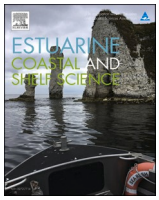
Estuarine, Coastal and Shelf Science 329 (2026) 109678

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



An invader chronicles: local ecological niche of *Mnemiopsis leidyi* in the Venice Lagoon

F. Piccardi [a,b,*], S. Girardello [b], S.M. Bussard [a], V. Tirelli [c,d], D. Borme [c], A. Barausse [b,d], C. Mazzoldi [b,d]

[a] Department of Comparative Biomedicine and Food Science, University of Padova, Viale dell'Università, 35020 Legnaro, Italy
[b] Hydrobiological Station "Umberto D'Ancona", Department of Biology - University of Padova, Isola San Domenico, 30015 Chioggia, Italy
[c] National Institute of Oceanography and Applied Geophysics – OGS, Via Auguste Piccard 54, 34151 Trieste, Italy
[d] National Biodiversity Future Center (NBFC), Piazza Marina 61, 90133 Palermo, Italy

ARTICLE INFO

Keywords:
Invasive alien species
Spatial distribution
Warming
Salinity
Survival

ABSTRACT

The invasive ctenophore *Mnemiopsis leidyi* poses ecological threats in invaded coastal ecosystems such as the Venice Lagoon due to its high fecundity and adaptability to various climates. Although its dynamics have been studied in other regions, information from Mediterranean lagoons, which are characterized by strong spatial and seasonal variability in environmental conditions, remains limited. This study provides the first integrated field and laboratory investigation of the species' ecological niche in the Venice Lagoon, combining two years of spatial distribution monitoring with controlled experiments to define key environmental thresholds for its survival. Our results shows that the species displays a seasonal pattern, blooming in late spring and late summer-early autumn, likely related to warmer temperatures and optimal salinity; indeed, its abundance positively correlated with water temperature and salinity. The controlled laboratory results integrated field observations by showing that *M. leidyi* can survive across a wide range of temperatures (10–32 °C) and salinities (10–34), but the extreme conditions of this range, such as very high temperatures (32 °C) or low salinity (10), markedly reduced its survival. By integrating *in situ* observations with experimentally estimated thresholds, this study provides novel insights into the ecological niche of *M. leidyi* in a Mediterranean lagoon. The results suggest that ongoing climate change may shift the lagoon towards more favorable conditions for this species, potentially intensifying bloom events and their cascading ecological impacts. These findings highlight the need for targeted monitoring and adaptive management to mitigate the ecological and socio-economic consequences of *M. leidyi* expansion.

1. Introduction

The sea walnut *Mnemiopsis leidyi* is a lobate ctenophore listed as one of the 100 most invasive species worldwide by the International Union for Conservation of Nature (IUCN) (Lowe et al., 2000). Native to the Atlantic American coasts, it expanded beyond its native range since the 80's, due to the increasing maritime traffic and global trade, and started a massive invasion of European seas (Ghabooli et al., 2013; Bayha et al., 2015; Shiganova et al., 2019; Putelli et al., 2025). A number of biological and ecological characteristics are the basis for the success of this species in the invaded areas. Its eurythermal and euryhaline characteristics enable the species to tolerate a wide range of salinity and temperature values in native areas as well as in Eurasian seas (Costello et al., 2012; Shiganova, 2020), with the growth optimum regionally depending on the combination of temperature, salinity, and prey availability. Moreover, *M. leidyi* can successfully establish in the invaded habitats due to its high fecundity rate and its capacity to self-fertilize. This species is, indeed, a simultaneous hermaphrodite that can produce up to 14000 eggs per day (highest fecundity observed in the coastal areas of the Northern Adriatic Sea; Malej et al., 2017). These characteristics can lead to massive blooms of the species, which can cause severe damages to species and ecosystems and the associated services. The first invaded area where the impact of this species was disruptive was the Black Sea, where the first massive bloom was recorded in 1989 (the biomass of ctenophores was around 840 million tonnes) (Shiganova et al., 2019). Favoured by the warming of the sea, the ecosystem experienced a strong regime shift with the collapse of the European anchovy *Engraulis encrasicolus* stock and cascading impacts on fisheries as well as

* Corresponding author. Department of Comparative Biomedicine and Food Science, University of Padova, Viale dell'Università, 35020 Legnaro, Italy.
E-mail address: filippo.piccardi@unipd.it (F. Piccardi).

https://doi.org/10.1016/j.ecss.2025.109678
Received 5 June 2025; Received in revised form 17 December 2025; Accepted 20 December 2025
Available online 20 December 2025
0272-7714/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

socio-economic consequences for local communities (Vinogradov and Shushkina, 1992; Shiganova et al., 2019).

In the Northern Adriatic Sea few individuals of *M. leidyi* were first observed in the Gulf of Trieste in October 2005 (Shiganova and Malej, 2009) and then not seen again for a decade. There, from 2016, blooms of this species reappeared every summer (Malej et al., 2017; Pestorić et al., 2021; Tirelli et al., 2021), possibly correlating with a decrease in anchovy population due to competition for zooplankton (Budiša et al., 2021) as observed also in the Black Sea (Vinogradov and Shushkina, 1992; Shiganova et al., 2019). Impacts have been highlighted also in lagoons, in particular in the Venice Lagoon, where small-scale fishery landings decreased concurrently with the massive presence of *M. leidyi* and water warming (Piccardi et al., 2024). Little is still known about the relation between climate change and the spread of this invasive ctenophore, a relevant issue considering the accelerating changes in sea water conditions, in particular in shallow and enclosed areas such as lagoons.

Despite the growing relevance of *M. leidyi* invasion in the Mediterranean, some research gaps still remain; little is known about the actual tolerance thresholds to temperature and salinity and the spatial distribution of *M. leidyi* in Mediterranean transitional systems, where environmental gradients may shape its establishment and spread. The Venice Lagoon offers an ideal model system to address these gaps due to its unique hydrodynamics, shallow morphology, high socio-economic importance, and its spatio-temporal variability of temperature and salinity (Solidoro et al., 2010; Zirino et al., 2014; Tagliapietra et al., 2018). Understanding the environmental preferences of *M. leidyi* and its survival to different combinations of temperature and salinity is therefore fundamental to predict its future spread in the Venice Lagoon, the nearby Adriatic Sea, and other coastal areas, under ongoing climate change. Indeed, the aim of this study was to characterize the local ecological niche of *M. leidyi*, focusing on two key environmental factors, water temperature and salinity, and their possible interactions. This goal was achieved by 1) investigating the spatial distribution of *M. leidyi* in relation to environmental parameters in the Venice Lagoon during two

Fig. 1. Map of the sampling sites in the Venice Lagoon (Italy). Aerial pictures from Google Earth Pro (v. 7.3.4.8642). The map markers show the start ("1") and end ("2) of each transect (identified by a letter, with the alphabetical order reflecting the chronological order of surveys); the letters "S", "C" and "N" at the end of the transect code indicate the surveyed lagoon part.

years of field sampling before and during the season of massive aggregations of the species, and 2) conducting laboratory experiments to verify the findings derived from the field observations with the ultimate goal of finding out whether and which combinations of temperature and salinity could inhibit the survival of *M. leidyi*.

2. Materials and methods

2.1. Study area and sampling sites

The Venice Lagoon (Italy) is the largest lagoon of the entire Mediterranean Sea, situated along the north-western coasts of the Adriatic Sea and hosting a complex ecosystem (Fig. 1) (Ravera, 2000). The lagoon can be divided in three areas according to the 3 inlets connecting it to the sea (Fig. 1): northern (Lido), middle (Malamocco). and southern (Chioggia). With a mean depth throughout the shallow parts of the lagoon of about 1 m, it is highly subjected to temperature and salinity variations influenced by the seasons, tidal shifts and rainfall events. Especially close to river mouths, salinity can be highly influenced by river runoff, and in particular the northern area of the lagoon generally has a lower salinity than the central and southern areas (Zirino et al., 2014). The Venice Lagoon hosts an important vegetal and animal biodiversity, being used as a nursery area by many local fish species (Marani et al., 2006), frequented by many waterbirds, and characterized by various important coastal habitats such as mudflats and salt marshes, endangered by human-driven erosion and sea level rise, and seagrass meadows (Tagliapietra et al., 2018; Tommasini et al., 2019). This ecosystem has a high socio-economic value for the local fishery and aquaculture activities (Rossetto, 2000; Solidoro et al., 2010; Piccardi et al., 2024).

To understand the spatial distribution of the invasive ctenophore *M. leidyi* in relation to abiotic parameters, field survey campaigns were carried out in 2022 and 2023, starting shortly before what in our experience was the seasonal period of ctenophore appearance in the lagoon: from June 2022 to October 2022 in the southern part of the lagoon, and from April 2023 to October 2023 in the northern, central and southern parts of the lagoon (see SI). In each lagoon part, 15 transects were surveyed to collect ctenophores using a bongo net (mouth of the net 18 cm, mesh size of 200 μm and 300 μm respectively, with a flowmeter attached to one of the nets). Considering the size of *M. leidyi* adult individuals (≥1 cm), we assumed that the two different mesh size did not affect the collection. Each transect had an average length from start to end point of approximately 200 m; the first transect was selected as the furthest inland of all the three-lagoon areas, while the last transect was selected as the closest to the sea. The tows were performed with the boat going backwards at minimum speed (approx. 2.22 km/h), to avoid entangling the bongo net with the boat propeller. All tows were conducted during high tide and lasted less than 2 h.

At the start and at the end of each transect, the abiotic parameters were measured at a depth of approximately 10 cm using a HANNA multiparametric probe, specifically: water temperature (°C), dissolved oxygen concentration as percentage of saturation and mg/L, and salinity. The initial and final depths of each transect were recorded using the acoustic depth gauge installed in the boat "D'Ancona" of University of Padova. The data collected at the beginning and end of the transect were averaged to estimate the water parameters and depth of the entire transect. The total number of ctenophores collected at each transect was recorded and, according to the sample size, all specimens or a randomly selected subsample of 100 adult specimens was brought to the laboratory of the Hydrobiological station "Umberto D'Ancona" (Department of Biology, University of Padova) in Chioggia, where their length (LT) and width (LW) were measured in centimetres using a calliper (±0.1 cm).

To calculate the volume of water (m^3) sampled during each tow, the following formulas were used:

$$Sampled\ Water\ volume = 2 \times 0.3 \times 0.0254 \times number\ of\ revolutions$$

Where 2 are the bongo nets, 0.0254 is the area of the mouth of the net expressed in m^2, 0.3 is a constant characterizing the HydroBios flow meter used and the number of revolutions made by the flowmeter is obtained as the difference between initial and final counts.

The number of ctenophores per m^3 was computed as:

$$\frac{Number\ of\ ctenophores\ caught}{Sampled\ water\ volume}$$

2.2. Experimental set up for the survival experiments in the laboratory

To evaluate the tolerance of *M. leidyi* to different combinations of temperature and salinity in the Venice Lagoon, a survival experiment was carried out at the facilities of the University of Padova's Hydrobiological Station "Umberto D'Ancona". Four temperature values were chosen: 10 °C, 18 °C, 28 °C and 32 °C. Temperature 18 °C is the mean water temperature of the lagoon in November of the last 10 years (data have been recorded at the Hydrobiological Station approximately every day since 1973 with a multiparametric probe, see https://chioggia.biologia.unipd.it/en/the-database/parameters-of-lagoon/for details); the temperature of 28 °C was chosen because it represents the upper limit at which *M. leidyi* is reproductively active according to previous studies (Costello et al., 2012). Temperature 32 °C and temperature 10 °C are the warmest and coldest temperatures measured in the last 10 years in the summer and winter months in the southern part of the Venice Lagoon (data have been recorded at the Hydrobiological Station approximately every day since 1973 with a multiparametric probe, see https://chioggia.biologia.unipd.it/en/the-database/parameters-of-lagoon/for details). Four salinity values were chosen: 10, 20, 30 and 34. The northern lagoon displays the lowest salinity values (10 and 20) (Zirino et al., 2014), as most of the rivers discharging freshwater into the Venice Lagoon are located in the northern part of the lagoon; 30 is approximately the average salinity in the central and southern part of the Venice lagoon, while 34 was chosen as one of the highest salinity values recorded at the Hydrobiological Station as described above, and is representative of marine conditions (Zirino et al., 2014).

The experiment consisted of a one-week survival test for the ctenophores at each combination of temperature and salinity and took place in July and August 2023 and 2024. A total of 240 specimens were tested, 15 specimens for each combination of temperature and salinity. Ctenophores were collected with a hand net in the canals of Chioggia in July and August 2023 and 2024. Each specimen was first measured in length and width using a caliper (±0.1 cm) and then placed in a plastic container (25x18 × 13 cm) filled with filtered (1.2 μm) lagoon water at approximately *in situ* conditions (temperature: 28 °C; salinity: 34). The temperature was changed within 24 h by moving the containers to their respective thermo-regulated laboratories: one laboratory at 10 °C, another at 18 °C and the last at 28 °C; to reach 32 °C, the containers were moved to a larger tank with heaters that could hold 4 small plastic containers (each with the ctenophore inside). Salinity was changed manually by adding filtered (1.2 μm) freshwater every 6 h until the target salinity was reached for each experimental condition; this time interval was chosen considering the tidal regime in the Venice Lagoon (Cucco et al., 2009).

Once the target temperature and salinity were reached, the experiment started. The environmental parameters were recorded every 12 h with a "HANNA" multiparametric probe, and the vitality of the specimens was checked twice per day in each container. The movement of the cilia was used as an indicator of the animal's vital status (Tamm, 2014). Once per day, after completing the measurements and checking the survival status of the animal, all ctenophores were fed with approximately 200–1000 *Artemia salina* nauplia per individual (Soto-Angel et al., 2024). The survival rate of each specimen was then evaluated as the cumulative hours the specimen was alive. The experiment lasted up to a maximum of 168 h.

2.3. Data analysis

All data were included in a spreadsheet database, then analyses were conducted using Microsoft Excel, Google Earth (https://earth.google.com/web/) mapping, R (Vers. 4.0.5) and RStudio (Vers. 1.4.1106). T-tests were used to evaluate differences in temperature, salinity, or ctenophore abundance between 2022 and 2023 (considering samplings from June to October) in the southern part of the lagoon. Two-way ANOVA and post-hoc Tukey tests were used to evaluate differences in temperature, salinity, or ctenophore abundance between months and different lagoon areas (north, central, south) in 2023, and to test for any difference in ctenophore survival between the different experimental combinations of temperature and salinity. In all the analyses July and August were combined into 1 month as, in one case, the July sampling was carried out in early August for logistical issues. To assess the relationship between ctenophore abundance and *in situ* environmental variables, we fitted a Generalized Linear Mixed Model (GLMM) using the lme4 package in R (Vers. 4.0.5) and RStudio (Vers. 1.4.1106), assuming a Poisson distribution for the response variable (Bates et al., 2015). The Poisson GLMM was initially fitted to model the effects of Temperature and Salinity on organism abundance, with Month and Area included as random intercepts. Diagnostic checks indicated substantial over-dispersion in the initial model. To address this, we added an observation-level random effect (OLRE), which eliminated the over-dispersion. All results reported are based on the corrected model. Abundance in each transect was modelled as a function of temperature and salinity (taken as average of measures at the start and at the end of each point of the transect) as fixed effects. To account for repeated sampling and potential spatio-temporal patterns and autocorrelation, we included months and lagoon sub-basins as random effects.

3. Results

3.1. Sampling campaigns

The temperature was significantly different in the southern Lagoon between the two years, 2022 and 2023. Specifically, differences were found in July/August, September and October (with positive or negative

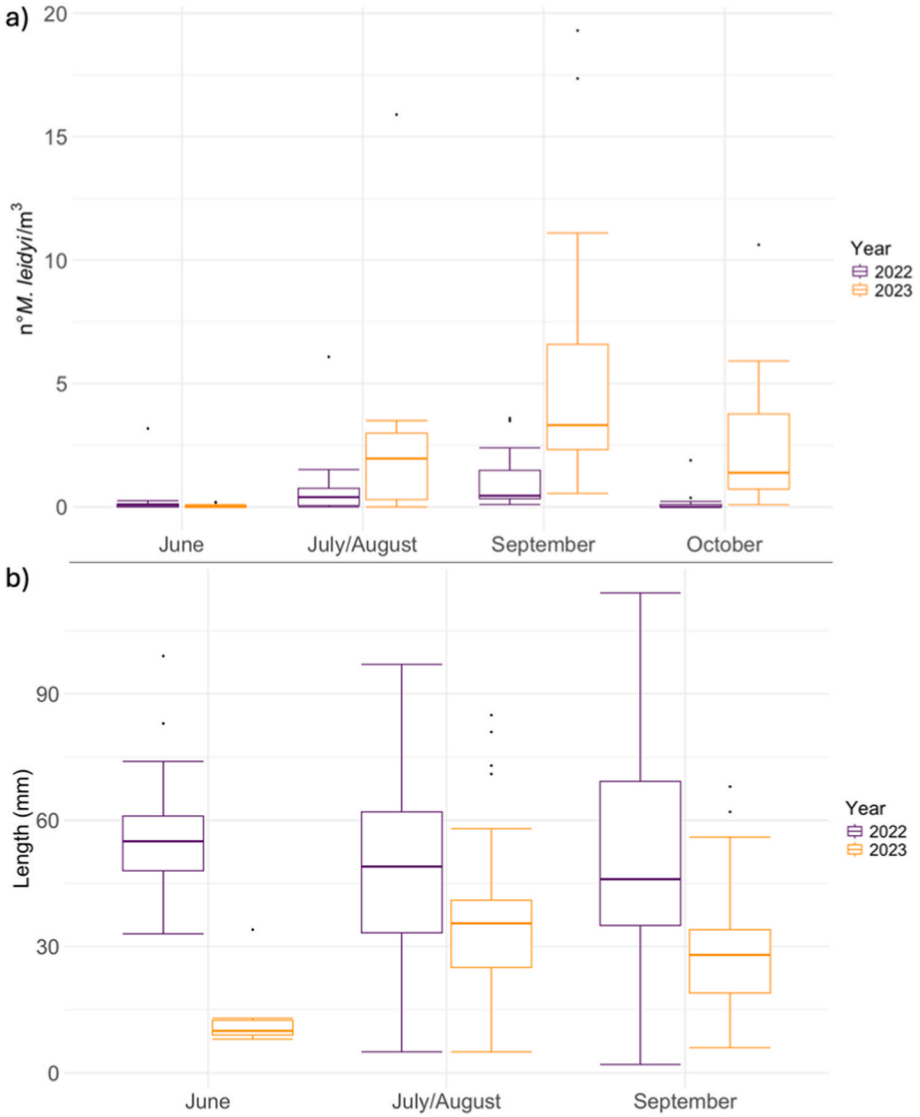


Fig. 2. Ctenophore sampling results in the southern Lagoon **a)** Boxplots representing the number per unit volume of captured ctenophores in different months and years (from June to October 2022 in purple and 2023 in orange). **b)** Boxplots representing the length of the captured ctenophores (expressed in millimeters) in the different months and years (from June to September 2022 in red and 2023 in blue). The box plots show the median (the thick colored line), the interquartile range (the box), and the outliers (dots), while whiskers represent the lowest and the uppermost quartile. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

differences depending on the month, Table S1 & Fig. S1). The salinity was significantly different between years in all months except June (Table S2, Fig. S1). In both years salinity was very high, generally above 30, especially in 2022 when it was mostly above 35.

In the southern Lagoon, very few ctenophores were found in June 2022 and 2023. From July until the end of October they were more abundant. The number of specimens in June and July/August did not differ between 2022 and 2023, while September and October showed a significant difference, with more ctenophores found in 2023 (Table S3). Caught specimens showed a significant difference in size between the two years in all sampling months, with the ctenophores caught in 2023 being significantly smaller than those caught in 2022 (Fig. 2; Table S4).

In 2023, there was a significant difference in the water temperature of the three lagoon sub-basins. Specifically, the central area was significantly warmer than the northern and southern areas in April, the southern area was colder in June, and the northern area was the coldest part of the lagoon from July to October (Fig. 3; Tables S5 and S6).

Regarding salinity, there was a significant difference between the northern and the southern areas of the lagoon in June, July/August and September 2023, with the southern area being saltier (Fig. 3; Tables S7 and S8). In general, in the southern Lagoon salinity levels were never below 26, unlike in the other areas.

The analysis of the captures of *M. leidyi* in 2023 showed a difference in the abundance of ctenophores across months, reflecting the trend of their seasonal appearance and peak, as well as a significant interaction between the lagoon sub-basins and months (Table S9). The post-hoc analysis showed a significant difference in the number of ctenophores only in July/August with animals caught in the southern part of the lagoon being in lower number than in the central and northern parts (Fig. 4; Tables S9 and S10).

The GLMM applied to the field samples revealed a significant positive effect of temperature and salinity on *M. leidyi* abundance (Table 1). The inclusion of month and lagoon sub-basin as random effects also accounted for substantial unexplained temporal and spatial variability. The marginal R^2 was 0.702, indicating that fixed effects (temperature and salinity) explained a major proportion of the variance in ctenophore abundance. Moreover, the conditional R^2 was 0.976, suggesting that fixed effects together with random effects (month and lagoon sub-basin) accounted for nearly all of the variability in the data. Another GLMM run adding the interaction between temperature and salinity provided

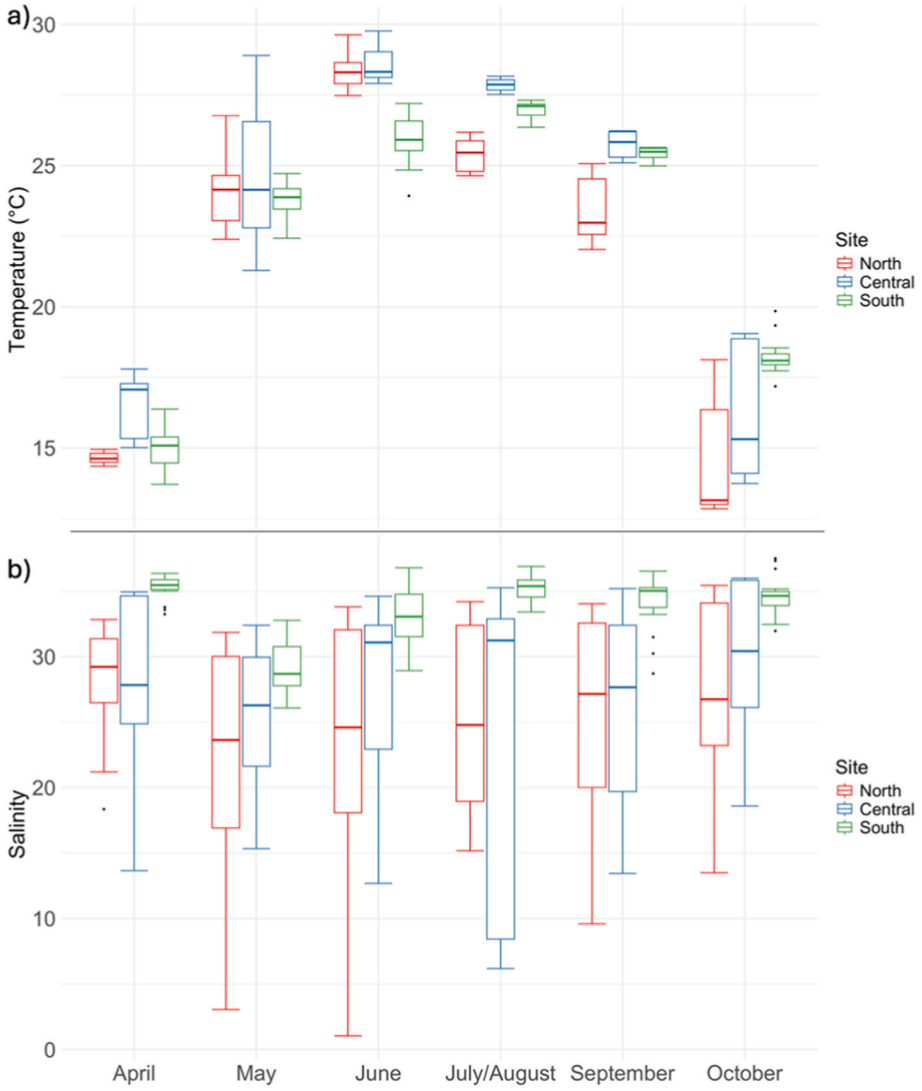


Fig. 3. Environmental data across the Lagoon in 2023. **a)** Box plots representing the temperature (expressed in °C) in the different months (from April to October 2023) in the three different sub-basins of the Venice Lagoon. **b)** Box plots representing the salinity in the different months (from April to October 2023) in the three different sub-basins of the Venice Lagoon. North in red, Central in blue, and South in green.: Box plots show the median (the thick colored line), the interquartile range (the box), and the outliers (dots), while whiskers represent the lowest and the uppermost quartile. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

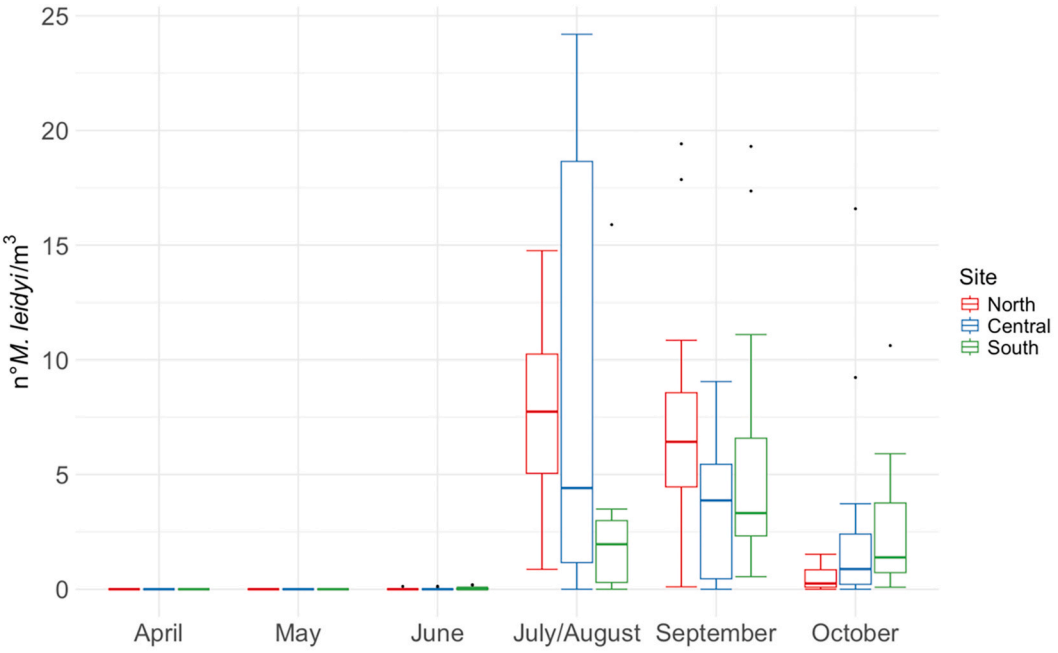


Fig. 4. Number of ctenophores in the different months (from April to October 2023) and in the three different Venice Lagoon sub-basins: North in red, Central in blue, and South in green. Box plots show the median (the thick colored line), the interquartile range (the box), and the outliers (dots), while whiskers represent the lowest and the uppermost quartile. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Summary of fixed effects from the generalized linear mixed model (GLMM) assessing the relationship of ctenophore abundance with environmental variables. Estimates are shown on the log scale; N sample size = 180. Std. Error represents standard errors. P-values (*<0.05) show the statistical significance.

	Estimate	Std. Error	z-value	p-value
Intercept	−0.178	2.450	−0.713	0.476
Temperature	0.115	0.005	23.539	<0.001*
Salinity	0.039	0.002	19.196	<0.001*

similar results respect to the previous one, therefore the results are not reported for the sake of brevity.

3.2. Survival experiments

The results of the laboratory experiment highlighted differences in the survival rate of ctenophores at different temperatures and salinities, with a significant interaction between salinity and temperature (Fig. 5; Tables S11 and S12): at each temperature, survival rates were lower in low salinity treatments. Moreover, survival rates were lower at higher temperatures. In general, all 240 animals survived for at least 12 h during the experiments.

4. Discussion

This study revolved around the relationship between temperature, salinity, spatial distribution and survival of *M. leidyi* in the Venice Lagoon. Our experimental findings provide crucial insights into the ecology of the massive invasion of this species in this lagoon (Piccardi et al., 2024), which are potentially transferable to other marine and transitional water bodies. It also underscores the potential role of climate change with its impact on temperature, precipitation and evaporation patterns (Vargas et al., 2017; IPCC et al., 2023) in amplifying the impact of biological invasions on coastal ecosystems, a connection already hypothesized in the northern Adriatic coastal area for another invasive species, the blue crab *Callinectes sapidus*, whose invasion which could possibly be linked to warmer and saltier waters (Chiesa et al., 2025). Indeed, the sampling in our study took place in 2022 and 2023, which were drought years in north-eastern Italy (Chiesa et al., 2025).

In agreement with Schroeder et al. (2023), our results show a strong seasonal pattern in the occurrence and abundance of *M. leidyi* in the Venice Lagoon in terms of temporal and spatial distribution, with a consistent absence in the coldest seasons, followed by an increase in abundance in late spring, peaking in summer and continuing into autumn. These observations reflect the species preference for warmer months, as individuals thrive in the warm temperatures of the lagoon during these periods (Shiganova et al., 2019; Marchessaux and Belloni, 2021; Schroeder et al., 2023). Although it is not possible to draw definitive conclusions based on two years of observations, the higher abundance and smaller body size of the individuals observed in 2023 compared to 2022 may indicate massive reproductive events even at smal size possibly linked also to the high temperature recorded in 2023. Variations in adult body size have also been reported for other invaded areas (Finenko et al., 2006; Delpy et al., 2016), and indeed Edgar et al. (2022) recently showed that, under adequate environmental conditions, this species begin to reproduce at a small body size (cydippid stage) and continue to spawn continuously. In our study area, in 2023, during the months of high abundance, mainly 2–4 cm long specimens formed the population structure.

In this study we have focused on temperature and salinity, which are among the most important factors for the development of *M. leidyi* populations (Fenoglio et al., 2010; Herbert et al., 2015). The northern, central and southern sub-basins of the Venice Lagoon differ considerably in their temperature and salinity patterns, as also shown by our data, as well as in their trophic conditions due to the different freshwater inflows (which are higher in the northern lagoon) and their proximity (geographical and hydrodynamic) to the Adriatic Sea (Zirino et al., 2014). The lagoon's spatial gradients in environmental conditions offered an opportunity to test whether such heterogeneity structures ctenophore distribution. Despite these gradients, *M. leidyi* occurred throughout the lagoon (similarly to what found by Schroeder et al., 2023) without displaying any clear patterns, indicating that spatial

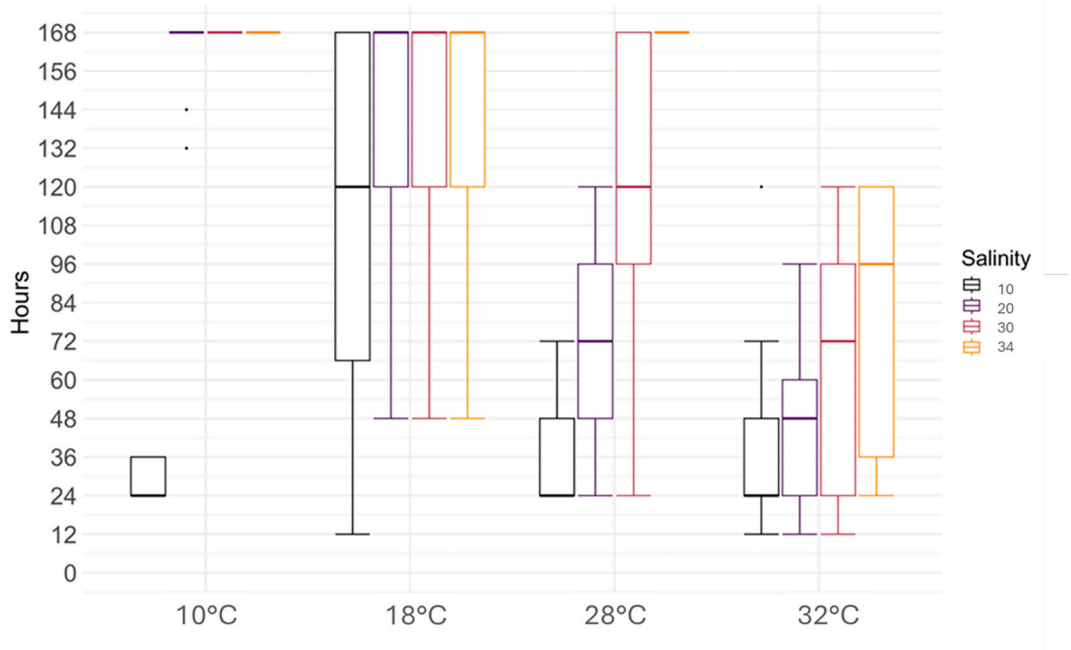


Fig. 5. Individual hours of survival for ctenophores exposed to different combinations of temperature and salinity. The experiments lasted 168 h at maximum. Boxplots show the median (the thick colored line), the interquartile range (the box), and the outliers (dots), while whiskers represent the lowest and the uppermost quartile.

variability in environmental conditions does not strongly constrain its distribution at the scale of our sampling design. This finding contrasts with the previous observation that fyke nets placed by local fishers tend to be less clogged with *M. leidyi* in the northern lagoon than in the other areas (Piccardi et al., 2024), a difference which may be linked to differences in sampling methods. Indeed, the data collection in this study took place in channels, while the fyke nets examined by Piccardi et al. (2024) were generally placed in shallower areas. Also, the sampled fyke nets were not placed with a standardized sampling design but were instead placed by professional fishers as part of their working routine in locations expected to maximize commercial catch and, presumably, to minimize clogging according to theirknowledge, suggesting that there may be some particular areas in the northern lagoon where *M. leidyi* is less abundant. Finally, the sampling years of the study by Piccardi et al. (2024) and this work differ, being 2020 and 2023 respectively, and it could well be that over this time span the invasion has spread more to the northern Lagoon.

The GLMM results revealed that both temperature and salinity had positive strong effects on ctenophore abundance in the field, explaining a large fraction of its overall variability, thus supporting the crucial influence of these environmental parameters on the distribution of this invasive species. Nonetheless, sampling months and the Venice lagoon sub-basins emerged as important explanatory factors, suggesting a more complex spatial and temporal distribution of the species in the different areas, with other factors, such as the hydrodynamics and productivity of the lagoon sub-basins, potentially playing an important role.

The results of the laboratory experiments complement the observations in the field by singling out the effects of the two environmental factors and their interaction and showing that the survival of *M. leidyi* is highly dependent on specific combinations of temperature and salinity. In particular, the species is negatively impacted by extreme warm temperatures while it shows remarkable survival rates at low temperatures, except at very low salinity. At higher temperatures, a clear salinity-dependent trend emerges, with survival rates decreasing significantly at salinities of 20 or lower. Interestingly, at a temperature of 18 °C, *M. leidyi* shows exceptional resistance in almost all the salinity conditions which were tested, suggesting that this temperature is close to the optimal value for its survival and potential expansion. This combination of laboratory results and field observations emphasizes the ecological processes driving the blooms of *M. leidyi*. The field survey data demonstrates that the species can withstand a wide range of salinity changes, consistent with its wide distribution throughout the Venice Lagoon. Combined with the observed species' ability to tolerate a wide range of salinities (20–34) at a wide range of temperature conditions (10–28 °C) in controlled conditions, these results confirm the species' adaptability to different coastal-marine ecosystems, while highlighting thresholds that could limit its dispersal under extreme environmental scenarios. On the positive side, consistent with recent findings showing that extreme thermal treatment of ballast water can reduce *M. leidyi* survival (Budiša et al., 2023), our results confirm the effectiveness of high-temperature exposure in decreasing the survival of this ctenophore and highlight its potential as a starting point for managing the invasions of this species. An important finding is that all 240 specimens tested in the laboratory survived the first 12 h of treatment, which corresponds to the duration of an entire half-day tidal cycle in the Venice lagoon (Ferrarin et al., 2017). The ability of ctenophores to withstand low salinity conditions for at least 12 h suggests that they can survive even in critical areas of transitional systems such as the inner parts of the northern lagoon near estuaries, with the next high tide transporting them to areas with more tolerable salinity levels. These findings are consistent with previous research in other ecosystems (e.g., Costello et al., 2012) and emphasize the potential of *M. leidyi* to exploit changing climatic conditions, thereby influencing marine community dynamics and ecosystem resilience.

While temperature and salinity are key drivers of *M. leidyi* population trends, trophic conditions are also known to play a fundamental role. Despite its capacity to resist and reproduce also during period of starving (Jaspers et al., 2015), changes in the abundance of zooplankton can have a significant impact on population dynamics and size distribution of *M. leidyi*, due to its carnivorous feeding habit (Finenko et al., 2006; Mavrič et al., 2025), with periods of high ctenophore abundance often corresponding to increased availability of zooplankton (Costello et al., 2006). Conversely, grazing by adult *M. leidyi* can strongly reduce mesozooplankton biomass and produce a cascading effect on primary

producers, resulting in increased phytoplankton and microzooplankton biomass (e.g. Dinasquet et al., 2012; McNamara et al., 2013, Tiselius and Møller, 2017). In turn, the increase of microplankton support an increase of cydippid larvae.

5. Conclusions

Our results evidenced a positive relationship between temperature, salinity, and abundance of *M. leidyi*, moreover, laboratory experiments highlighted how this ctenophore can survive well within the 10–28 °C and 20–34 salinity range but experiences reduced survival at extreme conditions. These findings suggest that climate change may increase the seasonal time span and intensity of the blooms of *M. leidyi* in the Venice Lagoon through its combined effects on water temperature and salinity. Warmer spring-summer temperatures combined with droughts, which reduce freshwater supply and accelerate evaporation, could create increasingly favorable conditions for this species. The ecological consequences of these blooms in the Venice lagoon, such as cascading impacts on fisheries (Piccardi et al., 2024), mirror the negative effects observed in other invaded ecosystems such as the Black Sea, where the ctenophore caused the collapse of the anchovy stock with a consequent socio-economic crisis (Shiganova, 1998). The two-year observation period of this study captures only a short portion of the invasion timeline, limiting our ability to assess long-term trends. Future studies integrating trophic and environmental monitoring and considering additional measurements to better understand the fine-scale hydrodynamics of lagoon ecosystem also in relation to prey availability, will be necessary to fully understand bloom dynamics in transitional systems. The response of *Mnemiopsis* to salinity changes observed in this study supports the idea that restoring natural salinity gradients in the lagoon (Boscolo Brusà et al., 2022; Feola et al., 2022) to improve habitats and overall environmental conditions could also reduce the bloom intensity of this invasive species. This study provides the first integrated field–laboratory assessment of *M. leidyi* ecology in the Venice Lagoon and establishes a starting point for predictive modeling and management of gelatinous invasions in Mediterranean transitional systems.

CRediT authorship contribution statement

F. Piccardi: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **S. Girardello:** Methodology, Data curation. **S.M. Bussard:** Investigation, Data curation. **V. Tirelli:** Writing – review & editing, Validation, Methodology. **D. Borme:** Writing – review & editing, Methodology. **A. Barausse:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **C. Mazzoldi:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Funding

FP was supported by the PhD fellowship “PON research and innovation” (funded by the European Union) on “Marine Invasive Species and fisheries in lagoons of the Northern Adriatic Sea”. AB, VT and CM acknowledge the support of the National Biodiversity Future Center—NBFC, funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender 3138 of 16/12/2021, rectified by Decree n.3175 of 18/12/2021 of Italian Ministry of University and Research funded by the EU – NextGenerationEU (Project code CN_00000033, Concession Decree 1034 of 17/06/2022 adopted by the Italian Ministry of University and Research, Project “National Biodiversity Future Center – NBFC”). This study was partly carried out (AB) within the RETURN Extended Partnership and received funding from the European Union Next-GenerationEU (National Recovery and Resilience Plan – NRRP, Mission 4, Component 2, Investment 1.3 – D.D. 1243 2/8/2022, PE0000005).

Declaration of competing interest

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

Acknowledgements

We thank Andrea Sambo, Cristina Breggion, and Mattia Panin for their unvaluable support in laboratory work and boat trips. We thank Claudia Gattolin and Marta Paganin for their contribution during their thesis works.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109678.

Data availability

Data will be made available on request.

References

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Bayha, K.M., Chang, M.H., Mariani, C.L., Richardson, J.L., Edwards, D.L., DeBoer, T.S., Moseley, C., Aksoy, E., Decker, M.B., Gaffney, P.M., Harbison, G.R., McDonald, J.H., Caccone, A., 2015. Worldwide phylogeography of the invasive ctenophore *Mnemiopsis leidyi* (Ctenophora) based on nuclear and mitochondrial DNA data. Biol. Invasions 17, 827–850. https://doi.org/10.1007/s10530-014-0770-6.

Boscolo Brusà, R., Feola, A., Cacciatore, F., Ponis, E., Sfriso, A., Franzoi, P., Lizier, M., Peretti, P., Matticchio, B., Baccetti, N., Volpe, V., Maniero, L., Bonometto, A., 2022. Conservation actions for restoring the coastal lagoon habitats: strategy and multidisciplinary approach of LIFE Lagoon Refresh. Front. Ecol. Evol. 10, 979415. https://doi.org/10.3389/fevo.2022.979415.

Budiša, A., Paliaga, P., Juretić, T., Lučić, D., Supić, N., Pasarić, Z., Djakovac, T., Mladinić, M., Dadić, V., Tičina, V., 2021. Distribution, diet and relationships of the invasive ctenophore *Mnemiopsis leidyi* with anchovies and zooplankton, in the northeastern Adriatic sea. Mediterr. Mar. Sci. 22, 827. https://doi.org/10.12681/mms.23305.

Budiša, A., Burić, E., Blecich, P., Matulja, T., Millotti, G., Iveša, N., Najdek, T.M., Mičić, M., Paliaga, P., 2023. Treating ballast waters to limit Mnemiopsis leidyi access to new habitats. Management of biological invasions 14 (3). https://doi.org/10.3391/mbi.2023.14.3.12.

Chiesa, S., Petochi, T., Boscolo Brusà, R., Raicevich, S., Cacciatore, F., Franceschini, G., Antonini, C., Vallini, C., Bernarello, V., Oselladore, F., Ciani, M., Di Blasio, L., Campolunghi, M.P., Baldessin, F., Boldrin, L., Marino, G., 2025. Impacts of the blue crab invasion on Manila clam aquaculture in Po Delta coastal lagoons (Northern Adriatic Sea, Italy). Estuar. Coast Shelf Sci. 312, 109037. https://doi.org/10.1016/j.ecss.2024.109037.

Costello, J.H., Sullivan, B.K., Gifford, D.V., Van Keuren, D., Sullivan, L.J., 2006. Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Limnol. Oceanogr. 51 (4), 1819–1831. https://doi.org/10.4319/lo.2006.51.4.1819.

Costello, J.H., Bayha, K.M., Mianzan, H.W., Shiganova, T.A., Purcell, J.E., 2012. Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. Hydrobiologia 690, 21–46. https://doi.org/10.1007/s10750-012-1037-9.

Cucco, A., Umgiesser, G., Ferrarin, C., Perilli, A., Canu, D.M., Solidoro, C., 2009. Eulerian and lagrangian transport time scales of a tidal active coastal basin. Ecol. Model. 220 (7), 913–922. https://doi.org/10.1016/j.ecolmodel.2009.01.008.

Delpy, F., Albouy-Boyer, S., Pagano, M., Thibault, D., Blanchot, J., Guilhaumon, F., Molinero, J.C., Bonnet, D., 2016. Identifying the drivers of abundance and size of the invasive ctenophore *Mnemiopsis leidyi* in Northwestern Mediterranean lagoons. Mar. Environ. Res. 119, 114–125. https://doi.org/10.1016/j.marenvres.2016.05.026.

Dinasquet, J.V., Titelman, J., Møller, L.F., Setälä, O., Granhag, L., Andersen, T., Båmstedt, U., Haraldsson, M., Katajisto, T., Kragh, T., Kuparinen, J., Schrøter, M.L., Søndergaard, M., Tiselius, P., Riemann, L., 2012. Cascading effects of the ctenophore *Mnemiopsis leidyi* on the planktonic food web in a nutrient limited estuarine system. Mar. Ecol. Prog. Ser. 460, 49–61. https://doi.org/10.3354/meps09770.

Edgar, A., Ponciano, J.M., Martindale, M.Q., 2022. Ctenophores are direct developers that reproduce continuously beginning very early after hatching. Proc. Natl. Acad. Sci. 119 (18), e2122052119. https://doi.org/10.1073/pnas.2122052119.

Fenoglio, S., Bo, T., Cucco, M., Mercalli, M., Malacarne, G., 2010. Effects of global climate change on freshwater biota: a review with special emphasis on the Italian situation. Ital. J. Zool. 77 (4), 374–383. https://doi.org/10.1080/11250000903176497.

Feola, A., Ponis, E., Cornello, M., Boscolo Brusà, R., Cacciatore, F., Oselladore, F., Matticchio, B., Canesso, D., Sponga, S., Peretti, P., Lizier, M., Maniero, L., Volpe, V., Sfriso, A., Ferla, M., Bonometto, A., 2022. An integrated approach for evaluating the restoration of the salinity gradient in transitional waters: monitoring and numerical modeling in the life lagoon refresh case study. Environments 9 (3), 31. https://doi.org/10.3390/environments9030031.

Ferrarin, C., Maicu, F., Umgiesser, G., 2017. The effect of lagoons on Adriatic Sea tidal dynamics. Ocean Model. 119, 57–71. https://doi.org/10.1016/j.ocemod.2017.09.009.

Finenko, G.A., Kideys, A.E., Anninsky, B.E., Shiganova, T.A., Roohi, A., Tabari, M.R., Rostami, H., Bagheri, S., 2006. Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. Mar. Ecol. Prog. Ser. 314, 171–185. https://doi.org/10.3354/meps314171.

Ghabooli, S., Shiganova, T.A., Briski, E., Piraino, S., Fuentes, V., Thibault-Botha, D., Angel, D.L., Cristescu, M.E., MacIsaac, H.J., 2013. Invasion pathway of the Ctenophore *Mnemiopsis leidyi* in the Mediterranean sea. PLoS One 8, e81067. https://doi.org/10.1371/journal.pone.0081067.

Herbert, E.R., Boon, P., Burgin, A.J., Neubauer, S.C., Franklin, R.B., Ardón, M., Hopfensperger, K.N., Lamers, L.P.M., Gell, P., 2015. A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. Ecosphere 6 (10), 206. https://doi.org/10.1890/ES14-00534.1.

IPCC, 2023. Climate change 2023: synthesis report. In: Lee, H., Romero, J. (Eds.), Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team. IPCC, Geneva, Switzerland, p. 184. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Jaspers, C., Møller, L.F., Kiørboe, T., 2015. Reproduction rates under variable food conditions and starvation in *Mnemiopsis leidyi*: significance for the invasion success of a ctenophore. J. Plankton Res. 37 (5), 1011–1018. https://doi.org/10.1093/plankt/fbv017.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the World's Worst Invasive Alien Species: a Selection from the Global Invasive Species Database). Published by the Invasive Species Specialist Group (ISSG) a Specialist Group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens 12, December 2000.

Malej, A., Tirelli, V., Lučić, D., Paliaga, P., Vodopivec, M., Goruppi, A., Ancona, S., Benzi, M., Bettoso, N., Camatti, E., Ercolessi, M., Ferrari, C.R., Shiganova, T., 2017. *Mnemiopsis leidyi* in the northern Adriatic: here to stay? J. Sea Res. 124, 10–16. https://doi.org/10.1016/j.seares.2017.04.010.

Marani, M., Belluco, E., Ferrari, S., Silvestri, S., D'Alpaos, A., Lanzoni, S., Feola, A., Rinaldo, A., 2006. Analysis, synthesis and modelling of high-resolution observations of salt-marsh eco-geomorphological patterns in the Venice lagoon. Estuarine. Coastal and Shelf Science 69 (3–4), 414–426. https://doi.org/10.1016/j.ecss.2006.05.021.

Marchessaux, G., Belloni, B., 2021. Expansion of *Mnemiopsis leidyi* in the French mediterranean lagoons along the Gulf of Lion. J. Sea Res. 168, 7. https://doi.org/10.1016/j.seares.2021.101995.

Mavrič, B., Ivajnšič, D., Lučić, D., Malej, A., Lipej, L., 2025. Feeding Habits of the Invasive Ctenophore *Mnemiopsis leidyi* in the Gulf of Trieste (Adriatic Sea). Water 17 (4), 470. https://doi.org/10.3390/w17040470.

McNamara, M.E., Lonsdale, D.J., Cerrato, R.M., 2013. Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. Estuar. Coast Shelf Sci. 133, 2–10. https://doi.org/10.1016/j.ecss.2013.04.019.

Pestorić, B., Lučić, D., Bojanić, N., Vodopivec, M., Kogovšek, T., Violić, I., Paliaga, P., Malej, A., 2021. Scyphomedusae and ctenophora of the eastern adriatic: historical overview and new data. Diversity 13, 186. https://doi.org/10.3390/d13050186.

Piccardi, F., Poli, F., Sguotti, C., Tirelli, V., Borme, D., Mazzoldi, C., Barausse, A., 2024. Assessing the impact of the invasive ctenophore *Mnemiopsis leidyi* on artisanal fisheries in the Venice Lagoon: an interdisciplinary approach. Hydrobiologia 852, 2387–2405. https://doi.org/10.1007/s10750-024-05505-6.

Putelli, E., Costantini, F., Tirelli, V.A., 2025. First molecular insight into the invasive ctenophore *Mnemiopsis leidyi* in the northern Adriatic Sea. Hydrobiologia 852, 2263–2276. https://doi.org/10.1007/s10750-024-05597-0.

Ravera, O., 2000. The Lagoon of Venice: the result of both natural factors and human influence. J. Limnol. 59 (1), 19–30. https://doi.org/10.4081/jlimnol.2000.19.

Rossetto, L., 2000. The management of fishery in the Lagoon of Venice. In: https://ir.library.oregonstate.edu/concern/conference_proceedings_or_journals/8p58pd90c.

Schroeder, A., Camatti, E., Pansera, M., Pallavicini, A., 2023. Feeding pressure on meroplankton by the invasive ctenophore *Mnemiopsis leidyi*. Biol. Invasions 25 (6), 2007–2021. https://doi.org/10.1007/s10530-023-03023-5.

Shiganova, T.A., 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fish. Oceanogr. 7, 305–310. https://doi.org/10.1046/j.1365-2419.1998.00080.x.

Shiganova, T., Malej, A., 2009. Native and non-native ctenophores in the Gulf of Trieste, Northern Adriatic Sea. J. Plankton Res. 31, 61–71. https://doi.org/10.1093/plankt/fbn102.

Shiganova, T.A., Sommer, U., Javidpour, J., Molinero, J.C., Malej, A., Kazmin, A.S., Isinibilir, M., Christou, E., Siokou- Frangou, I., Marambio, M., Fuentes, V., Mirsoyan, Z.A., Gülsahin, N., Lombard, F., Lilley, M.K.S., Angel, D.L., Galil, B.S., Bonnet, D., Delpy, F., 2019. Patterns of invasive ctenophore *Mnemiopsis leidyi* distribution and variability in different recipient environments of the Eurasian seas: a review. Mar. Environ. Res. 152, 8. https://doi.org/10.1016/j.marenvres.2019.104791.

Shiganova, T.A., 2020. Adaptive strategies of *Mnemiopsis leidyi* A. Agassiz 1865 in different environments of the Eurasian seas. Mar. Pollut. Bull. 161, 111737. https://doi.org/10.1016/j.marpolbul.2020.111737.

Solidoro, C., Bandelj, V., Aubry Bernardi, F., Camatti, E., Ciavatta, S., Cossarini, G., Facca, C., Franzoi, P., Libralato, S., Melaku Canu, D., Pastres, R., Pranovi, F., Raicevich, S., Socal, G., Sfriso, A., Sigovini, M., Tagliapietra, D., Torricelli, P., 2010. Response of Venice lagoon ecosystem to natural and anthropogenic pressures over the last 50 years. In: Paerl, H.W., Kennish, M.J. (Eds.), Coastal Lagoons: Systems of Natural and Anthropogenic Change. CRC press, Boca Raton, pp. 483–511.

Soto-Angel, J.J., Nordmann, E.L., Sturm, D., Sachkova, M., Pang, K., Burkhardt, P., 2024. Stable laboratory culture system for the ctenophore *Mnemiopsis leidyi*. In: Ctenophores: Methods and Protocols. Springer US, New York, NY, pp. 123–145. https://doi.org/10.20944/preprints202202.0341.v1.

Tagliapietra, D., Baldan, D., Barausse, A., Buosi, A., Curiel, D., Guarneri, I., Pessa, G., Rismondo, A., Sfriso, A., Smania, D., Ghirardini, A.V., 2018. Protecting and restoring the salt marshes and seagrasses in the lagoon of Venice. In: Quintana, X., Boix, D., Gascón, S., Sala, J. (Eds.), Management and Restoration of Mediterranean Coastal Lagoons in Europe. Recerca i Territori, vol. 10. Museu de la Mediterrània, Girona, pp. 39–65. ISSN: 2013-5939.

Tamm, S.L., 2014. Cilia and the life of ctenophores. Invertebr. Biol. 133 (1), 1–46. https://doi.org/10.1111/ivb.12042.

Tirelli, V., Goruppi, A., Riccamboni, R., Tempesta, M., 2021. Citizens' eyes on *mnemiopsis*: how to multiply sightings with a click! Diversity 13, 224. https://doi.org/10.3390/d13060224, 2021.

Tiselius, P., Møller, L.F., 2017. Community cascades in a marine pelagic food web controlled by the non-visual apex predator *Mnemiopsis leidyi*. J. Plankton Res. 39 (2), 271–279. https://doi.org/10.1093/plankt/fbw096.

Tommasini, L., Carniello, L., Ghinassi, M., Roner, M., D'Alpaos, A., 2019. Changes in the wind-wave field and related salt-marsh lateral erosion: inferences from the evolution of the Venice Lagoon in the last four centuries. Earth Surf. Process. Landf. 44 (8), 1633–1646. https://doi.org/10.1002/esp.4599.

Vargas, C.I., Vaz, N., Dias, J.M., 2017. An evaluation of climate change effects in estuarine salinity patterns: application to Ria de Aveiro shallow water system. Estuar. Coast Shelf Sci. 189, 33–45. https://doi.org/10.1016/j.ecss.2017.03.001.

Vinogradov, M.E., Shushkina, E.A., 1992. Temporal changes in community structure in the open Black Sea. Oceanology 32, 485–491.

Zirino, A., Elwany, H., Neira, C., Maicu, F., Mendoza, G., Levin, L.A., 2014. Salinity and its variability in the Lagoon of Venice, 2000–2009. Adv. Oceanogr. Limnol. 5 (1), 41–59. https://doi.org/10.1080/19475721.2014.900113.