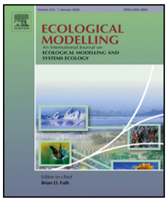
Ecological Modelling 505 (2025) 111109

Contents lists available at ScienceDirect

Ecological Modelling

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



Spatially explicit individual-based model reveals the mauve stinger jellyfish distribution in the Mediterranean Sea

Martin Vodopivec *, Alenka Malej

Marine Biology Station, National Institute of Biology, Fornače 41, Piran, 6330, Slovenia

ARTICLE INFO

Dataset link: https://gitlab.com/mvodopivec/pelagiaibm, https://figshare.com/articles/software/PelagiaIBM/27605307, https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1, https://doi.org/10.25423/cmcc/medsea_multiyear_bgc_006_008_medbfm3

Keywords:
Individual-based model
Agent-based model
Zooplankton
Lagrangian particle tracking
Ocean circulation
Jellyfish

ABSTRACT

The mauve stinger *Pelagia noctiluca* is a holoplanktonic oceanic jellyfish known for its painful sting and large outbreaks at irregular intervals. As jellyfish field observations are almost exclusively limited to coastal regions, there are many unknowns about the spatial and temporal dynamics of most species. We approach the problem using a spatially explicit individual-based model for the mauve stinger in the Mediterranean Sea. The newly developed module for the OpenDrift Lagrangian particle tracking tool includes diel vertical migrations, food-dependent growth modeled on Michaelis–Menten kinetics, and custom mortality related to shallow waters and stranding. In the first part of the study, we analyze the resulting parameter space searching for solutions that ensure a stable *Pelagia noctiluca*population in the western Mediterranean Sea. In the second part, we conducted several 21-year simulations. Despite its relative simplicity, the model reveals for the first time the dynamic spatio-temporal distribution of *Pelagia noctiluca*. We demonstrate how spatially explicit individual-based model can be used to generate a realistic spatio-temporal distribution of marine zooplankton, even with a limited set of observations and loosely constrained parameters. The model code is easy to modify and freely available.

1. Introduction

Pelagia noctiluca is one of the bloom-forming jellyfish (Scyphozoan) species in the Mediterranean Sea. Due to its painful sting, abundance, economical and ecological role it is often considered to be the most important jellyfish species in this area (Daly Yahia et al., 2010; Canepa et al., 2014). It consumes large volumes and variety of prey, primarily zooplankton and including fish larvae (Malej et al., 1993; Gordoa et al., 2013; Purcell et al., 2014; Tilves et al., 2016), importantly controlling its abundance. Contrary to the large majority of scyphozoans, the *Pelagia noctiluca* does not have an attached polyp phase in its life cycle (Jarms and Morandini, 2019). Therefore, it is a holoplanktonic (pelagic or free-swimming) species and does not require a solid substrate for completing the life cycle. The impacts of *Pelagia noctiluca* blooms on human activities are direct and indirect and affect tourism, fisheries, aquaculture, energy and ecosystem functioning (Canepa et al., 2014). The painful sting makes *Pelagia noctiluca* a factor of huge importance in coastal tourism. Swarms of jellyfish have been known to cause significant harms in aquaculture where they damage the gills of farmed fish (Baxter et al., 2011). They also cause significant losses to fisheries when clogging fishing nets and damaging the catch (Long et al., 2024).

There is a growing evidence that jellyfish blooms could importantly contribute to the biological carbon pump and therefore significantly influence the level of CO_2 in the atmosphere (Lebrato et al., 2019; Luo et al., 2020; Wright et al., 2021; Tinta et al., 2023). It has also been shown that jellyfish blooms importantly influence the structure of the ecosystem and microbial community (Tinta et al., 2020, 2021, 2023).

Since we have no means available that would allow us to perform direct large scale observations of jellyfish in the 3-dimensional ocean, the large majority of available observations are performed from or near the coast by human observers who scan the ocean surface. The black dots in Fig. 1 show recorded observations of *Pelagia noctiluca* in the Global Biodiversity Information Facility (GBIF, 2024). It is very obvious that only a small part of observations are made in the open ocean. And furthermore, only a fraction of these are performed with vertical hauls of underwater cameras or zooplankton nets that give us information of the jellyfish presence in the deeper water layers. Therefore, our knowledge of *Pelagia noctiluca* distribution in the Mediterranean Sea is largely derived from surface observations in coastal waters which is a serious drawback.

Due to scarcity and difficulty of obtaining in situ data on the occurrence of jellyfish, modeling is currently the only tool that can give us a holistic view of their spatio-temporal distribution. Although *Pelagia noctiluca* is one of the most studied jellyfish species, there are major gaps in our understanding of its spatial distribution and

---

* Corresponding author.
E-mail address: martin.vodopivec@nib.si (M. Vodopivec).

https://doi.org/10.1016/j.ecolmodel.2025.111109
Received 13 November 2024; Received in revised form 18 March 2025; Accepted 26 March 2025

phenology and *Pelagia noctiluca* presence in some areas seems to be very variable (Daly Yahia et al., 2010; Kogovšek et al., 2010; Marambio et al., 2021; Violić et al., 2022; Bergamasco et al., 2022). Given the available data, there is high likelihood of a permanent population in the Western Mediterranean Sea, while presence in other areas likely depends on environmental factors. These could be food availability, temperature, predation and transport by currents.

Individual-based models (IBM, Jørgensen and Fath, 2011; Grimm and Railsback, 2013) have been in use in plankton ecology since the 80's (Gentleman, 2002). In several instances IBMs were used to model jellyfish dispersal and population dynamics. The most simplistic approach employs passive Lagrangian particle tracking to model jellyfish dispersal (Dawson et al., 2005; Lee et al., 2013; Janßen et al., 2013; Bergamasco et al., 2022). Prieto et al. (2015) added wind drift to study Portuguese man o' war (*Physalia physalis*) intrusions into the Mediterranean Sea. Diel vertical migrations add an important feature affecting the transport: Berline et al. (2013) studied the mechanisms that bring the *Pelagia noctiluca* in the Western Mediterranean Sea from the open sea to the coastal waters; Vodopivec et al. (2017) studied the impact of offshore platforms on the moon jellyfish (*Aurelia* s.l.) population in the Adriatic Sea. El Rahi et al. (2020) created a complex *Pelagia noctiluca* IBM using the OpenDrift Lagrangian particle tracking toolbox (Dagestad et al., 2018) to model different *Pelagia noctiluca* life stages to test the role of marine canyons in jellyfish transport from ocean depths to the nearshore.

The main idea behind the presented work is to construct a spatial IBM that would faithfully reproduce the spatio-temporal distribution of *Pelagia noctiluca* in the Mediterranean Sea. The goals are to identify the geographical areas that are capable of supporting a permanent population, the interannual variance in size of the population and the geographical location of its core. If properly tuned, such a model could maybe also explain the irregular blooms outside the permanent population area, e.g. the sporadic occurrences (Malej and Malej, 2004) in the northern Adriatic Sea (Fig. 1).

We developed a new Pleagia IBM module for OpenDrift (Dagestad et al., 2018), which incorporates sun-synchronized diel vertical migrations, food-dependent growth using Michaelis–Menten kinetics, and beaching mortality. These elements provide a more ecologically realistic representation of Pelagia noctiluca compared to previous jellyfish distribution models. The diel vertical migrations of *Pelagia noctiluca* are well known (Arai, 1997; Berline et al., 2013), however other traits such as feeding and mortality in the natural environment are poorly constrained. Therefore, we follow the "as simple as possible, but as complicated as necessary" approach (Sun et al., 2016; Jakeman et al., 2024) in formulation of a few relatively simple principles that provide satisfactory results without excessive complexity. We address the ambiguity of model parameters by performing a 4-year calibration run. The latter is used for rigorous parameter space exploration to stabilize population dynamics. Knowing the approximate geographical area of the permanent population, we use this knowledge to deduce a set of realistic mortality and growth values. These are then used in longer simulations which reveal the geographic distribution of the species and its temporal variations.

Using the above-mentioned approach, we demonstrate how a relatively simple individual-based model with poorly constrained parameters can be used in combination with relatively scarce field data to obtain a realistic and holistic spatio-temporal distribution of marine zooplankton. Furthermore, the parameter space exploration and calibration in combination with relatively scarce and descriptive knowledge enabled us to quantify realistic mortality and growth values (Jakeman et al., 2024). Such an approach and our model code could also be used in future studies on the distribution of marine zooplankton and the effects of climate change, in forecasting of blooms or as a part of the digital twin of the ocean (Bauer et al., 2021).

2. Methods

In this study we model the trajectories of virtual particles which represent large groups of *Pelagia noctiluca* jellyfish (super-individual; Scheffer et al., 1995). The particles are transported horizontally by ocean currents while their vertical movement is programmed in accordance with observed diel vertical migrations. This approach is based on the assumption that large scale horizontal swimming is negligible, which is supported by observed lack of oriented swimming in *Pelagia noctiluca* individuals (Malej, 1989).

2.1. Transport and primary production models

Currents used for propagation of OpenDrift particles were obtained from Copernicus Marine Service (CMEMS). Daily values of Mediterranean Physics Reanalysis were used (MEDSEA_MULTIYEAR_PHY_006_004) in the simulations. The model reanalysis by the Med MFC (Escudier et al., 2021; Pinardi et al., 2003) provides currents at 141 vertical z levels in 1/24° (approx. 4.5 km) horizontal resolution. Monthly primary production values (expressed as carbon per unit volume in sea water) were also downloaded from CMEMS. The coupled NEMO-BFM model reanalysis (Cossarini et al., 2021) of the Mediterranean Sea biogeochemistry (MEDSEA_MULTIYEAR_BGC_006_008) is available in 125 vertical z levels and at the same horizontal resolution as the physics reanalysis. Primary production was used as a proxy for food availability as zooplankton concentration values are not available at the web service. This approximation is supported by observed strong correlation of Pelagia noctiluca abundance with chlorophyll concentration and primary production (Canepa et al., 2014; Ottmann et al., 2021).

2.2. Lagrangian model

OpenDrift is a freely available highly modular Lagrangian particle tracking tool written in Python programming language (Dagestad et al., 2018). The clearly structured code encourages the creation of new modules which modulate the behavior of individual particles. Such an approach is highly suitable for the implementation of individual-based models coupling transport physics with biological and ecological interactions.

The timestep of particle propagation was set to 1 h, the particle-coastline interaction was set to "previous" which allows particles to "slip" along the coastline preventing beaching. As each particle represents a large group of jellyfish, the beaching was already accounted for in increased mortality in shallow waters and proximity to dry land (see Section 2.3).

2.2.1. Size of the group

The initial average distance between the neighboring particles in the long runs (Section 2.5) is 14 km and when the particles mass exceeds a preset threshold, it is split into several particles that are randomly distributed through an area of 0.5° (approx. 50 km) in size. The 'nearshore' value used for mortality due to stranding (Section 2.3.2) reaches its maximum value when the particle is one grid cell (approx. 4.5 km) away from the land mask and then falls linearly towards 0 at the next 'wet' cell (approx. 9 km away from land). When comparing model results with observations in the northern Adriatic (Section 3.2.2) the particle presence is matched with observations within an area roughly 200 km in size (red area in Fig. 1).

Based on the information given above, each particle represents a group of individuals of all life stages with the size that spans from kilometers to tens of kilometers and positional uncertainty that can reach up to 100 km. As the size of the group matches the spatial resolution of the ocean model there was no need to account for unresolved subgrid scale processes (Peliz et al., 2007) and no additional horizontal diffusion was used.

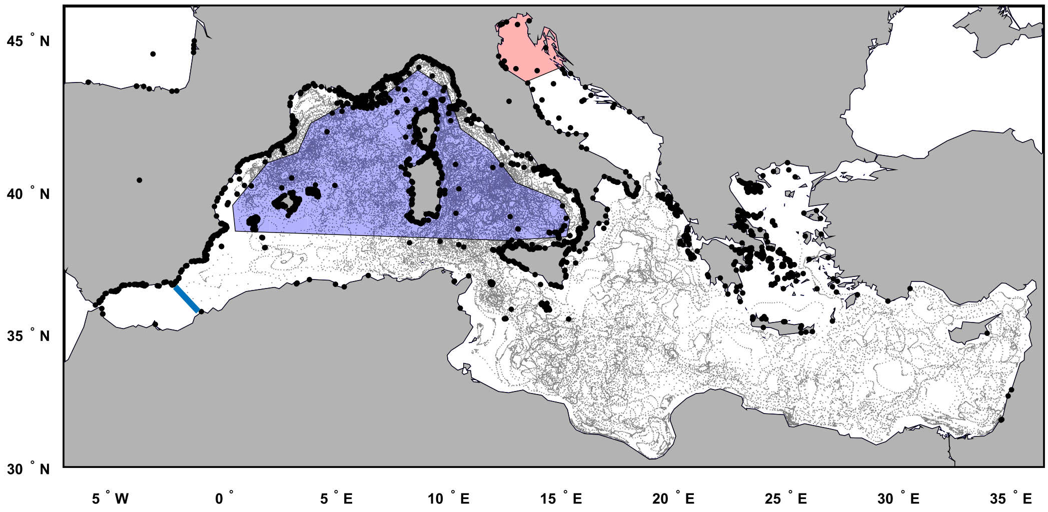


Fig. 1. Map of the Mediterranean Sea including the trajectories of the initial run (see Section 3.1). Only 0.5% of trajectories are shown. The initial release area is marked in light blue color. The light red area marks the Northern Adriatic. Locations of observations recorded in the Global Biodiversity Information Facility (GBIF, 2024) are shown as black dots. The blue line in the western part of the basin indicates the position of the Almeria-Oran front.

2.3. The individual-based model

A new PelagiaIBM module was written in Python programming language and is freely available in the repository (see Software and data availability section). Several additional scripts were written to perform different runs and these are available in the repository as well. The new IBM module introduces *Pelagia noctiluca* super-individuals, performs diel vertical migrations, changes particle's dimensionless biomass according to food availability and mortality and avoids including excessive details (Jakeman et al., 2024). The total *Pelagia noctiluca* biomass in the Mediterranean Sea is unknown and therefore the biomass of a particle cannot be scaled and we cannot make an estimate of how many individuals are represented by each particle. All the calculations are made in the units of initial particle mass or initial total biomass of the population. Active horizontal swimming is negligible as in other similar studies (Berline et al., 2013; Janßen et al., 2013; Vodopivec et al., 2017; Bergamasco et al., 2022).

2.3.1. Vertical migrations

The particle represents a whole group of individuals including all life stages. Adult *Pelagia noctiluca* are known to perform pronounced diel vertical migrations (Franqueville, 1970; Arai, 1997), while ephyrae stay close to the surface (Pastor-Prieto et al., 2021). Diel vertical migration of the particles was modeled following the behavior of adult organisms (Berline et al., 2013) as these represent the majority of the group's biomass. The migration of each particle was synchronized with local sunrise and sunset. The suncalc (https://github.com/kylebarron/suncalc-py) Python class was used to determine the sunrise and sunset timing at exact location of each particle. The particles vertical velocity is set to 2 m/min (Arai, 1997). After sunrise particles dive until they reach 500 m depth or stop 5 m above the bottom where the depth is smaller than 500 m. After sunset they swim towards the surface until they reach 2 m depth.

2.3.2. Growth and mortality

The change in biomass in relation to local primary production, which is used as a proxy for food availability, is modeled using Michaelsen–Menten a.k.a. Monod kinetics (Jørgensen and Fath, 2011; Strniša et al., 2024). The principle is based on the assumption that increased food concentration accelerates the growth of the group's biomass. However, this is valid only to a certain threshold (unknown model parameter) above which other factors than food availability limit the growth and reproduction. The maximum primary production value in the water column at the location of each particle is used in the equation. This is based on the assumption that the individuals feed in the water layer where the concentration of prey is the highest.

An additional mortality term is added to the Michaelis–Menten equation to represent combined predation and natural mortality of the individuals. The mortality is constant and is reflected in reduction of biomass of the super-individual. As the particle represents a large group of individuals of all life stages, the mortality value is an estimate for average mortality over the whole life span of *Pelagia noctiluca*. Combining the Michaelis–Menten growth and mortality, the equation for the change in biomass can be written as:

$$\frac{dM}{dt} = \left(\frac{k_1 P}{k_2 + P}\right) M - k_3 M \tag{1}$$

where M is the dimensionless biomass represented by each particle, P represents primary production obtained from the MedBFM model (in mg m^{-3} day^{-1}) and k_1, k_2 and k_3 are the unknown coefficients that have yet to be determined. k_1 is the growth rate, k_2 is the half-saturation constant and k_3 is the mortality rate.

An additional mortality term is added when the particle resides in waters shallower than 200 m. This term represents increased mortality due to inability to dive to deep waters to avoid predation, increased concentration of predators and higher possibility of stranding. The mortality coefficient k_S was set to -0.03 day^{-1} which halves the population in about three weeks.

To account for stranding regardless of water depth, an additional shore-proximity variable nearshore_mask was created and added to the MED-MFC netCDF (Rew and Davis, 1990) mask file. All the MedMFS (see Section 2.1) grid cells with at least one neighboring dry (land) cell were marked with 'nearshore' value 1. The nearshore value of each particle was multiplied by -0.05 day^{-1}, to produce an additional mortality coefficient k_B due to beaching. Therefore the maximum beaching mortality is $k_B = -0.05$ day^{-1}, which halves the population in two weeks.

Conducting a sensitivity test for both k_S and k_B would be too computationally expensive. Both values were chosen on the basis of our field observations (Malej and Malej, 1992) and some of the experimental runs. We ran a few simulations using smaller k_S and k_B values which produced unrealistically large populations in near-shore areas (Marambio et al., 2021). We also ran four simulations using larger values ($k_S = -0.05$ day^{-1}, $k_B = -0.10$ day^{-1}) but the results turned out to be unstable in the longer runs. Large near-shore mortality meant that the population could quickly go extinct when in vicinity of land.

At the same time the resulting growth was high to compensate for the additional mortality, which meant that the offshore populations exploded very quickly.

Including additional mortality due to shallow waters (k_S) and beaching (k_B) renders a combination of Michaelis–Menten equation and three additional mortality terms:

$$\frac{dM}{dt} = M\left(\frac{k_1 P}{k_2 + P}\right) - k_3 M - k_S M - k_B M \tag{2}$$

2.4. Short run - model calibration

Initially we ran a 4-year simulation for 10 000 particles without the growth/mortality calculations to obtain the particle trajectories and corresponding food availability. At the start of the run particles were equally distributed through the initial release area (blue area in Fig. 1) and only the trajectories that ended within the same area were used for further analysis. A large set of simulations was ran on these data using MATLAB code (Section 3.1), daily time-step and different values of k_1, k_2 and k_3 to find out which combinations render a stable *Pelagia noctiluca* population in the Western Mediterranean Sea.

2.5. The long run

Long-term (21-year) simulations were performed using the new OpenDrift module (PelagiaIBM). The k_1, k_2 and k_3 parameter values were chosen from the set of successful 4-year runs (Section 2.4). With no obvious clusters of favorable solutions (Section 3.1), we chose several different coefficient combinations from the set of solutions to run the 21-year-long simulations. Six parameter combinations were chosen using the k-means (Arthur and Vassilvitskii, 2006) clustering algorithm (C1 to C6; Fig. 2). Due to the curvature of the 2D surface, the values of successful run closest to the cluster centroid were used (Fig. 2 and Table 1). The clustering algorithm was used in the hope there are areas with higher density of stable solutions and as an alternative to picking random points. After these six configuration ran for the whole 21-year period, another three points were hand-picked from the 2D surface (C7 to C9; Fig. 2 and Table 1).

The mortality-growth dynamics (Eq. (2)) was implemented into the new OpenDrift Pelagia IBM module, the biomass change, vertical migrations and transport were calculated in hourly time-steps. Daily output values were written into netCDF files.

The long-term simulations ran in yearly segments. In the beginning of each year-long run the positions and biomass of particles were read for the last time-step from the previous year output file. If the biomass of the particle was smaller than 0.2% of the initial biomass, the group represented by the particle was considered too depleted and the particle was removed from the simulation. If the biomass of the particle was larger than twice the initial biomass, the group represented by the particle has grown to the extent that it should be represented by more than one particle. In this case the particle was replaced by several particles, each of them having the biomass equal to the initial biomass, and an additional particle with a smaller biomass. The sum of biomass of all the new particles matched the biomass of the particle that was removed and replaced. E.g. a particle with biomass five-times the initial biomass was replaced by five new particles. The latitude and longitude of new particles was randomly perturbed for up to 0.5°. If the total number of particles in the simulation fell below 50 or rose above 200 000, the total *Pelagia noctiluca* population was considered extinct or exploded and the simulation was stopped.

The C1 to C9 runs started with the initial population of 2000 particles limited to the western Mediterranean Sea (blue area, Fig. 1). The idea was that the initial population will spread quickly throughout the Mediterranean Sea and establish permanent presence where the conditions would prove suitable. The C7 configuration was chosen as most suitable and in accordance with good modeling practice (GMP, Jakeman et al., 2024) several runs were performed using the same parameters (C7a, C7b and C7c) to analyze the model uncertainty. An additional simulation was performed with the initial positions throughout the whole Mediterranean Sea (configuration C7M, Table 1). 8000 particles were released to keep the initial particle density the same as in the other runs. The C7a, C7b and C7c simulate how an initial localized permanent population spreads throughout the basin, while C7M simulates where permanent populations would be established from an initial population that inhabits the whole basin. If the connectivity throughout the Mediterranean is high enough, the end distribution should be similar in all the C7 runs.

3. Results

3.1. Calibration of model parameters

10 000 particles were released from predetermined area that was chosen as the approximate location of permanent Pelagia presence (blue area in Fig. 1). The simulation ran with hourly time-step for four years from 2000 to 2003 and particle locations and maximum primary production value at each location were recorded every 24 h into an output netCDF file. At the end of the simulation 1605 particles were located inside the release polygon (blue area in Fig. 1). With the assumption that the biomass in the starting area is more or less constant – ensuring a permanent population – the trajectories of these particles were used for parameter space analysis.

A replicate IBM in MATLAB was written for parameter space analysis. The MATLAB code used the daily PP, depth and shore proximity values recorded in the output netCDF file to simulate the growth and mortality using Eq. (2). A range of values was used for each of the coefficients (minimum value : step : maximum value):

$$\begin{aligned} &k_1 \in [0.001 : 0.002 : 0.2]\ \mathrm{day}^{-1} \\ &k_2 \in [0.1 : 0.05 : 7]\ \mathrm{mg\,m}^{-3}\ \mathrm{day}^{-1} \\ &k_3 \in [0.07 : 0.002 : 0.15]\ \mathrm{day}^{-1} \end{aligned} \tag{3}$$

The mortality rate range k_3 was set according to Wright et al. (2021), Acevedo et al. (2013) and Malej and Malej (1992). While Acevedo et al. (2013) and Malej and Malej (1992) cite a mortality rate between 0.006–0.026 day^{-1}, Wright et al. (2021) used a much higher value of 0.12 day^{-1} to achieve best fit of model data to observations. The growth parameter range k_1 was set on a wide interval (0.1% day^{-1} to 20% day^{-1}) to balance the mortality. The half-saturation coefficient range k_2 was chosen to cover typical primary production values in MedBFM model.

This resulted in 1 542 900 runs for 1605 particle trajectories for 4 years using daily output values. The coefficients that produced the end total biomass that matched the initial total biomass inside the polygon with less than 20% difference, were recorded in the aim to search for parameters values that ensured the stability of the initial population. 1894 runs matched this criteria. We present this values in the k_1, k_2, k_3 space in Fig. 2. The aim was to identify clusters of parameter values that would ensure a stable population. However, the resulting dots in the parameter space form a 2-dimensional, slightly curved plane. The inclination of the plane in relation to k_1 and k_3 can be easily explained. Greater mortality (k_3) demands greater growth (k_1) in order to keep the population stable. The half-saturation constant (k_2) is determined by these two values and follows accordingly.

3.2. Long runs

We ran the chosen parameter configurations (Table 1, Figs. 2 and 3) for a 21-year period from 2000 to 2020 and three of them stopped before reaching the final year. The C1, C5 and C6 populations exploded before reaching the end of the run. Others ran the whole length of the simulation. The C7 gave most promising results and therefore we ran the same configuration two additional times, to test the sensitivity

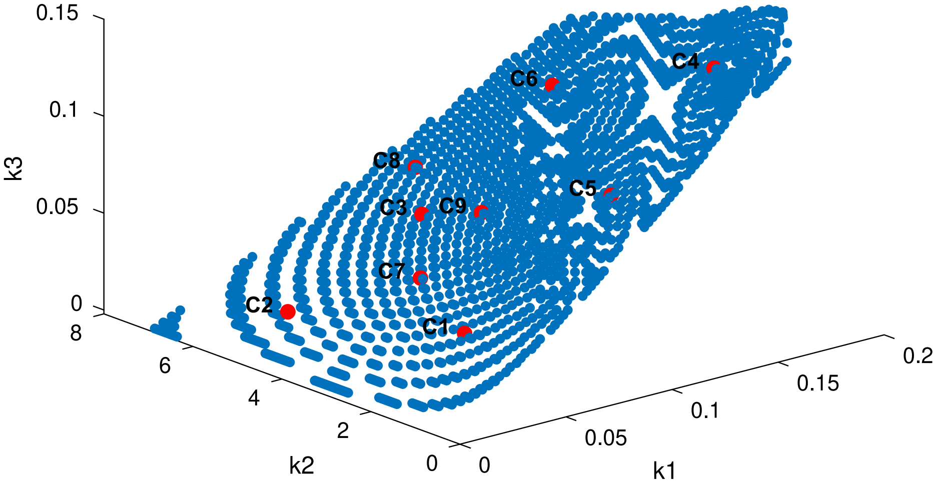


Fig. 2. The parameter values (k_1, k_2 and k_3) that result in a stable population in the area of initial release in the 4-year run (blue dots). The red dots mark the chosen values for the long runs — C1 to C9 respectively.

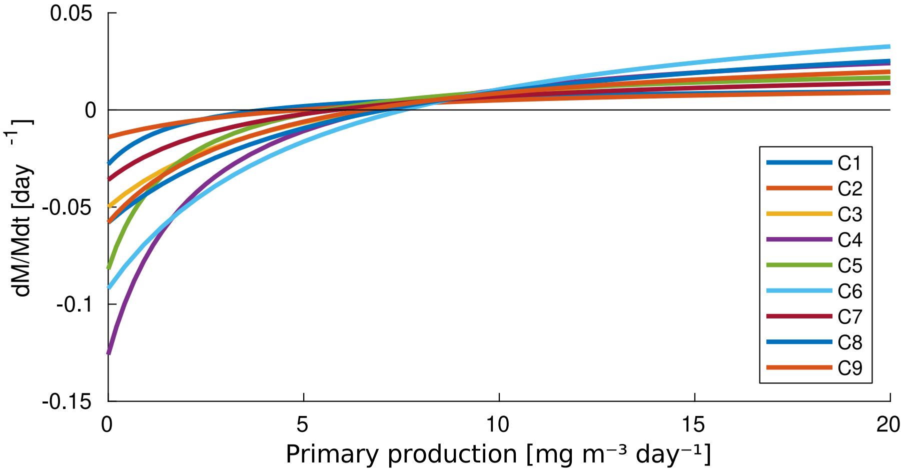


Fig. 3. The growth-mortality curves for the C1 to C9 experiments based on Eq. (2).

Table 1
Parameter configurations used in the 21-year simulation (N - initial number of particles).

Run name	Release area	N	k_1	k_2	k_3
C1	W Med.	2000	0.041	1.9	0.028
C2	W Med.	2000	0.029	5.2	0.014
C3	W Med.	2000	0.087	5.0	0.050
C4	W Med.	2000	0.167	2.2	0.126
C5	W Med.	2000	0.107	1.7	0.082
C6	W Med.	2000	0.159	5.5	0.092
C7 (a,b,c)	W Med.	2000	0.059	3.7	0.036
C7M	Med.	8000	0.059	3.7	0.036
C8	W Med.	2000	0.109	6.2	0.058
C9	W Med.	2000	0.093	4.0	0.058

of the results to the uncertainty introduced when each year massive particles are split into smaller ones (Section 2.5) - new particles are randomly distributed inside a 0.5° area and their positions differ each time the model is run. We present the results marked as C7a, C7b and C7c. The last of the runs was C7M, which uses the same C7 parameters but with the initial release of particles throughout the whole Mediterranean Sea. The rest of the results are available in the repository (see Software and data availability section). The C7 parameters:

$$
\begin{aligned}
k_1 &= 0.059\ \mathrm{day}^{-1} \\
k_2 &= 3.7\ \mathrm{mg\,m}^{-3}\,\mathrm{day}^{-1} \qquad (4) \\
k_3 &= 0.036\ \mathrm{day}^{-1}
\end{aligned}
$$

The total biomass of the whole population (Fig. 4) shows high interannual variations and seasonal oscillations with maximums in the summer months (usually August) and minimums in the winter months (January or February). There is high seasonal variance with sometimes more than 2-fold increase of the total biomass in the summer. There is considerable difference between the runs, although the dynamics is the same. Therefore there is considerable sensitivity of the population size to slight changes in positioning of the particles. The highest total biomass during the simulation was reached in summer 2010 when the population for C7c grew up to 52 times the initial mass. The C7M run reached a higher maximum mass but started with 4-times the usual initial population (8000 particles instead of 2000 particles) and unsurprisingly maintained a slightly higher total biomass. However, it exhibits the same dynamics. Although the total biomass seems to stabilize between 10 and 20-times of the initial mass after 2013, it starts to grow again after 2019.

3.2.1. Spatial distribution

The average biomass distribution for C7a (Figs. 5 and 6; it is almost identical for C7b and C7c – plots are available in the repository) shows that the majority of Mediterranean *Pelagia noctiluca* population resides in the Northwestern Mediterranean Sea – from Catalan coast to Ligurian

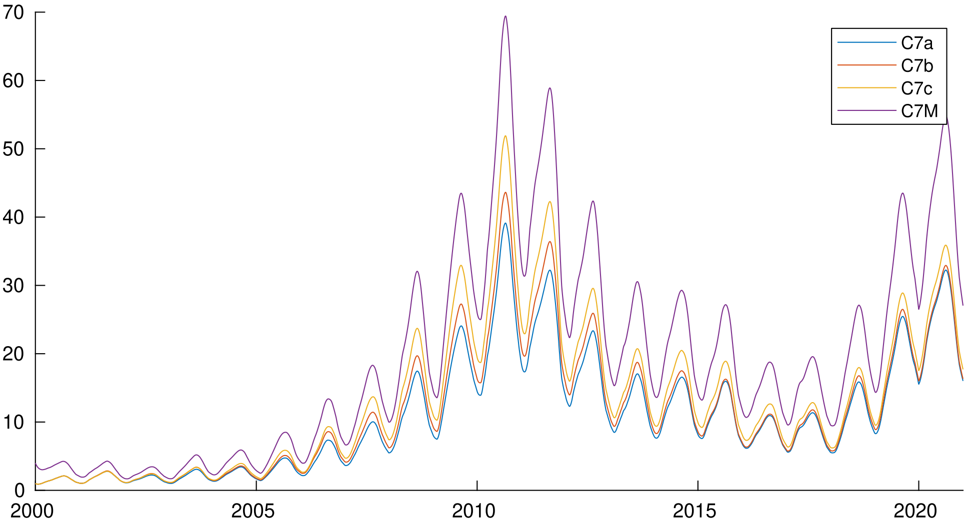


Fig. 4. Total *Pelagia noctiluca* normalized biomass throughout the simulation for C7a, C7b, C7c and C7M. The biomass shown is units of the total biomass of the initial population inside the blue area in Fig. 1.

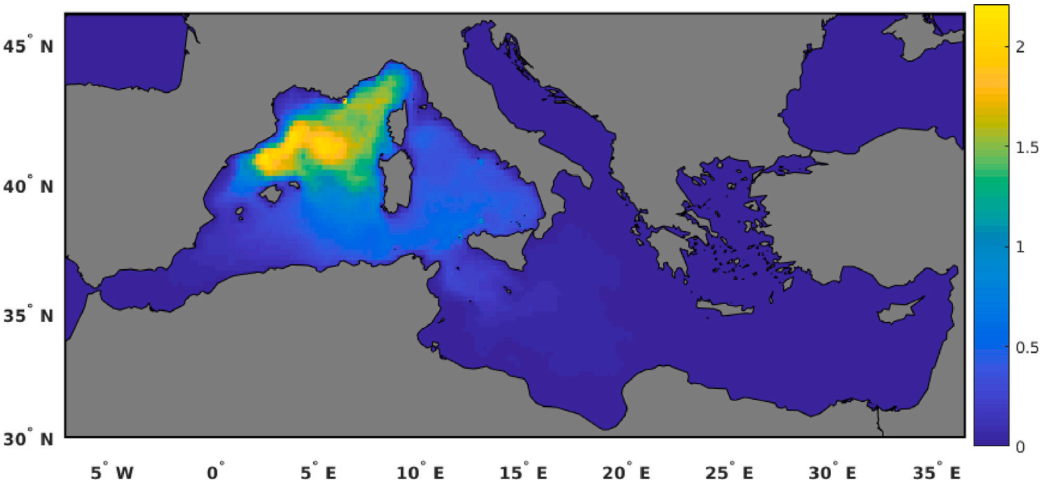


Fig. 5. Distribution of average *Pelagia noctiluca* biomass throughout the 21-year long simulation (C7a). Average biomass in units of initial particle mass per deg^2 is shown.

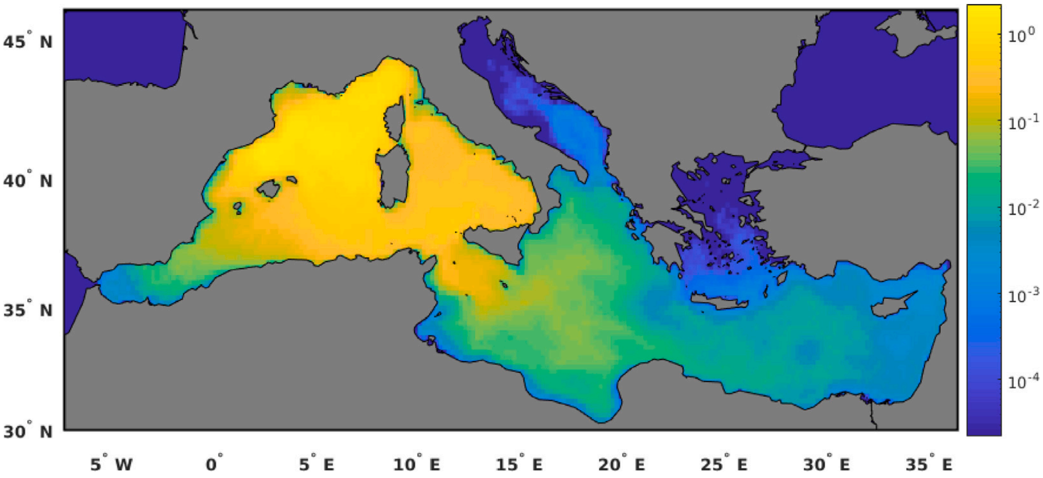


Fig. 6. Same as Fig. 5 but in logarithmic scale.

Sea in the north and from Balearic Islands to Sardinia in the south. However, the simulation shows large interannual variations in total biomass (Fig. 4) and its distribution in this area which is in accordance with observations (Goy et al., 1989; Bernard et al., 2011; Ottmann et al., 2021; Daly Yahia et al., 2023). Yearly biomass distribution plots are available in the repository (see Software and Data Availability

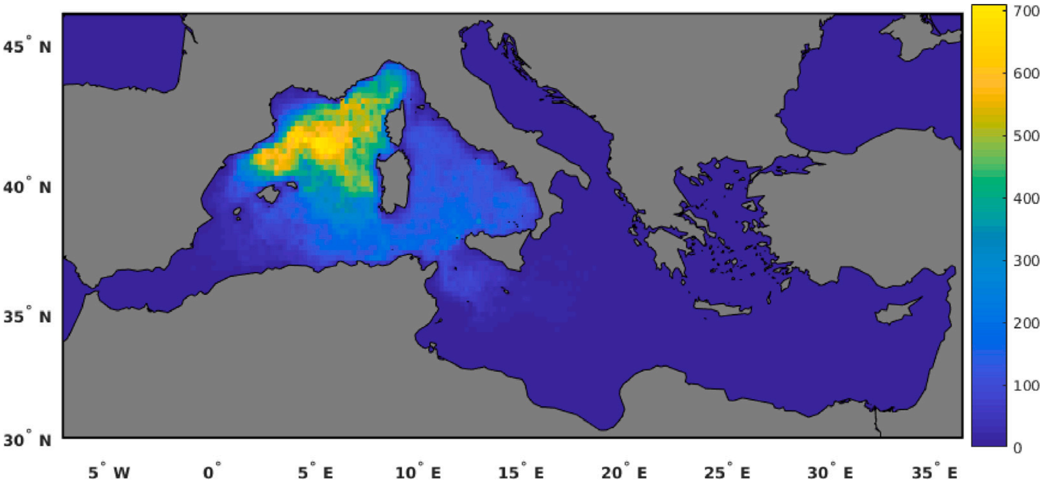


Fig. 7. Distribution of median *Pelagia noctiluca* biomass (in units of initial particle mass per deg^2) throughout the 21-year long simulation (C7a).

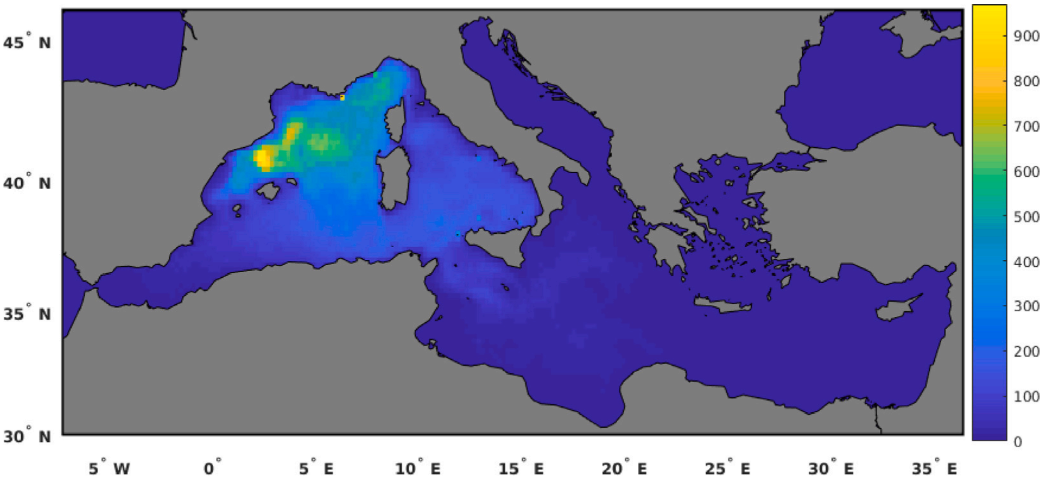


Fig. 8. Distribution of standard deviation of *Pelagia noctiluca* biomass (in units of initial particle mass per deg^2) throughout the 21-year long simulation (C7a).

section) and show that the core of the population is moving inside the above-mentioned area. The median distribution plot (Fig. 7) shows a bit different picture with the core centered a bit more eastward and a bit more dispersed throughout the area. The distribution of the standard deviation (Fig. 8) confirms that the average distribution was heavily influenced by the position of the core in the years when the population was at its maximum.

Throughout the rest of the Western Mediterranean the biomass density is somewhat lower but still considerable. It decreases significantly towards the Gibraltar strait and through the Strait of Sicily towards the Eastern Mediterranean. As expected, the Eastern Mediterranean proves to be too oligotrophic to support a significant *Pelagia noctiluca* population. According to biomass density plots, the *Pelagia noctiluca* was not able to establish a permanent population in any other location besides the release area. The Adriatic and Aegean Sea show extremely low biomass concentrations. Again, the observations qualitatively support the results for the Adriatic Sea, where *Pelagia* is somewhat frequent in the SE part of the basin, whereas sightings in other parts are relatively rare (Kogovšek et al., 2010; Violić et al., 2022).

The average distribution produced by C7M is virtually indistinguishable from C7a (plot in the repository). This demonstrates that the connectivity throughout the Mediterranean is quite high and that an initial population would quickly spread to areas where the conditions are favorable.

3.2.2. Comparison with observations in the northern Adriatic Sea

Total normalized biomass (sum of biomass of all particles divided by the initial mass of single particle) of all particles within the northern Adriatic area (red area in Fig. 1) is shown in Fig. 9. We decided to count the particles north of the Ancona-Zadar line as this should roughly match with the area of observations. Red dots represent the sightings index (Pestorić et al., 2021; Violić et al., 2022; Malej et al., 2022) of *Pelagia noctiluca* in this area for the same period (own observations). There is significant difference between the results of the three simulations (C7a, C7b and C7c) although the model configuration was exactly the same (Eq. (4)). The solutions show high sensitivity to randomness in particle positioning when accounting for growth (Section 2.5). This is less surprising, given the length of the simulation and the distance of the northern Adriatic from the release area.

However, there are some prominent similarities. All the three simulations fail to produce *Pelagia noctiluca* presence before the autumn 2006. It is reasonable to assume that the initial population has to reach sufficient size to migrate to far areas of the basin and this could be considered as a spin-up time of the model. The prominent peak in the autumn 2006 and the peaks in the beginning of 2012 and 2018 are present in all three simulations and match well with the observations. This indicates that in these situations the circulation was strongly favorable for the transport of *Pelagia noctiluca* to the northern Adriatic.

There are other observations (2008, 2011 and 2013) that are matched with peaks in two out of three runs. This indicates that these intrusions are likely a consequence of more random processes.

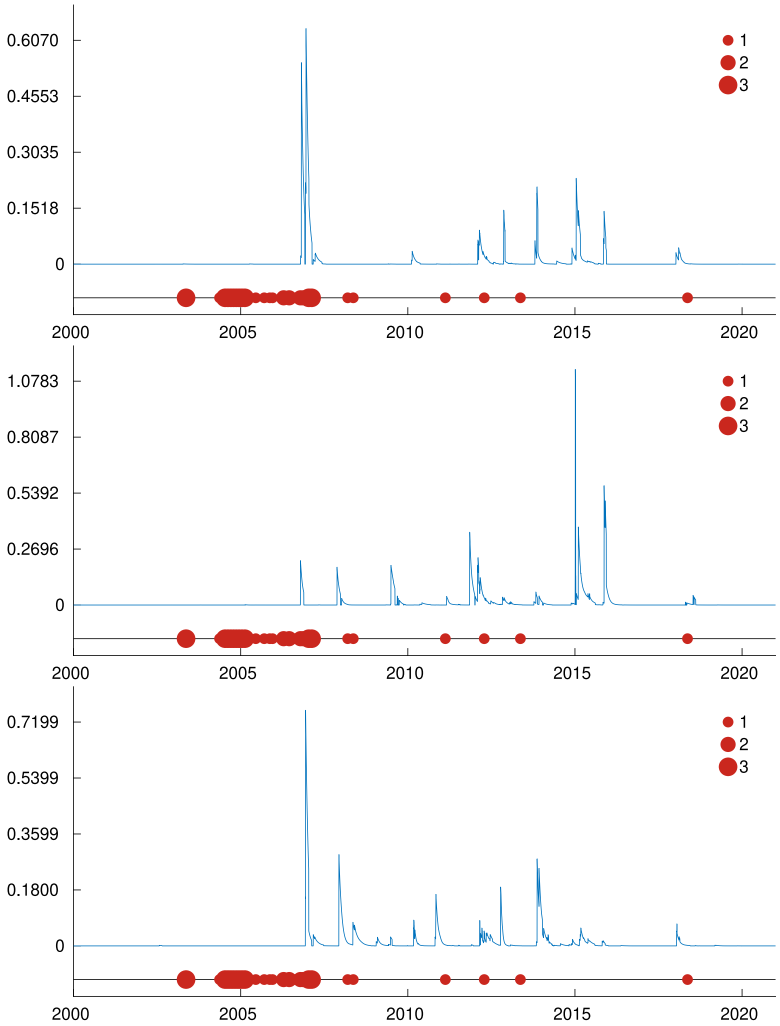


Fig. 9. Total normalized biomass within the Northern Adriatic area (see Fig. 1 - light red color) drawn in blue. All the results were obtained using the C7 configuration. Top to bottom: C7a, C7b, C7c. Red dots represent sightings index as in Pestorić et al. (2021) and Violić et al. (2022): 1—sporadic occurrence of individual organisms; 2—frequent occurrence of individual jellyfish specimens and/or small aggregations; 3—frequent occurrence of large jellyfish aggregations/blooms.

On the other hand, there is a peak in winter 2015 present in all three runs with no matching observations. These peaks could be caused by underestimated mortality in shallow waters (k_S) or beaching (k_B). However, such events are not necessarily model errors. It has to be emphasized that jellyfish observations are difficult to perform and scarce. In large majority of cases they are limited to the surface of the water column and coastal waters. Therefore, the lack of observations does not necessarily imply lack of presence of *Pelagia noctiluca* in that period. It is completely possible that *Pelagia noctiluca* were in the area without being noticed.

4. Discussion

Contrary to our initial expectations, the solutions that ensured a stable population in the Western Mediterranean Sea did not form isolated clusters in the 3-dimensional parameter space. Such cluster or several clusters would indicate that only isolated set or sets of parameters maintain permanent *Pelagia noctiluca* presence in the Western Mediterranean Sea. This would allow us to speculate about the true interactions between *Pelagia noctiluca* and its environment related to our parameter constraints.

However, the resulting homogeneous 2-dimensional surface indicates an infinite range of stable solutions (Fig. 2). The results of the C7 run which form a realistic pattern throughout the Mediterranean Sea (Figs. 5 and 6) starting from a very limited area in the Western Mediterranean, indicate that the model has reached a certain level of realism.

Observations in the northern Adriatic in years 2006, 2012 and 2018 are matched with modeled presence in this area in all three C7 runs. This indicates the presence of circulation patterns that strongly favor transport of *Pelagia noctiluca* towards the northern Adriatic. Observations in years 2008, 2011 and 2013 were matched only in two out of three C7 runs. This indicates that the circulation was less favorable and the presence in these years was likely more random.

The discrepancies in the first part of the run likely stem from the model spin-up. One also has to keep in mind that the observations are scarce and only partially reflect the true concentration of jellyfish in a given area. Given the above, it seems very plausible that the C7 configuration provides realistic k_1, k_2 and k_3 values. The mortality rate in the presented C7 long-term simulation (Eq. (4)) is $k_3 = 0.036$ day^{-1} and is closer to values obtained (Malej and Malej, 1992) (0.006 day^{-1} to 0.02 day^{-1}) than those by Wright et al. (2021) (0.12 day^{-1}). This seems reasonable as the former were obtained from a *Pelagia noctiluca* Leslie matrix model (Leslie, 1945), while the latter are from a global biogeochemical model with a single jellyfish plankton functional type that represents all jellyfish species. Lilley et al. (2014) observed maximum laboratory growth of 0.015 day^{-1} to 0.04 day^{-1} for adults and 0.3 day^{-1} for ephyrae, while Rosa et al. (2013) observed maximum growth of 0.04 day^{-1} for adults in the Straits of Messina (Central Mediterranean Sea). Since a particle in the simulation represents a

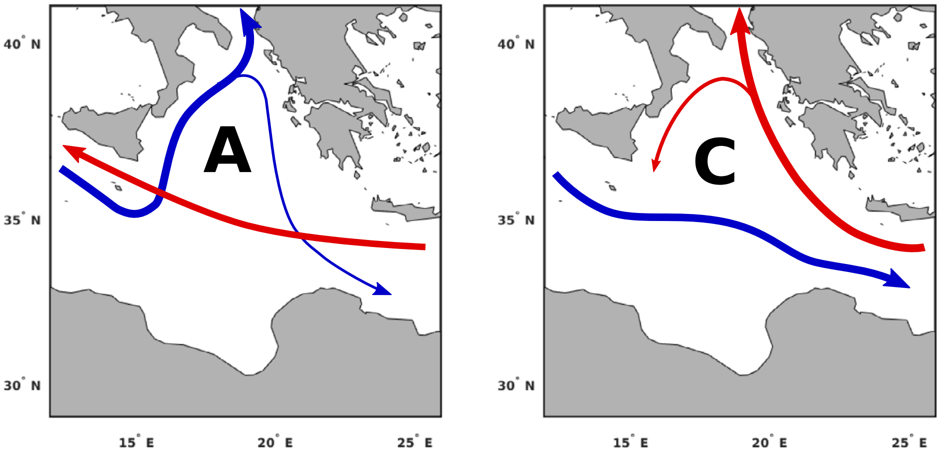


Fig. 10. Schematic representation of the BiOS mechanism. Left: anticyclonic phase, right: cyclonic phase. In the anticyclonic phase the water entering the Adriatic Sea is coming from the western Mediterranean Sea, while in the cyclonic phase the water is coming from the eastern Mediterranean Sea.
Source: The image was adapted from Figure 6 in Civitarese et al. (2023).

large group of individuals of all life stages, the obtained value of maximum growth rate $k_1 = 0.059$ day^{-1} matches incredibly well with observations. Taking in consideration the simplicity of the theoretic foundations our model is based on, the results are truly impressive.

4.1. *Pelagia noctiluca and Mediterranean circulation*

The multiyear presence of *Pelagia noctiluca* in the northern Adriatic, followed by long periods of absence, resembles the BiOS (Adriatic-Ionian Bimodal Oscillating System; Fig. 10) mechanism (Gačić et al., 2010; Civitarese et al., 2023): water from the eastern Mediterranean Sea is carried into the Adriatic Sea when the circulation in the northern Ionian Sea is cyclonic, while in the anticyclonic phase the water from western Mediterranean Sea is transported into the Adriatic basin. Therefore, the anticyclonic phase should favor the transport of *Pelagia noctiluca* from the western part of the Mediterranean basin into the Adriatic Sea as was observed for some other organisms (Civitarese et al., 2010). The north Ionian circulation was primarily cyclonic throughout the simulation period, except for the 2006–2009 period when it was anticyclonic (Mihanović et al., 2021; Denamiel et al., 2022). This does not match with our *Pelagia noctiluca* sightings (Fig. 9). However, the processes involved are more complex and it is possible that the jellyfish travel through the eastern part of the Ionian Sea before entering the Adriatic. Furthermore, Denamiel et al. (2022) observed a 1–2 year lag in Adriatic water properties following the transition of BiOS. The relation between BiOS and *Pelagia noctiluca* in the Adriatic Sea is beyond the scope of this paper and should be studied more thoroughly.

The model shows surprisingly small concentration of *Pelagia noctiluca* in the Alboran Sea (the western-most part of the Mediterranean Sea; area westward from the green line in Fig. 1) which is in stark contrast with frequent observations in the area (Bellido et al., 2020; Dobson et al., 2023; Gutiérrez-Hernández and Gómez, 2023). The Alboran Sea is under strong influence of the Atlantic water flowing in through the Strait of Gibraltar. The Atlantic inflow forms two large anticyclonic gyres in the Alboran sea and the convergence of the Atlantic and Mediterranean water masses forms the Almeria-Oran front (green line in Fig. 1; Tintore et al., 1988) which likely prevents the particles to enter this area from the east. This is in accordance with observed genetic divergence between other species on both sides of the front (Patarnello et al., 2007; Garcia-Cisneros et al., 2018; Pérez-Portela et al., 2019). Therefore, we can assume that the Alboran *Pelagia noctiluca* population is mainly influenced by the inflow from the Atlantic and that the inflow from the Mediterranean population is very limited.

4.2. *Model limitations*

As emphasized in the introduction, the model accounts only for vertical migrations, food availability and stranding. As such it cannot be used to test the impact of marine canyons on *Pelagia noctiluca* transport (Canepa et al., 2014; Benedetti-Cecchi et al., 2015; El Rahi et al., 2020) or other complex interactions between environment and different life stages (Bergamasco et al., 2022). Mortality in this study is kept constant (k_3) with additional mortality in shallow waters (k_S) and in proximity to dry land (k_B). Therefore the model does not account for spatially and temporally variable predation or the effects of temperature on growth and mortality (Malej and Malej, 2004).

Primary production was used as a proxy for food availability (Fig. 11). This might seem far fetched, as gut content and stable isotope studies have shown that the main diet of Pelagia is mesozooplankton (Malej et al., 1993; Sabatés et al., 2010; Rosa et al., 2013; Milisenda et al., 2018). However, zooplankton concentration reanalysis is not available at the CMEMS web service. Using primary production as a proxy is supported by observed and modeled correlation between mesozooplankton and chlorophyll *a* (Mazzocchi et al., 2014; Liu et al., 2024) and observed strong correlation of *Pelagia noctiluca* abundance with chlorophyll concentration and primary production (Canepa et al., 2014; Ottmann et al., 2021).

As already noted, the western part of the Mediterranean basin is more productive than the oligotrophic eastern part and unsurprisingly there are certain similarities between the average primary production distribution (Fig. 11) and the *Pelagia noctiluca* distribution produced by the model (Figs. 5–7). The core of the population is located in the area of high primary production between the Catalan coast, Ligurian Sea, Balearic Islands and Sardinia. There are also obvious differences — e.g. in the coastal areas where the primary production is high, but the increased mortality and ocean dynamics prevent the existence of large populations.

The surface-averaged primary production (Fig. 12) shows peaks in the summer months as does the total *Pelagia noctiluca* biomass (Fig. 4). However, the former peaks between April and July, while the latter reaches its maximum with a bit of a delay (usually in August). The use of primary production introduces some additional uncertainties, but should suffice to serve the purpose of this study, namely to elucidate the *Pelagia noctiluca* distribution in the Mediterranean Sea.

Our model ignores the effects of temperature on growth, reproduction and mortality of jellyfish, which has been implemented in some other models (Vodopivec et al., 2017; El Rahi et al., 2020; Wang et al., 2025). El Rahi et al. (2020) also used OpenDrift to study *Pelagia noctiluca* in the Mediterranean Sea. However, the focus

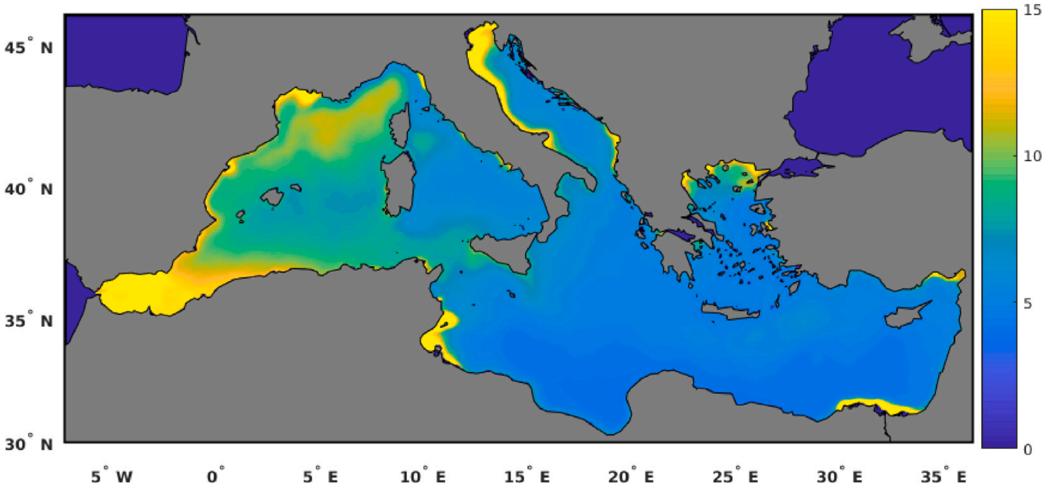


Fig. 11. Multi-year average (2000–2020) of monthly primary production (in mg m^{-3} day^{-1}). Maximum monthly value in the top 500 m layer is used.

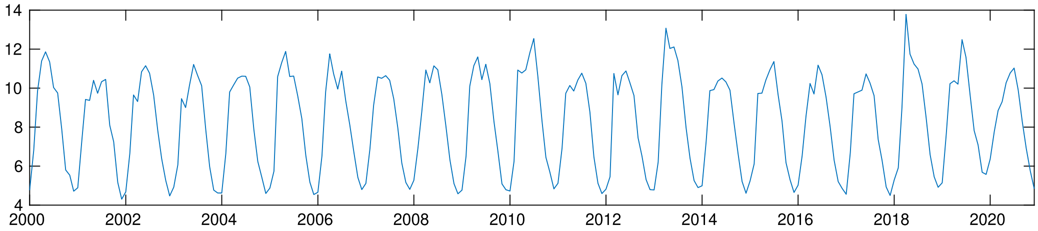


Fig. 12. Surface-averaged monthly primary production value (in mg m^{-3} day^{-1}). Maximum primary production in the top 500 m is used.

of the study was different from ours and so was the model design. The IBM included different life stages, vertical migrations and temperature-dependent development. The study area was much smaller and the simulation spanned 8 months. The implementation of stage-specific behavior benefited the model which was developed to study *Pelagia noctiluca* stranding events in the Mediterranean Coastal waters of Spain. In our case, the geographical domain is much larger and the time span much longer and for our purpose of studying the long-term geographical distribution, food-dependent growth is of primary importance and a different modeling approach is needed.

The importance of jellyfish in the ecosystem, and therefore the need to study their ecological role and distribution, was demonstrated by Calhoun-Grosch et al. (2024) who used a depth-resolved food web model to study the trophic dynamics of the oceanic Gulf of Mexico. Increased biomass of large jellyfish in the model decreased the biomass of most other forage functional groups. Such modeling approach gives no insight into spatial distribution of jellyfish, however it includes feedback between predator and prey biomass, which is missing in our model.

This study is based on the assumption that the population in the Western Mediterranean is stable. This is supported by frequently observed presence in this area (Goy et al., 1989; Ferraris et al., 2012; Rosa et al., 2013; Prieto, 2018; Daly Yahia et al., 2023; Canepa et al., 2014). However, the model does not account for possible exchange of *Pelagia noctiluca* between the Atlantic Ocean and the Mediterranean Sea (Licandro et al., 2010; Stopar et al., 2010; Glynn et al., 2016; Pastor-Prieto et al., 2021). The exchange might have significant influence on their abundance in the Western Mediterranean Sea.

One limitation of our simulations is the removal of particles with small biomass and splitting of particles with high biomass that happens in the beginning of each year-long run segment (Section 2.5). This approach was necessary because OpenDrift does not allow changes in the number of particles during a simulation. Ideally, removal or splitting should occur as soon as a particle reaches the threshold biomass.

Despite relative simplicity of the PelagiaIBM model (Sun et al., 2016; Jakeman et al., 2024), the emerging distribution is very realistic and matches very well with expectations. The partial match with observations in the Northern Adriatic is encouraging. The most obvious further steps will be to employ zooplankton biomass instead of primary production for food-related growth. The model could be further improved with the effects of temperature on reproduction, mortality and growth, which are particularly important to study the effects of climate change on some jellyfish species.

Using PelagiaIBM in combination with a thorough parameter exploration and calibration has provided impressive insight into *Pelagia noctiluca* distribution in the Mediterranean Sea and produced new growth and mortality estimates. Our code and approach can be extended to other zooplankton species that exhibit similar behavior. The model could help forecast species distributions under future climate scenarios (especially with the addition of temperature effects) or be used in marine resource management (fisheries management, jellyfish bloom forecasting, etc.). The encouraging results confirm the value of integrating biological traits into particle tracking simulations, forming individual-based models, to study the spatial distribution of organisms.

5. Conclusions

We present a novel individual-based model (IBM) to simulate and elucidate the spatio-temporal distribution of *Pelagia noctiluca* (mauve stinger) in the Mediterranean Sea. The model addresses significant gaps in the field observation data that traditionally limit jellyfish population studies. Previous research has shown substantial limitations in understanding *Pelagia noctiluca* distribution, largely due to the scarcity of in situ data from the open ocean. A custom OpenDrift module introduces sun-synchronized diel vertical migrations, food-dependent growth modeled on Michaelis–Menten kinetics, and custom mortality parameters. The model produces a realistic representation of mauve stinger dispersal and population dynamics and provides new growth and mortality estimates.

A 21-year simulation revealed a very clear geographical distribution of *Pelagia noctiluca* population in the Mediterranean Sea, with a strong core in the northern part of the Western Mediterranean Sea, between the Catalan coast, Balearic Islands, Corsica and Gulf of Lions. The simulation also shows strong seasonal and interannual variations in the total biomass of *Pelagia noctiluca* population, which confirms the conclusions deduced from spatially very nonhomogeneous in situ observations. The core of the population is also constantly moving, but stays within the above-mentioned area limits.

The model partially reproduces the sightings in the northern Adriatic. While the pattern of occasional intrusions into the area is reproduced by the model, the timing and intensity exhibit high sensitivity to small randomness introduced in positioning of the particles. This is not surprising given the large distance from the permanent population.

Our work demonstrates how spatially explicit IBMs can model complex ecological phenomena in marine environments with limited in situ data by dynamically integrating environmental and behavioral factors in a high-resolution spatial context. The model addresses previously identified shortcomings by realistically replicating jellyfish movement and also capturing interannual variations and potential “hotspot” regions that align well with observed *Pelagia noctiluca* distribution.

The model’s ability to generate realistic spatial patterns and interannual variations indicates that it has reached a high level of realism even with initially poorly constrained parametrizations. The initial parameter space analysis ensures the model’s robustness and flexibility. The model code is freely available, enabling interested users to adapt and extend the model to other marine species and environmental scenarios. The presented spatial individual-based model could be improved with further *Pelagia noctiluca* traits and adapted to different locations. As demonstrated, PelagiaIBM is capable of explaining the distribution of jellyfish and therefore also forecast jellyfish blooms which should prove invaluable in tourism and fisheries management. With suitable modifications it can be used for other zooplankton species and with adequately modulated release of particles also for other jellyfish species that originate from attached polyps.

Software and data availability

The PelagiaIBM code, adjacent scripts, land proximity mask and plots of simulation results (C1–C9) are freely available. Due to ongoing development, the updated version of the code is available on GitLab: https://gitlab.com/mvodopivec/pelagiaibm

Supplementary plots, step by step guide and the code used for the production of figures in this article are available on Figshare: https://figshare.com/articles/software/PelagiaIBM/27605307.

Mediterranean Sea Physics Reanalysis (MEDSEA_MULTIYEAR_PHY_006_004) was obtained from Copernicus Marine Service: https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1

Mediterranean Sea biogeochemical reanalysis (MEDSEA_MULTIYEAR_BGC_006_008) was obtained from Copernicus Marine Service: https://doi.org/10.25423/cmcc/medsea_multiyear_bgc_006_008_medbfm3

CRediT authorship contribution statement

Martin Vodopivec: Writing – review & editing, Writing – original draft, Software, Methodology, Conceptualization. **Alenka Malej:** Writing – review & editing, Methodology, Conceptualization.

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.

Acknowledgments

The authors acknowledge the financial support from the Slovenian Research Agency (research core funding No. P1-0237 and project DECOMB J7-2599). Image of *Pelagia noctiluca* for the graphical abstract was provided by Tihomir Makovec. We thank Tinkara Tinta for the valuable discussions and insightful advice. This study took advantage of netCDF software developed by UCAR/NSF Unidata (https://doi.org/10.5065/D6H70CW6) and has been conducted using E.U. Copernicus Marine Service Information.

Appendix. Code description

In line with Janssen et al. (2020) and Jakeman et al. (2024) the PelagiaIBM, adjacent scripts and some of the results are freely available (see Software and data availability section). The repository includes a README file with detailed description on how to use the OpenDrift module, run the simulations and perform the analysis of results. The code and run scripts are written in Python programming language and users are encouraged to modify them according to their own needs or new findings about jellyfish-environment interactions. The repository also includes the MATLAB scripts that were used for the analysis of the results and plotting the figures.

A.1. PelagiaIBM

PelagiaIBM.py is an OpenDrift (Dagestad et al., 2018) module and should be placed in the ‘models’ directory inside the OpenDrift folder. It introduces a ‘PelagiaElement’ class which extends the native Lagrangian3DArray class. All the variables of each super-individual are defined here. These will also be stored in the output netCDF files in form of 2-dimensional arrays, the first dimension being the number of individuals and the second the time. ‘biomass’ is the dimensionless biomass of the particle; ‘p_production’ is the highest primary production value in the water column at the location of the particle; ‘kb’ is the k_B parameter value (mortality due to beaching); ‘ks’ is the k_S parameter value (mortality due to shallow water):

```
variables = Lagrangian3DArray.add_variables([
  ('biomass', {'dtype': np.float32,
         'units': '',
         'default': 10000.0}),
  ('p_production', {'dtype': np.float32,
         'units': '',
         'default': 0.0}),
  ('kb', {'dtype': np.float32,
         'units': '',
         'default': 0.0}),
  ('ks', {'dtype': np.float32,
         'units': '',
         'default': 0.0})])
```

The second class is ‘Pelagia_IBM’ that extends the native OceanDrift class and governs the behavior of the particles. It contains the following functions: ‘diel_vertical_migration’, ‘update_pelagia_state’ and ‘update’.

The ‘diel vertical migrations’ function sets the vertical position of each particle. The beginning of downward and upward migration can be determined by the clock or the position of the sun at the location of each particle, or completely omitted by setting the ‘MigrationType’ parameter. Here you can set also the vertical swimming speed, maximum depth and minimum distance from the sea floor.

The ‘update_pelagia_state’ function calculates the biomass of each particle using the modified Michaelis–Menten kinetics:

$$\frac{dM}{dt} = M\left(\frac{k_1 P}{k_2 + P}\right) - k_3 M - k_S M - k_B M \tag{A.1}$$

The group of jellyfish represented by the particle gains mass (M) in areas with higher primary production (P) and looses mass due to the mortality terms (k_3, k_S, k_B). The $k_S M$ and $k_B M$ terms are calculated separately using the bathymetry and near-shore mask respectively. For in depth description see Section 2.3.

The 'update' function is the main function of the class and calls the functions that change the location and properties of the particles.

A.2. OpenDrift run scripts

Three run scripts are included: Run_baserun.py, Run_pelagia.py and Restart_pelagia.py. The first is used for the 4-year run that is needed for the calibration of model parameters (Section 3.1). It runs the model for the 2000–2003 period using 10 000 particles. The second executes the first year of the long simulation (year 2000) using 2000 particles. The third executes each following year of the long-term simulation (from 2001–2020). This one includes the code for removal of particles with the biomass below the threshold and multiplication of particles with biomass above the threshold.

Each of the scripts is well commented and the commentaries should provide enough information to guide the user through the code. A bash script Longrun.sh was used to run the long-term simulation. It invokes the Run_pelagia.py first, followed by a sequence of Restart_pelagia.py calls. Longrun.sh is also included in the repository.

Data availability

The PelagiaIBM code, adjacent scripts, land proximity mask and plots of simulation results (C1-C9) are freely available. Due to ongoing development, the updated version of the code is available on GitLab: https://gitlab.com/mvodopivec/pelagiaibm Supplementary plots, step by step guide and the code used for the production of figures in this article are available on Figshare: https://figshare.com/articles/software/PelagiaIBM/27605307. Mediterranean Sea Physics Reanalysis (MEDSEA_MULTIYEAR_PHY_006_004) was obtained from Copernicus Marine Service: https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1 Mediterranean Sea biogeochemical reanalysis (MEDSEA_MULTIYEAR_BGC_006_008) was obtained from Copernicus Marine Service: https://doi.org/10.25423/cmcc/medsea_multiyear_bgc_006_008_medbfm3.

References

Acevedo, M.J., Fuentes, V.L., Olariaga, A., Canepa, A., Belmar, M.B., Bordehore, C., Calbet, A., 2013. Maintenance, feeding and growth of Carybdea marsupialis (Cnidaria: Cubozoa) in the laboratory. J. Exp. Mar. Biol. Ecol. 439, 84–91.

Arai, M.N., 1997. A Functional Biology of Scyphozoa. Springer Science & Business Media.

Arthur, D., Vassilvitskii, S., 2006. k-means++: The Advantages of Careful Seeding. Technical Report. Stanford.

Bauer, P., Stevens, B., Hazeleger, W., 2021. A digital twin of earth for the green transition. Nat. Clim. Chang. 11 (2), 80–83.

Baxter, E.J., Sturt, M.M., Ruane, N.M., Doyle, T.K., McAllen, R., Harman, L., Rodger, H.D., 2011. Gill damage to Atlantic salmon (Salmo salar) caused by the common jellyfish (Aurelia aurita) under experimental challenge. PLoS One 6 (4), e18529.

Bellido, J.J., Baez, J.C., Souviron-Priego, L., Ferri-Yanez, F., Salas, C., López, J.A., Real, R., 2020. Atmospheric indices allow anticipating the incidence of jellyfish coastal swarms. Mediterr. Mar. Sci. 21 (2), 289–297.

Benedetti-Cecchi, L., Canepa, A., Fuentes, V., Tamburello, L., Purcell, J.E., Piraino, S., Roberts, J., Boero, F., Halpin, P., 2015. Deterministic factors overwhelm stochastic environmental fluctuations as drivers of jellyfish outbreaks. PLoS One 10 (10), e0141060.

Bergamasco, A., Cucco, A., Guglielmo, L., Minutoli, R., Quattrocchi, G., Guglielmo, R., Palumbo, F., Pansera, M., Zagami, G., Vodopivec, M., et al., 2022. Observing and modeling long-term persistence of P. noctiluca in coupled complementary marine systems (southern Tyrrhenian sea and Messina strait). Sci. Rep. 12 (1), 14905.

Berline, L., Zakardjian, B., Molcard, A., Ourmières, Y., Guihou, K., 2013. Modeling jellyfish *Pelagia noctiluca* transport and stranding in the Ligurian Sea. Marine Poll. Bull. 70 (1), 90–99.

Bernard, P., Berline, L., Gorsky, G., 2011. Long term (1981–2008) monitoring of the jellyfish Pelagia noctiluca (Cnidaria, Scyphozoa) on the french Mediterranean Coasts. J. Ocean. Res. Data 4 (1).

Calhoun-Grosch, S., Ruzicka, J.J., Robinson, K.L., Wang, V.H., Sutton, T., Ainsworth, C., Hernandez, F., 2024. Simulating productivity changes of epipelagic, mesopelagic, and bathypelagic taxa using a depth-resolved, end-to-end food web model for the oceanic Gulf of Mexico. Ecol. Model. 489, 110623.

Canepa, A., Fuentes, V., Sabatés, A., Piraino, S., Boero, F., Gili, J.-M., 2014. Pelagia noctiluca in the Mediterranean Sea. Jellyfish Bloom. 237–266.

Civitarese, G., Gačić, M., Batistić, M., Bensi, M., Cardin, V., Dulčić, J., Garić, R., Menna, M., 2023. The BiOS mechanism: History, theory, implications. Prog. Oceanogr. 216, 103056.

Civitarese, G., Gačić, M., Lipizer, M., Eusebi Borzelli, G., 2010. On the impact of the bimodal oscillating system (BiOS) on the biogeochemistry and biology of the Adriatic and Ionian Seas (Eastern Mediterranean). Biogeosciences 7 (12), 3987–3997.

Cossarini, G., Feudale, L., Teruzzi, A., Bolzon, G., Coidessa, G., Solidoro, C., Di Biagio, V., Amadio, C., Lazzari, P., Brosich, A., et al., 2021. High-resolution reanalysis of the Mediterranean Sea biogeochemistry (1999–2019). Front. Mar. Sci. 8, 741486.

Dagestad, K.-F., Röhrs, J., Breivik, Ø., Ådlandsvik, B., 2018. OpenDrift v1. 0: a generic framework for trajectory modelling. Geosci. Model. Dev. 11 (4), 1405–1420.

Daly Yahia, M.N., Batistic, M., Lucic, D., Fernández de Puelles, M.L., Licandro, P., Malej, A., Molinero, J.C., Siokou-Frangou, I., Zervoudaki, S., Prieto, L., Goy, J., Daly Yahia-Kéfi, O., 2010. Are the outbreaks of Pelagia noctiluca (Forsskål, 1775) more frequent in the Mediterranean basin? In: Gislason, A., Gorsky, G. (Eds.), Proceedings of the "Joint ICES/CIESM Workshop To Compare Zooplankton Ecology and Methodologies Between the Mediterranean and the North Atlantic (WKZEM)". International Council for the Exploration of the Sea.

Daly Yahia, N.M., Gueroun, S.K., Malej, A., Cucco, A., Granata, A., Prieto, L., Letterio, G., Lucic, D., Mourre, B., Vodopivec, M., Minnutoli, R., Leon Cobo, M.J., Bergamasco, A., 2023. Exploring the potential ecological niche of Pelagia noctiluca in Mediterranean ecoregions. In: 7th Jellyfish Bloom Symposium.

Dawson, M.N., Gupta, A.S., England, M.H., 2005. Coupled biophysical global ocean model and molecular genetic analyses identify multiple introductions of cryptogenic species. Proc. Natl. Acad. Sci. USA 102 (34), 11968–11973.

Denamiel, C., Tojčić, I., Pranić, P., Vilibić, I., 2022. Modes of the BiOS-driven Adriatic sea thermohaline variability. Clim. Dyn. 59 (3), 1097–1113.

Dobson, J.Y., Fonfría, E.S., Palacios, R., Blasco, E., Bordehore, C., 2023. Citizen science effectively monitors biogeographical and phenological patterns of jellyfish. Ocean & Coastal Management 242, 106668.

El Rahi, J., Weeber, M.P., El Serafy, G., 2020. Modelling the effect of behavior on the distribution of the jellyfish Mauve stinger (Pelagia noctiluca) in the Balearic Sea using an individual-based model. Ecol. Model. 433, 109230.

Escudier, R., Clementi, E., Cipollone, A., Pistoia, J., Drudi, M., Grandi, A., Lyubartsev, V., Lecci, R., Aydogdu, A., Delrosso, D., et al., 2021. A high resolution reanalysis for the Mediterranean Sea. Front. Earth Sci. 9, 702285.

Ferraris, M., Berline, L., Lombard, F., Guidi, L., Elineau, A., Mendoza-Vera, J., Lilley, M., Taillandier, V., Gorsky, G., 2012. Distribution of Pelagia noctiluca (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). J. Plankton Res. 34 (10), 874–885.

Franqueville, C., 1970. Etude comparative de macroplancton en Méditerranée nord-occidentale par plongées en soucoupe SP 350, et pêches au chalut pélagique. Mar. Biol. 5, 172–179.

Gačić, M., Borzelli, G.E., Civitarese, G., Cardin, V., Yari, S., 2010. Can internal processes sustain reversals of the ocean upper circulation? The Ionian Sea example. Geophys. Res. Lett. 37 (9).

Garcia-Cisneros, A., Palacin, C., Ventura, C.R.R., Feital, B., Paiva, P.C., Pérez-Portela, R., 2018. Intraspecific genetic structure, divergence and high rates of clonality in an amphi-Atlantic starfish. Mol. Ecol. 27 (3), 752–772.

GBIF, 2024. Global biodiversity information facility (25 july 2024) GBIF.org occurrence download. URL: https://doi.org/10.15468/dl.rw5jf5.

Gentleman, W., 2002. A chronology of plankton dynamics in silico: how computer models have been used to study marine ecosystems. Hydrobiologia 480, 69–85.

Glynn, F., Houghton, J.D., Bastian, T., Doyle, T.K., Fuentes, V., Lilley, M.K., Provan, J., 2016. High-resolution genetic analysis reveals extensive gene flow within the jellyfish Pelagia noctiluca (Scyphozoa) in the North Atlantic and Mediterranean Sea. Biol. J. Linnean Soc. 117 (2), 252–263.

Gordoa, A., Acuña, J.L., Farrés, R., Bacher, K., 2013. Burst feeding of Pelagia noctiluca ephyrae on Atlantic bluefin tuna (Thunnus thynnus) eggs. PLoS One 8 (9), e74721.

Goy, J., Morand, P., Etienne, M., 1989. Long-term fluctuations of Pelagia noctiluca (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. Deep. Sea Res. Part A Ocean. Res. Pap. 36 (2), 269–279.

Grimm, V., Railsback, S.F., 2013. Individual-based modeling and ecology. In: Individual-Based Modeling and Ecology. Princeton University Press.

Gutiérrez-Hernández, O., Gómez, A.R., 2023. Jellyfish distribution and abundance on the Southern Coast of the Iberian peninsula. In: Sustainable Development Goals in Europe: A Geographical Approach. Springer, pp. 281–299.

Jakeman, A.J., Elsawah, S., Wang, H.-H., Hamilton, S.H., Melsen, L., Grimm, V., 2024. Towards normalizing good practice across the whole modeling cycle: its instrumentation and future research topics. Soc.-Environ. Syst. Model. 6, 18755–18755.

Janßen, H., Augustin, C., Hinrichsen, H.-H., Kube, S., 2013. Impact of secondary hard substrate on the distribution and abundance of *Aurelia aurita* in the western Baltic Sea. Marine Poll. Bull. 75 (1), 224–234.

Janssen, M.A., Pritchard, C., Lee, A., 2020. On code sharing and model documentation of published individual and agent-based models. Environ. Model. Softw. 134, 104873.

Jarms, G., Morandini, A., 2019. World Atlas of Jellyfish. Dolling und Galitz Verlag.

Jørgensen, S.E., Fath, B.D., 2011. Fundamentals of Ecological Modelling: Applications in Environmental Management and Research. Elsevier.

Kogovšek, T., Bogunović, B., Malej, A., 2010. Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time series. Hydrobiologia 81–96.

Lebrato, M., Pahlow, M., Frost, J.R., Küter, M., de Jesus Mendes, P., Molinero, J.-C., Oschlies, A., 2019. Sinking of gelatinous zooplankton biomass increases deep carbon transfer efficiency globally. Glob. Biogeochem. Cycles 33 (12), 1764–1783.

Lee, P.L., Dawson, M.N., Neill, S.P., Robins, P.E., Houghton, J.D., Doyle, T.K., Hays, G.C., 2013. Identification of genetically and oceanographically distinct blooms of jellyfish. J. R. Soc. Interface 10 (80), 20120920.

Leslie, P.H., 1945. On the use of matrices in certain population mathematics. Biometrika 33 (3), 183–212.

Licandro, P., Conway, D.V., Daly Yahia, M.N., Fernandez de Puelles, M.L., Gasparini, S., Hecq, J.-H., Tranter, P., Kirby, R.R., 2010. A blooming jellyfish in the northeast Atlantic and Mediterranean. Biol. Lett. 6 (5), 688–691.

Lilley, M.K., Ferraris, M., Elineau, A., Berline, L., Cuvilliers, P., Gilletta, L., Thiéry, A., Gorsky, G., Lombard, F., 2014. Culture and growth of the jellyfish Pelagia noctiluca in the laboratory. Mar. Ecol. Prog. Ser. 510, 265–273.

Liu, K., Xu, Z., Liu, X., Huang, B., Liu, H., Chen, B., 2024. Modelling global mesozooplankton biomass using machine learning. Prog. Oceanogr. 229, 103371.

Long, A., Bastian, T., Haberlin, D., Stokes, D., Lyashevska, O., Brophy, D., Lawton, C., Doyle, T., 2024. Regular widespread aggregations of the oceanic jellyfish Pelagia noctiluca in the northeast Atlantic over 11 years. Estuar. Coast. Shelf Sci. 108805.

Luo, J.Y., Condon, R.H., Stock, C.A., Duarte, C.M., Lucas, C.H., Pitt, K.A., Cowen, R.K., 2020. Gelatinous zooplankton-mediated carbon flows in the global oceans: a data-driven modeling study. Glob. Biogeochem. Cycles 34 (9), e2020GB006704.

Malej, A., 1989. Behaviour and trophic ecology of the jellyfish Pelagia noctiluca (Forsskål, 1775). J. Exp. Mar. Biol. Ecol. 126 (3), 259–270.

Malej, A., Faganeli, J., Pezdič, J., 1993. Stable isotope and biochemical fractionation in the marine pelagic food chain: the jellyfish Pelagia noctiluca and net zooplankton. Mar. Biol. 116, 565–570.

Malej, A., Lučić, D., Bojanić, N., Vodopivec, M., Paliaga, P., Pestorić, B., Violić, I., Supić, N., 2022. The occurrence of the jellyfish Aequorea cf. forskalea in the Adriatic Sea: comparison of historical and recent data. Acta Adriat. 63 (2), 175–192.

Malej, A., Malej, M., 1992. Population dynamics of the jellyfish Pelagia noctiluca (Forsskål, 1775). In: Colombo, G., Ferrari, I., Ceccherelli, V., Rossi, R. (Eds.), Proceedings of the 25th EMBS. Olsen & Olsen, Fredensborg, Denmark.

Malej, A., Malej, A., 2004. Invasion of the jellyfish Pelagia noctiluca in the northern Adriatic: a non-success story. In: Dumont, H., Shiganova, T.A., Niermann, U. (Eds.), Aquatic Invasions in the Black, Caspian, and Mediterranean Seas. Kluwer Academic Publishers, Dordrecht, pp. 273–285.

Marambio, M., Canepa, A., Lòpez, L., Gauci, A.A., Gueroun, S.K., Zampardi, S., Boero, F., Yahia, O.K.-D., Yahia, M.N.D., Fuentes, V., et al., 2021. Unfolding jellyfish bloom dynamics along the Mediterranean basin by transnational citizen science initiatives. Diversity 13 (6), 274.

Mazzocchi, M.G., Siokou, I., Tirelli, V., Bandelj, V., de Puelles, M.F., Örek, Y.A., de Olazabal, A., Gubanova, A., Kress, N., Protopapa, M., et al., 2014. Regional and seasonal characteristics of epipelagic mesozooplankton in the Mediterranean Sea based on an artificial neural network analysis. J. Mar. Syst. 135, 64–80.

Mihanović, H., Vilibić, I., Šepić, J., Matić, F., Ljubešić, Z., Mauri, E., Gerin, R., Notarstefano, G., Poulain, P.-M., 2021. Observation, preconditioning and recurrence of exceptionally high salinities in the Adriatic Sea. Front. Mar. Sci. 8, 672210.

Milisenda, G., Rossi, S., Vizzini, S., Fuentes, V.L., Purcell, J.E., Tilves, U., Piraino, S., 2018. Seasonal variability of diet and trophic level of the gelatinous predator Pelagia noctiluca (Scyphozoa). Sci. Rep. 8 (1), 12140.

Ottmann, D., Álvarez-Berastegui, D., Prieto, L., Balbín, R., Alemany, F., Fiksen, Ø., Gordoa, A., Reglero, P., 2021. Abundance of Pelagia noctiluca early life stages in the western Mediterranean Sea scales with surface chlorophyl. Mar. Ecol. Prog. Ser. 658, 75–88.

Pastor-Prieto, M., Bahamon, N., Sabatés, A., Canepa, A., Gili, J.-M., Carreton, M., Company, J.B., 2021. Spatial heterogeneity of Pelagia noctiluca ephyrae linked to water masses in the Western Mediterranean. PLos One 16 (4), e0249756.

Patarnello, T., Volckaert, F.A., Castilho, R., 2007. Pillars of Hercules: is the Atlantic–Mediterranean transition a phylogeographical break? Mol. Ecol. 16 (21), 4426–4444.

Peliz, A., Marchesiello, P., Dubert, J., Marta-Almeida, M., Roy, C., Queiroga, H., 2007. A study of crab larvae dispersal on the Western Iberian Shelf: Physical processes. J. Mar. Syst. 68 (1–2), 215–236.

Pérez-Portela, R., Wangensteen, O.S., Garcia-Cisneros, A., Valero-Jiménez, C., Palacín, C., Turon, X., 2019. Spatio-temporal patterns of genetic variation in Arbacia lixula, a thermophilous sea urchin in expansion in the Mediterranean. Heredity 122 (2), 244–259.

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 (5), 186.

Pinardi, N., Allen, I., Demirov, E., De Mey, P., Korres, G., Lascaratos, A., Le Traon, P.-Y., Maillard, C., Manzella, G., Tziavos, C., 2003. The Mediterranean ocean forecasting system: first phase of implementation (1998–2001). In: Annales Geophysicae. vol. 21, Copernicus GmbH, pp. 3–20, 1.

Prieto, L., 2018. Diagnosis, prognosis, and management of jellyfish swarms. In: Chassignet, E., Pascual, A., Tintoré, J., Verron, J. (Eds.), New Frontiers in Operational Oceanography. GODAE OceanView, pp. 737–758. http://dx.doi.org/10.17125/gov2018.ch28.

Prieto, L., Macías, D., Peliz, A., Ruiz, J., 2015. Portuguese man-of-war (*Physalia physalis*) in the Mediterranean: A permanent invasion or a casual appearance? Sci. Rep. 5.

Purcell, J.E., Tilves, U., Fuentes, V.L., Milisenda, G., Olariaga, A., Sabatés, A., 2014. Digestion times and predation potentials of Pelagia noctiluca eating fish larvae and copepods in the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. 510, 201–213.

Rew, R., Davis, G., 1990. NetCDF: an interface for scientific data access. IEEE Comput. Graph. Appl. 10 (4), 76–82.

Rosa, S., Pansera, M., Granata, A., Guglielmo, L., 2013. Interannual variability, growth, reproduction and feeding of Pelagia noctiluca (Cnidaria: Scyphozoa) in the Straits of Messina (Central Mediterranean Sea): Linkages with temperature and diet. J. Mar. Syst. 111, 97–107.

Sabatés, A., Pages, F., Atienza, D., Fuentes, V., Purcell, J.E., Gili, J.-M., 2010. Planktonic cnidarian distribution and feeding of pelagia noctiluca in the NW mediterranean sea. Hydrobiologia 645, 153–165.

Scheffer, M., Baveco, J., DeAngelis, D., Rose, K.A., van Nes, E., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. Ecol. Model. 80 (2–3), 161–170.

Stopar, K., Ramšak, A., Trontelj, P., Malej, A., 2010. Lack of genetic structure in the jellyfish Pelagia noctiluca (Cnidaria: Scyphozoa: Semaeostomeae) across European seas. Mol. Phylogenet. Evol. 57 (1), 417–428.

Strniša, F., Tinta, T., Herndl, G.J., Kosec, G., 2024. Dynamic population modeling of bacterioplankton community response to gelatinous marine zooplankton bloom collapse and its impact on marine nutrient balance. Prog. Oceanogr. 103312.

Sun, Z., Lorscheid, I., Millington, J.D., Lauf, S., Magliocca, N.R., Groeneveld, J., Balbi, S., Nolzen, H., Müller, B., Schulze, J., et al., 2016. Simple or complicated agent-based models? A complicated issue. Environ. Model. Softw. 86, 56–67.

Tilves, U., Purcell, J.E., Fuentes, V.L., Torrents, A., Pascual, M., Raya, V., Gili, J.-M., Sabatés, A., 2016. Natural diet and predation impacts of Pelagia noctiluca on fish eggs and larvae in the NW Mediterranean. J. Plankton Res. 38 (5), 1243–1254.

Tinta, T., Klun, K., Herndl, G.J., 2021. The importance of jellyfish–microbe interactions for biogeochemical cycles in the ocean. Limnol. Oceanogr. 66 (5), 2011–2032.

Tinta, T., Zhao, Z., Bayer, B., Herndl, G.J., 2023. Jellyfish detritus supports niche partitioning and metabolic interactions among pelagic marine bacteria. Microbiome 11 (1), 156.

Tinta, T., Zhao, Z., Escobar, A., Klun, K., Bayer, B., Amano, C., Bamonti, L., Herndl, G.J., 2020. Microbial processing of jellyfish detritus in the ocean. Front. Microbiol. 11, 590995.

Tintore, J., La Violette, P., Blade, I., Cruzado, A., 1988. A study of an intense density front in the eastern Alboran Sea: the Almeria–Oran front. J. Phys. Oceanogr. 18 (10), 1384–1397.

Violić, I., Lučić, D., Bojanić, N., Pestorić, B., Gangai Zovko, B., Onofri, I., Hure, M., 2022. Long-term monitoring of carnivorous gelatinous macrozooplankton in the area of Dubrovnik–Neretva county (Croatia). NAŠE more: Znan. Cas. Za more I Pomor. 69 (1), 22–29.

Vodopivec, M., Peliz, Á.J., Malej, A., 2017. Offshore marine constructions as propagators of moon jellyfish dispersal. Environ. Res. Lett. 12 (8), 084003.

Wang, W., Wang, M., Wang, H., 2025. Effects of temperature on asexual reproduction and jellyfish booms of Aurelia aurita: Insights from mathematical modeling. Ecol. Model. 499, 110915.

Wright, R.M., Le Quéré, C., Buitenhuis, E., Pitois, S., Gibbons, M.J., 2021. Role of jellyfish in the plankton ecosystem revealed using a global ocean biogeochemical model. Biogeosciences 18 (4), 1291–1320.