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Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean

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Jellyfish are important predators of fish eggs and larvae and predation is believed to be the main factor determining fish recruitment. The diet of different life stages of *Pelagia noctiluca* and their potential predation impact on ichthyoplankton were investigated in the NW Mediterranean Sea. In June, the spatial distribution of jellyfish and fish larvae, particularly those of anchovy, overlapped in the study area. Gut content analyses showed relatively high abundance of ichthyoplankton in large medusae, while siphonophores were the most numerous prey of ephyrae. Gut contents, digestion times (DT), and prey and predator abundances were used to estimate predation effects (% of standing stock consumed time^{-1}) of *P. noctiluca*. Medusae consumed 0.1–0.9% h^{-1} of the anchovy larvae, while ephyrae consumed 1.5–2.7% h^{-1} of all fish larvae and 1.5–10.4% h^{-1} of anchovy larvae. We estimate that medusae and ephyrae consumed 0.02–3.2% h^{-1} and 0.4–7.1% h^{-1} of fish eggs, respectively. *P. noctiluca* can reach extremely high numbers and in a bloom situation it can be an important predator of fish larvae, in particular anchovy. Hence it may play an important role in the planktonic food web with a possible impact on anchovy populations.

KEYWORDS: jellyfish; ichthyoplankton; diet; predation; competition

INTRODUCTION

Jellyfish are considered harmful to fish populations due to competition for food and by direct predation on fish eggs and larvae (Möller, 1980; Purcell and Sturdevant, 2001; Brodeur *et al.*, 2008). Predation by pelagic cnidarians (mainly hydrozoans and scyphozoans) and ctenophores on ichthyoplankton has been reported in many areas of the world (Purcell *et al.*, 1999; Purcell and Arai, 2001; Sabatés *et al.*, 2010). These interactions are of particular interest due to the potential effects that these organisms could have on fish populations, especially those of commercial value (Graham *et al.*, 2014).

Predation on early life stages of fish is believed to be the main factor determining fish recruitment (Bailey and Houde, 1989), and several species of fish larvae have been affected by predation by different species of jellyfish. Herring larvae were shown to be heavily predated by *Aurelia aurita* and *Aequorea victoria* in Kiel Bight and in waters of British Columbia, respectively (Möller, 1984; Purcell and Grover, 1990). *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* also were shown to be important predators of bay anchovy, *Anchoa mitchilli*, eggs and larvae in Chesapeake Bay (Purcell *et al*., 1994). Feeding of jellyfish, their diet composition and predation on ichthyoplankton have been studied around the world, but only a few studies calculate the magnitude of this predation and the potential competition with fishes for food (Purcell and Grover, 1990; Purcell and Sturdevant, 2001; Brodeur *et al*., 2008; Sabatés *et al*., 2010; Purcell *et al*., 2014).

Pelagia noctiluca (Forsskål, 1775) is recognized as one of the most abundant and widespread jellyfish species in the Mediterranean (reviewed in Canepa *et al*., 2014), and it has had massive outbreaks in recent years (Gili and Pagés, 2005; Daly Yahia *et al*., 2010; Kogovšek *et al*., 2010; Bernard *et al*., 2011). *Pelagia noctiluca* is deleterious to human activities, especially tourism and fisheries in the Mediterranean Sea (Canepa *et al*., 2014) and causes important economic damage to aquaculture in northern Europe (Doyle *et al*., 2008; Purcell *et al*., 2013). Although it is an oceanic species, it can be found in coastal areas (Goy *et al*., 1989; Doyle *et al*., 2008; Licandro *et al*., 2010) at densities that can even exceed 500 medusae m^{-3} (Zavodnik, 1987). This jellyfish species can be abundant on the Catalan coast (NW Mediterranean), mainly during spring and summer (Gili *et al*., 1987; Benedetti-Cecchi *et al*., 2015), over the shelf-slope region where high concentrations of zooplankton occur (Sabatés *et al*., 2004). *Pelagia noctiluca* performs diel vertical migration, staying at the surface at night and in deep water, below 300 m, during the day (Franqueville, 1971; Ferraris *et al*., 2012). This vertical distribution pattern coincides with the migration of zooplankton, their main prey (Malej, 1989; Rottini Sandrini and Avian, 1989).

Pelagia noctiluca has been described as an opportunistic predator that feeds on a wide variety of prey (Malej, 1989; Rottini Sandrini and Avian, 1989; Rosa *et al*., 2013) including ichthyoplankton (Sabatés *et al*., 2010; Purcell *et al*., 2014). It can also be a competitor of fish larvae and zooplanktivorous fish, due to its consumption of zooplankton (Purcell *et al*., 2014). In the NW Mediterranean, copepods were the most numerous prey of *P. noctiluca* ephyrae (Sabatés *et al*., 2010) and also the main diet component of different species of fish larvae, including the European anchovy, *Engraulis encrasicolus* and sardine, *Sardina pilchardus* (Sabatés and Saiz, 2000; Morote *et al*., 2010; Costalago *et al*., 2012).

The spring-summer period in the NW Mediterranean is characterized by high ichthyoplankton diversity. Most coastal fish species (e.g. from Sparidae, Mullidae, Serranidae and Carangidae families), as well as small pelagics, such as anchovy and round sardinella, *Sardinella aurita*, spawn during that period. Eggs and larvae of these species are located in the surface waters above the thermocline (Olivar and Sabatés, 1997) and co-occur there with *P. noctiluca* during the night (Sabatés *et al.* 2010). Small pelagic fishes are widespread and support important fisheries globally. They are essential elements of marine ecosystems due to their significant biomass at intermediate levels in the pelagic food web, playing important roles in connecting the lower and upper trophic levels (e.g. Bakun, 1996; Cury *et al*., 2000). In the NW Mediterranean, the small pelagic anchovy and sardine are the most important species in terms of both biomass and commercial interest (Palomera *et al*., 2007). Because fisheries along the Catalan coast and many Mediterranean countries depend economically on small pelagic fish, it is necessary to understand jellyfish trophic interactions and their potential effects in the pelagic food web.

In this context, the objectives of this study were (1) to assess the possible spatial overlap between *P. noctiluca* (ephyrae and medusae) and fish larvae along the Catalan coast, (2) to analyse the natural diet and feeding selectivity of *P. noctiluca* and (3) to estimate the *in situ* potential predation impact of *P. noctiluca* on ichthyoplankton communities.

METHOD

Field sampling

Sampling of *P. noctiluca*, medusae and ephyrae, and their zooplankton prey was conducted along the Catalan coast (NW Mediterranean) in summer 2011 (17 June–4 July) on board the RV “García del Cid”. To determine the spatial distribution and abundance of *P. noctiluca* and zooplankton, 81 stations were sampled on 17 transects perpendicular to the shoreline from near the coast to the slope. Stations on each transect were placed 7.5 nautical miles apart and the distance between transects was 10 nautical miles. Vertical profiles of the basic hydrographic parameters (temperature, salinity and fluorescence) were obtained by means of CTD casts equipped with a fluorometer.

Pelagia noctiluca ephyrae and zooplankton were sampled at each station by oblique tows from a maximum depth of 200 m to the surface using a bongo net with of 60 cm diameter opening and a mesh size of 300 µm. Samples were collected continuously during the cruise regardless of the time of the day. The volume of water filtered was estimated by means of a flowmeter placed in the centre of the net mouth. Zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

Abundances of adult medusae, which were near the surface mainly at night, were recorded through visual observations during net sampling stations and during transit between stations from the ship's deck. During the night, a light (ADIR, 10 000 000 cd) was used to illuminate an observation area of 10 m^2. The ship's speed during net sampling was 2 knots and in transit it was around 10 knots. A total of 17.3 h of observations were made over 19 days, averaging 54.5 min per day. The jellyfish abundance was estimated by visual counts of the numbers of jellyfish observed in the illuminated area. Three abundance categories were established based on the Medusa Project sighting protocol: $<$1 medusa 10 m^{-2}, $>$1 medusa10 m^{-2}, $>$10 medusa 10 m^{-2} (Canepa *et al.* 2014).

Pelagia noctiluca medusae (30–75 mm) for gut content analyses were collected at eight sampling stations where they were numerous (see Fig. 1). Specimens were individually collected from the vessel's deck during the night using a long-handled dip net. Immediately after collection, medusae were rinsed with filtered seawater to remove any attached zooplankton and preserved individually with 5% buffered formalin solution. Sampling of ephyrae (2–9 mm) for stomach content analyses was by bongo net during day and night and samples were preserved as described above (Fig. 1). In the laboratory, those ephyrae were removed from the samples and their gut contents analysed. Additionally, ephyrae were also collected at night by drifting a neuston net (1.5 m^2 mouth, 1 mm mesh) at the surface for short periods of time (10 min) and dipping them individually from the surface using a long-handled dip net. These ephyrae were preserved individually in 3 mL centrifuge vials with formalin.

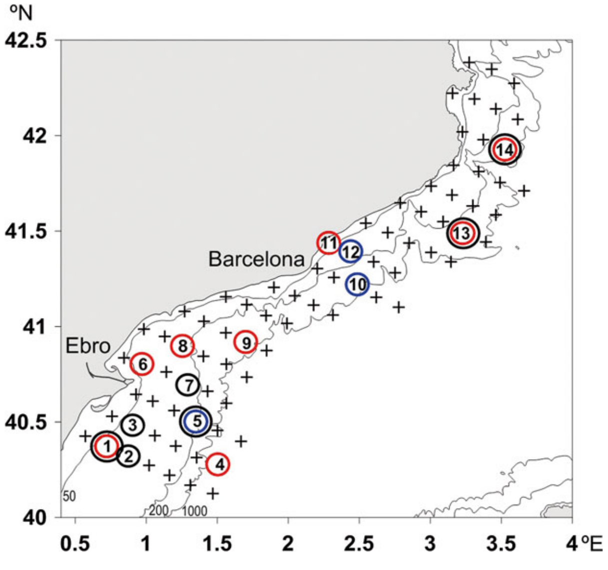

Fig. 1. Stations where medusae of *Pelagia noctiluca* (red circles) and ephyrae (collected by bongo net: black circles; dipped or collected drifting a neuston net: blue circles) were collected for gut content analyses during the oceanographic cruise conducted in the northwest Mediterranean Sea during 17 June – 4 July 2011.

Laboratory analysis

Zooplankton was sorted for all the stations and quantified by major taxonomic groups. Different aliquots were taken from the bongo net samples to obtain at least 100 individuals of each group. All jellyfish ephyrae and fish larvae were sorted from the samples and identified to species level. Only anchovy eggs could be identified to species, due to their oval shape. The numbers of zooplankton, *P. noctiluca* and ichthyoplankton at each station were standardized to number 10 m^{-2}.

A total of 91 *P. noctiluca* medusae and 1198 ephyrae were analysed to determine their gut contents from different stations (Fig. 1). Prior to dissection, the maximum diameter of each specimen was measured with a ruler (medusae) or with an ocular micrometre (ephyrae). For the diet composition analyses, the gastric pouches were carefully removed using forceps and a scalpel and placed in petri dishes. The oral arms of medusae and the formalin were also examined for prey. Prey were counted and identified to major taxonomic groups with the aid of a dissecting microscope; fish larvae and anchovy eggs were identified to species level.

Data analyses

The feeding incidence (FI) of each stage of *P. noctiluca* was calculated as the proportion of specimens with at least one prey item in their gastric pouches. The diet composition was described as the percentage of frequency of occurrence (%FO) and the percentage of numerical abundance (%N) of prey items in each stage (excluding medusae with no prey). The percentage of the product of these two factors was taken as an index of relative dietary importance (IRI) (Laroche, 1982). To allow easy comparison among prey items, the IRI was then standardized to %IRI for each prey item (Sassa and Tsukamoto, 2012). Diversity of the diet was calculated using the Shannon Weaver diversity index, H' (Zar, 1984). Prey selectivity by *P. noctiluca* for or against specific prey was calculated using Pearre´s index (C) (Pearre, 1982).

To calculate the jellyfish feeding rates on fish eggs and larvae, we used the average digestion times (DT) obtained by Purcell *et al.* (2014) in the same area and during the same period. For ephyrae, 3.0 h was used for all fish larvae (mean size 6.1 ± 9.2 mm standard length (SL)), 3.5 h for anchovy larvae (8.5 ± 6.3 mm SL) and 8.2 h for fish eggs (0.6 mm ± 0.1 diameter). In the case of medusae, 2.1 h was used for fish larvae (11.1 ± 27.7 mm SL) and anchovy larvae (14.4 ± 34.2 mm SL). Because rates for fish eggs digested by medusae were unavailable, we used the above rates obtained for ephyrae, which we believe to be conservative estimates, because digestion times decreased with jellyfish size (Purcell *et al.*, 2014). The individual feeding rates (prey eaten jelly^{-1} h^{-1}) of *P. noctiluca* on each prey type were calculated from their number in the gut contents at each station divided by the digestion times of these prey types (Purcell *et al.*, 2014).

In order to determine the predation effects at the population level (% standing stock consumed h^{-1}), individual feeding rates were multiplied by ephyra and medusa abundances and divided by prey abundances at each station. For calculation of predation impacts of *P. noctiluca* medusae, the following abundances from the above categories were used for the low, medium and high abundances, respectively: 1 medusa 10 m^{-2}, 5 medusae 10 m^{-2}, 10 medusae 10 m^{-2}.

Non-parametric tests (Mann Whitney) were used to test for differences in diets between ephyrae collected at day and at night and ephyrae collected using different methodologies, using SPSS software for Windows (IBM SPSS, 2011).

RESULTS

The sea surface temperature during the study showed a marked thermal front across the shelf that separated the cool northern waters (19°C) with few *P. noctiluca* medusae or ephyrae from the warmer southern waters (24°C) with more jellyfish (Fig. 2). *Pelagia noctiluca* medusae were observed during the night, near the surface, scattered throughout the area, both in coastal and open sea stations (Fig. 2A). Their abundances mainly ranged between <1 medusa and >1 medusa 10 m^{-2}, although in some stations, abundances of >10 medusa 10 m^{-2} were recorded (Fig. 2a). The spatial distribution of *P. noctiluca* ephyrae was uneven in the study area. Ephyrae were particularly abundant over the shelf off the Ebro River in the southern part of the Catalan coast, reaching concentrations of 12 209 ephyrae 10 m^{-2}. A high abundance peak was also detected in the central part of the study area over the slope where the highest concentration was recorded (33 693 ephyrae 10 m^{-2}) (Fig. 2)B.

Fish larvae were widely distributed along the Catalan coast (Fig. 2D). The highest abundances appeared in the north and the south where the shelf is wider, while their lowest concentrations were detected in the central region. Larvae of anchovy, *E. encrasicolus*, the most abundant species, were present along the entire coast over the shelf, being particularly abundant in the north where they reached abundances up to 3000 larvae 10 m^{-2} (Fig. 2c).

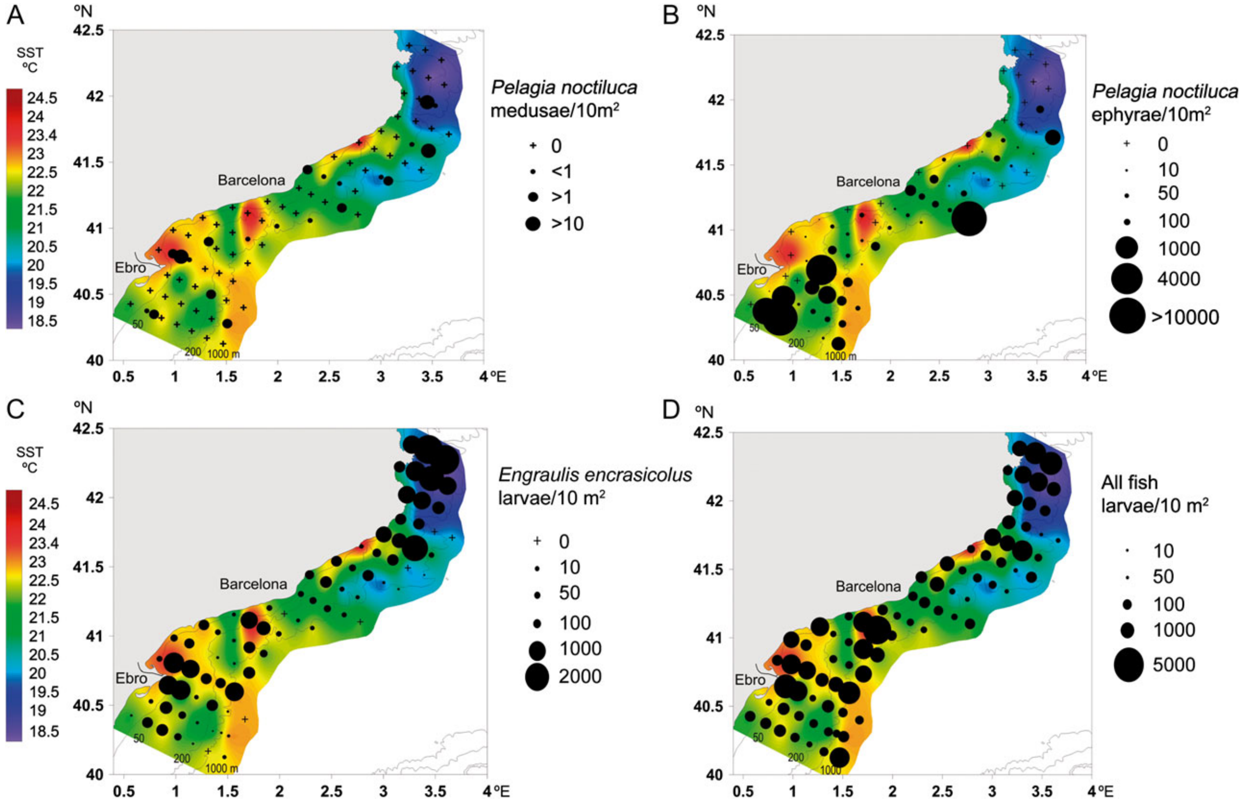

Fig. 2. Distributions of *Pelagia noctiluca* and fish larvae, overlaid on maps of sea surface temperature, in the northwest Mediterranean Sea during 17 June– 4 July 2011. (**A**) *Pelagia noctiluca* medusae determined from surface counts. (**B**) *Pelagia noctiluca* ephyrae determined from plankton tows. (**C**) *Engraulis encrasicolus* larvae determined from plankton tows. (**D**) All fish larvae determined from plankton tows.

Table I: Mean abundances (ind 10 m^{-2} ± SD) of zooplankton groups in the NW Mediterranean Sea during 17 June- 4 July 2011

Taxa	All stations	Stations where gut contents were analysed
Copepoda	32 981 ± 22 893	29 880 ± 22 085
Cladocera	20 017 ± 12404	19 789 ± 8170
Euphausiacea	68 ± 166	44 ± 55
Mysidacea	2 ± 10	1 ± 3
Decapoda	3 ± 5	6 ± 8
Amphipoda	17 ± 28	15 ± 17
Isopoda	2 ± 6	0 ± 1
Crustacean larvae	14 167 ± 13 618	12 724 ± 8375
Echinodermata	1127 ± 2877	590 ± 959
Mollusca	4447 ± 4744	5776 ± 4564
Ostracoda	527 ± 1018	483 ± 788
Radiolaria	9820 ± 10 338	7471 ± 8271
Appendicularia	8758 ± 6852	10 132 ± 4614
Chaetognatha	1840 ± 2361	2498 ± 1457
Doliolida	7649 ± 9712	6020 ± 5107
Salpida	1453 ± 2788	432 ± 646
Siphonophora	3951 ± 4809	3540 ± 3498
Hydromedusae	2214 ± 2947	2818 ± 2295
P. noctiluca ephyrae	749 ± 3978	349 ± 642
Fish larvae	1020 ± 889	1033 ± 630
Fish eggs	799 ± 847	838 ± 715
Total zooplankton	111 610 ± 103288	104 476 ± 72 898

High abundances were also detected in the south over the Ebro shelf, reaching concentrations up to 1000 larvae 10 m^{-2} in stations close to the river mouth. Over the study area, the distribution of both groups of organisms showed a high degree of overlap, particularly in the southern part. *P. noctiluca* medusae coexisted with all fish larvae and with anchovy larvae in 25% of the sampled stations, while ephyrae co-occurred with fish larvae and anchovy larvae in 72.5% of the stations. Overall, during the study period *P. noctiluca* and fish larvae co-occurred in 77.5% of the stations. Nevertheless, in areas where anchovy larvae were very abundant, such as in the north, ephyrae were practically absent.

Information on zooplankton abundance during the cruise is summarized in Table I. The most abundant groups were copepods and cladocerans, representing 29.6% and 17.9% of the total zooplankton abundance, respectively. Larvae of crustaceans (decapods and euphausiids) (12.7%) and radiolarians (8.8%) were also generally abundant, followed by appendicularians and doliolids. Fish larvae and eggs represented 0.9% and 0.7%, respectively.

Gut content analyses

Medusae ranged from 30 to 75 mm in swimming bell diameter. A total of 91 medusae (52 ± 14 mm) were examined for gut content analyses. Feeding incidence (FI) was 100%, which means that all large jellyfish had at least one prey inside the gut. Although most ephyrae (86.9%) were collected during the night, no significant differences were detected in the FI between day (47%) and night (49%) ($U = 1108.5$, *p*-value = 0.201). 65% of the gut contents of large jellyfish was highly-digested material that could not be identified; therefore, diet descriptions and further analyses considered only identified prey items.

Table II: Diet composition of Pelagia noctiluca *medusae* (N = *91) in the Catalan Sea*

Prey type	%N	%FO	%IRI
Copepoda	15.9	287.9	24.7
Crustacean exoskeletons (unidentified)	3.7	67.0	1.3
Cladocera	4.0	72.5	1.6
Amphipoda (hyperiids excluded)	1.5	26.4	0.2
Decapoda/Euphausiacea larvae	13.3	240.7	17.3
Echinodermata	0.7	13.2	0.05
Mollusca	8.7	158.2	7.5
Ostracoda	9.1	164.8	8.1
Appendicularia	1.6	29.7	0.3
Chaetognatha	3.5	62.6	1.2
Doliolida	0.7	13.2	0.05
Salpida	4.4	79.1	1.9
Siphonophora	8.7	158.2	7.5
Hydromedusa	0.3	5.5	0.01
Fish eggs	16.1	291.2	25.3
Fish larvae	4.9	89.0	2.4
Others	3.0	53.8	0.9
Amphipoda			

%*N*, percentage of numerical abundance of prey items in the gut contents; %FO, percentage frequency of occurrence in the gut; %IRI, index of relative dietary importance. Feeding incidence = 100%; Shannon Diversity Index (H') = 2.9; Total prey = 1665.

The mean numbers of captured and ingested prey per jellyfish was 18.3 ± 43.2, and prey diversity (H') was 2.9. The diet of medusae was mainly composed of fish eggs (IRI 25.3%) and copepods (IRI 24.7%) (Table II). Decapod and euphausiid larvae (17.3%), ostracods (IRI 8.1%) and molluscs and siphonophores (IRI 7.5%) were also relatively abundant in their diet (Table II). Although fish larvae were not very numerous prey (IRI 2.3%), many species were eaten, with the most abundant being European anchovy and bullet tuna, *Auxis rochei* (Table III).

Significant differences were observed in the numbers of ingested prey between ephyrae collected by the bongo net (0.1 ± 0.4 prey ephyra^{-1}) and by dip net (1.0 ± 1.0 prey ephyra^{-1}) ($U = 27\,897$, *p*-value < 0.05), those from the bongo net having few prey. No significant differences were observed between the number of ingested prey in ephyrae collected by dip net (1.0 ± 1.0 prey ephyra^{-1}) and neuston net (0.5 ± 0.8 prey ephyra^{-1}) ($U = 2519.5$, *p*-value = 0.092); therefore, only the 145 ephyrae (4.1 ± 1.6 mm) collected in the dip and neuston nets were considered for the description of their diet and for feeding calculations. The numbers of prey in ephyrae were similar during day (0.7 ± 0.7 prey ephyra^{-1}) and

Table III: Fish larvae species found in Pelagia noctiluca *guts in the Northwest Mediterranean Sea during 17 June – 4 July 2011*

Fish species	%*N* large medusae	%*N* ephyrae	% of the species at the stations
Engraulis encrasicolus	63.9	38.5	36.7
Auxis rochei	8.2	0	3.6
Diplodus sp.	4.9	15.4	0.1
Unidentified	4.9	0	14.6
Mullus barbatus	3.3	7.7	0.5
Gobiidae	3.3	0	5.2
Trachurus mediterraneus	–	15.4	0.9
Arnoglossus sp.	1.6	0	1.8
Sparidae	1.6	15.4	1.5
Myctophidae	1.6	0	0.7
Blenniidae	0	7.7	0.1
Others	–	–	34.3

Table IV: Diet composition of Pelagia noctiluca *ephyrae (nday = 19; nnight = 126) in the Catalan Sea*

	Ephyrae **day**			Ephyrae **night**		
Feeding incidence (%)	47			49		
Shannon Diversity Index (*H*′)	1.13			2.37		
Total no. of prey	14			101		
Prey type	%N	%FO	%IRI	%N	%FO	%IRI
Copepoda	0	0	0	12.9	10.3	14.5
Cladocera	0	0	0	5.9	4.8	3.1
Euphausiacea	0	0	0	3.0	2.4	0.8
Mollusca	0	0	0	6.0	4.8	1.7
Appendicularia	14.3	10.5	4.5	5.9	4.8	3.1
Chaetognatha	7.1	5.3	1.1	0	0	0
Doliolida	0	0	0	3.0	2.4	0.8
Salpida	7.1	5.3	1.1	7.9	6.3	5.5
Siphonophora	64.3	47.4	92.0	14.9	11.9	19.3
Dinoflagellates	0	0	0	1.0	0.8	0.1
Tintinnids	0	0	0	1.0	0.8	0.1
Invertebrate eggs	0	0	0	1.0	0.8	0.1
Fish eggs	0	0	0	5.0	4.0	2.1
Fish larvae	0	0	0	12.9	10.3	14.5
Unidentified	7.1	5.3	1.1	19.8	15.9	34.0

%*N*, percentage of numerical abundance of prey items in the gut contents; %FO, percentage frequency of occurrence in the gut; %IRI, index of relative dietary importance.

night (0.8 ± 0.9 prey ephyra^{-1}), although the diversity of prey was higher during the night. Siphonophores were the most abundant and frequent prey in the daytime ephyra diet (IRI 92.0%), followed by appendicularians (Table IV). Ephyrae collected during the night had a wider variety of prey, with siphonophores, copepods, and fish larvae the most important groups (IRI = 19.3%, 14.5% and 14.5%, respectively) (Table IV), although 21% of the diet composition was unidentified highly digested material. Selectivity analysis showed that both *P. noctiluca* medusae and ephyrae fed unselectively on most prey taxa present in the zooplankton (Table V).

Table V: Prey selectivity coefficients (C, Pearre, 1982) of Pelagia noctiluca *calculated from their gut contents*

	Copepoda	Cladocera	Appendicularia	Chaetognatha	Mollusca	Siphonophora	Hydromedusa	Crustacean larvae	Fish eggs	Fish larvae	Salpida	Doliolida	Echinodermata	Euphausiacea
Medusae	0.00	−0.02	−0.01	0.01	0.01	0.02	−0.01	0.00	0.05	0.04	0.03	0.00	0.01	0.00
Ephyrae	−0.03	−0.04	−0.02	–	−0.02	0.05	–	–	0.06	0.11	0.13	−0.02	–	0.10

No values were significantly different from zero ($p < 0.05$), indicating no significant selection.

Table VI: Predation effects (% of standing stocks consumed h^{-1}) by P. noctiluca *on ichthyoplankton and copepods in the northwest Mediterranean during 17 June – 4 July 2011*

Prey type	Prey consumed (% h^{-1}) Medusae	Ephyrae
Fish larvae	0.1–1.5	1.5–2.7
Anchovy larvae	0.1–0.9	1.5–10.4
Fish eggs	0.02–3.2*	0.4–7.1

Values with * are estimated using ephyra digestion times.

Potential predation (% of the standing stock consumed h^{-1}) was calculated for *P. noctiluca* medusa and ephyrae feeding on ichthyoplankton. Fish larvae in the gut contents of medusae averaged 11.1 ± 27.7 mm SL and predation effects on them ranged from 0.1 to 1.5% h^{-1}; predation on anchovy larvae (14.4 ± 34.2 mm SL) was 0.1–0.9% h^{-1} (Table VI, S1). Potential predation by medusae on fish eggs ranged from 0.02 to 3.2% h^{-1}. The impacts of ephyrae were higher, ranging from 1.5 to 2.7% h^{-1} for all fish larvae (6.1 ± 9.2 mm SL), 1.5 to 10.4% h^{-1} for anchovy larvae (8.5 ± 6.3 mm SL), and from 0.4 to 7.1% h^{-1} for fish eggs.

DISCUSSION

The sampling strategy employed in the present study allowed us to evaluate the predation effects of different stages of *P. noctiluca* co-occurring with fish eggs and larvae in the NW Mediterranean. To our knowledge, this is the largest scale and most detailed study of predation on ichthyoplankton by medusae based on individual collection of the gelatinous predators for gut content analysis.

Gelatinous zooplankton outbreaks, including those of *P. noctiluca*, are seasonal events (Mills, 2001) and their processes of aggregation and dispersion are very rapid (Malej, 1989). On the Catalan coast, high abundances of *P. noctiluca* ephyrae and other gelatinous organisms have been reported over the slope probably due to the increased primary and secondary production associated with the shelf-slope front and its associated Northern Current flowing all along the continental slope (Gili *et al.*, 1988; Sabatés *et al.*, 2010). Nevertheless, this pattern may be subject to considerable spatio-temporal variability due to the mesoscale activity of the front, which can show seasonal variations in its location, strength, and width (Sabatés *et al.*, 2004; Sáiz *et al.*, 2014). In contrast to the trend in those studies, our observations showed *P. noctiluca* medusae and ephyrae were located both in coastal waters and the open sea (Fig. 1). In the Mediterranean, blooms of *P. noctiluca* have been reported to be driven by physical forcing, specifically winds and currents (e.g. Vučetić, 1984; Ferraris *et al.*, 2012; Rosa *et al.*, 2013; Canepa *et al.*, 2014). In our study, variability in the physical forcing together with mesoscale activity of the Northern Current, including meanders, filaments and eddies (Millot, 1991; Flexas *et al.*, 2002) would contribute to the observed distribution of *P. noctiluca* along the Catalan coast.

In the northernmost part of the study area north of the thermal front, the abundances of *P. noctiluca* were very low. By contrast, high densities of anchovy larvae were detected in that area. These differences in abundance between both groups of organisms could suggest that there was a causal relationship, such as possible predation on anchovy larvae by *P. noctiluca*. Lynam *et al.* (2005) reported a negative correlation between the abundance of *A. aurita* and herring larval survival and Brodeur *et al.* (2002) also observed a significant inverse relationship between the biomass of *Chrysaora melanaster* and forage fish. However, in the northern Catalan coastal waters, the presence of high concentrations of anchovy larvae is a regular phenomenon (Sabatés *et al.*, 2013), with these larvae advected by the Northern Current from the northern spawning grounds in the Gulf of Lions (Sabatés *et al.*, 2007). By contrast, these waters contained virtually no *P. noctiluca*. The intruding waters from the north are cold compared to the Catalan waters and form a temperature front across the shelf (Sabatés *et al.*, 2009). Temperatures north of the front may have been too low for *P. noctiluca*; low temperatures have been reported to slow swimming (Rottini Sandrini and Avian, 1989), reduce respiration and pulsation rates (Malej, 1989; Malej and Malej, 2004), and affect their abundance and reproduction (Canepa *et al.*, 2014). In any case, given the patchy distribution of this species, it cannot be excluded that this water mass did not contain ephyrae.

Feeding incidence (FI), defined by Arthur (1976) as the percentage of individuals containing at least one food particle in the gut, is considered to be measure of a predator ability to obtain food from the environment. The FI of ephyrae in our study (47% during day and 50% during night) were much higher than those (7–21%) obtained by Sabatés *et al.* using a bongo net in the same area (Sabatés *et al.*, 2010). These differences could be explained by the ephyra collection methods; the FI of ephyrae collected with the bongo net and processed by standard plankton sample methods in both studies were low and similar. As Purcell *et al.* (2014) suggested, ephyrae collected with the bongo net were damaged and their apparent feeding reduced. Problems related to collection methodology for jellyfish diet composition analyses, have also been described by Purcell (1997). For this reason, for dietary analyses we used only ephyrae collected by drifting the neuston net and those dipped individually from the surface to minimize damage to their body and loss of prey from the gastric pouches.

Medusae contained more prey items and had higher prey diversity than ephyrae. The average number of prey per medusa (18.3 ± 43.2) was similar to that obtained in the Messina Strait during the summer period (Rosa *et al.*, 2013; Milisenda, 2014). Differences in the captured and ingested number and diversity of prey between medusae and ephyrae would be attributable to the higher clearance and contact rates of larger individuals (Möller, 1984) and vulnerability of different types of prey, including swimming rates and escape abilities, in relation to medusa and prey size (Sullivan *et al.*, 1994; Purcell, 1997; Suchman and Sullivan, 2000; Graham and Kroutil, 2001). Different studies have shown that mixed diets typically produce the greatest growth responses due to the varied supply of essential nutrients derived from mixed prey populations (Helm, 1977; Hamburguer and Boëtius, 1987). Increasing numbers and diversity of prey as medusae grow has also been described in other species of scyphozoans, such as *A. aurita*, *C. quinquecirrha*, and *Chrysaora plocamia* (Costello and Colin, 1994; Graham and Kroutil, 2001; Riascos *et al.*, 2014). In our study, the numbers of captured and ingested prey in *P. noctiluca* medusae were lower than those found in *A. aurita* and *C. quinquecirrha* guts (Purcell *et al.*, 1994; Graham and Kroutil, 2001), which might be related to different feeding abilities or to differences in the densities of the zooplankton in each area, which were higher in the other two locations than in the present study.

The natural dietary composition of *P. noctiluca* medusae has been studied in different areas (including the NW Mediterranean) and the species has been described as a non-selective predator (Rosa *et al.*, 2013; Milisenda, 2014) feeding on almost all zooplankton groups, including ichthyoplankton, with copepods being the most important item (Giorgi *et al.*, 1991; Malej *et al.*, 1993; Sabatés *et al.*, 2010). In the present study gut contents contained a wide variety of prey, with fish eggs as the most important item in medusae and siphonophores in ephyrae, although copepods were also relatively abundant. The low incidence of fish eggs in ephyrae could be due to high rates of egestion of undigested eggs (52%), although some of them may be held for many hours (Purcell *et al.* 2014). While we do not know if *P. noctiluca* medusae also have difficulty in digesting some fish eggs or how long they require to digest them, the high proportion of fish eggs in medusae could also be due to the higher rates of clearance and encounters of larger individuals (Möller, 1984). In fact, many other types of medusae have also been shown to prey on fish eggs (reviewed in Purcell, 1985; Purcell and Arai, 2001; Purcell *et al.*, 2014). Although siphonophores were the major prey in ephyra gut contents, fish larvae were also an important component of its diet, particularly at night. Ichthyoplankton is often part of gelatinous zooplankton diets (reviewed in Purcell, 1985; Purcell and Arai, 2001) and several scyphozoan species have been described as predators of fish larvae (Barz and Hirche, 2007). In our study, 6 species of fish larvae were identified in the guts of *P. noctiluca*, most of them belonging to shelf dwelling species, although larvae of myctophids were also present.

The majority of ephyrae analysed for gut contents were collected during the night, when vertical migration of the zooplankton to upper layers occurs (Saiz *et al.*, 2014). In the study area, eggs and larvae of most fish species are located in the upper layers of the waters column (Olivar and Sabatés, 1997; Sabatés *et al.*, 2008) and anchovy, the most abundant species during the study period, migrate to the surface at night (Olivar *et al.*, 2001; Sabatés *et al.*, 2008). In our study, *P. noctiluca* ephyrae and medusae were observed at the surface mostly at night, as reported in other studies conducted in the NW Mediterranean (Ferraris *et al.*, 2012; Gordoa *et al.*, 2013) and in other areas of the world (Doyle *et al.*, 2008). Nevertheless, ephyrae were also detected at the surface during the day, although in much lower abundance. Thus, overlap between *P. noctiluca* and ichthyoplankton and zooplankton is high in the surface water during the night. The migration of zooplankton towards deeper waters during the day (Sáiz *et al.* 2014) would explain the absence of fish larvae and copepods in ephyrae collected in surface waters during daytime.

Analysis of prey selectivity showed that *P. noctiluca* is a non-selective predator, feeding on almost all zooplankton taxa, and confirming their opportunistic feeding (Giorgi *et al.*, 1991; Rosa *et al.*, 2013; Milisenda, 2014). Although Sabatés *et al.* (2010) found positive selection by ephyrae for some zooplankton groups; these differences could be due to the different methodological approaches used. The diversity of prey found in this study (15 major groups) is slightly higher than that reported by Giorgi *et al.*, (1991) and Rosa *et al.* (2013) (13 major groups) while 8 taxa were identified by Milisenda (2014) for the same period of the year. Selection for ichthyoplankton and copepods has been described in other species of jellyfish (Fancett, 1988; Purcell, 1989; Purcell *et al.*, 1994), but feeding and selection is probably affected by the digestion times which, in turn, differ among the prey type and also with the size of prey (Purcell *et al.*, 2014). Predation effects of *P. noctiluca in situ* have not been previously studied. The values of predation on fish larvae observed in medusae were much lower than those obtained for ephyrae. Medusae would consume between 0.1% and 1.5% of fish larvae standing stock h^{-1} and between 0.1% and 0.9% of anchovy larvae standing stock h^{-1}. Because all medusae analysed for gut contents were collected at night, if we assume that feeding and digestion of *P. noctiluca* was continuous during night

(8 h), then their consumption during this period would be between 0.4% and 11.9% of all larvae and between 0.5% and 7.3% of anchovy larvae. All these impact values are probably underestimated because abundances of *P. noctiluca* medusae used for the calculations came from individuals observed only at the surface at night and, presumably, jellyfish and their prey may overlap in the water column during daylight hours. Moreover, the use of oblique tows to determine ephyrae and fish larvae distributions during the cruise, did not allow investigation of the potential overlap of both groups at different levels of the water column since the abundance data are homogenized over the depth of the tows. Other studies have reported higher consumption rates than those reported in the present study, such as that of *C. quinquecirrha* in Chesapeake Bay (Purcell *et al.*, 1994). The higher abundances of larvae and medusae in the field and more rapid digestion (1 h) of the small fish larvae contributed to higher consumption in Chesapeake Bay than on the Catalan coast.

The percentages of fish larva standing stocks consumed h^{-1} by ephyrae ranged from 1.5% to 2.7%, while the potential impact on anchovy larvae was higher (1.5–10.4%). If we assume that feeding and digestion of *P. noctiluca* was continuous during the night (8 h), ephyrae would consume between 12.1% and 21.3% of all fish larvae night^{-1}, while consumption of anchovy ranged from 11.8 to 82.9% night^{-1}. These rates are much greater than predation impacts in Purcell *et al.* (2014), which ranged from 1 to 3% of fish larvae consumed per night (8 h). Both studies were performed in the same area and although fish larvae densities were similar, ephyra densities were much lower in our study, so the differences are probably due to bongo net *vs.* individual collection of ephyrae for gut contents.

Moreover, fish eggs were also consumed by ephyrae in a high proportion (0.1–7.1% h^{-1}, or 2.8–56.6% of eggs night^{-1}). There is no previous information about the potential predation impact of ephyrae of any species; however, high consumption rates have been reported for *P. noctiluca* ephyrae feeding on tuna eggs in the laboratory (Gordoa *et al.*, 2013). Estimations made for medusae, assuming the same digestion time as ephyrae, showed that their consumption of fish eggs was lower than that of ephyrae, with rates from 0.02 to 3.2% h^{-1} (or 0.1–25.7% eggs night^{-1}). These rates are high compared to other species of jellyfish, such as *C. quinquecirrha*, for which a predation impact of 7–17% on *A. mitchilli* eggs 20 h^{-1} was reported (Purcell *et al.*, 1994). Because we used egg digestion time of ephyrae for the medusae, the impacts could be underestimated if medusae digest eggs more rapidly than do ephyrae, as was true for fish larvae (Purcell *et al.*, 2014).

Pelagia noctiluca can bloom in the Mediterranean Sea, reaching very high numbers of individuals (reviewed in Canepa *et al.* 2014). During the cruise, the abundances of *P. noctiluca* observed generally were not as high as in a bloom, except in one station located in the central area (Fig. 2). To illustrate the potential predation of this jellyfish on fish larvae in a bloom situation, we have considered the abundance of *P. noctiluca* ephyrae encountered at this station (33 693 ephyrae 10 m^{-2}) and the abundance of fish larvae at the same station (645 fish larvae 10 m^{-2}). Based on the mean ephyrae individual feeding rates obtained in this study (0.18 prey med^{-1} h^{-1}, see S1), the ephyrae and fish larvae abundances at the bloom situation, and following the same methodology as above, the potential consumption would be $>$ 100% of fish larvae stock night^{-1}. Modelling exercises already suggested that in a scenario of frequent blooms *P. noctiluca*, anchovy landings off the Catalan coast would sensibly decrease though the impact on the regional economy would not be significant (Tomlinson *et al.*, in press). As this last study was based on anchovy larvae consumption rates from Sabatés *et al.* (2010), lower than those obtained in the present study, we might assume that the impact on anchovy fisheries could be higher than that previously estimated. Recent data from different areas of the Mediterranean indicate that blooms of *P. noctiluca* are occurring more frequently (Canepa *et al.* 2014), especially in the Western Mediterranean, so that, their impact on fish larvae populations could be extremely high.

CONCLUSIONS

Pelagia noctiluca is an opportunistic predator that consumes a wide variety of prey from most zooplankton groups and feeds on ichthyoplankton at very high rates. It can form extremely large blooms, especially at night in surface waters, and co-occur with fish eggs and larvae at the beginning of summer on the Catalan coast. The high potential predation of *P. noctiluca* calculated suggests that its impact on fish larvae populations, particularly anchovy, can be extremely high in a bloom situation. Most Mediterranean fish stocks are over exploited and current environmental conditions (e.g. sea warming, river runoff) have been demonstrated to have a direct impact on fish catches (e.g. Lloret *et al.*, 2001; Sabatés *et al.*, 2006). Because a combination of pressures is responsible for the decline of fish stocks, increasing our understanding of different sources of variability, including their predators such as *P. noctiluca*, as well as combinations of stressors, is essential for an effective management of fishery resources.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org

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