Vol. 591: 101–116, 2018
https://doi.org/10.3354/meps12332

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 19[§]

Contribution to the Theme Section 'Jellyfish bloom research: advances and challenges'

Trophic interactions of the jellyfish *Pelagia noctiluca* in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition

Uxue Tilves[1,*], Verónica L. Fuentes[1], Giacomo Milisenda[2], Christopher C. Parrish[3], Salvatrice Vizzini[4], Ana Sabatés[1]

[1]Institut de Ciències del Mar, CSIC, Pg. Maritim de la Barceloneta 37-49, 08003 Barcelona, Spain
[2]Dipartimento Terra e Ambiente, CNR–IAMC Mazara del Vallo, 91026 Italy
[3]Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada
[4]Department of Earth and Marine Sciences, University of Palermo, via Archirafi 18, 90123 Palermo, Italy

ABSTRACT: Jellyfish have the potential to dominate the pelagic biomass of marine ecosystems, thereby negatively affecting pelagic fish. We investigated the trophic interactions of *Pelagia noctiluca* (medusae and ephyrae), one of the most abundant and conspicuous jellyfish on the Catalan coast in the NW Mediterranean. A combination of stable isotope and fatty acid analyses was used to obtain a broad picture of the feeding habits of this jellyfish in order to understand its potential interactions with the most abundant fish species (larvae and adults) during the summer in the area. The results suggested that in addition to predation on fish larvae by *P. noctiluca*, this jellyfish had similar feeding requirements to those of most fish larvae, suggesting potential competition. The trophic niche of medusae and ephyrae overlapped highly with that of larval *Engraulis encrasicolus*, *Trachurus mediterraneus* and *Sardinella aurita* and to a lesser extent with that of *Serranus hepatus, Sparus pagrus* and *Mullus barbatus.* No overlap was observed with *Arnoglossus* sp. larvae and adult *E. encrasicolus, Sardina pilchardus, T. mediterraneus* and *S. aurita*. Our findings demonstrated that *P. noctiluca* could be an important predator and competitor for fish larvae, but not for adult fish. Moreover, salps were found to be a significant food source for *P. noctiluca*. This study provides information that should be considered in near-future ecosystem-based fishery management in regions where *P. noctiluca* thrives.

KEY WORDS: Medusae · Ephyrae · Predation · Competition · Fish larvae · Pelagic fish

INTRODUCTION

Jellyfish are common organisms living around the world, with populations increasing in some areas (Brotz & Pauly 2012, Duarte et al. 2013), which can influence bottom-up and/or top-down processes (Purcell et al. 2007). Different mechanisms are thought to drive the upward trend in gelatinous zooplankton, such as climate change (Brodeur et al. 1999, Lynam et al. 2004, Attrill et al. 2007), introduction of invasive species (Shiganova 1998, Graham & Bahya 2007), eutrophication (Xian et al. 2005) or removal of their predators and competitors (Daskalov et al. 2007). Regardless of whether the increase is due to any of these factors, the outcome of jellyfish blooms is that there are serious implications for ecosystem organization and functioning (Boero 2013).

Jellyfish, especially scyphozoan medusae, have the potential to dominate the pelagic biomass of marine ecosystems (Brodeur et al. 2008), negatively affecting pelagic fish, with economic implications in the case of commercial species. For this reason, different studies have focused on the potential interactions between jellyfish and fish (reviewed by Purcell & Arai 2001). Positive and negative interactions have been described between both groups, although negative ones seem to prevail due to competition for food or through direct predation by jellyfish on fish eggs and larvae

*Corresponding author: tilves@icm.csic.es
[§]Advance View was available online January 11, 2018. Methods were corrected in the present version. See www.int-res.com/abstracts/meps/v591/c_p101–116 for details

(Möller 1980, Purcell & Sturdevant 2001, Brodeur et al. 2008, Tilves et al. 2016). Likewise, jellyfish may share the same trophic level of many pelagic fish; therefore, any potential reduction of the latter (due to overfishing or competition for food) may allow jellyfish to occupy the entire trophic niche (Brodeur et al. 2008). As an example, in the California Current, years with high jellyfish biomass coincide with low forage fish biomass and vice versa (Brodeur et al. 2014). In the NW Mediterranean, Tilves et al. (2016) concluded that in a bloom situation the potential predation of *Pelagia noctiluca* on fish larvae, particularly on anchovy *Engraulis encrasicolus*, could be extremely high. Carnivorous jellyfish are mainly subject to bottom-up controls from their forage base (Pauly et al. 2009), suggesting that information on their feeding strategy is essential to understanding their ecophysiology and their trophic interactions within the ecosystem.

P. noctiluca is an important species in the Mediterranean Sea in terms of abundance and distribution (Canepa et al. 2014), and large blooms have been recorded in recent years (Gili & Pagès 2005, Daly Yahia et al. 2010, Kogovšek et al. 2010, Bernard et al. 2011). Although *P. noctiluca* is characteristic of warm waters, it also inhabits temperate and cold areas in the North Pacific, North Atlantic and North Sea (Mariottini et al. 2008). This species has been described as an opportunistic predator that feeds on a wide variety of prey (Malej 1989, Rottini Sandrini & Avian 1989), including ichthyoplankton (Sabatés et al. 2010, Rosa et al. 2013, Tilves et al. 2016). In fact, high feeding rates have been reported when feeding on fish larvae (Sabatés et al. 2010, Tilves et al. 2016), with a potential high impact on their populations, especially in a bloom situation (Tilves et al. 2016).

With only 2 exceptions (Malej et al. 1993, Milisenda 2014), studies on the feeding ecology of *P. noctiluca* have been based on the analysis of gut contents (Larson 1987, Malej 1989, Giorgi et al. 1991, Zavodnik 1991, Daly Yahia et al. 2010, Sabatés et al. 2010, Rosa et al. 2013, Tilves et al. 2016). However, as stomach content analysis can only identify the most recently ingested items, or items that require long digestion times, conclusions based on this approach may give biased results (Pitt et al. 2008). Furthermore, small microscopic prey are not easily detectable and may often be missed, leading to the loss of important information (Sullivan et al. 1994, Pitt et al. 2008). This is why, in recent years, molecular biomarkers, such as stable isotopes (SIs) of nitrogen and carbon and fatty acids (FAs), have increasingly been used as complementary approaches to gut content analysis. On the one hand, the SI approach for trophic analysis is based on the assumption that there are systematic and predictable changes in the isotopic signatures of a consumer, relative to its prey or food resource (Minagawa & Wada 1984). $\delta^{15}N$ values usually provide information about predator–prey relationships and the trophic level of an individual, while $\delta^{13}C$ values usually determine the primary production sources used by consumers (Vander Zanden & Rasmussen 2001, Mallela & Harrod 2008). On the other hand, some essential FAs are required for energy and the biological functioning of membranes and organs, but not all are synthesized de novo by animals so they have to be obtained from the diet. FAs consumed by a predator are transferred from the prey and assimilated with little modification by the predator, providing information on their feeding habits (Budge et al. 2006). Thus, biomarkers give a temporally and spatially integrated picture of feeding history and trophic position of a predator, and may allow identification of trophic relationships within the food web (Peterson & Fry 1987, Waite et al. 2007, Pitt et al. 2008). However, these markers have not been extensively used in studies involving gelatinous zooplankton (Pitt et al. 2008), although some work used these techniques in the study of different species, e.g. *Aurelia aurita, Stomolophus meleagris* and *Cyanea nozakii* (Ying et al. 2012), *Mnemiopsis leidyi* (Montoya et al. 1990), *Chrysaora melanaster* (Brodeur et al. 2002), *Catostilus mosaicus* (Pitt et al. 2008) and *P. noctiluca* (Malej et al. 1993, Cardona et al. 2012, Milisenda 2014).

The aim of our study was to determine the trophic interactions, i.e. predation and/or competition, between *P. noctiluca* (ephyrae and medusae) and the most abundant fish species (larvae and adults) during summer on the NW Mediterranean coast, using a combination of SI and FA analyses. Furthermore, we aimed to compare the results obtained with those from *P. noctiluca* gut content analysis (Tilves et al. 2016) carried out during the same samplings. As *P. noctiluca* inhabits different areas worldwide (Mariottini et al. 2008) and its outbreaks are becoming more frequent, the knowledge of its trophic interactions is important to predict the consequences of outbreaks on ecosystems and is essential for ecosystem-based fishery management (Robinson et al. 2014).

MATERIALS AND METHODS

Sampling

The study was conducted off the Catalan coast (NW Mediterranean) in June 2011, during an oceano-

graphic cruise on board the RV 'García del Cid'. Specimen collection was carried out in an area (40° 53′ 12″ N, 1° 15′ 12″ E) determined by the high presence of *Pelagia noctiluca* (medusae and ephyrae) and fish larvae. Medusae were individually collected at the surface from the vessel's deck during the night, using a long-handled dip net. Immediately after collection, they were placed in buckets filled with filtered seawater to remove any attached zooplanktonic organisms, then frozen in liquid nitrogen and stored at −80°C until further analyses.

Ephyrae and zooplankton samples (including ichthyoplankton) were collected by depth-stratified tows using a MOCNESS net with a 1 m^2 opening mouth and a 300 µm mesh, approximately every 10 h, avoiding sunset and sunrise hours. Two samplings were performed during the night and 2 during the day. The hauls were oblique, towing from deep to shallow layers at 2–2.5 knots. The depth strata sampled were: 150–100, 100–50, 50–25 m and 25–0 m, and the volume of water filtered was recorded by a flow meter attached to the mouth of the net. Zooplankton samples were split into 2 subsamples; one was used to determine plankton composition and to separate out major groups (copepods, euphausiids, mysidaceans, chaetognaths, siphonophores, salps and fish larvae of different species) for biochemical analyses, while the other was size-fractionated using a series of sieves (250, 500 and 1000 µm) and filtered on pre-combusted (500°C, 4 h) GF/F 47 mm filters (0.7 µm, Whatman). After these procedures, all samples were immediately frozen in liquid nitrogen and stored at −80°C.

Adult individuals of pelagic planktivorous fish, i.e. *Engraulis encrasicolus, Sardina pilchardus* and *Trachurus mediterraneus*, which are potential competitors of *P. noctiluca* for planktonic prey, were collected during the same period from commercial vessels that operate in the same area. All individuals were immediately frozen after capture and stored at −20°C until further analyses.

Laboratory analyses

SI analysis

Isotopic composition was determined from ~5 mg of whole medusae (n = 15), ~1 mg of size-fractionated zooplankton (n = 68), ~0.8 mg of white muscle of adult fish (n = 15) and entire individual organisms of zooplankton (including ephyrae and fish larvae; n = 110). Although the use of the whole organism for isotopic analysis is a controversial topic, as it has been suggested that different body tissue have different isotopic composition (Pitt et al. 2008, 2009), recent studies have demonstrated that whole medusae are a good indicator to quantify the isotopic signature (D'Ambra 2012, D'Ambra et al. 2013).

Prior to the analysis, the sizes of the organisms were measured. Medusae ranged from 40 to 97 mm, ephyrae from 3 to 10 mm and fish larvae from 3 to 8 mm standard length. Depending on the organism size, samples were treated individually or pooled to obtain sufficient material. Medusae were large enough to obtain the required weight from single samples. In the case of ephyrae <5 mm and fish larvae <4 mm, >1 individual was pooled. Copepods, fish eggs, chaetognaths and salps were also analysed by pooling >1 individual for each replicate. After storage (−80°C), samples were freeze-dried and ground to a fine powder. They were then weighed in tin cups, except for crustaceans and fractionated zooplankton samples, which were acidified (1 N HCl) to remove carbonate structures. $\delta^{13}C$ and $\delta^{15}N$ values were determined using an isotope ratio mass spectrometer (Thermo Delta Plus XP) coupled to an elemental analyser (Thermo Flash EA 1112) through an open split interface (CONFLO III). $\delta^{13}C$ and $\delta^{15}N$ values were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric N_2 standards, respectively, according to the formula:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3 \quad (1)$$

where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Instrumental precision based on the SD of replicates of internal standards (International Atomic Energy Agency IAEA-NO-3 for $\delta^{15}N$ and IAEA-CH-6 for δ^{13}) was ±0.2 for both $\delta^{13}C$ and $\delta^{15}N$ values.

FA analysis

Lipid extraction. Lipids were extracted from freeze-dried powdered samples. Approximately 100 mg of medusae, 100 mg of size-fractionated zooplankton, 100 mg of white muscle of adult fish and entire individual organisms of zoo- and ichthyoplankton were placed in test tubes, and 5 ml of extracting solution (methanol:chloroform:water 1:2:1 v/v/v) were added. The tube was sonicated over ice and centrifuged for 2–3 min. The organic layer was then removed and placed in new centrifuge vials. Addition of chloroform, sonication and centrifugation were repeated at least 3 times, and then the volume of the new vial was evaporated down under a gentle stream of nitro-

gen before storing in a freezer until lipid transmethylation.

Transmethylation and FA determination. The organic solution obtained from lipid extraction was blown dry under nitrogen at room temperature before adding 1.5 ml of methylene chloride and 3 ml of Hilditch reagent (0.5 N H_2SO_4 in methanol). The sample was then vortexed and sonicated to remove adsorbed lipids and heated at 100°C for 1 h. After cooling, 0.5 ml of saturated sodium bicarbonate solution and 1.5 ml of hexane were added. The tube was vortexed, and the upper, organic layer containing FA methyl esters (FAMEs) was transferred to a vial and blown dry. The extraction was repeated twice, blowing down in between. After addition of an internal injection standard (19:0 FAME), samples were analysed by gas chromatography (GC).

Samples were analysed using an Agilent Technologies 7890B GC equipped with an Equity™-1 fused silica capillary column (15 m × 0.1 mm internal diameter and 0. 1 µm film thickness), a flame ionization detector, a split/splitless injector, and an Agilent Technologies 7683B Series autosampler. Peaks were quantified using Agilent Technologies ChemStation software. FAMEs were identified by GC–mass spectrometry (GC/MS) using a Finnigan Thermoquest GCQ GC/MS fitted with an on-column injector and Thermoquest Xcalibur software. Procedures for FA derivatization, identification and quantification were based on Miller et al. (2006).

Indicators of trophic interactions

A number of established FA markers or ratios were used to understand diet preferences of *P. noctiluca*. Markers of diatoms include 14:0, 16:1ω7, 18:1ω7 and 20:5ω3, while markers of dinoflagellates include 22:6ω3, 18:4ω4 and 22:5ω3 (Dalsgaard et al. 2003, Parrish 2013). Relative ratios provide an indication of long-term trophic exchanges: the ratio of 16:1ω7 to 16:0 was used to discriminate between diatom and dinoflagellate feeding (Parrish et al. 2000, Rossi et al. 2006). Ratios of 16:1ω7 to 16:0 >2 are considered to represent a strong presence of diatoms, whereas ratios <0.3 suggest dinoflagellates. The 18:1ω9 to 18:1ω7 ratio, considered a copepod-consumption marker (Dalsgaard et al. 2003), was also used to indicate a potential carnivorous diet of *P. noctiluca*. High levels of 22:1ω11 and 20:1ω9 are present in large calanoid copepods (Dalsgaard et al. 2003), while high levels of 18:1ω9, 16:0 and 20:5ω3 are characteristic of small copepods (Kattner et al. 2003).

Statistical analysis

Differences in the SI signatures of the zooplankton samples collected during the day and night were assessed with the Mann–Whitney non-parametric test, and no differences were observed ($\delta^{13}C$: U = 659.5, p = 0.07; $\delta^{15}N$: U = 950.0, p = 0.26); consequently, samples were treated without day time distinction. Differences in the SI signatures between medusae and ephyrae (all individuals were collected at the surface) were analysed with the Mann–Whitney non-parametric test. ANOVAs or Kruskal–Wallis tests (when ANOVA assumptions were not met) were carried out to assess differences in SIs of potential prey between depths

In order to obtain the relative contributions of the different food sources to *P. noctiluca* diet, we used a Bayesian stable-isotope mixing model (SIAR; Parnell et al. 2008), which allows the inclusion of isotopic signatures, elemental concentrations and fractionation together with the uncertainty of these values within the model. In order to use mixing models, the isotopic values for food sources must be adjusted by appropriate fractionation factors (Gannes et al. 1998). Here, we used fractionation values for *P. noctiluca* determined in the laboratory ($\Delta\delta^{15}N$ = 2.4‰; $\Delta\delta^{13}C$ = 0.7‰; Tilves et al. unpublished data). The position of a species in a $\delta^{13}C$:$\delta^{15}N$ biplot is representative of its ecological niche (Newsome et al. 2007) and can be established by calculating the standard ellipse area for small sample sizes (SEAc) from individual measurements. These size-corrected SEAc are bivariate equivalents to SDs in a univariate analysis (Jackson et al. 2011). We evaluated the total trophic niche of jellyfish and fish (larvae and adults), and the potential niche overlap between them was estimated as the percent of overlapping SEAc (Parnell et al. 2008). These analyses were performed using the SIAR package (Parnell et al. 2008) for the R statistical computing package.

FA relationships were investigated using Plymouth Routines in Multivariate Ecological Research (PRIMER) software. Differences in the FA profiles between both life stages of jellyfish were determined using permutational multivariate ANOVA (PERMANOVA) and principal components analysis (PCA). Relationships between the composition of *P. noctiluca* and its potential prey were explored using non-metric multidimensional scaling (nMDS). Similarity percentages (SIMPER) analyses were used to identify individual FA contributions to average dissimilarities among groups.

RESULTS

SI analysis

Medusae and ephyrae of *Pelagia noctiluca* were not significantly different from each other in terms of their $\delta^{13}C$ and $\delta^{15}N$ (Fig. 1, Table 1). Moreover, both stages fed at a similar average trophic level, as indicated by similar $\delta^{15}N$ values (5.5 ± 0.5‰ for medusae and 4.5 ± 0.5‰ for ephyrae; Fig. 1, Table 1). Each fraction of zooplankton (which comprised a mix of different groups of zooplankton) except for 500–1000 µm was statistically different among depths in terms of $\delta^{15}N$ and $\delta^{13}C$ (Table 1), so data from each depth were treated independently. However, major zooplankton groups (e.g. fish larvae, copepods, euphausiids) did not differ between depths (Table 1), apart from marginal differences in Mysidacea, so they were treated without distinction by depth.

A comparison of the differences in the patterns of $\delta^{13}C$ and $\delta^{15}N$ isotopic composition between *P. noctiluca* (medusae and ephyrae) and other planktonic components (fish larvae, size-fractioned zooplankton and individual zooplanktonic groups) and adult fish was carried out (Fig. 1). *P. noctiluca* (medusae and ephyrae) and fish larvae were characterized by similar values of $\delta^{13}C$ (–20.55 ± 0.4‰, –20.87 ± 0.2‰, –20.60 ± 0.4‰ for medusae, ephyrae and fish larvae, respectively). Their $\delta^{15}N$ signatures (5.5 ± 0.5‰, 4.5 ± 0.5‰, 5.6 ± 0.4‰ for medusae, ephyrae and fish larvae, respectively) highlighted a shared trophic level for *P. noctiluca* and fish larvae, which was lower than that of adult fish (9.3 ± 1.1‰; Fig. 1). Adult fish had a higher $\delta^{13}C$ value (–18.8 ± 0.3‰) than both life stages of *P. noctiluca* (Fig. 1). Zooplankton fractions from all depths belonged to a comparable trophic level as *P. noctiluca*, showing similar values of $\delta^{15}N$ (from 4.2 ± 0.2‰ to 6.0 ± 0.2‰), but they were more ^{13}C-enriched (from –21.7 ± 0.5‰ to –20.7 ± 0.2‰; Fig. 1). Among all groups analysed, salps showed the lowest $\delta^{15}N$ signature (Fig. 1). With respect to $\delta^{13}C$, salps and copepods were farthest from *P. noctiluca* medusae, while salps and siphonophores had signatures farthest away from ephyrae (Fig. 1).

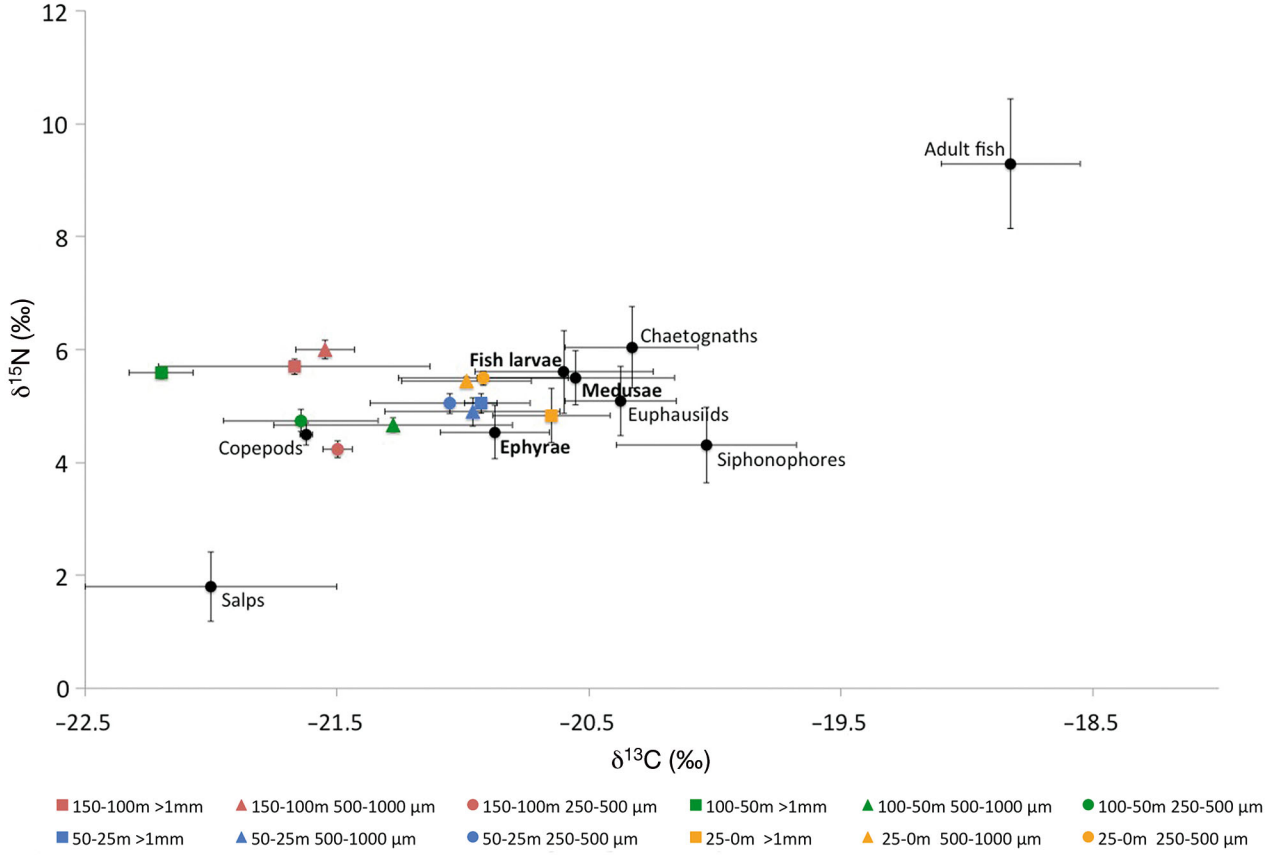

Fig. 1. $\delta^{13}C$ and $\delta^{15}N$ (mean ± SD) of *Pelagia noctiluca* (medusae and ephyrae), fish (adults and larvae) and their potential zooplanktonic prey. Symbols and colours differentiate size-fractionated zooplankton and the depths at which they were collected. Major zooplankton groups (such as fish larvae and copepods) did not differ between depths; these groups are represented by black circles and are individually labelled in the figure

Table 1. Results of Kruskal–Wallis tests on $\delta^{13}C$ and $\delta^{15}N$ values of major zooplankton groups performed to assess differences between collection depths, and results of Mann–Whitney tests performed to assess differences between *Pelagia noctiluca* medusae and ephyrae. *U*-values correspond to Mann–Whitney tests; *F*-values correspond to 1-way ANOVAs; χ^2-values correspond to Chi-squared tests. Values in **bold** are significant at $p < 0.05$

Functional groups	Collection depth (m)	$\delta^{13}C$ Test statistic	$\delta^{13}C$ p	$\delta^{15}N$ Test statistic	$\delta^{15}N$ p
Zooplankton 250–500 µm	150–100 (n = 3) 100–50 (n = 10) 50–25 (n = 3) 25–0 (n = 6)	$\chi^2 = 12.679$	**0.005**	$F = 49.140$	**<0.001**
Zooplankton 500–1000 µm	150–100 (n = 6) 100–50 (n = 6) 50–25 (n = 6) 25–0 (n = 6)	$\chi^2 = 3.746$	0.290	$\chi^2 = 13.520$	**0.004**
Zooplankton >1000 µm	150–100 (n = 6) 100–50 (n = 6) 50–25 (n = 4) 25–0 (n = 6)	$\chi^2 = 6.231$	**0.044**	$\chi^2 = 8.423$	**0.015**
Copepods	100–50 (n = 3) 50–25 (n = 3) 25–0 (n = 3)	$\chi^2 = 5.015$	0.051	$\chi^2 = 6.455$	0.214
Siphonophores	50–25 (n = 3) 25–0 (n = 7)	$F = 0.123$ df =1	0.452	$F = 0.236$	0.794
Salps	50–25 (n = 5) 25–0 (n = 7)	$F = 19.906$ df =1	0.070	$F = 2.875$	0.121
Fish larvae	150–100 (n = 3) 50–25 (n = 6) 25–0 (n = 32)	$\chi^2 = 2.909$	0.113	$\chi^2 = 4.216$	0.077
Euphausiids	100–50 (n = 2) 50–25 (n = 3) 25–0 (n = 3)	$\chi^2 = 2.134$	0.125	$\chi^2 = 2.555$	0.053
Mysidaceans	100–50 (n = 1) 50–25 (n = 3) 25–0 (n = 3)	$\chi^2 = 4.143$	**0.049**	$\chi^2 = 2.687$	**0.048**
Medusae vs. Ephyrae	25–0 ($n_{medusae}$ = 15) 25–0 ($n_{ephyrae}$ = 20)	$U = -1.610$	0.108	$U = -1.360$	0.233

Based on SI-mixing models, medusae presented a more varied diet compared to ephyrae (Fig. 2). Salps were the major contributor to the assimilated diet of both *P. noctiluca* medusae and ephyrae, with an average contribution reaching almost 70% in both stages (Fig. 2). The other prey types included in the model constituted the remaining proportions of the medusae diet, with no single prey type dominating. Copepods and siphonophores were relevant to the ephyrae diet, with a maximum contribution of 33 and 25%, respectively (Fig. 2B).

The trophic niche of *P. noctiluca* medusae overlapped that of almost all fish larvae, although the degree of overlap differed among species. High niche overlap, between 18 and 51%, was detected with *Engraulis encrasicolus* (18.1%), *Trachurus mediterraneus* (51.2%) and *Sardinella aurita* larvae (35.5%; Fig. 3A). Although in lower proportions, medusae also overlapped with *Serranus hepatus* (14.3%), *Sparus pagrus* (0.1%) and *Mullus barbatus* (4.1%), while *Arnoglossus* sp. niche ellipses did not touch that of medusae (Fig. 3B). No niche overlap was observed between medusae and adult fish, with the adult fish being more ^{15}N- and ^{13}C-enriched than *P. noctiluca* medusae (Fig. 3E). Ephyrae showed a lower degree or even no overlap with fish larvae. The ephyrae niche did not overlap with those of *Arnoglossus* sp., *M. barbatus* or *S. pagrus* (Fig. 3D), while there was a high overlap with *T. mediterraneus* (21.0%), *E. encrasicolus* (16.9%) and *S. aurita* niches (19.4%; Fig. 3C). As with medusae, no niche overlap was observed between ephyrae and adult fish (Fig. 3F).

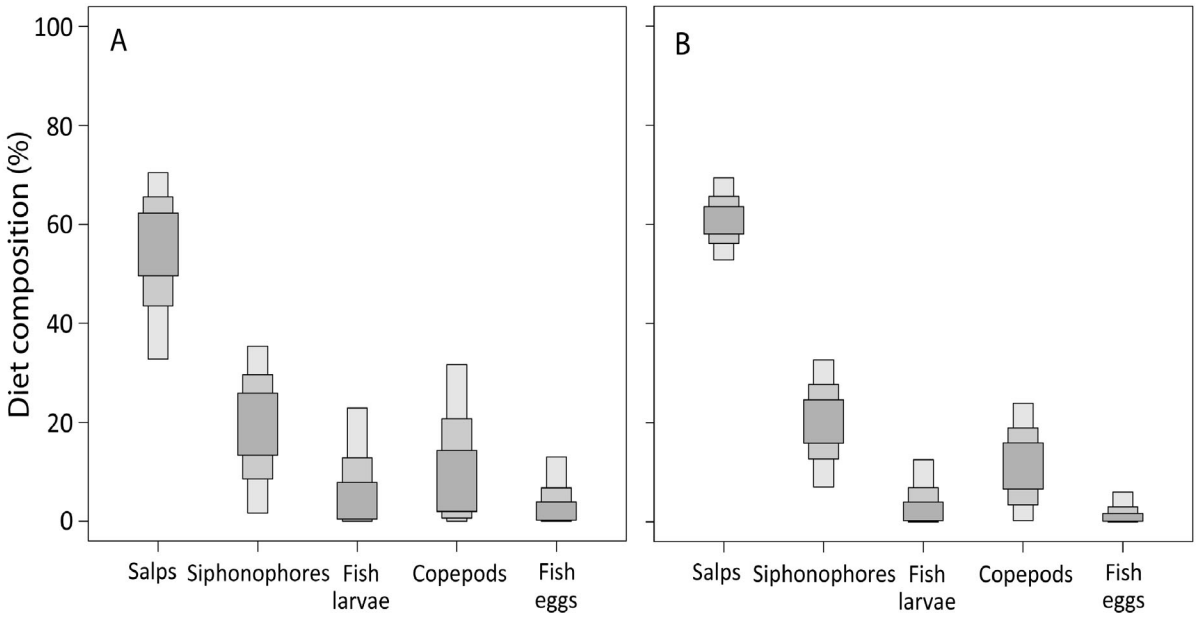

Fig. 2. Contribution of major zooplankton groups to the diet of *Pelagia noctiluca* (A) medusae and (B) ephyrae on the Catalan coast calculated using SIAR. Grey scale (from light to dark) indicates 95, 75 and 25% confidence intervals, respectively

FA analysis

FA compositions of the different groups analysed are presented in Table 2. In medusae, saturated FAs (SFAs) were the most abundant compounds, accounting for 65 ± 7% of the total FAs. Monounsaturated FAs (MUFAs) were the second most abundant FA group, followed by polyunsaturated FAs (PUFAs) (Table 2). For ephyrae, however, the composition followed the opposite trend, with PUFAs comprising the major proportion of the FAs (Table 2). Fish (adults and larvae), size-fractionated zooplankton and all individual planktonic organisms, except salps, also had a high PUFA content. In the case of salps, SFA were the most abundant compounds, as was observed in medusae. Diatom markers (e.g 16:1ω7, 20:5ω3) were present in all organisms, but the Σ16:1 to 16:0 ratio was <0.3 in all analysed organisms, with the exception of salps, copepods and size-fractionated zooplankton, which possessed values of 0.4 (values <0.3 indicate dominance of dinoflagellates). Dinoflagellate markers, such as 22:6ω3, were elevated in all groups of organisms. Medusae showed a higher 18:1ω9 to 18:1ω7 ratio (zooplankton marker) than ephyrae, although differences were not significant (U = 20.00; p = 0.26), and significantly lower ratios than fish larvae (U = 24.00; p < 0.01) and adult fish (U = 29.00; p < 0.01; Table 2).

PERMANOVA on log+1-transformed FA concentrations suggested that the medusae diet differed significantly from ephyrae diet (t = 2.0533, df = 18, p = 0.007), but the SIMPER test showed a similarity of 74.2% between both groups (Table 3). The MUFAs 18:1ω11, 20:1ω11 and 22:1ω9 were strongly associated with medusae (Fig. 4), while the PUFAs 20:4ω3, 20:5ω3, 21:5ω3, 22:5ω3 and 22:6ω3 were associated with ephyrae. PCA results based on the FA profiles suggested 2 main groups differentiating medusae and ephyrae diets (Fig. 4). Medusae were potentially feeding on salps and fish larvae, while ephyrae were deriving nutrients from a mix of siphonophores and zooplankton, like adult fish. The similarity between FA profiles of all organisms quantified by SIMPER showed that medusae had similarities of >69% with the rest of the groups of organisms, whereas ephyrae showed similarities >74% (Table 3). Fish larvae and adult fish had slightly higher similarity percentages with other organisms (>75% and >71%, respectively). SIMPER analyses also showed that 16:0 and 22:6ω3 were always among the top 4 contributors to the similarity among the different gelatinous groups, each contributing >4%. In the case of zooplanktonic crustaceans and fish (adults and larvae), 22:6ω3. 20:5ω3 and 18:1ω9 contributed most to their dissimilarity. When comparing *P. noctiluca* medusae with the zooplankton groups, salps were located closest in the nMDS plot (Fig. 5), and this is reflected in medusae and salps having the highest similarity (79%). Fish larvae were also close to medusae, with almost 75% similarity between them. In the case of

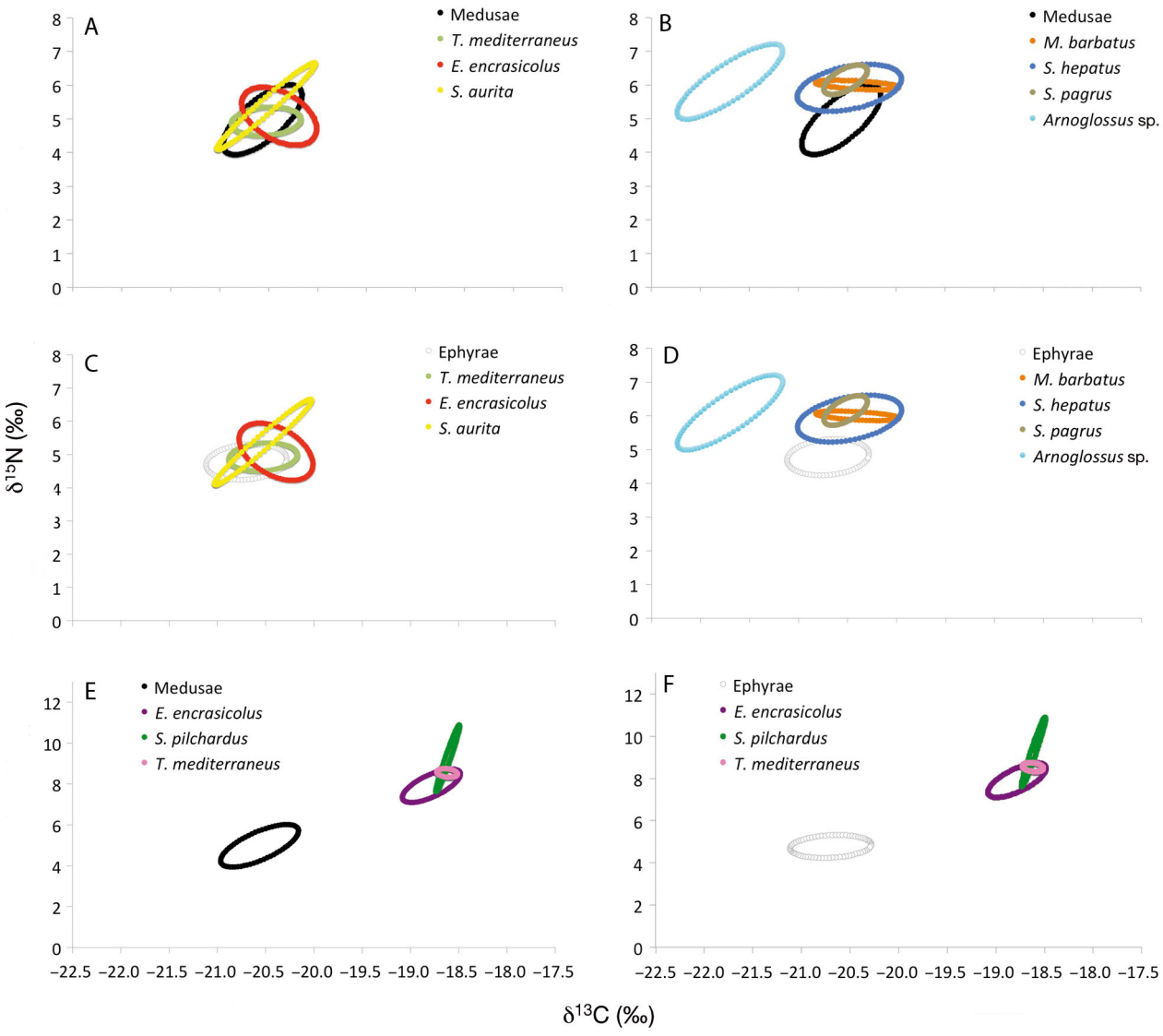

Fig. 3. Trophic niche (as size-corrected standard ellipse area) of *Pelagia noctiluca* (medusae or ephyrae, as indicated in each panel) and (A–D) fish larvae and (E, F) adult fish species on the Catalan coast

ephyrae, size-fractionated zooplankton and siphonophores seemed to be important, which was also observed in the SIMPER analysis (Table 3).

DISCUSSION

Studies based on gut content analysis of the dietary composition of *Pelagia noctiluca* in the Mediterranean Sea have described this jellyfish as a non-selective predator feeding on almost all zooplankton groups (Malej et al. 1993, Sabatés et al. 2010). Recently, Tilves et al. (2016) reported that stomach contents of *P. noctiluca* medusae and ephyrae, collected during the same oceanographic cruise as that of the present study, contained a wide variety of prey, with ichthyoplankton, siphonophores and copepods being the most important items. In the present study, biochemical trophic markers (SIs and FAs) were used for the first time to estimate dietary composition and the trophic interactions of *P. noctiluca* and different fish species (larvae and adults) in the NW Mediterranean Sea.

Some authors included *P. noctiluca* as part of the trophic web analysed (Pinnegar & Polunin 2000, Cardona et al. 2012, 2015, Syväranta et al. 2012), and the SI signatures obtained were similar to those observed in the present study. In line with this, $\delta^{13}C$ and $\delta^{15}N$ values recorded for size-fractionated zooplankton and individual groups were in the mid-range of val-

Table 2. Fatty acid (FA) composition (% of total FAs ± SD) of *Pelagia noctiluca* (medusae and ephyrae), fish (larvae and adults) and their potential prey collected on the Catalan coast. SFA: saturated FA, MUFA: monounsaturated FA, PUFA: polyunsaturated FA

FA	Medusae	Ephyrae	Salps	Siphono-phores	Cope-pods	Euphau-siids	Mysida-ceans	Fish larvae	Adult fish	Size-fractionated zooplankton
14:0	3.0 ± 0.7	1.9 ± 1.1	13.2 ± 3.4	4.4 ± 0.6	5.6 ± 1.4	4.1 ± 1.1	4.5 ± 1.5	3.7 ± 1.6	2.4 ± 2.4	6.2 ± 2.7
15:0	2.4 ± 0.6	1.0 ± 0.1	1.8 ± 0.5	0.9 ± 0.0	0.5 ± 0.3	0.7 ± 0.1	1.0 ± 0.0	0.9 ± 0.3	0.5 ± 0.3	1.0 ± 0.3
16:0	33.2 ± 4.0	16.1 ± 0.5	28.3 ± 2.9	18.6 ± 1.8	14.4 ± 3.3	17.6 ± 1.4	18.3 ± 0.6	23.8 ± 5.4	22.5 ± 5.4	21.5 ± 4.0
17:0	4.9 ± 1.4	1.9 ± 0.1	1.7 ± 0.2	1.5 ± 0.4	0.8 ± 0.2	0.8 ± 0.0	0.9 ± 0.2	1.4 ± 0.4	0.7 ± 0.3	1.2 ± 0.2
18:0	18.0 ± 2.3	10.3 ± 1.4	5.4 ± 1.1	7.6 ± 1.4	4.1 ± 0.8	2.6 ± 0.9	2.9 ± 0.4	7.6 ± 2.6	6.3 ± 3.5	5.0 ± 1.0
20:0	0.6 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	0.5 ± 0.6	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
i17:0	0.3 ± 0.5	0.8 ± 0.3	0.5 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.5 ± 0.1	0.3 ± 0.2	0.3 ± 0.2
ai17:0	1.1 ± 0.4	0.6 ± 0.2	0.4 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.2
ΣSFA	**63.4 ± 10.0**	**33.0 ± 3.8**	**51.8 ± 8.5**	**33.6 ± 4.5**	**25.8 ± 6.3**	**26.7 ± 4.2**	**28.3 ± 3.0**	**38.3 ± 10.6**	**33.0 ± 12.3**	**35.6 ± 8.7**
16:1ω9	1.2 ± 0.5	0.8 ± 0.2	0.5 ± 0.1	0.5 ± 0.2	0.3 ± 0.4	0.5 ± 0.1	0.8 ± 0.3	0.5 ± 0.3	0.4 ± 0.4	0.4 ± 0.2
16:1ω7	2.1 ± 0.8	2.2 ± 0.4	11.2 ± 4.3	3.2 ± 2.2	5.2 ± 0.4	2.2 ± 0.3	3.3 ± 1.0	3.9 ± 0.9	3.0 ± 3.6	7.8 ± 2.6
16:1ω5	0.3 ± 0.1	0.6 ± 0.1	0.8 ± 0.2	0.3 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1
18:1ω9	5.7 ± 2.5	3.2 ± 2.1	5.3 ± 1.1	5.2 ± 1.7	5.7 ± 1.2	11.3 ± 1.0	10.2 ± 1.5	6.4 ± 2.8	6.1 ± 2.7	6.4 ± 1.4
18:1ω7	4.2 ± 0.9	2.6 ± 0.2	2.5 ± 0.5	1.7 ± 0.9	1.4 ± 0.8	3.8 ± 0.2	3.8 ± 0.4	2.6 ± 0.8	2.0 ± 0.8	3.0 ± 0.4
20:1ω11	0.8 ± 0.6	0.1 ± 0.1	0.4 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.3	0.1 ± 0.1	0.1 ± 0.1
20:1ω9	1.6 ± 1.0	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.0	0.9 ± 0.5	0.9 ± 0.4	1.8 ± 2.1	0.3 ± 0.3	0.5 ± 0.4	0.4 ± 0.2
22:1ω11	2.2 ± 0.6	1.0 ± 1.9	0.6 ± 0.6	0.3 ± 0.1	2.7 ± 2.9	0.2 ± 0.4	0.3 ± 0.4	0.4 ± 0.7	0.4 ± 0.6	0.5 ± 0.7
22:1ω9	2,7 ± 1.0	0.0 ± 0.1	0.3 ± 0.3	0.0 ± 0.0	0.8 ± 1.7	0.1 ± 0.1	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 1.0
24:1	0.5 ± 0.3	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.4	1.3 ± 0.7	0.6 ± 0.2	0.6 ± 0.6	0.6 ± 0.4	0.9 ± 0.4	1.0 ± 0.7
ΣMUFA	**21.1 ± 8.3**	**11.0 ± 5.3**	**22.3 ± 7.7**	**12.1 ± 5.6**	**18.6 ± 8.8**	**20.1 ± 2.9**	**21.5 ± 7.0**	**15.2 ± 6.6**	**13.6 ± 9.1**	**20.3 ± 7.4**
16:2ω4	1.0 ± 0.2	0.6 ± 0.4	0.8 ± 0.0	0.3 ± 0.5	0.6 ± 0.2	0.4 ± 0.0	0.2 ± 0.4	0.7 ± 0.2	0.6 ± 0.3	0.7 ± 0.3
16:3ω4	0.6 ± 0.4	0.4 ± 0.6	0.2 ± 0.2	0.6 ± 0.2	0.4 ± 0.2	0.6 ± 0.1	0.8 ± 0.3	0.6 ± 0.4	0.3 ± 0.1	0.5 ± 0.4
16:3ω3	0.9 ± 0.3	0.4 ± 0.2	0.6 ± 0.2	0.4 ± 0.0	0.2 ± 0.1	0.3 ± 0.0	0.4 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.1
16:4ω3	0.5 ± 0.6	0.4 ± 0.3	0.5 ± 0.5	1.6 ± 2.2	1.6 ± 1.8	0.3 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.3 ± 0.2	0.9 ± 1.3
18:2ω6	0.9 ± 0.9	1.4 ± 0.3	1.4 ± 0.0	1.3 ± 0.3	1.6 ± 0.6	2.3 ± 0.3	2.1 ± 0.1	1.6 ± 0.6	0.8 ± 0.4	1.7 ± 0.5
18:3ω6	1.1 ± 0.5	0.7 ± 0.0	0.3 ± 0.1	0.1 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0
18:3ω3	0.5 ± 0.4	0.4 ± 0.1	0.5 ± 0.1	0.7 ± 0.0	0.8 ± 0.1	1.1 ± 0.1	1.2 ± 0.5	0.4 ± 0.2	0.3 ± 0.3	0.7 ± 0.1
18:4ω3	0.1 ± 0.1	0.5 ± 0.1	0.9 ± 0.4	0.7 ± 0.1	1.6 ± 0.8	1.1 ± 0.0	1.5 ± 1.5	0.6 ± 0.4	0.5 ± 0.5	0.9 ± 0.4
20:2ω6	0.5 ± 0.4	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.5 ± 0.1	0.4 ± 0.2	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.1
20:4ω6	0.8 ± 0.5	6.0 ± 1.0	0.7 ± 0.3	4.7 ± 2.7	0.8 ± 0.6	1.2 ± 1.1	1.8 ± 0.7	0.8 ± 0.4	1.5 ± 0.6	1.2 ± 0.3
20:4ω3	0.1 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.6 ± 0.2	0.3 ± 0.3	0.5 ± 0.1	0.5 ± 0.4	0.2 ± 0.1	0.3 ± 0.2	0.3 ± 0.2
20:5ω3	1.1 ± 0.7	19.0 ± 1.4	4.7 ± 3.3	11.5 ± 2.2	12.6 ± 1.5	13.3 ± 2.3	12.5 ± 5.1	8.1 ± 2.8	7.3 ± 2.5	13.1 ± 3.7
22:4ω6	0.1 ± 0.1	1.5 ± 0.6	0.0 ± 0.0	0.2 ± 0.3	0.0 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	0.2 ± 0.3	0.0 ± 0.0
22:5ω6	0.4 ± 0.9	0.8 ± 0.1	0.4 ± 0.3	6.0 ± 5.0	1.1 ± 0.6	1.0 ± 0.1	1.0 ± 0.1	1.0 ± 0.5	1.3 ± 0.7	0.6 ± 0.3
22:4ω3	0.2 ± 0.3	0.1 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 2.2
22:5ω3	0.7 ± 1.8	4.9 ± 1.1	0.0 ± 0.0	0.3 ± 0.1	3.8 ± 4.2	0.4 ± 0.1	0.5 ± 0.1	0,5 ± 0.2	1.0 ± 0.7	0,5 ± 0.6
22:6w3	0.7 ± 0.3	14.7 ± 1.6	9.6 ± 8.5	22.9 ± 1.2	27.4 ± 1.9	26.6 ± 1.8	24.2 ± 2.4	28.7 ± 2.9	36.9 ± 12.5	18.9 ± 4.4
ΣPUFA	**10.2 ± 8.7**	**52.1 ± 8.2**	**21.0 ± 14.2**	**52.3 ± 15.2**	**53.2 ± 13.0**	**50.0 ± 6.2**	**47.6 ± 12.1**	**44.1 ± 9.4**	**51.8 ± 19.6**	**41.6 ± 14.9**
16:1ω7/16:0	0.1 ± 0.02	0.2 ± 0.03	0.4 ± 0.2	0.2 ± 0.1	0.4 ± 0.1	0.1 ± 0.01	0.2 ± 0.05	0.2 ± 0.03	0.1 ± 0.2	0.4 ± 0.1
18:1ω9/18:1ω7	1.4 ± 1.6	1.2 ± 0.7	2.1 ± 0.2	3.1 ± 0.7	4.0 ± 1.5	3.0 ± 0.4	2.7 ± 0.1	2.5 ± 0.4	3.1 ± 11.1	2.2 ± 0.5

Table 3. Average similarity between/within groups (SIMPER values, %) for fatty acid proportions in *Pelagia noctiluca* (medusae and ephyrae), fish (larvae and adults) and their potential prey

	Medusae	Ephyrae	Siphono-phores	Salps	Cope-pods	Euphau-siids	Mysida-ceans	Fish larvae	Adult fish	Size-fractionated zooplankton
Medusae	78.0									
Ephyrae	74.2	85.0								
Siphonophores	72.1	79.2	76.0							
Salps	79.2	76.5	76.0	90.7						
Copepods	69.8	74.2	75.9	77.2	83.2					
Euphausiids	73.6	77.6	77.8	78.5	80.4	85.0				
Mysidaceans	73.0	78.4	78.1	78.1	80.0	84.6	77.4			
Fish larvae	75.0	78.1	78.0	81.2	78.9	83.8	82.5	85.0		
Adult fish	71.2	78.2	77.0	75.2	75.9	76.6	76.5	77.3	78.1	
Size-fractionated zooplankton	74.7	79.3	80.7	75.2	80.0	81.9	81.1	82.4	78.7	84.1

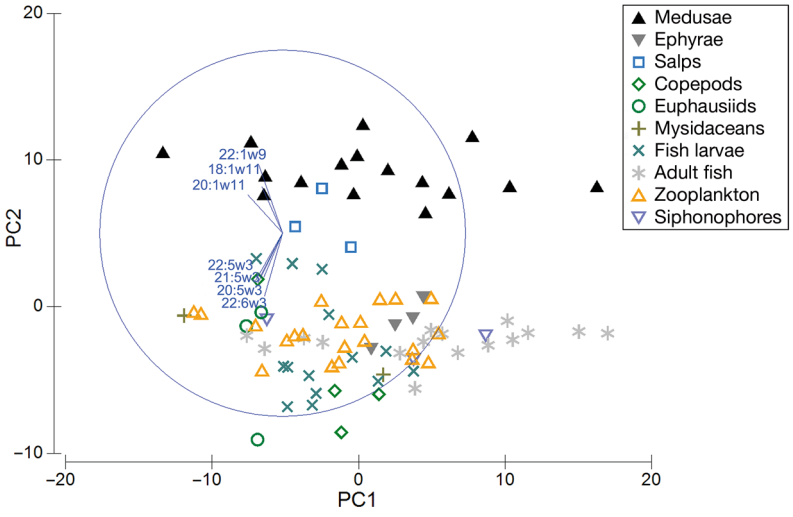

Fig. 4. Principal component analysis (PCA) of fatty acid proportions in *Pelagia noctiluca* medusae and ephyrae. The large circle represents the correlation between fatty acids and principal components 1 and 2

ues reported from the Mediterranean Sea (Costalago et al. 2012, Syväranta et al. 2012). Concerning fish larvae, Costalago et al. (2012) reported higher values of both $\delta^{13}C$ and $\delta^{15}N$ for *Engraulis encrasicolus* larvae during the same period of the year, although in their study, larger individuals were analysed. Considering the ontogenetic shift in the diet of anchovy (Costalago et al. 2012), the differences observed would be related to the different developmental stages analysed.

In our study, the $\delta^{15}N$ signatures recorded for size-fractionated zooplankton, fish larvae and *P. noctiluca* were quite similar. Although $\delta^{15}N$ in the tissues of jellyfish is typically enriched relative to their prey (Post

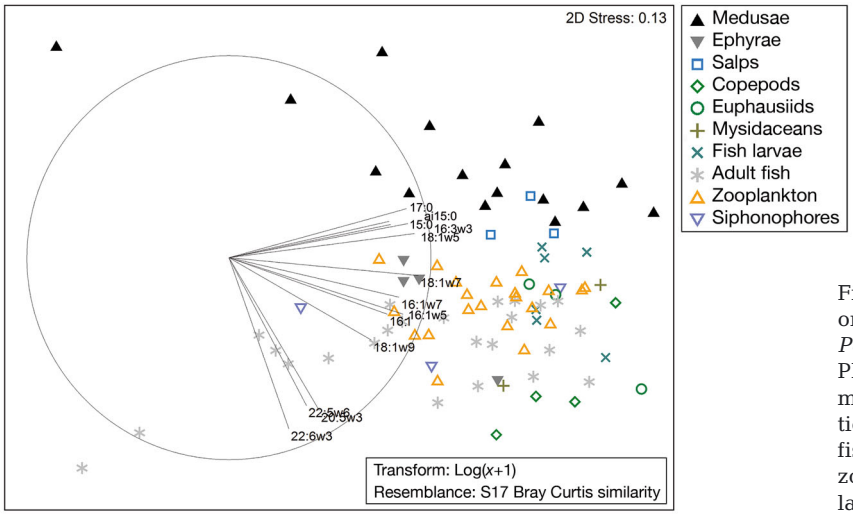

Fig. 5. Non-metric multidimensional scaling ordination of fatty acid composition for *Pelagia noctiluca* medusae and ephyrae. Plot is based on Bray-Curtis resemblance matrix of log-transformed fatty acid proportions of *P. noctiluca* (medusae and ephyrae), fish (larvae and adults) and major groups of zooplankton. The circle represents a correlation between fatty acids and nMDS axes

2002), the $\delta^{15}N$ overlap between gelatinous zooplankton and their potential prey has been previously reported in *P. noctiluca* (Milisenda 2014) and *Aurelia aurita* (D'Ambra et al. 2013). Salps were the only group of potential prey with significantly lower $\delta^{15}N$ values than jellyfish, reflecting their herbivorous feeding behaviour (Vargas & Madin 2004). On the other hand, adult fish presented values about 4–5‰ higher, similar to those reported by Costalago et al. (2012) and Albo-Puigserver et al. (2016) for the same species, reflecting a more carnivorous diet (Stergiou & Karpouzi 2002, Šantić et al. 2004, Costalago et al. 2015). *P. noctiluca* and fish larvae had similar $\delta^{13}C$ values, suggesting they feed on the same food resources, while adult fish were slightly ^{13}C-enriched (≤2‰) compared to medusae and ephyrae. This can be due to a higher trophic level of adult fish ($\delta^{15}N$ is higher), which causes a contextual increase of $\delta^{13}C$ (based on a +1‰ enrichment per trophic level, Post 2002).

According to SIAR model results, salps were the most important prey for *P. noctiluca,* contrasting with the stomach content analysis where salps were not the major food item (Tilves et al. 2016). This discrepancy between the 2 approaches likely reflects differences between recently ingested prey (gut content analysis) and assimilated diet (SIs) (Pitt et al. 2008). Salps are soft-bodied animals, which are more rapidly digested by medusae and ephyrae than copepods (Purcell et al. 2014), hindering their detection and/or identification in stomachs. In fact, Tilves et al. (2016) found that 65% of the stomach content of *P. noctiluca* medusae was unidentifiable digested material, probably composed of gelatinous prey. Moreover, when interpreting SIAR results, the isotopic turnover rate of *P. noctiluca* should be considered, and it is important to note that experiments conducted in the laboratory showed that for *P. noctiluca* medusae, this rate was equal to 22 d (Tilves et al. unpublished data). This time period coincided with the time elapsed between the characteristic bloom of salps in the area (from May to June: Calbet et al. 2001, Pascual 2016) and the sampling period. Thus, the results of the SIAR model would reflect the diet of *P. noctiluca* prior to the cruise, when the salp bloom occurred, while gut content analysis showed recently consumed prey. Salps have been previously described as part of the diet of young and adult *P. noctiluca* (Rosa et al. 2013, Tilves et al. 2016), and Purcell et al. (2014) described the digestion times of *P. noctiluca* ephyrae when feeding on *Thalia democratica*, demonstrating the capability of ingestion and digestion of this type of prey in the youngest stages.

P. noctiluca, especially medusae, had different degrees of isotopic niche overlap with larvae of pelagic fish, i.e. *E. encrasicolus, Sardinella aurita* and *Trachurus mediterraneus*, suggesting shared dietary habits between both groups, while larvae of the benthic *Arnoglossus* sp. did not show overlap with *P. noctiluca.* This discrepancy could be related to the different habitat of these larvae that would affect the type of prey consumed. Thus, while larvae of pelagic fish inhabit the upper levels of the water column (Sabatés et al. 2008, Raya & Sabatés 2015), those of *Arnoglossus* sp. are found at deeper levels (Olivar & Sabatés 1997). In addition, medusae of *P. noctiluca* migrate to the surface at night (Ferraris et al. 2012), and ephyrae are located near the surface both day and night (Gordoa et al. 2013, Tilves et al. 2016), coinciding with fish larvae in the upper layers and their potential prey. Moreover, medusae had a wider isotopic niche than most fish larvae, probably due to their broader diet (Tilves et al. 2016), consuming prey with similar isotopic values, such as fish larvae and copepods, but also with lower isotopic values, such as salps. Diets of fish larvae are less varied and are similar among species, consisting mainly of herbivorous nauplii of copepods and copepodites (Morote et al. 2008, Sabatés et al. 2015). No niche overlap was observed between jellyfish and adult fish, clearly reflecting the different diet requirements of both groups. Although copepods are consumed by adult fish (Tudela & Palomera 1997, Costalago et al. 2012, 2015, Albo-Puigserver et al. 2016) and *P. noctiluca* (Tilves et al. 2016), the lack of niche overlap could be related to the consumption of different species. Moreover, cladocerans are also important prey in the diet of adult fish, while they are a minor component in the diet of *P. noctiluca* (Tilves et al. 2016).

FA profiles reflect baseline food web composition (e.g. diatoms vs. dinoflagellates) and can shed light on dominant food sources and carnivory levels of the organisms involved in the food web (Dalsgaard et al. 2003, El-Sabaawi et al. 2009, Parrish 2013). Markers of phytoplankton can be present even in organisms with a known carnivorous and/or omnivorous diet due to the imprint that their herbivorous prey leave on the tissues. In this study, phytoplankton markers (diatoms and dinoflagellates) were present in all analysed groups, but their proportions differed among the groups. Dinoflagellate markers were elevated in medusae, ephyrae and fish (larvae and adults), in agreement with previous reports (Rossi et al. 2006, Pethybridge et al. 2014, Cardona et al. 2015), indicating a dominance of dinoflagellates in their diet (ratios of 16:1ω7 to 16:0 were <0.3) (Parrish et al.

2000) or in the diet of their prey. This mixed diatom and dinoflagellate dietary signature agrees with the availability of diverse plankton during summer (Pethybridge et al. 2014). In contrast, salps did not present a dominance of dinoflagellates (ratios of 16:1ω7 to 16:0 = 0.4), since diatoms were another important food item, although not a dominant one. In order to consider diatoms dominant, the ratio of 16:1ω7 to 16:0 should be >2.

FA markers of copepods were present in both life stages of *P. noctiluca*, fish larvae and adult fish. The values of certain markers indicate that medusae consumed large (22:1ω11 and 20:1ω9) and small (18:1ω9, 16:0 and 20:5ω3) copepods with higher proportions of the latter. Ephyrae, however, specifically consumed small copepods, although proportions of these markers were lower than in large medusae. The presence of copepod markers in both stages agrees with the results of mixing models and with previous studies that reported the presence of these crustaceans in the stomachs of both life stages of the jellyfish (Sabatés et al. 2010, Rosa et al. 2013, Tilves et al. 2016). The ratio 18:1ω9 to 18:1ω7, which is specific for carnivory, was higher in medusae than in ephyrae, but lower than that observed in fish larvae. Nevertheless, all of these groups had ratios >0.5, which has been set as a threshold to distinguish herbivorous (<0.5) from carnivorous (>0.5) feeding (Nelson et al. 2000, Brett et al. 2008). The carnivory ratio of *P. noctiluca* was lower than that previously reported for this species in the Messina Strait (Milisenda 2014). FA composition can be influenced by several factors, such as environmental conditions and food availability (Dalsgaard et al. 2003) or age (Kattner et al. 1994) or size (Kainz et al. 2003), which may help explain the observed differences.

PUFAs represented the largest component of FAs of most organisms analysed, but not in medusae (Table 2). These particular FAs provide special conformational properties to the biological membranes, assist sensory cells in reacting to external stimuli (Cook 1985) and are the major FA component in marine organisms during summer in the NW Mediterranean (Costalago et al. 2011, Milisenda 2014, Pethybridge et al. 2014), including larval and adult fish (Rossi et al. 2006, Costalago et al. 2011, Pethybridge et al. 2014). PUFAs are important components of the eggs of *P. noctiluca* (Milisenda 2014), and as reported by that author, spawning events occur mainly twice a year, in May and October. Considering this information and the fact that the cruise was performed during June and July, lower values of these FAs in the medusae might be related to the fact that samples were collected after reproduction.

FA distributions differed by 26% between *P. noctiluca* medusae and ephyrae, reflecting different feeding habits of the 2 life stages. The MUFAs more strongly associated with medusae were those of carnivory, while ephyrae were characterized by PUFA markers of herbivory. A previous study indicated a higher diversity of prey in the diet of medusae (Tilves et al. 2016), which likely influenced the differences in the FA profiles. The 2 main groups based on FA markers were differentiated by PCA. In the first group, medusae seemed to feed mainly on salps, with almost 80% similarity between them, which agrees with the SI results. Feeding on gelatinous zooplankton by medusae is not new (Arai 2005), and *P. noctiluca* showed evidence of this behaviour when stomach contents were analysed (Malej 1989, Sabatés et al. 2010, Rosa et al. 2013, Tilves et al. 2016), indicating that they were able to feed on large soft-bodied organisms with low digestion times (Purcell et al. 2014). This ingestion/digestion capability, together with the high densities of salps prior to the cruise, would explain the prevalence of these tunicates in the diet of *P. noctiluca* medusae, considering the turnover time already mentioned. Moreover, diatom markers, which were important in salps, were also present in medusae, suggesting their trophic transfer. Although medusae and fish larvae were not assigned to the same group by the PCA, the high similarity between FA profiles of both groups (SIMPER, 75%) may indicate that they were feeding on the same type of prey or that fish larvae were part of the medusae diet. *P. noctiluca* has been suggested to be an important predator of fish larvae, with high consumption rates in bloom situations (Purcell et al. 2014, Tilves et al. 2016). Again, although copepods were not grouped with medusae in the PCA, the presence of copepod markers in the jellyfish tissue clearly indicates their consumption, while in lower proportions than salps, as observed by the SIAR mixing model.

The second group in the PCA comprised ephyrae, zooplankton (size-fractionated and major groups) and fish larvae and adults. Although SI analyses showed that salps were the major contributor to the diet of ephyrae, the highest similarities obtained between FA profiles were with size-fractionated zooplankton and siphonophores (79.2 and 79.3%, respectively). It must be noted that similarity between FA profiles of ephyrae and salps was 76.5%. These results agree with those previously reported by Tilves et al. (2016), who observed ephyrae diets based mostly on siphonophores. Despite siphono-

phores being carnivorous (Purcell 1981, Purcell 1982, Pagès & Madin 2010), they had high dinoflagellate marker values, which were probably reflected in ephyrae tissue. As mentioned above, ephyrae also fed on copepods, mostly on small ones. Although the percentage similarity with these organisms was the lowest, this could be because the copepods analysed were large individuals and thus not the preferred type of prey. The discrepancy between the 2 methodological approaches used in this study (SIs and FAs) regarding which organisms contribute most to the ephyrae diet, could be related to turnover rates of FAs in ephyrae tissue. It is reasonable to assume that the analysed ephyrae may present traces of adult females being grouped with other organisms rich in PUFAs by the PCA.

In conclusion, this study elucidates some important trophic interactions of different life stages of *P. noctiluca*. Each of the methodologies used presented some limitations by itself, but by combining all of the methods, these limitations can be overcome to obtain more accurate information. Gut content analysis of *P. noctiluca* showed that a high percentage of the contents comprised digested material with a gelatinous appearance, with fish larvae and copepods as important food items (Tilves et al. 2016). These food sources (in addition to salps and siphonophores) were included in the isotopic analysis, which demonstrated the importance of the salps in the diet of the jellyfish, contributing up to ~70%. Although salps have been previously described as part of the *P. noctiluca* diet, to our knowledge, this is the first description of such high consumption. Our results also showed similar isotopic signatures of jellyfish and fish larvae and overlapping trophic niches, whereas adult fish occupied a higher position in the trophic web with no overlap with *P. noctiluca*. FA analyses confirmed the presence of copepods in the diet of medusae and ephyrae and salps in medusae. Based on the 3 approaches, we corroborated omnivorous feeding habits of *P. noctiluca* and demonstrated that *P. noctiluca* could be an important predator and competitor of fish larvae, but not of adult fish. The broad global distribution of *P. noctiluca* in different oceans increases concern about their potential impact on fish populations, since many coastal areas inhabited by this species are exploited by different fisheries. In fact, replacement cycles of fish by jellyfish have been described (Robinson et al. 2014). The results obtained in this study provide information that should be considered in near-future ecosystem-based fishery management in the NW Mediterranean and in regions where *P. noctiluca* thrives.

Acknowledgements. We are grateful to people who contributed to the fieldwork, including the scientific team and crew on board the RV 'García del Cid'. We also thank Jeanette Wells (Department of Ocean Sciences, Memorial University of Newfoundland) and Adele Elisa Aleo (Department of Earth and Marine Science, University of Palermo) for their help with FA and SI analyses, respectively. This work was supported by the Spanish Ministry of Economy and Competitiveness (FISHJELLY project: CTM2010-18874), and U.T. was supported by a predoctoral fellowship of the FPI program (Spanish Ministry of Economy and Competitiveness).

LITERATURE CITED

Albo-Puigserver M, Navarro J, Coll M, Layman CA, Palomera I (2016) Trophic structure of pelagic species in the northwestern Mediterranean Sea. J Sea Res 117:27–35

Arai MN (2005) Predation on pelagic coelenterates: a review. J Mar Biol Assoc UK 85:523–536

Attrill MJ, Wright J, Edwards M (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol Oceanogr 52: 480–485

Bernard P, Berline L, Gorsky G (2011) Long term (1981–2008) monitoring of the jellyfish *Pelagia noctiluca* (Cnidaria, Scyphozoa) on the French Mediterranean Coasts (Principality of Monaco and French Rivera). J Oceanogr Res Data 4:1–10

Boero F (2013) Review of the jellyfish blooms in the Mediterranean and Black Sea. Report 92. General Fisheries Commission for the Mediterranean, FAO, Rome

Brett MT, Müller-Navarra DC, Persson J (2008) Crustacean zooplankton fatty acid composition. In: Arts MT, Brett MT, Kainz MJ (eds) Lipids in aquatic ecosystems. Springer, New York, NY, p 115–145

Brodeur RD, Mills CE, Overland JE, Walters GE, Schumacher JD (1999) Substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish Oceanogr 8:296–306

Brodeur RD, Sugisaki H, Hunt GL Jr (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar Ecol Prog Ser 233:89–103

Brodeur RD, Suchman CL, Reese DC, Miller TW, Daly EA (2008) Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Mar Biol 154:649–659

Brodeur RD, Barceló C, Robinson KL, Daly EA, Ruzicka JJ (2014) Spatial overlap between forage fishes and the large medusa *Chrysaora fuscescens* in the northern California Current region. Mar Ecol Prog Ser 510:167–181

Brotz L, Pauly D (2012) Jellyfish populations in the Mediterranean Sea. Acta Adriat 53:213–232

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mamm Sci 22: 759–801

Calbet A, Garrido S, Saiz E, Alcaraz M, Duarte C (2001) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. J Plankton Res 23:319–331

Canepa A, Fuentes V, Sabatés A, Piraino S, Boero F, Gili JM (2014) *Pelagia noctiluca* in the Mediterranean Sea. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 237–266

Cardona L, Álvarez de Quevedo I, Borrell A, Aguilar A (2012) Massive consumption of gelatinous plankton by Mediterranean apex predators. PLOS ONE 7:e31329

Cardona L, Martínez-Iñigo L, Mateo R, Gonzalez-Solís J (2015) The role of sardine as prey for pelagic predators in the western Mediterranean Sea assessed using stable isotopes and fatty acids. Mar Ecol Prog Ser 531:1–14

Cook H (1985) Fatty acid desaturation and chain elongation in eukaryotes. In: Vance DE, Vance JE (eds) Biochemistry of lipids and membranes. Elsevier, Amsterdam, p 129–152

Costalago D, Tecchio S, Palomera I, Álvarez-Calleja I, Ospina-Álvarez A, Raice-vich S (2011) Ecological understanding for fishery management: condition and growth of anchovy late larvae during different seasons in the Northwestern Mediterranean. Estuar Coast Shelf Sci 93: 350–358

Costalago D, Navarro J, Álvarez-Calleja I, Palomera I (2012) Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. Mar Ecol Prog Ser 460:169–181

Costalago D, Garrido S, Palomera I (2015) Comparison of the feeding apparatus and diet of European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological implications. J Fish Biol 86:1348–1362

D'Ambra I (2012) Applications of stable isotopes in the analysis of trophic interactions between jellyfish and fish. PhD dissertation. University of South Alabama, Mobile, AL

D'Ambra I, Graham WM, Carmichael RH, Malej A, Onofri V (2013) Predation patterns and prey quality of medusa in a semi-enclosed marine lake: implications for food web energy transfer in coastal marine ecosystems. J Plankton Res 35:1305–1312

Dalsgaard J, St. John M, Kattner G, Muller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

Daly Yahia MN, Batisti M, Lu i D, Fernandez de Puelles ML and others (2010) Are the outbreaks of *Pelagia noctiluca* (Forsskål, 1771) more frequent in the Mediterranean basin? In: Gislason A, Gorsky G (eds) Proceedings of the Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic (WKZEM). Cooperative Research Report 300. ICES, Copenhagen, p 8–14

Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proc Natl Acad Sci USA 104:10518–10523

Duarte CM, Pitt KA, Lucas CH, Purcell JE and others (2013) Is global ocean sprawl a cause of jellyfish blooms? Front Ecol Environ 11:91–97

El-Sabaawi R, Dower JF, Kainz M, Mazumder A (2009) Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. Mar Biol 156:225–237

Ferraris M, Berline L, Lombardi F, Guidi L and others (2012) Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). J Plankton Res 34:874–885

Gannes LZ, Martínez del Rio C, Koch P (1998) Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. Comp Biochem Physiol Part A Mol Integr Physiol 119:725–737

Gili JM, Pagès F (2005) Les proliferacions de meduses. Boll Soc Hist Nat Illes Balears 48:9–22

Giorgi R, Avian M, De Olazabal S, Rottini-Sandrini L (1991) Feeding of *P. noctiluca* in open sea. In: Jellyfish blooms in the Mediterranean. Proceedings of the 2nd Workshop on Jellyfish in the Mediterranean Sea. Tech Rep Ser 47. United Nations Environment Programme, Mediterranean Action Plan, Athens, p 102–111

Gordoa A, Acuña JL, Farrés R, Bacher K (2013) Burst feeding of *Pelagia noctiluca* ephyrae on Atlantic bluefin tuna (*Thunnus thynnus*) eggs. PLOS ONE 8:e74721

Graham WM, Bahya KM (2007) Biological invasions by marine jellyfish. In: Nentwing W (ed) Biological invasions. Ecological studies, Vol 193. Springer, Berlin, p 239–255

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

Kainz M, Arts MT, Mazumder A (2004) Essential fatty acids in the planktonic food web and their ecological role for higher trophic levels. Limnol Oceanogr 49:1784–1793

Kattner G, Graeve M, Hagen W (1994) Ontogenic and seasonal changes in lipid and fatty acid/alcohol compositions of the dominant Antarctic copepods *Calanus propinquus*, *Calanoides acutus* and *Rhincalanus gigas*. Mar Biol 118:637–644

Kattner G, Albers C, Graeve M, Schnack-Schiel SB (2003) Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: indication on feeding modes. Polar Biol 26:666–671

Kogovšek T, Bogunović B, Malej A (2010) Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time-series. Hydrobiologia 645:81–96

Larson R (1987) A note on the feeding, growth, and reproduction of the epipelagic scyphomedusa *P. noctiluca* (Forskål). Biol Oceanogr 4:447–454

Lynam CP, Hay SJ, Brierley AS (2004) Interannual variability in abundance of North Sea jellyfish links to the North Atlantic oscillation. Limnol Oceanogr 49:637–643

Malej A (1989) Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskål, 1775). J Exp Mar Biol Ecol 126:259–270

Malej A, Faganeli J, Pezdi J (1993) Stable isotope and biochemical fractionation in the marine pelagic food chain: the jellyfish *Pelagia noctiluca* and net zooplankton. Mar Biol 116:565–570

Mallela J, Harrod C (2008) $\delta^{13}C$ and $\delta^{15}N$ reveal significant differences in the coastal food webs of the seas surrounding Trinidad and Tobago. Mar Ecol Prog Ser 368:41–51

Mariottini GL, Giacco E, Pane L (2008) The mauve stinger *P. noctiluca* (Forsskål, 1775). Distribution, ecology, toxicity and epidemiology of stings. A review. Mar Drugs 6: 496–513

Milisenda G (2014) Ecophysiology, trophic ecology, reproductive biology and bioenergetics of *Pelagia noctiluca* (Forskål, 1775). PhD dissertation, Universitá del Salento, Lecce

Miller MR, Nichols PD, Barnes J, Davies NW, Peacock EJ, Carter CG (2006) Regiospecificity profiles of storage and membrane lipids from the gill and muscle tissue of Atlantic salmon (*Salmo salar* L.) grown at elevated temperature. Lipids 41:865–876

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140

Möller H (1980) Scyphomedusae as predators and food competitors of larval fish. Meeresforschung 28:90–100

Montoya JP, Horrigan SG, McCarthy JJ (1990) Natural abundance of ^{15}N in particulate nitrogen and zooplankton in the Chesapeake Bay. Mar Ecol Prog Ser 65:35–61

Morote E, Olivar MP, Villate E, Uriarte I (2008) Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. J Plankton Res 30:807–816

Nelson MM, Phleger CF, Mooney BD, Nichols PD (2000) Lipids of gelatinous Antarctic zooplankton: Cnidaria and Ctenophora. Lipids 35:551–559

Newsome SD, Del Rio CM, Bearhop S, Phillip DL (2007) A niche for isotopic ecology. Front Ecol Environ 5: 429–436

Olivar MP, Sabatés A (1997) Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. Mar Biol 129:289–300

Pagès F, Madin L (2010) Siphonophores eat fish larger than their stomachs. Deep Sea Res II 57:2248–2250

Parnell A, Inger R, Bearhop S, Jackson AL (2008) SIAR: stable isotope analysis in R. https://cran.r-project.org/web/packages/siar/

Parrish CC (2013) Lipids in marine ecosystems. ISRN Oceanogr 2013:1–16

Parrish CC, Abrajano TA, Budge SM, Helleur RJ, Hudson ED, Pulchan K, Ramos C (2000) Lipid and phenolic biomarkers in marine ecosystems: analysis and applications. In: Wangersky P (ed) The handbook of environmental chemistry. Springer, Berlin, p 193–223

Pascual M (2016) Spatio-temporal processes explaining salp aggregations and their role in the Catalan Sea, northwestern Mediterranean Sea. PhD dissertation. Universitat Politècnica de Catalunya, Barcelona

Pauly D, Graham W, Libralato S, Morissette L, Palomares MLD (2009) Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia 616:67–85

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Ecology 18:293–320

Pethybridge H, Bodin N, Arsenault-Pernet EJ, Bourdeix JH and others (2014) Temporal and inter-specific variations in forage fish feeding conditions in the NW Mediterranean: lipid content and fatty acid compositional changes. Mar Ecol Prog Ser 512:39–54

Pinnegar JK, Polunin NVC (2000) Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122:399–409

Pitt KA, Clement AL, Connolly RM, Thibault-Botha D (2008) Predation by jellyfish on large and emergent zooplankton: implications for benthic–pelagic coupling. Estuar Coast Shelf Sci 76:827–833

Pitt KA, Connolly RM, Meziane T (2009) Stable isotope and fatty acid tracers in energy and nutrient studies of jellyfish: a review. Hydrobiologia 616:119–132

Post DM (2002) Use of stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83: 703–718

Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar Biol 65:83–90

Purcell JE (1982) Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham, 1883). J Exp Mar Biol Ecol 62:39–54

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27–44

Purcell JE, Sturdevant MV (2001) Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Mar Ecol Prog Ser 210:67–83

Purcell JE, Uye S, Lo W (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174

Purcell JE, Tilves U, Fuentes VL, Milisenda G, Olariaga A, Sabatés A (2014) Digestion times and predation potentials of *Pelagia noctiluca* eating fish larvae and copepods in the NW Mediterranean Sea. Mar Ecol Prog Ser 510:201–213

Raya V, Sabatés A (2015) Diversity and distribution of early life stages of carangid fishes in the northwestern Mediterranean: responses to environmental drivers. Fish Oceanogr 24:118–134

Robinson KL, Ruzicka JJ, Decker MB, Brodeur RD and others (2014) Jellyfish, forage fish, and the world's major fisheries. Oceanography 27:104–115

Rosa S, Pansera M, Granata A, Guglielmo L (2013) Interannual variability, growth, reproduction and feeding of *Pelagia noctiluca* (Cnidaria: Scyphozoa) in the Straits of Messina (Central Mediterranean Sea): linkages with temperature and diet. J Mar Syst 111–112:97–107

Rossi S, Sabatés A, Latasa M, Reyes E (2006) Lipid biomarkers and trophic linkages between phytoplankton, zooplankton and anchovy (*Engraulis encrasicolus*) larvae in the NW Mediterranean. J Plankton Res 28:551–562

Rottini-Sandrini L, Avian M (1989) Feeding mechanism of *Pelagia noctiluca* (Scyphozoa: Semaeostomeae); laboratory and open sea observations. Mar Biol 102:49–55

Sabatés A, Zaragoza N, Grau C, Salat J (2008) Vertical distribution of early developmental stages in two coexisting clupeoid species, *Sardinella aurita* and *Engraulis encrasicolus.* Mar Ecol Prog Ser 364:169–180

Sabatés A, Pagès F, Atienza D, Fuentes V, Purcell JE, Gili JM (2010) Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. Hydrobiologia 645:153–165

Sabatés A, Zaragoza N, Raya V (2015) Distribution and feeding dynamics of larval red mullet (*Mullus barbatus*) in the NW Mediterranean: the important role of cladocera. J Plankton Res 37:820–833

Šantić M, Jardas I, Pallaoro A (2004) Diet composition and feeding intensity of Mediterranean horse mackerel, *Trachurus mediterraneus* (Osteichthyes: Carangidae), in the central Adriatic Sea. Acta Adriat 45:43–50

Shiganova TA (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fish Oceanogr 7:305–310

Stergiou KI, Karpouzi VS (2002) Feeding habits and trophic levels of Mediterranean fish. Rev Fish Biol Fish 11: 217–254

Sullivan BK, Garcia JR, Klein-MacPhee G (1994) Prey selection by the scyphomedusan predator *Aurelia aurita.* Mar Biol 121:335–341

Syväranta J, Harrod D, Kubicek L, Cappanera V, Houghton JDR (2012) Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators. J Fish Biol 80:225–231

Tilves U, Purcell JE, Fuentes VL, Torrents A and others (2016) Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. J Plankton Res 38:1243–1254

Tudela S, Palomera I (1997) Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea

(northwest Mediterranean). Mar Ecol Prog Ser 160: 121–134

Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46:2061–2066

Vargas CA, Madin LP (2004) Zooplankton feeding ecology: clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa cylindrica* on naturally occurring particles in the Mid-Atlantic Bight. J Plankton Res 26:827–833

Waite AM, Muhling BA, Holl CM, Beckley LE and others (2007) Food web structure in two counter-rotating eddies based on $\delta^{15}N$ and $\delta^{13}C$ isotopic analyses. Deep Sea Res II 54:1055–1075

Xian W, Kang B, Liu R (2005) Jellyfish blooms in the Yangtze Estuary. Science 307:41

Ying C, Ying W, Jing Z, Na W (2012) Potential dietary influence on the stable isotopes and fatty acid compositions of jellyfish in the Yellow Sea. J Mar Biol Assoc UK 92: 1325–1333

Zavodnik D (1991) On the food and feeding in the northern Adriatic of Pelagia noctiluca (Scyphozoa). Jellyfish blooms in the Mediterranean. In: Proceedings of the 2nd Workshop on Jellyfish in the Mediterranean Sea. Tech Rep Ser 47. United Nations Environment Programme, Mediterranean Action Plan, Athens, p 212–216

Editorial responsibility: Kelly Sutherland (Guest Editor), Eugene, Oregon, USA

Submitted: February 1, 2017; Accepted: September 6, 2017
Proofs received from author(s): November 2, 2017