

Interannual size changes of adult *Aurelia* sp.5 medusae stage in the Marine Protected Area of Mljet Island South Adriatic

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Aurelia aurita s.l. is the most widespread scyphozoan jellyfish that recurrently appear “en mass” and forms large aggregations mainly in coastal waters, embayments and estuaries. Beside anthropogenic factors controlling jellyfish populations climate change may play an important role. The aim of this study was to assess whether climate-related factors in absence of other anthropogenically induced stressor influence medusae size. We investigated seasonal and interannual changes in the size of Aurelia in a “jelly lake” in the National Park of Mljet Island (Croatia) where minimal human impact on the environment makes the Veliko Jezero a natural mesocosm for understanding the impact of climate change on the Aurelia population. The observed changes suggest Aurelia medusa population response to changing environment, in particular to enhanced temperature, by reduced body sizes. Comparison of Aurelia population dynamics from different regions in the Mediterranean Sea revealed the unique feature of the Veliko Jezero population. Despite the similarity of the environmental windows of medusae occurrences in the Veliko Jezero and regions in the Mediterranean Sea, medusae in the Veliko Jezero are present all year round. It seems that the lake bathymetry enables medusae to vertically migrate to deeper and cooler water layer, avoiding the limiting temperatures developed in the upper layer during the summer. These conditions may prolong the Aurelia medusae life span and together with continuous strobilation support the stability of the Aurelia medusae population all year round.

Key words: moon jellyfish, marine lake, climate-related factor, vertical migration, Mediterranean Sea

INTRODUCTION

Jellyfish are ubiquitous components of pelagic marine ecosystems, and pronounced changes in their population size are common in these ecosystems (GRAHAM *et al.*, 2001). Recent publications however, indicate more frequent jellyfish outbreaks worldwide (for a review see PURCELL, 2012), particularly in coastal areas affected by multiple anthropogenic stressors. Synergies between human-related perturbations in marine ecosystems (i.e. eutrophication, overfishing and habitat modification) and climate changes have been shown as plausible causal factors of the jellyfish increase (RICHARDSON *et al.*, 2009).

Compared to fish, jellyfish have short generation times with medusae life span of usually less than one year, therefore populations of gelatinous species may respond to climate forcing without a time-lag (LYNAM *et al.*, 2005). Linkages to variations in climate suggest that jellyfish abundances could change following ocean basin-scale climate oscillations (for a review see PURCELL, 2005). For instance, in the Mediterranean Sea, changes in abundance in the last three decades appear to be related to climate modifications, in particular to rising temperatures (i.e. MOLINERO *et al.* 2008). Besides changes at ecosystem and population levels, global warming may also act at level of individuals. DAUFRENSE *et al.* (2009) showed that populations may respond to increases in temperature with reduced body sizes. Also, previous studies showed that increased temperature may act directly on the metabolic rates of the medusae (MØLLER & RIISGÅRD, 2007) or indirectly on their food supply (LUCAS & LAWERS, 1998). Food availability in medusae natural environment is an important controlling factor for the medusae growth. It was demonstrated that during the periods of scarce food medusae growth rate decreased and maturation occurred at smaller sizes than in well-fed individuals (ISHII & BÄMSTEDT, 1998). Besides food availability, ambient temperature was reported to be controlling the size of medusae at sexual maturity for *Aurelia aurita* s.l. medusae population from Horsea

Lake (LUCAS, 1996), with decreased sizes at maturity with increased temperature.

Among scyphozoan jellyfish that recurrently appear “en masse”, *Aurelia aurita* s. l. is the most widespread. This species forms large aggregations mainly in coastal waters, embayments and estuaries worldwide where water depth, temperature and salinity, and trophic conditions can vary greatly (LUCAS, 2001). *Aurelia aurita* s.l. is the most common scyphozoan jellyfish in the northern Adriatic Sea (KOGOVSĚK *et al.*, 2010) and its recurrence in this region stabilized after 2002 (MALEJ *et al.*, 2012). However, information on the *Aurelia aurita* biological cycle in the Mediterranean is scarce (but see BONNET *et al.*, 2012; MALEJ *et al.*, 2012) and the foundations of the growing abundance of this species remain elusive. Among plausible factors controlling the *Aurelia aurita* populations are overfishing, changes at the base of food web and the bottom-up effects, new marine constructions (MALEJ *et al.*, 2012).

None of these factors seem to influence resident population of *Aurelia* identified as sp. 5 (RAMŠAK *et al.*, 2012) in enclosed marine lake Veliko Jezero on the southern Adriatic island Mljet. The Veliko Jezero lies within protected area with minimal human impact since establishment of Mljet Protected area more than 50 years ago. It therefore represents an ideal location to study structure and functioning of complex marine systems (GRAHAM *et al.*, 2009) including impacts of different factors on jellyfish population. We provide here an assessment of seasonal and interannual changes in the size of adult *Aurelia* sp.5 medusae. We examined these results in regard to environmental variability as indexed by sea surface temperature. These results are then compared to other Mediterranean locations where *Aurelia aurita* s.l. were studied.

MATERIAL AND METHODS

Study area

The study area is located on Mljet Island (Croatia), in a Marine protected area where

Aurelia sp. 5 is known to occur all yearlong (BENOVIĆ *et al.*, 2000) (Fig. 1). The Veliko Jezero is connected with the open sea through a shallow channel (2.5 to 4 m depth) approximately 1 km long. Due to limited water exchange between the Veliko Jezero and the southern Adriatic Sea, its hydrographic features are defined primarily by bathymetry and atmospheric forcing (VILIBIĆ *et al.* 2010). The lake is divided into two >40m deep depressions separated by a 15 m deep reef. The hydrography is characterized by large temperature fluctuations in the surface layer (between 8 and 28 °C), which allow a pronounced seasonal stratification, whereas salinity does not show large variations (BULJAN & ŠPAN, 1976). The development of the thermocline is stronger in summer months and separates the water column in a colder (10-12 °C) and more saline (37.5-38.5) layer below ca. 15 m from the upper layer where temperature and salinity show larger variations (VUČETIĆ, 1953; BULJAN & ŠPAN, 1976). Species composition and abundance of phytoplankton in the Veliko Jezero is comparable to the open waters of the South Adriatic (JASPRICA *et al.*, 1995), while the zooplankton community is characterized by higher abundance and lower species diversity (MILOSLAVIĆ *et al.*, 2010).

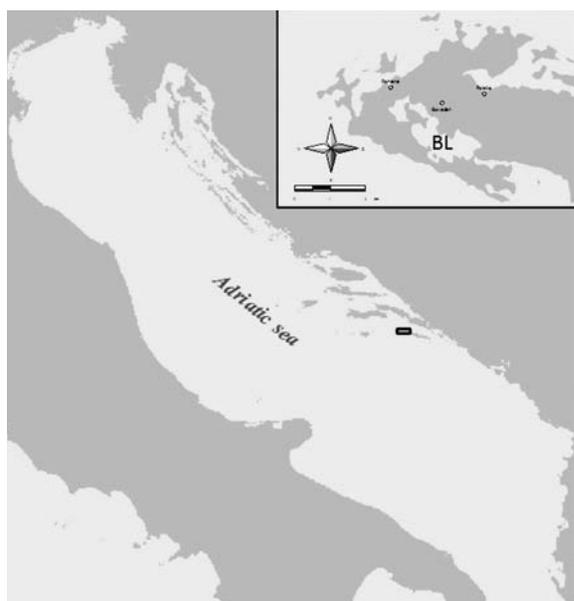


Fig 1 Study area a) Location of Mljet Island, Croatia, in the Adriatic Sea, and b) the Veliko Jezero Lake (BL) at the western tip of the Island

Sampling and data compilation

We used satellite data of sea surface temperature (SST) for southern Adriatic as a proxy of environmental variability. SST has been closely related to climate change and is further associated with modifications in plankton community structure (M. MILOSLAVIĆ pers. comm). The salinity window in the Veliko jezero was constructed on published values (BENOVIĆ *et al.*, 2000; MALEJ *et al.*, 2007). Two complementary sampling methods, zooplankton vertical tows (WP2, 200 µm mesh size) and scuba diving, were used to collect *Aurelia* medusae. The sampling was carried out in 2003 (July), 2004 (May), 2005 (July), 2006 (March and October), 2008 (May), 2009 (May) and 2010 (January). Medusae were stored in a plastic bucket in a shaded place and immediately transferred to the laboratory. Bell diameters were measured to the nearest 1 mm on freshly collected medusae flattened on a glass plate with the oral side facing up before wet weight was determined (± 1 g). A total of 488 individuals were measured.

Vertical tows for zooplankton were taken in three locations in the Veliko Jezero from February 2008 to February 2009 with two nets (200 µm and 125 µm mesh size). The samples were preserved with 4% buffered formalin and checked for ephyrae.

Data analysis

Environmental changes, as indexed by SST, were assessed by means of traffic light plots in the following way: first SST data were standardized to zero mean and unit variance, and the range of values was quantile divided. We tracked variations through changes in quantiles 0.25, 0.5 and 0.9. These quantiles represent low, median and high values, and are therefore suitable for identifying thermal changes in the upper layer. The colours in the traffic light plots represent: red (quantil 0.9), yellow (quantil 0.5) and light blue (quantil 0.25).

The interannual pattern of *Aurelia* adults' size was assessed by means of box and whisker plots. A nonparametric stationary bootstrap

method for correlation analysis (HSIEH *et al.*, 2005) was used to identify the potential relationship between SST and adult size.

RESULTS AND DISCUSSION

The Veliko Jezero is located in a protected national park where human activities are negligible. Hence changes in *Aurelia* sp.5 population structure might be related to natural environmental variations and ecological interactions. The SST shows marked interannual and seasonal variability (Fig 2a). During the first years of the 2000s the SST was lower than the long term mean except in summer 2003, spring and late autumn 2004, and autumn 2006. An abrupt increase of SST in 2007 was observed. This year was characterized by high temperatures almost all year long. Afterwards SST showed

generally higher values than the long term average. It is worth nothing that the changes in SST were observed mostly during the winter (Fig 2b), whereas no significant changes in summer temperatures were observed.

Aurelia aurita s.l. bell diameter can reach > 30 cm in the open areas while in the enclosed environments the average diameter is smaller, commonly less than 10 cm (ISHII & BÅMSTEDT, 1998). *Aurelia* sp.5 from the Veliko Jezero mean size showed a marked variability throughout the sampling periods; however an abrupt change in the size of individuals was observed (Fig 2c). During the period 2003-2006 the medusae sizes ranged between 3.2 cm and 18.8 cm, and more than 90% of all medusae measured during this period fell in the range of 5-15 cm. After the abrupt increase in SST in 2007, the medusae sizes recorded were smaller with bell diameters ranging from 2.1 cm to 11.8 cm, with

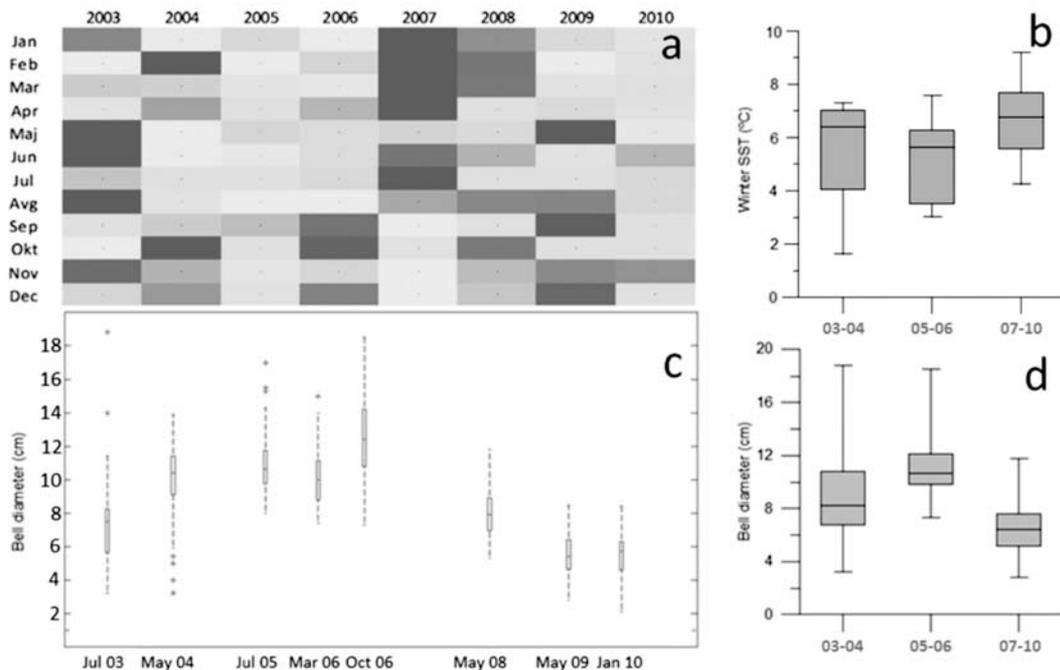


Fig 2. Sea surface temperature and bell diameter of *Aurelia* adults. a) Monthly and interannual variability of sea surface temperature in the Veliko Jezero displayed as a traffic light plot; red represents quantil .9, yellow quantil .5 and light blue quantil .25. b) box-whiskers plot of winter temperatures in periods before (2000-2004 and 2005-2006) and after the marked increase in temperature in 2007 (2007-2010); c) Interannual variations of bell diameter size of adult stages; a noticeable dome-shape pattern characterizes the study period; d) box-whiskers plot of bell size according to the periods before (July 2003 and May 2004; and July 2005 and March and October 2006) and after the marked increase in temperature in 2007 (data from May 2008, May 2009 and January 2010)

most of the values (74%) in the range of 5-10 cm. The close covariation of both variables suggests a potential medusae size-temperature relationship. This was investigated by using a nonparametric correlation test. A negative effect of global warming on the body size of ectotherm organisms has been previously emphasized by DAUFRENSE *et al.* (2009). Temperature can in part contribute indirectly to a smaller body size of the secondary producers in the pelagic food chain, due to the low food quality of small sized primary producers in warmer waters (SOMMER & LENGFELLNER, 2008), changing the energy transfer to higher trophic level. The changes in temperature observed in the recent years in the Veliko Jezero may have caused the changes in the plankton community at the base of the trophic chain, moderating the quality of jellyfish food. Such changes in the food quality may have been the cause of the reduction of medusae individual size observed in the Veliko Jezero. While during this study the zooplankton biomass and abundance in the Veliko Jezero was not measured, we can only speculate about the indirect influence of temperature on adult *Aurelia* medusae size from the lake.

The environmental windows that favour medusae in different locations of the Mediterranean Sea where the species has been investigated show a common general pattern of temperatures and salinities (Fig 3). The temperature and salinity windows that favour *Aurelia aurita* s.l. presence vary from 7 to 28 °C and 32 to 38, respectively. In the lagoons of the W Mediterranean, Bizerte (Tunisia) and Thau (France), the temperature range inhabited by *Aurelia* medusae is between 12.5 and 27.5 °C and between 7 and 24 °C, respectively. Similarly, the salinity ranges overlap (32.5 – 38 and 32.5 – 39.3, respectively) (BONNET *et al.*, 2012). In the Veliko Jezero salinity annually fluctuates between 36.3 and 39 and temperature between 11 and 28 °C. Although medusae in the Veliko Jezero were also observed in the surface layer, the bulk of the population is concentrated below or just above the thermocline layer with temperatures not exceeding 19 °C and salinities between 38 and 39 (MALEJ *et al.*, 2007). In contrast to the shallow lagoons of

the W Mediterranean Sea, the bathymetry of the Veliko Jezero enables medusae to migrate vertically; avoiding higher temperatures in the upper layer during summer and preferentially locates in an environment that might provide metabolic advantages.

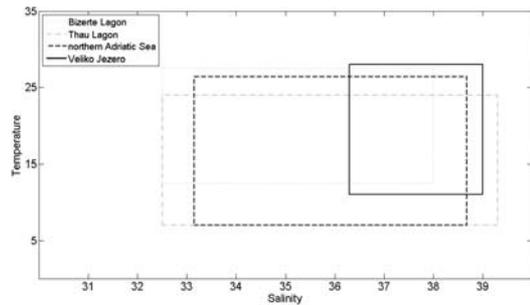


Fig 3. Temperature - Salinity plots of *Aurelia* sp. from different locations in the Mediterranean Sea. Modified from BONNET *et al.* (2012)

Most of the Scyphozoa life cycle comprises a planktonic sexually-reproducing medusae and a benthic asexually reproducing polyp. Scyphistomae in the Veliko Jezero were found attached to rocky substrate below 20 m depth (I. ONOFRI, personal observation). The recruitment from the benthic stage occurs almost all year-round with the peak of ephyrae abundance in May to August (maximum abundance 16 ind. m⁻³ in May 2008), but little is known about the seasonality of juvenile medusae and planulae production (Fig 4a). The presence all year-round of medusae and ephyrae, however, suggests continuous strobilation throughout the year, which makes the Veliko Jezero ecosystem a possible hotspot for *Aurelia* sp. 5 production. Such seasonality is in contrast to previous reports from other temperate regions (LUCAS, 2001), where strobilation occurs mostly during the colder period of the year. For instance, in the north Adriatic (MALEJ *et al.*, 2012) ephyrae have been found in the water column from November to February (Fig 4b) while in the Western Mediterranean, Thau lagoon, that stage is present until April (BONNET *et al.*, 2012) (Fig 4c). While in the Veliko jezero medusae are observed all year-round, in the northern Adriatic Sea and Thau lagoon, the first adult medusae occur in February or April, respectively.

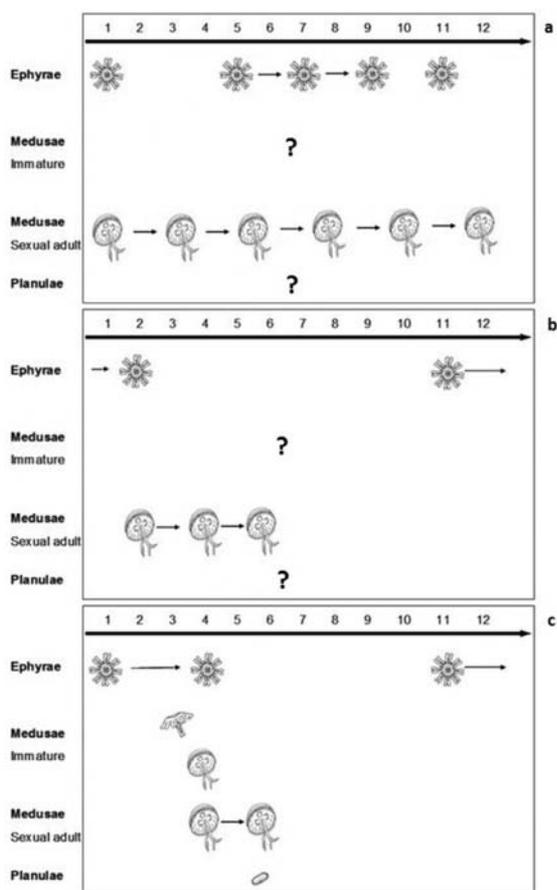


Fig 4 Seasonal succession of *Aurelia* sp. stages in different locations of the Mediterranean Sea: a) Mljet Veliko Jezero (this study), b) the northern Adriatic Sea (MALEJ et al., 2012), c) Thau Lagon, France (BONNET et al., 2012).

Several factors, such as changing temperature, food availability and light intensity are reported to be the cause for the onset of *Aurelia* strobilation (LUCAS, 2001). Even though little is known about the combined effects of the environmental parameters, it is more likely that more than one factor is responsible for triggering the asexual reproduction of the scyphistoma. LUCAS (2001) speculated that a combination of critical environmental conditions is specific to individual populations, and that the response of the benthic stage is partly governed by its genotype. It is possible that the environmental conditions of the Veliko Jezero have caused the selection of certain alleles making the *Aurelia* sp.5 population adaptable to this particular environment. The

isolation of the lake in Holocene (WUNSAM et al., 1999) isolated the *Aurelia* population for around 10 000 years limiting mixing of the gene. This may have yielded a gene combination that differs from those of the *Aurelia* population from other coastal areas in the Mediterranean Sea.

Aurelia sp. 5 medusae in the Veliko jezero preys mostly on small copepods (*Paracalanus parvus* and *Oithona nana*), copepodites and nauplii but also naked ciliates were found in medusae gut contents (MALEJ et al., 2007). By feeding on crustacean zooplankton and ciliates, medusae can indirectly favour phytoplankton. In this ecosystem, former investigations have focused on interactions between *Aurelia* and microbial communities (TURK et al., 2008; TINTA et al., 2010), however little is known about potential predators and top down forces acting on *Aurelia* sp. 5. Nevertheless, recent observations hypothesize that the population size may be in part affected by parasitism rather than predation or food limitation (D'AMBRA et al., 2009).

In addition to a direct impact on the classical food web, indirect trophic linkages to the microbial loop have been shown in the Veliko Jezero by TURK et al. (2008) through consumption of bacteriovores and by release of inorganic and dissolved organic nutrients. A large *Aurelia* sp. 5 population provides an amount of nutrients continuously released to the water column through excretion (CONDON et al., 2011) and by the decay of dead medusae modulating also bacterial dynamics (TINTA et al., 2012). BENOVIĆ et al. (2000) observed higher nutrient concentrations in the bottom layer in the Veliko Jezero suggesting a relationship with *Aurelia* sp. 5 swarms. Besides nutrient accumulation in the bottom layer during periods of *Aurelia* sp. 5 proliferation, the microbial degradation of jellyfish carcasses may impact the oxygen dynamic (TINTA et al., 2010) especially during summer stratification. Potential warming may enhance and prolong the summer stratification which may lead to more frequent anoxic conditions (BENOVIĆ et al., 2001).

Due to the long isolation of the Veliko Jezero from the open sea (WUNSAM et al., 1999), the ecosystem has reached stability and *Aurelia* seems to play a crucial role in its maintenance

(BENOVIĆ *et al.*, 2000). Therefore the change in external forcing i.e. climate, may have a drastic impact on this ecosystem.

CONCLUSIONS

The year round presence of *Aurelia* in the Mljet “jelly-lake” is a unique characteristic never observed thus far in the Mediterranean. We hypothesize that the factors controlling continuous recruitment from benthic to pelagic stages may be linked to other factors than temperature and that lake bathymetry may be an important factor controlling the stability and seasonality of the *Aurelia* sp. 5 population. *Aurelia* polyps were found at depths below the thermocline where the temperature is relatively stable throughout the year. Therefore light and/or food availability may be important factors controlling strobilation in the Veliko Jezero. The lake’s bathymetry enables medusae to vertically migrate to deeper and cooler water layers, avoiding the limiting temperatures for the medusae which establish in the upper layer during the summer. These conditions may prolong the *Aurelia* medusae life span and together with continuous strobilation support the stability of the *Aurelia* medusae population all year round.

Here we hypothesize that medusae in the Veliko Jezero may respond to warmer conditions by reduced medusae body size. Body size

is a biological feature relating many ecological properties, such as fecundity, population growth rate and metabolic rate. The temperature-size rule (ATKINSON, 1994) predicts a negative effect of warming on size at maturity and a positive effect on growth rate, leading to smaller sizes late and larger sizes early in the ontogeny (DAUFRENSE *et al.*, 2009). In this study the age structure of the population and the size at which medusae reached maturity was not investigated. Further investigations would be necessary to identify the possible mechanism that link temperature and sizes of the organisms in the Veliko Jezero, keeping in mind the possible indirect cascading effect through change in food quality that could also contribute to the changes in sizes of organisms.

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Godišnje promjene veličine adultnih primjeraka meduze *Aurelia* sp.5 u zaštićenom području otoka Mljeta, južni Jadran

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SAŽETAK

Aurelia aurita s.l. je najrasprostranjenija vrsta meduze unutar razreda režnjaka (*Scyphozoa*) koje se opetovano pojavljuje u nakupinama. Stvaraju velike agregacije većinom u obalnim vodama, zaljevima i estuarijima. Osim antropogenog, važan utjecaj na populaciju meduza mogu imati i klimatske promjene. Cilj ovog istraživanja je procijeniti u kolikoj mjeri utjecaji povezani s klimatskim promjenama, u odsutnosti drugih antropogeno induciranih stresova, utječu na veličinu meduza. Istraživali smo sezonske i godišnje promjene veličine vrste *Aurelia* u morskim jezerima Nacionalnog parka Mljet (Hrvatska), gdje se Veliko jezero pokazalo kao idealan prirodni mezokosmos za istraživanje i razumijevanje utjecaja klimatskih promjena na populaciju ove vrste.

Uočene promjene ukazuju da populacija meduze *Aurelia* odgovara na promjene okoliša, posebno na povišenu temperaturu smanjujući veličinu tijela. Usporedba dinamike populacije *Aurelia* u različitim dijelovima Sredozemlja otkriva jedinstvenu značajku populacije u Velikom jezeru. Unatoč sličnosti uvjeta okoliša u kojima se meduze pojavljuju u Velikom jezeru i ostalim područjima Sredozemlja, u Velikom jezeru su prisutne tijekom cijele godine.

Očigledno, batimetrija jezera omogućava meduzama avertikalnu migraciju u dublje i hladnije slojeve, izbjegavajući površinski sloj sa povišenim vrijednostima temperature koje se razvijaju tijekom ljeta. Ovi uvjeti mogu utjecati na produžen životni vijek meduza te omogućiti stalnu strobilaciju i stabilnost populacije ove vrste tijekom cijele godine.

Ključne riječi: morsko jezero, klimatske promjene, vertikalna migracije, Sredozemno more