



Abundance of *Pelagia noctiluca* early life stages in the western Mediterranean Sea scales with surface chlorophyll

Daniel Ottmann^{1,*}, Diego Álvarez-Berastegui², Laura Prieto³, Rosa Balbín¹, Francisco Alemany⁴, Øyvind Fiksen⁵, Ana Gordo⁶, Patricia Reglero¹

¹Centre Oceanogràfic de les Balears, Instituto Español de Oceanografía (COB-IEO), Moll de Ponent s/n, 07015 Palma de Mallorca, Spain

²Balearic Islands Coastal Observing and Forecasting System (ICTS-SOCIB), Parc Bit, Naorte, Bloc A 2º, 07121 Palma de Mallorca, Spain

³Instituto de Ciencias Marinas de Andalucía, Consejo Superior de Investigaciones Científicas (ICMAN-CSIC), Republica Saharaui 2, 11519 Puerto Real, Spain

⁴International Commission for the Conservation of Atlantic Tunas, Corazón de María 8, 28002 Madrid, Spain

⁵Department of Biological Sciences, University of Bergen, 5020 Bergen, Norway

⁶Centro de Estudios Avanzados de Blanes, Spanish National Research Council (CEAB-CSIC), 17300 Blanes, Spain

ABSTRACT: *Pelagia noctiluca* is the most successful and well-studied jellyfish in the Mediterranean Sea. This species tolerates a wide range of water temperatures and succeeds in low to medium food regimes, but factors driving its distribution and population dynamics remain poorly understood. Here we applied a multiscale analytical approach using survey data and a physical–biochemical coupled model to assess how environmental factors affect the 3-dimensional distribution and seasonal abundance of *P. noctiluca* early life stages. The surveys took place after the spring bloom, when warm water favors fecundity and growth, but food shortage limits the reproductive investment and early survival. We found that most early life stages of *P. noctiluca* remained above the shallow thermocline and upper mixed layer where temperature is warm. Their spatial distribution was positively correlated with surface chlorophyll concentration, and over 90 % of the variation in interannual abundance was explained by basin-scale productivity in June. Warmer water during winter and spring seasons coupled with protracted spring blooms increase the population of *P. noctiluca*, and this explains the trend of increasing outbreaks observed in the western Mediterranean Sea over the past decades.

KEY WORDS: Jellyfish · Ephyra · Metaephyrae · Spatial distribution · Diel vertical migration · Temperature · Chlorophyll concentration

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1. INTRODUCTION

How will gelatinous zooplankton respond to environmental and global change? This question often relates to jellyfish blooms, as their consequences range from ecosystem changes to direct impacts on tourism,

energy supply, fisheries and aquaculture (Purcell et al. 2007, Boero 2013, Rossi et al. 2019). Water temperature and food availability are known to influence the reproductive activity of cnidarians (Rossi et al. 2019). However, the question of whether jellyfish blooms are increasing remains controversial (Duarte et al. 2015),

and we need better understanding of how these organisms respond to environmental factors.

Pelagia noctiluca is a holopelagic scyphozoan that extends across all oceans between 58° N and 34° S, and it is the most common jellyfish in the Mediterranean Sea (Licandro et al. 2010, Miller et al. 2012). Its wide tolerance to temperature and food availability may explain why *P. noctiluca* is so broadly distributed across all oceans. Laboratory experiments show that early life stages can develop at water temperatures as low as 13°C, and growth and survival increase as temperature rises up to at least 24°C (Avian 1986, Morand et al. 1992, Rosa et al. 2013, Augustine et al. 2014). On the other hand, *P. noctiluca* is an opportunistic predator that feeds on micro- and mesozooplankton, including fish eggs and larvae and other gelatinous plankton (Malej 1989, Milisenda et al. 2018b, Tilves et al. 2018). This species is resilient to starvation by shrinking in size during periods of food depletion, a trait that enables it to thrive in a wide spectrum of food regimes (Morand et al. 1987, Augustine et al. 2014, Lilley et al. 2014b). Outbreaks of *P. noctiluca* in the Mediterranean Sea are region specific, and climate anomalies in the North Atlantic can create particular conditions in the western Mediterranean, i.e. mild winters, low rainfall and high temperature in spring and summer, where bloom frequency increases (Goy et al. 1989, Daly Yahia et al. 2010, Canepa et al. 2014). In fact, population outbreaks of this jellyfish appear to follow deterministic processes (Benedetti-Cecchi et al. 2015), although the mechanisms remain elusive.

What drives the population dynamics of such a resilient species? High temperature increases gonad activity (Milisenda et al. 2018a), accelerates growth and improves survival of early life stages (Avian 1986, Rosa et al. 2013, Augustine et al. 2014). Thus, warm water presumably enhances population growth by increasing fecundity and accelerating recruitment of new individuals to the spawning population. A clear example of how warm temperature favors population growth occurs in the northeast Atlantic Ocean, where periods of warm anomalies are associated with increased abundances of *P. noctiluca* in plankton observations (Licandro et al. 2010). In the Mediterranean Sea, however, the effect of water temperature is more ambiguous as it varies over the season: temperature-driven increases in growth rate and fecundity have been found in winter and spring, when water is relatively cold, but fecundity drops during the warm summer months (Rosa et al. 2013, Milisenda et al. 2018a), indicating that food supply limits reproduction as well as growth.

Compared to adult *P. noctiluca*, relatively little is known about the abundance and distribution of early life stages (ephyrae and metaephyrae) or the natural conditions favoring their occurrence. For instance, it is known that adult individuals engage in sexual reproduction near the surface and conduct diel vertical migrations down to several hundred meters (Zavodnik 1987). However, identifying the degree to which early life stages follow similar migratory behavior has been hampered by methodologies that are too coarse to detect minor vertical migrations (Morand et al. 1992, Buecher & Gibbons 1999).

Even less is understood about the spatial distribution of early life stages. For instance, surveys of cross-shore transects in the Ligurian Sea and off eastern Spain found that early life stages of *P. noctiluca* tended to be more abundant near a shelf-slope front where plankton is generally abundant (Morand et al. 1992, Sabatés et al. 2010), but a more recent study off eastern Spain found them widely distributed over both shelf and slope areas (Sabatés et al. 2018). Water temperature in this study area also had mixed correlations with the distribution of early life stages, as they were more abundant on the warmer side of the study area (Tilves et al. 2016), but overall less abundant in warmer years (Guerrero et al. 2018).

To cast more light on conditions enhancing the abundance of *P. noctiluca* early life stages, we evaluated the relationship between physical variables and chlorophyll concentration and the distribution and abundance of early life stages in the western Mediterranean Sea. Habitat variability in the study area is fostered by the seasonal occurrence of a front between 2 water masses that originate in the Atlantic Ocean but differ in salinity and time of residence in the Mediterranean basin (Balbín et al. 2014). We first linked the summer vertical distribution of early life stages to temperature and fluorescence in the water column and tested whether they conduct diel vertical migrations. We then applied statistical modeling to evaluate how physical and biological variables influence spatial distribution over 6 continuous years. The models combined data recorded *in situ* (CTD) and obtained from coupled physical–biological models, and the analyses were conducted at the mesoscale (10 nautical miles [n miles]) to determine patchy distributions in relation to the local hydrography. Finally, we scaled up the analyses and related their overall abundance with environmental variables averaged over the whole study area (190 × 160 n miles) to identify factors driving annual reproductive output at the regional level.

2. MATERIALS AND METHODS

2.1. Biological samples

To evaluate the vertical distribution and daily migration patterns of *Pelagia noctiluca* early life stages, we conducted 8 stratified sampling tows from 2–4 July 2019 using a Multinet Midi (Hydro-Bios) with 0.25 m² mouth opening and 200 µm mesh size. The sampling station was located about 25 n miles northwest of the island of Ibiza (Fig. 1) and was selected based on the high abundance of *P. noctiluca* revealed by a previous plankton tow using bongo nets. We towed the Multinet in circles of about 900 m in diameter at a cruising speed of 2 knots, sampling each 20 m stratum from 0 to 100 m depth (see Section S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m658p075_supp.pdf). Sampling took place throughout 48 consecutive hours, and included 2 replicate samples of sunrise, daylight, sunset and night, considering astronomical twilight phases of 3 July at 39° N latitude. All Multinet samples were preserved in 99% ethanol and stored for further lab processing.

Spatial distribution of *P. noctiluca* early life stages was based on plankton samples collected between 17 June and 22 July over 6 yr (2012–2017) on a 10 × 10 n mile grid in the Balearic Islands (Fig. 1). The hydrodynamic landscape of the study area during this time of the year is typically dominated by the confluence of the resident, saltier water that streams from the Northern Current, and a fresher water inlet that flows from the Atlantic Ocean towards the islands (Balbín et al. 2014). Consequently, a mosaic of fronts and eddies fosters variable conditions of temperature and salinity that shape the associated plankton community. We conducted a total of 540 oblique plankton tows from 0 to approximately 30 m depth, covering the mixed layer and thermocline portions of the water column. Bongo nets of 90 cm frame diameter and 500 µm mesh size were equipped with independent flowmeters and deployed at a cruising speed of 2 knots. One replicate was immediately preserved in 2% formalin buffered with borax and the other in ethanol. Both replicates were stored for further lab processing, but only samples in formalin were used in this

study. In the laboratory, we used a dissecting microscope to sort and count early life stages (<10 mm) of *P. noctiluca* from both the bongo and Multinet samples. When samples appeared to contain >500 ind., we subsampled aliquots taken with a Folsom plankton divider and calculated the total number of individuals, applying the corresponding multiplication factor.

2.2. Environmental data

Immediately after all bongo and Multinet tows, we deployed a CTD rosette down to alternating depths of 600 and 350 m to record vertical profiles of water temperature and salinity (and fluorescence for the vertical profiles following stratified plankton tows). Seasonal thermal stratification in the area is known to separate 2 distinct communities above and below the thermocline, including phyto- (Mena et al. 2019) and ichthyoplankton (Olivar et al. 2014). We used the vertical profiles of water temperature and salinity to identify the mixed layer depth (MLD), and then calculated mean temperature (Temp) and salinity (Sal) of the upper mixed layer. To parametrize regional hydrodynamic activity, we calculated the module of the geostrophic velocity (GVel) by differentiating the dynamic height derived from the temperature and salinity profiles (Olivar et al. 2014).

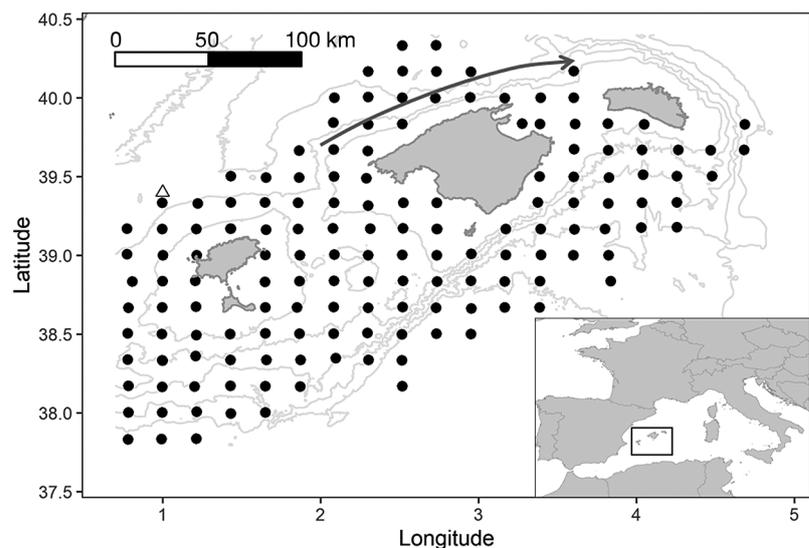


Fig. 1. Study area where 540 oblique bongo tows (filled dots) and 8 stratified tows (white triangle) were conducted in 2012–2017 and 2019, respectively. Oblique bongo tows were distributed on a 10 × 10 nautical mile grid, and not all sites could be sampled every year due to logistical constraints. Stratified tows were conducted over 48 h, encompassing dawn, daylight, dusk and night. Arrow indicates the direction of the Balearic Current; thin contour lines indicate the bathymetry at 500 m depth intervals

In addition to *in situ* data, sea surface (1.5 m) temperature and chlorophyll *a* (chl *a*) concentration data were obtained from the Mediterranean Sea (Med Sea) physical (v1.4) and biogeochemistry (v2.2) model re-analyses of the EU Copernicus Marine Environment Monitoring Service (Simoncelli et al. 2014, Teruzzi et al. 2014). Re-analysis modeling is a technique that combines multi-source information archived over decades with a general ocean model to generate assimilated numerical values of the system. The Med Sea re-analysis products have a 5–6 km resolution based on a Nucleus for European Modelling of the Ocean (NEMO) ocean general circulation model assimilated with satellite and *in situ* recorded data, including information on chlorophyll concentration. An additional advantage of using a re-analysis model is that it retains information when cloud coverage hampers use of direct satellite data. Because phytoplanktonic organisms are the main primary producers fueling subsequent trophic levels in marine pelagic systems (Boero et al. 2008), we used chlorophyll concentration as an indicator of biological productivity. Given that June partially encompasses the period when adult *P. noctiluca* invest energy obtained from food in reproduction, as well as the lifetime of the young individuals collected in the surveys, we used monthly mean chl *a* concentration in June as a biological indicator of their food abundance. This was confirmed by a sensitivity analysis, showing that monthly mean chlorophyll concentration of each of April, May and June had a positive and significant relation with the interannual abundance of *P. noctiluca*, and that chlorophyll concentration in June was the most powerful predictor among the 3 months (Table S1).

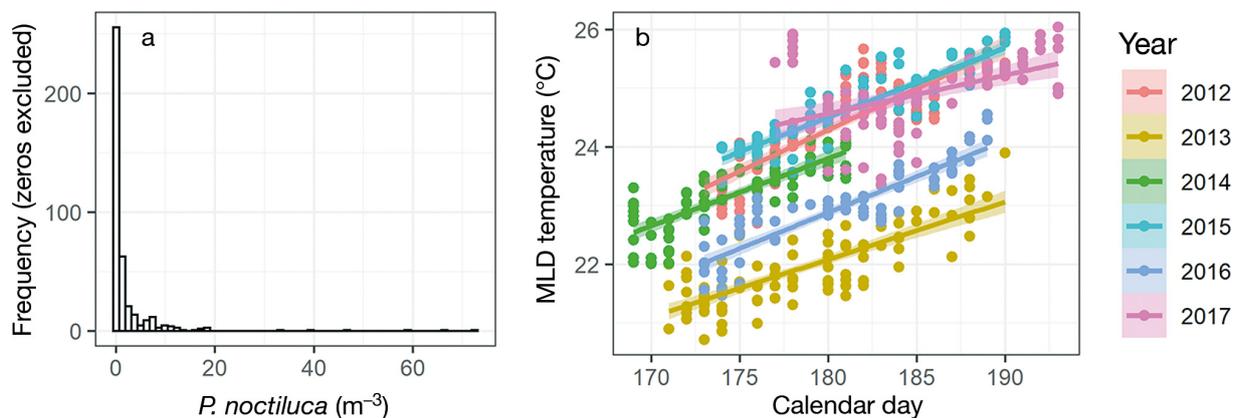


Fig. 2. (a) Frequency distribution of observed densities (24.4% zeros excluded) of *Pelagia noctiluca* early life stages drawn from 540 oblique bongo tows around the Balearic Islands in 2012–2017. (b) Annual variation of mean temperature of the mixed layer as the sampling season (17 June to 11 July) progressed in 2012–2017. MLD: mixed layer depth; dots: observations; lines: annual regressions of temperature against calendar day; shading around lines: 95% confidence intervals

2.3. Data exploration

Prior to the analyses, the data were explored following standard statistical procedures (Zuur et al. 2010). This process revealed that *P. noctiluca* abundances were overdispersed (Fig. 2a) and zero inflated (24.4%), and that there was excessive correlation ($\text{cor} = 0.7$) and variance inflation factor ($\text{VIF} = 2.6$) between calendar day (Day) and Temp. A common approach to deal with this correlation is to use temperature residuals of each year (TempR), instead of absolute values of temperature (Reglero et al. 2012, Ingram et al. 2017, Alvarez-Berastegui et al. 2018). Residuals were obtained regressing Temp over Day using year (Yr) as a discrete interaction covariate to allow for different intercepts and slopes every year (Model M1, Eq. 1; Fig. 2b):

$$\text{Temp}_i = \beta_0 + \beta_1(\text{Day}_i) + \beta_2(\text{Yr}_i) + \beta_3(\text{Day}_i \times \text{Yr}_i) + \varepsilon_i \quad (1)$$

Where for each observation i , β_0 is the intercept, β_{num} are each of the variable slopes and ε is the model error. As such, this new variable cannot be used to estimate the quantitative effect of water temperature on the presence or abundance of *P. noctiluca*, but it can tell if they show a functional response to warmer ($\text{TempR} > 0$) or colder ($\text{TempR} < 0$) water masses, regardless of year and calendar day.

2.4. Data analyses

2.4.1. Vertical distribution

For each Multinet tow, *P. noctiluca* density was calculated by dividing the number of individuals in each

stratum by its filtered volume (m^3), and the MLD was derived from CTD temperature and salinity profiles. To evaluate potential diel vertical migration patterns, we calculated the weighted mean depth (WMD) of each tow following Frost & Bollens (1992), where n_i is the density of *P. noctiluca* at depth d_i , taken to be the midpoint of each depth stratum:

$$\text{WMD} = \frac{\sum n_i d_i}{\sum n_i} \quad (2)$$

Welch's 2-sample *t*-tests were used to evaluate variation in WMD between the different daylight periods. We considered differences to be significant at a Bonferroni-adjusted *p*-value < 0.008.

2.4.2. Mesoscale analysis

To evaluate how environmental conditions affect the distribution of *P. noctiluca* early life stages, we modeled their presence and abundance in response to 4 physical and 1 biological variable following a 2-step approach. First, we ran the models excluding the geographic position to assess the direct effect of the environment assuming no spatial effect. Then we added the geographic position to investigate potential spatial correlation or the effect of other variables not included in the models. Presence and abundance models were run separately, because presence indicates the effect limits to a variable while abundance reflects the effect magnitude.

Given that early life stages of *P. noctiluca* were absent in 24.4% of the sampled stations, presence can be modeled with a frequentist approach applying the following general additive model (GAM) with Bernoulli distribution (Model M2, Eq. 3; Zuur et al. 2009):

$$\begin{aligned} P_{iYr} = & \beta_0 + s_1(\text{Time}_i) + s_2(\text{Day}_i) \\ & + s_3(\text{MLD}_i) + s_4(\text{Sal}_i) + s_5(\text{TempR}_i) \\ & + s_6(\text{Gvel}_i) + s_7(\text{Chl}_i) + Yr_i + \varepsilon_{iYr} \end{aligned} \quad (3)$$

For each observation i , P is the probability of presence of *P. noctiluca*, Time is the normalized circadian time of day (GMT), Yr is a random effect covariate of year, ε is the model residual, and the other covariates are as defined above. All smoothing parameters are indicated with s , and were restricted to 3 knots to prevent over-fitting the model. A model selection was conducted applying sequential *F*-tests with a *p*-value threshold of 0.05 and crosschecked with values of Akaike's information criterion (Zuur et al. 2009, Wood 2013).

Because our count data were heavily over-dispersed and zero inflated (Fig. 2a), modeling abundances of early life stages of *P. noctiluca* required the use of zero-inflated models with negative binomial distri-

bution. Frequentist statistical approaches have a limited performance evaluating additive models with such data. Thus, we modeled abundances applying a Bayesian approach (Model M3, Eq. 4):

$$\begin{aligned} N_{iYr} = & \beta_0 + s_1(\text{Time}_i) + s_2(\text{Day}_i) \\ & + s_3(\text{MLD}_i) + s_4(\text{Sal}_i) + s_5(\text{TempR}_i) \\ & + s_6(\text{Gvel}_i) + s_7(\text{Chl}_i) + Yr_i \\ & + \text{of}(\ln(\text{Vol}_i)) + \varepsilon_{iYr} \end{aligned} \quad (4)$$

Here, N is the number of *P. noctiluca* in each observation i , and the natural log of volume (m^3) is included as an offset, $\text{of}(\ln(\text{Vol}_i))$, to standardize for the different volumes filtered per sampling tow. Bayesian models were fitted with uninformative priors, and coded to draw 10 000 post warm-up samples (4 chains of 3500 iterations, of which the first 1000 were discarded as warm-up for chain convergence). Post warm-up samples were thinned at 1/10 to reduce autocorrelation, and all full and reduced models presented good mixing of chains. Leave-one-out cross-validation and the widely applicable information criterion were applied to conduct stepwise model selection (Vehtari et al. 2017). To measure the model fit, Bayesian R^2 was applied as an alternative to the classical R^2 , which is not an appropriate measurement in Bayesian statistics (Gelman et al. 2019).

To describe the spatial distribution of *P. noctiluca* early life stages in the study area, we added a variable that accounted for geographic position of each sampling station, LatLon (Model M4 [Eq. 5] and Model M5 [Eq. 6],) to models M2 and M3. The same model-selection processes described above were applied to these models.

$$\begin{aligned} P_{iYr} = & \beta_0 + s_1(\text{Time}_i) + s_2(\text{Day}_i) \\ & + s_3(\text{MLD}_i) + s_4(\text{Sal}_i) + s_5(\text{TempR}_i) \\ & + s_6(\text{Gvel}_i) + s_7(\text{Chl}_i) + s_8(\text{LatLon}_i) \\ & + Yr_i + \varepsilon_{iYr} \end{aligned} \quad (5)$$

$$\begin{aligned} N_{iYr} = & \beta_0 + s_1(\text{Time}_i) + s_2(\text{Day}_i) \\ & + s_3(\text{MLD}_i) + s_4(\text{Sal}_i) + s_5(\text{TempR}_i) \\ & + s_6(\text{Gvel}_i) + s_7(\text{Chl}_i) + s_8(\text{LatLon}_i) \\ & + Yr_i + \text{of}(\ln(\text{Vol}_i)) + \varepsilon_{iYr} \end{aligned} \quad (6)$$

2.4.3. Interannual variability and regional analysis

Several studies have identified a peak in reproduction during late spring to early summer, in synchrony with the spring blooming of lower trophic level organisms (Morand et al. 1992, Hecq et al. 2009, Milisenda et al. 2018a). To evaluate how the overall chlorophyll concentration and water temperature in June affect the interannual abundance of *P. noctiluca* early life

stages, we scaled up the analysis using averaged values of the entire study area with data from the reanalysis models. First, we compared the mean *P. noctiluca* density (mDens) of each year (Yr) against the June chlorophyll concentration (mChl) and sea surface water temperature (mSST) of the hydrodynamic models averaged over the whole study area (Model M6, Eq. 7):

$$\text{mDens}_{Yr} = \beta_0 + \beta_1(\text{mChl}_{Yr}) + \beta_2(\text{mSST}_{Yr}) + \beta_3(\text{mChl}_{Yr} \times \text{mSST}_{Yr}) + \varepsilon_{Yr} \quad (7)$$

This model used density averages, which is good to identify general patterns, but neglects the effect of time and calendar day when stations were sampled, as well as their variability. Therefore, we also modeled the *P. noctiluca* abundance (N) of each station *i* as a function of mChl and mSST, including the calendar day (Day) and time (Time) of the day when each station was sampled (Model M7, Eq. 8):

$$N_i = \beta_0 + s(\text{Time}_i) + s_2(\text{Day}_i) + s_3(\text{mChl}_i) + s_4(\text{mSST}_i) + s_5(\text{mChl}_i \times \text{mSST}_i) + \text{of}(\ln(\text{Vol}_i)) + \varepsilon_i \quad (8)$$

We conducted a model selection following standard procedures described above (Zuur et al. 2009, Wood 2013, Vehtari et al. 2017). To evaluate the predictive power using area-averaged variables, we predicted *P. noctiluca* densities for each station.

2.4.4. Software and model diagnostics

All analyses and figures were made in R v3.6.1 (R Core Team 2019) using the packages ‘tidyverse’ v1.2.1 (Wikham 2017), ‘mgcv’ v1.2.28 (Wood 2011), ‘brms’ v2.9.0 (Bürkner 2017), ‘rstanatm’ v2.18.2 (Goodrich

et al. 2018), ‘maps’ v3.3.0 (Becker et al. 2018), ‘raster’ v3.7.0 (Hijmans 2019), ‘ncdf4’ v1.16.1 (Pierce 2019) and ‘MBA’ v0.0.9 (Finley et al. 2017). Model diagnostics of models M2–M7 are shown in Figs. S2–S7, respectively.

3. RESULTS

3.1. Vertical profiles of temperature and salinity and *Pelagia noctiluca* early life stage distribution

The thermocline was compressed between 9 and 15 m depth throughout the 48 h of stratified sampling, and temperature continued to drop towards deeper waters until stabilizing to 13.5°C at about 70 m depth (Fig. 3). Chlorophyll concentration was very low (<0.02 mg m⁻³) within the upper mixed layer, and the deep chlorophyll maximum occurred at 60–85 m depth, where temperature was always lower than 15°C. Our stratified plankton tows revealed that 98.3% of the early life stages of *P. noctiluca* remained in the top 40 m depth. In fact, they were most predominant (89.5%) in the 0–20 m stratum and spread more evenly between the 0–20 and 20–40 m strata in only 1 tow conducted during day hours. We found no significant diel vertical migration pattern in the top 100 m, as all pairwise *t*-tests of WMD yielded *p*-values >0.008.

3.2. *P. noctiluca* early life stage abundances and habitat characteristics

Presence and abundance of *P. noctiluca* early life stages varied from year to year (Table 1), being most

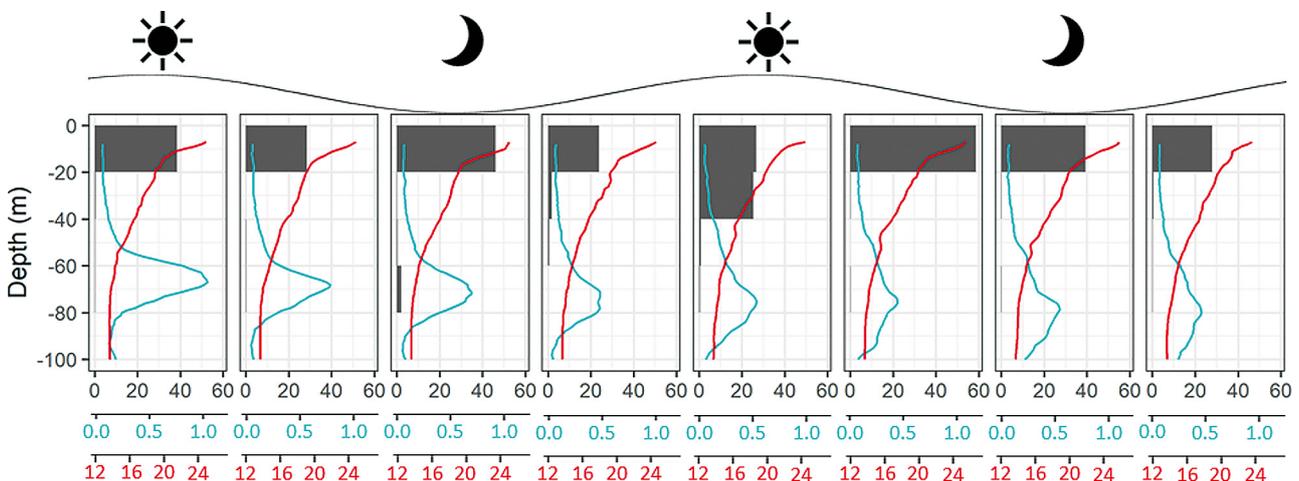


Fig. 3. Vertical distribution of *Pelagia noctiluca* early life stages (bars; *P. noctiluca* m⁻³) sampled throughout 48 h in 2019 with a Multinet Midi (Hydro-Bios®) at 25 nautical miles off northwest Ibiza. Fluorescence (blue; mg m⁻³) and water temperature (red; °C) profiles show a deep chlorophyll maximum at 65–80 m depth and a thermocline at 10–15 m

Table 1. Summary of *Pelagia noctiluca* abundances ($P. noctiluca\ m^{-3}$), and range of model covariates surveyed from 17 June to 8 July of 2012–2017 around the Balearic Islands. MLD: mixed layer depth; T: temperature; Sal: salinity; Gvel: geostrophic velocity; Chl: average sea surface chlorophyll concentration in June

Year	<i>P. noctiluca</i>				Ranges of covariate values				
	Absences (%)	Max	Mean	Median	MLD (m)	T (°C)	Sal (psu)	Gvel (cm s ⁻¹)	Chl (mg m ⁻³)
2012	49.2	11.3	0.4	0.002	8.2–20.3	22.5–25.7	37.0–38.5	1.8–28.6	0.031–0.052
2013	7.1	72.5	3.5	0.678	8.0–28.3	20.7–23.9	37.4–38.2	0.5–27.6	0.046–0.070
2014	47.3	17.9	0.9	0.002	8.4–20.2	22.0–24.1	37.2–38.3	1.2–16.2	0.042–0.057
2015	17.3	66.2	2.0	0.160	7.8–19.2	23.4–25.9	37.1–38.1	1.7–25.6	0.041–0.063
2016	17.7	58.8	2.9	0.110	8.2–26.4	21.5–24.6	37.1–38.3	0.0–29.8	0.040–0.065
2017	4.5	33.4	1.14	0.157	7.8–25.4	23.3–26.0	36.6–38.0	0.5–28.5	0.044–0.055
Overall	24.4	72.5	1.8	0.067	7.8–28.3	20.7–26.0	36.6–38.5	0.0–29.8	0.040–0.070

prevalent in 2017 (presence = 95.5%), most abundant in 2013 (mean = 3.5 $P. noctiluca\ m^{-3}$, median = 0.678 m^{-3}) and scarcest in 2012 (presence = 50.8%; mean abundance = 0.4 $P. noctiluca\ m^{-3}$, median = 0.002 m^{-3}). Six exceptional stations had more than 30

$P. noctiluca\ m^{-3}$ (Fig. 2a), of which the greatest density (72.5 m^{-3}) occurred in 2013 at about 20 n miles west of Ibiza. Regarding environmental variables, years with shallower ranges of MLD tended to coincide with those with warmer ranges of water temperature, and salinity ranged from about

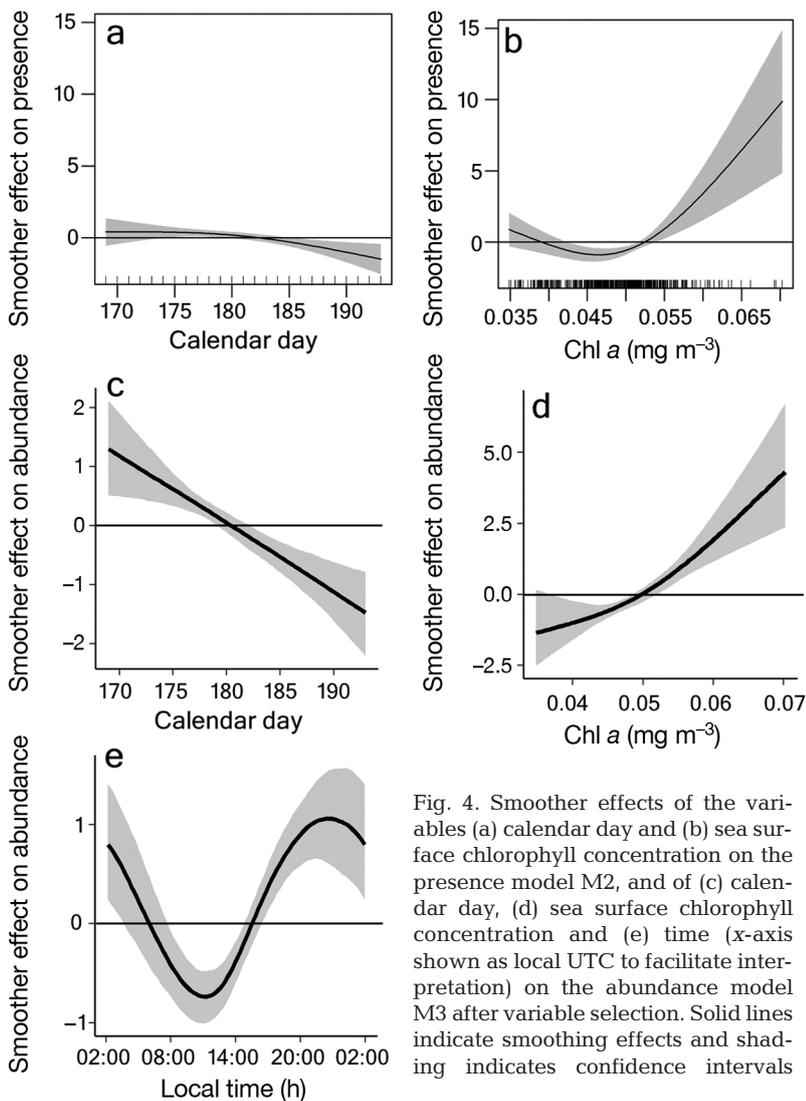


Fig. 4. Smoother effects of the variables (a) calendar day and (b) sea surface chlorophyll concentration on the presence model M2, and of (c) calendar day, (d) sea surface chlorophyll concentration and (e) time (x-axis shown as local UTC to facilitate interpretation) on the abundance model M3 after variable selection. Solid lines indicate smoothing effects and shading indicates confidence intervals

37 to 38 in all years, confirming that resident and newly arrived water masses from the Atlantic were sampled every year. Following common patterns described by Balbín et al. (2014), the boundary between both water masses ranged from more than 40 n miles south of the archipelago in 2012 to about 10 n miles off northern Mallorca in 2016. Indeed, geostrophic velocities varied from year to year in the different parts of the study area, with maximum speeds of almost 30 cm s⁻¹, and with some stations where there was virtually no geostrophic movement (Table 1). Such high variability reflects the complexity and fluctuating dynamics of the frontal zone. Regarding the water productivity, sea surface chlorophyll concentration indicates that June productivity was lowest in 2012 and highest in 2013.

3.3. Mesoscale analysis

While presence of *P. noctiluca* early life stages was only influenced by the effects of calendar day and sea surface chlorophyll (Fig. 4a,b; F -test, $p < 0.05$), abundance was also affected by time of the day (Fig. 4c–e). Early life stages were more prevalent and abundant towards

the beginning of the sampling season and in waters with greater concentration of chlorophyll and they were more abundant during the night tows. None of the other variables (MLD, mean water temperature and salinity, or geostrophic velocity) showed a significant effect on either presence or abundance of *P. noctiluca*.

Models including the geographic position (Models M4 and M5) showed that *P. noctiluca* tended to be more prevalent and abundant on the northwestern side of the study area (Fig. 5a). Variable selection for these models resulted in discarding the calendar day variable, which was retained in the models lacking the geographic position (Models M2 and M3). However, the proportion of variance explained by the abundance models was slightly greater in the one lacking the spatial position (Model M3, Bayesian $R^2 = 0.48$) than in the model including it (Model M5, Bayesian $R^2 = 0.45$). This indicates that the model-selected variables describing the environmental conditions in each sampling station can explain the observed abundances, and that sampling position by itself does not add any further information. In fact, similarities between model-predicted and field-observed abundances become more and more apparent at increasing spatial scales (Fig. 5a,b), showing how *P. noctiluca* tended to be more abundant in areas with greater chlorophyll concentration (Fig. 5c).

3.4. Interannual variability and regional analysis

At the regional level, mean surface chlorophyll concentration of the study area had a distinctively positive relation with the overall abundance of *P. noctiluca* (Model M6; Fig. 6a; F -test, $p < 0.05$; $R^2 = 0.91$), while mean sea surface temperature had no significant effect (F -test, $p > 0.05$). This shows that June productivity has a direct and much stronger regional effect on the early summer abundance and spatial distribution of *P. noctiluca* early life stages than water temperature. Consistently, modeled abundances of each station considering area-averaged variables were affected by chlorophyll concentration and not temperature, and predicted densities increased almost linearly with chlorophyll concentration (Model M7; Fig. 6b).

4. DISCUSSION

Our results showed that almost all early life stages of *Pelagia noctiluca* remained in the top 40 m of the water column at the onset of summer, mainly in the first 20 m, where water temperature is warm and

chlorophyll concentration is low. However, their spatial distribution was determined by mesoscale (10 n miles) surface chlorophyll concentration, and their overall interannual abundance was correlated with the chlorophyll concentration of the entire study area. Given that greater primary productivity supports a greater community of food items in the micro- and mesozooplankton community, these findings show that while *P. noctiluca* early life stages remain at the layer where high temperature favors growth and survival, it is food availability that determines their abundance and horizontal distribution.

Our stratified sampling data confirm the previously suggested hypothesis (Morand et al. 1992, Buecher & Gibbons 1999, Tilves et al. 2016) that early life stages of *P. noctiluca* do not follow major vertical migrations of several hundred meters like the adult medusae (Fig. 3). The fact that most early life stages of *P. noctiluca* remain in the top layers of the water column confirms that the use of sea-surface and sub-surface variables in our models was a good proxy to link habitat conditions with their spatial distribution.

Adult *P. noctiluca* can reproduce throughout the year (Rottini Sandrini & Avian 1991, Rosa et al. 2013, Milisenda et al. 2018a), but at the onset of summer, early life stages face a tradeoff between food availability and water temperature, as the vertical stratum where temperature is optimal for growth and survival is different from the depth with higher food concentration. Laboratory experiments have shown that eggs can develop to ephyrae at 13°C (Avian 1986), but they do so 3 times slower than at 24°C and with 5 times greater chances of dying (Morand et al. 1992, Rosa et al. 2013, Augustine et al. 2014). We observed that *P. noctiluca* early life stages were most abundant in the water portion where temperature was 18–26°C, and they were rarely observed in the deep chlorophyll maximum, where water temperature was always lower than 15°C. It seems that faster temperature-derived growth is a priority to maximize survival of *P. noctiluca* offspring at the onset of summer, and that the species has adapted its spawning behavior by releasing the gametes in the warmer layers of the upper water column (Zavodnik 1987). Furthermore, although most plankton organisms remain at deeper waters, a number of food sources exist in the top 25 m of the water column during the summer season, including nutritious fish eggs and larvae (Olivar et al. 2014).

The average sea surface chlorophyll concentration in June showed a distinctively positive relation with presence and abundance of *P. noctiluca* early life stages at both regional and mesoscale levels. This

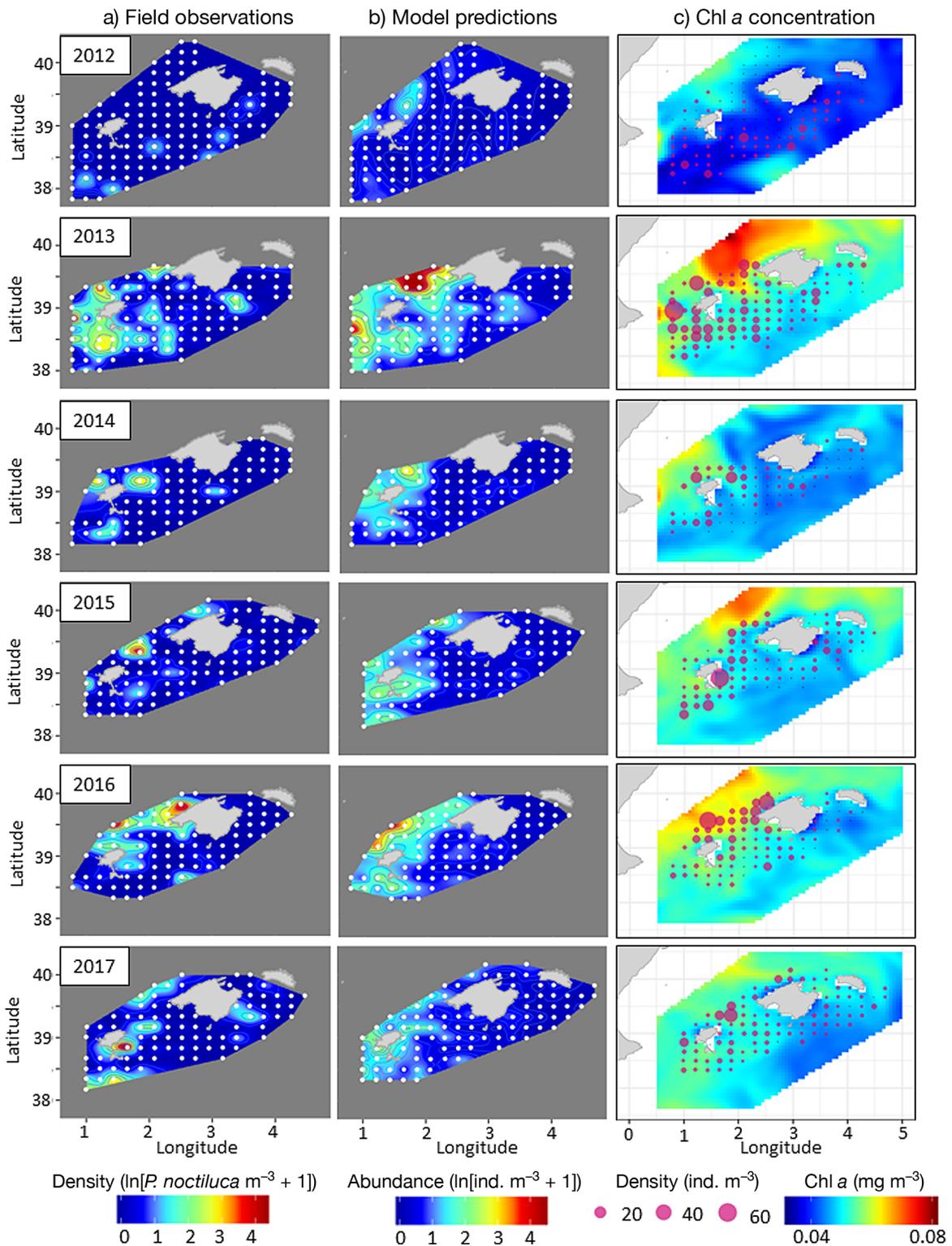


Fig. 5. (a) Observed and (b) predicted abundances of *Pelagia noctiluca* early life stages around the Balearic Islands from 17 June to 11 July of 2012–2017. Predictions of density are drawn from Model M5 (Bayesian $R^2 = 0.48$), and all values are log-transformed to facilitate visualization. White dots ($n = 540$) indicate sampling stations, and a multilevel B-spline approximation was applied for the interpolation. (c) Density of *P. noctiluca* early life stages (magenta circles) overlaying the monthly mean sea surface chlorophyll concentration of the study area. Chlorophyll data were obtained from the Mediterranean Sea biogeochemistry reanalysis product v2.2 of the EU Copernicus Marine Environment Monitoring Service

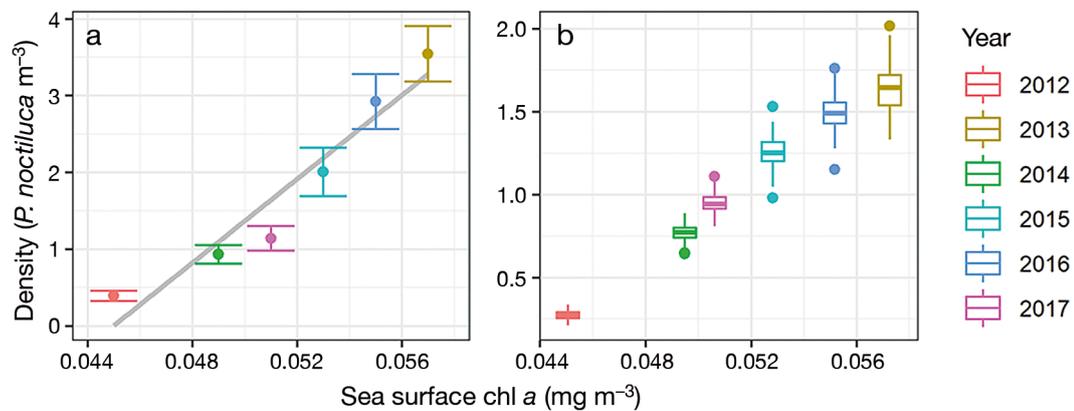


Fig. 6. Regional analysis outputs. (a) Mean annual density of *Pelagia noctiluca* early life stages (\pm SE) regressed against the June-averaged sea surface chlorophyll (Model M6; $y = 312.3 + 272.8\text{Chl}$; $R^2 = 0.91$). (b) Annual predicted *P. noctiluca* densities of Model M7 including June-averaged sea surface chlorophyll concentration, calendar day and sampling time. Horizontal line in box: median; bottom and top of boxes: 1st (Q1) and 3rd (Q3) quartiles, respectively; lower and upper whiskers: minimum ($Q1 - 1.5 \times$ interquartile range) and maximum ($Q3 + 1.5 \times$ interquartile range) values, respectively; dots: outliers. June-averaged regional data were obtained from the Mediterranean Sea biogeochemistry reanalysis product of the EU Copernicus Marine Environment Monitoring Service, and averaged over the study area around the Balearic Islands

relation passed unnoticed in similar studies of shorter duration and deeper plankton tows which focused on currents and water temperature (Tilves et al. 2016, Guerrero et al. 2018, Sabatés et al. 2018). However, comparing their results with the mean surface chlorophyll concentration in June (Teruzzi et al. 2014), we found that *P. noctiluca* early life stages also tended to be more abundant in the years and parts of their study area with higher chlorophyll concentrations.

In our study, none of the other habitat variables (i.e. salinity and temperature, geostrophic velocity and MLD) directly explained the abundance and distribution of *P. noctiluca* early life stages. The effect of calendar day determining the presence and abundance of *P. noctiluca* was no longer important when the spatial dimension was included in the models. It is statistically difficult to separate the partial effects of chlorophyll concentration and calendar day, but from a mechanistic perspective, it makes sense that a drop in observed abundance as the summer progresses reflects a decrease in reproduction and early life survival as food becomes scarcer and metabolic demands increase (Morand et al. 1987, Lilley et al. 2014b).

With the caveat of lacking information on micro- and mesozooplankton biomass, we suggest that the strong, positive relation between surface chlorophyll concentration of June and abundance of *P. noctiluca* early life stages can be explained by bottom-up trophic energy transfer throughout the food chain. In the western Mediterranean Sea, phytoplankton usually bloom around February–March when nutrients are well mixed in the water column and the sunlight hours increase daily (García-Martínez et al. 2019).

This pulse of phytoplankton biomass supports a community of micro- and mesozooplankton, including copepods and other food sources of adult *P. noctiluca* (Boero et al. 2008, Milisenda et al. 2018b, Ramírez-Romero et al. 2020). Such food abundance fuels growth and reproductive investment of adult *P. noctiluca*, leading to increased egg production (Milisenda et al. 2018a). For the early life stages of *P. noctiluca*, increased abundance of micro- and mesozooplankton also provides nourishment to grow faster and with less mortality (Lilley et al. 2014a, Purcell et al. 2014, Ramondenc et al. 2019). Further, small ephyrae of other jellyfishes can directly ingest phytoplankton cells (Båmstedt et al. 2001, Miranda et al. 2016) which could be an important food source for the smaller *P. noctiluca* ephyrae that have not fully developed their tentacles and oral arms. The bloom and subsequent increase in secondary productivity make food abundant when water temperature is low; thus, temperature is the limiting factor, as it promotes slow gonadal development (Milisenda et al. 2018a), increased stage duration and predation due to slow early life growth rate (Avian 1986), and increased early life mortality (Rosa et al. 2013). As such, warmer water temperature in winter and spring will increase the overall reproductive success and abundance. Towards the end of spring, water temperature will be closer to optimal, and food will still be available, making this time of the year the most successful in terms of reproductive output (Rottini Sandrini & Avian 1991, Morand et al. 1992, Buecher & Gibbons 1999, Hecq et al. 2009, Milisenda et al. 2018a). By June, the spring bloom has dropped, and food has become the main

limitation. Because of this limitation, years with a more productive June can sustain a community of prey that fuels some reproduction and early life survival of *P. noctiluca*. This explains the strong relation between surface primary productivity and early life stages of *P. noctiluca* found in this study. Enduring conditions of low food availability and high metabolic demand will remain until the fall storms break the thermocline and productivity rises again, enabling an occasional second peak of reproduction before water temperature drops too much (Malej & Malej 1992, Rosa et al. 2013, Milisenda et al. 2018a). By then, some of the spring offspring have reached sexual maturity and contribute to the population recruitment (Ramondenc et al. 2019).

Seasonal trade-offs in growth from water temperature and food availability have been identified before (Purcell et al. 2007, Hecq et al. 2009, Rossi et al. 2019). Increased coastal productivity due to fluvial input of nutrients such as in the Ebro River plume or in the northern Adriatic Sea can sustain greater reproduction throughout summer (Malej & Malej 1992, Kogovšek et al. 2010, Sabatés et al. 2018), while cold downwelling areas like the Gulf of Lions are less likely to sustain a high reproduction output (Guerrero et al. 2018). Accordingly, our mesoscale analysis identified the influence of increased surface productivity along the peninsular coast driven by the Ebro plume and brought to our study area by the Northern and Balearic currents, as well as the more oligotrophic waters off southwest Balearic Islands (Fig. 5c).

For a tolerant species like *P. noctiluca*, the ability to detect environmental signals driving the abundance and distribution of early life stages at the mesoscale requires a relatively large sample size (Gerrodette 1987). Our best model could only explain about half of the observed deviance, which means that the abundance of *P. noctiluca* did not perfectly align with the surface chlorophyll concentration at a given station (Fig. 5c). However, resemblances between the observed and model-estimated abundances become more conspicuous at increasing spatial scales. At the regional level, we found that surface chlorophyll concentration explained 91 % of the variability in interannual abundance (Fig. 6a). Indeed, interannual abundance of copepods and other important food sources of the same study area are correlated with primary productivity, supporting the trophic link between phytoplankton and *P. noctiluca* (Fernández de Puelles et al. 2007, García-Martínez et al. 2019). The remaining unexplained mesoscale variance is likely caused by other more stochastic variables not considered in this study, such as fine-scale surface currents

and convergence forces (Berline et al. 2013) or inter-specific interactions such as predation or competition. Resolving such fine-scale processes requires an adaptive sampling approach combining *in situ*, high-resolution data acquisition with remote-sensing and Lagrangian modeling methods (Marrec et al. 2018).

Sea surface temperature in the Mediterranean Sea has increased over the past decades due to climate change (Pastor et al. 2018), and this trend is expected to continue for all seasons of the year (Bindoff et al. 2019). Such warming may foster a better match between food availability and the optimal temperature for reproduction success in winter and spring. Simultaneously, surface chlorophyll concentration and the period of phytoplankton growth has increased in the western Mediterranean Sea while decreasing in the eastern Mediterranean Sea (Salgado-Hernanz et al. 2019). On the western side, the protracted period of phytoplankton growth occurs along with changes in its community structure that increase food availability for *P. noctiluca* through bottom-up control (Ramírez-Romero et al. 2020). Both of these phenomena may accentuate the match between warmer temperature and food availability that favors reproduction success in winter and spring, but whether this increase in productivity will be enough to compensate for the increase in summer metabolic demands is difficult to predict at this point. On the other hand, warmer water temperature and lower food availability in the eastern Mediterranean will probably reduce the summer fecundity, as the decrease in food supply will not be enough to sustain the higher metabolic demand.

Overall, the growing synchrony between the optimal temperature for reproduction with the seasonal period of greater food availability leads to the prediction that the population of *P. noctiluca* has increased in recent decades, particularly in the northwestern Mediterranean Sea (Rossi et al. 2019). This is supported by the observation that *P. noctiluca* outbreaks have increased over the last decades (Daly Yahia et al. 2010, Kogovšek et al. 2010, Bernard et al. 2011). This trend may continue if water gets warmer in winter and spring (Bindoff et al. 2019). In the northeast Atlantic, where productivity is generally higher than in the Mediterranean Sea, increases in water temperature resulted in unusual outbreaks of *P. noctiluca* (Licandro et al. 2010). Here, water temperature and not food availability is the limiting factor of population dynamics. Given the current projections of rising water temperature (Bindoff et al. 2019), this area may also experience an increase in blooms of *P. noctiluca*.

Predicting mass arrivals of *P. noctiluca* to coastal areas is challenging, because it depends on processes

acting at different spatial and temporal scales (Gibbons & Richardson 2013). The formation of dense aggregations depends on fine-scale physical forcing and behavioral traits (Zavodnik 1987, Malej 1989, Berline et al. 2013), but estimates of annual reproductive success are more accurate at a regional level than at smaller spatial scales. Furthermore, regional and mesoscale currents also play an important role, propelling swarms of adult *P. noctiluca* across the continental shelf and towards coastal areas (Sabatés et al. 2018), especially when underwater canyons act as funnels of adult jellyfish (Canepa et al. 2014, Benedetti-Cecchi et al. 2015). It is unknown whether the effect of canyons is widespread across the entire Mediterranean basin, but linking offshore abundances of early life stages with coastal blooms and topographic information can help understand the underlying mechanisms. Thus, future research aiming to predict mass arrivals of *P. noctiluca* to coastal areas should integrate estimates of adult jellyfishes and the conditions favoring their fecundity during the preceding months, along with accurate models of current dynamics and underwater topography. Across the Mediterranean Sea, platforms for monitoring essential ocean variables and hydrographic dynamics at different scales have experienced a rapid development in recent years (Tintoré et al. 2019). These promising advances feature downstream services that can be combined with ecological understanding of *P. noctiluca* to forecast their abundances in coastal areas. This work provides valuable insights to understand how water temperature structures the vertical distribution of young *P. noctiluca* and how surface chlorophyll concentration drives their spatial distribution and regional abundance in the Western Mediterranean Sea.

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