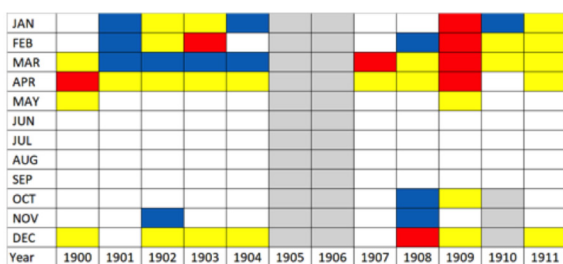
Fig. 5. Temporal variability (month/year) of semi-quantitative abundance of Aequorea cf. forskalea *for historical data in the Gulf of Trieste. Categories of semi-quantitative abundance: empty (0, medusae not seen at all); yellow (1, sporadic occurrence of single medusae); blue (2, frequent occurrence of single medusae and/or small aggregations), red (3, regular occurrence of large aggregations/blooms). Grey boxes indicate no reported observations (no data).*

Multivariate data analysis and comparison of recent and historical data

Temperature

Comparison of seasonal temperature variations between the historical (H) records from the beginning of the 20th century (1900-1911) and the current period (2003-2020, R) shows an increase in average values in all seasons (Fig. 6, Table 1). However, due to the high temperature variations in spring and autumn, the one-way ANOSIM test confirmed significant differences between the H and R records only for winter (R=0.407, p=0.001) and summer (R=0.300, p=0.002) temperatures.
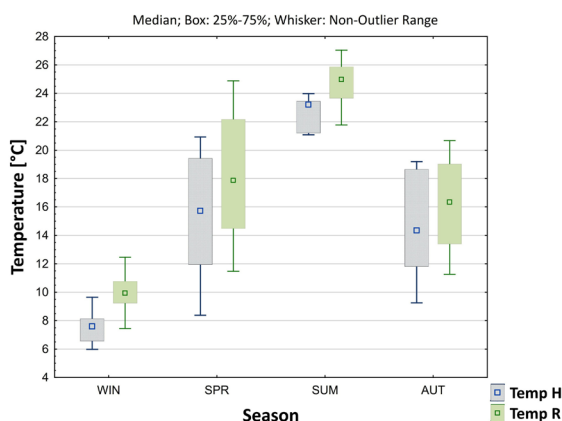

Fig. 6. Comparison of historical (H) and recent (R) temperature data from the Gulf of Trieste in different seasons

Aequorea cf. forskalea seasonal distribution

In recent years (2000-2020), *A. cf. forskalea* medusae have been observed in winter and spring, with few exceptions: in October 2001, September 2014 and August 2020 (Fig. 3). In contrast, the historical records (1900-1911) show that *A. cf. forskalea* medusae were regularly observed not only in winter and spring but also in autumn (Fig. 5), and in 1908 the highest semi-quantitative abundance (categories 2 and 3) were reported in October-December (STIASNY, 1909). The current occurrence of *A. cf. forskalea* was significantly different from the historical data (R=0.089, p=0.002), for which precisely the differences in abundance of the species in autumn (R=0.302, p=0.0001) and winter (R=0.06, p=0.017) were responsible. At the same time, the seasonal length of the plankton phase of *A. cf. forskalea* (medusae) has recently decreased from 4-7 months in the historical data set to 2-5 months currently, indicating a significant temporal change in life cycle events.

To examine the degree of similarity in the seasonal distribution pattern of *A. cf. forskalea*, the four abundance categories were subjected to hierarchical clustering and MDS ordination (Fig. 7). According to the SIMPROF test, the following clusters were statistically significant
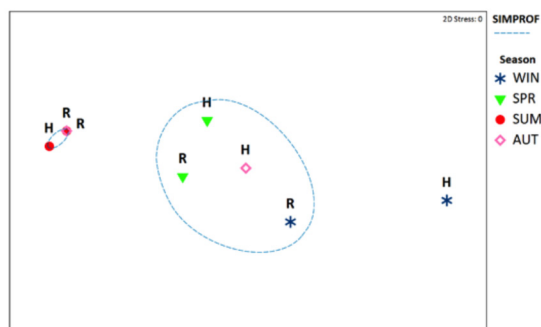

Fig. 7. Non-metric multidimensional scaling (MDS) ordination of seasons for two periods (H and R) based on Euclidean distance of semi-quantitative abundance data of Aequorea cf. forskalea. *Statistically significant separations are indicated by the dashed line at Euclidean distance of 0.31, Π = 0.03 and a significance level of 0.0004. (WIN, winter; SPR, spring; SUM, summer and AUT, autumn)*

Table 1. Descriptive statistics for the temperature parameter over four seasons in the historical (H) 1900-1911 and recent (R) 2003-2020 periods.

Statistic	AUT H	AUT R	SPR H	SPR R	SUM H	SUM R	WIN H	WIN R
Number of observations	10	54	12	54	12	54	12	54
Minimum	9.250	11.264	8.380	11.471	21.090	21.779	5.990	7.445
Maximum	19.190	20.668	20.930	24.876	23.970	27.030	9.650	12.465
Range	9.940	9.404	12.550	13.405	2.880	5.251	3.660	5.020
1st Quartile	12.083	13.433	12.373	14.533	21.845	23.672	6.950	9.265
Median	14.345	16.331	15.715	17.861	23.190	24.974	7.590	9.931
3rd Quartile	18.310	18.901	19.255	22.159	23.375	25.850	8.095	10.760
Mean	14.740	16.247	15.358	18.173	22.645	24.751	7.636	10.036
Variance (n-1)	13.727	8.372	17.948	16.221	1.088	1.900	1.233	1.160
Standard deviation (n-1)	3.705	2.893	4.236	4.028	1.043	1.379	1.110	1.077

Table 2.Results of one-way ANOSIM test for differences between semi-quantitative abundance of Aequorea cf. forskalea *in four seasons in two time periods (H) 1900-1911 and (R) 2000-2020 (n.s., non-significant).*

Group	Period H Global R=0.162, p=0.01%		Period R Global R=0.081 p=0.01%	
	R Statistic	Significance level [%]	R Statistic	Significance level [%]
Winter, Spring	0.173	0.1	0.037	0.5
Winter, Summer	0.473	0.01	0.179	0.01
Winter, Autumn	0.101	0.9	0.179	0.01
Spring, Summer	0.065	1.0	0.046	0.01
Spring, Autumn	-0.006	n.s.	0.046	0.01
Summer, Autumn	0.132	0.08	-0.001	n.s.

Table 3. Results of one-way ANOSIM test for differences between semi-quantitative abundance of Aequorea cf. forskalea *in four seasons in two times periods (H) 1900-1911 and (R) 2000-2020 (n.s., non-significant). .*

Group	Period / Season Global R=0.122, p=0.01%	
	R statistic	Significance level [%]
Winter H *vs.* Winter R	0.06	1.7
Spring H *vs.* Spring R	-0.01	n.s.
Summer H *vs.* Summer R	-0.012	n.s.
Autumn H *vs.* Autumn R	0.302	0.01

Fig. 8. The proportion of each category of semi-quantitative abundance of Aequorea cf. forskalea *during the four seasons in the historical (H) and recent (R) periods based on frequency of occurrence. (WIN, winter; SPR, spring; SUM, summer and AUT, autumn) (For interpretation of categories, see the Material and methods chapter.)*

at p=0.0004 (indicated by the dashed line): the first cluster includes the summer season of both periods and the recent autumn, the second cluster includes the spring of both periods, the historical autumn and the recent winter, while the historical winter is grouped in a separate cluster.
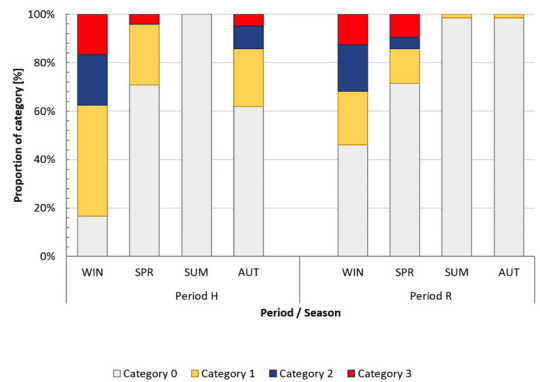
The proportion of each category in each season for the historical and recent periods shows the differences in seasonal distribution and the reason for this grouping (Fig. 8, Table 2). While the differences between the historical and recent periods were not significant for summer and spring, significant differences were found in winter and especially in autumn (Table 3). They were characterized by a less frequent sporadic occurrence (category 1) in winter and an almost complete absence of the species in autumn in the most recent period (Fig. 8).

DISCUSSION

Spatial and temporal patterns in recent period

Although species belonging to the genus *Aequorea* are distributed worldwide, their medusa stage is conspicuous, forms blooms in some years, and is a strong competitor for fish, knowledge of these hydrozoans is limited to only a few locations in the world's oceans (see PURCELL, 2018).

In temperate latitudes, higher abundances of *A. forskalea* have been observed most frequently in winter and spring (SPARKS *et al.,* 2001; PURCELL, 2018; GIBBONS *et al.,* 2021). Very few data are available for *A. forskalea* in the Mediterranean Sea. GÜRLEK *et al.* (2013) provided data on *A. forskalea* in Iskenderun Bay (eastern Mediterranean) in January and June 2012, while DEIDUN & PIRAINO (2021) reported a brief but intense occurrence of *A. forskalea* (last week of March – first week of April 2021) in nearshore waters of the Maltese archipelago. According to historical records, higher abundances of *A. forskalea* in the Mediterranean Sea are known for the northern Adriatic and western Mediterranean (MAAS, 1904; NEPPI & STIASNY, 1912).

The results of our study, conducted over a 21-year period (2000 to 2020), show that *A. cf. forskalea* occurs regularly, albeit with varying abundance, in the Adriatic Sea, and are also the first evidence of its occurrence in the southern part of the Adriatic. The northern Adriatic (NEA) and especially the Gulf of Trieste (TB)

seem to be the subregions of the Adriatic where this hydrozoan species occurs most frequently and has the highest relative abundance, while in other subregions, it occurs only occasionally.

In assessing distribution and phenological changes, it is critical to recognize the bipartite life cycle (benthic polyps and planktonic medusae) of *A. cf. forskalea*. Hydroids (polyps), especially in temperate waters, show apparent seasonality in their growth, and their reproductive periods are predominantly seasonal (COMA, 2000). Hydrozoans produce medusae in response to various environmental stimuli (PRUSKI & MIGLIETTA, 2019), of which temperature is one of the most important (GILI & HUGHES, 1995). In the Mediterranean, there tends to be more hydroids in autumn and winter and less in summer, although other patterns may exist (BAVESTRELLO *et al.*, 2006). In the absence of field and/or experimental data, we can surmise from the seasonal pattern of medusae of *A. cf. forskalea* that the best time for hydroids to produce medusae is autumn to early winter. Furthermore, as with some other cnidarian species (ROSSI *et al.*, 2019), a cold trigger is likely required to stimulate medusa production by *A. cf. forskalea*. Based on our observations over a 21-year period, we assume that the hydroids (polyps) are most likely established in the northernmost area (TB and NEA) and that the sporadic occurrence in other parts of the Adriatic is due to the transport of the medusae with the ocean currents.

The rapid transport between TB and NEA could occur in the presence of an atmospheric anticyclonic gyre and a well-developed northeasterly flow along the Istrian coastline, as evidenced by the models of BUDIŠA *et al.* (2021). Such a circulation pattern is also typical for colder winters (SUPIĆ *et al.,* 2012). *A. cf. forskalea* appeared in large numbers in February at both TB and NEA in 2005, 2012, and 2015, indicating that it was rapidly transported across NEA during these years of colder-than-average winters (https://meteo.hr) and that the circulation type mentioned above was likely present. Considering the prevailing cyclonic circulation (ARTEGIANI *et al.,* 1997; CUSHMAN-ROISIN *et al.,* 2001) of the Adriatic Sea, we speculate that

medusae originating from the northern Adriatic Sea (TB and NEA) were first transported westward and then migrated southward along the western Adriatic coast with the strong and very persistent western Adriatic current (WAC, Fig. 1). Cross-basin transport from the WAC region to the eastern part of the basin (CEA and SEA) is likely provided by less persistent circulation features. These include a fairly persistent cyclonic gyre in the southern Adriatic (SAG) and a less permanent gyre (MAG) in the central Adriatic (ARTEGIANI *et al.*, 1997). The occasional strong north-easterly winds (LIČER *et al.*, 2016; DENAMIEL *et al.*, 2020) blowing through the gaps on the mountainous eastern coasts transport the medusae towards the WAC region (MALAČIČ & PETELIN, 2009). On the other hand, there is a considerable leeward sea current (in NE direction) between the strong bora jets (KUZMIĆ *et al.*, 2006; BOICOURT *et al.*, 2021). These currents and the above-mentioned gyres should allow part of the *Aequorea* medusae, originating from the northernmost part of the Adriatic and migrating southward along the western part of the basin (WAC), to reach the CEA and SEA. Indeed, simulations of the dispersal and connectivity of scyphozoan *Aurelia* during the five-year model run have shown considerable eastward transport of medusae across the basin (VODOPIVEC *et al.*, 2017). The high interannual variability of MAG, SAG and bora events, affects the occurrence of *Aequorea* medusae outside the northernmost areas of the Adriatic Sea. Nevertheless, following the recent publication of MICARONI *et al.* (2022), who reported a bloom of *Aequorea forskalea* in the western coastal Ionian Sea, a possible transport of specimens in SEA during the corresponding BIOS phase cannot be excluded (CIVITARESE *et al.*, 2010).

It is widely believed that warming in temperate zones is reflected in temperature-induced changes in species phenology, manifested by various life cycle events being "brought forward," i.e., occurring earlier in the season (HUGHES, 2000). We hypothesize that the deviation from this picture in *A. cf. forskalea* is related to the benthic phase of their bipartite life cycle. The hydroids of *A. cf. forskalea* probably require a cold trigger, i.e., a critical temperature drop for medusa production. If warm periods persist longer in the autumn, medusa production can be expected to begin later and not appear in the water column until winter/early spring. This delayed medusa production by hydroids also affects the duration of the *Aequorea* medusae season in a year that has recently become shorter and limited to winter-spring. An unavoidable caveat to confirming these observations is the lack of experimental evidence for *Aequorea* polyps.

On the other hand, we observed a similar change in phenology in the scyphozoan moon jellyfish (*Aurelia*) by comparing historical records and current occurrences in the Gulf of Trieste (PESTORIĆ *et al.,* 2021). Laboratory and field data have shown that *Aurelia* polyps require a temperature drop for strobilation and medusa production (FUCHS *et al.*, 2014; HOČEVAR *et al.,* 2018). While moon jellyfish were observed in the autumn in the early 20th century, their more recent occurrence is restricted to winter-spring. Although several other factors could be responsible for these changes in phenology, warming and persistence of higher temperatures in autumn/early winter seems to be the most plausible explanation. Experimental evidence for such a pattern was recently provided by LOVERIDGE *et al.* (2021), who showed that minimal *Aurelia* polyps strobilation (production of young medusae) was observed following incubation at warmer than average temperatures.

Mass occurrences of gelatinous organisms in the northern Adriatic, recorded since the 19th century, have become more frequent and massive in recent decades and are ubiquitous in all seasons. Blooms of autochthonous species *A. cf. forskalea* (this article) in winter-autumn, *Cotylorhiza tuberculata* in summer, and *Rhizostoma pulmo* in some years without pronounced seasonality (PESTORIĆ *et al.*, 2021) have been "joined" by allochthonous invasive species in recent years. In the summer-autumn period from 2016, large masses of Ctenophora *Mnemiopsis leidyi* (MALEJ *et al.,* 2017) are constantly present, which led to a decrease in the density of anchovy populations in the northern Adriatic (BUDIŠA

et al., 2021). New molecular techniques have proven that the Indo-Pacific species *Aurelia solida* (SCORRANO *et al.,* 2017) is present in the Adriatic Sea, rather than the cosmopolitan *A. aurita*. Recently, a completely new species of *Aurelia* was discovered, identified as *A. pseudosolida* (GARIĆ & BATISTIĆ, 2022). Previously, *Pelagia benovici* (PIRAINO *et al.,* 2014) had been described in the northern Adriatic Sea, which was later assigned to the new genus *Mawia* (AVIAN *et al.,* 2016). Therefore, a comparison of historical and recent data (PESTORIĆ et al., 2021; this article) shows that the northern Adriatic is a specific area where significant changes in the life cycles of various macrogelatinous organisms occur in response to environmental pressures, which may affect ecosystem balance and organic matter fluxes. In addition, the observed phenological changes suggest a long-term restructuring of plankton community dynamics and a likely link to warming. As the example of *A. cf. forskalea* shows, it is not only the year-round temperature increase that is important, but also its seasonal changes.

CONCLUSIONS

The present work shows that *A. cf. forskalea* occurs in the Adriatic Sea between one and five months of the year, generally from early winter (January) to late spring (May) and only exceptionally in any other month. The cold-water affinity of *A. cf. forskalea* is confirmed by its high abundance in the cold season and a significant negative correlation with temperature. Based on our data, we estimated the average temperature optimum of *A. cf. forskalea* medusae to be 11.33±2.81°C. The high abundance of *A. cf. forskalea* medusae was regularly observed only in the subregions TB and NEA, which are characterized by the lowest winter temperatures. Their sporadic occurrence in other parts of the

Adriatic Sea suggests the influence of advection from the source population in the north. The seasonal length of the plankton phase (medusa) has decreased in recent decades compared to historical dataset. A significant change in the occurrence of *Aequorea* medusae was observed in the autumn and to a lesser extent in the winter. The polyps, which are probably found only in the northernmost part of the Adriatic Sea, require a critical temperature drop (cold trigger) to start medusae production. If warm periods in autumn last longer, as has been the case in recent decades, medusae production can be expected to start later and not appear in the water column until late winter/early spring. While warming is emerging as a driver of the observed shift in phenology of this meroplanktonic cnidarian, similar effects on other cold-loving species will likely lead to restructuring of plankton communities.

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Nalazi meduze *Aequorea cf. forskalea* u Jadranskom moru: usporedba povijesnih i recentnih podataka

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SAŽETAK

Meduze postaju sve važnija komponenta globalnog proučavanja morskog okoliša, budući da njihove česte masovne pojave utječu na održanje ekosustava, a imaju ekonomske i zdravstvene posljedice. Najnovija su istraživanja usmjerena prvenstveno na masovnu pojavu režnjaka (Scyphozoa) i rebraša (Ctenophora), dok se manje pažnje posvećuje masovnim pojavama hidromeduza, koje također mogu imati veliki utjecaj na morski ekosustav sa značajnim ekonomskim posljedicama. Poput mnogih pripadnika Scyphozoa i Ctenophora, vrste roda *Aequorea* se mogu javljati u visokim brojnostima te njihovu pojavu možemo opisati kao masovnu („bloom"). Na temelju podataka prikupljenih tijekom istraživanja Jadrana u razdoblju od 2000. do 2020. godine te informacija dobivenih od stručnjaka koji se bave istraživanjem mora, razmatrali smo višegodišnju i sezonsku varijabilnost kao i obrasce prostorne raspodjele slabo proučavane vrste *Aequorea cf. forskalea* (Hydrozoa: Leptothecata) koja nastanjuje umjerena klimatska područja. Pretpostavili smo da je ova makro-želatinozna meduza, s bipartitnim životnim ciklusom (bentoski polipi i planktonske meduze), osjetljiva na sezonske i dugoročne promjene temperaturne, budući da temperatura igra ključnu ulogu za izmjenu generacija u životnom ciklusu žarnjaka (Cnidaria). Afinitet *A. cf. forskalea* prema hladnoj morskoj vodi potvrđuje značajna negativna korelacija s temperaturom te učestalo pojavljivanje tijekom zimsko-proljetnog razdoblja. Podaci o temperaturi mora i abundancijama vrste su dostupni za sjeverni Jadran (Tršćanski zaljev) za prvo desetljeće 20. stoljeća, što je omogućilo usporedbu povijesnih podataka (1900.-1911.) s novim setom podataka. U usporedbi s povijesnim zapisima, recentna se pojava *A. cf. forskalea* značajno razlikuje. Sa zatopljenjem sjevernog dijela Jadranskog mora od početka 20. stoljeća se mijenja sadašnja fenologija vrste *A. cf. forskalea*, što je vjerojatno povezano sa zakašnjelom proizvodnjom meduza u jesen, izostankom tijekom jeseni i njihovom rjeđom pojavom tijekom zime.

Ključne riječi: hidromeduze; masovne pojave; dugoročno praćenje; višegodišnja varijabilnost; Sredozemno more