Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea)

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The scyphozoan *Pelagia noctiluca* reproduces by direct development without a benthic stage. Typically, this jellyfish is found offshore with a holoplanktonic life-cycle, vertical migration and feeding behaviours. Frequent outbreaks have been well documented on the Mediterranean shores since the 19th century; however, the offshore distribution of this species remains mostly unknown. In this study, we performed a bimonthly monitoring of *P. noctiluca* surface density, at high resolution, from a sailboat, along a 35-km coastal to offshore transect in the Ligurian Sea, between February and October 2011. During daylight, *P. noctiluca* was rarely seen. At night, offshore, *P. noctiluca* was always present, while within 5 km of the coast, *P. noctiluca* was rarely observed. *Pelagia noctiluca* aggregations were most abundant within the Northern Current of the Ligurian Sea. Our findings suggest that *P. noctiluca* outbreaks observed on Mediterranean shores may result from the transport of the permanent offshore population inshore by specific hydrodynamic conditions.

KEYWORDS: jellyfish; diel vertical migration; mauve stinger; blooms; gelatinous zooplankton; surface observations; glider

INTRODUCTION

Reports of jellyfish blooms worldwide have increased dramatically in both the scientific literature and mass media since the 1950s (Condon *et al.*, 2012). These blooms have become increasingly problematic with conferences organized to discuss their consequences worldwide (e.g. Pitt and Purcell, 2009; Mianzan *et al.*, 2012). In many cases, the abundances have become a real economic problem for local populations (reviewed in Purcell *et al.*, 2007). These increases result in a simultaneous negative impact on tourism, aquaculture and fisheries (Mills, 2001) and have been potentially attributed to climate change (Brodeur *et al.*, 1999; Purcell, 2005), eutrophication (Arai, 2001) and overfishing (Purcell and Arai, 2001; Hay, 2006; Lynam *et al.*, 2011). In the Mediterranean Sea, problems were experienced in the early 1980s and several United Nations programmes were set up to address the issues (UNEP, 1984; UNEPMA, 1991; CIESM, 2001). In the absence of background data, the study of jellyfish abundance, physiology, distribution and population dynamics are of high priority (Sabatés *et al.*, 2010).

In many cases, regular sampling of gelatinous zooplankton populations has found considerable interannual variability related to climatic factors, e.g. North

Atlantic Oscillation (Lynam *et al.*, 2004; Brodeur *et al.*, 2008; Lynam *et al.*, 2011). In the Mediterranean, it is thought that similar climatic drivers affect the occurrences of the mauve stinger *Pelagia noctiluca* (Molinero *et al.*, 2005), particularly the Atlantic surface water (Licandro *et al.*, 2010). Warm and dry conditions have been correlated with the abundance of *P. noctiluca* across the Mediterranean over a 200-year timescale (Goy *et al.*, 1989). Gelatinous zooplankton typically undergo short lifecycles and have the ability to colonize empty ecological niches rapidly (Boero *et al.*, 2008); however, these same variables also result in considerable spatial variability of populations. Although the benthic polyps drive the abundance of most scyphozoan jellyfish species in coastal waters, the holoplanktonic lifecycle of *P. noctiluca*, i.e. without a benthic polyp stage, leads to a wide distribution across ocean basins (Russell, 1970; Arai, 1997; Purcell, 2005), which is not limited to nearshore reproductive areas. Among jellyfish, *P. noctiluca* is the most abundant and the most venomous jellyfish species in the Western Mediterranean (Mariottini *et al.*, 2008). However, its distribution in this basin remains largely unknown.

Pelagia noctiluca lives offshore, migrating vertically in response to the migration pattern of their zooplankton prey (Giorgi *et al.*, 1991; Zavodnik, 1991; Malej *et al.*, 1993). This migration pattern results in medusae being reported at considerable depth by day and reaching the surface at night (Franqueville, 1971; Larson *et al.*, 1991; Mariottini *et al.*, 2008). In the Western Mediterranean, it has been suggested that *P. noctiluca* is abundant mostly in the vicinity of the Northern Current (Morand *et al.*, 1992), a permanent geostrophic current present in the Ligurian Sea; however, this hypothesis was based on irregular sampling over several years and poor data resolution. Moreover, the few available observations of *P. noctiluca* suggest that their presence in the Mediterranean follows a pluriannual cycle of ∼11−12 years, with 5−6 years presence/absence oscillations (Goy, 1984; Morand and Dallot, 1985; Goy *et al.*, 1989).

Contrasting with this cycle, *P. noctiluca* has been quasi continuously observed on the southern coasts of France since the 1990s (Bernard *et al.*, 2011). These coastal outbreaks are sporadic (Bernard *et al.*, 2011) and may originate from local patchy populations or from a single permanent offshore population (Vucetic, 1984). Mechanisms leading to these coastal outbreaks are still poorly understood, mainly because of a lack of observations and knowledge on the annual *P. noctiluca* distribution in the northwestern Mediterranean Sea.

In order to fill this gap, we monitored the abundance of *P. noctiluca* bimonthly from February to October 2011, at night on a transect from Villefranche sur Mer, France, and heading towards Calvi, on the island of Corsica, and compared the observed distributions with the hydrological characteristics of the area surveyed.

METHOD

Study site

Abundance of *P. noctiluca* was monitored in the Ligurian Sea on a ∼35-km bimonthly transect from Villefranche sur Mer (43°41′N, 7°18′E) heading towards Calvi (42°34′N, 8°45′E) (Fig. 1). This area was selected because it is well known in terms of its hydrodynamics and hydrology. The Ligurian Sea has a permanent cyclonic circulation (Millot, 1999) with an associated thermohaline front enclosing a central divergence zone. The French and Italian Rivieras to the north, and Corsica to the south, bound the Ligurian Sea. This basin is characterized by three main hydrographic zones (Prieur, 1981; Béthoux and Prieur, 1983; Prieur and Tiberti, 1985): (i) a peripheral zone (Pz) with weak and variable current; (ii) a frontal zone (Fz) characterized by a sharp horizontal change in density and a ∼ 0.4 m/s jet called the Northern Current; (iii) an offshore central zone (Cz) where the surface water density and salinity are high (∼28.9 kg/m^3 and ∼38.3‰, respectively; Fig. 1).

Monitoring strategy

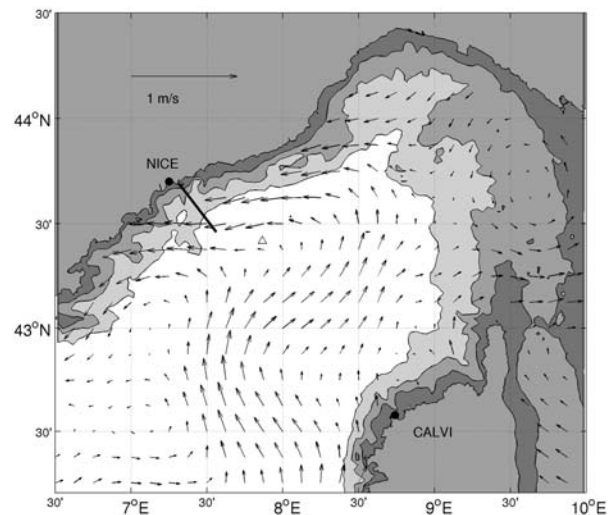The monitoring of abundance and distribution was carried out bimonthly from February 2011 to October

Fig. 1. Map of the study area showing the location of the monitored transect and the geostrophic current field from AVISO (aviso. oceanobs.com) for 22 June 2011. The background shows the 300, 1000 and 2000 m bathymetry isocontours. The triangle indicates the DYFAMED point (43°25′N, 7°52′E).

2011 (Table I), on board of the "Alchimie", an 11-m long sailboat. Each survey started in the evening around 6 p.m. and ended at ∼3 a.m. of the next day. The outward and return routes lasted 4 h each. The boat cruised on the Nice-Calvi transect at an average speed of 5 knots (maximum cruising speed: 6.5 knots), allowing good observations of the sea surface. Timing and location of our monitoring were constant for all our surveys (except two) to limit the variables of our study, to facilitate comparisons and guarantee the statistical significance of our findings.

Surveys were conducted only under very good sea conditions (wave height < 0.20 m). This criterion was been selected because, during other studies and preliminary personal observations, we noted that *P. noctiluca* individuals tend to stay deeper in the water when the wave height exceeds 0.20 m, preventing their detection from the boat and biasing the estimation of their abundance. To plan the surveys, forecasts of wave heights from PREVIMER system website (Lecornu and De Roeck, 2009) and real-time measurements from the Cote d'Azur meteorological buoy were used (Rolland and Blouch, 2002). Wind and sea conditions during surveys were always low (wave height < 0.20 m), with the exception of the return leg on 25 February and 15 June (Table I).

Observations were conducted from the side of the deck of the sailboat, at a height of ∼2 m above the sea surface. At night, a floodlight mounted on deck illuminated an area of 10–12 m², for a depth of ∼2 m. The jellyfish abundance was estimated by eye count as the number of adult individuals observed in the illuminated area and reported as an index from 0 to 2: 0 for zero individuals, 1 for 1–10 individuals and 2 for more than 10 individuals. These three categories of abundance were considered sufficient to describe realistically the offshore distribution of *P. noctiluca*. We used abundance classes of the same order of magnitude as Doyle *et al.* (Doyle *et al.*, 2008), but the maximum observed never exceeded 30–40 individuals per unit of surface, so we considered that further categories were not necessary. Two observers were on the deck of the boat and at least one constantly observed the sea surface along the outward and the return legs of the surveys. Only adult *P. noctiluca* were considered for abundance estimations, because only adults were detectable.

Global positioning system (GPS) coordinates were noted when the density of *P. noctiluca* changed or at least every 10 min. Sunset, astronomical twilight, civil twilight, sunrise, astronomical dawn, civil dawn, moonrise, moon to the meridian and moonset local time were noted for every cruise.

We defined three periods during each day depending on the sun illumination: "day" corresponded to the time from astronomical dawn until the sunset, "dusk" to the time between the sunset and astronomical twilight and "night" to the time between astronomical twilight and the astronomical dawn.

Table I: Summary of the surveys

Survey date	Departure	Astronomical twilight	Arrival	Transect distance (km)	Instruments[a]	Date of ADCP records	Date of glider transect	Waves height (m)	Moon[b]
25–26 February	06:50 p.m.	07:49 p.m.	03:00 a.m.	32.4	ADCP, Gd, M	25 February	24–26 February	0.1–2	nv
9–10 March	06:40 p.m.	08:04 p.m.	03:00 a.m.	28.2	Gd, M		6–9 March	0.1–0.15	nv
31 March–1 April	06:15 p.m.	08:35 p.m.	03:15 a.m.	22.7	M			0.05	nv
9–10 April	06:04 p.m.	09:49 p.m.	03:30 a.m.	28.2	M			0.05–0.15	nv
28–29 April	05:45 p.m.	10:21 p.m.	03:00 a.m.	31.8	ADCP, Gd, M	28 April	25–28 April	0.05–0.1	nv
18–19 May	05:40 p.m.	10:58 p.m.	03:00 a.m.	34.9	ADCP, M	18 May		0.1	v
25–26 May	06:45 p.m.	11:10 p.m.	03:00 a.m.	30.3	M			0.1–0.15	nv
15–16 June	06:25 p.m.	11:37 p.m.	03:40 a.m.	29.3	ADCP, Gd, M	15 June	13–14 June	0.15–0.35	v
9–10 July[c]	11:00 a.m.	11:31 p.m.	18:15 p.m.	38.4	ADCP, M	9 July		0.15–0.20	v[d]
2–3 August	08:15 p.m.	10:53 p.m.	04:15 a.m.	25.0	M			0.05	nv
24–25 September	06:30 p.m.	09:02 p.m.	03:30 a.m.	28.5	Gd, M		23–25 September	0.1	nv
2 October[e]	02:05 a.m.	–	06:30 a.m.	26.8	ADCP, Gd, M	3 October	30 September–2 October	0.1–0.15	nv
11–12 October	06:30 p.m.	08:30 p.m.	03:30 a.m.	28.5	Gd, M		10–12 October	0.1	v

[a]Instruments available to determine the position of the hydrological zone (ADCP, Acoustic Doppler Current Profiler; Gd, glider; M, Mercator model outputs); the one selected for the analysis is in bold.
[b]Presence/visibility of the moon (v, visible; nv, not visible). In case of moon absent or covered by clouds we have recorded moon "not visible" (nv).
[c]Nocturnal monitoring on board of the Téthys-II starting 5 km away from the coastline.
[d]Visible on the outward leg, but not on the return leg.
[e]Unusual departure and return times.

Exceptions to the regular protocol occurred on 9 July and 2 October 2011. On 2 October, the survey started at 2 a.m. and ended at 6:30 a.m. during sunrise. On 9 July, we combined the nocturnal monitoring with another scientific campaign, in the same area of the Ligurian Sea, but requiring a larger boat. This survey was carried out starting 25 km away from the shoreline at 11 p.m., going further offshore than usual (38.4 km) and ending 5 km from the coast at 4 a.m., on board Téthys-II, a 24.9-m long oceanographic vessel cruising at 10 knots (observational area $\sim$20 m^2). The use of powerful lighting and good sea conditions allowed accurate monitoring at this cruising speed.

Identification of the hydrological zones

Because the vessel was not equipped for physical and hydrographical measurements, data from parallel projects/campaigns or models of the Ligurian Sea were used to identify the hydrological zones crossed during the cruises.

Acoustic Doppler Current Profiler (ADCP) current velocity and direction were obtained from the INSU SAVED database (saved.dt.insu.cnrs.fr), for the BOUSSOLE cruises (Antoine *et al.*, 2008) simultaneous to our campaigns (Table I), along a transect between Nice and the DYFAMED station, very close to our transect (Fig. 1).

Physical properties of the water were obtained from gliders cruising monthly along a similar transect (Fig. 1), as part of the MOOSE project (Niewiadomska *et al.*, 2008). Conductivity, temperature and depth data were used to characterize the density and slope of isopycnals and identify the location of the Northern Current.

Finally, the location of the Northern Current was also identified using ocean circulation model outputs from the Mercator forecasting system (Bahurel, 2006). The MERCATOR system is based on three components: the ocean model, the surface forcing fields and the observations (remotely sensed sea surface temperature and altimetry; *in situ* temperature and salinity profiles). These components are routinely integrated through an assimilation method, the objective being to provide the best possible description of the real ocean (Brasseur *et al.*, 2005).

A transect across the Northern Current would be segmented in three zones: a Pz (low current velocity, <0.2 m/s and weak 28.9 isopycnal slope); an Fz (high current velocity, ≥0.2 m/s and significant 28.9 isopycnal slope) and a Cz (low current velocity, <0.2 m/s and weak 28.9 isopycnal slope) (Prieur, 1981; Béthoux and Prieur, 1983; Prieur and Tiberti, 1985; Boucher *et al.*, 1987; Niewiadomska *et al.*, 2008; Stemmann *et al.*,

2008). The Cz was never crossed during this survey and therefore was not considered during analysis.

The hydrological zones were identified using the available data on (i) current velocity estimations from ADCP, (ii) slope of the 28.9 isopycnal from gliders density section and (iii) the Mercator surface current models outputs. Current velocity from ADCP at 28 m depth is considered as the most reliable parameter, followed by the slope of the 28.9 isopycnal. Mercator velocity outputs were used when none of the previous information was available. Table I summarizes the available instruments and the one selected to determine the hydrological zones for each survey.

We fixed the coastal zone (Co) at 5 km off Villefranche sur Mer, because of the lack of hydrological data in this area, whatever the source of data taken into account.

To map the along-track distribution of *P. noctiluca*, the distance from Villefranche sur Mer harbour was computed for each GPS position. Along track abundance data were binned in 5 km bins. For each bin, frequencies of the abundance indices (0, 0 ind./10 m^2; 1, ≤10 ind./10 m^2; 2, >10 ind./10 m^2) were computed. Frequencies of the abundance indices were also computed for each survey and each zone (Co, Pz and Fz).

RESULTS

Adult *P. noctiluca* were observed on all 13 surveys conducted between 25 February and 11 October in the Ligurian Sea. Abundances of *P. noctiluca* varied as a function of the distance from the coast, and with the time of day (Figs 2 and 3).

Co, Pz and Fz positions

Positions of the three hydrological zones were identified using current velocities from ADCP (6 of 13 surveys, Table I), automated glider density sections (three surveys) and Mercator surface current model alone for the remaining surveys, when no *in situ* data were available (Table I).

The Mercator currents were compared using ADCP and glider data for all available survey dates and agreed in seven of nine cases (e.g. Fig. 4B and D), except on 18 May and 2 October. In all the surveys, the Fz was always entered but never totally crossed, and the Cz of the Ligurian basin has never been reached. Considering our data set, the boundary between the peripheral region and the Fz of the Northern Current displayed a strong spatial oscillation from 5 km (15 June) to 19.4 km (2 August) offshore, with an average of 11.2 km.
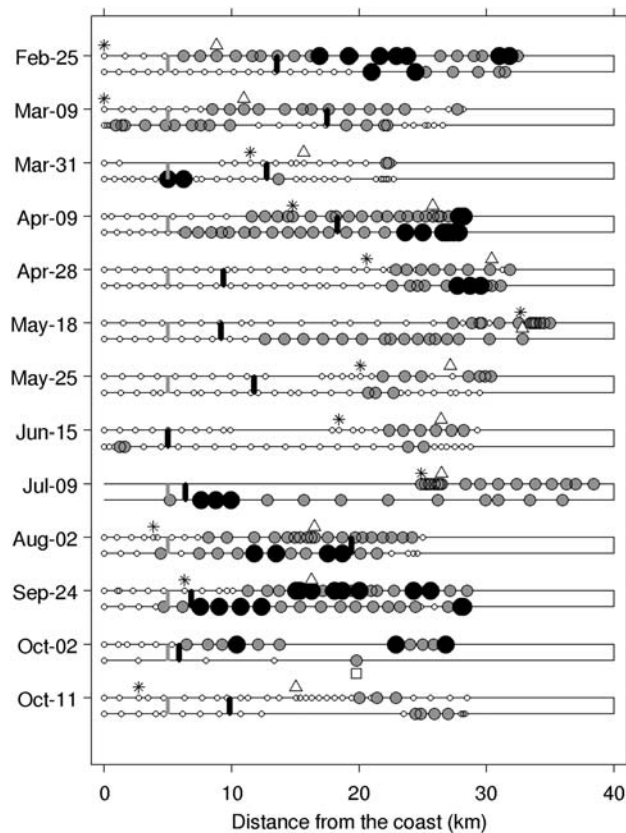
Fig. 2. *Pelagia noctiluca* abundance for the 13 surveys from 25 February to 2 October 2011 as a function of distance to Villefranche sur Mer harbour along outward and return tracks. Jellyfish abundance is coded as the size and colour of the dot (white, 0; grey, ≤ 10 ind./$10m^2$; black, > 10 ind./$10m^2$) along forward (upper line) and return (lower line) tracks of the transect. The location at the time of sunset (star), astronomical twilight (triangle) and astronomical dawn (square) are plotted on the track. The Co is fixed at 5 km off Villefranche sur Mer as a grey vertical line. The limit between Pz and Fz is indicated as a black vertical line.

On 9 July, 24 September and 2 October, the current, i.e. the near edge of Fz, was very close to the coast (Fig. 2), shrinking Pz to the point that it could not be detected, as on the 15th June survey, when the Fz reached the coastal limit (Fig. 2).

Average day–night *P. noctiluca* distribution

All surveys left Villefranche sur Mer harbour before sunset (except 9 July and 2 October) thereby observing the transition between both day- and night-time distributions of *P. noctiluca*.

During the day, *P. noctiluca* was encountered only during one survey, on 9 April, between 10 and 15 km offshore (Figs 2 and 3A). Additionally, on 2 October, we were able to span astronomical dawn and noted an absence of *P. noctiluca* immediately after this time (Fig. 2).

Typically, *P. noctiluca* started to appear in the surface layer after twilight (Figs 2 and 3B) and mostly away from the coast. During the night, higher densities were more frequent for all distance bins

(Fig. 3C). During dusk and night, abundances increased to seaward. On average, largest abundances were observed during the night between 30 and 35 km offshore (Fig. 3C).

Pelagia noctiluca was only observed within 5 km from the coast during the night-time on 9 and 31 March. For the whole transect, differences of abundances between day, night and dusk were significant (χ^2 test, $P < 0.001$), with higher abundances when the moon was not visible at night (Table I; two-sample t-test, $P = 0.015$).

In some cases, the jellyfish abundances detected on the outward and the return tracks were different and resulted from changing sea conditions, in addition to the effect of light already noted. For example, on 25 February, sea conditions deteriorated rapidly during the monitoring, waves increased from a height of $0.1–2$ m, in less than an hour, at ~ 20 km offshore, rendering the detection of *P. noctiluca* difficult on the return track (Fig. 2). On other occasions, small changes in the sea state were noted, but their effect was less clear. On 9 July, because of a parallel experiment, the vessel was stopped
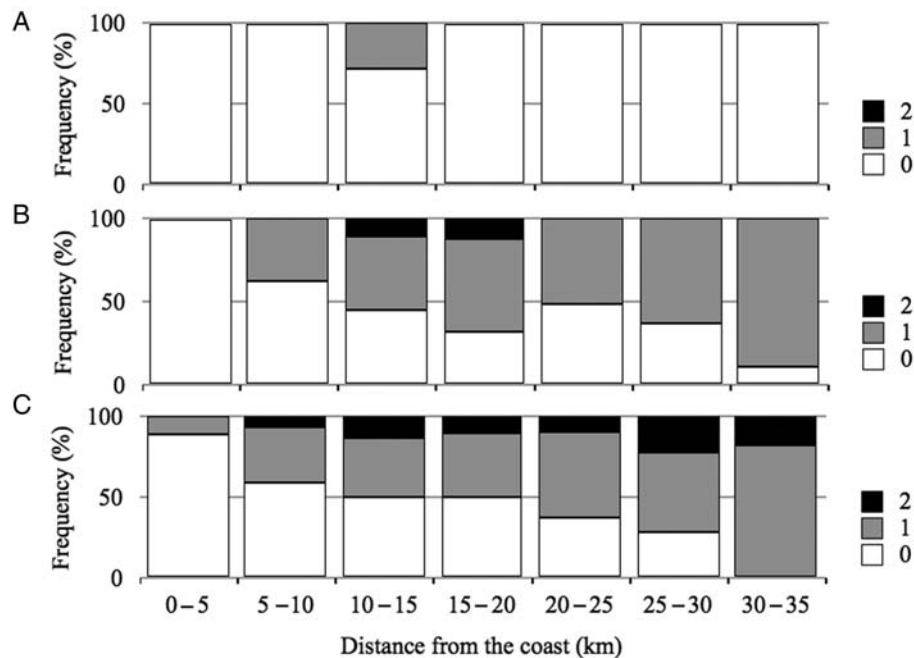
Fig. 3. Frequency of the abundance index for all surveys as a function of the distance from the coast: (**A**) day (total number of observations: 96), (**B**) dusk (total number of observations: 155), (**C**) night (total number of observations: 414). Abundance indices: 0, 0 ind./10 m^2; 1, $\leq$10 ind./10 m^2; 2, >10 ind./10 m^2.

between dusk and sunset thus covering a shorter distance during this period than for the other surveys (Fig. 2).

Pelagia noctiluca along-track distribution versus hydrological zones

In the majority of surveys (8 of 13 cases, Fig. 5), *P. noctiluca* was absent at the coast and increased in abundance to seaward (e.g. 28 April; Fig. 4A). In two cases, 9 and 31 March (Fig. 5), we observed a homogeneous distribution of the jellyfish throughout the transect (e.g. 9 March; Fig. 4C and D). In addition to these general trends, there were three notable variations. On 15 June, *P. noctiluca* abundance was very low in Co and Fz, but totally absent in Pz. On 2 August, jellyfish were absent in Co but considerably more abundant in Pz than in Fz. Finally, on 9 July, abundance was recorded in both Pz and Fz, but Co was not explored therefore preventing the classification of this part of the transect. Overall, *P. noctiluca* were most abundant in the Fz in most cases (Fig. 5) with significant differences between the abundances in the three zones (χ^2 test, $P < 0.001$).

DISCUSSION

Adult *P. noctiluca* were present offshore in the Ligurian Basin throughout the 9-month period surveyed in 2011.

However, spatially and temporally their distribution varied with the time of day, distance from the coast and the location of the Northern Current.

Impact of light on *P. noctiluca* vertical distribution

Our observations showed that, in the open sea, *P. noctiluca* is visible at the surface layer after dark. This confirms the few previous observations, suggesting that *P. noctiluca* perform daily vertical migrations from considerable depth (Pérès, 1958; Franqueville, 1971), reaching the surface at night (Morand *et al.*, 1992). Our surveys confirm this behaviour over 9 months for *P. noctiluca*. These migrations can be attributed to feeding (following the zooplankton community; Lampert, 1989) or survival strategies (avoiding predator during day; Harrison, 1984; Purcell and Arai, 2001). *Pelagia noctiluca* have been identified as a prey of a number of Mediterranean apex predators, including tuna, swordfish, sunfish and loggerhead turtles (Cardona *et al.*, 2012); however, depth is unlikely to provide a refuge from these deep-diving predators (e.g. Teo *et al.*, 2007; Sims *et al.*, 2009). Most likely the migration of *P. noctiluca* is to maximize the feeding duration on planktonic crustacean prey (Giorgi *et al.*, 1991). Diel vertical migration (DVM) is a common trait within many zooplankton species to avoid predation by larger visual predatory organisms while utilizing the prey resources at
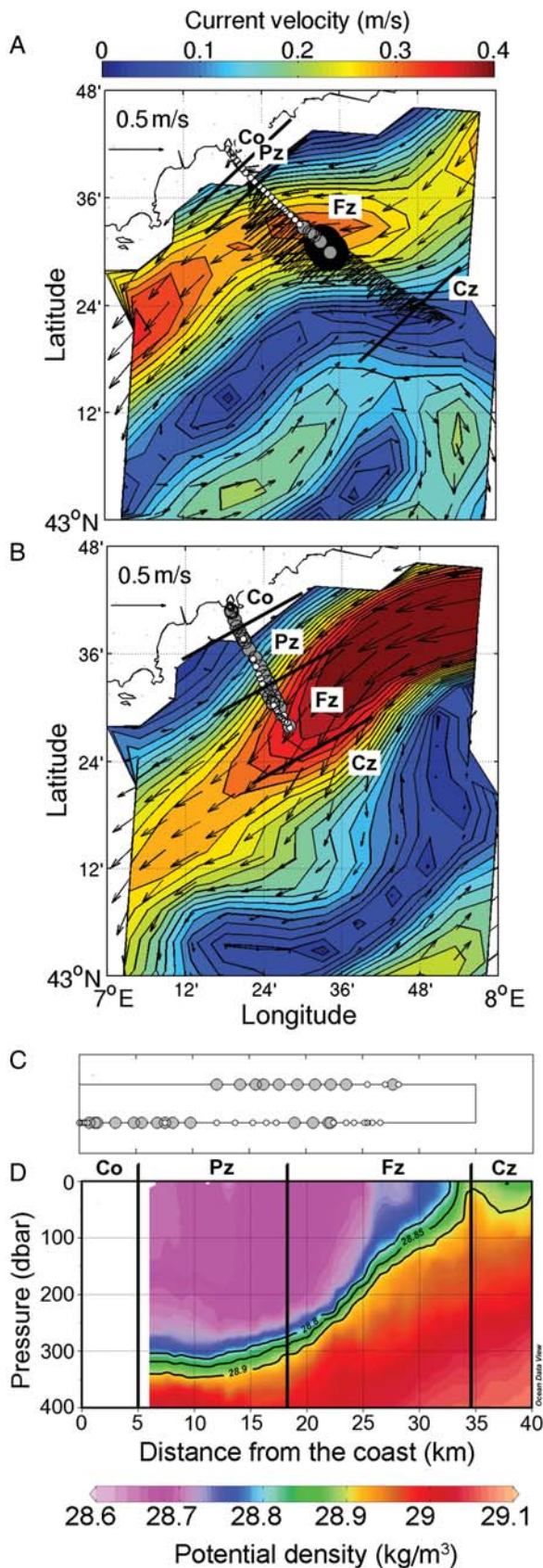
the surface (reviewed by Hays, 2003), but it is less common in scyphozoan jellyfish which are frequently observed at the surface by day, e.g. from aerial surveys (Graham *et al.*, 2003; Houghton *et al.*, 2006) or ship observations (Doyle *et al.*, 2007; Bastian *et al.*, 2011). The tactile predation by cruising predators, such as jellyfish, removes the need for visual predation. Indeed, other deep water species such as *Periphylla periphylla* have also shown regular DVM (Kaartvedt *et al.*, 2011).

Cohen and Forward (Cohen and Forward, 2009) reviewed the factors controlling causes of DVM and noted that some gelatinous species followed constant isolumes. In our study, *P. noctiluca* were less abundant when at least one quarter of the moon rose on the horizon. This type of situation was only detected during 3 and a half of the 13 surveys (Table I), but nevertheless *P. noctiluca* were 50% more likely to be seen when there was no moon visible. Moonlight has also been demonstrated to negatively affect the vertical migration of other planktonic organisms (Tarling *et al.*, 1999; Anokhina, 2006). This apparent behavioural change as a response to increasing light has also been seen in laboratory studies (Axiak, 1984; Schuyler and Sullivan, 1997) and would further support the isolume hypothesis; however, the mechanism of light reception has yet to be identified in *P. noctiluca*. Salps (*Salpa* sp.) have also been observed to respond to a decrease in downwelling irradiance, ascending over 100 m through the water column following a constant isolume as a result of a turbid water influx (Frank and Widder, 2002). Potentially, *P. noctiluca* may also follow similar isolumes, explaining their appearance at the surface around twilight and disappearance at dawn on 2 October, but equally chemical stimuli emitted by prey could also be a significant driver. Future parallel studies of the predator and prey fields could elucidate this further.

In other areas, *P. noctiluca* has been recorded offshore at the sea surface also during daytime, e.g. in western Irish offshore waters (Doyle *et al.*, 2008) and in the Adriatic Sea (Zavodnik, 1987). Such findings suggest that other factors, in addition to light and prey/predator

Fig. 4. Jellyfish abundances (circles: white, 0; grey, ≤10 ind./10 m²; black, >10 ind./10 m²) are represented along outward and return routes of the transect. We fixed the Co at 5 km off Villefranche sur Mer. Only nocturnal observations are considered, i.e. dusk and night data. (**A**) Example of *P. noctiluca* increasing distribution offshore, observed on 28 April 2011. The Pz and Fz have been identified using ADCP data (thin solid lines) overlaid on surface currents from Mercator. (**B**–**D**) Example of *P. noctiluca* ubiquitous distribution, observed on 9 March 2011. Mercator surface currents are shown in (B) for comparison with the hydrological zones identified using the slope of the 28.9 isopycnal (bold black line) from the glider density section (D).
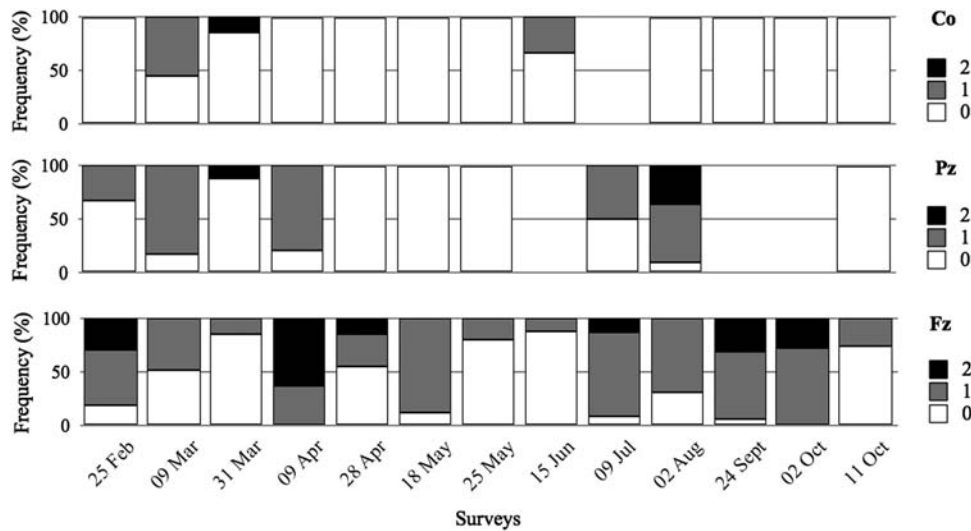
Fig. 5. Frequency of *P. noctiluca* abundance index (0, 0 ind./10 m^2; 1, $\leq$10 ind./10 m^2; 2, >10 ind./10 m^2) observed per Co, Pz and Fz, and per survey. Only nocturnal data are considered, i.e. since astronomical dusk.

relationships, affect the distribution and the migration of this scyphomedusa in the water column. The reproductive behaviour could be one of these factors. Ephyra and young stages of *P. noctiluca* are mostly observed in the sea surface layers (Morand *et al.*, 1992), but they are thought to be unable to make large migrations (Hecq *et al.*, 2009). It may be plausible that adults migrate in the superficial layers of the water column to release gametes, providing the new larvae with a suitable environment for their development.

Large-scale distribution

Adult *P. noctiluca* were observed on every survey throughout this study, with no obvious seasonal cycle in abundance. This confirms the hypothesis of a permanent offshore population in the Ligurian Sea and supports the view of Morand *et al.* (Fig. 1 in Morand *et al.*, 1992) that there is a permanent jellyfish belt in the Ligurian Sea. However, long-term studies have found interannual oscillations in the abundance of *P. noctiluca* in the Mediterranean and some years when the species is absent (Goy *et al.*, 1989; Kogovšek *et al.*, 2010). This apparent disparity is likely to be the result of the source of the historical data. The long-term time-series come predominantly from shore-based or near-shore observations, which may not record the presence of *P. noctiluca* if it is only present offshore. Certainly, the population within the Adriatic Sea is not self-sustaining and the population is sourced from the Mediterranean (Kogovšek *et al.*, 2010), with no genetic differences between the Adriatic and Mediterranean individuals

(Stopar *et al.*, 2010). Whether the *P. noctiluca* population studied here is permanently entrained in the cyclonic circulation observed in the Ligurian Sea (Millot, 1999) or part of a Mediterranean-wide population as suggested by Licandro *et al.* (Licandro *et al.*, 2010) is not proven.

The lifecycle of *P. noctiluca* has been suggested to be between 9 months (Kogovšek *et al.*, 2010) and 1 year (Franqueville, 1971; Morand *et al.*, 1992). Licandro *et al.* (Licandro *et al.*, 2010) suggested that *P. noctiluca* abundance peaks near Villefranche sur Mer in summer, while ephyrae observed in the water column peaked in April and June (Morand *et al.*, 1992), making a continuous annual cycle feasible; however, further research is required to establish where the various life stages occur. With a strong NE-SW Northern Current, it is unlikely that the lifecycle is completed entirely in the Ligurian Sea, but across different regions of the Western Mediterranean basin. The population offshore near Villefranche sur Mer will be fed by source populations located upstream in the current, e.g. in the East Ligurian Sea, Western Corsica Current and Tyrrhenian Sea, and will feed populations downstream along the path of the Northern Current (Licandro *et al.*, 2010). To extend this study, particle tracking models could be used for predicting the path of jellyfish particles, including a DVM of ∼500 m. A particle tracking model developed by Qiu *et al.* (Qiu *et al.*, 2010) for the region showed a small proportion of particles being retained in the Ligurian Sea over a 90-day particle life. Such models should significantly affect our understanding of *P. noctiluca* distribution and the capacity for stranding along the Mediterranean shoreline.

Coastal-open sea distribution with respect to the Fz

Excluding particular situations and the light effect discussed above, the density of *P. noctiluca* often differed between the outward and the return legs of the surveys. This may be due to the typical patchiness of zooplankton in general (Omori and Hamner, 1982) and jellyfish in particular (Graham *et al.*, 2001; Magome *et al.*, 2007). For the same transect, Molinero *et al.* (Molinero *et al.*, 2008) found across shelf patch size ranging from 1 km (euphausiids) to 10 km (salps). Another factor that could presumably affect the presence of *P. noctiluca* is the wave height, with two of our surveys potentially supporting this assertion. While the wind did not change significantly during any of the surveys (except 25 February), the sea conditions worsened in two cases, on 25 February and 15 June (Fig. 2), with an apparently concomitant decrease in *P. noctiluca* detectable. The presence of *P. noctiluca* may be disturbed by the sea state, disappearing from the surface when the sea surface is not completely smooth, as is the case with *Rhizostoma octopus*, which responds to vibrations by diving (Russell, 1970). Zavodnik (Zavodnik, 1987) also noted that *P. noctiluca* individuals rarely swam at the surface to avoid wave damage. This presumed sensitivity to the conditions could be an interesting aspect to explore more in detail.

In terms of average abundances, *P. noctiluca* were more abundant in the Fz than in the Co and Pz (Fig. 5). A seaward increase in zooplankton abundance was also observed in the Ligurian Sea for *P. noctiluca* by Morand *et al.* (Morand *et al.*, 1992) and for several copepod species (Boucher, 1984; Molinero *et al.*, 2008). While *P. noctiluca* may increase with distance from the shore, we would expect a lower abundance in the Cz of the Ligurian Sea, resulting from declining current intensity (Fig. 1 in Morand *et al.*, 1992). Whether this higher abundance associated with the Fz is a result of the biological prey field or caused by physical aggregating factors requires further study. Biologically, this Fz is a favourable feeding environment, indeed upwelling of nutrients by divergent circulation cells occurs parallel to the front (Prieur, 1979; Boucher, 1984; Stemmann *et al.*, 2008). The surface nutrient enrichment fuels primary (Béthoux and Prieur, 1983) and secondary production (Boucher, 1984; Boucher *et al.*, 1987; Ibanez and Boucher, 1987; McGehee *et al.*, 2004; Molinero *et al.*, 2008); therefore, the whole Northern Current path is a favourable region for *P. noctiluca* growth and maintenance (Morand *et al.*, 1992; Sabatés *et al.*, 2010). Physically, vertical circulation coupled with the Fz of the Northern Current is characterized by divergent and convergent flows (Boucher *et al.*, 1987; Stemmann *et al.*,

2008). These cross-frontal flows are weak; however, they may have an influence on migrating and swimming organisms (Franks, 1992). A model developed by Franks (Franks, 1992) showed that in a convergent flow an increase in the concentration of vertical migrators is found at the surface and near the convergence for strong swimmers (maximal speeds of ca. 2–20 mm/s) during the upward phase of the migration, since the surface forms a barrier to migration. *P. noctiluca* are strong swimmers *sensu* Franks (Franks, 1992), as they migrate at ∼33 mm/s (i.e. 2 m/min; Arai, 1997); therefore, convergence zones would aggregate both crustacean prey and jellyfish predators in this region. Unfortunately with our *in situ* observations, the convergent cells cannot be easily identified, as they are a three-dimensional phenomenon constantly evolving with time.

Pelagia noctiluca was present only episodically in the Co (3 of 13 surveys, Fig. 5), while it was always present in the frontal one. Abundance onshore is also known to be erratic (Bernard *et al.*, 1988; Bernard *et al.*, 2011) and may be associated with strong wind effects driving individuals ashore. Frequently observed in poor condition close to shore (Zavodnik, 1987; Hecq *et al.*, 2009), it is unknown whether these individuals are damaged during transport or transported as a result of damage or starvation. In any case, there is an apparent uncoupling between offshore and onshore abundance. The hypothesis of a permanent population of *P. noctiluca* offshore with sporadic transport to the coast is therefore plausible. Episodic transport could be linked to coastal intrusions of the current. In this regard, modelling studies coupling physical transport and coastal jellyfish outbreak monitoring for the Ligurian basin should be pursued. A better understanding of the population dynamics of *P. noctiluca* and conditions leading to its major outbreaks close to shore may allow anticipation and the taking of precautions prior to their arrival, perhaps limiting potential damage to the tourism industry.

CONCLUSIONS

We have shown the importance of night-time observations to study the distribution of vertically migrating *P. noctiluca*. *Pelagia noctiluca* were found throughout the year, but rarely in close proximity to the coast. Surface occurrence of this species in the Ligurian Sea was driven by the physical conditions of the Northern Current and may be linked to the presence of the moon.

Future work should extend the surveys into the Cz of the Ligurian Basin, possibly utilizing autonomous vehicles, and explore the coastal region to determine the physical forces affecting the occurrence of *P. noctiluca*.

Finally, an understanding of the vertical distribution and the association of medusae with the prey field will complement the observed surface distributions.

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