

Modelling the effect of behavior on the distribution of the jellyfish Mauve stinger (*Pelagia noctiluca*) in the Balearic Sea using an individual-based model

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ABSTRACT

Jellyfish behavior and physiology significantly influence spatial distribution and aggregations in the marine environment. However, current models used to study these transport patterns have a limited incorporation of these physiological and behavioral variables. In this paper, the life cycle and movement of the mauve stinger, *Pelagia noctiluca*, is simulated from fertilized egg up to the adult stage using an individual-based model (IBM). Our model combines available knowledge on the mauve stinger with inputs of ocean currents and temperature from the CMEMS hydrodynamic model. Horizontal transport is solely governed by ocean currents, but vertical distribution is controlled by diel vertical migration, motility and stage of development. Particle agents are released along the submarine canyons in the Spanish Mediterranean waters during the spring reproduction period, to later disperse and develop through an interplay between physical and biological processes. When compared with a simpler model, that omits behavior and physiology, the biophysical model is able to qualitatively better predict stranding events in the Balearic Sea. Our results expose the potential for operational life stage and distribution modelling of jellyfish.

1. Introduction

Jellyfish are a known nuisance for tourism, fisheries and water intakes (Graham et al., 2014; Purcell et al., 2007; Richardson et al., 2009). Although they are a natural feature of a healthy ecosystem, an increasing trend in jellyfish blooms is caused by a combination of warmer waters, eutrophication, over fishing and disturbance to natural habitats (Mills, 2001; Pauly et al., 2009). Better prediction of these blooms and their area of impact will support the previously mentioned industries to mitigate their effect or alter their course of action.

Jellyfish are gelatinous zooplankton, present in a large variety of marine environments where their transport is controlled by the flow direction and velocity of their surrounding environment (e.g., ocean and tidal currents) (Graham et al., 2001). However, the biology of jellyfish can also strongly influence their vertical displacement (Fossette et al., 2015; Lilley et al., 2014), which, combined by environmental forces, effects their horizontal movement (Werner et al., 2015). In view of this, understanding biophysical jellyfish displacement would improve knowledge on their biology, dispersion, and stranding locations.

One instance of jellyfish nuisance is the invading swarms of *Pelagia*

noctiluca (Cnidaria: Scyphozoa, Forskal, 1775) which tend to form in the Western Mediterranean (Brotz and Pauly, 2012; Mills, 2001) and cause harm to the tourism and fishing industries through beach closures, clogged fishing nets and economic harm to aquaculture (Aznar et al., 2017; Bosch-Belmar et al., 2017; Ghermandi et al., 2015). *Pelagia noctiluca* (hereinafter referred to as *P. noctiluca*), also known as the mauve-stinger, resides offshore in deep waters and is characterized by a holoplanktonic life cycle, diel vertical migrations and reproduction by direct development without a benthic stage (Ferraris et al., 2012; Mariottini et al., 2008).

To model biological impact on the horizontal displacement of *P. noctiluca*, one must consider the ontogenetic development and include the effects of life stages, swimming speeds and behavioral patterns (Werner et al., 2015). Starting with non-motile fertilized eggs, free swimming planulae hatch to later develop into ephyrae and then adult medusae. Throughout these stages, swimming capabilities develop, due to increased pulsations and bell size, and behavioral patterns are established, shaping a well-defined diel vertical migration pattern. While horizontal transport is critically dependent on the physical environment (currents) (Chapman et al., 2011; Qiu et al., 2010); *P. noctiluca* can actively swim in the vertical direction (diving during the day and

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Fig. 1. Study area and model boundaries. Coastlines are classified geographically according to the administrative units (NUTS2016) published by Eurostat, the statistical office of the European Union. Regions with in situ observations of stranding events are highlighted with green.

surfacing at night) in a pattern that reduces predation and provides a feeding advantage (Berline et al., 2013; Ferraris et al., 2012).

Numerical modelling has been successfully applied to simulate: (i) the spatial and temporal variations in distributions of jellyfish (Ferrer and Pastor, 2017; Jaspers et al., 2018; Johnson et al., 2014; J. Moon et al., 2010), (ii) and biophysical processes such as growth, fecundity or mortality in other marine organisms like fish (e.g., integration of bioenergetics in an individual-based model for anchovy, (Bueno-Pardo et al., 2019)). Thus, complex biophysical models have the capacity to include the effect of jellyfish biology on distribution, a feature ignored in previous models which strictly treated released particle agents as jellyfish in the adult form (Berline et al., 2013; Dupont et al., 2009; Moon et al., 2010; Wei et al., 2015). As a result, such models (e.g., *P. noctiluca* model of Berline et al. (2013)) over simplify vertical migration by ignoring the effect of development stages, bell size, and motility on swimming speeds and diving limits. While using the principles of physiological ecology is the norm to incorporate this biological growth, our work uses a data driven approach based on field observations and laboratory studies of *P. noctiluca* (Augustine et al., 2014; Avian, 1986; Rosa et al., 2012; Sandrini and Avian, 1983). The Mediterranean Coastal waters of Spain, including the Balearic Islands, were selected for the biophysical modelling approach to study the mauve stinger, a jellyfish native to these waters (Fuentes et al., 2010; Rosa et al., 2012). This study area is well known for its high dependency on tourism and coastal economic activities; two sectors impacted by *P. noctiluca* blooms (Ghermandi et al., 2015).

The aim of this study is to improve jellyfish distribution and stranding modelling by including jellyfish specific behavior and development. For this we developed an individual-based Lagrangian particle model for *P. noctiluca* distribution based on life cycle, motility and behavior applied to the Spanish Mediterranean Coast. Based on the

model results we determine if the accuracy with which models can predict stranding events is improved by incorporation of: (1) detailed behavioral and motility information and (2) the full life cycle.

2. Methods and materials

In this study we will develop an individual-based Lagrangian particle model to predict the stranding events of the jellyfish species *P. noctiluca*. These models have been widely used to simulate the biophysical behavior of organisms (Bueno-Pardo et al., 2019; Garcia et al., 2013; Le Port et al., 2014; Santos et al., 2018). The developed biophysical model (available online on <https://github.com/joeelrahi/pelagianoctiluca>) is built over the general Python-based framework for Lagrangian particle modelling, OpenDrift (Dagestad, Röhrs, Breivik, & Ådlandsvik, 2018, github.com/opendrift). Changes in the biological characteristics of jellyfish (e.g., development stage) will be added to our model through a growth function which in turn influences swimming speed, buoyancy and diurnal migration. This approach is effective in reproducing the transport of jellyfish under the influence of environmental cues (currents) and abiotic factors like temperature and luminosity.

Our “Methods and Materials section” consists of four subsections: “Study area”, “Model description”, “Comparison with alternative model structures” and “Model validation”. Of these subsections our model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2020, 2006).

2.1. Study area

The Mediterranean Coastal waters of Spain, including the Balearic

Islands, were selected for the biophysical modelling approach to study the mauve stinger. The predominant circulation patterns in the Spanish Mediterranean waters are a characteristic of the Western Mediterranean basin, a semi isolated oceanic system exchanging water with the North Atlantic Ocean. Marine water from the Atlantic flows through the strait of Gibraltar into the basin and becomes denser because of the intense evaporation, thus producing a stronger saline water layer near the sea bed (Robinson et al., 2001). This results in weak stratification and deep vertical mixing of up to 2000 m (Schroeder, 2018). On the surface, the circulation is characterized by surface eddies along the African coast and a steady along shore current at the European coast (Buffett et al., 2013). Additionally, seasonal storms and wind bursts can induce cross-shore surface currents.

The marine topography of the area is characterized by a shallow continental shelf spanning up to 70 km with a depth of 100 m, followed by deep waters of up to 3000 m. Connecting the two zones are marine canyons that act as vertical conveyor belts between deep and shallow waters, enhancing marine biodiversity and function for marine species including *P. noctiluca* (Allen and Durrieu De Madron, 2009; Flexas et al., 2008; Harris and Whiteway, 2011; Würtz, 2012). Offshore model boundaries and the Spanish coastline including the cities of Barcelona and Valencia in addition to the Balearic Islands are shown in Fig. 1.

2.2. Model description

2.2.1. Purpose and patterns

The purpose of our biophysical model is to improve the accuracy of stranding events predictions of *P. noctiluca* through hydrodynamic forcing in combination with biophysical modelling features; mainly life cycle, motility, and behavior.

We evaluate our model by its ability to reproduce the pattern of *P. noctiluca* stranding events, based on the assumption that hydrodynamic forcing, the moment of spawning along the marine canyon ridge, diurnal migration and the effect of biological growth on horizontal and vertical distribution all have major influence on the final outcome. The resulting stranding events are compared spatially and temporally to in-situ stranding, as described in Section 2.4.

2.2.2. Entities, state variables, and scales

The biophysical model is composed of two entities: (1) the agents representing *P. noctiluca*, and (2) the 3-dimensional grid cells representing the host environment. Each agent is a super individual representing an equal percentage of the *P. noctiluca* population. Agents are characterized by the state variables: identification number [nr], stage [nr], time_stage [hr], location [X,Y], swimming speed [m/d] and depth [m]. In turn, each of these state variables is dependent on constant stage properties such as vertical swimming speed, buoyancy and total stage time. The host grid cell state variables include: location [X,Y,Z], current velocity [m/s], current direction [°], water depth [m], luminosity simplified to time of sunrise and sunset [time], and land-mask, a Boolean which returns “true” for coastline and “false” for water. Information about the environmental state variables is obtained through the Copernicus Marine Environment Monitoring Service (CMEMS, <http://marine.copernicus.eu>), and communicated to our model through a structured grid consisting of discrete rectilinear cells and a z-vertical grid. The horizontal resolution is 1/24° (ca. 4 km) and consists of 141 unevenly spaced vertical levels. This feature provides enhanced vertical resolution that can handle steep topography and resolve deep water exchanges. Results are available at hourly intervals in a 3-Dimensional domain covering the whole vertical profile (Clementi et al., 2018). The biophysical model runs on spatial and temporal resolution of the input hydrodynamic model, whereas the agents are traced by coordinated and therefore operate on a finer resolution.

2.2.3. Process overview and scheduling

The biophysical model runs in discrete time steps, and in each step all entities and their corresponding state variables are updated. The processes included are spawning, development stage, diurnal vertical migration, horizontal transport, and stranding. The biophysical model is started with the release of particle agents representing fertilized eggs. These agents will develop over time into planulae, ephyrae, and mature medusae. Each of these stages of development has a specified buoyancy and swimming velocity. During development between stages the buoyancy and swimming velocity will be interpolated based on the agent's development time. The progression of development time is affected by the water temperature, which in extreme cases leads to a complete halt in development. Swimming velocity is affected by the agent's motility, which is in turn affected by the experienced water temperature. Diurnal vertical migration is dependent on luminosity and stage development. Agents dive during the day and ascend during the night at a vertical swimming speed relative to the stage (an ephyra swims slower than an adult), with a maximum diving depth relative to the bathymetry. The vertical transport is a result of the agents' vertical direction of migration, buoyancy and swimming velocity. On the other hand, horizontal transport depends exclusively on advection from horizontal currents. Agents that reach the land boundary of the hydrodynamic model are considered stranded, and agents that reach the water boundary leave the domain.

During each time step the processes are executed in the following order: (1) development stage and resulting buoyancy and swimming velocity; (2) motility; (3) vertical direction based on day or night time; (4) maximum diving depth limit. As a result, state variables are updated and will thereby directly affect the movement of the entity (particle agents). Transport of agents is based on flow velocity as experienced by the hydrodynamic forcing in addition to the vertical movement based on the diurnal vertical migration process. The scheduling of these processes is depicted in Fig. 2.

2.2.4. Design concepts

Based on the description of the ODD protocol (Grimm et al., 2020, 2006) the design concepts Objectives, Learning, Prediction, Stochasticity, and Collectives do not apply to this model.

2.2.4.1. Basic principles. The model uses a data driven approach to capture the growth and transport of *P. noctiluca* (particle agents) which is influenced by an interaction of environmental variables (temperature, luminosity, sea water depth) on the vertical displacement of agents and hydrodynamic variables (currents) on the horizontal advection induced displacement of agents. This is achieved through the several submodels presented in Section 2.2.7.

Mortality, effects of predation and grazing patterns are not part of this model. Reproduction is also disregarded since sex is not a state variable of the agents, and simulation time represents only one life cycle.

2.2.4.2. Emergence. The variation in mobility patterns, development stage and stranding events emerge from the adaptive traits of the particle agents and the environmental conditions. Different sea water temperatures will dictate how fast the agents will develop from one stage to another and build up their vertical swimming capabilities respectively.

2.2.4.3. Adaptation. The vertical swimming pattern of the particle agents is an adaptive trait influenced by luminosity and development stage. Agents take decisions to dive or surface based on the time of the day; and their ability to reach the surface or the limiting dive depth is function of their development. In turn, development stage is an adaptive trait influenced by the sea water temperature. Both traits do not explicitly seek to increase individual success, for example, particle agents will not actively migrate towards warmer waters to achieve

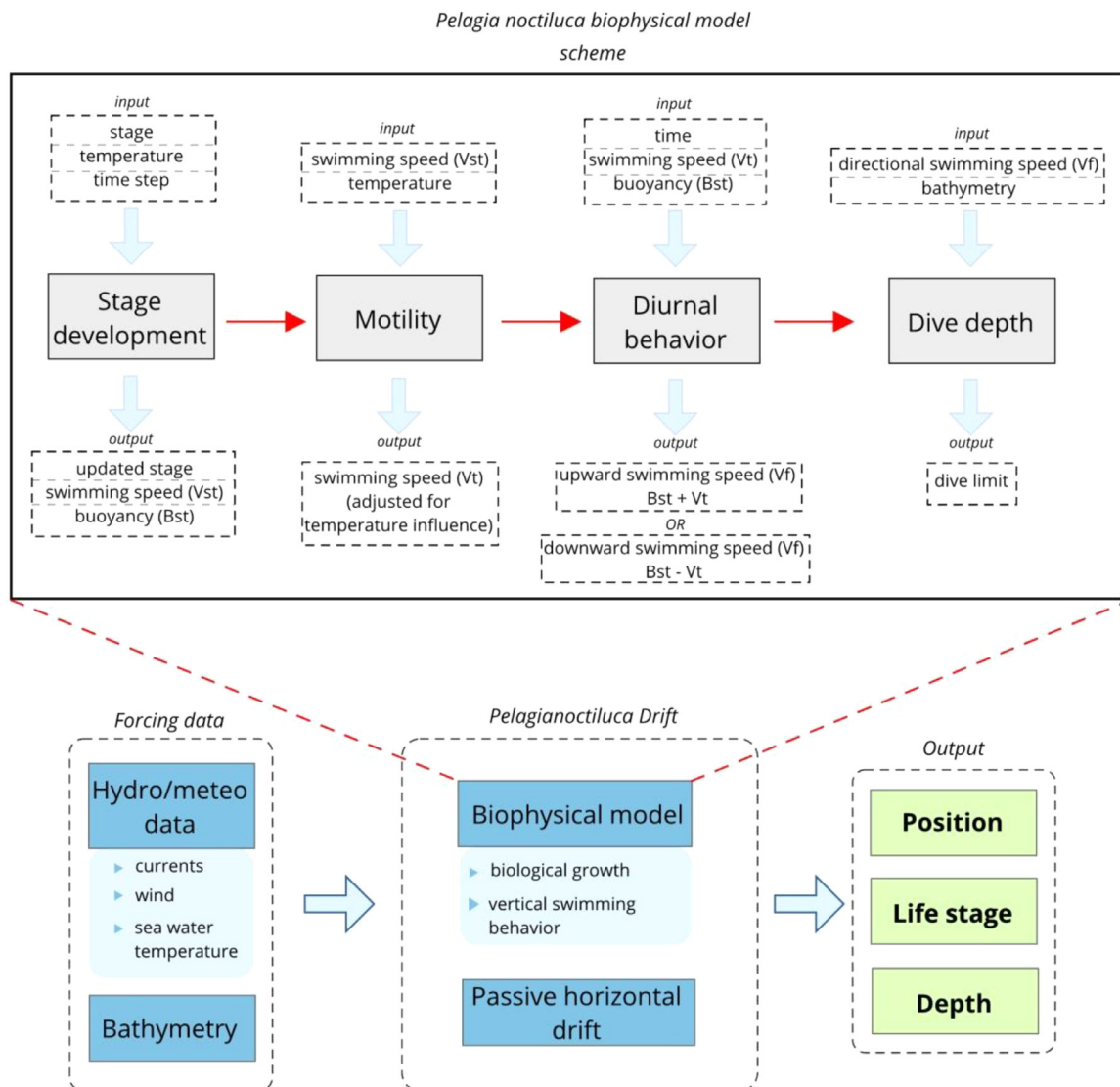


Fig. 2. Design and implementation scheme of the biophysical model.

faster development.

2.2.4.4. Sensing. Each particle agent is capable of locally sensing the environmental state variables of the 3-dimensional grid cell in which it is located. The sensed variables are sea water temperature, luminosity (day or night) and sea water depth. Each agent senses these values accurately, hence the model does not represent the mechanism of sensing and the uncertainty associated.

2.2.4.5. Interaction. *P. noctiluca* swimming pattern is sometimes directed towards maintaining large aggregations or swarms (Dawson and Hamner, 2009), but this is not reproduced in our biophysical mode. There is no interaction nor communication between particle agents and they do not affect each other's decisions.

2.2.4.6. Observation. The three-dimensional location of the particle agents is recorded at every time step. This is also applicable to stranding events which are temporally and spatially logged. To monitor biological growth, stage development, complemented by the water temperature and motility, are also recorded at every time step. This helps understand and analyze the link between spatial distribution, development stage and temperature.

2.2.5. Initialization

Agents representing fertilized eggs are released into our model during the peak spawning period which occurs during spring and peaks at temperatures of 17°C (Augustine et al., 2014). The spatial extent of this release is limited to the presence of marine canyons, which provide a reproductive advantage by transporting jellyfish from deep to surface layers through enhanced upwelling (Benedetti-Cecchi et al., 2015). Thus, fertilized eggs are released in our model top layer at a depth of 0 m evenly distributed within the spatial extent of the marine canyon ridge (Fig. 3). Release occurs over a period of 10 days after the first reproduction peak moment in spring and follows the warming of the Mediterranean waters from South to North along the marine canyon ridge, as detected in the CMEMS hydrodynamic-wave model. According to the monthly mean temperature data from CMEMS (Fig. 3), peak spawning occurs sometime between March and April. Thus, a total of 10 000 particles are continuously released during the 10 day period; at a rate of 1000 particle per day from May 8, 2018 until May 18, 2018.

2.2.6. Input data

Our model is coupled offline with the CMEMS hydrodynamic-wave model velocity vectors and temperature data at hourly intervals to supply the information needed to resolve the physical and behavioral effects on the agents. Horizontal current data and seawater temperature

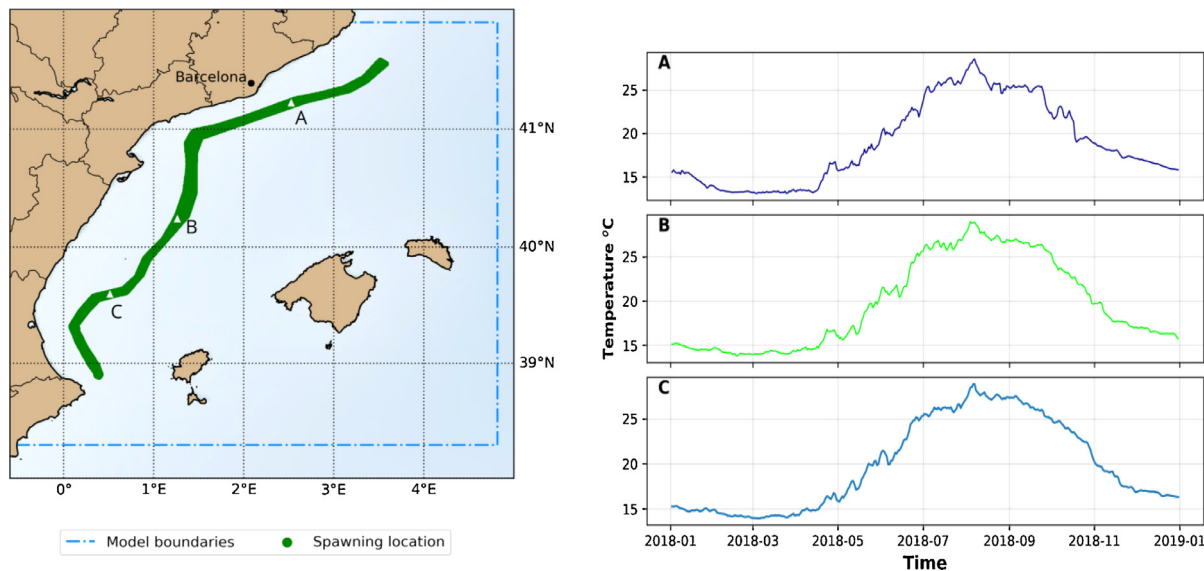


Fig. 3. . Spawning locations (where individuals are released) and annual sea water temperature trend.

along the vertical grid provide information for all water depth in our model. The exact time of sunrise and sunset are calculated using the astronomical computational package PyEphem (<http://rhodesmill.org/pyephem/>). This information is provided to every agent.

2.2.7. Submodels

2.2.7.1. Development. The biophysical model is designed to capture the development stage and corresponding behavior throughout *P. noctiluca*'s life cycle. Field observations, laboratory studies and DEB (Dynamic Energy Budget) simulations display a strong influence of temperature on development time (Augustine et al., 2014; Avian, 1986; Rosa et al., 2012; Sandrini and Avian, 1983). This link is shown in Table 1 and the growth ratio is presented graphically in Fig. 4 by linearly interpolating the growth rates corresponding to the different temperatures. Growth ratio appears to increase exponentially before reaching a threshold, and then declines. This would be expected following principles of enzyme kinetics and is frequently modelled using an Arrhenius equation (Boyd et al., 2018; Bueno-Pardo et al., 2019; Politikos et al., 2015). Nevertheless, in this biophysical model a data-driven approach has been applied to define the influence of temperature on development. The linear interpolation equation for the growth factor is:

$$G = G_1 + \frac{(G_2 - G_1)}{(T_2 - T_1)} \times (T - T_1)$$
 (1)

Where G = growth factor of agent (%), T = water temperature detected by agent (°C), and G₁ and G₂ are the growth factors at the theoretical temperatures T₁ and T₂ shown in Table 2.

Maximum growth corresponds to fastest development which is equivalent to a development period of 1 day from fertilized egg to planula, 2 days from planula to ephyra (Rosa et al., 2012), and 2 months from ephyra to mature medusa (Augustine et al., 2014). Growth comes to a halt as water temperatures exceed 25 °C (Malej, 1989) or drop below 4.5 °C (Avian, 1986). The term mature medusa or adult

jellyfish is used to refer to an individual with reproductive capabilities, and is not established on anatomy. Following that, *P. noctiluca* can live for up to 12 months (Ferraris et al., 2012); hence mortality will not be included into our model.

To describe this development numerically, each released particle is characterized by two properties, termed “stage” and “time_stage”. At the initial instance *t*₀, the “stage” variable is set to the default value of 1 and “time_stage” to 25 h, corresponding to a fertilized egg. Afterwards, with every numerical loop the variable “time_stage” is reduced by a factored time step, corrected by the growth factor which adds the influence of water temperature, until it reaches a value of 0. At this point, the variable “stage” is increased by one and “time_stage” takes a new value analogous to the development time of a planula. By doing so each particle develops independently with a development speed influenced by the water temperature. The same process is applied to the planula which develops into an ephyra, and then in turn into an adult jellyfish. The contribution of development stage in the transport of particles is interpreted through the behavioral processes and effect on vertical swimming speed explained in Section 2.7.2.

2.2.7.2. Vertical swimming speed. Vertical swimming speed is derived from the development stage of the agent, and then adjusted to the temperature of the environment. No studies thoroughly document the swimming speed of *P. noctiluca*, so estimations from other publications and studies performed on other jellyfish species were used (Conley and Uye, 2015; Garaventa et al., 2010). During the first stage, fertilized eggs drift passively with currents. Afterwards, during the second stage particles gradually develop swimming capabilities eventually achieving maximum speeds of 5 m/h; in agreement with reported swimming speeds of *Aurelia aurita* (moon jelly) planulae (Conley and Uye, 2015). As they develop into ephyrae, swimming capabilities are expected to further improve reaching a maximum of 100 m/h in stage 4 (adult stage). This speed has been already used in a previously published *P. noctiluca* model (Berline et al., 2013). Moreover, it is

Table 1
Reported development time at different sea water temperatures.

	13.5 °C(Avian, 1986)	17 °C(Rosa et al., 2012)	19 °C(L. Sandrini and Avian, 1983)	20 °C(Rosa et al., 2012)
Appearance of sensory organ (Rhopalium)	120 h		72 h	
First pulsations	142 h		60 h	
Ephyra stage (diameter 1.1 mm)	168 h	72 h	92 h	96 h

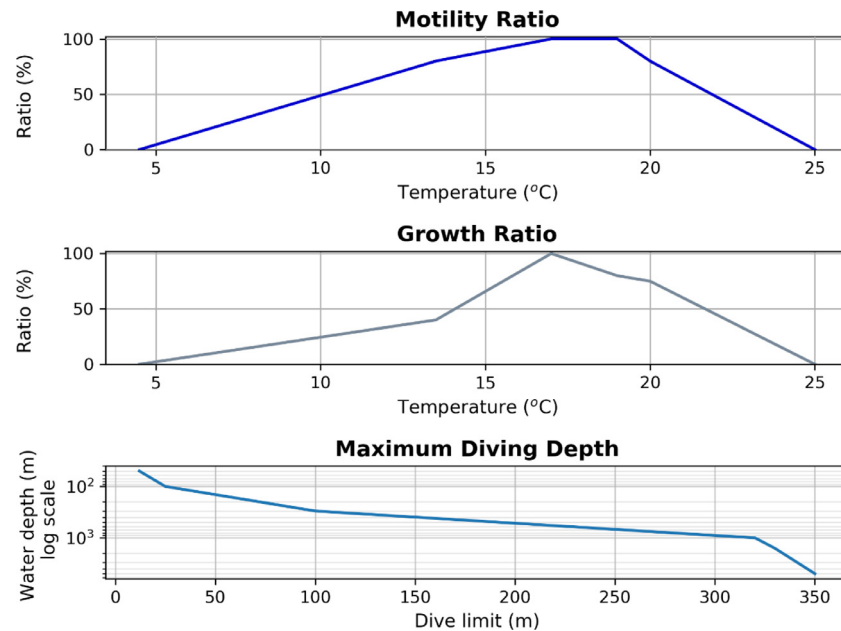


Fig. 4. Temperature induced behavior and maximum depth.

Table 2

Overview of the parameters used in the biophysical model. Derivation and references are listed in the corresponding subsections

Parameter	Value
Development stage specifics (Section 2.7.1)	
Egg	
Buoyancy of egg (m/d)	24
Vertical swimming velocity of egg (m/d)	0
Planula	
Development time form egg to planula – stage 2 (in days)	1
Buoyancy of planula (m/d)	-24
Vertical swimming velocity of planula (m/d)	120
Ephyra	
Development time form planula to ephyra – stage 3 (in days)	2
Buoyancy of ephyra (m/d)	-80
Vertical swimming velocity of ephyra (m/d)	1800
Mature medusa	
Development time from ephyra to mature medusa – stage 4 (in days)	60
Buoyancy of mature medusa (m/d)	-259
Vertical swimming velocity of mature medusa (m/d)	2,400
Spawning (Section 2.5)	
Spawning initiation based on water temperature (in °C)	17.0
Motility (Section 2.7.2)	
Motility at 4.5 °C water temperature (in %)	0
Motility at 13.5 °C water temperature (in %)	80
Motility at 17.0 °C water temperature (in %)	100
Motility at 19.0 °C water temperature (in %)	100
Motility at 20.0 °C water temperature (in %)	80
Motility at 25.0 °C water temperature (in %)	0
Development (Section 2.7.1)	
Development speed at 4.5 °C water temperature (in %)	0
Development speed at 13.5 °C water temperature (in %)	40
Development speed at 17.0 °C water temperature (in %)	100
Development speed at 19.0 °C water temperature (in %)	80
Development speed at 20.0 °C water temperature (in %)	75
Development speed at 25.0 °C water temperature (in %)	0
Bathymetry dependent maximum diving depth (Section 2.7.3)	
Diving depth at 0 m bathymetry depth (m)	0
Diving depth at 50 m bathymetry depth (m)	12
Diving depth at 100 m bathymetry depth (m)	25
Diving depth at 300 m bathymetry depth (m)	100
Diving depth at 900 m bathymetry depth (m)	300
Diving depth at 1000 m bathymetry depth (m)	320
Diving depth at 1600 m bathymetry depth (m)	330
Diving depth at 5000 m bathymetry depth (m)	350

coherent with the average swimming speed of 180 m/h, recorded by attaching an accelerometer to the much larger jellyfish *Rhizostoma octopus* (Fossette et al., 2015). The calculation of swimming speed is as follows:

$$V_i = V_{i-1} + (V_{i+1} - V_{i-1}) \times (SD) \quad (2)$$

Where subscript i represents the stage of the agent, V_i is the swimming speed of the agent, V_{i-1} is the swimming speed at stage $i-1$, V_{i+1} is the swimming speed at stage $i+1$, and SD is the stage development factor of agent i expressed in percentage (%). SD values are between 0 and 100 and represent the status of development of the agent within a stage.

The influence of seawater temperature on vertical swimming speed is then added through the so-called motility ratio obtained through a linear fit between percent motility (relative to number of pulsations) and water temperature values recorded in laboratory tests (Avian et al., 1991). Thus, each particle has a swimming speed equivalent to an absolute speed relative to the biological development adjusted for the effect of temperature using the motility ratio trend shown in Fig. 4. The following equation is used for the calculation of the motility ratio:

$$M = M_1 + \frac{(M_2 - M_1)}{(T_2 - T_1)} \times (T - T_1) \quad (3)$$

Where M = motility ratio of agent (%), T = water temperature detected by the agent (°C), and M_1 and M_2 are the growth factors at the theoretical temperatures T_1 and T_2 shown in Table 2.

Last, the temperature adjusted agent swimming speed is obtained by multiplying the motility ratio (M) by the swimming speed (V_i) (Eq. (4)).

$$V = V_i \times M \quad (4)$$

For the calculation of the vertical swimming speeds used in the diurnal vertical migration (Section 2.7.3), an additional buoyancy parameter is added. Buoyancy is calculated according to Eq. (5) and is factored by the stage development factor SD .

$$B_i = B_{i-1} + (B_{i+1} - B_{i-1}) \times (SD) \quad (5)$$

Where subscript i represents the stage of the agent, B_i is the buoyancy of the agent, B_{i-1} is the buoyancy at stage $i-1$, B_{i+1} is the buoyancy at stage $i+1$, and SD is the stage development factor of agent i expressed in percentage (%).

2.2.7.3. Diurnal vertical migration. Agents in the biophysical model are programmed to perform diurnal vertical migration, a feature of *P. noctiluca* (Berline et al., 2013; Ferraris et al., 2012). This is translated into the numerical model by adding a diurnal function which prompts the particles to dive during the day and surface during the night. In the water column, luminosity, dissolved oxygen, turbidity, and water density contribute in defining the boundaries of the vertical movement (Cartes et al., 2013; Graham et al., 2003; Jansson and Källander, 1968; Macquart-Moulin and Castelbon, 1990). However, in our model this is simplified into a positive correlation between bathymetry and dive limit: in deep offshore waters exceeding 1500 m particles migrate until 350 m (Berline et al., 2013; Kanda et al., 1989), and when bathymetry becomes shallower the dive limit decreases accordingly (Dafni et al., 1987; Kanda et al., 1989), the maximum depth trend is shown in Fig. 4. Agents are programmed to dive 1 h after sunrise and ascend 1 h after sunset (Anokhina, 2006) at a rate equivalent to the vertical swimming speed adjusted to buoyancy.

The vertical swimming speed for diving and ascending is calculated by adding the influence of buoyancy according to the following equation:

$$V_z = B_i + V, \text{ for ascending agents} \quad (6)$$

$$V_z = B_i - V, \text{ for diving agents} \quad (7)$$

2.2.7.4. Stranding. Stranding events are recorded when the agents hit the coastline; once agents are stranded they cannot become active again. This approach does not take into consideration the transport patterns abundant in shallow waters like breaking waves and rip currents. Stranding is a default function that comes with the *OpenDrift* model. At each time step the location of the agents is checked by the “landmask” function which then identifies the agents that are stranded.

2.3. Comparison with alternative model structures

Additionally, and for comparison, we developed a simple drift model and fixed diurnal vertical behavior model (fixed-diurnal-behavior model hereafter (Berline et al., 2013)). The biophysical model and simple drift model were configured to run starting from the spring reproduction period for a total of 8 months, while the fixed-diurnal-behavior model was configured to start when strong vertical behavior became present in the biophysical model.

A similar initial release along submarine canyons is used for the biophysical and simple drifting models: 10 000 agents (particles) are released linearly in time starting on the 8th of May 2018 from the Southern (Lon = 0.388°, Lat = 38.884°) up to the Northern edge (Lon = 0.3819°, Lat = 38.907°). In the fixed diurnal behavior model, initial release locations of agents are obtained from the positions of active agents in the biophysical model on the 1st of June, this coupling procedure intends to disregard reproduction and early life stages when diurnal vertical migration is absent. In all three simulations the models run until the 15th of December 2018. All models are summarized in Table 3. The fixed diurnal behavior model starts later in the year and with fewer agents, as the model is initialized on current locations of the biophysical model and a portion of the agents has moved across the

Table 3
Summary of models.

Model	Initial release	Simulation period	Number of agents
Biophysical	submarine canyons	May 8 – December 15	10 000
Simple drifting	submarine canyons	May 8 – December 15	10 000
Fixed diurnal behavior	Location of active entities obtained from the biophysical model	June 1 – December 15	9784*

* Number of agents (particles) is an input parameter from the biophysical, the lower number of agents is because some agents left the model domain by that time.

Table 4

Summary of state-of-agent results for the three different simulations.

Status	Biophysical	Simple	Fixed diurnal*
Active	2543	518	1862
Stranded	1577	3909	1989
Out of domain	5880	5573	5933

* Fixed diurnal behavior: Simulation started on the 1st of June with 9784 agents (particles)

model water boundary.

2.4. Model validation

To validate the simulated stranding events, online published sightings data are used. The spatial and temporal distribution of these sightings were collected from the jellyfish monitoring program set up by the Mediterranean Science Commission (www.ciesm.org/marine/programs/jellywatch.htm) and the citizen science jellyfish program (www.jellywatch.org). Gathered information was classified according to location and time and then compiled into the georeferenced map shown in Fig. 1. For the time interval of May until December 2018, there are 8 stranding events recorded over 4 different administrative units.

3. Results

In this section, results of the biophysical model showing transport, growth and stranding are presented and then confronted with simple drifting and fixed diurnal behavior (Berline et al., 2013). A résumé of the results is presented in Table 4.

3.1. Biophysical model

Output of the biophysical model focuses on transport, biological growth and vertical behavior. First, the final spatial distribution of the agents by the end of the run-time is presented in Fig. 5. More than half (58.8%) of the released agents leave the model domain, while the remaining agents either end up stranded on beaches (15.77%) or active (25.43%). Active agents are mostly concentrated in the offshore deep waters (between Lon = 2° and Lon = 5°), with the remaining minority sparsely divided along the coasts. While stranded agents are spread with a more complex pattern:

On the spatial level, stranding events are evenly distributed along the coastlines of the three islands (from South to North: Ibiza, Mallorca and Menorca) but unevenly spread along the Spanish mainland coast. Stranding events are non-existent North of Barcelona, while one single event is recorded just South of the city. Further South (starting from Lat = 41.2 °), the frequency of stranding events increases and becomes geographically more consistent all the way until the Southern border of the model; with a peak along the coastal section in the vicinity of Valencia (Lat = 39 ° up to Lat = 40°).

The temporal distribution of the stranding events is variable throughout the simulation period (Fig. 6). Fewest events occur during the months of May and June, with a significant increase in July

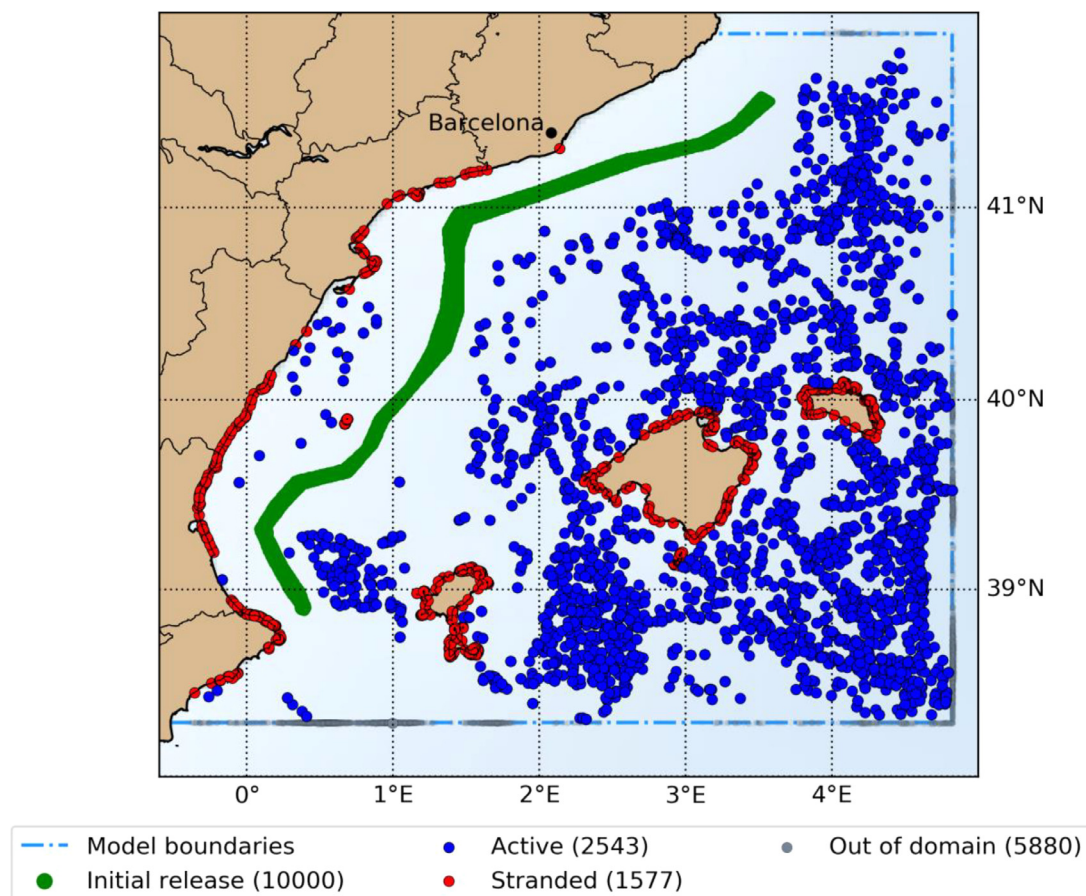


Fig. 5. Map of the results of the biophysical model: (i) initial release is along the green area, (ii) stranding events are represented by red circles, (iii) active particles (that haven't left the model domain) by blue circles and (v) particles that left the model boundaries by grey circles.

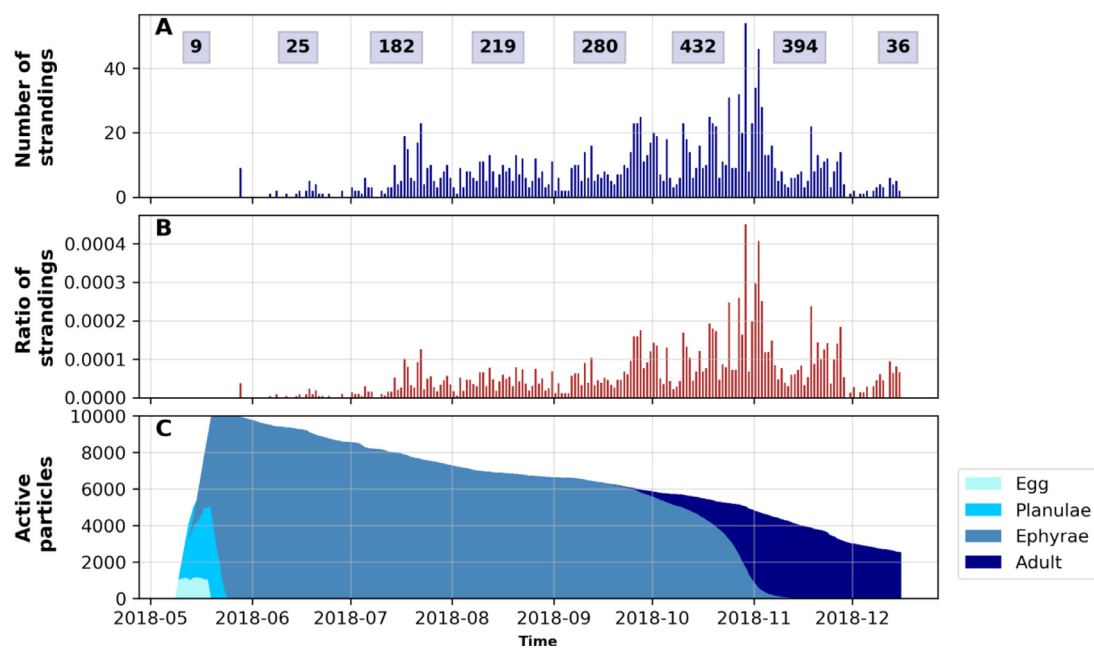


Fig. 6. Temporal distribution of stranding events and biological growth. (A) Number of stranding events per day; numbers in boxes are the sum of monthly events; while (B) shows the ratio of stranding events calculated by dividing the number of events by the total number of active agents (particles). Last, (C) shows the stage development of agents (particles) over time.

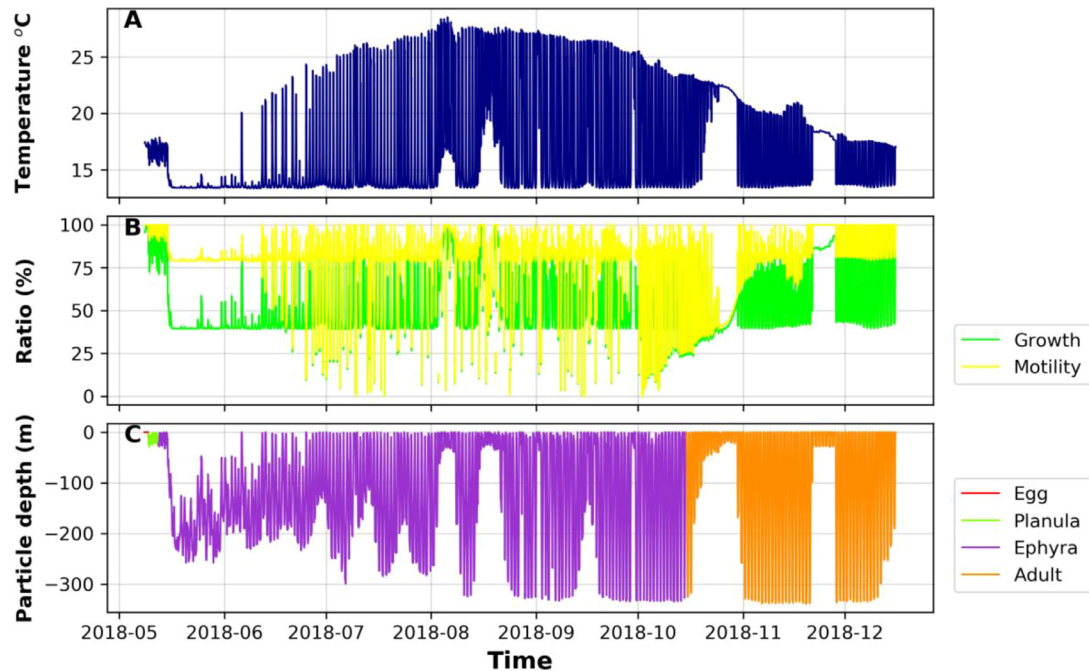


Fig. 7. Temperature, development ratio and dive depth of one particle. (A) Fluctuation of sea water temperature experienced over time, (B) Growth and motility ratios over time and (C) Diurnal vertical migration displayed through agent dive depth, with colors expressing stage. Longer periods of a shallow depth show that the agent was unable to dive deep due to bathymetry.

followed by a steady sum of events in August and September. Following that is a spike, resulting in the peak number of events during October (432), with a relatively small number of events during November (394). A steep decrease follows in the month of December with only 36 events. All agents stranded in the period spanning from April to September are exclusively stage 3 (ephyrae); agents stranded in October are of stage 3 or stage 4 (adults), with exclusive adult stranding events during November and December.

3.1.1. Biological growth

Biological growth is interpreted through the different development stages shown in Fig. 6 (for all 10 000 agents) and Fig. 7 (for 1 randomly selected agent). During the initial release, all agents representing fertilized eggs (stage 1) quickly develop into planulae (stage 2) which in turn become ephyrae (stage 3) by the end of May. For the majority of their lifecycle the agents remain in stage 3, with the first stage 4 agents emerging in the beginning of October. The transition from stage 3 to stage 4 continues throughout October, until all agents become adults in November. Growth ratio (check Fig. 7B) varies between a maximum of 100%, an average somewhere between 75 and 50%; and a minimum that drops to 0 during small intervals.

3.1.2. Diurnal vertical migration

Diurnal vertical migration is expressed through the variation in agent depth (Fig. 7C), and is function of biological growth, ratio of motility and bathymetry. During the first period, through stage 1 and well into stage 2, the agent remains on the surface before sharply diving to deeper than 200 m during the initial phase of stage 3. Afterwards, a rebound phase in which the agent starts pushing more towards the surface initiates. This phase ends around the mid/end of June, giving way to a new vertical swimming behavior characterized by well-defined patterns of surface to bottom fluctuations. An additional feature of the diving pattern is the difference in dive depth, which varies from shallow dives of few tens of meters to maxima of 350 m.

3.2. Comparison across models

3.2.1. Spatial distribution of agents

In this section the results of the spatial distribution of the biophysical, simple drift and fixed diurnal behavior models are compared. The spatial occurrence probability maps of the different models are used to evaluate the likelihood of the presence of agents in a given grid cell; the maps are generated by averaging the hourly occurrence data over the whole simulation period. The purpose of this comparison is to identify the geographic areas with the highest occurrence probability across the different models, therefore the results presented in Fig. 8 will be interpreted visually. The biophysical model (Fig. 8 A) exhibits a strong probability of occurrence concentrated offshore in between latitudes 39°N and 40°N characterized by a clearly defined central eddy. While the simple model (Fig. 8B) demonstrates a contrasting probability map which is spread out in space and indicates tracks that are similar in form to surface currents. Similarly, a spatial probability map is produced for the fixed diurnal behavior model in Fig. 8 (C and D), displaying the occurrence probability starting from the 1st of June. Once again, the results show divergent probabilities between the two models. While the location of the high occurrence zone in the fixed diurnal behavior model matches that of the biophysical, its size is significantly smaller, and it does not show the spiral shape attributed to the local hydrodynamics.

3.2.2. Stranding events

The total number of stranding events predicted in different administrative units (see Fig. 1) are shown in Table 5. The simple drifting model reports more than a thousand stranding events during the month of May (zone ES514) and more than 500 stranding events during the months of June and July (zone ES533). In contrast, the biophysical and fixed diurnal behavior model report stranding events in the order of 10. The inconsistency in the spatial and temporal distribution of the results, combined with the difference in the magnitude of the reported stranding events, eliminate the option of producing meaningful statistical results. The performance of models in terms of predicting stranding events will be further discussed in Section 4.

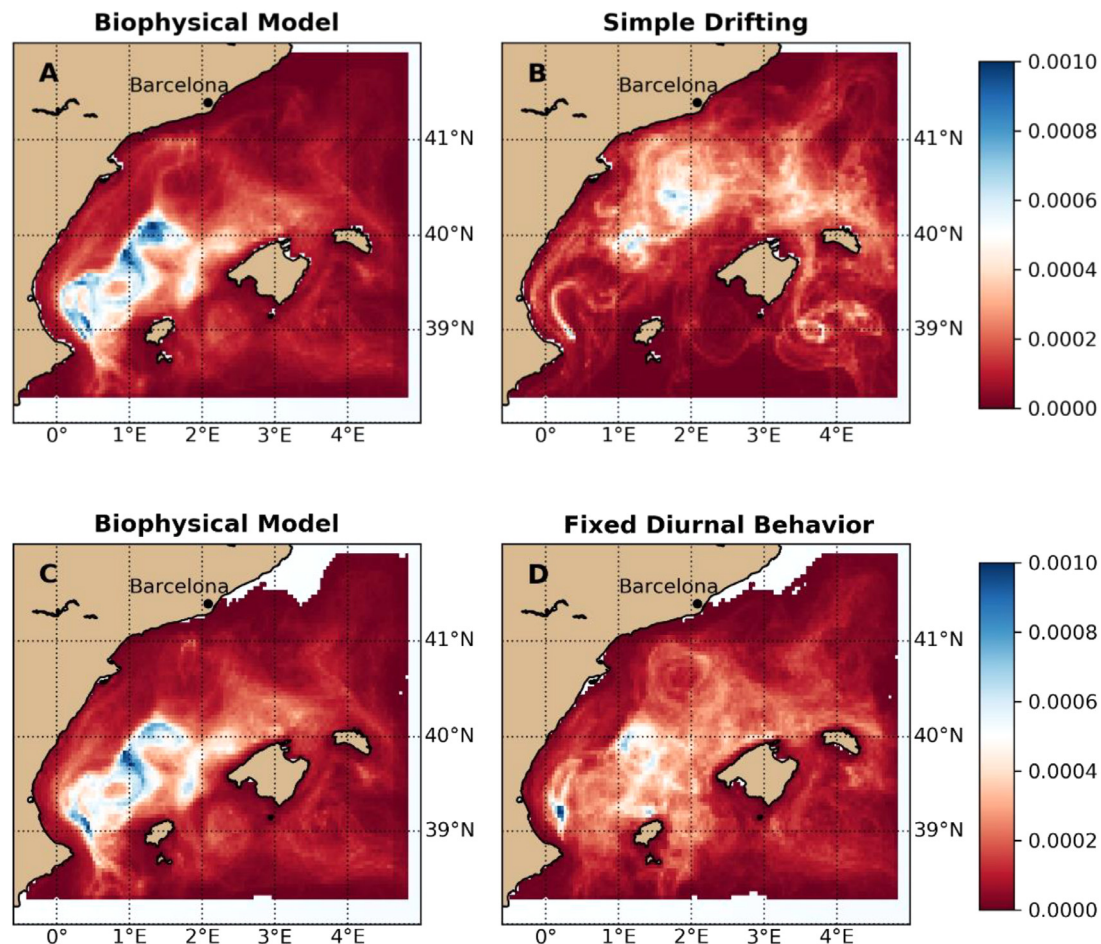


Fig. 8. Agent occurrence probability. (A) shows the results of the biophysical model while (B) shows those simple drifting model. These results are based on the period May till December; (C) shows the results of the biophysical model while (D) shows those of the fixed diurnal behavior, these results are for the period June till December. The probabilities were calculated based on hourly occurrence data gridded on a 4 km x 4 km grid.

3.3. Model validation with in situ stranding observations

Since data obtained through “citizen science” approaches relies on the contributions from volunteers, the available data set of in situ observations is limited in number of stranding events and characterized by discrepancies in time and space. The nature of this data set makes the validation process approximative. Hence, a general qualitative analysis of stranding data obtained from all three simulations will be used in the following comparison. Data shown in Table 5 shows the stranding events per geographic zone and not for a particular location. Starting with zones where in situ observations are available (from North to South), in ES522 the biophysical model (II) is the most accurate with the highest number of stranding events during August when compared to the other two models. In zone ES523 the simple drifting model (III) provides the best approximation for the month of July, followed by better results from the biophysical model for the months of August and September, while the fixed diurnal model (IV) outputs no stranding events. Last, in zone ES521 all three models completely fail to capture the stranding in June, and only the fixed diurnal behavior model partially captures stranding in August. In July, the simple drifting model gives better prediction while the biophysical model is the sole model to forecast stranding in September. In short, the biophysical model ranks first in capturing the spatial pattern of stranding events, predicting 6 out of the 8 jellyfish sightings, followed by the simple drift model with 4 out of 8 and last the fixed diurnal behavior model with 3 out of 8.

4. Discussion

The purpose of this study is to include biological traits and assess the interaction between physical dispersion and physiological behavior. The role of biological processes is believed to be crucial with significant effect on transport and population dynamics (Tremblé et al., 2007). Implementing these behavior regimes and growth stages requires information which is species specific, thus creating a range of possibilities in the amount of influence biology has on dispersion. Regarding *P. noctiluca*, results of the simulations performed in this study expose the sensitivity of agents to biological behavior and the impact it has on spatial dispersion. This is clearly visible in the contradicting transportation patterns followed by agents released in the biophysical and simple drifting models, which reflects the importance of considering vertical movement in spatially predicting individual-based particle tracking models for this jellyfish species. Additionally, when comparing the results of the biophysical model to that of the fixed behavior model, the impacts of variation in swimming speed and temperature in diurnal migration on the spatial distribution are exposed. By including this variation in the biophysical model, the accuracy of spatially predicting stranding events improved in comparison to the fixed diurnal behavior model.

Within this study, our aim was to develop a methodology for a temporally and spatially explicit *P. noctiluca* stranding model including key behavioral processes to their distribution capable of supporting a screening-level baseline assessment. Nevertheless, there were several simplifications and limitations in our analyses. It was necessary to

Table 5
Stranding events across model simulations in number of agents and in-situ data.

Zone		2018 May	June	July	August	September	October	November	December
ES511	I								
	II	0	0	0	0	1	0	0	0
	III	37	7	2	4	45	28	0	0
	IV	0	0	0	0	1	2	0	0
ES514	I								
	II	9	3	7	0	40	15	0	0
	III	1306	24	10	6	28	83	0	0
	IV	X	1	0	0	1	27	0	0
ES522	I				B				
	II	0	0	0	10	20	22	0	0
	III	0	7	60	3	1	0	0	0
	IV	X	0	0	0	0	0	0	0
ES523	I			B	B	A			
	II	0	0	2	7	30	34	5	0
	III	6	91	234	4	0	0	0	0
	IV	X	0	0	0	0	5	4	0
ES521	I		A	B	B	A			
	II	0	0	26	0	24	0	40	14
	III	0	0	51	0	0	0	2	0
	IV	X	0	3	3	1	14	7	0
ES531	I								
	II	0	0	130	108	23	83	68	0
	III	0	9	2	0	1	0	0	0
	IV	X	28	483	273	94	49	45	1
ES532	I								
	II	0	8	17	65	94	157	130	21
	III	0	128	40	29	115	6	25	1
	IV	X	132	259	86	34	85	76	5
ES533	I								
	II	0	5	4	13	39	15	119	15
	III	0	684	504	147	44	94	3	0
	IV	X	46	8	29	34	72	48	11
CI*	I								
	II	0	9	5	18	10	3	0	0
	III	5	9	1	9	1	5	3	0
	IV	X	5	1	13	2	1	0	0

* CI: Columbretes Islands

Zones are divided according to the administrative units (NUTS2016) published by Eurostat, the statistical office of the European Union, and presented from North to South (I) refers to in situ observations, (II) biophysical model, (III) simple drifting and (IV) fixed diurnal behavior. For the in situ observations the letters indicate the quantity of *P.noctiluca* individuals in recorded strandings: (A) is 1000 individuals and (B) is 100 individuals. Note that this data is collected through a citizen science application which uses letters for the ease of users. This means letters are approximate and do not necessarily reflect an exact number. For this reason, we refrain from using exact numbers in the table but adhere to the form of data as provided (i.e., A and B instead of 1000 and 100). For the models the numbers represent stranded agents and “X” a not modelled period. Each agent is a super individual. Only a qualitative assessment between models and in-situ data is made based on stranding events.

select a single hydrodynamic year for the baseline assessment to reduce the amount of computational and postprocessing time required. Running multiple year cycles of our model, maintaining a single spawning moment, would provide insight in the influence of the hydrodynamic year on model results. This would allow for inclusion of multiple years of in-field data for comparison, potentially enabling a statistical model evaluation. Through a sensitivity analysis the derived jellyfish model characteristics could be tested for their influence on the model result.

There are multiple methods to calibrate and evaluate individual-based models (MacPherson and Gras, 2016; van der Vaart et al., 2016); nevertheless, the lack of coherent and in-field data and the quality and amount of in situ observations do not permit for any quantitative assessment. This lack of in-field data (Table 5) prohibits the possibility to derive a statistical based goodness-of-fit for our model, as the data that is available (8 measurements) appears to have a strong spatial correlation between stranding events (ES521, ES522, ES523), and recorded stranding amounts vary widely (100 or 1000 strandings). The biophysical model results predict yearlong stranding events while observations are mainly available during summer period. Seasonality of these observations is potentially related to the activeness of observations along the coasts during the summer months, or could be otherwise attributed

to the theory of Pitt and Lucas (2014) that *P. noctiluca* migrate to deeper waters during winter. However, observations in literature suggest otherwise, as stranding events of *P. noctiluca* are reported during the winter months (Fleming et al., 2013; Mariottini et al., 2008; Yahia et al., 2003); thus justifying the yearlong stranding events in the biophysical model. Additionally, and when data is available, the biophysical model provides predictions with reasonable accuracy in qualitative terms and performs better than both the simple drifting and fixed diurnal behavior models.

Looking into the spatial and temporal distribution of the stranding events, another fact which stands out is the high number of stranding events along the three islands in all three models. This is most likely related to the fact that islands are not shielded from the winds and currents from either direction; thus cross shore forcing, a major factor in stranding, is more frequent (Keesing et al., 2016; Ourmieres et al., 2018). Temporally, the simplistic model yields more stranding events in the first period (first 2 months) of simulation. This exposes the intrinsic property of simplistic models: susceptibility to temporal changes in meteorological conditions. For example, an interval of cross-shore currents can cause a high number of beach stranding events over a small period of time. This disturbance to realistic dispersion is surpassed by the biophysical model through an increased retention period

and a reduction in the influence of hydraulic and environmental parameters. Another benefit of biophysical modelling is the information it delivers regarding growth and development stage. This development of egg towards adult jellyfish seems to be accurate as agents reach the adult stage starting from October and peaking in number during November, corresponding to the time window of the autumn reproduction period (Milisenda et al., 2016). It requires notion that in this study the employed models only captured the spring reproduction period of one year (2018). This year has been selected for the availability of data in Valencia, since the port of Valencia is a partner in this project. Whereas running these models over longer periods with multiple reproduction cycles is likely to give better results for stranding in the early spring and summer season. Moreover, the spawning period used in our model corresponds to the peak release of eggs achieved at an optimum temperature. The missing aspect of this approach is the non-peak spawning events that occur throughout time at different temperatures and are not included in this work.

Additionally, the findings of this work give a strong indication about the population connectivity in the Western Mediterranean basin, signalled by the large proportion of agents (more than 50%) that exit the model domain. This implies that the local populations of *P. noctiluca* in the Spanish Western Mediterranean waters subsidize other sub-populations in adjacent waters. In turn, adult jellyfish are also sourced adjoining waters into the Spanish waters, thus creating an interexchange of individuals in the Western Mediterranean as a whole (Aglieri et al., 2014). Nevertheless, this does not abolish the connectivity driven through self-recruitment attributed to the active agents present at the end of the simulation. Combined, both self-recruited and subsidized individuals are an indication of the reproductive connectivity that links one season to the other. This link could be only revealed through biophysical modelling, as the number of active particles by the end of the simulation is the most sensitive variable to agent behavior. Last, population connectivity is not the main purpose of the study and a larger big-scale model would be required to adequately represent the exchange between population sources. This would be achievable through an additional “identity letter” state variable for the agents which would differentiate between jellyfish of different subpopulations, and could be used to study genetic diversity (e.g., individual-based genetic model (Baggio et al., 2018)).

It is important to note that the diurnal vertical migration is simplified, and this could have effects on both spatial distribution and stranding events. In the biophysical model, a maximum diving depth, adjusted to allow for a well-defined vertical pattern at different temperatures and stages was used. This approach does take into consideration deviations in the diving patterns due to seasonality, or other hydrodynamic phenomena. *P. noctiluca* samples have been collected in the summer period at depths of up to 1200 and 1400 m (Cartes et al., 2013). A possible explanation is the hypothesis that jellyfish purposely dive to deeper water in order to avoid very warm unpleasant surface temperatures (Pitt and Lucas, 2014). Future hydrodynamic models that capture deep sea thermal fronts could provide an opportunity to further study dive depth as a function of temperature.

Additional processes not included in this biophysical model, and necessary to mention in the discussion, are predation and feeding. These effects mainly influence survival and to a lesser extent development stage and vertical migration (Augustine et al., 2014). Feeding and predation have been already quantified and included in jellyfish models (Kristiansen et al., 2007; Legovic, 1987; Neumann et al., 2016; Qiu et al., 2010), but have been left out of this biophysical model to limit probabilistic factors and complexity.

Together with the biological and behavioral processes, the quality and resolution of the hydrodynamic model has a large influence on the dispersion patterns (Kvile et al., 2018). Resolving shallow water currents and coastal interactions is a delicate process that requires models of higher resolution than that used in this study, and preferably curvilinear or unstructured grids that can accurately trail the coastline. A

key constituent in the beaching process is wave action, causing stranding events especially in shallow waters. By increasing the spatial resolution and integrating wave action, the biophysical model could be further improved for modelling the physical aspect of *P. noctiluca* strandings.

5. Conclusion

By including life cycle development and behavior in jellyfish modelling our study has shown better prediction of *P. noctiluca* stranding events compared to a simple drift and fixed-diurnal behavior model. This biophysical model approach is likely to be of use for occurrence prediction of other jellyfish species, especially those with strong vertical behavior. Future research that tackles the knowledge gaps we encountered should address (1) in situ field measurements which provide more accurate *P. noctiluca* stranding events records; (2) monitoring campaigns to study seasonality in *P. noctiluca* dive depth and spatial distribution; and (3) laboratory research to validate the assumptions on buoyancy, swimming velocities, motility and time requirements for the development stages.

This biophysical model could be further developed by including multiple spawning periods, switching from seasonal simulations to multiannual lifecycle runs where populations are linked through reproduction. Through the incorporation of jellyfish sightings to test and adjust model predictions a comprehensive operational model could be setup. This model would then be predicting the full lifecycle of jellyfish, giving insight on the likeliness of jellyfish spatial and temporal distributions and predicting jellyfish stranding locations; thereby contributing to one of the goals of the ODYSSEA project that has funded this study. The societal benefits of such a model would be numerous, from early warnings to beachgoers, industry intakes and fisheries to potential to mitigate upcoming jellyfish blooms and to determine the current state of the ecosystem.

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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.

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