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A *Cladocora caespitosa* bank (National Park Mljet, Adriatic Sea) under climate and anthropogenic impacts: a 20-year survey

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Abstract

The Mediterranean endemic stony coral *Cladocora caespitosa* (Linnaeus, 1767) is the only reef-building and obligate zooxanthellate coral in the Mediterranean Sea. This endangered species is threatened by climate and anthropogenic impacts affecting the coastal zone of the Mediterranean Sea. Growth rates and colony state were monitored over 20 years on a *C. caespitosa* bank in the Marine Protected Area of Veliko Jezero in the Adriatic Sea (Mljet National Park, Croatia). The growth rate of corallites (from 2.02 mm to 5.32 mm annually) was similar to relevant studies in different areas of the Mediterranean Sea and showed a positive correlation with the average annual sea temperature. The coral colonies formed a highly aggregated bank and beds on rocky and sandy bottoms, from 6 to 18 m depth, within a semi-enclosed bay with high water exchange caused by tides. The marine area has experienced abnormally warm summers during the last two decades, with sea temperatures reaching up to 30°C driving population damage to the coral bank. Mortality events of *C. caespitosa* colonies caused by polyp bleaching and tissue necrosis, showed a positive correlation with high sea temperature anomalies during summer and autumn resulting in complete or partial mortality of the colonies. The excessive growth of macroalgal species on coral colonies seems to be a direct consequence of sewage discharges from nearby villages. The present climate-warming trend together with urbanization has severely and negatively affected the *C. caespitosa* coral bank in the Mljet National Park causing concerns for future viability.

Keywords: Scleractinia; bioconstruction; coral bank; ecological impacts; Marine protected area; Adriatic Sea.

Introduction

Corals, together with long-living organisms such as encrusting red algae, polychaetes and bryozoans, are major carbonate producers, or bioengineers, in the Mediterranean Sea (Laborel, 1987; Bianchi, 1997, 2002; Peirano *et al.*, 1998, 2004; Bianchi & Morri, 2000, 2004; Cocito & Ferdeghini, 2001; Kružić *et al.*, 2012; Kružić, 2014). Depending on ecological factors, these organisms may grow to a large size, such as banks of corals or bioherms of red algae (like *Lithophyllum stictiforme* (Areschoug) Hauck 1877)) or bryozoans (Ballesteros, 2006; Biacchi *et al.*, 2022). The colonial scleractinian coral *Cladocora caespitosa* (Linnaeus, 1767) occurs on rocky and sandy bottoms mostly from 5 to 30 m depth (Zibrowius, 1980). This endemic Mediterranean coral has characteristics of zooxanthellate and hermatypic tropical corals. It can be present in the form of individual colonies, beds of a large number of colonies, or coral banks produced by the fusion of large adjacent colonies, covering a wide surface area (Schiller, 1993; Morri *et al.*, 1994; Peirano *et al.*, 1998, 2001; Kružić & Požar-Domac, 2003; Kersting & Linares, 2012; Kružić *et al.*, 2012; Kružić, 2014; Chefaoui *et al.*, 2017; Kersting *et al.*, 2023;Mačić *et al.*, 2024). It is a slow-growing coral with corallite extension rates from 1.3 to 6 mm per year (Peirano *et al.*, 1999; Kružić & Benković, 2008; Kružić *et al.*, 2012; Kersting & Linares, 2012) or calcification rates of 0.8 mg cm^2 per day and 1.7 kg $CaCO_3$ m^2 per year (Peirano *et al.*, 2001; Rodolfo-Metalpa *et al.*, 2006). According to Peirano *et al.* (2001), carbonate production of *C. caespitosa* can reach up to 10 kg $CaCO_3$ per m^2 per year, similar to tropical corals. *Cladocora caespitosa* supports marine biodiversity by building stable carbonate frameworks and adding 3D complexity to the habitat (Pitacco *et al.*, 2014, 2021).

Living and fossil banks of *C. caespitosa* have been found off the coasts of Tunisia, the Columbretes and Balearic Islands in Spain, and in the Aegean and Ligurian seas (Laborel, 1961; Zibrowius, 1980; Peirano *et al.*, 1998; Antoniadou & Chintiroglou, 2010; Kersting &

Linares, 2012; Kersting *et al*., 2023). In the Adriatic Sea, large banks of *C. caespitosa* occur in the Lim Channel on the Istrian peninsula, near the islands of Prvić and Pag, and in the Veliko Jezero Lake in Mljet National Park on the island of Mljet (Abel, 1959; Pax & Müller, 1962; Zibrowius, 1980; Kružić & Požar-Domac, 2003). Large *C. caespitosa* formations are now rare in the Mediterranean Sea, compared to the Pleistocene when *C. caespitosa* formed true "reefs" during warmer climatic stages (Bernasconi *et al*., 1997; Kružić, 2014). The reason for this impoverishment could be related to climatic changes, eutrophication, pollution, habitat degradation and high sedimentation rates (Kružić e*t al*., 2014, 2016; Kersting *et al*., 2014a; Casado de Amezua *et al*., 2015; Zunino *et al*., 2018; Roveta *et al*., 2023; Gutierrez *et al*., 2024).

Cladocora caespitosa was included on the IUCN Red List in 2008 and its current status is endangered (A4bc) (Casado de Amezua *et al*., 2015; Otero *et al*., 2017). Anthropogenic activities such as industrial and sewage discharge, fishing, and coastal development (damaging the colonies by physical impact from rock and building rubble) are major threats to *C. caespitosa*, and have already caused a major decline in the Mediterranean Sea (Casado de Amezua *et al*., 2015; El Kateb *et al*., 2017; Kersting *et al*., 2023). Illegal trawling and dredging result in physical damage to coral colonies and habitat destruction, while small-scale fisheries cause more localised impacts to bioconstructors like *C. caespitosa* (Kersting *et al*., 2022; Ganias *et al*., 2023).

Stress and mortality events of *C. caespitosa* colonies due to seawater temperature changes are well-known and widely described (Rodolfo-Metalpa *et al*., 2005, 2011; Garrabou *et al*., 2009; Kružić *et al*., 2012, 2014; 2016; Kersting *et al*., 2013a, 2015; Jiménez *et al*., 2014; Hadjioannou *et al*., 2019; Azzola *et al*., 2022; Antoniadou *et al*., 2023). Temperature anomalies, related to climate warming and expressed as an extremely high seawater temperature in the Mediterranean Sea, have had a severe impact on the survival of *C. caespitosa* colonies and banks (Rodolfo-Metalpa *et al*., 2005; Kružić *et al*., 2012; Kersting *et al*., 2013a, 2023; Zunino *et al*., 2018). The species endures a high thermal range, with low winter temperatures in the northern Adriatic Sea (as low as 6°C) and high summer temperatures in the southern Adriatic Sea (up to 28°C) (Kružić & Benković, 2008; Kružić, 2014; Kružić *et al*., 2014; Zunino *et al*., 2018). Marine heatwaves with prolonged high sea temperatures (up to three months with surface temperatures above 28°C) caused polyp necrosis and death of 10% of colonies in Veliko Jezero Lake (Kružić & Benković, 2008; Kružić *et al*., 2012, 2016). In the Columbretes Islands of Spain, thermal anomalies between 2002 and 2012 killed off more than 50% of *C. caespitosa* colonies (Kersting *et al*., 2013a). Thermal anomalies also caused polyp bleaching (lack of symbiotic zooxanthellae) in the eastern Adriatic Sea, in Veliko Jezero Lake, and Piran Bay (Slovenia) (Kružić *et al*., 2014). While the death of bleached colonies showed no recovery in Veliko Jezero, most bleached colonies in Piran Bay showed tissue necrosis but successfully recovered. In Cyprus, 24% of *C. caespitosa* colonies suffered polyp bleaching or necrosis due to temperature anomalies of summer 2012 (Jiménez *et al*., 2014), while in the Aegean Sea, 27.49% of the coral colonies were partially bleached (Antoniadou *et al*., 2023). Bleached corals are not dead, but face a higher risk of starvation (Jiménez *et al*., 2014; Kružić *et al*., 2014).

Since habitat-forming species like encrusted algae, sponges, bryozoans, scleractinians and gorgonians are directly affected by mass mortalities in the Mediterranean Sea, long-term studies of the negative impacts of climate change on these species are important to adopt large-scale conservation plans (Garrabou *et al*., 2009; Kružić *et al*., 2012, 2014, 2016; Kersting *et al*., 2013a, 2015; Jiménez *et al*., 2014; Hadjioannou *et al*., 2019; Azzola *et al*., 2022; Antoniadou *et al*., 2023). The present study presents and summarises the results of a 20-year monitoring programme of a *C. caespitosa* bank in Veliko Jezero Lake on the island of Mljet in Mljet National Park, one of the oldest marine protected areas in the Mediterranean (Fig. 1). Growth rate variations and negative impacts

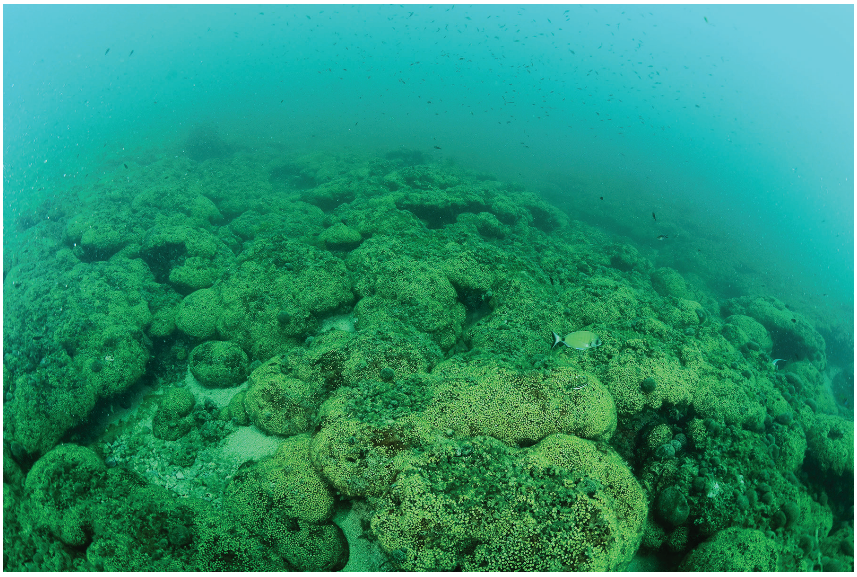

Fig. 1: The *Cladocora caespitosa* bank in National Park Mljet (Photo credits: P. Kružić).

on the coral bank, such as polyp bleaching and mortality, after high-temperature anomalies are presented. The results are discussed with relevant published data from other Mediterranean areas, providing new comparative information on the biological and ecological features of this endangered coral.

Materials and Methods

Main study area

The special natural attractions of Mljet National Park are two marine lakes (called Veliko Jezero and Malo Jezero), created when karst depressions were flooded by the sea in the postglacial period (Fig. 2A). Veliko Jezero (meaning Great Lake) has a maximum depth of 47 meters. These marine lakes communicate with the open sea through the narrow Soline channel constructed of stone blocks, about 60 meters long, 12 meters wide and 3.5 meters deep (Kružić & Benković, 2008). The bank of *C. caespitosa* is located near the channel entrance of Veliko Jezero (42.76888°N, 17.37388°E), and ranges from 6 to 18 meters depth, covering around 650 m^2 (Kružić, 2002; Kružić & Požar-Domac, 2003; Kružić & Benković, 2008). The strong bottom currents occurring as a result of tidal exchange in the Soline channel, appear to enhance coral growth and favour the formation of the bank (Kružić & Požar-Domac, 2002; Kružić & Benković, 2008). The Mljet bank is one of the largest *C. caespitosa* banks known in the Mediterranean Sea and may be comparable to coral reefs in tropical seas (Pax & Müller, 1962; Kružić, 2002; Kružić & Požar-Domac, 2003; Kružić & Benković, 2008).

Research methods

Monitoring of the *C. caespitosa* bank in Veliko Jezero followed the methods described by Kružić (2005), Kružić & Benković (2008), and Kružić *et al*. (2012, 2013, 2014, 2016). Accordingly, data from the last 20 years of study on the coral bank were directly comparable.

The seawater temperature database consists of

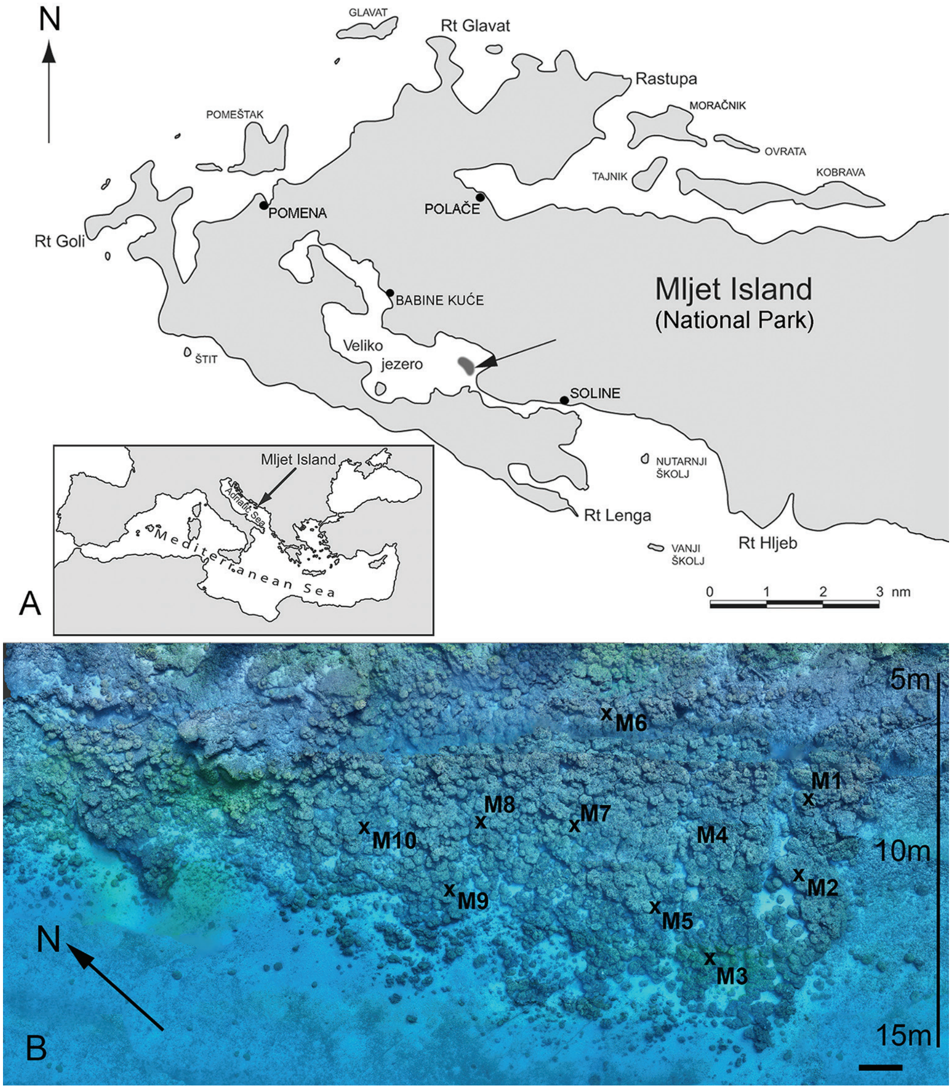

Fig. 2: A) Map of the Mljet National Park with the location of the *Cladocora caespitosa* bank (arrow). B) 2D photo of *C. caespitosa* bank in Veliko Jezero and investigated stations with depth range (Scale bar- 2 m; N-North) (Photo credits: P. Kružić).

high-frequency (1 h intervals) time series obtained using HOBO Pendant temperature loggers (Onset Computers Corporation) with an accuracy of ±0.2°C. The obtained daily data series presents the temporal coverage for the period 2003 to 2021. Temperature loggers were fixed at 10-meter depth with plastic ties to an electrical cable no longer in use. The data were downloaded annually. Older measurements (from 1970 to 2000) of daily average sea surface temperatures (SST) were obtained from the Institute for Marine and Coastal Research (University of Dubrovnik) and the Croatian Meteorological and Hydrological Institute. SST data were used to compare the growth rate over the past 50 years.

Oxygen saturation and dissolved nutrients were measured during summer (monthly from June to October) at 10 m depth, in the central part of the coral bank. Oxygen was measured with a WTW Oxi 197i oximeter and salinity with a WTW CTD probe. Ammonium, nitrate, nitrite, and phosphate in seawater samples were determined in the laboratory (Institute of Public Health) with spectrophotometric methods by Strickland & Parsons (1968).

Sampling surveys were conducted by SCUBA diving during summer periods from 2000 to 2021. The mean growth rates were obtained through corallite X-ray analyses of ten colonies scattered at depths from 6.1 to 14.2 m (stations M1 to M10, Fig. 2B). At each station, 20 to 30 corallites per colony were collected from the coral bank in 2022 for measurements of annual growth rate. Corallites were cleaned in 20% peroxide solution to remove polyp tissue and x-rayed with a medical unit (Siemens Mammomat 300). Coral growth rates were calculated from positive images with *Coral XDS* image analysing software (National Coral Reef Institute of Florida, USA; http://www.nova.edu/ocean/ncri//projects/coralxds/index.html) (Peirano *et al*., 1999, 2005; Kružić & Benković 2008; Kersting & Linares, 2012). Since separate corallites provide noticeable density banding (Peirano *et al*., 1999; Kružić & Požar-Domac, 2002; Peirano & Kružić, 2004; Kružić *et al*., 2012), the linear corallite growth rate was obtained by summing the lengths of HD (high-density in the winter period) and LD (low-density in the summer period) bands on x-rayed corallites, and together representing one year of corallite growth (Peirano *et al*., 1999). Growth rate data obtained by the radiographic method from longer corallites (up to 30 cm long collected from large colonies) allowed for a comparison of the relationship with sea temperature over the last 50 years.

For each surveyed colony, the following data were obtained: depth, size (as colony diameter) and percentage of the colony affected by polyp bleaching and/or necrosis (obtained through photographs of 50 x 50 cm squares).

In each September during the study period, *C. caespitosa* colonies were photographed (with 50 x 50 cm or 25 x 25 cm metal quadrats, depending on colony size) at 10 meters depth along 12 random 10-metre transects. Further, 25 colonies marked for long-term monitoring were photographed. ImageJ software (Schneider *et al*., 2002) was used to calculate the polyp area-percentage cover of healthy tissue and polyp necrosis or polyp bleaching. Four categories were used to assign affected colonies according to the percentage of the colony's surface area affected by polyp necrosis: (I) minor, less than 30%, (II) intermediate, 30% to 60%, (III) severe, 61% to 90%, or (IV) complete, 91% to 100% (Kružić *et al*., 2016).

The algal cover on living *C. caespitosa* colonies on the coral bank was calculated for each study, starting in 2001. Four transect lines marked at 5-metre intervals were used to make 25 m^2 squares (a total of 36 frames were investigated). Moving the frames over the whole coral bank allowed for an estimation of the percentage of algal cover and possible bleaching and necrosed areas on *C. caespitosa* colonies over the bank. Transect lines were also used to monitor polyp bleaching and necrosis over the entire coral bank, and to estimate the algal mucilage carpet on coral colonies.

Statistical methods

Mean values and standard deviation were calculated for coral growth data. The data were tested for normality and homogeneity using the Levene test. Differences between sampling sites within the bank and differences in summer sea temperature changes (anomalies of mean daily values) were analysed with one-way analysis of variance (ANOVA). Tukey posthoc comparison was used when significant differences were found. Kruskal-Wallis analysis was used to test for differences in bleaching and necrosis between colony diameter size classes (<25 cm, 25–50 cm, >50 cm). Differences in the mortality impact and investigated years amongst surveyed stations were analysed using the Kruskal–Wallis test. One-way ANOVA and Kolmogorov-Smirnov test were used to determine whether there were significant differences in polyp bleaching and necrosis between those years (mortality periods) in which necrosis was observed. The significance level was set at $p < 0.05$ throughout. The Pearson r correlation was used to test the correlation between the tested parameters. Statistical analysis and statistical graphics were performed using Statistica 14.0 (StatSoft Inc., Tulsa, OK, USA).

Results

Hydrographic Conditions

The summer sea temperature (June to October) measured at 10 m depth on the coral bank varied significantly over the study period (one-way ANOVA $F_{4,\ 1172} = 3.615$, $p<0.05$). Annual summer cycles showed maximum values from 29.9°C in 2003 to 26.4°C in 2015 (Table 1). The warmest years (by mean value) were 2003, 2009, and 2021 (Fig. 3A). These years significantly differed from all warm summers during the study period, and were also the warmest in the last 40 years in the Adriatic (according to SST data from the Croatian Meteorological and Hydrological Service). The highest sea temperatures at 10 m depth were measured in August 2003 (29.95°C), July

Table 1. Sea temperature values (in °C) at 10 m depth during summer (from June to October) and during the whole year on *Cladocora caespitosa* bank in National Park Mljet.

Year	Tmean (June to October)	Tmin	Tmax	Tmean (January to December)
2003	26.14 ± 2.57	20.27	29.95	20.39 ± 4.03
2006	24.14 ± 3.74	19.75	27.82	19.06 ± 2.56
2009	25.76 ± 2.79	21.63	28.59	20.40 ± .2.19
2012	24.79 ± 3.39	19.05	28.13	19.91 ± 2.36
2015	23.26 ± 3.37	18.33	26.44	19.01 ± 3.04
2018	23.23 ± 3.93	18.59	27.29	18.53 ± 2.12
2021	25.08 ± 3.15	19.88	28.48	19.44 ± 2.71

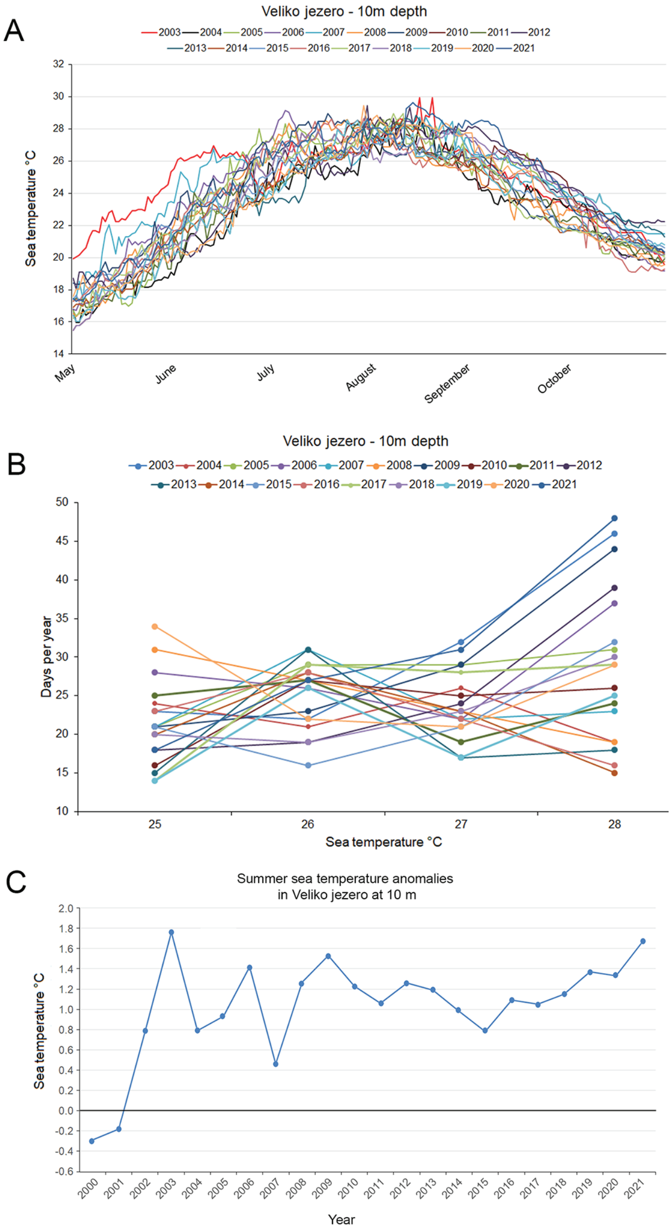

Fig. 3: A) Summer sea temperature values (mean values in °C) at 10 m depth on *Cladocora caespitosa* bank in National Park Mljet from May to October. B) Number of days per year with the highest values of sea temperatures at 10 m depth. C) Summer sea temperature anomalies (from June to October, in °C) at 10 m depth on *C. caespitosa* bank from 2000 to 2021.

2009 (28.59°C), and August 2021 (28.48°C) (Table 1).

The number of days with temperatures over 28°C at 10 m depth was also assessed (Fig. 3B). The longest periods were observed in summer 2021 with 48 consecutive days, followed by 2003 (46 consecutive days), 2009 (44 consecutive days) and 2012 (39 consecutive days). The coral bank was exposed to 100 days of temperatures above 26°C in 2003, and 96 days in 2009.

The frequency of positive thermal anomalies at 10 m depth from June to October has increased since 2002 (Fig. 3C), and these anomalies varied significantly over time (one-way ANOVA $F_{12,\,1571} = 15.207$, $p<0.001$). The maximum differences were found between 2003 with the rest of the studied years, except for 2006, 2009 and 2021. The summer of 2003 was the warmest of the 20-year-long measured data series, with an average positive anomaly of 1.76°C, followed by 2021 (1.67°C) and 2009 (1.53°C).

Oxygen concentrations indicated general healthy conditions of the coral bank area. A significant difference (one-way ANOVA $F_{3,\,2264} = 4.127$, $p<0.05$) was found between October and all other months. The highest oxygen concentrations in the summer period were measured in June (8.27 mg/L in 2018 and 8.24 mg/L in 2006), while the lowest values were measured in October (5.27 mg/L in 2006) (Table 2). The highest mean dissolved oxygen value was measured in 2018 (7.31 ± 1.07 mg/L). The lowest mean oxygen concentration during the summer period was measured in the warmest year, 2003 (6.67 ± 1.78 mg/L). Salinity ranged from 37.29‰ (June 2012) to 38.58‰ (October 2009) (Table 2).

Nitrate concentrations recorded at 10 metres depth were highest in August and October, and lowest in June. The highest mean summer value was measured in 2018 (2.05 ± 0.41 μM). Similar monthly relationships (August and October vs June) were measured for nitrite concentrations, with the highest mean summer value measured in 2006 (0.45 ± 0.12 μM). The highest ammonia concentration was measured in 2018 (1.91 μM), and the highest phosphate concentration in 2003 (0.19 μM). Ammonia fluctuated significantly throughout the sampling period (mean summer values from 1.12 μM in 2003 to 1.91 μM in 2018), showing constant summer growth over the last 20 years. Phosphate concentrations in Veliko Jezero Lake were generally higher in late summer and early autumn. Lower phosphate concentrations in October were presumably the result of the rapid recycling of phosphorus in this ecosystem. Ammonia and phosphate concentrations were significantly higher in August than in June and October (one-way ANOVA $F_{3,\,4226} = 3.534$, $p<0.05$) in all studied years.

Coral growth rates

The highest mean corallite growth rate at the Veliko Jezero bank over the study period was measured at stations M4 (5.32 ± 2.86 mm/year) and M7 (5.23 ± 1.59 mm/year) in 2012 (Table 3). The maximum mean annual growth rates at all stations were 4.39 mm in 2012 and 3.94 mm in 2015, respectively. The lowest mean annual growth rates were measured at station M7 (2.02 ± 0.16 mm/year) in 2009 and M3 (2.24 ± 0.16 mm/year) in 2003. These two years also featured the lowest annual growth rates at all stations (mean 3.11 ± 0.34 mm/year in 2003 and 3.27 ± 0.49 mm/year in 2009) over the 20-year survey. Mean values of corallite linear growth showed significant differences between years at all stations, especially between the two warmest years (2003 and 2009) and the remaining years ($F_{10,\,1302} = 14.782$, $p<0.001$; Tukey post hoc test $p<0.05$). A direct relationship between corallite growth and sea temperature was found, with lower growth rates during the warmer years, 2003 and 2009 (Fig. 4A). Significant spatial differences (between stations) in growth rate were also found (one-way ANOVA $F_{2,\,2257} = 2.034$, $p<0.05$). At the station level, there were no significant differences in corallite growth between colonies from each station (Kolmogorov–Smirnov two-sample test, $p=0.1$).

The corallite growth rate was significantly and positively correlated with sea surface temperature from 1970 to 2021 (r = 0.65; $p < 0.05$) as well in the period between 2000 and 2021 (r = 0.58; $p < 0.05$) (Fig. 6 A, B).

Polyp mortality

Cladocora caespitosa polyp mortality resulted from either direct tissue necrosis or necrosis after bleaching (Fig. 5). While polyp necrosis occurs gradually, bleaching is sudden with an onset of just 2 to 3 days. The first signs of bleaching in the Mljet coral bank were usually detected during August and lasted till late October, ending with polyp mortality. The strongest bleaching event was observed in summer 2003 (Table 4, Fig. 4B), with bleached polyps in more than 27% of observed colonies (27.14 ± 12.33%) over the coral bank. Extensive coral bleaching events were also recorded during the summers of 2009 (15.38 ± 14.21%), 2006 (14.49 ± 9.67%) and 2015 (12.22 ± 7.54%). The number of bleached colonies within the coral bank was positively correlated (r = 0.81; $p<0.01$) with seawater temperatures (at 10 m depth) from 2000 to 2021 (Fig. 6C). There was a direct relationship of coral bleaching both with seawater temperatures and with the number of days of sea temperatures >27°C. Similar results were obtained for the percentages of bleaching in individual colonies, with bleaching values ranging between 22.56 ± 31.78% (2003) and 6.23 ± 10.95% (2018) (Table 4). Significant differences were found in the amount of polyp bleaching over the entire study period among years (Kolmogorov-Smirnov test, $p<0.001$). There were no significant differences in polyp bleaching between depth ranges during the study period within the *C. caespitosa* bank (one-way ANOVA $F_{2,\,2134} = 0.307$, $p=0.732$). No significant differences were found between polyp bleaching and colony size (Kruskal-Wallis test, H = 8.97, df = 7, $p=0.611$). The average percentage of coral bleaching was significantly higher from August and September to October (Kolmogorov-Smirnov test, $p<0.01$).

An extended period of high sea temperatures produces gradual necrosis of polyp tissue without bleaching,

Table 2. Mean summer variations of dissolved oxygen (mgl^{-1}), salinity and nutrient contents (µM) on the *Cladocora caespitosa* bank at 10 m depth. Measurements were made at the beginning of each month. SD = Standard deviation.

Oxygen (mgl^{-1})	**June**	**August**	**October**	**Mean**	**± SD**
2003	7.53	7.16	5.33	6.67	1.78
2006	8.24	7.66	5.27	7.06	1.57
2009	7.47	7.21	5.98	6.89	0.79
2012	7.73	7.32	5.29	6.78	1.31
2015	7.59	7.06	5.76	6.80	0.94
2018	8.27	7.49	6.16	7.31	1.07
2021	7.89	7.33	6.09	7.10	0.92
Salinity					
2003	37.86	38.27	38.44	38.19	0.29
2006	37.56	38.32	38.56	38.15	0.52
2009	37.52	38.23	38.58	38.11	0.54
2012	37.29	38.33	38.36	37.99	0.61
2015	37.44	38.12	38.29	37.95	0.45
2018	37.68	38.29	38.55	38.17	0.44
2021	37.77	38.36	38.52	38.22	0.40
NO_3^- (µM)					
2003	1.29	1.77	1.93	1.66	0.33
2006	1.21	1.33	1.46	1.33	0.12
2009	1.53	2.17	1.87	1.85	0.32
2012	0.86	1.47	1.64	1.32	0.41
2015	1.08	1.38	1.44	1.30	0.41
2018	1.79	2.52	1.85	2.05	0.41
2021	1.77	2.47	2.26	2.17	0.36
NO_2^- (µM)					
2003	0.22	0.37	0.63	0.41	0.21
2006	0.35	0.41	0.59	0.45	0.12
2009	0.17	0.26	0.44	0.29	0.14
2012	0.31	0.39	0.61	0.44	0.16
2015	0.09	0.19	0.46	0.25	0.19
2018	0.27	0.29	0.55	0.37	0.16
2021	0.23	0.27	0.67	0.39	0.24
NH_4^+ (µM)					
2003	0.83	1.56	0.96	1.12	0.39
2006	1.06	1.63	1.29	1.32	0.29
2009	1.07	2.15	1.12	1.45	0.61
2012	0.97	1.92	1.53	1.47	0.48
2015	1.27	2.09	1.84	1.73	0.42
2018	1.62	2.23	1.89	1.91	0.31
2021	1.06	1.24	1.07	1.12	0.10
PO_4^{3-} (µM)					
2003	0.083	0.323	0.163	0.19	0.12
2006	0.077	0.249	0.105	0.14	0.09
2009	0.052	0.261	0.193	0.17	0.11
2012	0.095	0.197	0.118	0.14	0.05
2015	0.049	0.201	0.107	0.12	0.08
2018	0.063	0.229	0.136	0.14	0.08
2021	0.072	0.234	0.143	0.15	0.08

Table 3. Depth of investigated stations and mean *Cladocora caespitosa* corallite growth of sampled colonies (SD - standard deviation).

			Mean corallite growth (mm/year) ± SD						
Station	**Depth (m)**	**Number of corallite per colony**	**2003**	**2006**	**2009**	**2012**	**2015**	**2018**	**2021**
M1	7.7	22	3.18 ± 0.49	3.27 ± 1.14	3.06 ± 0.29	2.49 ± 2.03	3.32 ± 0.84	3.27 ± 2.15	3.44 ± 1.67
M2	10.2	20	3.34 ± 0.28	2.88 ± 1.56	3.33 ± 0.46	2.83 ± 1.27	2.88 ± 0.77	3.03 ± 1.36	3.17 ± 1.29
M3	14.2	25	2.24 ± 0.16	3.28 ± 0.64	3.19 ± 0.33	4.31 ± 1.44	3.94 ± 0.79	3.66 ± 1.08	3.82 ± 1.74
M4	12.2	25	3.19 ± 0.33	4.09 ± 1.33	3.62 ± 1.02	5.32 ± 2.86	4.31 ± 2.16	3.98 ± 1.19	4.12 ± 2.06
M5	12.6	28	3.27 ± 1.05	3.91 ± 1.28	3.56 ± 0.62	4.92 ± 2.17	4.07 ± 1.29	3.56 ± 1.22	3.93 ± 1.63
M6	6.1	20	2.83 ± 0.39	3.94 ± 0.96	3.47 ± 0.37	4.58 ± 1.56	3.96 ± 0.66	4.27 ± 1.94	4.26 ± 2.08
M7	11.9	26	3.08 ± 0.77	3.46 ± 0.51	2.02 ± 0.16	5.23 ± 1.59	4.27 ± 2.53	4.04 ± 0.69	4.17 ± 1.34
M8	10.1	25	3.24 ± 0.51	4.18 ± 1.77	3.11 ± 0.46	4.68 ± 2.12	4.51 ± 0.97	3.67 ± 0.74	3.84 ± 1.27
M9	12.9	28	3.45 ± 1,12	4.23 ± 1.08	3.71 ± 1.21	4.58 ± 1.84	3.98 ± 0.75	3.83 ± 1.29	3.92 ± 0.94
M10	11.3	24	3.29 ± 1.03	3.61 ± 0.82	3.63 ± 1.38	4.99 ± 2.56	4.16 ± 1.12	3.29 ± 0.36	3.63 ± 1.49

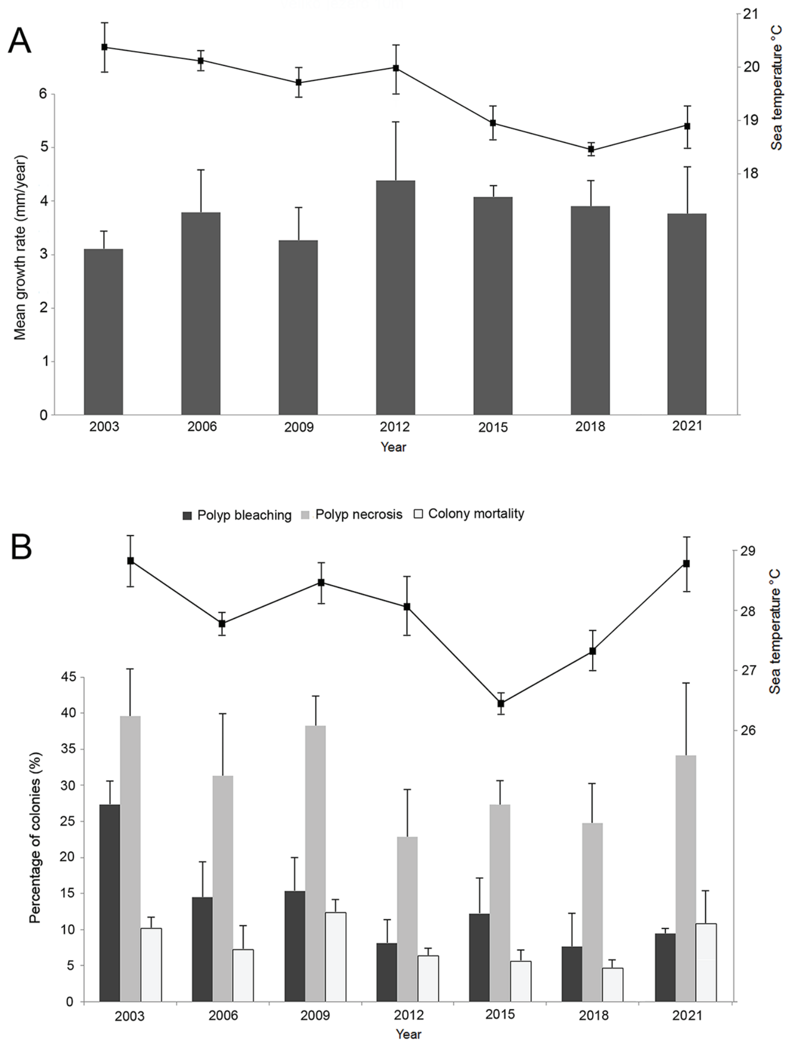

Fig. 4: A) Annual coral growth (bars: mean ± SD) compared with mean annual seawater temperatures (± SD) measured at 10 m depth. B) Percentage of affected colonies with polyp bleaching, polyp necrosis and colony mortality (dead colony) (bars: mean ± SD) compared with mean summer (June to October) seawater temperature (bars: mean ± SD) at 10 m depth in Veliko Jezero (Mljet National Park).

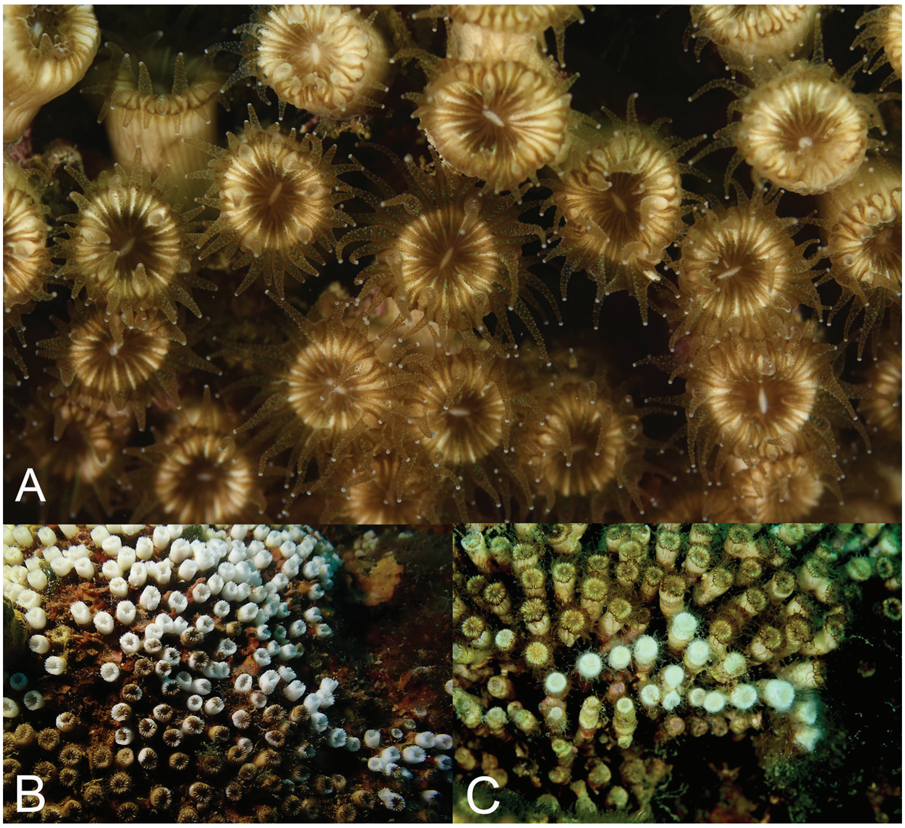

Fig. 5: A) *Cladocora caespitosa* healthy polyps. B) *C. caespitosa* polyp necrosis C) Partially bleached colony of *C. caespitosa* (translucent polyps) at the bank at Mljet National Park (Photo credits: P. Kružić).

Table 4. Percentage of colonies with polyp bleaching (mean on colony and total on coral bank % ± SD), polyp necrosis (mean on colony and total on coral bank % ± SD), colony mortality (%), summer maximum sea temperatures and during summer (in °C) on *Cladocora caespitosa* bank in National Park Mljet.

Year	Polyp Bleaching (colony)	Polyp Bleaching (bank)	Polyp necrosis (colony)	Polyp necrosis (bank)	Total mortality	Tmax	Tmean (June to October)
2003	22.56 ± 31.78	27.14 ± 12.33	27.63 ± 19.86	39.59 ± 21.55	10.16	29.33	26.14 ± 2.57
2006	18.24 ± 23.34	14.49 ± 9.67	29.35 ± 26.74	31.28 ± 18.52	7.23	27.82	24.14 ± 3.74
2009	15.75 ± 27.18	15.38 ± 14.21	31.06 ± 25.83	38.26 ± 16.38	12.37	28.59	25.76 ± 2.79
2012	11.38 ± 16.07	8.16 ± 9.31	23.29 ± 25.44	22.86 ± 17.96	6.38	28.13	24.79 ± 3.39
2015	9.69 ± 14.08	12.22 ± 7.54	22.89 ± 26.15	27.35 ± 22.28	5.59	26.44	23.26 ± 3.37
2018	6.23 ± 10.95	7.67 ± 5.38	19.81 ± 23.27	24.72 ± 12.08	4.62	27.29	23.23 ± 3.93
2021	14.18 ± 26.62	9.69 ± 4.37	33.19 ± 36.27	27.22 ± 16.46	9.14	28.48	25.08 ± 3.15

leaving the bare coral skeleton. The first signs of polyp necrosis were detected in early August at all stations of the coral bank, usually continuing until late October. As with polyp bleaching, direct polyp necrosis showed a high correlation with the number of days of exposure to sea temperatures >27°C (Fig. 6D). There were no significant differences in polyp mortality between depths during the study period for the *C. caespitosa* bank (one-way ANOVA $F_{3,\,3504} = 0.133$, p=0.918).

At the central part of the coral bank, at 10 m depth, 465 colonies were surveyed in the Mljet bank. The highest percentage of colonies with complete necrosis was found in 2021 (152 colonies; 4.63% with complete colony necrosis), 2003 (158 colonies; 3.21% with complete colony necrosis) and 2006 (121 colonies; 2.34% with complete colony necrosis) (Table 5). In total, 465 colonies were surveyed from 10 meters depth at Mljet bank. The lowest values of complete colony necrosis were found in 2018 (1.48%) and 2015 (1.53%). The highest mean values of polyp necrosis events on the bank were recorded during 2003 (39.59 ± 21.55% necrosed polyps) and 2009 (38.26 ± 16.38% necrosed polyps). During these two warmest

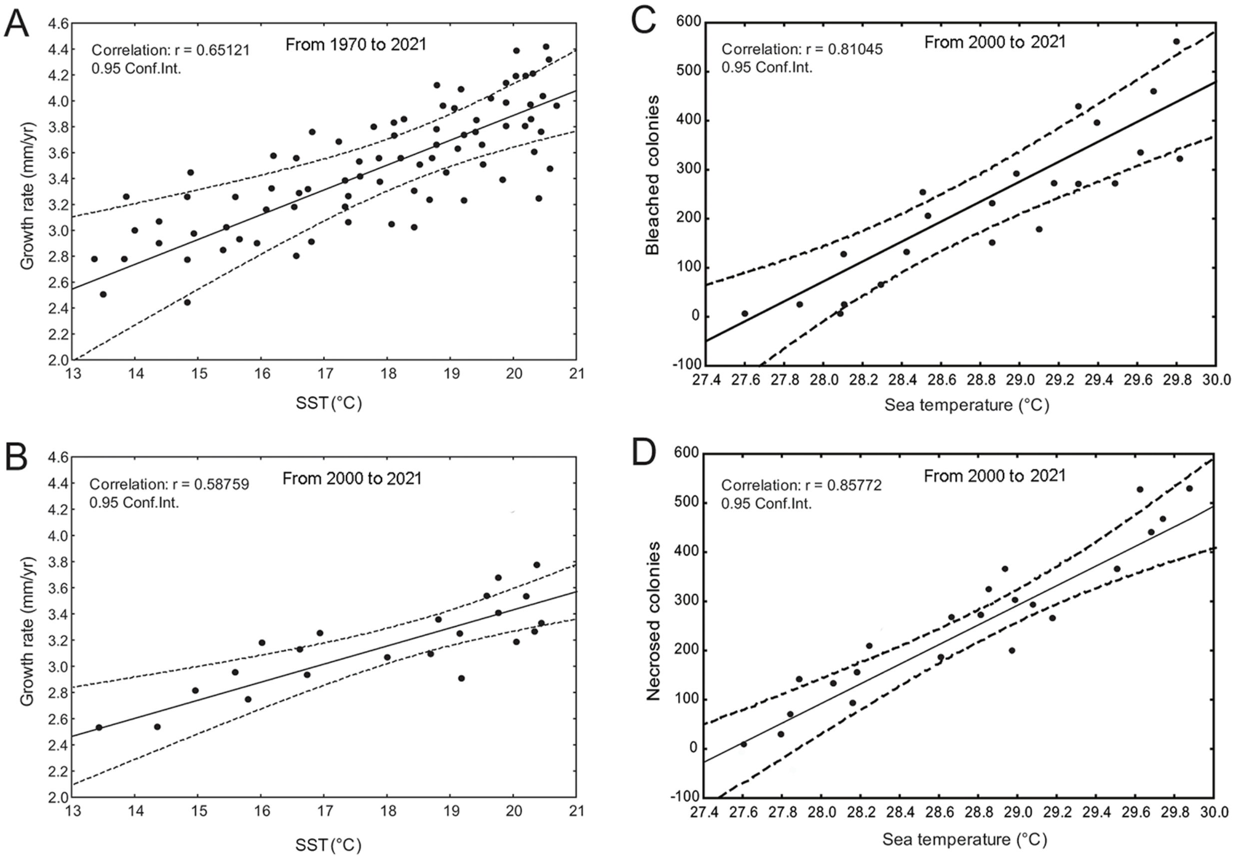

Fig. 6: *Cladocora caespitosa*. A) Relation between mean coral growth rate and sea surface temperature (SST) from 1970 to 2021. B) Relation between mean coral growth rate and SST from 2000 to 2021. C) Relation between bleached colonies and maximum values of seawater temperature at (10 m depth) from 2000 to 2021. D) Relation between necrosed colonies and maximum values of seawater temperature (10 m depth) from 2000 to 2021.

Table 5. The number of affected colonies by polyp necrosis (**minor** – less than 30% of the colony surface area was affected; **intermediate** – 30% to 60% of the colony surface area was affected; **severe** – 61% to 90%; **complete** – 91% to 100% of the colony surface area was affected) on *Cladocora caespitosa* bank in National Park Mljet at 10 m depth. The total number of surveyed colonies at Mljet bank at 10 m depth is 465.

Year	*n* colonies with necrosis	% affected colonies			
		Minor	Intermediate	Severe	Complete
2003	158	20.18	58.26	18.35	3.21
2006	121	42.56	41.77	13.33	2.34
2009	166	51.04	31.24	16.04	1.68
2012	102	59.09	26.33	12.82	1.76
2015	93	60.37	28.54	9.56	1.53
2018	77	55.03	35.16	8.33	1.48
2021	152	12.85	61.33	21.19	4.63

years, 12.37% of the surveyed colonies on the coral bank died completely in 2009 and 10.16% in 2003 (Table 4). Important mean values of polyp mortalities caused by necrosis occurred in 2006 (31.28 ± 18.52%) and 2015 (27.35 ± 22.28%). Lower percentages of necrosis were recorded in 2012 (22.86 ± 17.96%) and 2018 (24.72 ± 12.08%), with only 4.62% of total colony mortality in 2018. Results from 10 m depth showed significant differences between years at the Mljet bank, especially between the two warmest years (2003 and 2009) and other studied years ($F_{9,\ 0492} = 14.755$, $p<0.001$; Tukey post hoc test $p<0.05$). The number of colonies that suffered polyp necrosis within the Mljet bank was positively correlated with seawater temperatures from 2000 to 2021 ($r = 0.85772$, $p<0.01$) (Fig. 6D). A higher impact was observed during years with a longer period (days per year) with a sea temperature >27°C.

There were no significant differences in necrosis over the entire study period between stations (Kolmogorov-Smirnov test, *p = 0.33*) or between polyp necrosis and colony size (Kruskal-Wallis test, *p = 0.526*).

Values of polyp necrosis for individual colonies ranged between 19.81 ± 23.27% (in 2018) and 33.19 ± 36.27 (in 2021) (Table 4). Significant differences were found in polyp necrosis for individual colonies over the study period among the colony depth ranges (from 6 to 18 m depth) (Kolmogorov-Smirnov test, $p<0.001$). None of these necrosed colony areas of the coral bank recovered.

Local threats

The increased nutrient content during the summer period, mostly caused by tourism in adjacent villages (Soline and Babine Kuće) along the marine lake Veliko Jezero and Soline Channel, enhances phytoplankton and macroalgal bloom, reducing light availability. Due to the algal bloom, the coral bank was interspersed and covered with a carpet of algae (mucilage carpet) (Fig. 7C). Three species of pluricellular filamentous algae were identified in the mucilage aggregates: the Pheophyceae *Acinetospora crinita* (Carmichael) Sauvageau, and the Pelagophyceae *Chrysonephos lewisii* (W.R. Taylor) W.R. Taylor and *Nematochrysopsis marina* (J. Feldmann) C. Billard, together with a mix of benthic dinoflagellates (species of the genera *Gonyaulax*, *Prorocentrum*, *Dinophysis* and *Ostreopsis*, including *Ostreopsis* cf. *ovata*). *Acinetospora crinita* was the most dominant algal species on the mucilage covering the coral bank. Light deprivation caused by the algal carpet starves the coral (inability to feed and uptake food through symbiotic zooxanthellae), leading to necrosis. The results of transect lines (25 m^2 square) enabled an estimate that about 10% of *C. caespitosa* colonies on the bank perished from algal bloom smothering in the period from 2000 to 2021.

Frondose macroalgae compete for living space with the coral on the Veliko Jezero bank. The most common macroalgae on the Mljet coral bank were species of the genus *Codium* (i.e., *C. bursa* (Olivi) C. Agardh, *C. coralloides* (Kützing) P.C. Silva, *C. fragile* (Suringar) Hariot and *C. vermilara* (Olivi) Delle Chiaje), *Flabellia petiolata* (Turra) Nizamuddin, and *Halimeda tuna* (J. Ellis & Solander) J.V. Lamouroux (Fig. 7B). During the study period, these algal species increased their surface area on the coral bank from 9.3% in 2003 to 19.8% in 2021 (Fig. 8). Algae grew mostly in the interstices of the *C. caespitosa* colonies, increasing the shaded area, and on parts of colonies that died due to polyp necrosis. Another green alga identified on the coral bank was the invasive *Caulerpa cylindracea* Sonder (Fig. 7A). Since September 2004, when this species was recorded in Veliko Jezero for the first time, it has spread through Veliko Jezero Lake and overgrown the marginal part of the coral bank consisting of smaller colonies. It smothers live coral col-

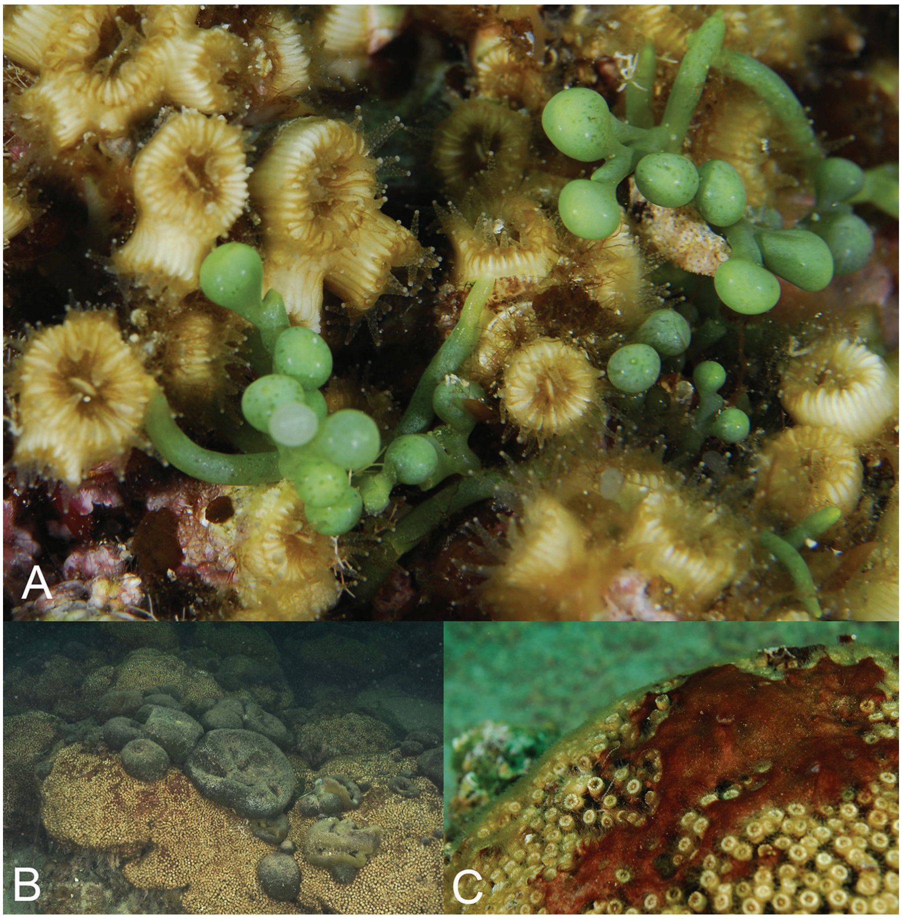

Fig. 7: A) Invasive green alga *Caulerpa cylindracea* on *Cladocora caespitosa* colony in National Park Mljet. B) Green alga *Codium bursa* on *C. caespitosa* colonies. C) Algal carpet on *C. caespitosa* colony (Photo credits: P. Kružić).

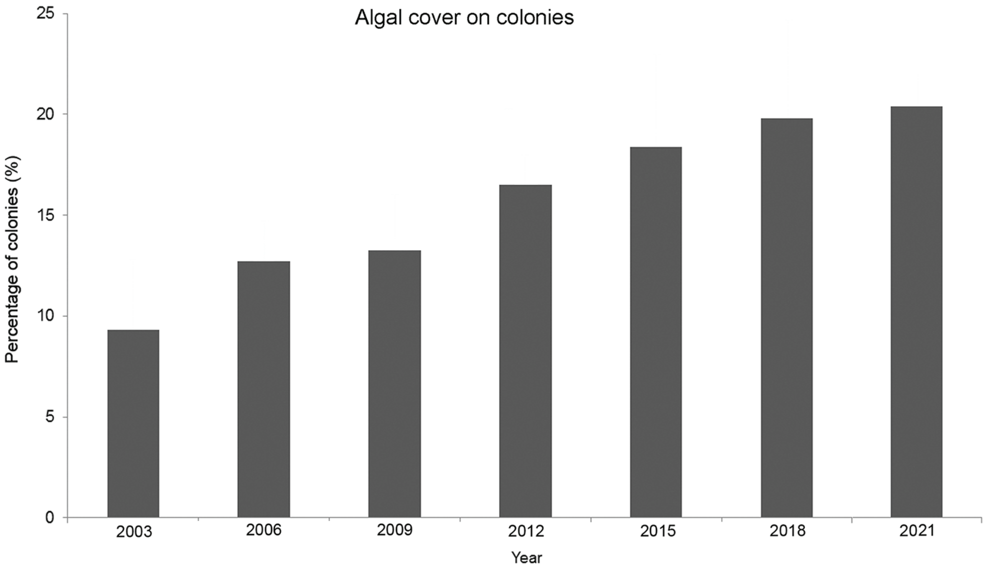

Fig. 8: The percentage of algal cover on *Cladocora caespitosa* colonies on the bank in the Mljet National Park.

onies, leaving the calyx rim deprived of tissue coverage (Fig. 9). In 2016, *C. cylindracea* achieved a homogeneous distribution throughout the entrance of Veliko Jezero Lake and marginal parts of the coral bank at all depths, with high abundances and nearly 100% seabed coverage.

Discussion

The scleractinian coral *Cladocora caespitosa* plays an important ecological role as a bioconstructor in the Mediterranean Sea. With a strong habitat-building capacity, this colonial coral species can build banks that resemble the reefs of tropical seas. It is also one of the most important benthic carbonate producers in the Mediterranean Sea (Peirano *et al.*, 2001). The skeleton of *C. caespitosa* is a source of important biochronological information about climate change in the Mediterranean Sea (Peirano *et al.*, 1999, 2004, 2009; Rodolfo-Metalpa *et al.*, 2008; Kružić *et al.*, 2012; Kersting *et al.*, 2013a; Vergotti *et al.*, 2025). Monitoring long-lived ecosystem engineering species like *C. caespitosa* is crucial, especially given the ongoing climate change and anthropogenic stressors harshly affecting the Mediterranean Sea. A similar long-term monitoring programme of *C. caespitosa* populations in the Mediterranean has been carried out in the Columbretes Islands, Spain (Kersting & Linares, 2019).

Large coral banks, like the one in Veliko Jezero Lake on Mljet Island, develop under specific environmental conditions, including strong bottom currents (Kružić & Benković, 2008). The bottom sea current in Veliko Jezero Lake near the channel is stronger during high than low tide (1.03 vs 0.83 ms^{-1}, respectively) (Kružić & Benković, 2008). The bottom sea currents have a marked influence on sedimentation, on the morphology of the coral colonies within the bank in Veliko Jezero Lake, and on the morphology of the bank itself. The relation between bottom hydrodynamic conditions, morphology and *C. caespitosa* populations has been also described from other sites in the Mediterranean Sea (Laborel, 1961; Kersting & Linares, 2012).

Climate change, especially related to changes in sea

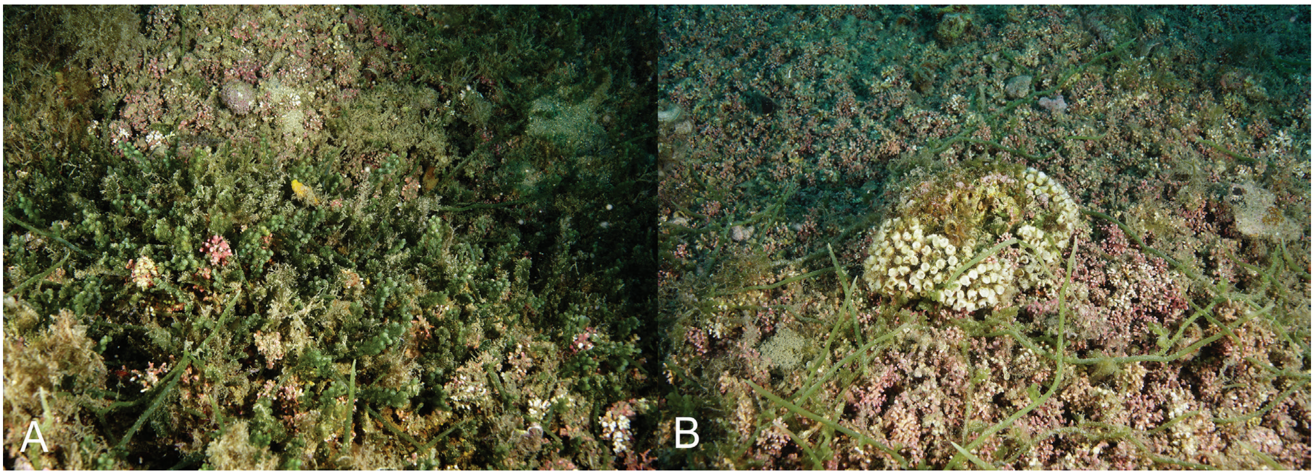

Fig. 9: A) Algal carpet of the invasive green alga *Caulerpa cylindracea* near the coral bank in National Park Mljet. B) Dead colony of *Cladocora caespitosa* colonies after removing algal carpet (Photo credits: P. Kružić).

temperature, affects marine communities, including coral colonies as a combination of 1) the direct impact on organisms, affecting their reproduction, behaviour and survival (Kersting *et al*., 2013a, 2013b; Kružić *et al*., 2014), 2) impact on interrelationships of organisms, such as the introduction of new organisms adapted to the newly created environmental conditions (Kersting *et al*., 2014b; Pons-Fita *et al*., 2020, 2021), and 3) indirect impact through sea currents, given that climate change affects alterations in the thermohaline circulation (Kružić, 2014). All these influences can be observed in the study area of Veliko Jezero Lake, especially expressed as coexistence with macroalgae overgrowth on coral colonies (Kružić & Benković, 2008).

Coral *Cladocora caespitosa* is well adapted to the temperature seasonality of the Mediterranean Sea, though extreme seawater temperatures in winter and summer have an evident impact on this endemic coral along the entire coast of the Adriatic Sea (Kružić *et al*., 2012). The lower sea temperatures measured in the eastern Adriatic Sea during winter are influenced mostly by the cold north-easterly Bora wind. In the Mljet lakes, low winter temperatures on the coral bank are also enhanced by the tides (Kružić & Benković, 2008).

Positive thermal anomalies were recorded at 10 meters depth on the Mljet coral bank every year from June to October starting in 2002. A rising trend of high sea temperature anomalies has been also reported in other Mediterranean areas (Cerrano *et al*., 2000; Rodolfo-Metalpa *et al*., 2005; Sparnocchia *et al*., 2006; Garrabou *et al*., 2009; Jiménez *et al*., 2013, 2014; Kersting *et al*., 2013a, 2014a, 2023; Kružić *et al*., 2014, 2016; Roveta *et al*., 2023; Martínez *et al*., 2023). The warming trend with positive sea surface temperature anomalies in the Mediterranean Sea started in the late 1990s and triggered ecological disturbances, such as mortality events in populations of sessile benthic organisms like sponges, corals and bryozoans (Garrabou *et al*. 2009, 2022; Darmaraki *et al*., 2024). Similar to other Mediterranean regions, during 2003, 2009, 2012 and 2021, sea temperatures were higher than average and the warm and stable conditions lasted for an unusually long time (more than 1 month) with the highest values recorded in August 2003 (29.3°C) (Kružić *et al*., 2016). Although bottom currents mix the seawater around the bank, elevated sea temperatures are a major threat to coral colonies in Veliko Jezero.

Temperature anomalies in the Mediterranean Sea were usually limited to 20 m depth owing to the calm weather conditions between June and August, and played a key role in widespread mortality events (Sparnocchia *et al*., 2006; Garrabou *et al*., 2009; Kružić *et al*., 2016). Several effects were found during exposure of sessile organisms to high temperatures, such as metabolic dysfunction, physiological stress, and development of pathogens (Kushmaro *et al*., 1998; Coma *et al*., 2002; Banin *et al*., 2003; Coma & Ribes, 2003; Bally & Garrabou, 2007; Torrents *et al*., 2008). Another threat to the coral bank is seen in the high sea temperature oscillations measured in Veliko Jezero during summer (up to 5.9°C per day in August) and winter (up to 3.6°C per day in January). Winter sea temperature oscillations usually lead to *C. caespitosa* polyp bleaching (Kružić & Benković, 2008; Kružić *et al*., 2014).

Environmental changes like eutrophication also affect *C. caespitosa* (Kružić *et al*., 2012). Higher eutrophication reduced coral growth on the Mljet coral bank during the experimental fertilisation of Veliko Jezero Lake in 1953 (Kružić, 2005). Around 17 tons of phosphates (117 kg per hectare) were discharged into Veliko Jezero that year, creating large deposits of organic mud on the bottom (Buljan, 1957; Buljan & Špan, 1976; Kružić, 2005; Kružić *et al*., 2012). The constant anoxic conditions in the deeper (40–45 m) part of Veliko Jezero are likely due to this experiment, and additionally, lower growth rates of corallites were measured between 1954 and 1958 on the Mljet bank (Kružić, 2005). The high input of phosphates, nitrates and nitrites into the seawater has been shown to decrease and even stop the process of coral calcification (Simkiss, 1964; Iglesias-Prieto *et al*., 1992; Yamashiro, 1995; Fabricius, 2005). The effects of nutrient enrichment and eutrophication beyond certain thresholds are negative for coral bank functioning and can contribute to loss of coral cover and diversity and increased coral diseases, potentially leading to the disappearance of the coral bank in Veliko Jezero (Kružić & Benković, 2008; Hadjioannou *et al*., 2019). High phytoplankton densities and macroalgae bloom could impose light limitation (shading) on zooxanthellae in coral polyps, resulting in reduced calcification rates.

Algal "blooms" (mostly dinoflagellates) covered colonies of coral in a rag form, wrapping the coral colonies and inhibiting the process of photosynthesis by zooxanthellae and feeding of coral polyps (Kružić & Benković, 2008). Algal bloom events increase polyp necrosis, suggesting that benthic mucilaginous aggregates may be a serious threat to *C. caespitosa* colonies (De Biasi *et al*., 2021). Benthic algae dominate in the struggle for living space, reducing light and growing over colonies (Kružić & Benković, 2008). The algal carpet deprives the coral colonies of light, resulting in starvation (inability to feed and take food through symbiotic zooxanthellae) which can be lethal for the polyps.

None of the measured nutrient values showed large deviations over 20 years of research, though there was a significant difference between June and October values, as a direct impact of tourism (increased tourist load in the national park). The data obtained from the study period show a decrease in oxygen concentration and temperature and an increase in salinity at the end of summer at depths between 10 and 15 m (thermocline area).

Phosphate and ammonia concentrations were significantly higher in August than in June or October, caused mostly by sewage discharge from the villages around Veliko Jezero during the tourism season. Although the experimental fertilisation of the lake in 1953 affected coral growth, winter nutrient enhancement most likely contributes to coral growth in Veliko Jezero, as previously recorded by Schiller (1993) and Peirano *et al*. (2005).

At the Mljet bank, the availability of zooplankton and organic particle ingestion by polyps is surely increased by strong eddy currents during high tide, driving particulate organic matter down towards the coral colonies (Kružić & Benković, 2008). Laborel (1961) observed the maximum development of *C. caespitosa* banks in the North Euboean Gulf (Aegean Sea) in the presence of strong sea currents and high water turbidity. Similar conditions were described in La Spezia (Ligurian Sea) by Peirano *et al.* (1998).

A high number of small *C. caespitosa* colonies occur on coarse sand and algal carpet below the main bank (more than 18 metres deep) and accumulate in depressions as free-living coral nodules or corallites, called "rolling corals" (Kersting *et al.*, 2017a) (Fig. 10), as these small colonies simply roll into the depressions. This is one way of expanding and growing the bank. Many studies have shown that the growth of *C. caespitosa* colonies correlates with climate fluctuations (Morri *et al.*, 2001; Peirano *et al.*, 2009; Rodolfo-Metalpa *et al.*, 2011; Kersting & Linares, 2012, 2019; Kersting *et al.*, 2013b, 2014a, 2014b; Kružić *et al.*, 2012). At the Mljet bank, the correlation between coral growth and sea temperatures in Veliko Jezero showed that higher growth rates of *C. caespitosa* coincided with the warmer period of the year (Kružić *et al.*, 2012). The only threat is represented by elevated temperatures in the Veliko Jezero when coral growth is inhibited due to thermal stress or polyp tissue necrosis.

The growth rates of *C. caespitosa* in Veliko Jezero (range 2.02 ± 0.16 to 5.32 ± 0.86 mm/year) are similar to those measured by Kersting & Linares (2012) near the Columbretes Islands (1.41–5.19 mm/year), Peirano *et al.* (1999) in the Ligurian Sea (1.30–4.03 mm/year), Lipej *et al.* (2013) in Strunjan Nature Reserve in the Gulf of Trieste (3.00–5.70 mm/year), and Vergotti *et al.* (2025) reporting values for the Columbretes Islands (2.93–3.39 mm/year with the highest value of linear extension of 3.20 mm/year), Montgri (2.29–2.90 mm/year) and Cap de Creus (1.56–2.79 mm/year) in Spain. The only deviations from the average in the present study were found at stations constantly under the direct influence of strong bottom sea currents (depending on the bank morphology), such as stations M1 and M2. Mean corallite growth at bank stations has not changed significantly over the last 20 years and continues to correlate with changes in sea temperature, except for the two warmest years (2003 and 2009) that showed slightly lower values. The cause of lower growth values in those two warmer years, perhaps food scarcity or other factor, requires further investigation. Vergotti *et al.* (2025) reported similar results of the long-term impacts of warming on coral growth indicating a decrease in linear extension and calcification rates, which might suggest possible physiological stress events.

Mortality of the coral *C. caespitosa* and other sessile marine invertebrates caused by elevated seawater temperatures has been previously described (e.g., Rodolfo-Metalpa *et al.*, 2000, 2005, 2006; Garrabou *et al.*, 2009; Jiménez *et al.*, 2013, 2014; Kersting *et al.*, 2013a, 2014a; Kružić *et al.*, 2016). Another impact of high sea temperature on *C. caespitosa* polyps is their bleaching, an event that is more common in tropical symbiotic corals. Polyp bleaching was recorded for the first time in 1997 in Veliko Jezero, and this was the first coral bleaching event reported for the Mediterranean Sea (Kružić *et al.*, 2014). Polyp bleaching begins during summer periods (usually in August), when temperatures in Veliko Jezero rise above 27°C, usually to a depth of 15 m, indicating a negative impact of positive temperature anomalies. A high percentage of polyp bleaching in Veliko Jezero was observed during summer 2003, when *C. caespitosa* colonies were exposed to temperatures of 29°C continuously for 46 days (Kružić *et al.*, 2014). A total of 465 colonies experienced partial bleaching and 133 colonies died due to complete bleaching at 10 m depth. Bleaching rates within the coral bank showed high variability be-

Fig. 10: Coral nodule of *Cladocora caespitosa* on the algal carpet near the bank at Mljet National Park (Photo credits: P. Kružić).

tween colonies, possibly due to bank morphology (large fused colonies) and bottom sea currents. Polyp necrosis was found mostly on the central, massive part of the *C. caespitosa* bank, while polyp bleaching was more abundant on smaller colonies surrounding the main bank and in areas not influenced by bottom sea currents. Polyp necrosis is more likely with prolonged exposure to elevated sea temperatures, while polyp bleaching is more likely to result from sudden changes in sea temperature. Another event of polyp bleaching was also found during the summer period. Due to the tidal exchange, the thermocline in Veliko Jezero varies in depth, with cold layers occasionally reaching the lower part of the coral bank (16 m depth), lowering the surrounding water temperature from 26 to 9–12°C and causing polyp bleaching (Kružić *et al*., 2014). These "cold-bleached" corals seem to cope better with prolonged exposure to cold temperatures than "heat-bleached" corals do during prolonged high temperatures, and can successfully recover (Kružić *et al*., 2014). In monitoring the same colonies through the study period, all sections of colonies that suffered "heat-bleaching" ended up in necrosis and died, with no recovery of bleached polyps observed. Kersting & Linares (2019) observed a survival strategy when some polyps in the colony reduced their size (as a transitory resistance phase) after heatwaves in the Columbretes Islands. This process may facilitate faster recovery of colonies severely affected by sea warming.

Shallow-water populations of *C. caespitosa* were decimated after the 2003, 2009 and 2021 sea temperature anomalies in Veliko Jezero. The recorded variations in polyp necrosis amongst the surveyed areas at the coral bank could also be the result of different environmental conditions within the habitat in terms of sea currents and food availability. Under the present climate warming trend in the Mediterranean Sea, new mortality events of the coral *C. caespitosa* might be expected to occur even more frequently in the coming decades (Kružić *et al*., 2016).

Shallow rocky habitats in the Mediterranean are usually dominated by macroalgae. Several papers have described *C. caespitosa* populations thriving among well-developed macroalgal communities and have demonstrated a positive relationship between zooxanthellate corals and macroalgae (Kersting & Linares 2012; Kersting *et al*., 2017b; Pons-Fita *et al*., 2020; 2021). Bank growth could be also limited by the presence and dominance of macroalgae as mentioned by Peirano *et al.* (1998) and Kersting *et al.* (2015). The lower part of the Mljet bank (between 12 and 15 m depth) was overgrown by algal communities (mostly species of the genus *Codium*). Macroalgae on the Mljet bank have increased their coverage in the last 20 years. The reason for the competition between coral *C. caespitosa* and macroalgae could be the lack of hard substrate for algal growth. These interactions are possible within coral beds, but on coral banks where large colonies are connected, there is competition for substrate and macroalgae overgrow coral colonies, causing further colony mortality and reduction of coral growth. The algae start growing on the dead parts of the colonies (after polyp mortality due to necrosis caused by elevated sea temperature) or in the crevices between colonies (between living corallites) and continue to grow. The combination of the elevated sea temperature and algal growth could have an even more negative effect on the coral bank in Veliko Jezero in the future.

Local threats on the coral bank in Veliko Jezero are usually related to eutrophication (village sewage) and illegal fishing trends (many fish are found above and around the bank) in the area of the bank. Algae tend to grow rapidly under high nutrient availability resulting in a high concentration of dead organic matter that starts to decay (Kružić, 2014). The decay process consumes dissolved oxygen in the water, resulting in hypoxic conditions in the deeper part of the Veliko Jezero (40–45 m depth) (Benović *et al*., 2000; Vilibić *et al*., 2010). However, this process has not yet affected the coral bank.

In September 2004, the invasive green alga *C. cylindracea* was found in Veliko Jezero between 8 and 14 m depth, affecting the deeper, marginal part of the coral bank (Kružić *et al*., 2008). This alga was observed to overgrow and smother living coral colonies in the deeper part of the bank not affected by necrosis or bleaching due to elevated temperatures. The strong sea currents appear to favour the input of algal fragments into Veliko Jezero from the open sea and Soline channel. During recent surveys in Mljet, this alga has spread aggressively and increased its coverage to as much as 1500 m^2 in the Channel Soline and approximately 1000 m^2 in Veliko Jezero in the past decade. It can reproduce from fragments, usually as a consequence of tourist boat anchors and the crumbling of the algae in shallow areas during sea storms (Kružić *et al*., 2008; Kružić, 2014). Kersting *et al*. (2014b) found that *C. cylindracea* avoids growing over living polyps of *C. caespitosa,* and did not find any lethal effects of this invasive alga. In Veliko Jezero, smaller dead colonies overgrown by algae were found near the coral bank, but to date, it has not affected the main bank. According to the annual monitoring programme, these colonies were alive before being overgrown with algae. Since 2017, the cleaning of *C. cylindracea* around the coral bank has been successfully carried out as the algae can be easily removed from the sedimentary bottom around the bank. The algae population is constantly checked and cleaned.

Another threat for *C. caespitosa* is linked to the corallivorous gastropods *Coralliophila meyendorffi* (Calcara, 1845) and *Babelomurex cariniferus* (Sowerby, 1834). High abundance of the former gastropod can drastically reduce coral cover (Kružić *et al*., 2013). While *B. cariniferus* is quite rare at the Mljet coral bank, specimens of *C. meyendorffi* (shell length from 5–40 mm) are abundant and feed exclusively on live polyp tissue. Possible outbreaks of *C. meyendorffi* could cause considerable damage to the *C. caespitosa* bank, especially during summer high sea temperatures (Kružić *et al*., 2013).

The Mljet coral bank provides a nursery area for a large number of fish, including the groupers *Epinephelus marginatus* (Lowe, 1834) and *E. costae* (Steindachner, 1878), which are common in the area, while *E. caninus* (Valenciennes, 1843) is occasionally present (Lipej *et* *al*., 2024). Groupers attract illegal fishers, despite a strict fishing ban in Veliko Jezero. Fishing gear (longlines, trolling lines and traps) are often found in the area, with fishing lines damaging the coral colonies by turning them upside down.

The coral bank of *C. caespitosa* in Veliko Jezero could be used as a reference sites for future research on the changing Mediterranean climate, allowing for the study of climate cycles (Kružić *et al*., 2014). The species is a good indicator of climate change and further research will lead to a better understanding of what the Mediterranean Sea is expected to face and withstand in the near future.

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