Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea

Ana Sabatés · Francesc Pagès · Dacha Atienza · Verónica Fuentes · Jennifer E. Purcell · Josep-María Gili

Abstract Pelagic cnidarians are important consumers of zooplankton and ichthyoplankton in the world's oceans, and thus harm fisheries as competitors and predators of fish. This study examined the inshore-offshore distribution of pelagic cnidarians and the trophic ecology of *Pelagia noctiluca* ephyrae (<12 mm diameter) and larger medusae in late spring 1995 in the NW Mediterranean Sea. The distribution of pelagic cnidarians was closely related to the presence of the shelf-slope front with most species mainly concentrated close to the front. Meroplanktonic antho- and leptomedusae predominated in coastal waters and more holoplanktonic trachy- and narcomedusae occurred both in shelf and open sea waters.

P. noctiluca was more abundant than other medusae, including hydromedusae. Siphonophores, particularly *Muggiaea atlantica*, outnumbered medusae at most stations. The diet of *P. noctiluca* ephyrae contained mainly copepods, but ~12% of the prey were fish larvae. *P. noctiluca* exhibited positive prey selection for chaetognaths and mollusc larvae in day and night samples, but fish larvae were positively selected only at night. These differences may be related to the diel vertical distributions of *P. noctiluca* and their prey. Most of the ingested fish larvae belonged to the family Myctophidae, but anchovy and sparid larvae also were found in the gastric pouches. The size of ingested fish larvae increased as ephyra diameter increased; however, in the larger medusae (>12 mm) the number of prey increased with medusa size rather than the size of the larvae. The temporal and spatial co-occurrence of *P. noctiluca* with early life stages of fish suggests that *P. noctiluca* may be an important predator on summer ichthyoplankton.

Keywords Jellyfish · Ichthyoplankton · Fish · Front · Siphonophore · Hydromedusae

A. Sabatés (✉) · F. Pagès · D. Atienza ·
V. Fuentes · J.-M. Gili
Institut de Ciències del Mar, CSIC, P. Marítim 37-49,
08003 Barcelona, Spain
e-mail: anas@icm.csic.es

J. E. Purcell
Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Rd, Anacortes, WA 98221, USA

J. E. Purcell
Coastal and Marine Resources Centre, University College Cork, Naval Base, Haulbowline Island, Cobh, Co. Cork, Ireland

Introduction

High concentrations of gelatinous plankton are a natural phenomenon in coastal and oceanic waters. Increased reports about jellyfish suggest that their

numbers have increased in recent years (Purcell et al., 2007). This is cause for concern because jellyfish cause serious problems in some economic sectors and in the management of natural resources (Mills, 2001). Modern commercial fishing removes predators and competitors of jellyfish with increasing efficiency enabling many gelatinous zooplankton species to proliferate. When jellyfish occur in large numbers, their predation impact can be very important and may even control the population sizes and compositions of their prey organisms (Behrends & Schneider, 1995). They also may compete with zooplanktivorous fish and fish larvae by eating the same prey items (Purcell & Grover, 1990). Thus, studies of gelatinous zooplankton abundances, population dynamics and feeding ecology are of high priority in all oceans.

The diets of various jellyfish taxa consist primarily of copepods, but may also include meroplankton, ichthyoplankton, and gelatinous plankton (Purcell, 1985, 1997; Purcell & Mills, 1988). There is considerable evidence that scyphomedusae, hydromedusae, siphonophores and ctenophores consume fish eggs and fish larvae (Möller, 1980; Purcell, 1989, 1990; Purcell et al., 1994; reviewed by Purcell & Arai, 2001). Indeed, all jellyfish species tested have shown positive selection for ichthyoplankton (Fancett, 1988; Purcell et al., 1994; Purcell & Sturdevant, 2001), with prey selection being defined as consumption of prey types in disproportion to their abundance in the environment.

In the northwestern Mediterranean, the abundances and distributions of gelatinous zooplankton, especially planktonic cnidarians, have been studied for many years (e.g. Gili et al., 1987a; Dallot et al., 1988). In recent decades, an increase in jellyfish outbreaks in this region has been related to climatic forcing, particularly warming temperatures and dry conditions (Molinero et al., 2005). In the western Mediterranean, pelagic cnidarians are most abundant during spring and summer (Gili et al., 1987a). The distributions of the dominant species are closely related to the hydrographic heterogeneity, the geomorphology of the continental shelf and the presence of mesoscale permanent hydrographic features (Gili et al., 1988).

In the Catalan Sea (NW Mediterranean), the scyphomedusa, *Pelagia noctiluca* (Forsskål), is the most abundant jellyfish species in the summer months and its abundance has increased in recent years (Gili & Pagès, 2005). This species is especially abundant on the shelf-slope where concentrations of plankton occurs (Sabatés et al., 1989). On the shelf-slope, *P. noctiluca* occurs near the surface, especially at night, as observed in other parts of the Mediterranean (review by Mariottini et al., 2008). Their vertical distribution pattern coincides with the nocturnal migration of zooplankton, their main prey (Malej, 1989; Rottini Sandrini & Avian, 1989). *P. noctiluca* is considered a top planktonic predator (Larson, 1987), feeding on almost all types of zooplankton and ichthyoplankton (Giorgi et al., 1991; Zavodnik, 1991; Malej et al., 1993); however, the dietary composition of *P. noctiluca* in the Catalan Sea has never been studied and its predatory effects on zooplankton and ichthyoplankton populations remain unclear.

The Catalan coast is characterized by a permanent shelf-slope front along the shelf edge. Typically the front is defined by salinity differences between waters of the open sea (salinity >38) and the shelf (salinity <38; Font et al., 1988; Salat, 1996). The front runs along the continental slope of the northwestern Mediterranean, reaching a depth of some 400 m where it intersects with the bottom. The associated geostrophic current flows in a strip about 10-km wide at the surface, parallel to the front on its coastal side, and roughly over the 1000-m isobath (García-Ladona et al., 1994). The roles of the front in phytoplankton distribution and primary production (Estrada & Margalef, 1988; Estrada et al., 1999) and in zooplankton distribution and metabolism (Alcaraz et al., 1994; Sáiz et al., 1999) have been documented. The highest densities of fish larvae are located at the edge of the continental shelf in association with the shelf-slope front (Sabatés, 1990). In some cases, the front has been found to delimit shelf and oceanic fish larvae populations and to act as a barrier preventing dispersal of fish larvae to the open sea (Masó et al., 1998).

In this study, we address the distribution of gelatinous zooplankton across the inshore–offshore gradient of the Catalan coast (NW Mediterranean) in relation to mesoscale physical processes, and the trophic ecology of *P. noctiluca* ephyrae (<12 mm diameter) and larger individuals, with particular attention to their predation on fish larvae.

Materials and methods

Sampling was conducted on a transect perpendicular to the coast, from near shore to the slope, in the Catalan Sea (western Mediterranean) during 18–23 June 1995 (FRONTS cruise; Fig. 1). Four stations were sampled in accordance with the general circulation in the Catalan Sea to detect spatial gradients. The first station was in coastal waters (40-m depth), the second was over the shelf (70–80-m depth), the third was over the slope (1000-m depth) near the front, and the last station was in the open sea (>2000-m depth; Fig. 1). This sampling was repeated three times at each station, regardless of time of the day. Thus, a total of 12 samplings were conducted (7 at day and 5 at night).

At each station, vertical profiles of temperature, salinity and chlorophyll fluorescence were obtained with a Neil Brown Mark III-CTD (WOCE standard) equipped with a Sea-Tech fluorometer. Zooplankton and fish larvae were sampled by oblique tows of a 60-cm diameter Bongo net with 500-µm mesh from near-bottom to the surface or from 200 m to the surface where the bottom was deeper than 200 m. The volume of water passing through the net was calculated by means of data obtained from a 2030R

Fig. 1 Map of the northwestern Mediterranean Sea showing with locations of the sampling stations along the coastal–open sea transect during 18–23 June 1995. *Open circles*: CTD casts; *crosses*: zooplankton tows

General Oceanics Inc. flowmeter mounted in the mouth of the net. Net samples were fixed in a 5% formaldehyde-seawater solution buffered with sodium tetraborate. Earlier on 10–14 June (VARI-MED cruise), CTD profiles were made at eight stations on the same transect for physical parameters.

In the laboratory, medusae, siphonophores and fish larvae were counted and identified to the lowest possible taxonomic level with the aid of a dissecting microscope. For physonect siphonophores, the number of colonies was estimated from the number of nectophores according to Totton (1965); for calycophorans, the number of colonies was determined by the number of anterior nectophores. *P. noctiluca* ephyrae (≤12 mm diameter) were counted. Some larger *P. noctiluca* were occasionally collected but not included in the abundance calculation because the net was inappropriate for collection of large medusae. Nevertheless, the large specimens were included for diet analyses. In addition, the most abundant zooplankton taxa were counted by means of a dissecting microscope from 1/256 to 1/32 aliquots obtained with a Motoda rectangular box splitter (Motoda, 1959). All individuals from each taxon were counted in an aliquot; densities were expressed as the number of individuals per 1000 m^3.

The gastric pouch contents of all *P. noctiluca* ephyrae in the samples were identified, counted, and measured with the aid of a dissecting microscope. We included only partly digested prey to ensure that the prey items had not been captured while in the net. Prior to dissection, the maximum diameter of each jellyfish was measured with an ocular micrometre. The proportion of *P. noctiluca* ephyrae containing food (feeding incidence) was calculated for each sampling station. One-way analysis of variance (ANOVA) was used to assess differences among sampling locations (independent of time of the day) and between day and night (independent of sampling location).

Prey taxon selectivity by *P. noctiluca* ephyrae was estimated by the α index (Chesson, 1978): $\alpha = (r_k/p_k)/\sum_1^n (r_i/p_i)$ where r_k and p_k are the proportions of prey k in the diet and in the field, respectively, and n is the number of prey taxa. Neutral selection would result in a constant $\alpha = 1/n$. This index is density independent and permits the determination of whether prey items were ingested in higher or lower proportion relative to what would be
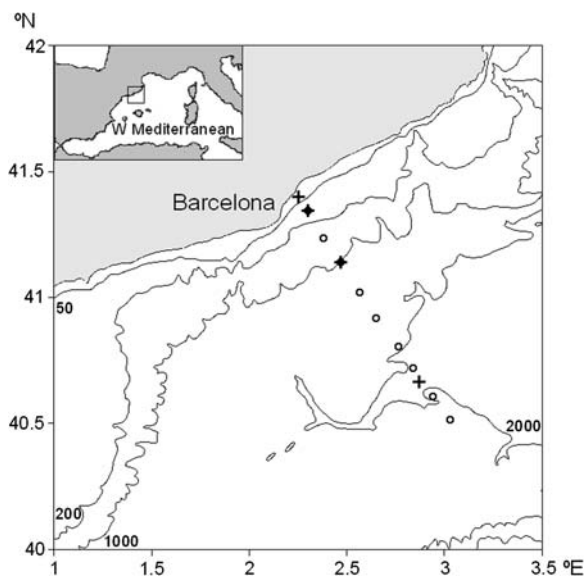
expected owing to their relative biomass in the field (Pearre, 1982). Chesson's α first was calculated for each tow and then averaged by sampling location and by day and night.

To analyse relationships between number and length of captured larval fish and *P. noctiluca* diameter (mm), both ephyrae and large medusae were included. Medusae were grouped into 1-mm size classes, and only classes with more than one prey item were used for further analysis.

Results

Hydrography

The vertical structure of the water column was dominated by thermal stratification, with a well-developed thermocline at around 60 m depth; below this depth temperature remained nearly constant at 14°C (Fig. 2). Vertical salinity distribution along the transect showed the presence of the shelf-slope front, determined by the horizontal gradient at 50–200 m depth (Fig. 2). The marked thermocline prevented the front from reaching the surface. A deep-chlorophyll fluorescence maximum was found near 60 m depth below the thermocline. The highest deep-fluorescence values always occurred on the oceanic side of the frontal system.

Pelagic cnidarian distribution

We identified a total of 31 cnidarian species, including 13 siphonophores and 18 medusae (Tables 1, 2). Siphonophores were almost always more abundant than medusae. The highest densities of siphonophores were recorded at the shelf and frontal stations, and medusae were more abundant in the front area.

Among siphonophores, the calycophoran, *Muggiaea atlantica*, predominated at all stations, especially at the shelf and front stations (Fig. 3). The asexual polygastric stage of *M. atlantica* was more abundant on the shelf, while the sexual eudoxid stage peaked at the front area. *Chelophyes appendiculata*, *Lensia conoidea*, *Lensia subtilis* and *Abylopsis tetragona* formed the bulk of the remaining species that showed a wide cross-shelf distribution (Table 1). *C. appendiculata* was absent in coastal waters but occurred at
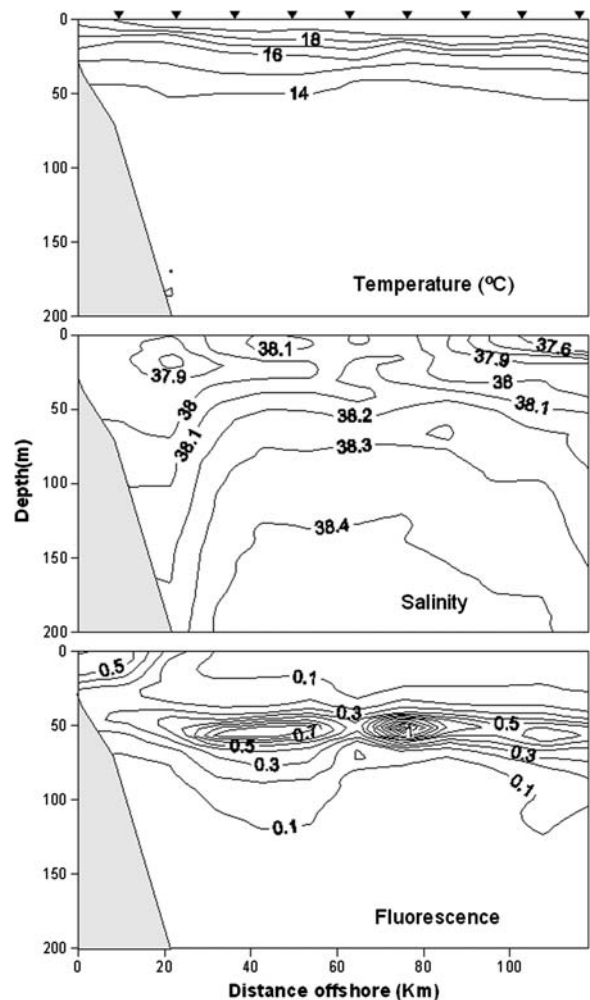

Fig. 2 Vertical distributions of temperature (°C), salinity and fluorescence (arbitrary units) on the coastal–open sea transect in the northwestern Mediterranean Sea during 18–23 June 1995. *Filled triangles* give the locations of hydrographic sampling stations shown in Fig. 1

the other stations. *L. conoidea* occurred in low numbers at the coastal and shelf stations and was more abundant in the frontal area and in the open sea. *L. subtilis* occurred at all stations in relatively high numbers, with peak abundances over the shelf.

Most of the medusa species occurred in lower densities than the siphonophores (Table 2). Only the ephyrae of *P. noctiluca* were abundant at all stations, except at the coastal station where they were virtually absent. The highest densities of *P. noctiluca* were observed at the front, but they also were abundant over the shelf and in the open sea. *P. noctiluca* abundance did not differ significantly

Table 1 Mean abundance $\pm$ SD of siphonophore colonies per 1000 m^{-3} in a coastal–open sea transect in the NW Mediterranean Sea during 18–23 June 1995

Species	Coast	Shelf	Front	Open sea
Physonectae				
Agalma elegans (Sars, 1846) Fewkes, 1880	–	1.6 ± 2.3	1.9 ± 1.5	1.3 ± 0.9
Agalma sp.	4.1 ± 5.7	–	–	–
Nanomia bijuga (delle Chiaje 1841)	2.3 ± 3.3	1.7 ± 2.4	1.9 ± 1.4	2.5 ± 0.8
Physophora hydrostatica Forskål 1775	–	–	–	0.7 ± 1.0
Calycophorae				
Muggiaea atlantica Cunningham 1892	1797 ± 270	8634 ± 2750	3304 ± 923.3	689.6 ± 160.9
M. atlantica eudoxids	211 ± 160	1728 ± 45.5	3070 ± 1844	248.4 ± 30.9
Lensia subtilis (Chun 1886)	48.5 ± 37	1694 ± 411.2	291 ± 181	298.3 ± 46.5
Lensia conoidea (Keferstein and Ehlers 1860)	5.4 ± 7.7	6.6 ± 9.3	74.8 ± 33.1	59.7 ± 37.4
Abylopsis tetragona (Otto 1823)	2.3 ± 3.3	56.1 ± 29.3	6.5 ± 4.6	37.0 ± 12.9
A. tetragona eudoxids	7.7 ± 6.7	88.9 ± 29.6	54.4 ± 28.1	48.2 ± 10.7
Eudoxoides spiralis (Bigelow 1911)	37 ± 3.7	–	0.7 ± 1.1	9.1 ± 1.1
E. spiralis eudoxids	–	1.6 ± 2.36	–	9.1 ± 10.7
Muggiaea kochi (Will 1844)	–	33.0 ± 28.8	14.6 ± 19.04	16.9 ± 7.3
M. kochi eudoxids	159.6 ± 175.1	20.1 ± 25.2	14.6 ± 20.6	–
Chelophyes appendiculata (Eschscholtz 1829)	–	238.7 ± 126	71.2 ± 8.7	166.4 ± 83.2
Lensia meteori (Leloup 1934)	–	–	10.0 ± 7.1	223.1 ± 13.8
Hippopodius hippopus (Forskål 1776)	–	–	1.1 ± 1.6	0.5 ± 0.8
Unidentified eudoxids	–	366 ± 199	323.1 ± 176.3	332.5 ± 193.6

Table 2 Mean abundances of medusae (individuals 1000 m^{-3} ± standard deviation) in a coastal–open sea transect in the NW Mediterranean Sea during 18–23 June 1995

| Species	Coast	Shelf	Front	Open sea
Podocoryne sp.	4.05 ± 7	–	–	–
Leptomedusa	4.1 ± 7.1	–	–	–
Eutima gegenbauri (Haeckel 1864)	2.7 ± 4.7	–	–	–
Leuckartiara octona (Fleming 1823)	2.3 ± 4	–	–	–
Obelia sp.	2.7 ± 4.7	–	1.1 ± 2.0	–
Aglaura hemistoma Perón & Lesueur 1810	2.3 ± 4	112.9 ± 18.8	59.2 ± 39.5	15.1 ± 13.2
Rhopalonema velatum Gegenbaur 1857	13.2 ± 17.3	377.2 ± 288.7	126.9 ± 43.7	99.3 ± 27.7
Solmundella bitentaculata (Quoy & Gaimard 1833)	9.6 ± 10.4	111.1 ± 145.5	68.1 ± 21.3	6.7 ± 5.9
Pelagia noctiluca (Forskål 1775)	–	469.5 ± 457.3	5012.3 ± 7216.8	646.3 ± 459.2
Pandea conica (Quoy & Gaimard 1827)	–	3.3 ± 5.8	4.6 ± 8.0	–
Helgicirrha schulzei Hartlaub 1909	–	1.6 ± 2.9	–	–
Nausithoe punctata Kölliker 1853	–	4.8 ± 4	–	–
Clytia sp.	–	–	8.1 ± 14.0	–
Persa incolorata McCrady 1859	–	–	20.4 ± 19.3	–
Liriope tetraphylla (Chamisso & Eysenhradt 1821)	–	–	1.9 ± 1.7	–
Solmissus flavescens (Kölliker 1853)	–	–	11.6 ± 10.7	–
Rhabdoon singulare Keferstein & Ehlers 1861	–	–	1.5 ± 2.7	–
Velella velella (Linnaeus 1758)	–	–	–	0.6 ± 1.0
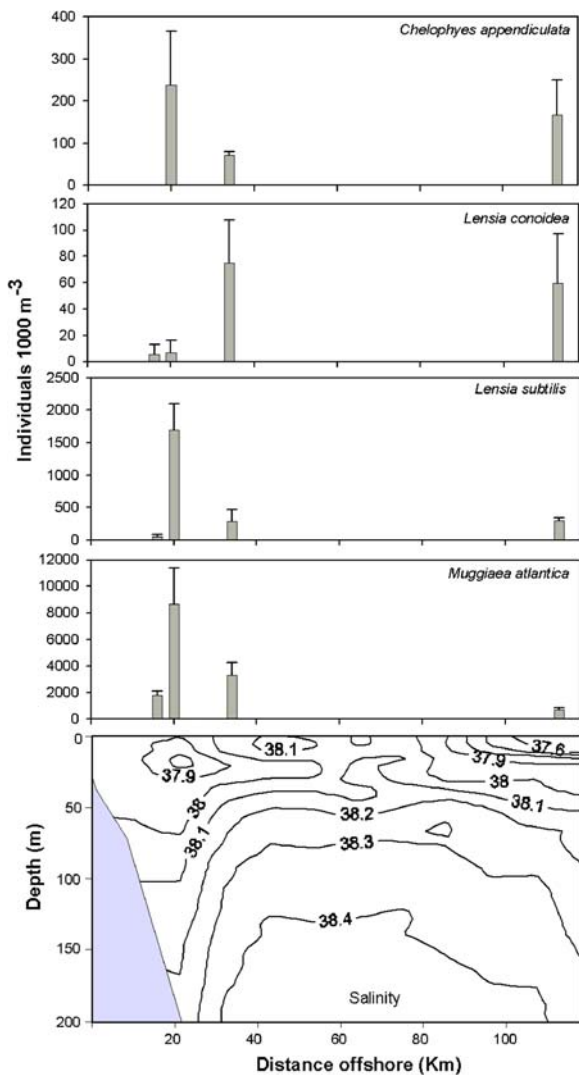
Fig. 3 Salinity distribution (*lower panel*) and abundances (means ± standard deviation) of the siphonophores *Chelophyes appendiculata*, *Lensia conoidea*, *Lensia subtilis* and *Muggiaea atlantica* at the sampling locations on the coastal–open sea transect in the northwestern Mediterranean Sea during 18–23 June 1995
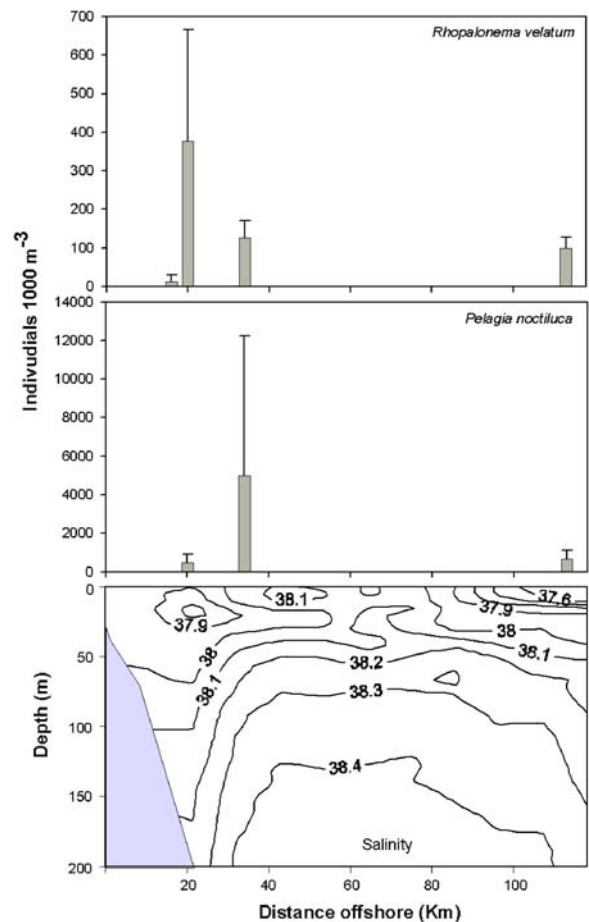

Fig. 4 Salinity distribution (*lower panel*) and abundances (means ± standard deviation) of the medusae *Rhopalonema velatum* and *Pelagia noctiluca* at sampling locations on the coastal–open sea transect in the northwestern Mediterranean Sea during 18–23 June 1995

between day and night tows ($F_{1,8} = 1.22$, $P = 0.31$). *Rhopalonema velatum* was very scarce in the coastal area and showed the highest concentrations over the shelf, with their abundance again decreasing offshore (Fig. 4).

Diet of *Pelagia noctiluca*

A total of 5680 *P. noctiluca* ephyrae were analysed for gastric pouch contents (Table 3). There were

significant differences in feeding incidence among the three sampled stations, ranging from 21% over the shelf to 7% in the front ($F_{2,8} = 6.19$, $P = 0.03$). No significant differences in feeding incidence were detected between day (14.0%) and night (14.7%) ($F_{2,8} = 0.01$, $P = 0.92$). The gastric pouches of *P. noctiluca* contained a wide variety of prey, mainly copepods, followed by juvenile euphausiids and fish larvae (Table 3).

Copepods were the most abundant zooplankton group at all sampled stations, with mean densities ranging between 48 and 159 individuals m^{-3} in the shelf and front areas, respectively (Table 4). The next most abundant crustaceans included decapod larvae and juvenile euphausiids. Appendicularians and

Table 3 Number of *Pelagia noctiluca* examined, feeding incidence (percentage of individuals containing prey), diet (percentage number of each prey type) and total number of prey of *Pelagia noctiluca* ephyrae in a coastal–open sea transect in the NW Mediterranean Sea during 18–23 June 1995
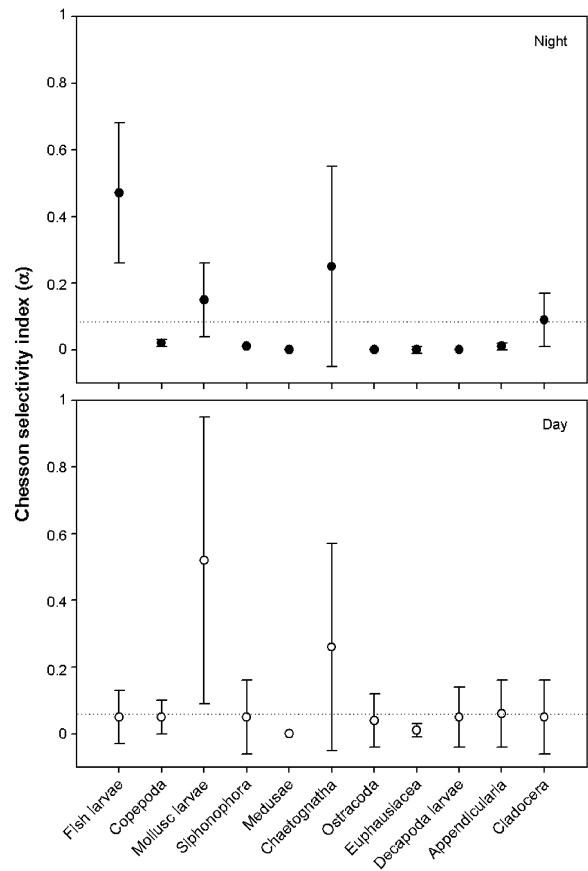
	Shelf	Front	Open sea
No. of *P. noctiluca*	145	4400	1135
Feeding incidence (%)	21	7	10
Diet (%)			
Copepoda	72	49	57
Mollusc larvae	8	3	5
Siphonophora	4	1	2
Chaetognatha	4	6	2
Ostracoda	0	1	2
Euphausiacea	0	20	7
Decapoda larvae	0	2	4
Appendicularia	0	4	12
Cladocera	4	3	2
Fish larvae	8	12	6
Total no. of prey	25	224	84

Table 4 Mean abundance of the major zooplankton taxa (individuals m^{-3} ± standard deviation) in a coastal–open sea transect in the NW Mediterranean during 18–23 June 1995

	Shelf	Front	Open sea
Copepoda	48.1 ± 20.9	159.4 ± 226.1	68.4 ± 88.7
Mollusc larvae	0.5 ± 0.2	0.7 ± 0.9	0.6 ± 0.9
Siphonophora	13.0 ± 3.1	7.3 ± 3.4	2.2 ± 0.4
Medusae	1.1 ± 0.2	5.3 ± 7.3	0.8 ± 0.5
Chaetognatha	0.2 ± 0.1	0.7 ± 1.0	0.5 ± 0.6
Ostracoda	0.9 ± 0.9	3.6 ± 4.6	3.9 ± 5.4
Euphasiacea	5.9 ± 1.2	26.4 ± 40.4	7.9 ± 10.2
Decapoda larvae	7.9 ± 3.6	38.0 ± 59.7	2.7 ± 3.5
Appendicularia	5.7 ± 1.8	6.8 ± 8.8	7.3 ± 10.2
Cladocera	5.7 ± 6.6	0.7 ± 0.3	0.2 ± 0.3
Fish larvae	1.0 ± 0.2	0.7 ± 0.1	0.6 ± 0.2

Fig. 5 Mean Chesson's α values (± standard deviation) for the most common prey items in *Pelagia noctiluca* during day and night in the northwestern Mediterranean Sea during 18–23 June 1995. Values above the *dashed line* indicate positive selection

siphonophores were also abundant; yet fish larvae, which were important in the ephyra diet, were clearly a minor group (Table 4). Most zooplankton taxa had highest densities in the front area, where most of the medusae and siphonophores species also occurred.

Selection by *P. noctiluca* ephyrae for certain prey taxa was evident when the gut content data were compared to the potential prey abundance data. At all stations with ephyrae, positive selection was observed for chaetognaths, mollusc larvae and fish larvae. Positive selection was shown for chaetognaths and mollusc larvae in both day and night, but fish larvae were positively selected only at night (Fig. 5). In contrast, selection for copepods was negative or neutral, in spite of the fact that they were the main group of ingested prey (Table 3).

Most species of fish larvae ingested by *P. noctiluca* belonged to the Family Myctophidae, but anchovy, *Engraulis encrasicolus* and Sparidae larvae also were found in the gastric pouches (Table 5). Higher diversity of fish larva prey occurred at the front station, and the species captured most often was *E. encrasicolus* (Table 5).

There was a significant positive correlation ($R^2 = 0.62$, $P < 0.05$; Fig. 6) between mean log

Table 5 Specific composition and relative frequency (% based on total number) of fish larvae found in stomachs of *Pelagia noctiluca* ephyrae during 18–23 June 1995

	Shelf	Front	Open sea
Ceratoscopelus maderensis (Lowe, 1839)	–	21	–
Hygophum benoiti (Cocco, 1838)	50	4	20
Lampanyctus crocodilus (Risso, 1810)	50	8	60
Lampanyctus pusillus (Johnson, 1810)	–	–	20
Myctophum punctatum Rafinesque, 1810	–	4	–
Vinciguerria sp.	–	4	–
Engraulis encrasicolus (Linnaeus, 1758)	–	38	–
Sparidae	–	4	–
Unidentified	–	17	–
Total number	2	26	5
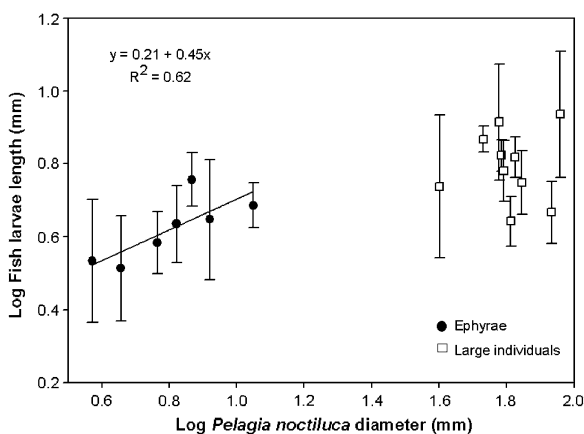
Fig. 6 Mean (± standard deviation) of log-transformed larval fish length (mm) in relation to log mean *Pelagia noctiluca* diameter (mm) in the north western Mediterranean Sea during 18–23 June 1995. *Black circles*: ephyrae (<12 mm diameter); *open squares*: larger individuals; *solid lines*: regressions

standard length of fish larvae ingested by *P. noctiluca* and the mean log diameter of *P. noctiluca* ephyrae (4–12 mm); however, there was no positive correlation between the length of ingested larvae and the diameter of larger *P. noctiluca* (40–90 mm). Nevertheless, the mean number of prey in the gastric pouches was greater for larger medusae (4.96 ± 2.64 SD) than for ephyrae (1.03 ± 0.16 SD), and these differences were statistically significant (Student's *t* test = −7.923, $P < 0.01$).

Discussion

The distribution of gelatinous zooplankton along the coastal to open sea transect was related to the presence of the shelf-slope front. The pelagic cnidarian community included representatives of all major taxonomic groups and was predominated by the siphonophore, *M. atlantica*. Coastal waters were populated mainly by meroplanktonic species (antho- and leptomedusae) whereas shelf and "offshore" water had more holoplanktonic species (trachy- and narcomedusae). This spatial pattern, characterized by increasing species diversity and abundance with distance from the coast, is a common trend in the northwestern Mediterranean (Gili et al., 1987a; Bouillon et al., 2004). The abundance of several species (Tables 1, 2) agrees with previous studies showing a high abundance of gelatinous carnivores in late spring or early summer in comparison with the rest of the year in the NW Mediterranean (Gili et al., 1987b).

During the last two decades, the neritic siphonophore, *M. atlantica*, and the oceanic scyphomedusan, *P. noctiluca*, have been reported as the most abundant gelatinous predators in the region (Razouls & Thiriot, 1968; Andersen et al., 2001). Moreover, Mackie et al. (1987) reported that *M. atlantica* is the predominant siphonophore species in temperate latitudes of the three major oceans. This species has replaced the previously predominant siphonophore, *Muggiaea kochi*, in the Mediterranean Sea (Riera et al., 1986; Bastić et al., 2007). *P. noctiluca* is the most conspicuous jellyfish in shelf waters of the western Mediterranean (Gili & Pagès, 2005) and in adjacent areas (Zavodnik, 1987). The high densities of most of the gelatinous species observed in this study are in accordance with the high productivity and hydrographic structure in the Mediterranean at the end of spring and early summer (Sabatés et al., 1989). Previous studies in the area corroborate the abundance of neritic species such as *L. subtilis*, *M. atlantica*, *Aglaura hemistoma* and *R. velatum* (Gili et al., 1987b, 1988).

High concentrations of coastal and offshore species of siphonophores and medusae (including hydromedusae) were found close to the shelf/slope front. These high concentrations could be related to increased primary and secondary production in the frontal area (Estrada et al., 1993; Sabatés et al.,

2004), as well as to the convergence associated with the front (Franks, 1992). Sabatés (1990) found high concentrations of shelf and oceanic fish larvae in the frontal area; however, this pattern was subject to considerable spatio-temporal variability, probably due to frontal mesoscale activity (Sabatés et al., 2004). Aggregations of gelatinous organisms around physical discontinuities have been reported in different geographical areas (e.g. Pagès et al., 2001; Lučić et al., 2005). The abundance of various types of gelatinous zooplankton at the front could be explained by interactions between physical and biological mechanisms occurring at local scales (Graham et al., 2001). Coastal hydromedusae would be concentrated at the front as a result of advection because those species do not produce new medusae in open waters far from shore. Siphonophores are holoplanktonic and able to proliferate in open waters at the productive front, thereby establishing large populations where prey are abundant (Purcell, 1982; Graham et al., 2001). In this study, the high concentration of gelatinous predators in the front area could have important trophic consequences for the planktonic communities. Surprisingly, although the abundance of zooplankton prey was highest in the frontal area, the feeding incidence of *P. noctiluca* was lowest there. This observation could be related to the high numbers of *P. noctiluca* and other planktonic predators in the front waters, which could result in low individual food availability. In the same area, Saiz et al. (1999) observed that copepod growth and abundance were uncoupled from phytoplankton abundance, and suggested that predation, rather than advection or physical retention, could explain the copepod distribution and production in the area.

Previous studies on *P. noctiluca* demonstrated that this species is an opportunistic predator that consumes a wide variety of prey (e.g. Malej, 1989). In our study, the diet of *P. noctiluca* ephyrae consisted mainly of copepods, but other prey such as euphausids, chaetognaths and fish larvae also were eaten. Predation on fish larvae was particularly important in the frontal area, where larvae of both shelf and oceanic species occurred (Sabatés et al., 2007a). Larvae of commercially important fish species, such as anchovy, are often removed in high proportions relative to the other taxa (Purcell, 1989; Purcell et al., 1994). In the Kiel Fjord, the calculated daily predation rate of *Aurelia aurita* medusae was as high as 5%

of the herring larvae (Möller, 1984). We were unable to estimate consumption rates of fish larvae in the NW Mediterranean because we lacked the length of time required by medusae to digest fish larvae; nevertheless, consumption of fish larvae clearly is important because they represented up to 12% of total prey captured by *P. noctiluca*.

Very few studies have examined natural prey consumed by ephyrae (Table 6). More microzooplankton prey (ciliates, rotifers and copepod nauplii) were consumed by ephyrae of *Chrysaora quinquecirrha* (Desor) and *A. aurita* (Linneaus) than by *P. noctiluca*, perhaps due to their small sizes relative to *P. noctiluca*. The prey available to the three species also differed because *P. noctiluca* ephyrae were in the open Mediterranean Sea but the others were in shallow estuaries. Even ephyrae only a few millimetres in diameter consumed large prey, including other gelatinous taxa (siphonophores, ctenophores, and hydromedusae) and larval fish.

Day–night variations in feeding could be related to the diel vertical migrations of *P. noctiluca* and their prey. In deep waters, *P. noctiluca* is distributed mostly between the surface and 150 m depth, but during the day it can also be found deeper, between 300 and 500 m (Mariottini et al., 2008). It is not known if ontogenetic changes in depth distribution occur in *P. noctiluca*. In the study area, at the end of spring and beginning of summer, chaetognaths and mollusc larvae are very abundant and concentrate between 60 and 150 m depth (Vives, 1966) and near the bottom in coastal waters (Martin et al., 1997). Fish larvae are mainly distributed in the surface layers above the thermocline (Olivar & Sabatés, 1997; Sabatés, 2004). Anchovy larvae, the most abundant species during spring–summer, are located around 50 m depth during the day and migrate to the surface at night (Olivar et al., 2001; Sabatés et al., 2008). Thus, fish larvae and *P. noctiluca* co-occur in surface waters at night, and our data indicate that prey selection was positive then. Positive selection for ichthyoplankton by other jellyfish species has been reported in other areas as well (Purcell, 1985, 1989; Purcell et al., 1994; Purcell & Sturdevant, 2001).

In this study, the size of ingested larval fish prey increased as ephyra diameter increased, although in the larger medusae, prey size was almost constant in the size range examined. This may be because the abundance of fish larvae in the field as well as their

Table 6 Numbers of ephyrae examined, ephyra diameter, in situ feeding incidence (percentage of individuals containing prey), diets (percentage number of each prey type), and total numbers of prey counted in ephyrae

	Pelagia noctiluca	*Chrysaora quinquecirrha*[a]	*Aurelia aurita*[b]
No. of ephyrae	5680	31	360
Ephyra diameter (mm)	4.0–12.0	3.8 ± 2.9	6.5–11.8
Feeding incidence (%)	8	50	0.2–0.6
Diet (%)			
Ciliates	NQ	48.4	NQ
Rotifers	NQ	22.4	87.5 +
Copepod nauplii	–	5.0	3.7 −
Copepoda	59.2 −	20.4	4.2 −
Mollusc larvae	4.3 +	0.9	NA
Gelatinous species	Siphonophores 3.7	Ctenophores NQ	Hydromedusae 4.1 +
Chaetognatha	4.7 +	NA	NA
Ostracoda	0.4	NA	NA
Euphausiacea	8.3	NA	NA
Decapoda larvae	0.6	NA	NA
Appendicularia	2.7	NA	NA
Cladocera	2.5	NA	NA
Fish larvae	13.7 +	2.0	NA
Total no. of prey	333	52	1387

NA not available, *NQ* not quantified; + = positive selection; − = negative selection

[a] Olesen et al. (1996)

[b] Sullivan et al. (1997)

susceptibility to predation decline with size (Cowan & Houde, 1992). The maximum size of most fish larvae in the plankton in that area and for the same period is ~10 mm (Sabatés et al., 2007b); therefore, large larvae were very scarce. In addition, digestion is more rapid for small than for large fish larvae, so small larvae would not be as easy to recognize in gut contents as would large larvae. Thus, availability, susceptibility and digestion would explain why large individuals of *P. noctiluca* contained almost a constant larval size range. Similarly, Cowan & Houde (1992) reported size-dependent predation rates on anchovy larvae by *C. quinquecirrha* medusae in controlled experiments. Unlike the larval size, the number of larvae in *P. noctiluca* gastric pouches increased with jellyfish size, presumably because larger medusae can catch a wider range of larval sizes and can effectively fish a larger volume of water than small ephyrae (Madin, 1988).

Our results not only indicate high predation on fish larvae by *P. noctiluca* medusae, which occur in high densities over wide reaches of the oceans (e.g. Doyle

et al., 2008), but also demonstrate the potential for competition for zooplankton prey between zooplanktivorous fish (e.g. anchovy) and *P. noctiluca* and other abundant planktonic cnidarians. Most pelagic cnidarians consume mostly copepods (Purcell, 1981, 1997; Purcell & Mills, 1988), and diet overlap between medusae and fishes have been documented (Purcell & Grover, 1990; Purcell & Sturdevant, 2001; Brodeur et al., 2008). Zooplankton predators and prey were concentrated in the front area, but fewer prey items were found in *P. noctiluca*, which suggests that prey might be limiting at the front.

In summary, this study has highlighted how different communities/species of gelatinous zooplankton are found in different habitat types at sea. The highest zooplankton abundances occurred at the frontal area, where some species are concentrated. The diet of the most abundant medusa, *P. noctiluca*, consisted mainly of copepods, but almost 12% of the prey items were fish larvae. Thus, this species may exert important trophic effects on plankton communities, including fish larvae, considering its

widespread occurrence. The abundant and diverse pelagic cnidarian fauna of the Mediterranean Sea is of great importance as both predators and competitors of fish populations.

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