Biological interactions between fish and jellyfish in the northwestern Mediterranean

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Barcelona 2018

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Interacciones biológicas entre meduas y peces y sus implicaciones ecológicas en el Mediterráneo Noroccidental

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Memoria presentada para optar al grado de Doctor por la Universitat Politècnica de Catalunya (UPC), Programa de doctorado en Ciencias del Mar (RD 99/2011). Tesis realizada en el Institut de Ciències del Mar (CSIC).

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This student has been supported by a pre-doctoral fellowship of the FPI program (Spanish Ministry of Economy and Competitiveness). The research carried out in the present study has been developed in the frame of the FISHJELLY project, CTM2010-18874 and CTM2015-68543-R.

Cover design by Laura López.
Visual design by Eduardo Gil.

THESIS CONTENTS

SUMMARY

Jellyfish are important components of marine ecosystems, being a key link between lower and higher trophic levels. Jellyfish blooms occur sporadically and unpredictably in coastal areas and often have important socio-economic consequences for fisheries and tourism. This PhD thesis addresses some questions regarding the potential impact, positive and/or negative, that jellyfish have on fish populations in the Catalan coast (NW Mediterranean). Firstly, the natural diet of one of the most abundant jellyfish in the area, the scyphomedusa *Pelagia noctiluca*, was studied analyzing its gut contents and conducting biomarker analyses (stable isotopes and fatty acids). These results were complemented with laboratory experiments to calculate their digestion times and also with the records of fish larvae and jellyfish abundances in the field. All together, these results were used to estimate the potential feeding impact of *P. noctiluca* on fish eggs and larvae and competition between both groups of organisms. Results suggest that the potential consumption of ichthyoplankton by the jellyfish and competition between them may be high. Secondly, the association between the jellyfish *Rhizostoma pulmo* and *Cotylorhiza tuberculata* and the carangid fishes *Trachurus mediterraneus, Trachurus trachurus* and *Caranx rhonchus* was studied in detail. For this purpuse, field observations of jellyfish and their hosted fish were carried out during

summer to describe fish behavior. Moreover, laboratory experiments were performed to determine the survival capability of the jellyfish-associated fish to the venom of their hosts. Finally, biomarker analyses were conducted to understand the significance of the association. All this information demonstrated the benefit of the association for the fish.

Las medusas son componentes importantes de los ecosistemas marinos ya que son un vínculo clave entre el zooplancton más pequeño y los niveles tróficos superiores. Las proliferaciones de medusas ocurren esporádica e impredeciblemente en áreas costeras y con frecuencia tienen importantes consecuencias socioeconómicas para la pesca y el turismo. Esta tesis doctoral aborda algunas cuestiones relacionadas con el potencial impacto de las medusas, tanto positivo como negativo, sobre las poblaciones de peces en la costa catalana (NO Mediterráneo). En primer lugar, se estudió la dieta natural de una de las medusas más abundante en la zona, *Pelagia noctiluca*, analizando su contenido estomacal y sus biomarcadores (isótopos estables y ácidos grasos). Estos resultados se complementaron con sus tiempos de digestión (obtenidos mediante experimentos de laboratorio) y también con las abundancias en mar abierto de larvas de peces y medusas. En conjunto, estos resultados demostraron que el potencial impacto de depredación de *P. noctiluca* sobre huevos y larvas de peces es alto y que existe una probable competencia entre ambos grupos por el alimento. En segundo lugar, se estudió la asociación entre las medusas *Rhizostoma pulmo* y *Cotylorhiza tuberculata* y los peces carángidos *Trachurus mediterraneus*, *Trachurus trachurus* y *Caranx rhonchus*. Para ello, se estudió durante el período de verano el comportamiento en el mar de los peces asociados. Además, se realizaron experimentos de laboratorio para determinar la capacidad de supervivencia de estos peces al veneno de sus medusas anfitrionas. Finalmente, se realizaron análisis de biomarcadores para comprender la importancia de estas asociaciones. Toda esta información demostró el beneficio obtenido por los peces cuando se asocian a medusas.

GENERAL INTRODUCTION

Gelatinous zooplankton: what is it?

Since **gelatinous zooplankton** refers to several groups of planktonic organisms, taxonomically and functionally diverse, and taking into account that different authors do not always refer to the same groups using this definition, it is important to define which groups we indicate in this work. The term **gelatinous zooplankton** comprises those organisms with similarities in their body (high water content and gelatinous consistency) and in having a planktonic stage within their life cycle. Thus, this terminology includes pelagic cnidarians and ctenophores (comb jellies), and pelagic tunicates (invertebrate chordates: salps, doliolids and pyrosomes). What is called **jellyfish** refers to the pelagic stages of four classes of the Cnidaria subphyla: Hydrozoa, Cubozoa, Scyphozoa and Staurozoa. As the rest of the members of the phylum Cnidaria, all of them possess mechanoreceptor cells called cnidocytes (stinging cells) that are used for defense/offense purposes when cnidarians interact with other organisms.

Gelatinous zooplankton is an important component of pelagic ecosystems (Mills 1995, Purcell et al. 2007), because they play a key role as predators and competitors that can modulate the structure and dynamics of planktonic food webs (Purcell 1997, Purcell & Arai 2001, Arai

2005). They have been considered a trophic dead-ends for decades (Sommer et al. 2002, Lynam et al. 2006) due to their high water (> 97%) and low carbon (up to 2.9%) content (Lucas et al. 2011), but nowadays several evidences highlighted the importance of these organisms as prey for diverse marine predators, such as sea birds, invertebrates, leatherback sea turtles and an underestimated number of fish species (Arai 1988, Purcell & Arai 2001, Arai 2005). As an example, *Pelagia noctiluca* has been found to be part of the diet of the fish *Boops boops* in the Mediterranean (Milisenda et al. 2014), although the scyphomedusae have 20 times less energy density than the co-occurring fish (Cardona et al. 2012). Another example is the bristle worm, *Hermodice carunculata,* which has been indicated as a consumer of *Cassiopea* spp. in the Bahamas (Stoner & Layman 2015).

Jellyfish blooms

Most jellyfish are considered as planktonic organisms, which means they live suspended in the water column with limited movements against the currents and occasionally form "blooms" (rapid increases in abundance within a short period of time) (Graham et al. 2001, Hamner & Dawson 2009). When these rapid changes in jellyfish abundance are due to a rapid population growth, they are considered a "true bloom" (hereafter called simply bloom) while the re-distribution or re-dispersion of a stable population by environmental forcing is called "apparent bloom" (Graham et al. 2001). Jellyfish blooms appear to be increasing in number and frequency in some areas of the world (Brodeur et al. 2002, Purcell 2005, Attrill et al. 2007), but there is still controversy about their increase at a global scale (Mills 2001, Brotz & Pauly 2012, Condon et al. 2012). Whether there is an increase of jellyfish blooms or not, evidences suggest that jellyfish populations experienced prolonged periods of high abundance (Condon et al. 2013).

Different mechanisms are thought to be responsible for the upward trend of gelatinous zooplankton and, although the increasing pattern may be local, the mechanisms involved could act at a global scale. These factors include climate change, which may enhance reproduction rates and favour species wider dispersion (Brodeur et al. 1999, Lynam et al. 2004, Purcell 2005, Attrill 2007); introduction of alien species (Shiganova 1998, Graham & Bahya 2007); eutrophication, which may increase nutrients and zooplankton availability (Arai 2005, Purcell & Benović 1999); habitat modification, by increasing suitable substrates for polyp settlement (Duarte et al. 2013); and removal of jellyfish predators by overfishing (Purcell & Benović 1999, Lynam et al. 2006).

Increase of gelatinous organisms is considered as a potential indicator of ecological changes in marine ecosystems (Mills 2001, Purcell 2005, Purcell et al. 2007, Richardson et al. 2009) usually dominated by forage fishes (Boero 2013). Jellyfish populations present extended periods of high abundance (Condon et al. 2013) and in ecosystems supporting major forage fish fisheries these periods of high jellyfish abundance coincide with low abundance of fish (Decker et al. 2014, Brodeur et al. 2014, Mianzan et al. 2014) suggesting a jellyfish-fish replacement cycles (Robinson et al. 2014). It should be pointed out that jellyfish are known to be able to survive in degraded environments due to different physiological and biological

attributes that give them an advantage over other animals (including fishes) and could explain the shift in ecosystem structure (Richardson et al. 2009)(Fig. 1). These characteristics are tissue regeneration, broad dietary composition, fast growth rates, shrinking ability when starving and the high tolerance to hypoxia, which could

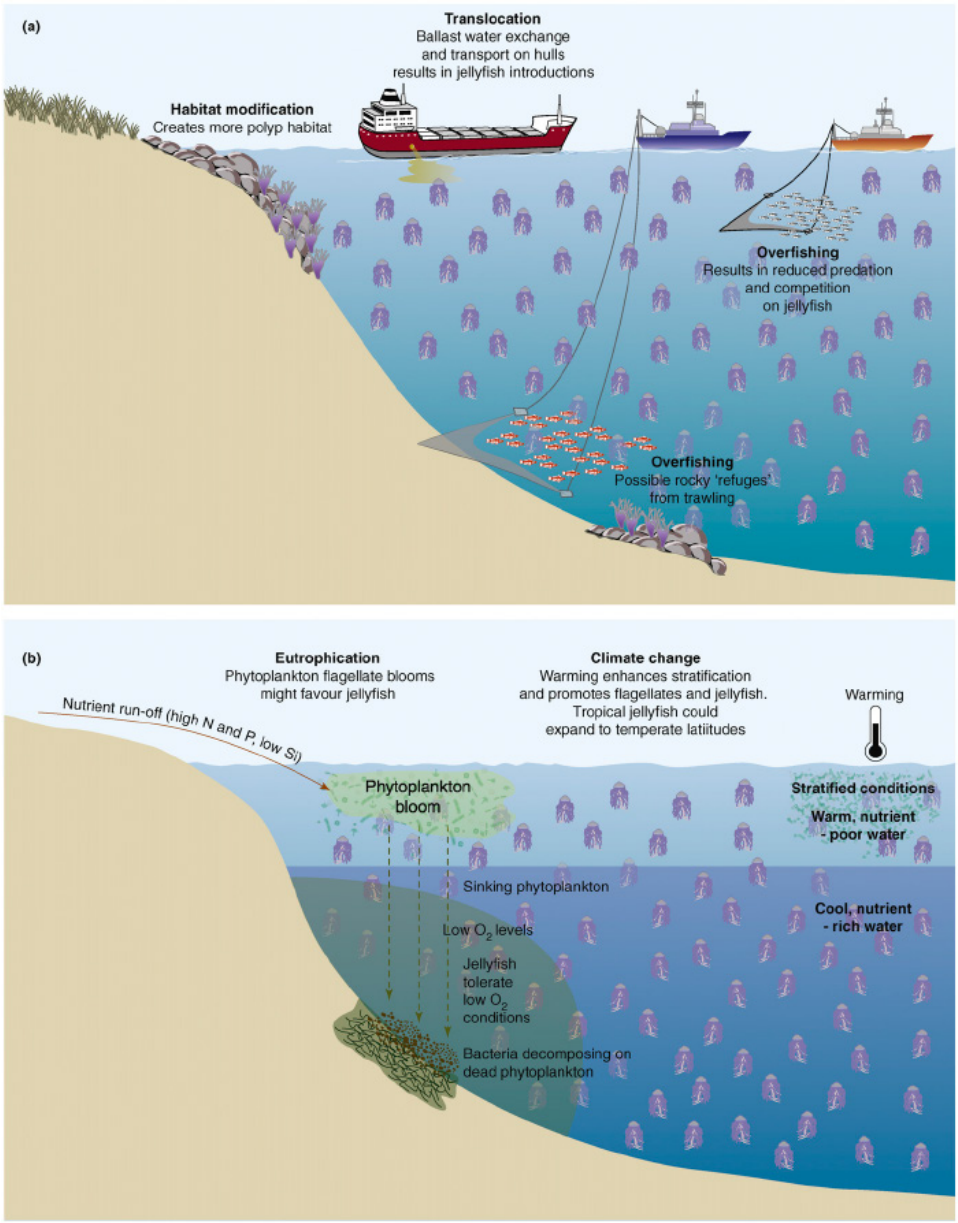

Fig 1 Summary of potential mechanisms promoting jellyfish blooms. (a) Habitat modification, species translocation and overfishing; (b) Eutrophication and climate. Jellyfish symbols represent jellyfish blooms. Source: Richardson et al.

give them advantage over other organisms (Richardson et al. 2009).

Although the causes of blooms are still under discussion (Purcell et al. 2007, Richardson et al. 2009, Purcell 2012, Duarte et al. 2013, Gibbons & Richardson 2013), their socio-economic impacts are well documented worldwide (Purcell et al. 2007, Quiñones et al. 2013, Graham et al. 2014, Lucas et al. 2014). Human activities in coastal areas are often affected by large aggregations of jellyfish. Thus, stings from pelagic cnidarians to beach users have become a problem worldwide (Burnett 2001, Canepa et al. 2014) and, in some cases, beaches must be closed due to the high abundances of these gelatinous organisms, which may result in a decrease of tourism and therefore in economic losses (Purcell et al. 2007). Jellyfish also cause problems by clogging the inflow of water systems in several energy plants, which results in significant power and thus economic loss (Purcell et al. 2007). In addition, jellyfish are known to generate problems in aquaculture, by causing massive dead of fishes in fish farms (Purcell et al. 2007, Baxter et al. 2011, Bosch-Belmar et al. 2016). However, the most reported problems in the interactions between jellyfish and human activities are those related to fishing, such as nets clogging and splitting due to the high densities of gelatinous material, injuries to fishermen and reduction of the quality of captured fish due to skin lesions (Purcell et al. 2007). All these difficulties result in high economic losses (Robinson et al. 2014).

Interactions between jellyfish and fish

From a socio-economic point of view, the main concern about the interactions between jellyfish and fish lies in the potential effects of the former on commercially important fisheries (Purcell & Arai 2001). Many fisheries all over the world are supported by forage fishes (Pikitch et al. 2014). These small pelagic

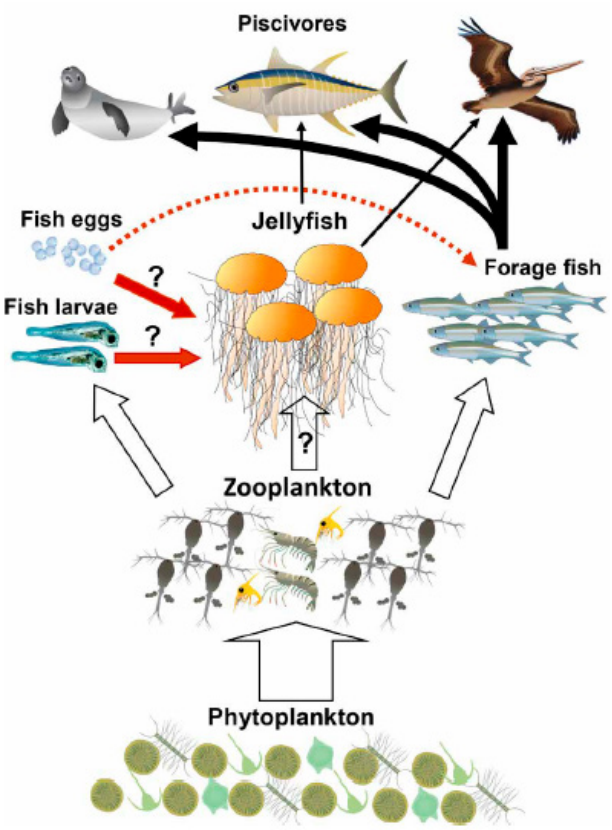

Fig 2 Simplified conceptual diagram illustrating energy transfer pathways in coastal pelagic food webs. The relative width of the arrows indicates the amount of energy flowing between functional groups. Red arrows are energy flows between members of the same trophic guild (i.e. intraguild predation). Dashed lines denote the probable consumption of fish eggs by planktivorous forage fish. Source: Robinson et al. 2014

fishes are essential elements of marine ecosystems since they are the primary food source for several marine predators including piscivorous fishes, mammals and sea birds and, in turn, they feed on phytoplankton and zooplankton (Springer & Speckman 1977) (Fig. 2). Thus, as they are positioned in the middle of the trophic webs, they are the link between the upper and lower trophic levels (e, g. Bakun 1996, Cury et al. 2000).

Jellyfish and small pelagic fish frequently overlap in space and time, giving rise to potential interactions. Most of the described effects of jellyfish on fish populations and fisheries are considered negative, but recent studies are demonstrating they can be both negative and positive. Negative effects include predation on fish eggs and larvae, competition between jellyfish and adult zooplanktivorous fish and fish larvae for prey, and parasite transmission to fish (Purcell & Arai 2001). Commensal associations between fish and scyphomedusae have been described as positive interactions enhancing the survival of juvenile fishes when associated to these gelatinous organisms (Lynam & Brierley 2007) (Fig. 3).

Predation by jellyfish on fish eggs and larvae

Predation on early life stages of fish is the main factor determining fish recruitment (Bailey & Houde 1989), and gelatinous zooplankton is one of the well documented predators of fish eggs and larvae (Purcell 1985, Purcell & Arai 2001). There is evidence that many species of scyphozoan and hydrozoan jellyfish as well as

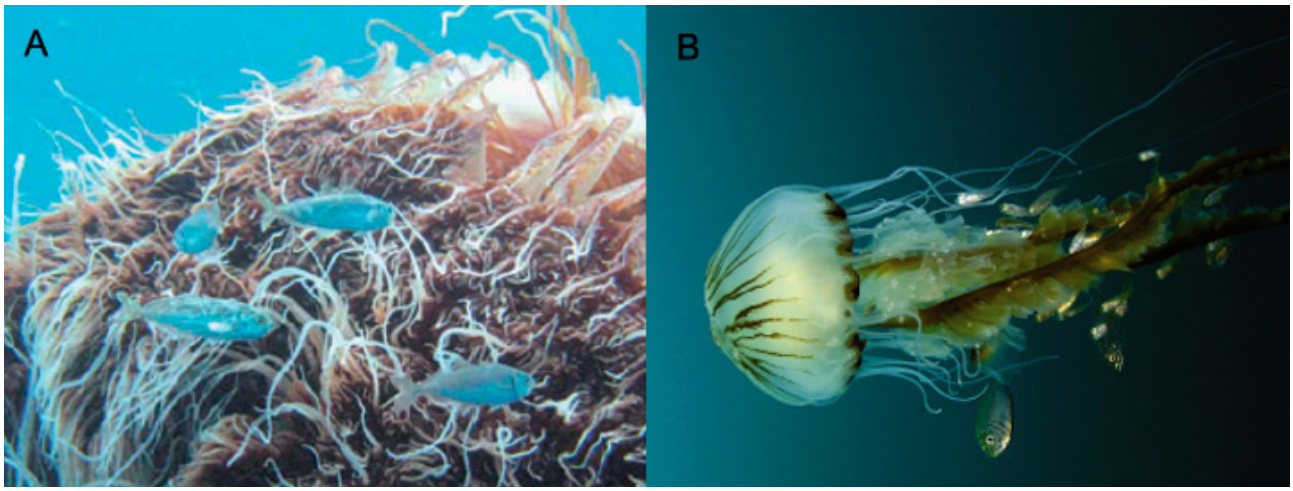

Fig 3 Fishes associated with medusae. (A) Jack mackerel *Trachurus japonicus* juveniles associated with giant jellyfish *Nemopilema nomurai*. Horse mackerel *Trachurus trachurus* associated with *Chrysaora* spp. Source: Masuda et al. 2008 (A) and Richardson et al. 2009 (B)

some ctenophores consume ichthyoplankton as part of their diet. This is the case of *Aequorea victoria* in British Columbia, which was described to feed on the Pacific herring larvae exerting a top-down control (Purcell & Grover 1990). *Chrysaora melanaster* exerted a relevant feeding pressure on the early life stages of walleye pollock, *Theragra chalcogramma,* in the Bearing Sea (Brodeur et al. 2002). Likewise, two species of *Cyanea* (*C. capillata* and *C. lamarckii*) showed high predation rates on larvae of plaice and salmon (Lynam et al. 2004) and *Aurelia aurita* have been described as the main predators of herring, *Clupea harengus*, larvae in the North Sea (Lynam et al. 2006). Similarly, the scyphomedusa *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi* caused as much as 50-100% of the daily mortality of bay anchovy, *Anchoa mitchilli,* eggs and larvae in Chesapeake Bay (Purcell et al. 1994).

Jellyfish predation rates (prey eaten predator^{-1} d^{-1}) when feeding on fish larvae and eggs are highly variable and several factors may affect them: predator and prey size, prey density and encounter rates between jellyfish and their prey (Purcell 1985, Purcell & Arai 2001). In general terms, increasing size of the predator (among and within species) leads on higher feeding rates (Möller 1984, Suchman & Sullivan 2000, Graham & Kroutil 2001). In similar manner, jellyfish showed higher feeding rates when ichthyoplankton in ambient waters was abundant (Titelman & Hansson 2006). It is important to take into account jellyfish abundance when evaluating the effect of jellyfish predation. When jellyfish occur in high numbers (jellyfish blooms), their collective prey-consumption rate could be so high that predation could control the population size of fish, either by direct predation or indirectly by competition.

Competition between jellyfish and fish for prey

Jellyfish are no visual predators that feed by filtering the water containing their potential prey or by direct contact with them. Conversely, fishes are visual predators affected by light and optical properties (Sørnes & Aksnes 2004). Although they have different predation mechanisms, both groups have shown similar respiration and clearance rates in terms of carbon (Pitt et al. 2013) and also similarities in the potential for growth and reproduction (Acuña et al. 2011). This capacity of jellyfish to compete with fishes is the result of the development of physiological characteristics (large bodies) that enhance the encounters with preys (Acuña et al. 2011), in addition to their swimming behaviour that reduces their metabolic demand (Hays et al. 2012).

Moreover, jellyfish and zooplanktivorous fish (e.g anchovies and sardines) often share diets, showing similar trophic requirements (Purcell & Studervant 2001, Brodeur et al. 2008). It has been suggested that the reduction in these vertebrate competitors can provide additional available food for the gelatinous organisms, taking over the vacated trophic niche (Brodeur et al. 2008), resulting in an increase of their populations (Purcell et al. 2007).

Although several authors have speculated on the importance of potential competition between zooplanktivorous fish and jellyfish (e.g. Uye 2008, Richardson et al. 2009), there are few studies comparing the diet of both groups. As an example, the scyphomedusa *Cyanea capillata*

and the pink salmon, *Oncorhynchus gorbuscha,* showed a diet similarity of 78.1%, and the jellyfish *Aurelia labiata* shared 75% of its diet with Pacific sandlance, *Ammodytes hexapterus* (Purcell & Sturdevant 2001). The competition between jellyfish and fish populations was studied by Brodeur et al. (2002) who reported that blooms of *Chrysaora melanaster* negatively affected recruitment and population size of walleye pollock, *Theragra chalcogramma*, in the Bering Sea. Another example is *Chrysaora fuscences*, which was able to consume an average of 32% and up to 61% of the standing stock of euphausiid eggs daily (Suchman et al. 2008), which would not be available for the co-occurring zooplanktivorous fish (Brodeur et al. 2008). These last authors reported a dietary overlap of jellyfish with the northern anchovy, *Engraulis mordax*, and pacific sardine, *Sardinops sagax,* of ~ 70%. Also D'Ambra et al. (2018) found a considerably high overlap between *Aurelia* sp. and the forage fish, *Brevoortia patrons,* in the northern Gulf of Mexico (up to 93%). However, to evaluating competition is not an easy task since many factors should be considered. Link and Auster (2013) concluded that opposing trajectories of the population size, spatio-temporal overlap, high dietary overlap, and resource limitation are factors affecting the potential competition.

Positive interactions between fish and jellyfish

Juveniles of different fish families associate to diverse species of scyphozoans and hydrozoans jellyfish (Mansueti 1963, Browne & Kingsford 2005, D'Ambra & Malej 2015). In the past, these associations were defined as a symbiosis, where jellyfish protect fishes from predators under their umbrellas (Mansueti 1963), but nowadays the meaning of these interactions is under discussion (Purcell & Arai 2001). Although most of the existing works is purely descriptive, different hypotheses regarding the ecological significance of the associations have been made: protection from predation (Masuda 2006), provisioning food by feeding on the zooplankton captured by jellyfish (Masuda 2009) or feeding on the jellyfish themselves (D'Ambra et al. 2015), transportation to favourable areas (Castro et al. 2002, Masuda 2009) and "meeting point" (Masuda 2009).

Associations can be favourable, deleterious, or without effect for the jellyfish (Purcell & Arai 2001) but they are positive for fishes in most of the cases, eventually increasing their recruitment. For example, in the North Sea, the survival of the early stages of whiting, *Merlangius merlangus*, that shelter beneath jellyfish, may be improved by high abundances of *Cyanea lamarckii* and *Cyanea capillata* (Lynam & Bierley 2007). On the other hand, these associations may benefit jellyfish by occasionally feeding on the hosted fish and by removal of their parasites by the guest fishes (Purcell & Arai 2001). Thus, a positive effect of the relationship was observed for *Rhizostoma octopus* in association with the young whiting, since the fish removed parasitic amphipods from infected individuals (Lynam & Brierley 2007).

The associations between juvenile fish and jellyfish are not species specific and both fish and jellyfish associate to one or more species of jellyfish and fish respectively (Purcell & Arai 2001). Thus, the mackerel, *Trachurus japonicus,* has been reported in association with *Aurelia aurita, Nemopilema nomurai* and *C. melanaster*

(Masuda 2009) and, in contrast, the whiting has been observed swimming exclusively with *C. capillata* (Hay et al. 1990, Lynam & Brierley 2007). The jellyfish *C. melanaster* can host more than one species of fish in the Bering Sea (Brodeur 1998). Moreover, ontogenetic shifts of fish observed during the association with the jellyfish resulted in changes in their ecological function (Purcell & Arai 2001, Masuda 2009). Thus, at the beginning of the association, some species of fish, such as *T. japonicus*, used the host jellyfish as a school formation area and as the fish grows, the jellyfish is used for predation avoidance and finally as food source (Masuda 2009).

Study Area: The Catalan coast (NW Mediterranean)

The Catalan coast is located in the North Western Mediterranean in the North Eastern part of the Iberian Peninsula, south of the Gulf of Lions. The northern sector, which is more directly influenced by strong northerly winds, is generally colder than the central and southern parts and a surface thermal front roughly coincides with the limit of frequent northerly winds (Sabatés et al. 2009). The Catalan coast is characterized by a continental shelf, which is, in general, quite narrow. It widens clearly in the southernmost part, in the vicinity of the Ebro River Delta, and in the north between the main submarine canyons, south of the Gulf of Lions. Input of continental water plays an important role in this region (Salat 1996). The southern shelf receives a significant river outflow from the Ebro River, while the northern areas are affected by the outflow of the Rhône River, which outflows into the Gulf of Lions.

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 associated geostrophic current, the Northern Current, flows parallel to the front on its coastal side, and roughly over the 1000-m isobath (García-Ladona et al. 1994). The role of the front in primary production (Estrada & Margalef 1988) and in zooplankton distribution (Sáiz et al. 1999, 2014) has been documented. High zooplankton biomass and fish larvae concentrations have been observed regularly along the shelf break in relation to the frontal convergence (Sabatés et al. 1989, 2010). The front may act also as a barrier preventing the dispersal of fish larvae towards the open sea (Sabatés et al. 2007).

In the NW Mediterranean, the highest abundance of jellyfish occurs in spring and summer (Buecher & Gibbons 1999, Gili & Pagès 2005) when the majority of fish species reproduce. Indeed, spawning of most neritic species (e.g. in the families Sparidae, Labridae, Blenniidae, Mullidae, Serranidae, Scombridae), as well as the small pelagic fish, anchovy (*Engraulis encrasicolus)* and round sardinella (*Sardinella aurita)*, takes place during this period. Thus, ichthyoplankton abundance and diversity are high during spring-summer (Sabatés 1990, Olivar et al. 2010), which coincides with the large populations of jellyfish. The summer period is characterized by a stratified water column, with a marked thermocline and pycnocline between 15 and 40m (Sabates et al. 2007), and fish larvae

of most species are distributed in surface waters above the thermocline (Olivar & Sabatés 1997).

Jellyfish in the Northwestern Mediterranean Sea

The maximum abundance of jellyfish along the Catalan coast has been reported during the spring and summer seasons (Gili & Pagès 2005) over the shelf-slope region, in relation to the increased primary and secondary production associated with the shelf-slope front (Gili et al. 1988, Sabatés et al. 2010). Nevertheless, this pattern may be subject to considerable spatio-temporal variability due to the mesoscale activity of the front, which can show seasonal variations in its location, strength, and width (Sabatés et al. 2004, Sáiz et al. 2014).

In the NW Mediterranean, the most abundant scyphozoan jellyfish are the oceanic species *Pelagia noctiluca* (Gili & Pagès 2005, Canepa et al. 2014) and the coastal species *Rhizostoma pulmo* and *Cotylorhiza tuberculata* (D'Ambra & Malej 2015, Fuentes et al. 2011). The three species are abundant during the summer season (Mariottini & Pane 2010), although *P. noctiluca* has been detected also in great abundances during spring (Gili et al. 1988, Benedetti-Cecchi et al. 2015).

Pelagia noctiluca

The scyphozoan *Pelagia noctiluca* (Fig. 4) is one of the most abundant blooming jellyfish in the Mediterranean and along the Catalan coast (Canepa et al. 2014). It is an oceanic species that

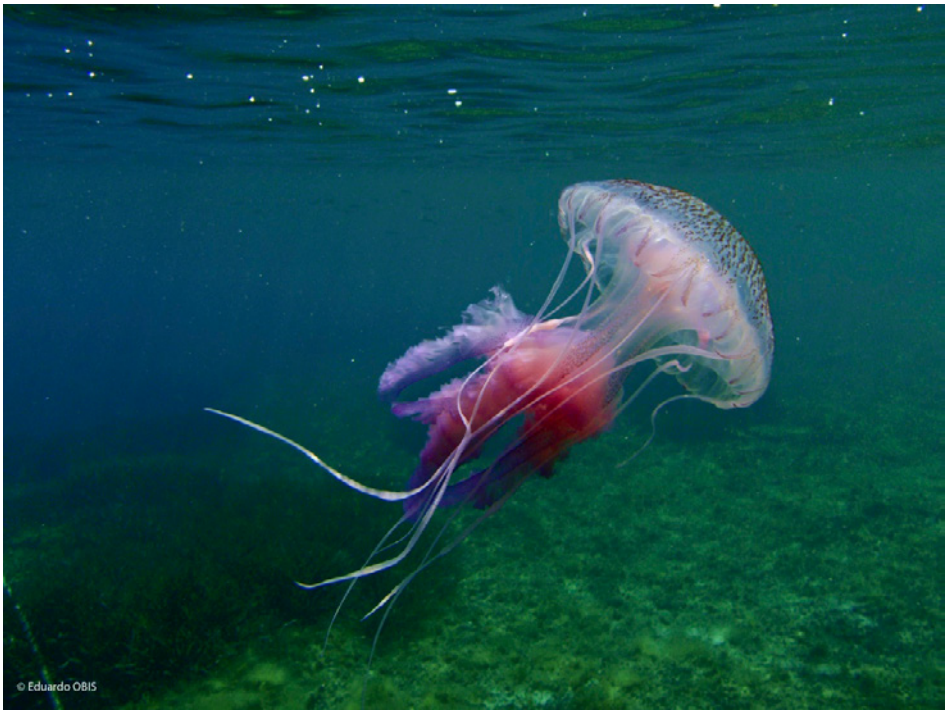

Fig 4 The scyphozoan *Pelagia noctiluca.* Picture: Eduardo Obis

lacks the polyp stage that limits the distribution of most scyphozoans to coastal areas (Arai 1997, Purcell 2005, Doyle et al. 2008). Although *P. noctiluca* is an oceanic species, it can be found in coastal areas as well (Goy et al. 1989, Doyle et al. 2008, Licandro et al. 2010) at high densities (Zavodnik 1987). Oceanographic conditions associated with the variability of the strength and position of the shelf-slope front have been reported to influence the arrival of the species to the coastal areas (Rubio & Muñoz 1997). Years with low precipitation and high solar radiation at the beginning of winter (which maximizes primary productivity) are correlated with blooms of the species in the offshore waters of the front. Then, if the wind blows perpendicular to the coast during the early spring, the first individuals arrive to the coast at the beginning of April (Rubio & Muñoz 1997). Finally, high temperatures and low precipitations at the beginning of summer weakens the density gradients of the front favouring the transport of jellyfish to coastal zones by means of winds and currents (Rubio & Muñoz 1997).

P. noctiluca is a non-selective predator that feeds on a variety of prey, including different groups of zooplankton (Giorgi et al. 1991, Malej 1993, Rosa et al. 2013, Milisenda 2014) and ichthyoplankton (Sabatés et al. 2010). In the NW Mediterranean, *P. noctiluca* adults and ephyrae have the potential to feed on fish larvae at very high rates, being larvae of anchovy, *E. encrasicolus,* the most consumed fish species (Sabatés et al. 2010). Moreover, this jellyfish performs nictemeral migrations, which lead jellyfish to co-occur with zooplankton and ichthyoplankton at the surface layers during the night (Malej 1989, Rottini Sandrini & Avian 1989). During the day, jellyfish have been found in deep waters, below 300 m (Ferraris et al. 2012).

Recent data show that *P. noctiluca* blooms are becoming more frequent in the western Mediterranean (Canepa et al. 2014) thus increasing its potential negative effects on the marine ecosystems and fish stocks.

Rhizostoma pulmo and Cotylorhiza tuberculata

Rhizostoma pulmo (Fig. 5A) and *Cotylorhiza tubercualata* (Fig. 5B) have the life cycle common to most scyphomedusae, composed by a benthic polyp, which asexually reproduces, and a free-swimming medusa stage (Fuentes et al. 2011, Astorga et al. 2012). The life cycle starts with the pelagic planula, sexually generated by adult medusa, which settles on suitable hard substrates (Fuentes et al. 2011, Astorga et al. 2012) where it metamorphoses into a benthic polyp. This polyp asexually reproduces (by polydisc strobilation in the case of *R. pulmo* and by a monodisc process in the case of *C. tuberculata*) and new ephyrae are detached (Fuentes et al. 2011, Astorga et al. 2012). Once the polyp is formed, they asexually reproduce by lateral budding, which can lead to the formation of colonies with hundreds of individuals (Fuentes et al. 2011, Astorga et al. 2012). Although less importance is given to the polyp stage when studying medusae, several authors have suggested that they are key for the development of jellyfish populations and their size (Boero et al. 2008, Purcell et al. 2007) and, thus, for the effects of jellyfish on the ecosystem.

During blooming years, *R. pulmo* and *C. tuberculata* may reach large numbers in different seas, for example the Northern and

Southern Adriatic Sea and the Eastern and Western Mediterranean (Mariottini & Pane 2010). They also reach very high abundances in enclosed or semi-enclosed areas, such as the Mar Menor coastal lagoon, in the southeastern Spain (NW Mediterranean) (Perez-Ruzafa et al. 2002), probably favoured by the degraded environment of this area due to the important inputs of nutrients (mainly coming from agricultural activities) (Fuentes et al. 2011). Morevoer, *R. pulmo* has shown an increasing trend in the frequency of blooming events across the whole Mediterranean (Kogovšek et al. 2010, Brotz & Pauly 2012). Both species are filter-feeders and feed mainly on zooplankton of different sizes, from diatoms <200 µm to copepods of 800-1000 µm (Lilley et al. 2009).

R. pulmo and *C. tuberculata* have been observed in association with juvenile fishes in the Mediterranean (D'Ambra & Malej 2015). In this region, *R. pulmo* has been described as host of three fish species, i.e. *Stromateus fiatola, Trachurus mediterraneus* and *Centrolophus niger*. *C. tuberculata* has been reported associated with *S. fiatola, T. trachurus, T. mediterraneus* and *Schedophilus medusophagus* (D'Ambra & Malej 2015). In other areas of the world, such as the North Atlantic, North Sea and Black Sea, other fish species (*Gadus morhua, Gadus merlangus, Merlangius merlangus, Trachurus trachurus* and *Trachurus mediterraneus*) have also been observed swimming together with *R. pulmo* (Mansuetti 1963, Purcell & Arai 2001).

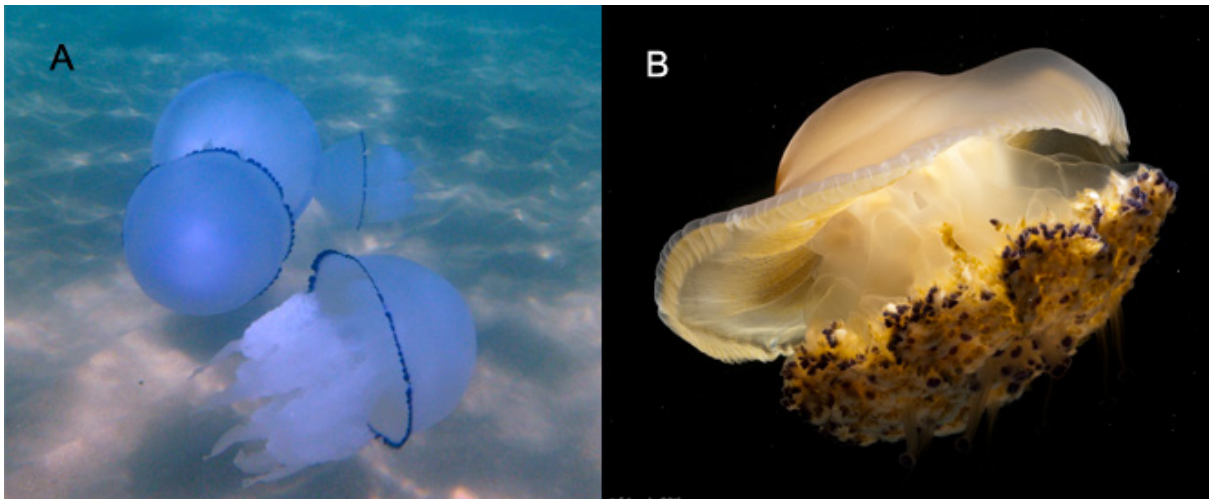

Fig 5 (A) The scyphozoans *Rhizostoma pulmo* and (B) *Cotylorhiza tuberculata*. Picture: Stefano Piraino (A) and Eduardo Obis (B)

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OBJECTIVES AND THESIS OUTLINE

The objective of the thesis has been to investigate the main interactions between fish and the most abundant jellyfish, *Pelagia noctiluca, Rhizostoma pulmo* and *Cotylorhiza tuberculata* along the Catalan coast (NW Mediterranean). The final aim is to provide the scientific basis that contribute to asses the consequences of jellyfish blooms in the coastal area. The research work has been structured in four chapters corresponding to four scientific publications (already published).

Chapter 1:

"Digestion times and predation potentials of *Pelagia noctiluca* eating fish larvae and copepods in the NW Mediterranean Sea" (Article I, published in MEPS) In this chapter we calculated the feeding rates (specifically digestion rates) of *P. noctiluca* when feeding on fish larvae and other zooplankton organisms necessary for the estimation of potential predation *in situ*. In order to assess this objective, an oceanographic cruise was performed off the Catalan coast, at the beginning of summer 2011, where hydrographic and biological samplings were performed, and experiments were conducted onboard. This approach allowed us to obtain information about *P. noctiluca* digestion times on different prey type, which is

essential to estimate feeding rates and predation impact.

Chapter 2:

"Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean" (Article II; published in JPR). In this chapter, we investigated the feeding habits of *P. noctiluca* along the Catalan coast. We analysed the gastric contents of the jellyfish collected during the oceanographic cruise mentioned above to identify and quantify the ingested prey. Moreover, using information obtained in Chapter I (digestion rates), we were able to calculate the potential predation impact of *P. noctiluca* on fish eggs and larvae.

Chapter 3:

"Trophic interactions of the jellyfish *Pelagia noctiluca* in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition" (Article III; published in MEPS). In this chapter, we used biomarker approaches (specifically stable isotopes and fatty acids analysis) to determine the potential predation and/or competition between *P. noctiluca* and the most common fish larvae and adult fish species along the Catalan coast. We complemented this work with the data obtained in Chapter 2, regarding the diet of this jellyfish, in order to obtain a broad picture of the feeding habits of this species and the potential trophic interactions between *P. noctiluca* and fish.

Chapter 4:

"Positive interactions between fish and jellyfish in NW Mediterranean" (Article IV; published in Marine Biology). In this chapter, we studied the association between carangid fish and *R. pulmo* and *C. tuberculata.* For this purpose, we conducted field observations of the fish behaviour, and samplings of jellyfish and associated fish off Barcelona were conducted during the summer period. In the laboratory, experiments were performed to determine the survival of the associated fish, and possible trophic interactions between fish and jellyfish were explored by mean of biomarkers (stable isotopes and fatty acids analysis).

The main results of each chapter are argued in the General Discussion. In that section, we discuss the positive and negative effects of jellyfish on fish populations in the Catalan coast. To conclude, we summarize and highlight the main Conclusions of the thesis.

Digestion times and predation potentials of Pelagia noctiluca eating fish larvae and copepods in the NW Mediterranean Sea
Chapter 1

CHAPTER 1

DIGESTION TIMES AND PREDATION POTENTIALS OF *PELAGIA NOCTILUCA* EATING FISH LARVAE AND COPEPODS IN THE NW MEDITERRANEAN SEA

Jennifer E. Purcell, Uxue Tilves, Verónica L. Fuentes, Giacomo Milisenda, Alejandro Olariaga, Ana Sabatés (2014) *Marine Ecology Progress Series 510: 201–213*

Abstract

Predation is the principal direct cause of mortality of fish eggs and larvae (ichthyoplankton). Pelagic cnidarians and ctenophores are consumers of ichthyoplankton and zooplankton foods of fish, yet few estimates exist of predation effects *in situ*. Microscopic analyses of the gastric 'gut' contents of gelatinous predators reveal the types and amounts of prey eaten and can be used with digestion time (DT) to estimate feeding rates (prey consumed predator^{-1} time^{-1}). We measured the DT and recognition time (RT) of prey for *Pelagia noctiluca*, an abundant jellyfish with increasing blooms in the Mediterranean Sea. DT of fish larvae averaged 2.5 to 3.0 h for *P. noctiluca* (4–110 mm diameter) and was significantly related to jellyfish and larval sizes. In contrast, DT of fish eggs ranged from 1.2 to 44.8 h for jellyfish ≤ 22 mm diameter ('ephyrae'), but DT was not significantly related to ephyra or egg diameter. Approximately half of the eggs ingested were not digested. DT of copepods averaged 4 h. We also measured DT and RT of salps, euphausiids, and miscellaneous zooplankton. Temperature

(20–25°C) generally did not significantly affect DT of any prey. Estimated potential predation effects of ephyrae on fish larvae in the Catalan Sea in 1995 showed great variability among 9 stations (0–3.7% consumed h^{-1}). We discuss how sampling methods contributed to variation in predation estimates and offer recommendations to improve accuracy. Our results enable estimation of predation on ichthyoplankton and competition for zooplankton prey, which can have extremely important effects on fish populations globally.

Keywords: Anchovy, jellyfish, salp, fish eggs, ichthyoplankton, zooplankton, competition.

Introduction

Much of fisheries research has been directed towards predicting annual recruitment of fish into a fishery. The Critical Period and Aberrant Drift hypotheses (Hjort 1914) inspired 20th-century recruitment fisheries oceanography research towards factors affecting the early life history of fish. The main factors believed to determine recruitment variability now include the interactions of temperature and other physical processes on prey availability and larval condition, which in turn determine their vulnerability to predators (Houde 2008). 'It is now evident that high and variable predation is the principal, [proximate] agent of mortality' (Bailey & Houde 1989, Houde 2008).

Many species of pelagic cnidarians and ctenophores eat fish eggs and larvae (ichthyoplankton) (reviewed by Purcell 1985, Purcell & Arai 2001), yet studies on the magnitude of this predation remain rare. During the 1980s and 1990s, several studies quantified removal rates of ichthyoplankton by pelagic cnidarians and ctenophores in containers ranging in size from 25 to 6300 l (reviewed by Purcell & Arai 2001). The results of those studies were affected by being conducted in artificial conditions (Purcell & Arai 2001). A second approach to estimate predation on ichthyoplankton by pelagic cnidarians and ctenophores is to collect the predators *in situ*, thereby preserving their natural prey without experimental interference. Calculation of ingestion rates (prey eaten $predator^{-1}$ $time^{-1}$) also requires estimation of the time prey can still be recognized in gut contents; calculation of predation effects (% prey standing stock consumed $time^{-1}$) further requires information about the abundances of the predators and prey *in situ*.

Interest in gelatinous species has resurged recently, probably because of their increasing interference with human enterprises in coastal oceans (Purcell et al. 2007). One species of particular concern is the holoplanktonic species *Pelagia noctiluca* that has caused economic damage to aquaculture in northern Europe (Doyle et al. 2008, Raffaele 2013) and to tourism, fisheries, aquaculture, and energy industries in the Mediterranean (reviewed by Mariottini et al. 2008, Canepa et al. 2014). *P. noctiluca* has a long history of blooms in the Mediterranean Sea (Goy et al. 1989) that appear to be increasing in frequency and duration (Daly Yahia et al. 2010, Kogovšek et al. 2010, Licandro et al. 2010, Bernard et al. 2011).

P. noctiluca consumes a variety of prey, including copepods and other crustaceans,

gelatinous zooplankton, pelagic mollusks, appendicularians, and fish eggs and larvae (Malej 1982, Vučetić 1982, Sabatés et al. 2010, Rosa et al. 2013). Copepods were the most numerous prey consumed by ephyrae in the NW Mediterranean Sea (Sabatés et al. 2010). Although fish larvae averaged <1% of the available mesozooplankton, they ranged from 5 to 32% of the prey in ephyrae; anchovy *Engraulis encrasicolus* larvae were the most frequently consumed (Sabatés et al. 2010). Thus, *P. noctiluca* is potentially important as a predator of ichthyoplankton and as a competitor of fish larvae and zooplanktivorous fish. Those effects are pervasive but difficult to evaluate. Because predation effects on prey populations increase with pelagic cnidarian and ctenophore population sizes (Purcell & Arai 2001, Purcell & Decker 2005), ichthyoplankton will likely suffer greater mortality as populations of these predators increase.

The *in situ* feeding rates of *P. noctiluca* were not calculated from gut contents in previous studies due to a lack of data on the digestion times of the various prey types. During cruises of the FishJelly project in 2011 and 2012, we measured digestion length of time and the times prey could be recognized in the gastric pouches ('guts') of *P. noctiluca* medusae and ephyrae. We emphasized ichthyoplankton, but also included common zooplankton organisms. Our objective was to measure digestion times in order to use this in formation in combination with gut content data for *P. noctiluca* collected at comparable temperatures to calculate predator feeding rates and predation effects on comparable prey. As an example, we used the gut content data for *P. noctiluca* ephyrae from Sabatés et al. (2010) to estimate their potential predation on fish larvae and copepods off the Catalan coast (NW Mediterranean) in 1995.

Materials and methods

Digestion measurements of fish larvae, fish eggs, and zooplankton by *Pelagia noctiluca* medusae and ephyrae were made in the Catalan Sea during cruises on board the RV 'García del Cid' (17 June to 4 July 2011 and 13 to 21 July 2012). Sea near-surface temperature and salinity were estimated by the ship's system. Near-ambient seawater temperature (T in °C) was maintained in the ship's laboratory by means of near-surface water pumped into kreisels and water baths containing the experimental containers. Fish larvae, fish eggs, and zooplankton used for digestion measurements were selected under magnification of a dissecting microscope from plankton tows of a 60 cm diameter bongo net with 300 µm mesh. Fish larvae were identified to the lowest taxon possible. Anchovy eggs were identified to species by their oval shape. Fish larva total length (TL), copepod cephalothorax length, and fish egg diameter were measured to the nearest 0.1 mm with calipers with the aid of a dissecting microscope immediately before they were fed to *P. noctiluca*. Body lengths of salps (excluding protrusions) and other large species were measured to the nearest 0.5 mm. Fish larval length was converted to dry mass by regressions for the most similar taxa in Pepin (1995) and Rossi et al. (2006). Our methods, outlined below, were considered 'natural feeding' as defined by FitzGeorge-Balfour et al. (2013) and differed for medusae (observed visually while in kreisels) and ephyrae (observed with a dissecting microscope).

P. noctiluca medusae (>22 mm diameter) were collected at night from the surface with a long-handled dip net and placed immediately in a bucket with seawater. They were kept on board in 300 l kreisels with weakly flowing seawater, as illustrated by Purcell et al. (2013). A prey item held with forceps and touched to the oral arms was ingested quickly, and the ingestion time was recorded. After ingestion, the prey item was observed continuously to track its final location in the gastric pouch. Thereafter, each rapidly digesting or transparent prey (i.e. fish larva, salp) was checked visually at ≤15 min intervals and each slowly digesting, conspicuous prey (i.e. euphausiid) at ≤60 min intervals. Only large fish larvae, euphausiids, and salps were visible once ingested by the medusae; therefore, fish eggs and copepods were not tested on medusae because they could not been seen after ingestion. The length of time that prey could still be seen in the guts was recorded and designated 'recognition time' (RT). Prey that could no longer be seen were considered to be digested, and the time was recorded and de signated 'digestion time' (DT). Egestion of the prey remains was occasionally observed (error = 0 min). Otherwise, the error (% of DT) was calculated from one-half of the final observation interval. After digestion of 1 prey item, each medusa was fed another prey and the process was repeated. Medusae appeared to be healthy for 3 to 4 d in the kreisels and were not used for digestion estimates afterwards. The swimming bell diameter then was measured to the nearest 1 cm by placing the medusa subumbrella down on a ruler.

Because we could not determine whether fish larvae digested by medusae on the cruise would be recognized in gut content analysis, we conducted an experiment at the Institut de Ciències del Mar in Barcelona, Spain (Table 1). Medusae from laboratory culture were placed in 300 l kreisels with weakly flowing ambient seawater and each was given 1 fish larva, as above. At 15 to 90 min intervals, 3 to 6 of the medusae were preserved in 5% formalin solution. Their gastric pouches were examined later with a dissecting microscope to determine whether the prey could be recognized as a fish larva. This experiment was conducted twice (18 and 25 July 2013) with 3 species of larvae: anchovy *Engraulis encrasicolus* (Engraulidae), round sardinella *Sardinella aurita* (Clu pidae), and bullet tuna *Auxis rochei* (Scombridae) that had been collected during the previous night using a Bongo net (60 cm diameter, 300 and 500 µm meshes) from nearby coastal waters. These results were compared to the digestion observations made on board ship. Medusae in

Species	Larval length (mm)	Time interval (min)				
		15	30	45	60	90
Anchovy & round sardinella	7-9	6/6	6/6	2/11	0/9	NT
Bullet tune	9-11	NT	3/3	3/3	3/3	0/6

Table 1 Numbers of single fish larvae recognizable in *Pelagia noctiluca* medusae following digestion and preservation at intervals of 15 to 90 min. Results are shown as the number recognizable/number tested. Number of larvae digested = number tested – number recognizable. '0' indicates that all larvae were completely digested. Temperature = 21.3°C. Species were anchovy *Engraulis encrasicolus*, round sardinella *Sardinella aurita*, bullet tuna *Auxis rochei*. NT: not tested

which the larvae could no longer be seen were also included in the analysis of digestion time.

P. noctiluca ephyrae and post-ephyrae with small oral arms and tentacles (hereafter, all referred to as 'ephyrae,' with a diameter ≤ 22 mm) were collected in short surface hauls with a Neuston net (1.5 m^2 mouth, 1 mm mesh). Undamaged ephyrae were kept individually in 25 to 350 ml glass bowls or beakers in which they could swim freely, with container size increasing with specimen size. A fish egg, larva, or zooplankter held with forceps and put in contact with each ephyra was ingested quickly. This time of in gestion was recorded, and each ephyra was checked under magnification of a dissecting microscope at 5 to 60 min intervals, with prey requiring prolonged digestion (fish eggs) being checked at the longer intervals. DT, RT, and % error were determined as described for me dusae. Ephyral diameter was measured to the nearest 1 mm with calipers under a dissecting microscope. We used multiple linear regressions to test whether DT was related to T, *P. noctiluca* diameter, or prey size (largest dimension). Regressions were made only when sufficient data were available. When data did not meet assumptions of normality and constant variance, we used $\log_{10}$ transformation before statistical analysis. One-way ANOVA was used to test for differences in digestion times among fish larval taxa and among fish egg diameters. Digested and undigested eggs were tested for differences in ephyral sizes and egg sizes with t-tests. When those data failed to meet assumptions after transformation, we used a non-parametric t-test (Mann-Whitney rank sum test). All data were presented as mean ± SD.

Results

To test when larvae digested by medusae (35.7 ± 2.1 mm diameter) could not be recognized as fish larvae with microscopic examination, we examined the gut contents of medusae preserved at intervals, as described above (Table 1). All larvae were easily recognizable after 15 and 30 min. The long, thin anchovy and round sardinella larvae could not be re cognized as fish larvae after 45 or 60 min. The larger bullet tuna larvae could still be recognized in the gut contents after 45 or 60 min, but not after 90min of digestion. Based on these results, we removed digestion data for 5 anchovy larvae >10 mm long that could not be seen within swimming medusae on board ship after 30 min.

DTs of *Pelagia noctiluca* medusae and ephyrae fed 1 fish larva averaged 2.5 to 3.0 h (Table 2). DTs of all medusae and ephyrae combined were significantly related to ephyral diameter (D) and larval length (L), but not to T ($R^2 = 0.258$, $F_{3,205} = 24.23$, $p < 0.001$; $\log_{10}D$ $t = -8.33$; $p < 0.001$; $\log_{10}L$ $t = 6.23$; $p < 0.001$; T $t = 0.66$; $p = 0.513$; $\log_{10}DT = 0.334 + 0.562 \times \log_{10}L - 0.620 \times \log_{10}D$). DT of combined medusae and ephyrae increased with larval length and de creased with the diameter of *P. noctiluca* (Fig. 1). Because our methods differed for medusae (>22 mm diameter) and ephyrae (≤22 mm), we considered the 2 groups separately in further analyses.

DTs of both ephyrae and medusae were significantly related to diameter and larval length; DTs were shorter for smaller larvae and larger *P. noctiluca*. DTs for fish larvae were not significantly related to T. Similar results were

Jellyfish							
Diameter (D, mm)	n	T (°C)	Prey length (L, mm)	DT (h)	Error (%)	Regression statistics	RT (h)
Medusae			**Fish larvae**				
48.6 ± 20.6	63	22.7 ± 1.3	14.1 ± 6.5	2.1 ± 2.2	13.3 ± 12.5	$R^2 = 0.425$	0.9 ± 0.8
(25 – 110)		(20.2 – 25.5)	(5 – 30.0)	(0.8 – 8.3)	(0 – 50)	$F_{3,59} = 14.55$; $p < 0.001$	(0.3 – 5.8)
						$Log_{10}D$ $t = -0.79$; $p = 0.432$ NS	
						$Log_{10}L$ $t = 6.41$; $p < 0.001$	
						T $t = -1.04$; $p = 0.300$ NS	
						$Log_{10}DT = 0.024 + 1.061 \times log_{10}L$	
Ephyrae			**Fish larvae**				
13.4 ± 5.2	107	23.4 ± 0.9	5.9 ± 2.6	3.0 ± 1.7	20.6 ± 25.2	$R^2 = 0.319$	1.2 ± 0.2
(4 – 22)		(20.7 – 24.4)	(1.5 – 13.0)	(0.3 – 8.3)	(0 – 50)	$F_{3,103} = 15.89$; $p < 0.001$	(0.2 – 5.8)
						$Log_{10}D$ $t = -2.73$; $p = 0.007$	
						$Log_{10}L$ $t = 5.71$; $p < 0.001$	
						T $t = -1.37$; $p = 0.172$	
						log_{10} DT = 1.213 + 0.662 x $log_{10}L$ – 0.379 x $log_{10}D$	
Medusae			**Salps**				
42.2 ± 11.4	30	22.2 ± 1.4	21.3 ± 12.0	2.0 ± 1.8	7.7 ± 9.0	$R^2 = 0.766$	1.8 ± 1.1
(15 – 60)		(19.6 – 23.7)	(1.5 – 40.0)	(0.4 – 6.9)	(0 – 35)	$F_{3,103} = 27.23$; $p < 0.001$	(0.2 – 5.0)
						D $t = 0.66$; $p = 0.515$ NS	
						L $t = 4.26$; $p < 0.001$	
						T $t = -2.87$; $p = 0.008$	
						DT = 12.217 – 0. 519 x T + 0.087 X L	
Ephyrae			**Salps**				
10.4 ± 0.6	5	23.4 ± 1.3	5.6 ± 2.6	3.2 ± 2.1	16.2 ± 8.8	NT	1.8 ± 1.4
(10 – 11)		(21.6 – 25.2)	(4.0 – 10.0)	(1.0 – 5.7)	(5 – 29)		(0.4 – 4.0)
Ephyrae			**1 copepod**				
11.8 ± 0.6	51	23.9 ± 0.7	1.3 ± 0.3	4.1 ± 1.3	10.2 ± 5.3	$R^2 = 0.131$	2.2 ± 1.2
(7 – 22)		(22.3 – 25.0)	(1.0 – 2.0)	(1.2 – 7.8)	(0 – 29)	$F_{3,44} = 2.20$; $p = 0.101$ NS	(0.7 – 5.0)
						D t = -1.66; $p = 0.105$ NS	
						L t = 1.20; $p = 0.235$ NS	
						T t = -1.10; p = 0. 276 NS	
Ephyrae			**2-4 copepods**				
17.0 ± 3.6	4	23.0	1.1	4.1 ± 0.5	11.4 ± 5.2	NT	1.8 ± 0. 4
(13 – 20)				(3.4 – 4.7)	(7 – 20)		(1.3 – 2.1)

Table 2 Digestion time (DT) and Recognition time (RT) for *Pelagia noctiluca* given single fish larvae, salps, and copepods unless noted otherwise. Errors (% of DT) and multiple regression statistics also given. Salps given to medusae were *Salpa fusiformis*; those given to ephyrae were *Thalia democratica*. Data are presented means ± SD, with ranges in parentheses. T = temperature; NS = not significant; NT = not tested

obtained for a multiple regression using larval dry mass (DM) instead of length; however, the relationship with DM ($R^2 = 0.288$, $F_{3,102} = 13.74$, $p < 0.001$, $\log_{10}$ DM $t = 3.85$; $p < 0.001$) was not as strong as with length (Table 2).

The DTs for ephyrae differed significantly ($F_{5,101} = 346.36$, $p < 0.001$) among different types of larvae (Table 3); pairwise comparisons of the DT of anchovy versus all other types of larvae were significantly different (Holm-Sidak method, $t = 18.12$ to 29.63, $p < 0.001$), and DTs of goby larvae also differed significantly from DTs of serranid and flatfish larvae ($t = 3.08$ and 2.80, respectively, $p < 0.01$). Thus, long, thin larvae (anchovies, sardinellas, gobies) were digested more rapidly

Jellyfish						
Diameter (mm)	n	T (°C)	Fish larvae length (mm)	Digestion (h)	Error (%)	Recognition (h)
Ephyrae			**Anchovy**			
12.9 ± 5.0	64	23.1 ± 0.9	7.3 ± 2.4	3.5 ± 1.7	13.0 ± 10.2	1.3 ± 0.8
(4 – 22)		(20.7 – 24.4)	(2.5 – 13.0)	(0.8 – 8.3)	(0 – 50)	(0.3 – 5.9)
			Serranid			
13.2 ± 0.6	6	24.2 ± 0.2	3.8 ± 0.11	2.7 ± 1.5	17.8 ± 6.9	1.8 ± 0.3
(9 – 13)		(23.7 – 24.4)	(3.5 – 4.0)	(1.3 – 2.6)	(0 – 24)	(1.4 – 2.2)
			Round Sardinella			
13.3 ± 4.2	7	23.7 ± 0.2	6.0 ± 1.4	1.7 ± 0.8	10.8 ± 7.9	0.8 ± 0.4
(10 – 22)		(23.3 – 24.4)	(4.0 – 8.0)	(1.0 – 2.8)	(9 – 24)	(0.4 – 1.5)
			Goby			
9.8 ± 2.8	6	24.1 ± 0.5	2.2 ± 0.9	1.2 ± 0.9	35.0 ± 18.2	0.6 ± 0.3
(8 – 15)		(23.5 – 24.4)	(1.5 – 4.0)	(0.5 – 2.7)	(6 – 50)	(0.3 –1.1)
			Mackerel, scianid, carangid			
13.5 ± 5.5	24	23.9 ± 0.8	3.6 ± 1.5	2.2 ± 1.2	22.0 ± 17.9	1.2 ± 0.6
(7 – 22)		(21.1 – 24.4)	(1.5 – 7.0)	(0.3 – 5.1)	(0 – 50)	(0.4 –2.5)
			Flatfish			
17.3 ± 5.8	6	23.8 ± 0.7	3.5 ± 0.6	2.8 ± 2.2	14.9 ± 19.0	1.3 ± 1.2
(10 – 22)		(23.0 – 24.4)	(3.0 – 4.0)	(0.9 – 5.6)	(0 – 50)	(0.2 – 3.3)

Table 3 *Pelagia noctiluca* ephyrae digestion time (DT) and recognition tiem (RT) of single fish larvae by taxon. Errors (% of DT) are also given. Prey were anchovy *Engraulis encrasicolus*, serranid *Serranus cabrilla*, round sardinella *Sardinella aurita*, mackerel *Trachurus mediterraneus*, myctophid *Ceratoscopelus maderensis*, flatfish *Aroglossus laterna*, and unidentified gobies, scianids, and carangids. Data are presented as means ± SD, withr ranges in parentheses. T: temperature

than short, thick larvae (scombrids, carangids, serranids, flatfish; Fig. 1). The lengths of time that they were recognizable as fish larvae in the guts (RTs) were approximately half of the DTs for both medusae and ephyrae.

Fish eggs were digested more slowly (1.2–44.8 h) than fish larvae by *P. noctiluca* ephyrae (Table 4, Fig. 2). About half of all eggs tested (29 of 56) were egested undigested after many hours, but interestingly, all anchovy eggs were digested. The sizes of ephyrae that had not digested eggs did not differ from those that had (t-test, t_{51} = 1.445, p = 0.155); thus, small ephyral size did not explain why some eggs were not digested.

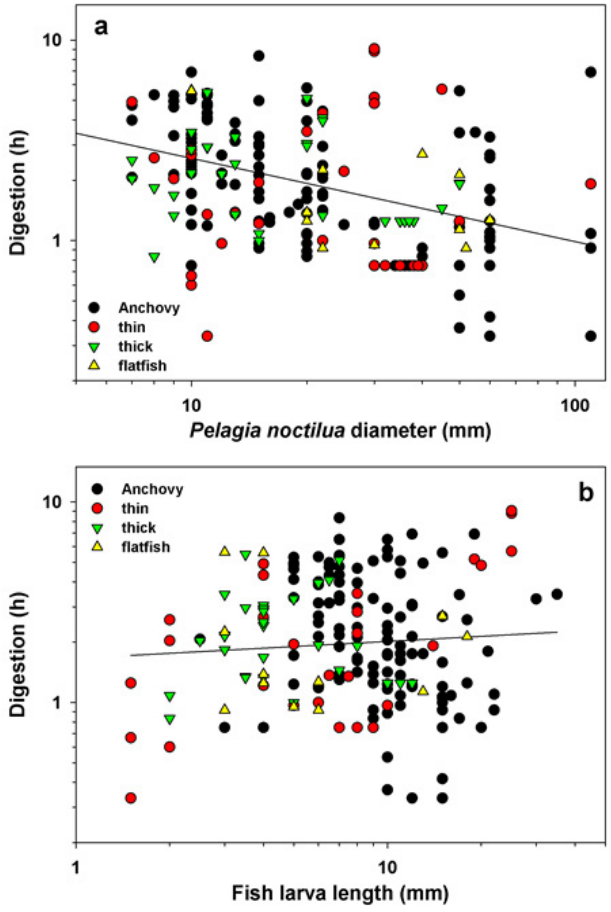

Fig 1 Digestion times of *Pelagia noctiluca* medusae and ephyrae of fish larvae by type: anchovy *Engraulis encrasicolus*, thin larvae (sardinellas, gobies), thick larvae (caran gids, sciaenids, serranids, scombrids), and flatfish *Arnoglossus laterna* with respect to (a) *P. noctiluca* diameter, and (b) fish larvae length. Trend lines are best fit linear regressions for all larvae. See Table 2 for multiple regression equations.

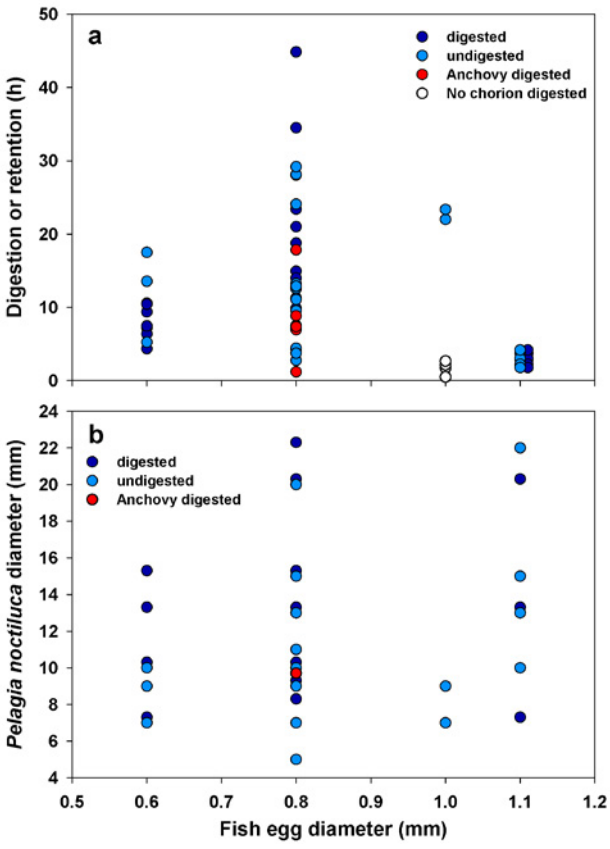

Fig 2 (a) *Pelagia noctiluca* ephyral digestion and retention times of fish eggs with respect to egg diameter. Time (h) that eggs were inside ephyrae. (b) Size of ephyrae compared to size of digested and undigested eggs. In (b), ephyral diameters for digested eggs were offset by +0.3 mm and only 1 point is shown for anchovy (of 6 at 9–10 mm) to enable them to be better seen.

Fish egg length (mm)	Digested eggs					Undigested eggs		
	Ephyra (mm)	n	DT (h)	RT (h)	Error (%)	Ephyra (mm)	n	Retention (h)
0.6 [75%]	9.9 ± 3.1 (7 – 15)	9	8.2 ± 2.2 (4.3 – 10.6)	6.1 ± 2.1 (3.2 – 9.5)	15.8 ± 2.2 (13 – 20)	8.7 ± 1.5 (7 – 10)	3	12.1 ± 6.3 (5.2 – 17.5)
0.8 [45.2%]	12.1 ± 4.3 (8 – 22)	14	17.4 ± 12.0 (3.8 – 44.8)	14.8 ± 13.0 (2.3 – 43.0)	19.0 ± 18.8 (6 – 50)	9.8 ± 3.7 (5 – 20)	17	12.6 ± 7.9 (2.8 – 29.2)
0.8 Anchovy [100%]	9.7 ± 0.5 (9 – 10)	6	8.5 ± 5.4 (1.2 – 17.8)	6.3 ± 3.1 (4.5 – 12.5)	19.8 ± 6.2 (15 – 30)	NA	0	NA
1.0 [0%]	8.0 ± 1.0 (7 – 9)	0	NA	NA	NA	8.0 ± 1.4 (7 – 9)	2	22.7 ± 1.0 (22.0 – 23.4)
1.1 [0%]	13.3 ± 6.5 (7 – 20)	0	NA	NA	NA	15.0 ± 5.1 (10 – 22)	6	3.0 ± 0.9 (1.8 – 4.2)

Table 4 *Pelagia noctiluca* ephyrae digestion time (DT) and recognition time (RT) of single fish eggs by diameter. Eggs 0.8 mm in diameter are presented in 2 groups (anchovy and those other than anchovy). Retention times are for undigested eggs that were egested. Errors (% of DT) are also given. Temperatures were 23.4 ± 0.5°C (22.3 – 25.2°C). Data are presented as means ± SD with ranges in parentheses. Percentages of each egg size digested are in square brackets. Errors reflect digested and undigested eggs; NA = not applicable

Similarly, egg sizes did not differ between those digested or undigested (Mann Whitney U = 296.50, p = 0.194) although no 1.0 or 1.1 mm eggs were digested. To test whether eggs would be digested without the chorion, it was dissected from 4 of the 1 mm eggs, which otherwise were not digested by ephyrae. These embryos were digested rapidly by the ephyrae (1.78 ± 0.46 h; Fig. 2), suggesting that the chorion protected the eggs from digestion. DTs of eggs differed significantly by diameter ($F_{3,29}$ = 5.68, p = 0.003), with 0.8 mm eggs requiring longer to digest than all others. One 3 mm diameter egg was digested in 22.4 h by a 22 mm ephyra. Neither DTs nor RTs of undigested eggs were significantly related to ephyral size, T, or egg size ($F_{3,28}$ = 1.071, p = 0.377 and $F_{3,22}$ = 0.622, p = 0.608, respectively). RT of digested fish eggs were 75–85% of the DT for ephyrae, and RT of undigested eggs were 100% of retention times.

DT and RT of copepods could only be measured for ephyrae (Table 2). DTs of single copepods by ephyrae averaged 4 h and were not

significantly related to prey or ephyral size, or T. We gave 2 to 4 copepods only to 4 ephyrae, but average digestion time remained ~4 h. RTs of copepods were about half of the DTs for ephyrae.

Salps were very abundant and were eaten by me dusae in 2011 (J. E. Purcell pers. obs.). DTs of large salps *Salpa fusiformis* by medusae averaged 2 h and were significantly related to salp length and temperature (Table 2). The few salps *Thalia democratica* small enough to be ingested by ephyrae were digested in ~3 h.

P. noctiluca eats a variety of zooplankton, but digestion times previously were unavailable. DTs of euphausiids (n = 10, 10–20 mm TL) by medusae averaged 5.0 ± 2.4 h. *Velella velella* colonies were eaten by medusae *in situ* (V. L. Fuentes et al. pers. obs.). DTs of 15 and 26 mm long colonies by 2 medusae were ~3.7 h, and those of 1 to 3 mm long colonies by 4 ephyrae were ~5.3 h. The chitin sail of *V. velella* was still recognizable after egestion. The necto phores of 2 polygastric colonies of the siphonophore *Muggiaea atlantica* were egested with their firm mesoglea intact from medusae after 5.0 and 6.5 h. Cladocerans (*Penilia* sp. and *Podon* sp.) were diges ted by ephyrae in 3.0 ± 1.7 h (n = 17). DTs of euphausiid furcilia larvae (n = 13, 3–11 mm TL) for ephyrae averaged 5.0 ± 0.9 h. DTs by ephyrae were short for 2 appendicularians (<1 h) and 1 chaetognath (1–2 h). Coiled pteropods (n = 3, 0.5 mm), whose shells were recognizable until egestion, were digested in ~4 h by ephyrae. RTs of the crustaceans were 45 to 65% of DTs. RTs of shelled pteropods and the cnidarians were 100% of DT.

Discussion

Digestion and recognition times

Gut contents of gelatinous predators in combination with DT can be used to determine *in situ* predation rates (prey consumed predator^{-1} time^{-1}), and in combination with population densities of the predators and prey, they can be used to estimate predation effects (% prey consumed time^{-1}). Even though *Pelagia noctiluca* blooms in tropical to temperate oceans around the world (Kramp 1961), few studies exist on DT. Gordoa et al. (2013) mentioned 18 ± 5 h as the DT of bluefin tuna *Thunnus thynnus* eggs by 'burst feeding' *P. noctiluca* ephyrae. We also only know the DT for *P. noctiluca* medusae consuming *Mnemiopsis leidyi* ctenophores (Tilves et al. 2012).

Martinussen & Båmstedt (2001) comprehensively summarized earlier studies on DTs of fish larvae, fish eggs, and zooplankton by gelatinous predators. The DTs of fish larvae in our study were similar to those in other studies that included larvae and medusae of comparable sizes, even when the temperatures were 10°C lower (Table 5). Few DTs were available for fish eggs, and no other studies used ephyrae and eggs. DT of anchovy eggs by *Chrysaora quinquecirrha* medusae (3.7–5.2 h, mean 4 h) and *Stomolophus meleagris* (3 h) were within the range for *P. noctiluca* ephyrae (1.2–17 h, mean 8.5 h), but shorter on average. DTs of ~1 mm copepods by *P. noctiluca* ephyrae were similar to those of other species of comparable sizes even at temperatures that were 10°C lower (Table 5). Our results are also comparable to other species digesting cladocerans and appendicularians. The cladoceran *Evadne* sp. was digested by

Predator species		Prey		T (°C)	DT (h)	Notes	Standing stock eaten		Reference
Diameter (mm)	n	Type (n)	Size (mm)				(% d^{-1})	(% of prey)	
		Fish larvae							
Aequorea victoria 49–68	204	*Clupea harengus pallasi* larvae (1–15)	9 – 14	8–12	1.6–5.2	DT increased with prey size and number, decreased with T	0.8–73	0–97	Purcell (1989), Purcell & Arai (2001)
Aurelia aurita 20–75	10	*C. harengus* larvae	11	9.5	3.9±0.5		NG	NG	Martinussen & Båmstedt (1999)
A. aurita 3–25 mm[a]	40[a]	*Pleuronectes americanus* larvae	NG	7	2.3±1.0		~1[a,c]	<2[a,c]	Sullivan et al. 1994
Chrysaora quinquecirrha NG	7	*Anchoa mitchilli* larvae (1–9)	3	26	1.1±0.5		29±14	0–8.8	Purcell et al. (1994)
Pelagia noctiluca 4–110	175	*Engraulis encrasicolus* & other larvae	1.5–30	20–25	0.7–8.3	DT decreased with jelly size & increased with larval size	1.2 –13.4	0–13.6	This study, Sabatés et al. (2010)
		Fish eggs							
Cyanea capillata ~2–100	~35	Fish eggs	NG	NG 20–25[b]	5.3		0.1–3.8	14.3	Fancett (1988) Fancett & Jenkins (1988)
Pseudorhiza haeckeli ~5–100	~35	Fish eggs	NG	NG 20–25[b]	3.3		0.1–2.4	40.8	Fancett (1988), Fancett & Jenkins (1988)
Stomolophus meleagris 15–100	165	Fish eggs	0.6–0.8	28–30	3		NG	<1	Larson (1991)
C. quinquecirrha 23–44	16	*A. mitchilli* eggs (9–52)	~1.0	26	3.7–5.2 3.9 ± 0.8	DT independent of egg numbers and medusa size	14±4	0.1–90	Purcell et al. (1994)
P. noctiluca 7–22	29	*E. encrasicolus* & unident. eggs	0.6–3	23–25	1.2–44.8	DT independent of ephyra & egg sizes and T	NG	NG	This study
Mnemiopsis leidyi *lg 50–75* sm 7–22	20 13	*A. mitchilli* eggs (1–2)	~1.0	24	lg 0.6 ± 0.1 sm 1.0 ± 0.4	DT	0–36 9±14	NG NG	Purcell et al. (1994)
		Copepods							
C. capillata ~2–100	~35	Copepods	NG	NG 20–25[b]	1.7	DT	0.1–1.6[d]	10.7	Fancett (1988), Fancett & Jenkins (1988)
P. haeckeli ~5–100	~35	Copepods	NG	NG 20–25[b]	1.7	DT	0.2–4.8[d]	32.8	Fancett (1988), Fancett & Jenkins (1988)
S. meleagris 15–100	165	Calanoids	0.3–1.5	28–30	1.5	DT	NG	4.3	Larson (1991)
A. aurita 4.5–13.5	24	*Pseudocalanus elongatus*	1.4	9.5	3.7 ± 1.7	DT	NG	NG	Martinussen & Båmstedt (1999)
A. aurita 8.7–13	6	*Temora longicornis*	1	9.5	3.2 ± 0.9	DT	NG	NG	Martinussen & Båmstedt (1999)
A. aurita 4.3–54	39	*Calanus finmarchicus*	2.3	9.5	1.5 – 7.7 5.2 ± 2.0	DT decreased with medusa size	NG	NG	Martinussen & Båmstedt (1999)
A. aurita 3–25 mm[a]	40[a]	*Acartia hudsonica*	NG	7	2.3±1.0	DT	< 25[a,c]	0–70	Sullivan et al. (1994)
C. quinquecirrha 25–126	16	*Acartia tonsa* (3–631)	1	20–27	1.1–6.2 3.5 ± 1.1	DT decreased with T	1–94	55–71	Purcell (1992)
P. noctiluca 7–22	53	Calanoids	1–2	22.3–25	1.2 – 7.8 4.1 ± 1.3	DT independent of ephyral and prey size and T	<0.1	43–86	This study
M. mccradyi = leidyi NG	39	*Acartia tonsa*	1	25–27	1	DT	12–82[c] 34±28[c]	13[c]	Larson (1988)

[a]In mesocosm; [b]estimated from Port Philip Bay summer water temperature; [c]calculated from data in paper; [d]laboratory feeding estimates

Table 5 Selected studies reporting digestion times for medusae and ctenophores eating fish larvae or eggs, plus copepods. The percentages of the standing stocks consumed and percentages of prey in the gut contents are reported if available. If more than 1 prey item was digested, the numbers are given in parentheses. T: temperature; NG: not given; lg: large; sm: small; n: number

Aurelia aurita ephyrae in 3.4 h at 4–5°C (Sullivan et al. 1997). Digestion of appendicularians was very rapid by hydromedusae (<2 h; Larson 1987b) and by *S. meleagris* at 28–30°C (1.5 h; Larson 1991). We are unaware of other DTs for gelatinous predators of salps, pteropods, or stages of euphausiids other than eggs or nauplii (see Martinussen & Båmstedt 2001).

Our estimates of DT and RT in *P. noctiluca* were constrained by the numbers and sizes of medusae available and the relatively narrow range of ambient seawater temperature. Too few medusae were present to allow repeated microscopic analysis to follow digestion over time, which could have damaged the specimens, or to preserve them for gut analysis to confirm complete digestion or recognition. *P. noctiluca* inhabits a wide range of temperatures from deep waters at <14°C to the surface at >26°C in the Mediterranean Sea. Therefore, DT and RT should be measured over that range of temperatures, which large medusae traverse on daily vertical migrations. Because we followed prey items in swimming medusae, 2 problems resulted. First, the end-point of digestion was usually very subjective. Second, we were unable to measure digestion of small prey (copepods, most fish larvae, and fish eggs) by medusae; therefore, additional experiments need to be conducted in which digestion of prey can be monitored more precisely. Our study was also limited by monitoring digestion of single prey items. Because of their small size, ephyrae may

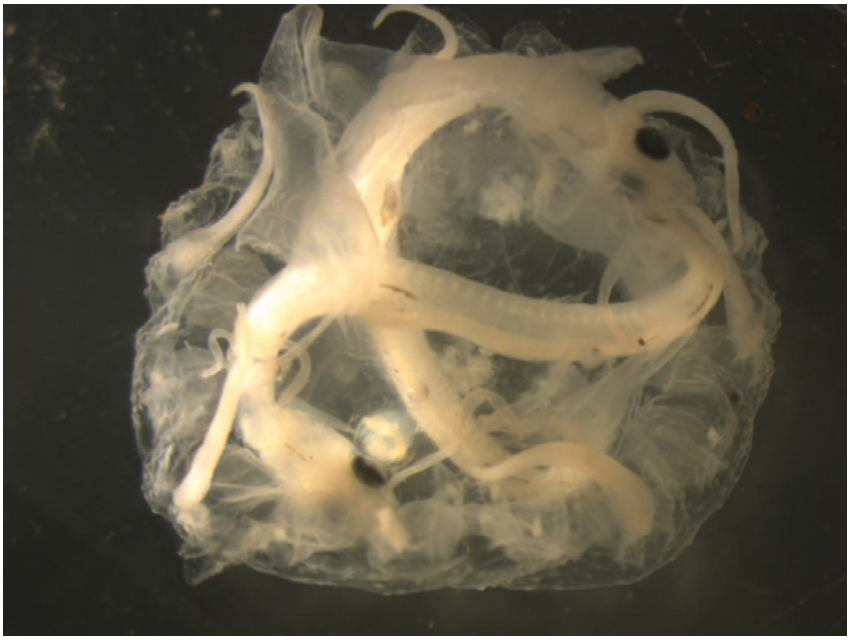

Fig 3 *Pelagia noctiluca* ephyra collected from the surface at night and immediately preserved on 4 July 2011. The ephyra contained 2 anchovy larvae (~10 mm long) and 1 unidentified fish egg (0.9 mm diameter; indicated by arrow). Ephyra preserved diameter is 7 mm.

not catch several prey items concurrently (but see Fig. 3); however, medusae usually contain numerous prey (J. E. Purcell & U. Tilves pers. obs.), which affected DT measured for small *A. aurita* (Martinussen & Båmstedt 2001, FitzGeorge-Balfour et al. 2013).

The lack of digestion of about 50% of the fish eggs by ephyrae raised interesting questions. Although small ephyral size did not explain that phenomenon (Fig. 2b), we could not measure digestion of fish eggs by medusae because we could not visually follow such small prey inside them. As ephyrae grew, the number and length of the digestive filaments in the gastric pouches increased (J. E. Purcell pers. obs.). The ephyrae collected by Sabatés et al. (2010) did not contain any fish eggs, although they were available for consumption (A. Sabatés pers. obs.). Therefore, we do not know whether *P. noctiluca* medusae >22 mm would digest all fish eggs.

On the other hand, the fish eggs may be resistant to digestion. Baltic cod *Gadus morhua callariasadu*s eggs were rejected by *M. leidyi* ctenophores; ctenophores that had ingested eggs subsequently ejected 12 of 14 eggs undigested after 2 h at 22°C and 3 d at 7°C (Jaspers et al. 2011). Plaice *Pleuronectes platessa* eggs similarly were ingested, but were egested undigested 'after some hours' by *Bolinopsis infundibulum* ctenophores (Gamble 1977). Most (98–99%) bivalve veligers were not digested or killed by *C. quinquecirrha* medusae (Purcell et al. 1991). 'Passing alive' of pelagic larvae of benthic invertebrates through their predators has been described previously (Mileikovsky 1974), but we could find no further information about fish eggs. Unfortunately, we were unable to determine whether the eggs had been killed by the ephyrae or remained viable.

Potential predation effects by Pelagia noctiluca on fish larvae and copepods

The DT and RT of *P. noctiluca* are valuable instruments for estimating predation on prey populations *in situ*. We, therefore, chose a study conducted in the Catalan Sea (Sabatés et al. 2010) to illustrate this method and problems we encountered. In the Sabatés et al. (2010) study, sampling was conducted on a transect perpendicular to the coast at 3 stations (Shelf: over the shelf; Front: over the slope at a shelf-break front; Open Sea: in the open sea) during 18 to 23 June 1995. Sampling was repeated 3 times at each station, and temperature was measured at each station with a CTD. Zooplankton, jellyfish, and fish larvae were sampled by oblique tows of a 60 cm diameter bongo net with a flowmeter and 500 m mesh from near bottom (70– 80 m) to the surface over the shelf or from 200 m to the surface at the front and in the open sea (≥1000 m depth). The duration of the tows ranged from 6 min at shallow shelf stations to 23 min at the front and open sea stations. Net samples were fixed in a 5% form aldehyde–seawater solution. *P. noctiluca* ephyrae (≤12 mm diameter), and fish larvae were counted and identified to the lowest possible taxonomic level from whole preserved samples aided by a dissecting microscope. All copepods were coun ted from 1/256 to 1/32 aliquots obtained with a plankton splitter. The gut contents of all ephyrae in the samples were identified, counted, and measured; only partly digested prey were included to ensure that the prey items had not been captured while in the net.

Although Sabatés et al. (2010) presented average predation by location (Shelf, Front, Open Sea), we calculated feeding at each of the 3 stations per location. Individual feeding rates of *P. noctiluca* ephyrae on fish larvae and copepods were calculated from the numbers of each prey type in the gut contents at each station divided by the DT of 107 fish larvae or 53 copepods at the mean surface water temperature in 1995 (20.4°C), as calculated from mean prey sizes and regression equations in Table 2. Individual feeding rates were multiplied by ephyral densities and divided by prey densities at each station to estimate the effects of the ephyrae on the prey populations (% prey standing stock consumed h^{-1}). To estimate the potential daily predation at each location, we assumed that feeding and digestion were continuous over the 8 h periods represented by the samples at each location (day, dawn/dusk, night) and multiplied the hourly rates by 8 and then summed the 3 stations.

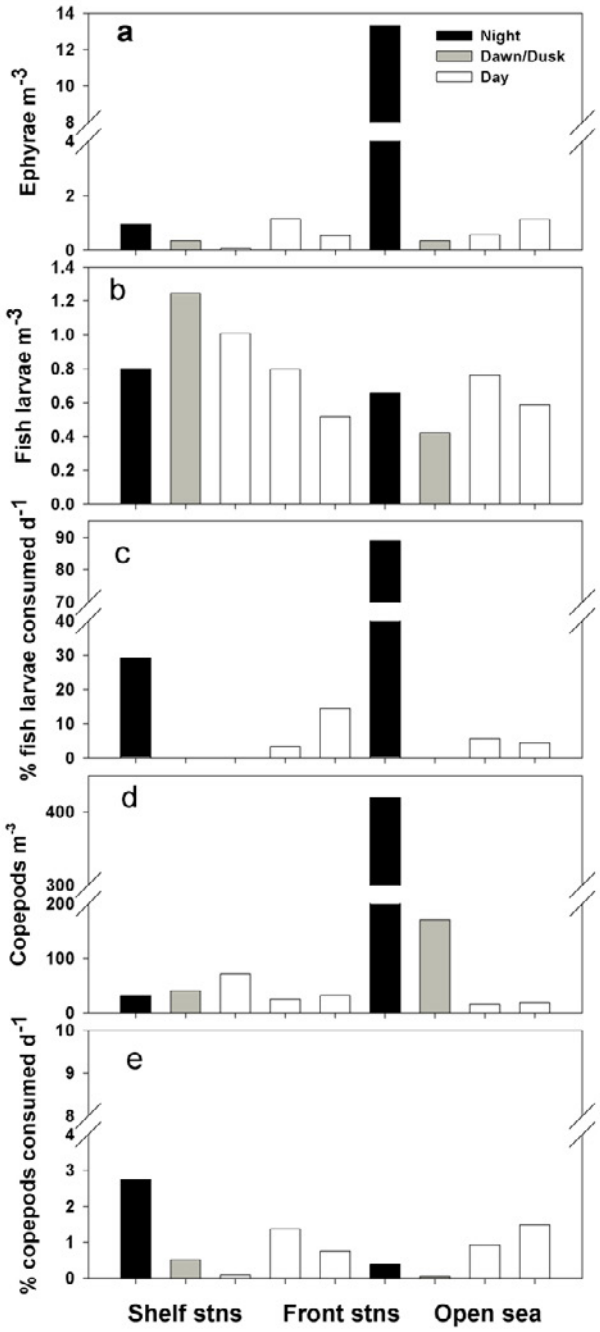

Fig 4 Abundances and predation effects of *Pelagia noctiluca* ephyrae on fish larvae and copepods according to station (stn) and time of day in the northwestern Mediterranean Sea during 18 to 23 June 1995. Three stations each were over the shelf, at a shelf-break front, or in the open sea along a transect perpendicular to the coast. (a) Ephyrae densities, (b) fish larvae densities, (c) predation effects on fish larvae, (d) copepod densities, and (d) predation effects on copepods.

Estimates of potential predation by ephyrae on fish larvae were highly variable among the 9 stations (Fig. 4). Ephyrae were much more abundant (13.4m^{-3}) at the Front at night (01:00 h) than at other stations (<1 m^{-3}). The incidences of feeding (ephyrae with prey) at the Front were only 6 to 13%, probably reflecting damage to the ephyrae and loss of prey in the 200 m depth tows. Fish larvae were of average abundance at that station, and the highest levels of predation (3.7% of the larvae h^{-1}) occurred there at night (Fig. 4). Although ephyrae were found at low densities on the Shelf (0–0.03 m^{-3}), fish larval densities were highest there (0.8–1.2 m^{-3}), and feeding incidences were high (14–33%) where tows were from only 70 to 80 m depth. Fish larvae were found in the ephyrae only at night (22:00 h) on the Shelf, when we estimated that 1.2% h^{-1} could have been consumed. In the Open Sea, ephyral densities, feeding incidences (9–10% in 200 m tows), and predation effects were low (0–0.7% h^{-1}; Fig. 4). Daily potential predation effects on fish larvae at each location ranged from 1.2 to 13.4% d^{-1}; Table 6).

Prey type	Location	Prey in guts (n)	Ephyrae examined (n)	Prey consumed (% d^{-1})
Fish larvae	Shelf	2	145	3.6
	Front	26	4400	13.4
	Open sea	5	1135	1.2
Copepods	Shelf	18	145	0.42
	Front	110	4400	0.31
	Open sea	48	1135	0.31

Table 6 Estimated potential predation effects (% prey consumed d^{-1}) of *Pelagia noctiluca* ephyrae on fish larvae and copepods in the northwest Mediterranean Sea in June 1995

Estimated potential predation effects by *P. noctiluca* ephyrae on copepods were much lower than on fish larvae (Fig. 4). Although copepods were very abundant at the Front station at night, the estimated potential predation effect was low (0.05% h^{-1}) because of the low feeding incidence. The highest predation effect (0.11% h^{-1}) was at night on the shelf, again probably because of the high feeding incidence (25%). The daily potential predation effects on copepods at each station ranged from 0.30 to 0.42% d^{-1}; Table 6). The predation effects of ephyrae on copepods were much lower (≤0.42% d^{-1}) than on fish larvae (≤13.4% d^{-1}) due to the 50- to 500-fold greater densities of copepods.

Even though the sampling methods of Sabatés et al. (2010) were standard for fisheries oceanography, they illustrated some problems for estimating predation effects on fish larvae by *P. noctiluca*. First, we believe that the net sampling damaged the ephyrae and reduced their apparent feeding. That was indicated by the higher feeding incidence on the shallow shelf where tows were half as deep as at the other stations. This likelihood also was clearly illustrated by the gut contents of ephyrae dipped from the surface in 2011 to 2012 (Fig. 3), which contained fish eggs and more fish larvae than in 1995. Additionally, the 60 cm diameter net was too small to adequately sample the larger medusae. Thus, feeding by *P. noctiluca* was underestimated with these net samples.

Other biases in the predation estimates resulted because the oblique tows of Sabatés et al. (2010) obscured the diel vertical migration patterns of *P. noctiluca* and their prey. The medusae are known to migrate near to the surface at night (Ferraris et al. 2012), and the ephyrae move near the surface during the night (Gordoa et al. 2013; V. L. Fuentes et al. pers. obs.). Anchovy larvae also migrate towards the surface at night (Sabatés et al. 2008). Thus, the oblique net tows in 1995 did not reflect the fine-scale patterns of overlap of ephyrae and larvae over 24 h, which were not known, but may have extended the duration of overlap. The variable sampling times at the different stations in 1995 also made predation estimates difficult to compare. If we had used RT instead of DT to calculate predation effects, the effects would have been approximately doubled. We consider the predation estimates presented here to be rough approximations.

Thus, our recommendations for use of the gut content method to estimate gelatinous predator consumption of ichthyoplankton and mesozooplankton are as follows:

- Collect specimens for gut contents individually, not in plankton nets, and preserve them immediately.

- Collect gut-content specimens from all appropriate depths, not only at the surface.

- Appropriate sampling methods should be chosen with consideration of the depth distribution patterns of predator and prey species during day and night.

- Use ambient temperature to measure digestion and recognition times.

- Different digestion methods may be best depending on predator and prey characteristics (e.g. Purcell et al. 1991, FitzGeorge-Balfour et al. 2013).

• The duration between ingestion and when prey can still be recognized in microscopic gut-content analysis (RT) is the most appropriate measure for use in feeding estimates using gut contents.

• Use data for ephyral size and ichthyoplankton species and size consumed for greatest accuracy.

• Determine densities, depths, and size distributions of the gelatinous species and their prey to estimate predation effects (% prey standing stock consumed d^{-1}).

Effects of gelatinous zooplankton as predators and competitors of fish

Surprisingly few studies have addressed consumption of fish eggs and larvae by gelatinous predators *in situ*. Whenever such studies were conducted, the predation effects were substantial (reviewed by Purcell 1985, Purcell & Arai 2001). Ichthyoplankton often constitutes large proportions of prey found in the gut contents (Table 5). *P. noctiluca* ephyrae and medusa could be important predators of fish eggs and larvae. Larson (1987a) stated that fish eggs were the most numerous prey items in 50 medusae, with as many as 10 eggs $medusa^{-1}$. Sabatés et al. (2010) found that fish larvae represented ~12% of the prey items in ephyral gut contents in the spring. Fish larvae and eggs represented 0.2 and 1.1%, respectively, of the prey in medusae collected through out a year (Rosa et al. 2013).

Gelatinous predators have been demonstrated to reduce populations of fish larvae (Purcell & Grover 1990). Gelatinous predators consume a variety of fish species in the plankton, including commercially valuable species. The siphonophore *Rhizophysa eysenhardti* consumed fish larvae in 5 families (Purcell 1981). The scyphomedusae *Cyanea capillata* and *Pseudorhiza haeckeli* consumed 4 kinds of larvae and eggs (Fancett 1988). *S. meleagris* con sumed 4 kinds of eggs (Larson 1991). Similarly, the large hydromedusan *Aequorea victoria* consumed larvae of at least 10 species of fishes and eggs of at least 3 species (Purcell 1989). Eight species of larvae were eaten by *P. noctiluca* ephyrae (Sabatés et al. 2010). Additional studies conducted since the reviews by Purcell (1985) and Purcell & Arai (2001) have shown that the cubomedusae *Chironex fleckeri, Tamoya haplonema*, and *Chiropsalmus quadrumanus* eat fish (Carrette et al. 2002, Nogueira Júnior & Haddad 2008). Young fish and fish eggs represented 5.2 and 1.2%, respectively, of the prey items in the pleustonic hydrozoan *Velella velella* (Purcell et al. 2012). Thus, the potential effects of gelatinous predators on fish are great.

Mesozooplankters are the main components of the diets of many fish and pelagic cnidarians and ctenophores, and dietary overlaps have been shown (Purcell & Grover 1990, Purcell & Sturdevant 2001, Brodeur et al. 2008). The small percentages of the cope pod standing stocks consumed by *P. noctiluca* ephyrae may seem unimportant, but the combined predation of the suite of gelatinous predators (Fuentes et al. 2010, Sabatés et al. 2010, Canepa et al.2014) removes food that otherwise could be consumed by fish. Studies of *in situ* predation by gelatinous species eating mesozooplankton are more numerous than studies on ichthyoplankton (e.g. Larson 1987b, 1988, Purcell 1997, 2009). Predation effects

on mesozooplankton, primarily copepods, vary greatly depending on the abundance of the predators (summarized by Purcell & Arai 2001). Competition for prey requires that prey are limiting, and when abundant, pelagic cnidarians and ctenophores can reduce copepod populations (e.g. Purcell & Decker 2005).

We believe that existing evidence of gelatinous species as important predators of ichthyoplankton and mesozooplankton covers only a small fraction of the extent of their predation. Past studies have considered only a few of the >1400 species of gelatinous predators that inhabit all depths of estuaries and oceans (Purcell et al. 2007). The studies were conducted only in near-surface waters, whereas concentrations of ichthyoplankton, mesozooplankton, and predators often occur at sub-surface hydrographic discontinuities (clines) (Graham et al. 2001, Purcell et al. 2014). The studies have also been limited spatially and temporally. Although *P. noctiluca* has been studied in only a few locations, primarily in Irish waters (Doyle et al. 2008, Bastian et al. 2011) and the Mediterranean Sea, this species is found in tropical to temperate oceans around the world (Kramp 1961). Studies suggest that blooms of *P. noctiluca* and other species have increased in frequency and duration in the Mediterranean Sea (Daly Yahia et al. 2010, Kogovšek et al. 2010, Licandro et al. 2010, Bernard et al. 2011). If cnidarian and ctenophore populations increase around the world, as evidence from some locations suggests (Brotz et al. 2012, Condon et al. 2013), there could be increasing predation on ichthyoplankton and mesozooplankton and increasing detrimental effects on fish populations.

Acknowledgments

We greatly appreciate the assistance of the crew of the RV 'García del Cid' and all the participants during the cruises. This study was supported by the project MAR-CTM2010-18874. V.L.F. was funded by a JAE-DOC contract of CSIC co-financed by the FSE (European Social Fund).

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

Chapter 2

CHAPTER 2

NATURAL DIET AND PREDATION IMPACTS OF PELAGIA NOCTILUCA ON FISH EGGS AND LARVAE IN THE NW MEDITERRANEAN

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Abstract

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

larvae, in particular anchovy. Hence it may play an important role in the planktonic food web with a possible impact on anchovy populations.

Keywords: Jellyfish, ichthyoplankton, diet, predation, competition

Introduction

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

Predation on early life stages of fish is believed to be the main factor determining fish recruitment (Bailey & Houde 1989), and several species of fish larvae have been affected by predation by different species of jellyfish. Herring larvae were shown to be heavily predated by *Aurelia aurita* and *Aequorea victoria* in Kiel Bight and in waters of British Columbia, respectively (Möller 1984, Purcell & Grover 1990). *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* also were shown to be important predators of bay anchovy, *Anchoa mitchilli*, eggs and larvae in Chesapeake Bay (Purcell et al. 1994). Feeding of jellyfish, their diet composition and predation on ichthyoplankton have been studied around the world, but only a few studies calculate the magnitude of this predation and the potential competition with fishes for food (Purcell & Grover 1990, Purcell & Sturdevant 2001, Brodeur et al. 2008, Sabatés et al. 2010, Purcell et al. 2014). *Pelagia noctiluca* (Forsskål, 1775) is recognized as one of the most abundant and widespread jellyfish species in the Mediterranean (reviewed in Canepa et al. 2014), and it has had massive outbreaks in recent years (Gili & Pagés, 2005, Daly Yahia et al. 2010, Kogovšek et al. 2010, Bernard et al. 2011). *Pelagia noctiluca* is deleterious to human activities, especially tourism and fisheries in the Mediterranean Sea (Canepa et al. 2014) and causes important economic damage to aquaculture in northern Europe (Doyle et al. 2008, Purcell et al. 2013). Although it is an oceanic species, it can be found in coastal areas (Goy et al. 1989, Doyle et al. 2008, Licandro et al. 2010) at densities that can even exceed 500 medusae m^{-3} (Zavodnik 1987). This jellyfish species can be abundant on the Catalan coast (NW Mediterranean), mainly during spring and summer (Gili et al. 1987, Benedetti-Cecchi et al. 2015), over the shelf-slope region where high concentrations of zooplankton occur (Sabatés et al. 2004). *Pelagia noctiluca* performs diel vertical migration, staying at the surface at night and in deep water, below 300m, during the day (Franqueville 1971, Ferraris et al. 2012). This vertical distribution pattern coincides with the migration of zooplankton, their main prey (Malej 1989, Rottini Sandrini & Avian 1989). *Pelagia noctiluca* has been described as an opportunistic predator that feeds on a wide variety of prey (Malej 1989, Rottini Sandrini & Avian, 1989, Rosa et al. 2013) including ichthyoplankton (Sabatés et al. 2010, Purcell et al. 2014). It can also be a competitor of fish

larvae and zooplanktivorous fish, due to its consumption of zooplankton (Purcell et al. 2014). In the NW Mediterranean, copepods were the most numerous prey of *P. noctiluca* ephyrae (Sabatés et al. 2010) and also the main diet component of different species of fish larvae, including the European anchovy, *Engraulis encrasicolus* and sardine, *Sardina pilchardus* (Sabatés & Saiz 2000, Morote et al. 2010, Costalago et al. 2012).

The spring-summer period in the NW Mediterranean is characterized by high ichthyoplankton diversity. Most coastal fish species (e.g. from Sparidae, Mullidae, Serranidae and Carangidae families), as well as small pelagics, such as anchovy and round sardinella, *Sardinella aurita*, spawn during that period. Eggs and larvae of these species are located in the surface waters above the thermocline (Olivar & Sabatés 1997) and co-occur there with *P. noctiluca* during the night (Sabatés et al. 2010). Small pelagic fishes are widespread and support important fisheries globally. They are essential elements of marine ecosystems due to their significant biomass at intermediate levels in the pelagic food web, playing important roles in connecting the lower and upper trophic levels (e.g. Bakun, 1996, Cury et al. 2000). In the NW Mediterranean, the small pelagic anchovy and sardine are the most important species in terms of both biomass and commercial interest (Palomera et al. 2007). Because fisheries along the Catalan coast and many Mediterranean countries depend economically on small pelagic fish, it is necessary to understand jellyfish trophic interactions and their potential effects in the pelagic food web. In this context, the objectives of this study were (1) to assess the possible spatial overlap between *P. noctiluca* (ephyrae and medusae) and fish larvae along the Catalan coast, (2) to analyse the natural diet and feeding selectivity of *P. noctiluca* and (3) to estimate the *in situ* potential predation impact of *P. noctiluca* on ichthyoplankton communities.

Materials and methods

Field Sampling

Sampling of *P. noctiluca*, medusae and ephyrae, and their zooplankton prey was conducted along the Catalan coast (NW Mediterranean) in summer 2011 (17 June–4 July) on board the RV "García del Cid". To determine the spatial distribution and abundance of *P. noctiluca* and zooplankton, 81 stations were sampled on 17 transects perpendicular to the shoreline from near the coast to the slope. Stations on each transect were placed 7.5 nautical miles apart and the distance between transects was 10 nautical miles. Vertical profiles of the basic hydrographic parameters (temperature, salinity and fluorescence) were obtained by means of CTD casts equipped with afluorometer. *Pelagia noctiluca* ephyrae and zooplankton were sampled at each station by oblique tows from a maximum depth of 200m to the surface using a bongo net with of 60 cm diameter opening and a mesh size of 300 μm. Samples were collected continuously during the cruise regardless of the time of the day. The volume of water filtered was estimated by means of a flowmeter placed in the centre of the net mouth. Zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

Abundances of adult medusae, which

were near the surface mainly at night, were recorded through visual observations during net sampling stations and during transit between stations from the ship's deck. During the night, a light (ADIR, 10000000cd) was used to illuminate an observation area of 10 m^2. The ship's speed during net sampling was 2 knots and in transit it was around 10 knots. A total of 17.3 h of observations were made over 19 days, averaging 54.5 min per day. The jellyfish abundance was estimated by visual counts of the numbers of jellyfish observed in the illuminated area. Three abundance categories were established based on the Medusa Project sighting protocol: <1 medusa 10m^{-2}, >1 medusa 10 m^{-2}, >10 medusa 10 m^{-2} (Canepa et al. 2014). *Pelagia noctiluca* medusae (30–75 mm) for gut content analyses were collected at eight sampling stations where they were numerous (see Fig. 1). Specimens were individually collected from the vessel's deck during the night using a long-handled dip net. Immediately after collection, medusae were rinsed with filtered seawater to remove any attached zooplankton and preserved individually with 5% buffered formalin solution. Sampling of ephyrae (2–9 mm) for stomach content analyses was by bongo net during day and night and samples were preserved as described above (Fig. 1). In the laboratory, those ephyrae were removed from the samples and their gut contents analysed. Additionally, ephyrae were also collected at night by drifting a neuston net (1.5 m^2 mouth, 1 mm mesh) at the surface for short periods of time (10 min) and dipping them individually from the surface using a long-handled dip net. These ephyrae were preserved individually in 3 mL centrifuge vials with formalin.

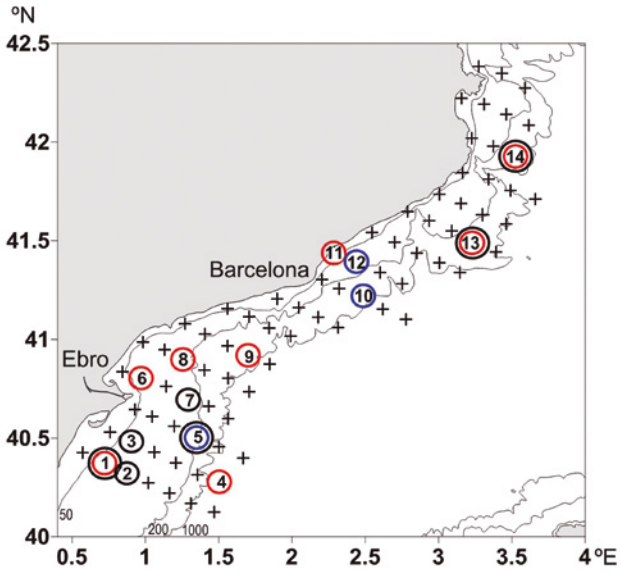

Fig 1 Stations where medusae of *Pelagia noctiluca* (red circles) and ephyrae (collected by bongo net: black circles; dipped or collected drifting a neuston net: blue circles) were collected for gut content analyses during the oceanographic cruise conducted in the northwest Mediterranean Sea during 17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

Laboratory analysis

Zooplankton was sorted for all the stations and quantified by major taxonomic groups. Different aliquots were taken from the bongo net samples to obtain at least 100 individuals of each group. All jellyfish ephyrae and fish larvae were sorted from the samples and identified to species level. Only anchovy eggs could be identified to species, due to their oval shape. The numbers of zooplankton, *P. noctiluca* and ichthyoplankton at each station were standardized to number 10 m^{-2}. A total of 91 *P. noctiluca* medusae and 1198 ephyrae were analysed to determine their gut contents from different stations (Fig. 1). Prior to dissection,

the maximum diameter of each specimen was measured with a ruler (medusae) or with an ocular micrometre (ephyrae). For the diet composition analyses, the gastric pouches were carefully removed using forceps and a scalpel and placed in petri dishes. The oral arms of medusae and the formalin were also examined for prey. Prey were counted and identified to major taxonomic groups with the aid of a dissecting microscope; fish larvae and anchovy eggs were identified to species level.

Data analyses

The feeding incidence (FI) of each stage of *P. noctiluca* was calculated as the proportion of specimens with at least one prey item in their gastric pouches. The diet composition was described as the percentage of frequency of occurrence (%FO) and the percentage of numerical abundance (%N) of prey items in each stage (excluding medusae with no prey). The percentage of the product of these two factors was taken as an index of relative dietary importance (IRI) (Laroche 1982). To allow easy comparison among prey items, the IRI was then standardized to %IRI for each prey item (Sassa & Tsukamoto 2012). Diversity of the diet was calculated using the Shannon Weaver diversity index, H´ (Zar 1984). Prey selectivity by *P. noctiluca* for or against specific prey was calculated using Pearre´s index (C) (Pearre 1982). To calculate the jellyfish feeding rates on fish eggs and larvae, we used the average digestion times (DT) obtained by Purcell et al. (2014) in the same area and during the same period. For ephyrae, 3.0 h was used for all fish larvae (mean size 6.1 ± 9.2 mm standard length (SL)), 3.5 h for anchovy larvae (8.5 ± 6.3 mm SL) and 8.2 h for fish eggs (0.6 mm ± 0.1 diameter). In the case of medusae, 2.1 h was used for fish larvae (11.1 ± 27.7 mm SL) and anchovy larvae (14.4 ± 34.2 mm SL). Because rates for fish eggs digested by medusae were unavailable, we used the above rates obtained for ephyrae, which we believe to be conservative estimates, because digestion times decreased with jellyfish size (Purcell et al. 2014). The individual feeding rates (prey eaten jelly^{-1} h^{-1}) of *P. noctiluca* on each prey type were calculated from their number in the gut contents at each station divided by the digestion times of these prey types (Purcell et al. 2014). In order to determine the predation effects at the population level (% standing stock consumed h^{-1}), individual feeding rates were multiplied by ephyra and medusa abundances and divided by prey abundances at each station. For calculation of predation impacts of *P.noctiluca* medusae, the following abundances from the above categories were used for the low, medium and high abundances, respectively: 1 medusa 10 m^{-2}, 5 medusae 10 m^{-2}, 10 medusae 10 m^{-2}. Non-parametric tests (Mann Whitney) were used to test for differences in diets between ephyrae collected at day and at night and ephyrae collected using different methodologies, using SPSS software for Windows (IBM SPSS, 2011).

Results

The sea surface temperature during the study showed a marked thermal front across the shelf that separated the cool northern waters (19°C) with few *P. noctiluca* medusae or ephyrae from the warmer southern waters (24°C) with more jellyfish (Fig. 2). *Pelagia noctiluca* medusae were observed during the night, near the surface, scattered throughout the

area, both in coastal and open sea stations (Fig. 2A). Their abundances mainly ranged between <1 medusa and >1 medusa 10 m^{-2}, although in some stations, abundances of >10 medusa 10 m^{-2} were recorded (Fig. 2A). The spatial distribution of *P. noctiluca* ephyrae was uneven in the study area. Ephyrae were particularly abundant over the shelf off the Ebro River in the southern part of the Catalan coast, reaching concentrations of 12209 ephyrae 10 m^{-2}. A high abundance peak was also detected in the central part of the study area over the slope where the highest concentration was recorded (33693 ephyrae 10 m^{-2}) (Fig. 2)B. Fish larvae were widely distributed along the Catalan coast (Fig. 2D). The highest abundances appeared in the north and the south where the shelf is wider, while their lowest concentrations were detected in the central region. Larvae of anchovy, *E. encrasicolus*, the most abundant species, were present along the entire coast over the shelf, being particularly abundant in the north where they reached abundances up to 3000 larvae 10 m^{-2} (Fig. 2C).

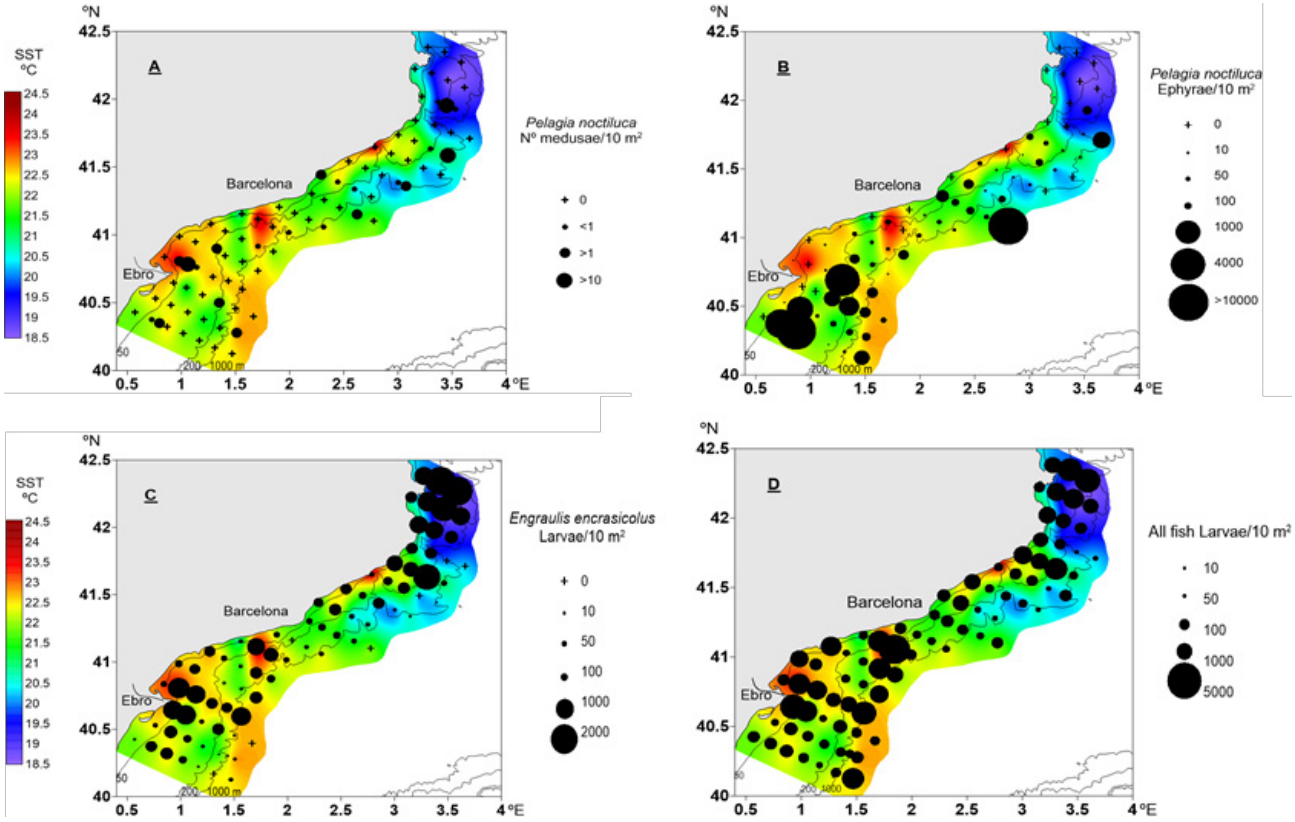

Fig 2 Distributions of *Pelagia noctiluca* and fish larvae, overlaid on maps of sea surface temperature, in the northwest Mediterranean Sea during 17 June – 4 July 2011. A: *Pelagia noctiluca* medusae determined from surface counts. B: *Pelagia noctiluca* ephyrae determined from plankton tows. C: *Engraulis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

High abundances were also detected in the south over the Ebro shelf, reaching concentrations up to 1000 larvae 10 m^{-2} in stations close to the river mouth. Over the study area, the distribution of both groups of organisms showed a high degree of overlap, particularly in the southern part. *P. noctiluca* medusae coexisted with all fish larvae and with anchovy larvae in 25% of the sampled stations, while ephyrae co-occurred with fish larvae and anchovy larvae in 72.5% of the stations. Overall, during the study period *P. noctiluca* and fish larvae co-occurred in 77.5% of the stations. Nevertheless, in areas where anchovy larvae were very abundant, such as in the north, ephyrae were practically absent. Information on zooplankton abundance during the cruise is summarized in Table I. The most abundant groups were copepods and cladocerans, representing 29.6% and 17.9% of the total zooplankton abundance, respectively. Larvae of crustaceans (decapods and euphausiids) (12.7%) and radiolarians (8.8%) were also generally abundant, followed by appendicularians and doliolids. Fish larvae and eggs represented 0.9% and 0.7%, respectively.

Gut content analyses

Medusae ranged from 30 to 75 mm in swimming bell diameter. A total of 91 medusae (52 ± 14 mm) were examined for gut content analyses. Feeding incidence (FI) was 100%, which means that all large jellyfish had at least one prey inside the gut. Although most ephyrae (86.9%) were collected during the night, no significant differences were detected in the FI between day (47%) and night (49%) ($U = 1108.5$, $p = 0.201$). 65% of the gut contents of large jellyfish was highly-digested material that could not be identified; therefore, diet descriptions and further analyses considered only identified prey items. The mean numbers of captured and ingested prey per jellyfish was 18.3 ± 43.2, and prey diversity (H´) was 2.9. The diet of medusae was mainly composed of fish eggs (IRI 25.3%) and copepods (IRI 24.7%) (Table II). Decapod and euphausiid larvae (17.3%), ostracods (IRI 8.1%) and molluscs and siphonophores (IRI 7.5%) were also relatively abundant in their diet (Table II). Although fish larvae were not very numerous prey (IRI 2.3%), many species were eaten, with the most abundant being European anchovy and bullet tuna, *Auxis rochei* (Table III). Significant differences were observed in the numbers of ingested prey between ephyrae collected by the bongo net (0.1 ± 0.4 prey $ephyra^{-1}$) and by dip net (1.0 ± 1.0 prey $ephyra^{-1}$)($U = 27897$, $p < 0.05$), those from the bongo net having few prey. No significant differences were observed between the number of ingested prey in ephyrae collected by dip net (1.0 ± 1.0 prey $ephyra^{-1}$) and neuston net (0.5 ± 0.8 prey $ephyra^{-1}$)($U = 2519.5$, $p = 0.092$); therefore, only the 145 ephyrae (4.1 ± 1.6 mm) collected in the dip and neuston nets were considered for the description of their diet and for feeding calculations. The numbers of prey in ephyrae were similar during day (0.7 ± 0.7 prey $ephyra^{-1}$) and night (0.8 ± 0.9 prey $ephyra^{-1}$), although the diversity of prey was higher during the night. Siphonophores were the most abundant and frequent prey in the daytime ephyra diet (IRI 92.0%), followed by appendicularians (Table IV). Ephyrae collected during the night had a wider variety of prey, with siphonophores, copepods, and fish larvae the most important groups (IRI = 19.3%, 14.5% and 14.5%, respectively) (Table IV), although 21% of the diet composition was unidentified

Taxa	All stations	Stations where gut contents were analysed
Copepoda	32981.0 ± 22893.0	29879.5 ± 22084.7
Cladocera	20016.8 ± 12403.8	19788.7 ± 8169.9
Euphausiacea	68.0 ± 166.2	43.9 ± 54.9
Mysidacea	1.7 ± 9.6	1.2 ± 3.0
Decapoda	2.7 ± 5.2	6.0 ± 8.1
Amphipoda	16.8 ± 28.1	15.0 ± 17 0
Isopoda	2.2 ± 6.1	0.3 ± 0.9
Crustacean larvae	14166.9 ± 13617.7	12724.2 ± 8375.3
Echinodermata	1127.0 ± 2876.5	590.2 ± 959.2
Mollusca	4447.1 ± 4743.7	5776.3 ± 4563.8
Ostracoda	527.4 ± 1018.2	482.9 ± 787.9
Radiolaria	9820.2 ± 10337.6	7471.4 ± 8271.0
Appendicularia	8758.4 ± 6851.9	10131.7 ± 4613.5
Chaetognatha	1839.8 ± 2361.0	2498.2 ± 1456.5
Doliolida	7649.2 ± 9712.0	6020.4 ± 5106.5
Salpida	1452.5 ± 2787.9	432.6 ± 645.8
Siphonophora	3951.2 ± 4808.7	3539.6 ± 3497.8
Hydromedusae	2213.9 ± 2946.5	2817.7 ± 2295.2
P. noctiluca ephyrae	749.2 ± 3977.8	349.3 ± 642.1
Fish larvae	1019.7 ± 889.3	1032.9 ± 630.1
Fish eggs	798.9 ± 846.9	837.7 ± 714.8
Total zooplankton	111610.1 ± 103287.8	104475.6 ± 72898.0

Table 1 Mean abundances (ind 10 m^{-2} ± SD) of zooplankton groups in the NW Mediterranean Sea during 17 June- 4 July 2011

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

Table 2 Diet composition of *Pelagia noctiluca* medusae (N = 91) in the Catalan Coast. %N, percentage of numerical abundance of prey items in the gut contents; %FO, percentage of frequency of occurrence in the gut; %IRI, index of relative dietary importance. Feeding incidence = 100%; Shannon Diversity Index (H′) = 2.9; Total prey = 1665

highly digested material. Selectivity analysis showed that both *P. noctiluca* medusae and ephyrae fed unselectively on most prey taxa present in the zooplankton (Table V).

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

Fish species	%N large medusae	%N ephyrae	% of the species at the stations
Engraulis encrasicolus	63.9	38.5	36.7
Auxis rochei	8.2	-	3.6
Diplodus sp.	4.9	15.4	0.1
Unidentified	4.9	-	14.6
Mullus barbatus	3.3	7.7	0.5
Gobiidae	3.3	-	5.2
Trachurus mediterraneus	-	15.4	0.9
Arnoglossus sp.	1.6	-	1.8
Sparidae	1.6	15.4	1.5
Myctophidae	1.6	-	0.7
Blenniidae	-	7.7	0.1
Others	6.6	-	34.3

Table 3 Fish larvae species found in *Pelagia noctiluca* guts in the Northwest Mediterranean Sea during 17 June – 4 July 2011

Discussion

The sampling strategy employed in the present study allowed us to evaluate the predation effects of different stages of *P. noctiluca* co-occurring with fish eggs and larvae in the NW Mediterranean. To our knowledge, this is the largest scale and most detailed study of predation on ichthyoplankton by medusae based on individual collection of the gelatinous predators for gut content analysis. Gelatinous zooplankton outbreaks, including those of *P. noctiluca*, are seasonal events (Mills 2001) and their processes of aggregation and dispersion are very rapid (Malej 1989). On the Catalan coast, high abundances of *P. noctiluca* ephyrae and other gelatinous organisms have been reported over the slope probably due to the increased primary and secondary production associated with the shelf-slope front and its associated Northern Current flowing all along the continental slope (Gili et al. 1988, Sabatés et al. 2010). Nevertheless, this pattern may be subject to considerable spatio-temporal variability due to the mesoscale activity of the front, which can show seasonal variations in its location, strength, and width (Sabatés et al. 2004, Sáiz et al. 2014). In contrast to the trend in those studies, our observations showed *P. noctiluca* medusae and ephyrae were located both in coastal waters and the open sea (Fig. 1). In the Mediterranean, blooms of *P. noctiluca* have been reported to be driven by physical forcing, specifically winds and currents (e.g. Vučetić 1984, Ferraris et al. 2012, Rosa et al. 2013, Canepa et al. 2014). In our study, variability in the physical forcing together with mesoscale activity of the Northern Current, including meanders, filaments and eddies (Millot 1991, Flexas et al. 2002) would contribute to the observed distribution of *P. noctiluca* along the Catalan coast. In the northernmost part of the study area north of the thermal front, the abundances of *P. noctiluca* were very low. By contrast, high densities of anchovy larvae were detected in that area. These differences in abundance between both groups of organisms could suggest that there was a causal relationship, such as possible predation on anchovy larvae by *P. noctiluca*. Lynam et al. (2005) reported a negative correlation between the abundance of *A. aurita* and herring larval survival and Brodeur et al. (2002) also observed a significant inverse relationship between the biomass of *Chrysaora melanaster* and forage fish. However, in the northern Catalan coastal waters, the presence of high concentrations

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

Table 4 Diet composition of *Pelagia noctiluca* ephyrae (n_{day}= 19; n_{night} = 126) in the Catalan Sea. %N, percentage of numerical abundance of prey items in the gut contents; %FO, percentage of frequency of occurrence in the gut; %IRI, index of relative dietary importance

of anchovy larvae is a regular phenomenon (Sabatés et al. 2013), with these larvae advected by the Northern Current from the northern spawning grounds in the Gulf of Lions (Sabatés et al. 2007). By contrast, these waters contained virtually no *P. noctiluca*. The intruding waters from the north are cold compared to the Catalan waters and form a temperature front across the shelf (Sabatés et al. 2009). Temperatures north of the front may have been too low for *P. noctiluca*; low temperatures have been reported to slow swimming (Rottini Sandrini & Avian, 1989), reduce respiration and pulsation rates (Malej 1989, Malej & Malej 2004), and affect their abundance and reproduction (Canepa et al. 2014). In any case, given the patchy distribution of this species, it cannot be excluded that this water mass did not contain ephyrae. Feeding incidence (FI), defined by Arthur (1976) as the percentage of individuals containing at least

	Copepo-da	Cladocera	Appendicu-laria	Chaetognatha	Mollusca	Siphono-phora	Hydrome-dusa	Crustacean larvae	Fish eggs	Fish larvae	Salpida	Doliolida	Echinoder-mata	Euphausi-acea
Medusae	0.00	-0.02	-0.01	0.01	0.01	0.02	-0.01	0.00	0.05	0.04	0.03	0.00	0.01	0.00
Ephyrae	-0.03	-0.04	-0.02	-	-0.02	0.05	-	-	0.06	0.11	0.13	-0.02	-	0.10

Table 5 Prey selectivity coefficients (*C*, Pearre, 1982) of *Pelagia noctiluca* calculated from their gut contents. No values were significantly different from zero ($p < 0:05$), indicating no significant selection

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

Table 6 Predation effects (% of standing stocks consumed h^{-1}) by *P. noctiluca* on ichthyoplankton and copepods in the northwest Mediterranean during 17 June – 4 July 2011. Values with * are estimated using ephyra digestion times.

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

Medusae contained more prey items and had higher prey diversity than ephyrae. The average number of prey per medusa (18.3 ± 43.2) was similar to that obtained in the Messina Strait during the summer period (Rosa et al. 2013, Milisenda 2014). Differences in the

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

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

The majority of ephyrae analysed for gut contents were collected during the night, when vertical migration of the zooplankton to upper layers occurs (Sáiz et al. 2014). In the study area, eggs and larvae of most fish species are located in the upper layers of the waters column (Olivar & Sabatés 1997, Sabatés et al. 2008) and anchovy, the most abundant species during the study period, migrate to the surface at night (Olivar et al. 2001, Sabatés et al. 2008). In our study, *P. noctiluca* ephyrae and medusae were observed at the surface mostly at night, as reported in other

studies conducted in the NW Mediterranean (Ferraris et al. 2012, Gordoa et al. 2013) and in other areas of the world (Doyle et al. 2008). Nevertheless, ephyrae were also detected at the surface during the day, although in much lower abundance. Thus, overlap between *P. noctiluca* and ichthyoplankton and zooplankton is high in the surface water during the night. The migration of zooplankton towards deeper waters during the day (Sáiz et al. 2014) would explain the absence of fish larvae and copepods in ephyrae collected in surface waters during daytime. Analysis of prey selectivity showed that *P. noctiluca* is a non-selective predator, feeding on almost all zooplankton taxa, and confirming their opportunistic feeding (Giorgi et al. 1991, Rosa et al. 2013, Milisenda 2014). Although Sabatés et al. (2010) found positive selection by ephyrae for some zooplankton groups, these differences could be due to the different methodological approaches used. The diversity of prey found in this study (15 major groups) is slightly higher than that reported by Giorgi et al. (1991) and Rosa et al. (2013) (13 major groups) while 8 taxa were identified by Milisenda (2014) for the same period of the year. Selection for ichthyoplankton and copepods has been described in other species of jellyfish (Fancett 1988, Purcell 1989, Purcell et al. 1994), but feeding and selection is probably affected by the digestion times which, in turn, differ among the prey type and also with the size of prey (Purcell et al. 2014). Predation effects of *P. noctiluca in situ* have not been previously studied. The values of predation on fish larvae observed in medusae were much lower than those obtained for ephyrae. Medusae would consume between 0.1% and 1.5% of fish larvae standing stock h^{-1} and between 0.1% and 0.9% of anchovy larvae standing stock h^{-1}. Because all medusae analysed for gut contents were collected at night, if we assume that feeding and digestion of *P. noctiluca* was continuous during night (8 h), then their consumption during this period would be between 0.4% and 11.9% of all larvae and between 0.5% and 7.3% of anchovy larvae. All these impact values are probably underestimated because abundances of *P. noctiluca* medusae used for the calculations came from individuals observed only at the surface at night and, presumably, jellyfish and their prey may overlap in the water column during daylight hours. Moreover, the use of oblique tows to determine ephyrae and fish larvae distributions during the cruise, did not allow investigation of the potential overlap of both groups at different levels of the water column since the abundance data are homogenized over the depth of the tows. Other studies have reported higher consumption rates than those reported in the present study, such as that of *C. quinquecirrha* in Chesapeake Bay (Purcell et al. 1994). The higher abundances of larvae and medusae in the field and more rapid digestion (1 h) of the small fish larvae contributed to higher consumption in Chesapeake Bay than on the Catalan coast.

The percentages of fish larva standing stocks consumed h^{-1} by ephyrae ranged from 1.5% to 2.7%, while the potential impact on anchovy larvae was higher (1.5–10.4%). If we assume that feeding and digestion of *P. noctiluca* was continuous during the night (8 h), ephyrae would consume between 12.1% and 21.3% of all fish larvae $night^{-1}$, while consumption of anchovy ranged from 11.8 to 82.9% $night^{-1}$. These rates are much greater than predation impacts in Purcell et al. (2014), which ranged from 1 to 3% of fish larvae consumed per night

(8 h). Both studies were performed in the same area and although fish larvae densities were similar, ephyra densities were much lower in our study, so the differences are probably due to bongo net vs. individual collection of ephyrae for gut contents.

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

Pelagia noctiluca can bloom in the Mediterranean Sea, reaching very high numbers of individuals (reviewed in Canepa et al. 2014). During the cruise, the abundances of *P. noctiluca* observed generally were not as high as in a bloom, except in one station located in the central area (Fig. 2). To illustrate the potential predation of this jellyfish on fish larvae in a bloom situation, we have considered the abundance of *P. noctiluca* ephyrae encountered at this station (33693 ephyrae 10 m^{-2}) and the abundance of fish larvae at the same station (645 fish larvae 10 m^{-2}). Based on the mean ephyrae individual feeding rates obtained in this study (0.18 prey med^{-1} h^{-1}, see S1), the ephyrae and fish larvae abundances at the bloom situation, and following the same methodology as above, the potential consumption would be >100% of fish larvae stock $night^{-1}$. Modelling exercises already suggested that in a scenario of frequent blooms *P. noctiluca*, anchovy landings off the Catalan coast would sensibly decrease though the impact on the regional economy would not be significant (Tomlinson et al. in press). As this last study was based on anchovy larvae consumption rates from Sabatés et al. (2010), lower than those obtained in the present study, we might assume that the impact on anchovy fisheries could be higher than that previously estimated. Recent data from different areas of the Mediterranean indicate that blooms of *P. noctiluca* are occurring more frequently (Canepa et al. 2014), especially in the Western Mediterranean, so that, their impact on fish larvae populations could be extremely high.

Conclusions

Pelagia noctiluca is an opportunistic predator that consumes a wide variety of prey from most zooplankton groups and feeds on ichthyoplankton at very high rates. It can form extremely large blooms, especially at night in surface waters, and co-occur with fish eggs and larvae at the beginning of summer on the Catalan coast. The high potential predation of *P. noctiluca* calculated suggests that its impact on fish larvae populations, particularly anchovy, can be extremely high in a bloom situation. Most

Mediterranean fish stocks are over exploited and current environmental conditions (e.g. sea warming, river runoff) have been demonstrated to have a direct impact on fish catches (e.g. Lloret et al. 2001, Sabatés et al. 2006). Because a combination of pressures is responsible for the decline of fish stocks, increasing our understanding of different sources of variability, including their predators such as *P. noctiluca*, as well as combinations of stressors, is essential for an effective management of fishery resources.

Supplementary data

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

Acknowledgments

We greatly appreciate the assistance of the crew of the R/V García del Cid and all the participants during the Cruise. U.T. was supported by a predoctoral fellowship of the FPI program (Spanish Ministry of Economy and Competitiveness).

Funding

Supported by the project MAR-CTM2010-18874. This study is a contribution of the Marine Zooplankton Ecology Group (2014SGR-498) at the Institut de Ciències del Mar– CSIC.

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Jellyfish	Station	Depth of trawls (m)	*P. noctiluca* abundance (ind 10 m^{-2})	All fish larvae abundance (ind 10 m^{-2})	*E. encrasicolus* larvae abundance (ind 10 m^{-2})	Fish eggs abundance (ind 10 m^{-2})	Individual feeding rate (prey/med/h)	Prey consumed (% h^{-1})
Adult	1	50	5	743.2	341.2	1113.3	2.2[a] 0.5[b] 0.2[c]	1.5[a] 0.7[b] 0.1[c]
Adult	4	65	5	729.6	22.1	326.1	0.2[c]	0.4[c]
Adult	6	90	5	2257.0	1307.9	175.4	0.6[a] 2.4[b] 10.1[c]	0.1[a] 0.9[b] 3.2[c]
Adult	8	100	5	756.5	292.7	674.2	0.3[a] 0.2[b] 0.03[c]	0.2[a] 0.1[b] 0.02[c]
Adult	9	200	5	2323.4	400.0	1821.3	0.2[a]	0.1[a]
Adult	11	30	1	802.2	238.8	2368.8	0.4[c]	0.1[c]
Adult	13	200	5	352.8	81.4	210.4	0.2[a] 0.4[c]	0.1[a] 1[c]
Adult	14	200	5	677.8	474.5	160.2	0.1[c]	0.4[c]
Ephyrae	5	130	937.7	903.3	383.8	175.4	0.02[a] 0.03[b] 0.01[c]	2.3[a] 1.5[b] 7.1[c]
Ephyrae	10	200	127.5	543.8	144.4	713.4		-
Ephyrae	12	60	216.1	1268.2	400.5	479.9	0.14[a] 0.07[b] 0.01[c]	1.5[a] 10.4[b] 0.4[c]

a: data refer to all larvae: b: data refer to anchovy larvae: c. data refer to fish eggs. Digestion times come from Purcell et al. (2014): Medusae: all larvae (2.5 h); anchovy larvae (2.5 h); fish eggs (8.2 h). Ephyrae: all larvae (3 h); anchovy larvae (2.5 h); fish eggs (8.2 h)

Table S1: Detailed information about the feeding impacts of *Pelagia noctiluca* the Northwest Mediterranean Sea during 17 June – 4 July 2011

Trophic interactions of the jellyfish Pelagia noctiluca in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition
Chapter 3

CHAPTER 3

TROPHIC INTERACTIONS OF THE JELLYFISH *PELAGIA NOCTILUCA* IN THE NW MEDITERRANEAN: EVIDENCE FROM STABLE ISOTOPE SIGNATURES AND FATTY ACID COMPOSITION

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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 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.

Keywords: Medsuae, 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 (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 oceanographic 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

(SL). 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:

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

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 nitrogen 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). 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).

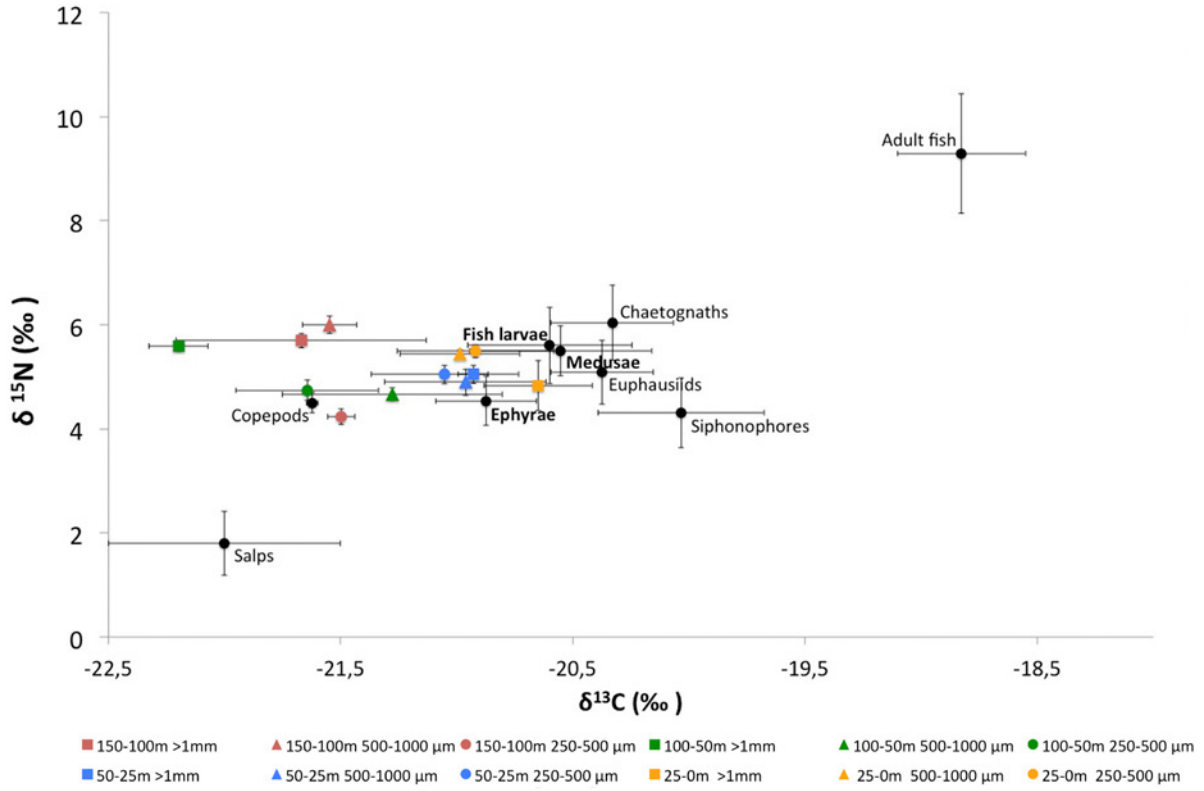

Fig 1 δ^{13}C and δ^{15}N (mean ± SD) of *Pelagia noctiluca* (medusae and ephyrae), fish (adults and larvae) and their potential zooplanktonic prey. Symbols and colours differentiate size-fractionated zooplankton and the depths at which they were collected. Major zooplankton groups (such as fish larvae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

Functional groups	Collection depth (m)	$\delta^{13}C$		$\delta^{15}N$	
		Test statistics	p	Test statistics	p
Zooplankton 250-500 µm	150-100 (n=3) 100-50 (n=10) 50-25 (n=3) 25-0 (n=6)	$\chi2$ = 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)	$\chi2$ = 3.746	0.290	$\chi2$ = 13.520	**0.004**
Zooplankton > 1000 µm	150-100 (n=6) 100-50 (n=6) 50-25 (n=4) 25-0 (n=6)	$\chi2$ = 6.231	**0.044**	$\chi2$ = 8.423	**0.015**
Copepods	100-50 (n=3) 50-25 (n=3) 25-0 (n=3)	$\chi2$ = 5.015	0.051	$\chi2$ = 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)	$\chi2$ = 2.909	0.113	$\chi2$ = 4.216	0.077
Euphausiids	100-50 (n=2) 50-25 (n=3) 25-0 (n=3)	$\chi2$ = 2.134	0.125	2.555	0.053
Mysidaceans	100-50 (n=1) 50-25 (n=3) 25-0 (n=3)	$\chi2$ = 4.143	**0.049**	$\chi2$ = 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

Table 1 Results of Kruskal–Wallis test 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 test performed to assess differences between *Pelagia noctiluca* medusae and ephyrae. *U*-values correspond to Mann–Whitney tests; *F*-values correspond to 1-way ANOVAs; $\chi2$-values correspond to Chi-squared tests. Values in **bold** are significant at $p < 0.05$

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

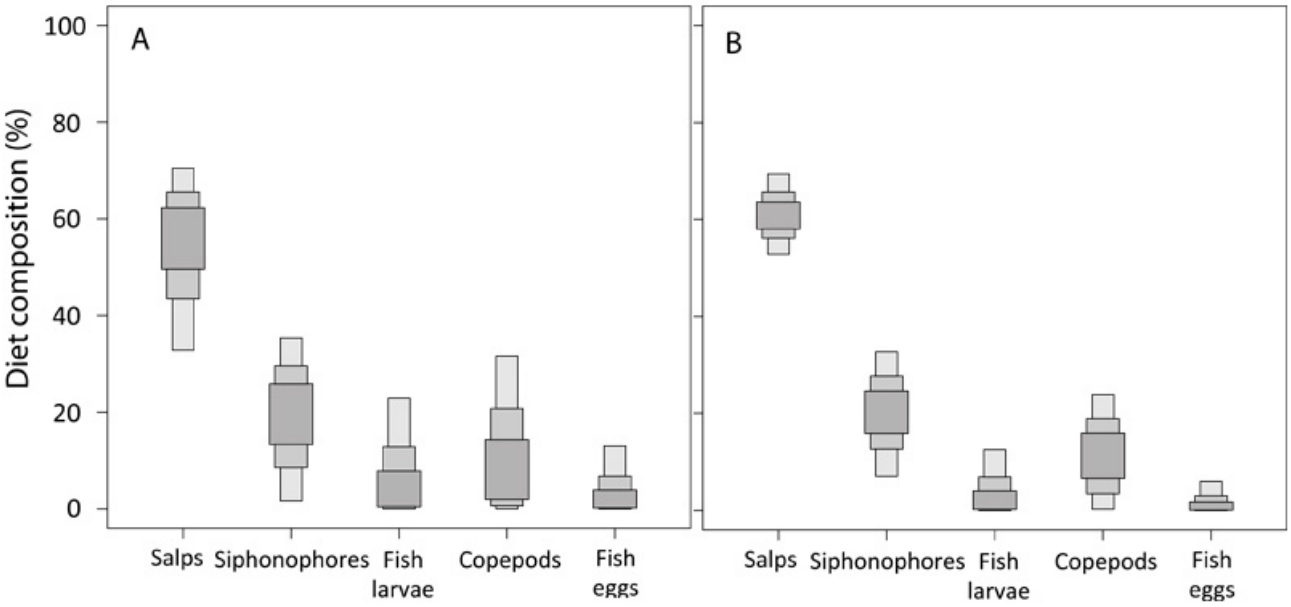

Fig 2 Contribution of major zooplankton groups to the diet of *P. noctiluca* (A) medusae and (B) ephyrae on the Catalan coast calculated using SIAR. Grey scale (from light to dark) indicates 95, 75 and 25% confidence intervals, respectively.

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.

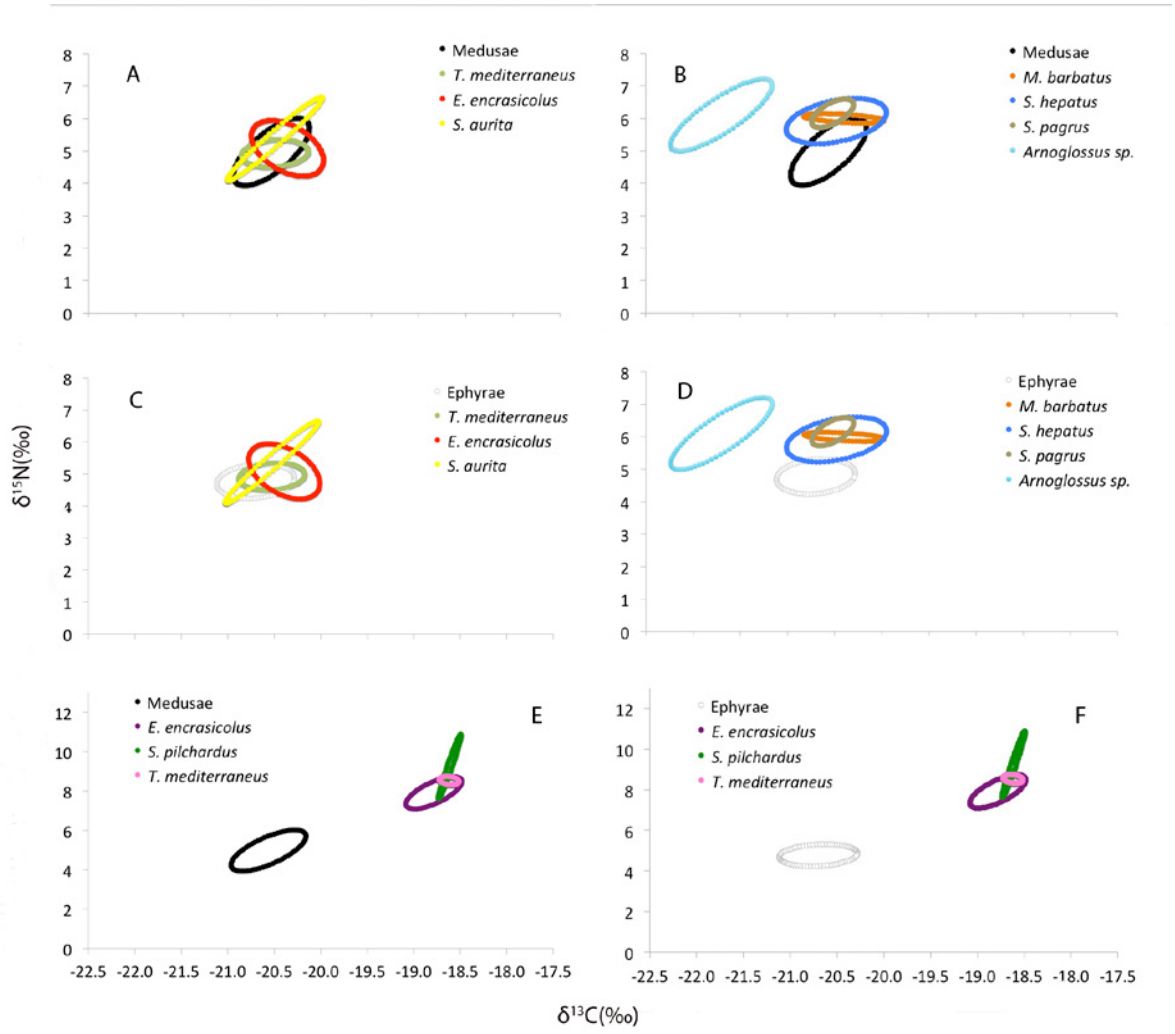

Fig 3 Trophic niche (as size-corrected standard ellipse area) of *Pelagia noctiluca* (medusae or ephyrae, as indicated in each panel) and (A–D) fish larvae and (E, F) adult fish species on the Catalan coast.

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.

%TFA	Medusae	Ephyrae	Salps	Siphonophores	Copepods	Euphausiids	Mysidaceans	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 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

Average Similarity between/within groups (%)										
	Medusae	Ephyrae	Siphonophores	Salps	Copepods	Euphausiids	Mysidaceans	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**

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

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 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

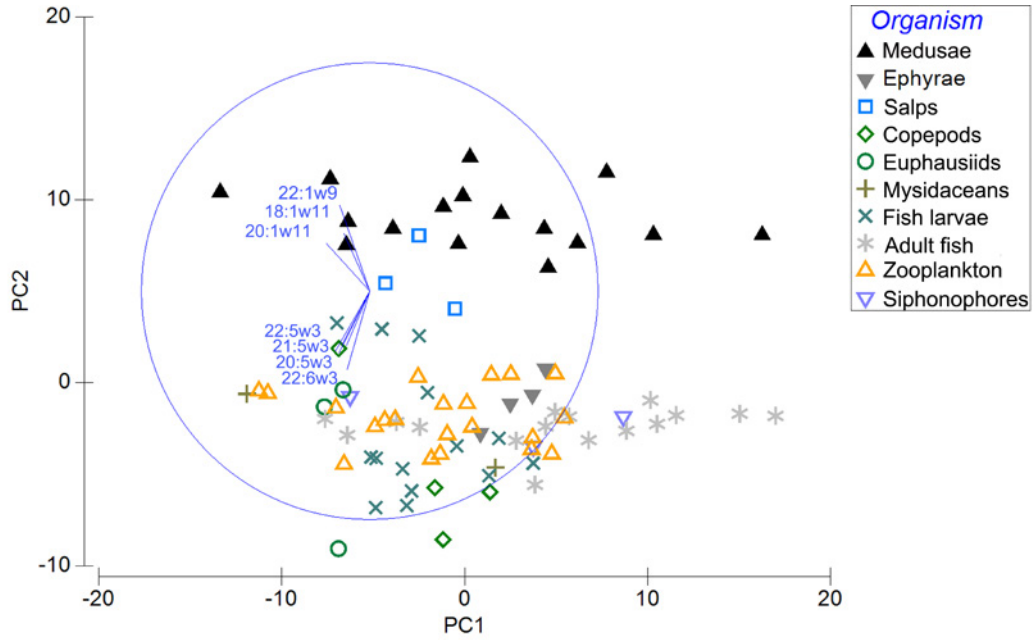

Fig 4 Principal component analysis (PCA) of fatty acid proportions in *Pelagia noctiluca* medusae and ephyrae. The large circle represents the correlation between fatty acids and principal components 1 and 2

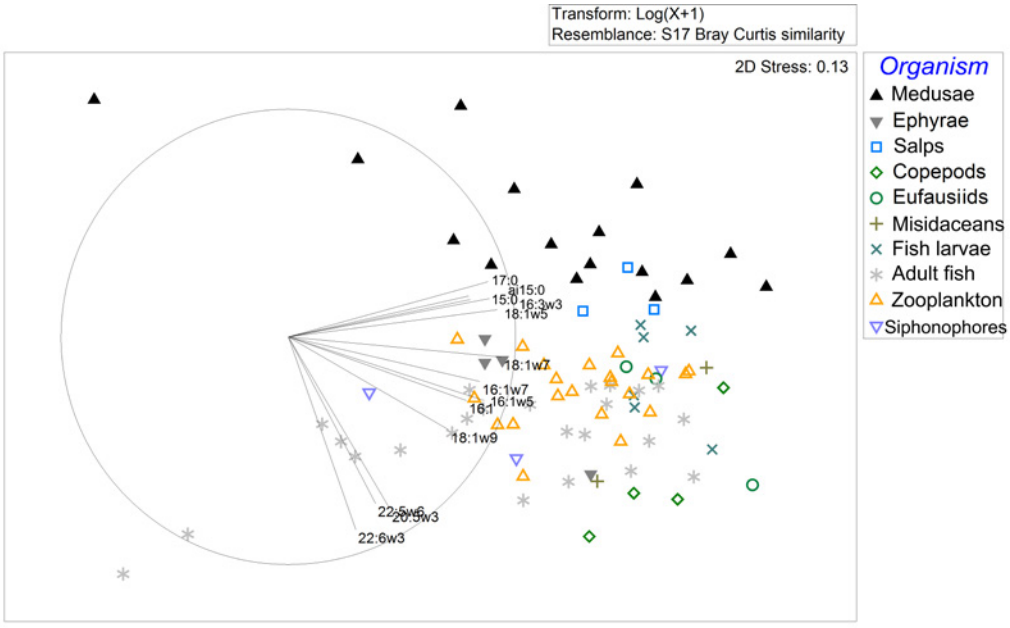

Fig 5 Non-metric multidimensional scaling ordination of fatty acid composition for *Pelagia noctiluca* medusae and ephyrae. Plot is based on Bray-Curtis resemblance matrix of log-transformed fatty acid proportions of *P. noctiluca* (medusae and ephyrae), fish (larvae and adults) and major groups of zooplankton.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

$\delta^{15}N$ values recorded for size-fractionated zooplankton and individual groups were in the mid-range of values 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 2002), the $\delta^{15}N$ overlap between gelatinous zooplankton and their potential prey has been previously reported in *P. noctiluca* (Milisenda 20141) 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), age (Kattner et al. 1993) 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 siphonophores 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).

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Chapter 4

CHAPTER 4

ASSOCIATIONS BETWEEN FISH AND JELLYFISH IN THE NW MEDITERRANEAN

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Marine Bology 165:127

Abstract

Fish-jellyfish associations were studied close to Barcelona (NW Mediterranean) during the summer period from 2008 to 2014. Jellyfish and their associate juvenile fish were collected, identified, counted and measured. Fish behaviour was described by visual field observations and laboratory experiments were performed to determine the survival of the associated fish after being in contact with the jellyfish. In addition, the possible contribution of jellyfish to the dietary composition of the fish was assessed using a combination of biomarkers. *Trachurus mediterraneus*, *Trachurus trachurus*, and *Caranx rhonchus* were associated with the jellyfish *Rhizostoma pulmo* and *Cotylorhiza tuberculata*. *T. mediterraneus* was the most frequent species and their size during the association ranged between 8.4 and 66 mm standard length (SL). The size and number of *T. mediterraneus* were slightly correlated with the size of *R. pulmo*, but not with that of *C. tuberculata*, although more numerous fish were found swimming with *C. tuberculata*. Behaviour studies showed that juvenile fish swam around jellyfish and into their oral arms seeking shelter without

suffering any pain. This survival capability was corroborated by experimental work in which all the specimens of *T. mediterraneus* survived after being in contact with both jellyfish species. Stable isotopes and fatty acids also revealed an important contribution of *R. pulmo* and *C. tuberculata* to *T. mediterraneus* diet. Defining better the associations between jellyfish and juvenile fish will help to understand the effects of the association on the survival and recruitment of fish species potentially ecologically and economically relevant.

Introduction

Although floating objects, both living and nonliving, often attract pelagic fish as cover in open waters, jellyfish potentially serve other ecological functions as possible predators or prey (Castro et al. 2002). Juveniles of different fish families (Carangidae, Stromateidae, Gadidae, Centrolophidae, Nomeidae, Girellidae, Centriscidae, Tetragonuridae and Zaproridae) associate with various species of scyphozoans (e. g *Cyanea* spp., *Rhizostoma* spp., *Chrysaora melanaster*, *Stygiomedusa gigantea, Catostylus mosaicus, Aurelia labiata, Pelagia noctiluca*) and hydrozoans (*Velella* sp., *Porpita* sp., *Physalia physalis, Aequorea forskalea*) (Mansueti 1963, Purcell & Arai 2001, Browne & Kingsford 2005, Greer et al. 2017).

These associations were earlier described as a short-term symbiosis between jellyfish that act as passive hosts and fish, which look for protection from predators (Mansueti 1963), but remain poorly understood at present (Purcell and Arai 2001). Most of the current studies are descriptive and different hypotheses regarding the ecological significance of the associations have been raised, including protection from predators (Masuda 2006), provisioning of food by feeding on the zooplankton captured by jellyfish (Masuda 2009) or feeding on the jellyfish (D'Ambra et al. 2015), transportation to favourable areas (Castro et al. 2002, Masuda 2009) and "meeting point" (Masuda 2009). These associations can be detrimental or without effect for the jellyfish but they are positive for fish and, in some cases, may increase their recruitment. For example, in the North Sea, the survival of the whiting (*Merlangius merlangus*) that shelters beneath jellyfish may be increased by high abundances of the scyphozoans *Cyanea lamarckii* and *Cyanea capillata* (Lynam & Brierley 2007). On the other hand, jellyfish may also benefit from these associations by occasionally feeding on the hosted fish and by removal of their parasites by the guest fishes (Purcell & Arai 2001 and references therein). This last benefit was observed for *Rhizostoma octopus* in association with young whiting, since the fish removed parasitic amphipods from infected individuals (Lynam & Brierley 2007).

The relationship between juvenile fish and jellyfish is not species specific, as a particular fish species usually associates with more than one species of jellyfish and *vice versa* (Purcell & Arai 2001). While the jack mackerel *Trachurus japonicus* has been reported in association with *Aurelia aurita, Nemopilema nomurai* and *C. melanaster* (Masuda 2009), the whiting has exclusively been observed swimming among the tentacles of *C. capillata* (Hay et al. 1990, Lynam & Brierley 2007). On the other hand, *C. melanaster* can host more than one fish species in the Bering Sea, specifically *Theragra*

chalcogramma and *Zaprora silenus* (Brodeur 1998). Moreover, the ontogenetic changes of the associated fish resulted in changes in the ecological function of the association (Purcell & Arai 2001, Masuda 2009). Thus at the beginning of the association, some fish species such as *T. japonicus* used the jellyfish as a school formation area, and as the fish grew the main role of the jellyfish was for predation avoidance and finally as food source (Masuda 2009).

In the Mediterranean, observations of fish sheltering underneath different scyphozoan bells have also been reported (D'Ambra & Malej 2015). *Rhizostoma pulmo* and *Cotylorhiza tuberculata* are two of the most abundant coastal scyphozoan species in the NW Mediterranean during the summer period (Gili et al. 2009, Fuentes et al. 2011, D'Ambra & Malej 2015) and they can reach large numbers during blooming years (Mariottini & Pane 2010). In particular, *R. pulmo* shows an increasing trend in the frequency of blooming events in the Mediterranean (Kogovšek et al. 2010, Brotz & Pauly 2012). In this region, *R. pulmo* has been described as host of three fish species, i.e. *Stromateus fiatola, Trachurus mediterraneus* and *Centrolophus niger,* while *S. fiatola, T. trachurus, T. mediterraneus* and *Schedophilus medusophagus* have been reported in association with *C. tuberculata* (D'Ambra & Malej 2015). In other areas, such as the North Atlantic, North Sea and Black Sea, other fish species (*Gadus morhua, Gadus merlangus, Merlangius merlangus, Trachurus trachurus* and *T. mediterraneus*) have also been observed while swimming together with *R. pulmo* (Mansuetti 1963, Purcell & Arai 2001).

Based on visual observations and laboratory experiments, hosted fish appear to feed on jellyfish (Mansueti 1963, Masuda 2009). However, this feeding behaviour has not been studied in detail due to methodological limitations. Although several fish species contain gelatinous prey items in their stomachs (Arai et al. 2003), the traditional preservation methods for gut content analysis, the rapid digestion rates of gelatinous tissue, and difficulties in the identification of this type of prey complicate obtaining accurate estimations of their feeding rates (Arai et al. 2003, Arai 2005). Furthermore, the low organic content of scyphozoans compared with other zooplanktonic organisms (Pitt et al. 2009, Lucas et al. 2011) has generally lead to the conclusion that scyphozoan tissue was not relevant for fish diet (Purcell & Arai 2001, Arai 2005). These difficulties in the identification of gelatinous tissue in fish stomachs led to the application of other approaches including the detection of nematocysts in the guts, although the information provided is qualitative (Sal Moyano et al. 2012). Alternatively, traceable biomarkers such as stable isotopes (SI) of carbon and nitrogen and fatty acids (FA), are useful approaches for detecting and quantifying soft body prey items like ciliates, flagellates (Rossi et al. 2006) and gelatinous organisms (D'Ambra et al. 2015, Tilves et al. 2018) as they provide information on assimilated diet in the predator tissue (Pitt et al. 2008).

The goal of the present work is to further deepen the study of the association between juvenile fish and *R. pulmo* and *C. tuberculata* in the Catalan Coast (NW Mediterranean) to elucidate the ecological function of these associations by investigating 1) the species involved in the association; 2) the size and number of fish *vs* the size of jellyfish; 3) the

ability of survival of the associated fish; and 4) the potential trophic interactions between fish and jellyfish.

Materials and methods

Field observations and specimen collections

Field observations of *R. pulmo* and *C. tuberculata* with their associated fish were conducted by scuba diving or snorkelling from June to November during six consecutive years (2008-2014) off the coast of Barcelona (NW Mediterranean; 41º 23´ 2.4´´N, 2º 12´ 17.1´´E, in a radius of 20 km), at depths of up to 20 m. A total of 37 periodic samplings were performed to collect jellyfish and their hosted fish for taxonomic identification, size measurements and biochemical analyses of stable isotopes (SI) and fatty acids (FA). Jellyfish and their associated fish were collected from the boat, using a hand net, or by snorkelling. They were carefully placed in plastic bags for transportation to the laboratory to avoid any damage to the jellyfish. From 2008 to 2010, the jellyfish (bell diameter) were measured with an accuracy of 1 mm and the hosted fish were preserved in formalin for species identification and size measurements (standard length) with an accuracy of 1 mm. From 2011 to 2014, each collected jellyfish together with its associated fish were individually placed in plastic bags in order to obtain information on the number of associated fish per jellyfish.

In July, August and September 2011, together with the sampling of fish and jellyfish, samples of zooplankton were collected for biochemical analyses (SI and FA). For this purpose, a bongo net (40 cm diameter opening mouth and 200 μm mesh size) was towed in surface waters for 10 minutes at 2 knots. Samples were size-fractionated using a series of sieves (250, 500, and 1000 μm) and then filtered on a pre-combusted GF/F 47 mm filter (0.7 μm, Whatman, 500 °C, 4 h). After these processes, all samples (including jellyfish and hosted fish) were immediately frozen in liquid nitrogen and stored at -80 °C until further analyses.

Laboratory experiments

A set of experiments was performed to determine the survival of *T. mediterraneus* after being in contact with jellyfish. Individuals of *T. mediterraneus* (22-54 mm SL) used in the experiments were collected in association with *R. pulmo* and *C. tuberculata* and immediately transported to our nearby experimental aquaria facilities (Area of Aquariums and Experimental Chambers (ZAE)) at the Institute of Marine Sciences, in Barcelona. Juveniles of *Mugil cephalus* (21-54 mm SL), a species never described to be associated with jellyfish, were hand netted from the Barcelona harbour to compare response to cnydocists. Eight trials of experiments using *R. pulmo* (trials 1 to 5) and C. *tuberculata* (trial 6 to 8) were carried out. In each trial, the oral arms of a single jellyfish were dissected and individually placed in glass bowls filled with seawater to completely cover each arm. With the aid of a tissue paper, individuals of both species were carefully held with the hand and placed in the bowls covered by water. They were kept in contact with the jellyfish oral arms during 10s, ensuring full contact between them. Following the exposure, fish were placed back in aquaria with clean seawater and their behaviour, degree of paralysis, and mortality

were compared to that of fish of the same species that were subjected to the same procedure but without contact with the oral arms. All fish were monitored at 0, 5, and 15 min after exposure and evaluated with different scores depending on the fish health situation: dead fish, 0; paralyzed fish on the bottom of the aquaria, 1; swimming but with paralysis symptoms, 2; and healthy fish, 3.

In total, 5 individuals of *R. pulmo,* 3 of *C. tuberculata,* 28 of *T. mediterraneus* and 28 of *M. cephalus* were used for the experiments. In four of the five trials using *R. pulmo* and in two of the three trials using *C. tuberculata,* 4 oral arms of each jellyfish species were put in contact with 4 juveniles of *T. mediterraneus* (one oral arm for each fish) and the other 4 oral arms with 4 juveniles of *M. cephalus.* In the fifth trial of *R. pulmo* and in the third trial of *C. tuberculata,* 2 oral arms were put in contact with 2 *T. mediterraneus* and other 2 oral arms with 2 *M. cephalus.*

Biomarker analyses

Stable isotopes

SI analyses of $\delta^{15}N$ and $\delta^{13}C$ were conducted in *R. pulmo*, *T. mediterraneus* and zooplankton of 3 different days representing the 2011 summer season (July, August, September). SI of *C. tuberculata* and their associated *T. mediterraneus* were only assessed in the samples from September 2011 due to the low abundance of *C. tuberculata* in previous months.

Determination of $\delta^{15}N$ and $\delta^{13}C$ signatures was performed on grounded freeze-dried samples. Isotopic composition was determined from ~5 mg of whole *R. pulmo* (n=12), ~5mg of whole *C. tuberculata* (n=4), ~ 0.5 mg of zooplankton (n=18) and ~ 0.5 mg of whole fish (n=19). Jellyfish and fish samples were loaded into tin capsules and analysed while size-fractionated zooplankton samples (with carbonate structures) were split in two subsamples. One set of subsamples, used to determine $\delta^{13}C$, was loaded in silver capsules, acidified by adding 1N HCl for 10 min, rinsed with distilled water and finally dried at 60ºC for 24-72 h. The other set of subsamples that was used to determine $\delta^{15}N$ was loaded in tin capsules and no acidification was performed, since the acidification procedure removes not only inorganic carbonates but also affects $\delta^{15}N$.

Values of $\delta^{15}N$ and $\delta^{13}C$ were determined using an isotope ratio mass spectrometer (Thermo Delta Plus XP) coupled with an elemental analyser (Thermo Flash EA 1112) through an open split interface (CONFLO III).). Content of both isotopes was expressed in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric N_2 standards, respectively, according to the formula:

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

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

Instrumental precision based on the SD of replicates of internal standards was ± 0.2 for both, $\delta^{13}C$ and $\delta^{15}N$. Because most of the tissues analysed had low-lipid content, lipids were not extracted from the samples, but a mathematical correction was applied to $\delta^{13}C$ when the carbon-to-nitrogen (C:N) ratio was > 3.5 ($\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N$) (Post et al. 2007).

Fatty acid analyses

FA analyses were conducted in both species of jellyfish and their associated *T. mediterraneus* collected in September 2011. Lipids were extracted from freeze-dried samples. About 100 mg of jellyfish of both species (n=5) and ~50 mg of fish (n=5) were extracted with 5 ml of methylating solution (methanol:chloroform:water 1:2:1 v/v/v). Samples were sonicated and centrifuged for 2-3 min at 3000 rpm. The organic layer was placed in fresh centrifuge vials and 2 ml of chloroform was added. This procedure was performed on ice and repeated at least 3 times. The final volume was concentrated down (being careful not to dehydrate the sample) under a gentle stream of nitrogen and stored in the freezer until trans-methylation process.

The organic solution obtained after lipid extraction was blown dry and then 1.5 ml of methylene chloride and 3 ml of Hilditch reagent (0.5N H_2SO_4 in methanol) were added. Absorbed lipids were removed by vortexing and heating (100ºC) the samples for 1h. After cooling, 0.5 ml of saturated sodium bicarbonate solution and 1.5 ml of hexane was added. The samples were vortexed and the upper organic layer containing fatty acid methyl esters (FAME) was transferred to a clean vial and blown dried. The procedure was repeated twice. Finally, after the addition of an internal injection standard (19:0 FAME) to the samples they were analysed by gas chromatography (GC) using an Agilent Technologies 7890BGC (Palo Alto, California USA). FAME 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 (Austin, Texas USA). Procedures for FA derivatization, identification and quantification were based on Miller et al. (2006).

Indicators of trophic interactions

Established FA markers were used to understand diet composition of jellyfish and their associated fish. 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). 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).

Data analyses

Spearman rank correlation analysis was used to identify the relationship between the jellyfish size and the size and number of associated *T. mediterraneus* and *C. rhonchus* from field collected specimens.

Differences between the survival scores of the associated *T. mediterraneus* and the non-associated *M. cephalus* from laboratory experiments were analysed by the Mann–Whitney non-parametric test performed separately for each observation time (0, 5 and 15 min).

Differences in the isotopic signature of *R. pulmo*, their associated *T. mediterraneus* and zooplankton throughout the summer were tested by the Kruskal Wallis non-parametric test, to analyse if fish and jellyfish shared the same food source (zooplankton). Moreover, in

order to obtain the relative contribution of the different food sources to *T. mediterraneu*s diet, we used a Bayesian stable-isotope mixing model (SIAR; Parnell et al. 2008), which allows for the inclusion of isotopic signatures, elemental concentrations, and trophic enrichment factors together with the uncertainty of these values within the model. To use mixing models, the isotopic values for predators must be adjusted by appropriate fractionation factors (Phillips and Koch 2002). The fractionation values used for fish tissues were $\Delta^{13}C = 1.4 \pm 1.0‰$ and $\Delta^{15}N = 3.0 \pm 1.0‰$ (McCutchan et al. 2003, Vanderklift & Ponsard 2003).

Differences in FA composition among *R. pulmo, C. tuberculata and T. mediterraneus* were tested using PERMANOVA analysis on square root transformed data based on Bray-Curtis similarities matrix. The SIMPER routine was used to identify the dissimilarity between the jellyfish and fish FA, as well as the FA responsible for the observed differences. In all statistical analyses, significant differences were set at $\alpha = < 0.05$.

Results

Field observations and description of the associations

Rhizostoma pulmo and their associated fish were observed from July to November, while *Cotylorhiza tuberculata* appeared from August to beginning of October swimming with fish (Fig. 1). *R. pulmo* was usually swimming horizontally at different levels of the water column, from the surface to near the bottom (up to 15 m), while *C. tuberculata* usually swam vertically in the first ~5 m of the water column.

Almost all individuals of *C. tuberculata* were hosting fish (95.8%) while the percentage of *R. pulmo* with associated fish was lower (43.1%). The biggest fish swam around the bell of the two jellyfish species and were located behind or below the oral arms, while the smaller ones swam closer and in some instances even between the oral arms. During jellyfish collections, fish rapidly sheltered into the bell and some large individuals moved over the bell. Once in the plastic bag, the fish left the bell and swam again around the oral arms. In some collection events, several fish escaped and sheltered again under the oral arms even if the jellyfish was inside the bag.

A total of 81 specimens of the jellyfish *R. pulmo* with 393 associated fish and 40 of the jellyfish *C. tuberculata* with 264 fish (Table 1) were collected for taxonomic identification and size measurements. The carangids *T. mediterraneus* and *C. rhonchus* were observed swimming with both jellyfish species, while *T. trachurus* was only found with *R. pulmo*. The most abundant species associated with *R. pulmo* was *T. mediterraneus*, representing 92.9% of the total fish, while *C. rhonchus* and *T. trachurus* represented 6.3% and 0.8%, respectively. Regarding *C. tuberculata*, *T. mediterraneus*was the most abundant species (91.6%) and *C. rhonchus* was present in low proportions (8.4%).

Different sizes of *T. mediterraneus* associated with both jellyfish species were observed during the studied period, with the presence of small specimens in July, August

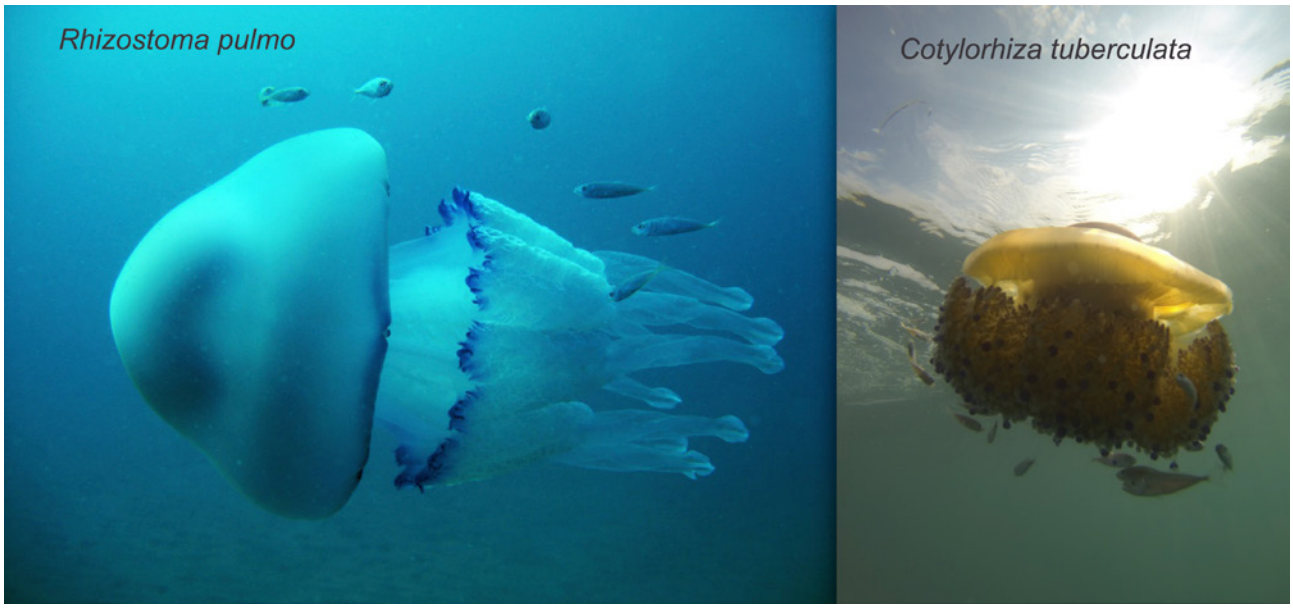

Fig 1 *Rhizostoma pulmo* and *Cotylorhiza tuberculata* with associated fish in the NW Mediterranean. Pictures: Alejandro Olariaga

and September (Table1). Overall, the number of specimens of this species associated with *R. pulmo* was higher than that observed with *C. tuberculata*. The size of this carangid associated with *R. pulmo* ranged between 8 mm to 66 mm (SL), the most abundant sizes being those between 20-23 mm and 40-47 mm (Fig. 2). The size of individuals of this species associated with *C. tuberculata* ranged between 9 and 60 mm SL, the most abundant sizes being those between 16 and 35 mm (Fig. 2). *C. rhonchus* ranged from 14.4 mm to 32.2 mm (SL) when associated with *R. pulmo*, and from 11.9 mm to 43 mm (SL) with *C. tuberculata*. The less abundant fish species, *T. trachurus*, ranged between 11.5 mm and 23.1 mm (SL).

	Rhizostoma pulmo		*C. tuberculata*	
	Trachurus mediterraneus	*Caranx rhonchus*	*Trachurus mediterraneus*	*Caranx rhonchus*
July	27.0 ± 11.4 (11–59)	25.7	n.f	n.f
August	36.7 ± 14.3 (8–66)	22.7 ± 6.1 (14–39)	29.0 ± 9.1 (11–60)	22.1 ± 4.9 (12–30)
September	29.4 ± 13.2 (9–62)	21.9 ± 5.4 (15–28)	28.2 ± 9.2 (10–54)	n.f
October	43.3 ± 10.8 (24–59)	n.f	22.8 ± 3.8 (17–33)	22.7 ± 1.5 (21–25)

Table 1 Size (mean ± SD and range) of fish associated with *Rhizostoma pulmo* and *Cotylorhiza tuberculata*
Data collected from 2008 to 2014. n.f: not found

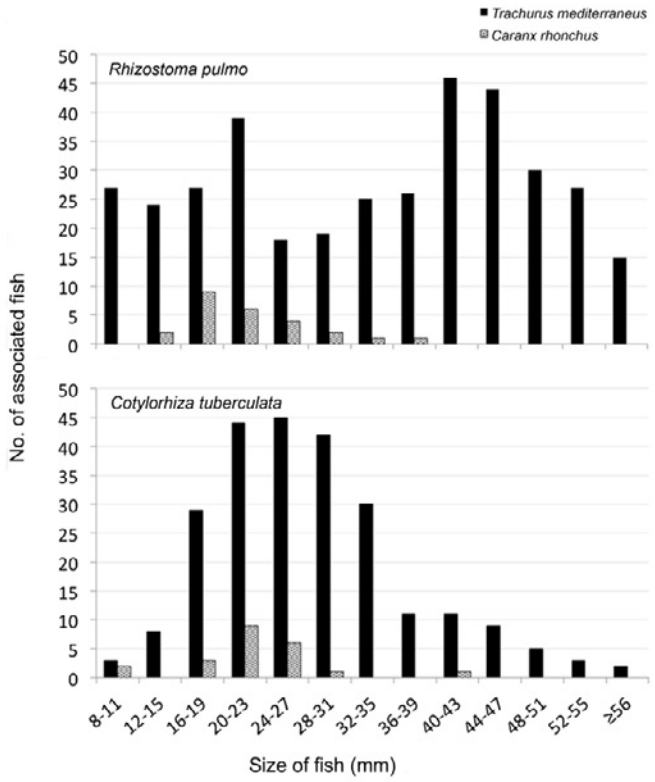

Fig 2 Number (no) of fish of different sizes (SL) associated with *Rhizostoma pulmo* and *Cotylorhiza tuberculata*

A weak but significant correlation was found between the size of *T. mediterraneus* and the size of *R. pulmo*, with larger jellyfish hosting bigger fish (Rho= 0.20, p= 0.03) whereas no correlation was found with the size of *C. tuberculata* (p= 0.73) (Fig. 3). Likewise, no correlation was found between the size of *C. rhonchus* and that of *R. pulmo* (p = 0.96). Unfortunately, due to the low number of *C. rhonchus* specimens collected, it was not possible to calculate their correlation with the size of *C. tuberculata*. There was also a weak but significant positive correlation between the number of *T. mediterraneus* and the size of *R. pulmo* (Rho = 0.31, p= 0.01), while no correlation was observed with the size of *C. tuberculata* (p= 0.45) (Fig. 4). The number of *C. rhonchus* associated with *R. pulmo* was not statistically correlated to jellyfish size (p= 0.28) (Fig. 4), while the low number of juveniles of this species associated with *C. tuberculata* prevented this calculation.

Laboratory experiments

The sizes of *R. pulmo* and *C. tuberculata* used for the experiments ranged between 29 and 34 cm and from 14 to 22 cm of bell diameter, respectively. *T. mediterraneus* and *M. cephalus* were similar in size, ranging

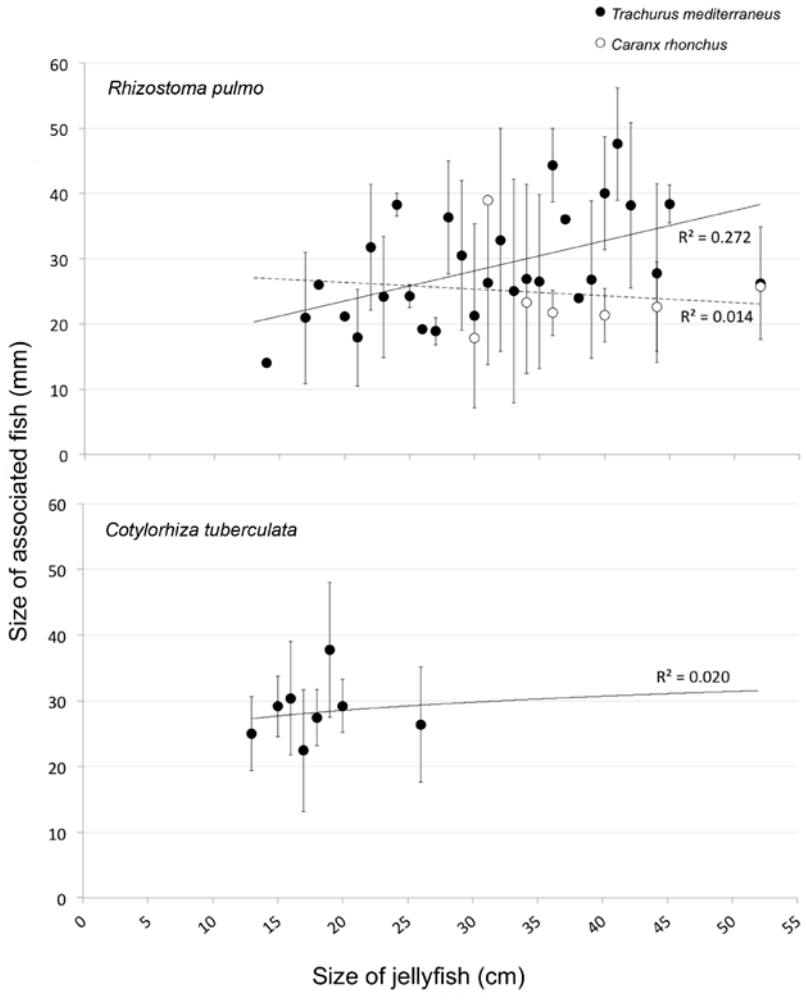

Fig 3 Relationship between the size (bell diameter) of *Rhizostoma pulmo* and the size (SL) of *Trachurus mediterraneus* and *Caranx rhonchus* and between the size (bell diameter) of *Cotylorhiza tuberculata* and the size (SL) of *Trachurus mediterraneus*. Data collected from 2011 to 2014, expressed as mean ± SD. *Trachurus trachurus* are not represented in the figure since they were very scarce (0.8% of the associated fish)

from 22 to 54 mm and from 21 to 54 mm SL, respectively. All individuals of *T. mediterraneus* survived after the contact with *R. pulmo* and *C. tuberculata*. When fish were released back in the aquaria with clean seawater after being in contact with jellyfish, their behaviour did not differ from that of fish with the same treatment but without any contact with the jellyfish. They swam fast and no symptoms of paralysis were observed. After 5 and 15 min, the experimental fish remained healthy in the experiment (Fig. 5). Conversely, *M. cephalus* showed paralysis after the contact. About half of the fish were paralyzed at the bottom of the aquaria while

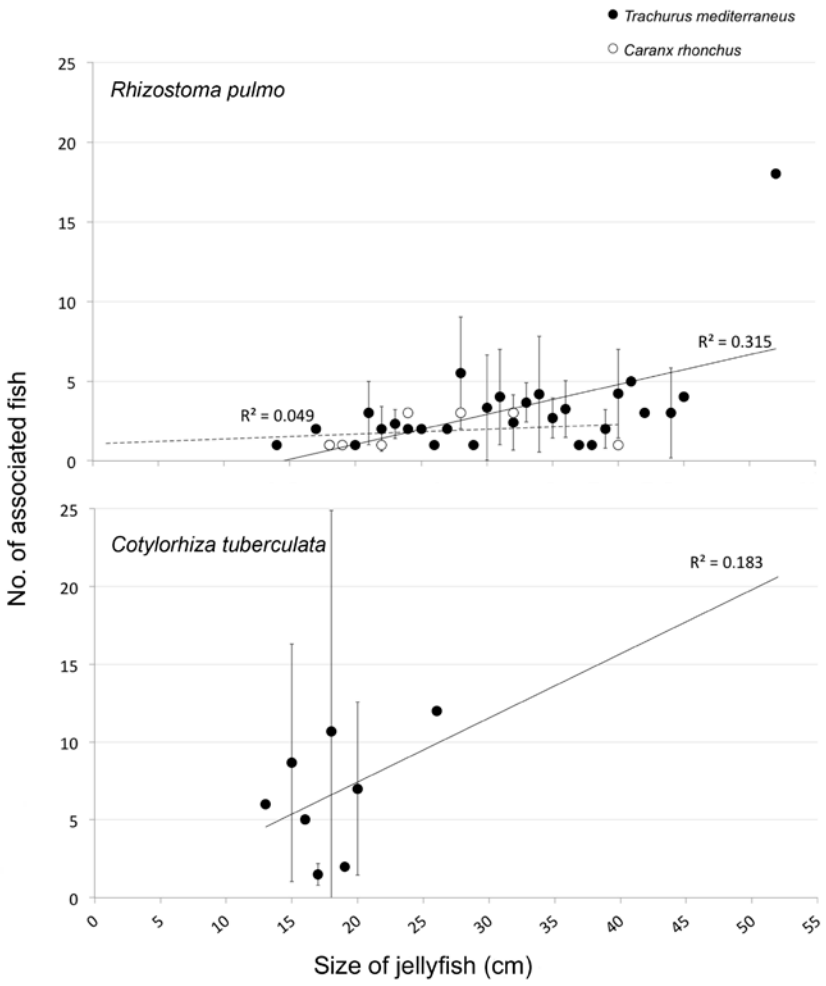

Fig 4 Relationship between the number of associated *Trachurus mediterraneus vs* the size (bell diameter) of *Rhizostoma pulmo* and *Cotylorhiza tuberculata.* Data collected from 2011 to 2014 and expressed as mean ± SD. *Trachurus* are not represented in the figure since they were very scarce (0.8% of the associated fish)

the rest remained swimming but with some sort of paralyses. These symptoms persisted after 5 and 15 minutes and death was observed in all but two individuals (Fig. 5). Statistical differences were observed between the health conditions of fish species after the contact with *R. pulmo* at each observation time ($U_{0'}$= 0; p= < 0.05; $U_{5'}$= 18.0; p= < 0.05; $U_{15'}$ = 0; p= < 0.05). *T. mediterraneus* showed the same healthy conditions after the contact with *C. tuberculata* with no symptoms of paralysis during and after the experiments. Although *M. cephalus* showed symptoms of paralysis after the contact with *C. tuberculata*, its resistance to the contact with

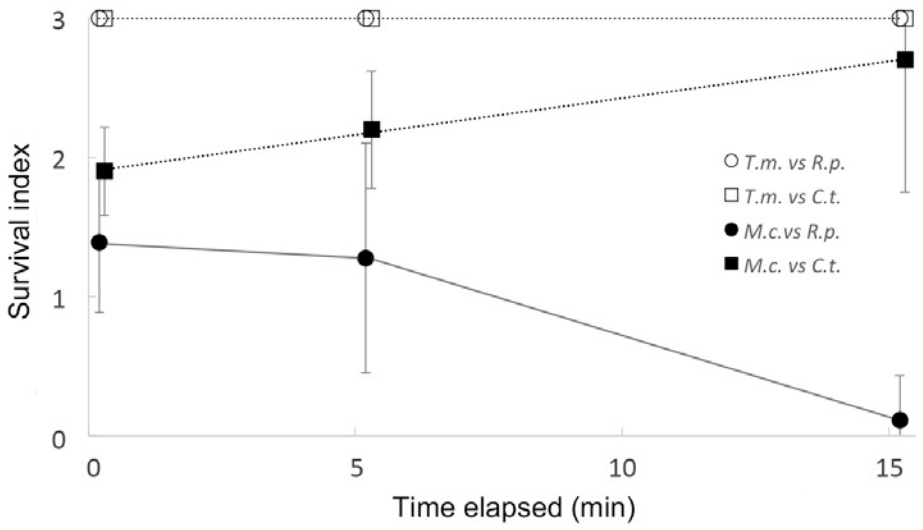

Fig 5 Survival rate (see text for more experimental details) of *Trachurus mediterraneus* (white squares and circles) and *Mugil cephalus* (black squares and circles) after being in contact for 10 s with *Rhizostoma pulmo* and *Cotylorhiza tuberculata*

nematocysts of this jellyfish was higher than that with nematocysts of *R. pulmo*. After 5 min, the exposed fish already showed recovery symptoms. Finally, after 15 min, all individuals except one were healthy and alive (Fig. 5). Significant differences in fish health conditions were observed between *T. mediterraneus* and *M. cephalus* right after being in contact with *C. tuberculata* and 5 min after ($U_{0'}$ = 0; p< 0.05; $U_{5'}$ = 9.0; p< 0.05) but no differences were observed 15 min after the exposure to the jellyfish (U = 36.0, p= 0.317).

Biomarker analyses

Signatures of $\delta^{15}N$ and $\delta^{13}C$ of *R. pulmo,* their associated *T. mediterraneus* and zooplankton did not change significantly through the summer 2011 (Table 2). For *C. tuberculata* and their associated fish this comparison was not possible to perform due to the low number of individuals during that year. SI values of *R. pulmo* ranged from 8.2 to 9.0‰ and from -20.7 to -19.4‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. The values of $\delta^{15}N$ of *C. tuberculata* ranged from 0.8 to 1.4‰ and from -19.3 to -18.9‰ in the case of $\delta^{13}C$. *R. pulmo* and their associated *T. mediterraneus* had similar values of $\delta^{15}N$ and $\delta^{13}C$, while *C. tuberculata* presented lower $\delta^{15}N$ and similar $\delta^{13}C$ values than those of their associated fish (Fig. 6, Table 2). Both zooplankton size fractions presented lower values of $\delta^{15}N$ than *R. pulmo* but higher than *C. tuberculata.* Their $\delta^{13}C$ values were similar to those of *R. pulmo* (mainly the fraction of 250-500 μm) but much lower than those of *C. tuberculata* (Fig. 6).

Dietary composition defined using SIAR indicated that the zooplankton represented the major contribution to the diet of *T. mediterraneus* associated with *R. pulmo* (32-

Organisms	$\delta^{15}N$	$\delta^{13}C$	Replicates	Statistics $\delta^{15}N$	Statistics $\delta^{13}C$	C:N ratio
Rhizostoma pulmo	8.7 ± 0.3‰	-19.7± 0.5‰	12	**H**25= 4.4 P > 0.05	**H**25= 2.1 P > 0.05	3.2± 0.2
Trachurus mediterraneus associated with *Rhizostoma pulmo*	8.0 ± 0.4‰	-19.2 ± 0.3‰	15	**H**25= 2.7 P > 0.05	**H**25= 1.34 P > 0.05	3.5± 0.1
Cotylorhiza tuberculata	1.2 ± 0.2‰	-19.1 ± 0.7‰	4	–	–	3.5± 0.2
Trachurus mediterraneus associated with *Cotylorhiza tuberculata*	4.6 ± 0.7‰	-19.2 ± 0.1‰	4	–	–	3.3± 0.1
Zooplankton of 250-500 µm	7.2 ± 0.1‰	-20.5 ± 0.3‰	9	**H**25= 2.8 P > 0.05	**H**25= 2.8 P > 0.05	4.9± 0.1
Zooplankton of 500-1000 µm	6.9 ± 0.1 ‰	-21.2 ± 0.2‰	9	**H**25= 5.2 P > 0.05	**H**25= 6.7 P > 0.05	4.6± 0.2

Table 2 Values (mean ± SD) of $\delta^{13}C$, $\delta^{15}N$ and C:N and statistics for the variation of the signatures throughout the summer ratio for *Rhizostoma pulmo, Cotylorhiza tuberculata, Trachurus mediterraneus* and size-fractionated zooplankton. $\delta^{13}C$ values are corrected for lipid content.

61% in the 250-500 µm fraction and 25-51% in the 500-1000 µm fraction) while *R. pulmo* contributed up to 31% (Fig. 7). *C. tuberculata,* nevertheless, contributed up to 61% to the diet of their associated *T. mediterraneus*, while both fractions of zooplankton contributed between 0 and 59% (Fig. 7).

Statistical analyses

PERMANOVA analysis on square root transformed FAs data suggested significant differences in the diet of both species of jellyfish and fish (F = 4.17, p = 0.009). SIMPER analysis conducted on Bray Curtis similarity

matrix pointed out a great homogeneity in FAs composition of both species of jellyfish (79.7% for *R. pulmo* and 81.2% for *C. tuberculata*) and *T. mediterraneus* (86.8%)(Table 3). FA profiles of *R. pulmo* differed in 34% of those of *T. mediterraneus* while the percentage of dissimilarity between fish and *C. tuberculata* was 42.4% (Table 3). The FAs that contributed most to differentiate *R. pulmo* samples from those of fish was 20:4ω3, which represented 17.3% of total FAs. In the case of *C. tuberculata*, the FA that contributed most to the difference between this jellyfish and fish was 22:6ω3. Both *R. pulmo and C. tuberculata* contained copepod (18:1ω9, 16:0, 20:5ω3 and 18:0) and dinoflagellate markers (20:4ω3, and 22:6ω4) in their tissues, although those of phytoplankton were more abundant in *C. tuberculata* (Table 4). Nevertheless, higher levels of zooplankton (copepods) than those of phytoplankton indicators were found in *T. mediterraneus* tissue (Table 4). Also in fish tissue, the copepod marker, 16:0, was the most abundant FA.

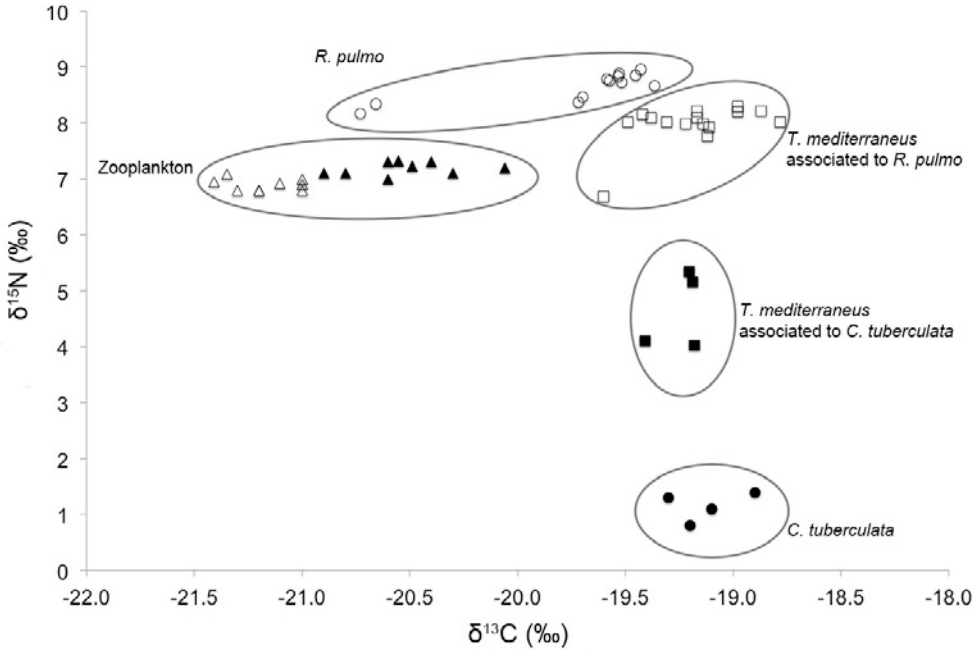

Fig 6 Isotope signatures of *Rhizostoma pulmo, Cotylorhiza tuberculata*, their associated *T. mediterraneus* and zooplankton (black triangles represent zooplankton fraction of 250-500 μm, and white triangles represent zooplankton fraction of 500-1000 μm)

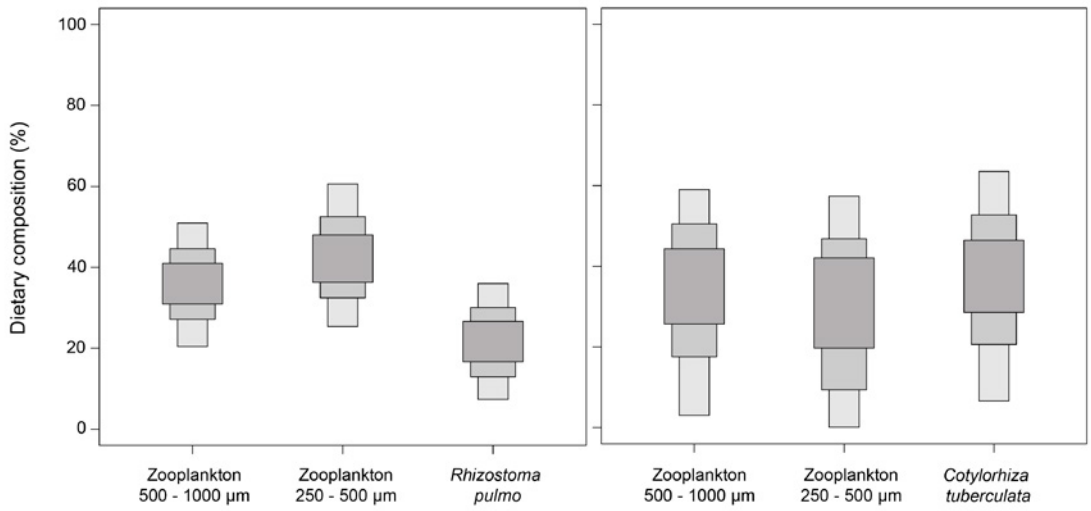

Fig 7 Contribution of different sources to the diet of *Trachurus mediterraneus* when associated with *Rhizostoma pulmo* and *Cotylorhiza tuberculata* calculated using SIAR. Grey scale (from light to dark) indicates 95, 75 and 25% confidence intervals, respectively

Average Similarity between/within groups (%)			
	Rhizostoma pulmo	*Cotylorhiza tuberculata*	*Trachurus mediterraneus*
Rhizostoma pulmo	**79.7**		
Cotylorhiza tuberculata	73.8	**81.2**	
Trachurus mediterraneus	66.0	57.6	**86.8**

Table 3 SIMPER analysis values for FA proportions in *R. pulmo, C. tuberculata* and *T. mediterraneus*

Discussion

Carangids are one of the most abundant fish families associated with floating objects (Mansueti 1963). Among them, different species of *Trachurus* and some of *Caranx* have been described associated with different scyphomedusae including *Pelagia noctiluca*, *Phylorhiza pacifica, Thysanostoma thysanura* and *Mastigietta* sp. (Mansueti 1963, Purcell & Arai 2001). Our field observations on the behaviour of associated fish demonstrated that they sought protection around and inside the jellyfish when they felt in danger (when we approached them), as has been reported in other associations (Bonaldo et al. 2004, Drazen & Robinson 2004, Lynam & Brierley 2007, Masuda 2009).

These associations have been found in different areas of the world and for different fish and jellyfish species. However, in the Mediterranean only six fish species (*T. mediterraneus, T. trachurus, Stromateus fiatola, Schedophilus medusophagus, Centrolophus niger and Tetragonorus atlanticus*) have been found associated with the scyphozoans *A. aurita, C. hysoscella, R. pulmo* and *R. octopus* (Mansueti 1963, D'Ambra & Malej 2015).

Our study shows that the most abundant fish species associated with jellyfish was *T. mediterraneus, T. trachurus* being very scarce. These two species are the most abundant Carangids in the Mediterranean, and while the spawning of *T. mediterraneus* takes place in spring-summer (Raya & Sabatés 2015), coinciding with the studied period, *T. trachurus* spawns in winter-spring, which limits the overlapping period between larvae-juveniles and jellyfish. Moreover, to the best of our knowledge, the present study is the first to report the association between *C. rhonchus* and Mediterranean jellyfish. Previous studies in the western Mediterranean have documented a northward spread and an increasing abundance of this thermophilic species in the northern sector of the basin as a consequence of sea warming (Azzurro 2008, Lloret et al. 2015, Raya & Sabatés 2015). Moreover, in the case of carangids, the increase of jellyfish blooms in the Mediterranean (Brotz & Pauly 2012), as well as of floating objects (Psomadakis et al. 2011), could have also contributed to its northward expansion, providing adequate conditions for recruitment and survival of young fish.

Kingsford (1993) and Masuda (2006)

%FA	*Cotylorhiza tuberculata*	*Rhizostoma pulmo*	*Trachurus mediterraneus*
14:0	2.3 ± 1.1	0.9 ± 0.1	5.7 ± 0.2
15:0	1.9 ± 1.8	0.2 ± 0.2	1.4 ± 0.1
16:0	18.7 ± 2.4	9.3 ± 2.1	23.9 ± 0.3
i17:0	2.8 ± 2.9	2.5 ± 1.4	0.5 ± 0.1
17:0	0.5 ± 0.3	0.6 ± 0.3	2.1 ± 0.0
18:0	14.5 ± 3.0	9.3 ± 4.7	12.2 ± 0.3
20:0	n.d	0.1 ± 0.1	0.6 ± 0.3
ΣSFA	40.7 ± 11.6	22.9 ± 9.0	46.3 ± 1.2
16:1ω9	3.8 ± 1.5	1.4 ± 0.2	0.7 ± 0.0
16:1ω7	n.d	0.9 ± 1.6	5.0 ± 0.1
18:1ω9	1.3 ± 0.5	1.8 ± 0.3	11.5 ± 0.1
18:1ω7	4.4 ± 1.0	3.3 ± 0.4	3.9 ± 0.0
20:1ω11	2.6 ± 5.0	0.1 ± 0.2	0.6 ± 0.1
20:1ω9	1.5 ± 1.0	1.8 ± 1.0	0.8 ± 0.0
22:1ω11	n.d	n.d	0.6 ± 0.0
24:1	1.1 ± 0.7	2.4 ± 1.3	1.1 ± 0.0
ΣMUFA	14.7 ± 9.6	11.6 ± 5.0	24.2 ± 0.5
16:2ω4	n.d	n.d	0.5 ± 0.0
16:3ω4	n.d	n.d	1.2 ± 0.0
16:3ω3	n.d	n.d	0.5 ± 0.0
18:2w6	2.0 ± 0.4	2.0 ± 0.4	0.7 ± 0.2
18:3ω3	9.6 ± 3.1	1.4 ± 0.2	0.1 ± 0.0
18:4ω3	n.d	n.d	0.2 ± 0.0
20:4ω6	0.3 ± 0.6	0.4 ± 0.4	0.3 ± 0.1
20:4ω3	9.1 ± 6.8	10.9 ± 8.5	0.1 ± 0.0
20:5ω3	6.1 ± 2.3	18.8 ± 12.8	3.5 ± 0.0
22:5ω6	n.d	1.5 ± 2.9	0.2 ± 0.0
22:5ω3	n.d	0.4 ± 0.7	0.3 ± 0.1
22:6ω3	4.0 ± 2.7	14.1 ± 8.6	18.1 ± 0.1
ΣPUFA	31.1 ± 15.8	49.3 ± 34.7	29.5 ± 0.7

Table 4 FA composition (area % of FA acids ± SD) of jellyfish and their associated fish. n.d: not detected

reported that the common size of *Trachurus* spp. and *Trachurus japonicus* associated with jellyfish ranged between 9-34 mm SL and 10-45 mm SL, respectively. Manuseti (1963) observed sizes of *T. mediterraneus* between 10 and 90 mm SL when associated with jellyfish in the Mediterranean. Our findings highlighted that the association started when *T. mediterraneus* were still larvae (8.4 mm SL) and lasted until 61 mm SL, the pre-recruitment stage (Karlou-Riga 2000). In this line, Masuda (2006) reported sporadic observations of larval *T. japonicus* in association with jellyfish. The size range of associated *C. rhonchus* was narrower, probably due to the smaller number of individuals collected. A single jellyfish contained fishes of different sizes, suggesting that fish larvae and juveniles use it as a "meeting point", since finding the blooming species *R. pulmo* and *C. tuberculata* would be easier for smaller individuals than finding another conspecific in the sea. In this line Masuda (2009) proposed that finding the giant jellyfish *N. nomurai* would be easier for *T. japonicus* than finding smaller conspecifics. Association of early juveniles with floating objects often leads into formation of schools (Masuda & Tsukamoto (1999)).

These last results agree with previous studies (Dempster & Kingsford 2004, Masuda 2009) in which the "meeting point" was the most feasible hypothesis proposed for the ecological function of the associations (Frèon & Dagorn 2000). The variability in fish sizes in our study was observed through the summer season, with small fish present at the beginning and the end of summer in relation to the reproductive period of the species (Raya & d Sabatés 2015). Based on our results, large individuals of *R. pulmo* had bigger and a higher number of associated fish swimming around, which is reasonable since large bells could host more fish than the small ones. Nevertheless, correlations between the bell diameter of *R. pulmo* and number and length of associated fish, although significant, were weak. It is important to consider that some fish might be able to escape in some collection events, which may lead to an underestimation of the number of associated fish. In addition, the wide size range of associated fish, due to the continuous presence of small individuals throughout the study period, could also affect the strength of the correlations.

T. mediterraneus was able to survive after being in contact with *R. pulmo* and *C. tuberculata*. Although both jellyfish species contain nematocysts in their oral arms (Mariottini & Pane 2010), fish seemed to remain unharmed after repeated contact with jellyfish bell and oral arms in the field, without any adverse reaction. This behaviour was also observed in the laboratory experiments where *T. mediterraneus* did not suffer any damage after being in contact with the oral arms of either jellyfish species. However, the non-associated *Mugil cephalus* suffered an important damage when being in contact with both jellyfish, and even death after contact with *R. pulmo.* Previous laboratory studies also reported the survival of the associated *Merlangius merlangus,* and the death of non-associated *Gobiusculus flavescens,* after contact with the scyphomedusa *Cyanea capillata* (Dahl 1961). In contrast, fishes associated with *Chrysaora quinquecirrha* and *Stomolophus meleagris* did not show different resistance to that of non-associated fish, finally all dying (Philips et al. 1969). Moreover, species-specificity fish resistance was reported for *Thalassobathia pelagica,* which survived its host *Stygiomedusa gigantea* but was affected

by *Aurelia aurita* (Drazen & Robinson 2004). Differences in the venom of the different hosts and in the defence mechanisms developed by each associated fish species would probably explain differences in their survival rate. It has been suggested that body surface of associated fishes, mucus or skin, could prevent the discharge of nematocysts or their penetration protecting fishes (Karplus 2014). For example, juvenile *T. japonicus* possess dense scales that seem to protect them from jellyfish nematocysts (Masuda 2009). Alternatively, fish could be resistant to nematocyst toxins (Arai 1988), as observed in some gadoids associated with jellyfish (Lynam & Berley 2007).

Many fish feed on jellyfish (Mianzan et al. 2001, Arai et al. 2003), and those associated with jellyfish can also be gelativorous at some developmental stage (Purcell & Arai 2001, D'Ambra et al. 2015). That is the case of *Peprilus burti* and *Chloroscombrus chrysurus* that feed on their hosts *C. capillata* and *A. aurita*, repectively (Philips et al. 1969, D'Ambra et al. 2015). Although the present study does not report any visual observation of this feeding behaviour, the biomarker analyses provide some evidence. Because the $\delta^{15}N$ is similar we argue that *R. pulmo* and their associated *T. mediterraneus* shared the same trophic level and both groups feed on the two sizes of zooplankton fractions analysed. These results correspond to the described diet of *R. pulmo*, a filter feeder consuming different sizes of zooplanktonic prey (Perez-Ruzafa et al. 2002), and to the diet of *T. mediterraneus* that mainly consists of different crustaceans, fish larvae and eggs (Šantić et al. 2013). Nevertheless, results of the mixing model suggest that *T. mediterraneus* would also feed on their host jellyfish, although in a smaller proportion than that of zooplankton. This would explain why both have similar $\delta^{15}N$ values without showing the typical enrichment in the fish tissue (Post 2002)

Results obtained from the FA analyses supported the findings of SI. The zooplankton consumption by *R. pulmo* and *T. mediterraneus* was corroborated by the presence of small copepod markers (18:1ω9, 16:0, 20:5ω3 and 18:0) (Kattner et al. 2003). Nevertheless, the FA distributions of the fish and jellyfish differed by 34% due to a higher concentration of the algal marker 20:4ω3 in the jellyfish tissue, being this FA the one that most contributed to this difference. The finding of this algal marker in the jellyfish in the present work is in agreement with previous studies that found diatoms in the stomach of *R. pulmo* (Perez-Ruzafa et al. 2002). Although in lower proportions the presence of herbivorous FAs (22:6ω3) in *T. mediterraneus* tissue suggests that as the diet of *T. mediterraneus* is mainly composed by crustaceans, this dinoflagellate marker could be transferred from the jellyfish.

Cotylorhiza tuberculata showed the lowest $\delta^{15}N$ values and their associated fish higher values, both being lower than those of the zooplankton, which would suggest that the jellyfish nor the fish were feeding on zooplankton. Although *C. tuberculata* has been described as a zooplankton consumer (Perez-Ruzafa et al. 2002), it has symbiotic algae (Visram et al. 2006, LaJeunesse et al. 2009) that could reduce their $\delta^{15}N$ values. Phytoplankton, in the baseline of aquatic food web, has very low $\delta^{15}N$ values (Post 2002), which means that a phytoplankton consumer or, as the present case, an organism having symbiotic algae would also

show low values of this biomarker.

Based on the results of mixing models, *T. mediterraneus* would feed on both size fractions of zooplankton and *C. tuberculata* would greatly contribute to its diet (up to 61%). This contribution was higher than that observed for *R. pulmo,* probably due to the lower toxicity of the nematocysts of *C. tuberculata* (Mariottini & Pane 2010). It has been reported that *A. aurita,* considered as a not very toxic species but more than *C. tuberculata* (Mariottini & Pane 2010), can reach up to 100% of the diet of their associated fish, *C. chrysurus* (D'Ambra et al. 2015). The presence of the symbiotic algae in *C. tuberculata* could also explain the lower values of $\delta^{15}N$ in their associated *T. mediterraneus* compared to those associated with *R. pulmo*, since more than half of their diet potentially consisted of *C. tuberculata.*

FA profiles suggested zooplankton consumption by *C. tuberculata* and their associated fish. The copepod marker 16:0 was the most abundant FA in the jellyfish and the presence of other copepod markers (18:1ω9, 20:5ω3) would demonstrate the zooplankton consumption described in the literature (Perez-Ruzafa et al. 2002), although not detected in our SI results. This discrepancy between both methodologies could be due to the presence of the symbiotic algae above mentioned, rather than a disagreement between both the methodologies. As most organisms are capable of synthesizing the 16:0 *de novo* (Kelly & Scheibling 2012) it is difficult to determine if the high values found could be due only to the diet. Moreover, the presence of several algal markers in the jellyfish, for example the 18:5ω3 (Bergé & Barnathan 2005, Parrish 2013) would corroborate the symbiosis between jellyfish and zooxanthellae. With regard to the possible predation of the jellyfish by the hosted fish, no clear markers of *C. tuberculata* nor *R. pulmo* were found in the FA profiles of the fish tissue. Further analytical work is needed to determine the specific FA that can be used as markers for the presence of jellyfish in the fish diet.

Several fish species have been described to practice kleptoparasitism, or feeding on planktonic prey collected by their jellyfish host. Thus, in laboratory conditions, *T. japonicus* was reported to feed on the prey items they remove from *A. aurita* (Masuda et al. 2008). Similarly, *M. merlangus* was described to feed on prey items collected by its jelly host (Hay et al. 1990). Comparative analyses of gut content of three fish species showed that while *Psenopsis anomala* and *Thamnaconus modestus* contained jellyfish tissue and nematocysts in their stomachs, *T. japonicus* did not show any trace of their hosts (Kondo et al. 2016, Miyajima et al. 2017). However, the presence of nematocysts has been reported in the stomach of *T. mediterraneus* (J. Mir personal observation) suggesting ingestion of jellyfish. These findings would be in line with our biomarker results which suggested that the ingestion of jellyfish tissue could not be only accidental, attached to the stolen prey, but also intentional since it represented a potential contribution of around 60% in the diet of the fish.

The ecological function of the association between fish and jellyfish may change through fish ontogeny (Masuda 2009). According to this author, *T. japonicus* started the association using the jellyfish as a meeting point, then as refuge and finally as food

collector. In the case of *Peprilus paru,* the fish use its host *C. quinquecirrha* as food collector at the beginning of the association and then consume the jellyfish tentacles (Mansueti 1963, Purcell & Arai 2001). In the present study, based on visual observations, small *T. mediterraneu*s would obtain refuge from their hosts; the presence of larvae together with juveniles in associations with a jellyfish would support the hypothesis of "meeting point"; from biomarker results, juveniles would also benefit from the zooplanktonic prey collected by jellyfish oral arms and, as the fish grows, and jellyfish are in a senescent phase, they would become part of their diet.

The present study describes the association between juveniles of *T. mediterraneus* and the scyphozoans *R. pulmo* and *C. tuberculata* in the NW Mediterranean and provides the first evidence of the association between the thermophilic species *C. rhonchus* and these jellyfish in the area. Through this work, the hypothesis of protection, meeting point and food provisioning is confirmed for *T. mediterraneus* and would all together favour the survival of early life stages of this fish species hence increasing their subsequent recruitment. Nevertheless, there is still the need for more studies to completely understand some aspects of the association between fish and jellyfish, and determine to what extent this association would enhance the recruitment of *T. mediterraneus* juveniles with respect compared to juvenile free-living fish.

Acknowledgements

We are especially grateful to Alejandro Olariaga, Giacomo Milisenda, Gastón Alurralde and Raül Golo for their contribution to the fieldwork. We also specially thank Dr. Amit Lotan for his contribution to the experimental work with his knowledge and advice. We also thank Miriam Gentile for maintaining the jellyfish and fish in the experimental aquariums and Joan Mir for his help during the experimental work. We thank all reviewers for their accurate and constructive comments, as also a second reviewer. This work was supported by the projects CTM2010-18874 and CTM2015-68543-R. UT was supported by a predoctoral fellowship of the FPI program (Spanish Ministry of Economy and Competitiveness).

Funding

This work was supported by the projects CTM2010-18874 and CTM2015-68543-R (Spanish Ministry of Economy and Competitiveness). UT was supported by a predoctoral fellowship of the FPI program (Spanish Ministry of Economy and Competitiveness).

Conflict of interest

The authors declare that they have no conflict of interests.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Fish were treated in agreement with the Spanish regulations (Royal Decree Act 53/2013) and the European legislation (2010/63 EU) concerning the protection of animals used for experimental and other scientific purposes. Animal experimental protocols were approved by the Animal Care and Use committee of the Generalitat de Catalunya under number DAAM8844. All steps were taken to reduce possible animal suffering.

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GENERAL DISCUSSION

This thesis is the result of the research conducted in the Catalan coast, NW Mediterranean, to determine the potential impact of jellyfish, both negative and positive, on fish populations. The jellyfish studied were *Pelagia noctiluca*, *Rhizostoma pulmo* and *Cotylorhiza tuberculata* that are the three most abundant species in the Catalan coast. From a biological and physiological perpective, *P. noctiluca* differs from *R. pulmo* and *C. tuberculata*. *P. noctiluca* is an oceanic species, high abundant in the open sea, while the distribution of the other two species is limited to coastal areas. Regarding their feeding mechanisms, *P. noctiluca* is a cruising predator while *R. pulmo* and *C. tuberculata* are active filter feeders. The results of this thesis have evidenced that their impact on fish population is also different. Thus we have evaluated that *P. noctiluca* exert a negative impact on several fish species, mainly anchovy, *Engraulis encrasicolus*, through predation and/or competition, and *R. pulmo* and *C. tuberculata* have shown to have a positive impact on some fish species, such as *Trachurus mediterraneus*, due to the association between these jellyfish and fish juvenile.

Trophic ecology of *P. noctiluca*

Predation and competition between fish and jellyfish

The scyphozoan *Pelagia noctiluca* feeds non-selectively on almost all zooplankton groups, including fish eggs and larvae (Giorgi et al. 1991, Malej et al. 1993, Rosa et al. 2013, Milisenda 2014). Based on previous studies, as well as on the analyses performed in the frame of this thesis (Chater II, Chapter III), we have concluded that *P. noctiluca*, both adult stage (medusa) and young stage (ephyrae), is a predator of fish eggs and larvae and competitor of larvae of several fish species. By one hand, results of gut contents analyses obtained in this thesis demonstrated that fish eggs represented the 25% of the medusa diet, while fish larvae were the second most important item in the diet of ephyrae, representing the 14.5% of it (Chapter II).

Although the presence of ichthyoplankton in gelatinous zooplankton diet has widely documented (Purcell, 1985, Purcell & Arai 2001), and several scyphozoan species have been described as predators of fish larvae (Brodeur et al. 2008, Barz & Hirche, 2007), in this thesis the *in situ* predation effects of *P. noctiluca* on fish eggs and larvae were estimated for the first time. For this purpose, by combining the jellyfish gut content information and its digestion times (DT) we estimated *in situ* predation rates (prey consumed predator^{-1} time^{-1}), which in combination with population densities of the predators and preys, allowed us to estimate the predation effects (% prey consumed time^{-1}) of *P. noctiluca* (Purcell et al. 2014).Thus, digestion times (DT) of *P. noctiluca* when feeding on fish eggs and larvae were obtained from experiments performed on-board (Chapter I). Our investigation showed that the highest predation effect showed by *P. noctiluca* medusa on fish larvae was up to 12% of fish larvae stock night^{-1} while that of ephyrae was higher, up to 21%, especially when feeding on on anchovy larvae that was of 83% (Chapter II). Moreover, the consumption rate of fish eggs by ephyrae was of 57% of fish eggs stock night^{-1}, which made the consumption rate of total ichthyoplankton very high. *P. noctiluca* is a blooming species that can reach very high numbers (Zavodnik 1987, Malej 1989, Canepa et al. 2014), as we detected during a oceanographic cruise, increasing its impact on fish population during these blooming episodes (Chapter II).

In addition, our results of the assimilated diet of *P. noctiluca* based on biomarker analyses, such as stable isotopes and fatty acid analyses, (Chapter III) demonstrate thatboth medusa and ephyrae, not only ingest ichthyoplankton prey but also digest these items. The information obtained about the assimilation is important since, on occasions, the ingested prey cannot be digested by the predator being finally egested, and if the gut content analysis are performed before egestion, results would be overestimated (Pitt et al. 2008). Thus, fish larvae contributed to the assimilated diet of medusa in ~20% and to the ephyrae´s diet in ~10% and fish eggs contributed ~10% and ~5% respectively.

In addition, our results pointed out that *P. noctiluca,* medusae and ephyrae and fish larvae occupy a similar trophic position in the food web (Chapter III), suggesting a potential competition between both groups.

Moreover, their trophic niches overlapped up to 51.2%, which means that they share many of their feeding habits. Diets of fish larvae are less varied than those of medusae and mainly consist on herbivorous nauplii of copepods and copepodites (Morote et al. 2008, Sabatés et al. 2015). Although these prey have not been directly identified in the diet of *P. noctiluca*, since this jellyfish species is a non-selective predator that feed on preys of several size fractions of almost all zooplankton groups (Sabatés et al. 2010, Rosa et al. 2013, Milisenda 2014), it is feasible that the jellyfish may feed on the same prey that fish larvae. Also, given the fast DT obtained for *P. noctiluca* (Chapter I), probably tiny prey, as nauplii of copepods and copepodites, do not last long in their stomachs, making difficult their encounter and identification.

It has been reported that scyphozoans jellyfish are potential competitors of zooplanktivorous fish (Purcell & Arai 2001, Purcell & Studervant 2001, Brodeur et al. 2008, Decker et al. 2018). Nevertheless our results confirm that *P. noctiluca* is not competitor of different adult pelagic fish species, such as *Engraulis encrasicolus*, *Sardina pilchardus*, *Trachurus mediterraneus* and *Sardinella aurita*. No niche overlap was observed between both groups, clearly reflecting their different diet requirements. Although some prey types, such as copepods, are common in the diets of fish and jellyfish (Tudela & Palomera 1997, Costalago et al. 2012, Albo-Puigserver et al. 2016) other prey, such as cladocerans, are consumed in very high rates by fishes, but not by *P. noctiluca*.

Pelagia noctiluca is widely distributed along different seas, inhabiting warm subtropical waters, as the Gulf of Mexico and the Mediterranean Sea, but also temperate waters, of the North Sea and Northeast Atlantic Ocean (Graham et al. 2003, Licandro et al. 2010, Bastian et al. 2011). Moreover, recent data from different areas of the Mediterranean indicate that blooms of *P. noctiluca* are occurring more frequently (Canepa et al. 2014), especially in the Western Mediterranean. This is specially concerning since, as commented in the Introduction, in some ecosystems supporting major forage fish fisheries it has been detected periods of high abundances of jellyfish in coincidence with low abundances of fish reflecting fish-jellyfish replacement cycles (Decker et al. 2014, Brodeur et al. 2014, Mianzan et al. 2014). In this line, some modelling exercises already suggested that in a scenario of frequent blooms of *P. noctiluca,* anchovy landings off the Catalan coast would sensibly decrease though the impact on the regional economy would not be significant (Tomlinson et al. 2015). Nevertheless, it is important to mention that results of this thesis have been obtained using appropriate methodologies, both of sampling and of analyses and we might assume that the impact on anchovy fisheries could be higher than that previously estimated.

The results obtained in the present thesis, together with the fact that the economies of many Mediterranean European countries depend on fisheries (among other activities) highlight the importance of effective management of jellyfish blooms. Our results provide important and useful information that can be considered in near-future ecosystem-based fishery management in the NW Mediterranean and in regions where *P. noctiluca* thrives.

Positive associations between fish and jellyfish

As commented in the Introduction not all the interactions between fish and jellyfish are detrimental for the first, existing commensal associations between juvenile pelagic fish and jellyfish (Purcell & Arai 2001, Ohtsuka et al. 2009).

These interactions has been reported as temporary (Lawley & Júnior 2018) and although it was first defined as symbiotic relationship (Mansueti 1963), described characteristics of the association is far from what is considered as symbiosis (Duffy 2008). The meaning of these interactions is under discussion (Purcell & Arai 2001) and different hypotheses regarding the ecological significance of the associations have been raised. Jellyfish may offer protection to associated fish from predation (Masuda 2006, Masuda et al. 2008, D'Ambra et al. 2015). They also may provide a food source for associate juveniles, either indirectlyfeeding on the zooplankton captured by jellyfish (which is defined as kleptoparasitism) (Masuda et al. 2008) or directly feeding on the jellyfish (Miyajima et al. 2011, D'Ambra et al. 2015). Juvenile fish may "use" their host jellyfish for transportation to favourable areas (Castro et al. 2002, Masuda 2009). Finally, jellyfish may provide associates a "meeting point" area for schooling (Masuda 2009).

In the frame of this thesis, juveniles of the carangids *Trachurus mediterraneus* and *Trachurus trachurus* have been found to be associated with the scyphozoans *Rhizostoma pulmo* and *Cotylorhiza tuberculata* (Chapter IV). In addition, we provide first evidences of the association between the thermophilic species *Caranx rhonchus*. Moreover, we have been able to elucidate the ecological significance of these associations corroborating some of the hypothesis raised:

- Meeting point: Our findings highlighted that *T. mediterraneus* was in association with jellyfish from larval to pre-recruitment stage. In the Catalan coast the reproductive period of this species takes place from June to September (Raya & Sabatés 2015), increasing the range of fish size along the studied period. The most common associations are among juvenile fish and scyphomedusae (Mansueti 1963, Arai 1997, D'Ambra & Malej 2015) being references to larval stages very scarce (Masuda 2006). In addition to the range of *T. mediterraneus* sizes found an individual of jellyfish contained fishes of different sizes, suggesting that fish larvae and juveniles use the jellyfish as a "meeting point". This is also the most feasible hypothesis proposed by several authors for the ecological function of the associations (Frèon & Dagorn 2000).

- Refuge: The hypothesis of refuge, that is the look for shelter and protection provided by the medusa, was corroborated by visual observations in the field. In "stress" situations, consisting on our approximation to the specimens for their collection, juvenile fish rapidly sheltered into the umbrella, which is a usual behaviour in fishes associated to floating objects (Kingsford 1993), including jellyfish (Bonaldo et al. 2004, Masuda 2009, D'Ambra & Malej 2015). During this fast movement, fishes apparently touch jellyfish body without any adverse reaction. From laboratory work, the resistance of *T. mediterraneus* to the jellyfish venom was corroborated (Chapter

IV) and therefore their ability to shelter under the umbrella without suffering any pain. The hypothesis of refuge benefits not only specimens individually but also may increase their recruitment, favouring the size of the populations (Lynam & Brierley 2007).

- Provisioning of food: Our investigation corroborated the hypothesis of provisioning of food by scyohozoans to fish juvenile. This hypothesis is controversial because, only with one exception (Mansueti 1963), there are no reports from visual observations on this feeding behaviour. Moreover, the difficulty in the identification of jelly tissue in gut contents of fish (Purcell & Arai 2001), added to the low organic content of scyphozoans compared to other groups of zooplankton (Pitt et al. 2009; Lucas et al. 2011), have led to the conclusion that scyphozoan tissue is not relevant in the diet of fish (Purcell & Arai 2001). Nevertheless, our results based on throphic biomarkers (specially stable isotopes), in agreement with those of D'Ambra et al. (2015), showed that the jellyfish contributed to the diet of associated *T. mediterraneus* in a high proportion. In addition, the presence of nematocysts has been reported in the stomachs of *T. mediterraneus* (J. Mir personal observation), suggesting ingestion of jellyfish tissue and supporting the findings of the present thesis.

The ecological function of the association between fish and jellyfish has been reported to vary through fish ontogeny (Masuda 2009). In line with this report and based on our findings, small *T. mediterraneus* would obtain refuge from their hosts; the presence of larvae together with juveniles in associations with a jellyfish would support the hypothesis of "meeting point"; from biomarker results, juveniles would also benefit from the zooplanktonic prey collected by jellyfish oral arms and, as the fish grows, and jellyfish are in a senescent phase, they would become part of their diet

Thus, in the Catalan coast, juveniles of different fish species may benefit from their association to scyphozoan jellyfish. The hypotheses regarding the association between fish and jellyfish confirmed in the frame of this thesis would favour the survival of the first life stages of fish, hence increasing their subsequent recruitment.

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GENERAL CONCLUSIONS

The main conclusions extracted from the investigations conducted in this PhD thesis are the following:

1 - The scyphozoan species studied along the Catalan coast play different ecological roles when interacting with the early life stages of fish. While *Pelagia noctiluca* is a predator and competitor of larvae of different fish species, *Rhizostoma pulmo* and *Cotylorhiza tuberculata* may enhance the survival of fish juveniles through a positive effect of the association with them.

2 - *P. noctiluca* can form extremely large blooms, especially at night in surface waters, and co-occur with fish eggs and larvae of several fish species at the beginning of summer along the Catalan coast.

3 – *P. noctiluca* is an opportunistic predator that feeds on a wide variety of prey from most zooplankton groups, including ichthyoplankton, being fish eggs and fish larvae very abundant in the medusae and ephyrae diet.

4 – Digestion times of fish larvae by *P. noctiluca* medusae and ephyrae averaged 2.5 to 3.0 h and were related to medusa diameter and larval length; Fish eggs were more difficult to digest and showed a high ejection rate.

5 - *In situ* predation rates (based on gut content analyses and digestion time calculations) combined with the population densities of predators and prey allowed to estimate the impact of *P. noctiluca* on the ichthyoplankton community along the Catalan coast.

6- Medusae consumed between 0.1 and 1.5% of fish larvae standing stock h^{-1} and between 0.1 and 0.9% of anchovy larvae standing stock h^{-1}, while ephyrae consumed 1.5–2.7% h^{-1} of all fish larvae and 1.5–10.4% h^{-1} of anchovy larvae. The estimated fish egg consumption rate was 0.02–3.2% h^{-1} for medusae and 0.4–7.1% h^{-1} for ephyrae.

7 – Biomarker analyses (stable isotopes and fatty acids) indicated that both medusae and ephyrae not only ingested ichthyoplankton. but also digested these items. Fish larvae contributed to the assimilated diet of the medusae up to ~20% and to the ephyrae diet up to ~10%, while fish eggs contributed ~10% and ~5%, respectively.

8 - *P. noctiluca* is not only a predator but also a potential competitor of fish larvae, in particular anchovy, *Engraulis encrasicolus*, and round sardinella, *Sardinella aurita*. Based on stable isotope analysis, this jellyfish feeds on prey with similar isotopic values to those of fish larvae.

9 – *P. noctiluca* is not a potential competitor of adult fish for food. Fish occupy a higher position in the trophic web than jellyfish indicating that they have different feeding requirements.

10 – In contrast to *P. noctiluca*, other species of Mediterranean jellyfish, specifically *R. pulmo* and *C. tuberculata,* have a beneficial role by hosting fish juveniles of three carangid species: *Trachurus mediterraneus, Trachurus trachurus* and *Caranx rhonchus*.

11 – *T. mediterraneus* is the fish species most frequently associated with jellyfish. This thesis provides the first evidence of the association between the thermophilic fish species *C. rhonchus* and the jellyfish *R. pulmo* and *C. tuberculata*.

12 - The association of *T. mediterraneus* with *R. pulmo* and *C. tuberculata* starts when the fish is still a larva and lasts until the pre-recruitment stage. The smallest size of fish found in the association is smaller than that described in the literature for the Mediterranean Sea.

13 -The resistance of *T. mediterraneus* to the jellyfish venom has been corroborated by laboratory work.

14 – Some of the hypotheses regarding the ecological function of the association between fish and jellyfish and their changes throughout the fish ontogeny have been confirmed:

- Protection: Fish juveniles find protection sheltering under the umbrella, around the oral arms, and inside the jellyfish when they feel in danger.

- Meeting point: A single jellyfish contained fish of different sizes, suggesting that fish use the jellyfish as a meeting point. Moreover, the size range of the hosted fish increased along the study period.

- Provisioning food: Jellyfish are a food source for the associated juvenile fish. Biomarkers results show that the jellyfish contribute in a high proportion to the diet of the associated *T. mediterraneus*.

ACKNOWLEDGMENTS

Por fin ha llegado el momento, ese momento en el que quiero decir tantas cosas… Ahora, que he llegado al final de este viaje quiero dedicar unas palabras a todo el que ha formado parte de él y me ha acompañado durante este tiempo. No ha sido un camino corto, ni fácil en algunos momentos. Pero lo que si ha sido es un viaje increíble en el que no sólo he aprendido profesional y personalmente, sino que también he reído, llorado, me he superado en muchas ocasiones y me ha ayudado a ser quien soy hoy en día. Por eso, quiero dar las gracias pero sobre todo quiero dedicar este trabajo, mi tesis.

Esta tesis va por ti Tío Xavier, quien no sólo me encaminó hacia este viaje sino quien junto a la Tía Carmen me enseñó a disfrutar del mar como nadie. Todo esos veranos en la Pelosa y en la Cala Tamariú, con las sandalias llenas de piedras corríamos a la orilla sabiendo que al primer aleteo salían; descubriendo lo que son las anémonas o las estrellas de mar y aprendiendo a no pisar las rocas para no destruirlas y para no pincharnos con los erizos.

No quiero dejar de dar las gracias a Mikel Z. por acompañarme en mis inicios. Y a ti Josep-Maria, no solo por abrirme las puertas del grupo y confiar en mi desde el

principio, sino por ser maestro en tantas ocasiones.

Por supuesto se la dedico a mis directoras, Ana y Vero, por la oportunidad que me disteis para hacer este doctorado. Entre las dos conseguisteis el equilibrio que me hizo disfrutar del mar como nunca lo había hecho. A ti Ana, por enseñarme a entender que cada detalle es importante. Por ayudarme a posar los pies en la tierra cuando he levantado demasiado el vuelo y porque con nuestras diferencias y similitudes hemos llegado juntas al final de este camino. A ti Vero, que me acogiste desde el principio como una mas de tu familia. Gracias por transmitirme esa pasión que me entusiasmó desde aquel primer momento en el que me subí al barco de Greenpeace y recibía tus ánimos cada día. Porque cuando llegué me enseñaste que cuando haces lo que te gusta no importa el tiempo, con la compañía y una buena banda sonora de fondo el tiempo vuela. Por darme alas para experimentar y disfrutar de esas estancias, congresos, charlas y demás formaciones que me han ayudado a crecer: desde un congreso en Donosti hasta una campaña en la Antártida!

A todo mi querido grupo de medusas del ICM - CSIC: Mely, Giacomo, Miriam, Ale, Laura, Maria, Raül, Toño, Mar, Gastón; y al grupo de bentos: Jordi, Carlos, Núria, Stefano, Martina, Andrea, Lorenzo; todos ellos mis compañeros de batalla con los que he compartido no solo horas (sí, muchas) sino risas, enfados, alegrías… todas y cada una de las emociones que forma parte de hacer una tesis. Por supuesto te doy las gracias a ti Maca, por cada una de nuestras salidas, charlas, confidencias, tirón de orejas, los ensayos de las mil y una charlas que hemos dado en tantos congresos. Por vivir cada logro a mi lado como si fuera tuyo y ayudar a levantarme en las caídas que he sufrido a lo largo del camino.

Gracias a Jenny, Chris, Steve, Titi y Alenka, por ser un ejemplo a seguir. Por enseñarme, inspirarme y ayudarme siempre a mejorar y acogerme y hacerme sentir como en casa. También gracias a todos lo co-autores de mis trabajos, por contribuir y ayudarme mejorarlos con su conocimiento y gran experiencia.

Tampoco puedo dejar nombrar a dos personas muy importantes para mí y que han sido de gran apoyo. Izaskun, eskerrik asko beti entzuteko prest egoteagatik. Baina batez ere, eskerrik asko zure animo, babes eta maitasunagatik. Silvia, mi luz y mi guía… gracias por enseñarme a conocerme y a sacar esa fuerza que a veces olvido que tengo. Por proporcionarme paz en momentos de caos y fuerza en momentos de debilidad.

Finalmente, quiero agradecer y dedicar este trabajo a mis padres, a mi hermana y a mi aitona, ¡por fin aitas! Porque no importó lo que quisiera estudiar, siempre que estuviera feliz haciéndolo; no importó si era en Donosti o en Cádiz, siempre que fuera feliz en el lugar; tampoco importó que viniera a hacer prácticas a Barcelona mientras me vierais contenta…. En todas y cada una de esas etapas vuestra respuesta siempre ha sido: “¡adelante, cariño!” y mirad ahora dónde estoy. Porque vuestra mirada de orgullo en cada una de las metas que

he alcanzado ha sido el mejor combustible para hacer siempre lo que me he propuesto. Eskerrik asko amatxo eta aitatxo. A mi hermana, Pati, quien me regaló mi primer álbum en blanco cuando aún estaba de prácticas para que fuera rellenando con mis artículos. A quien llamaba por teléfono a las tantas de la noche cuando salía de contar éfiras y me hacía compañía hasta llegar a casa… en esta etapa también juntas y bajo tu protección. Eskerrik asko ahizpa!

Y por último a ti, Martín, mi compañero de viaje. Porque sin ti no se dónde estaríamos en este momento. Ha sido un largo camino, a veces más llano y fácil y otras veces menos. Pero tú siempre has estado a mi lado dándome la mano, sin tirar demasiado fuerte pero sin dejarme caer nunca, respetándome y apoyándome. Me has visto en los momentos más eufóricos pero también en los menos alegres y tus palabras, pero también tus silencios, me han dado fuerzas para llegar a este punto. Por eso, ¡este trabajo va por ti!

Eskerrik asko bihotzez nere ondoan egon zareten guztioi!!

Appendices

APPENDICES

Vol. 510: 201–213, 2014
doi: 10.3354/meps10790

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 9

Contribution to the Theme Section 'Jellyfish blooms and ecological interactions'

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Digestion times and predation potentials of *Pelagia noctiluca* eating fish larvae and copepods in the NW Mediterranean Sea

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ABSTRACT: Predation is the principal direct cause of mortality of fish eggs and larvae (ichthyoplankton). Pelagic cnidarians and ctenophores are consumers of ichthyoplankton and zooplankton foods of fish, yet few estimates exist of predation effects *in situ*. Microscopic analyses of the gastric 'gut' contents of gelatinous predators reveal the types and amounts of prey eaten and can be used with digestion time (DT) to estimate feeding rates (prey consumed predator^{-1} time^{-1}). We measured the DT and recognition time (RT) of prey for *Pelagia noctiluca*, an abundant jellyfish with increasing blooms in the Mediterranean Sea. DT of fish larvae averaged 2.5 to 3.0 h for *P. noctiluca* (4–110 mm diameter) and was significantly related to jellyfish and larval sizes. In contrast, DT of fish eggs ranged from 1.2 to 44.8 h for jellyfish ≤22 mm diameter ('ephyrae'), but DT was not significantly related to ephyra or egg diameter. Approximately half of the eggs ingested were not digested. DT of copepods averaged 4 h. We also measured DT and RT of salps, euphausiids, and miscellaneous zooplankton. Temperature (20–25°C) generally did not significantly affect DT of any prey. Estimated potential predation effects of ephyrae on fish larvae in the Catalan Sea in 1995 showed great variability among 9 stations (0–3.7% consumed h^{-1}). We discuss how sampling methods contributed to variation in predation estimates and offer recommendations to improve accuracy. Our results enable estimation of predation on ichthyoplankton and competition for zooplankton prey, which can have extremely important effects on fish populations globally.

KEY WORDS: Anchovy · Jellyfish · Salp · Fish eggs · Ichthyoplankton · Zooplankton · Competition

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INTRODUCTION

Much of fisheries research has been directed towards predicting annual recruitment of fish into a fishery. The Critical Period and Aberrant Drift hypotheses (Hjort 1914) inspired 20th-century recruitment fisheries oceanography research towards factors affecting the early life history of fish. The main factors believed to determine recruitment variability now include the interactions of temperature and other physical processes on prey availability and larval condition, which in turn determine their vulnerability to predators (Houde 2008). 'It is now evident that high and variable predation is the principal, [proximate] agent of mortality' (Bailey & Houde 1989, Houde 2008, p 63).

Many species of pelagic cnidarians and ctenophores eat fish eggs and larvae (ichthyoplankton) (reviewed by Purcell 1985, Purcell & Arai 2001), yet studies on the magnitude of this predation remain rare. During the 1980s and 1990s, several studies quantified removal rates of ichthyoplankton by pelagic cnidarians and ctenophores in containers ranging in size from 25 to 6300 l (reviewed by Purcell &

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Arai 2001). The results of those studies were affected by being conducted in artificial conditions (Purcell & Arai 2001). A second approach to estimate predation on ichthyoplankton by pelagic cnidarians and ctenophores is to collect the predators *in situ*, thereby preserving their natural prey without experimental interference. Calculation of ingestion rates (prey eaten predator^{-1} time^{-1}) also requires estimation of the time prey can still be recognized in gut contents; calculation of predation effects (% prey standing stock consumed time^{-1}) further requires information about the abundances of the predators and prey *in situ*.

Interest in gelatinous species has resurged recently, probably because of their increasing interference with human enterprises in coastal oceans (Purcell et al. 2007). One species of particular concern is the holoplanktonic species *Pelagia noctiluca* that has caused economic damage to aquaculture in northern Europe (Doyle et al. 2008, Raffaele 2013) and to tourism, fisheries, aquaculture, and energy industries in the Mediterranean (reviewed by Mariottini et al. 2008, Canepa et al. 2014). *P. noctiluca* has a long history of blooms in the Mediterranean Sea (Goy et al. 1989) that appear to be increasing in frequency and duration (Daly Yahia et al. 2010, Kogovšek et al. 2010, Licandro et al. 2010, Bernard et al. 2011).

P. noctiluca consumes a variety of prey, including copepods and other crustaceans, gelatinous zooplankton, pelagic mollusks, appendicularians, and fish eggs and larvae (Malej 1982, Vućtić 1982, Sabatés et al. 2010, Rosa et al. 2013). Copepods were the most numerous prey consumed by ephyrae in the NW Mediterranean Sea (Sabatés et al. 2010). Although fish larvae averaged <1% of the available mesozooplankton, they ranged from 5 to 32% of the prey in ephyrae; anchovy *Engraulis encrasicolus* larvae were the most frequently consumed (Sabatés et al. 2010). Thus, *P. noctiluca* is potentially important as a predator of ichthyoplankton and as a competitor of fish larvae and zooplanktivorous fish. Those effects are pervasive but difficult to evaluate. Because predation effects on prey populations increase with pelagic cnidarian and ctenophore population sizes (Purcell & Arai 2001, Purcell & Decker 2005), ichthyoplankton will likely suffer greater mortality as populations of these predators increase.

The *in situ* feeding rates of *P. noctiluca* were not calculated from gut contents in previous studies due to a lack of data on the digestion times of the various prey types. During cruises of the FishJelly project in 2011 and 2012, we measured digestion length of time and the times prey could be recognized in the gastric pouches ('guts') of *P. noctiluca* medusae and ephyrae. We emphasized ichthyoplankton, but also included common zooplankton organisms. Our objective was to measure digestion times in order to use this information in combination with gut content data for *P. noctiluca* collected at comparable temperatures to calculate predator feeding rates and predation effects on comparable prey. As an example, we used the gut content data for *P. noctiluca* ephyrae from Sabatés et al. (2010) to estimate their potential predation on fish larvae and copepods off the Catalan coast (NW Mediterranean) in 1995.

MATERIALS AND METHODS

Digestion measurements of fish larvae, fish eggs, and zooplankton by *Pelagia noctiluca* medusae and ephyrae were made in the Catalan Sea during cruises on board the RV 'García del Cid' (17 June to 4 July 2011 and 13 to 21 July 2012). Sea near-surface temperature and salinity were estimated by the ship's system. Near-ambient seawater temperature (T in °C) was maintained in the ship's laboratory by means of near-surface water pumped into kreisels and water baths containing the experimental containers. Fish larvae, fish eggs, and zooplankton used for digestion measurements were selected under magnification of a dissecting microscope from plankton tows of a 60 cm diameter bongo net with 300 µm mesh. Fish larvae were identified to the lowest taxon possible. Anchovy eggs were identified to species by their oval shape. Fish larva total length (TL), copepod cephalothorax length, and fish egg diameter were measured to the nearest 0.1 mm with calipers with the aid of a dissecting microscope immediately before they were fed to *P. noctiluca*. Body lengths of salps (excluding protrusions) and other large species were measured to the nearest 0.5 mm. Fish larval length was converted to dry mass by regressions for the most similar taxa in Pepin (1995) and Rossi et al. (2006). Our methods, outlined below, were considered 'natural feeding' as defined by FitzGeorge-Balfour et al. (2013) and differed for medusae (observed visually while in kreisels) and ephyrae (observed with a dissecting microscope).

P. noctiluca medusae (>22 mm diameter) were collected at night from the surface with a long-handled dip net and placed immediately in a bucket with seawater. They were kept on board in 300 l kreisels with weakly flowing seawater, as illustrated by Purcell et al. (2013). A prey item held with forceps and touched to the oral arms was ingested quickly, and the ingestion time was recorded. After ingestion, the prey item

was observed continuously to track its final location in the gastric pouch. Thereafter, each rapidly digesting or transparent prey (i.e. fish larva, salp) was checked visually at ≤15 min intervals and each slowly digesting, conspicuous prey (i.e. euphausiid) at ≤60 min intervals. Only large fish larvae, euphausiids, and salps were visible once ingested by the medusae; therefore, fish eggs and copepods were not tested on medusae because they could not been seen after ingestion. The length of time that prey could still be seen in the guts was recorded and designated 'recognition time' (RT). Prey that could no longer be seen were considered to be digested, and the time was recorded and designated 'digestion time' (DT). Egestion of the prey remains was occasionally observed (error = 0 min). Otherwise, the error (% of DT) was calculated from one-half of the final observation interval. After digestion of 1 prey item, each medusa was fed another prey and the process was repeated. Medusae appeared to be healthy for 3 to 4 d in the kreisels and were not used for digestion estimates afterwards. The swimming bell diameter then was measured to the nearest 1 cm by placing the medusa subumbrella down on a ruler.

Because we could not determine whether fish larvae digested by medusae on the cruise would be recognized in gut content analysis, we conducted an experiment at the Institut de Ciències del Mar in Barcelona, Spain (Table 1). Medusae from laboratory culture were placed in 300 l kreisels with weakly flowing ambient seawater and each was given 1 fish larva, as above. At 15 to 90 min intervals, 3 to 6 of the medusae were preserved in 5% formalin solution. Their gastric pouches were examined later with a dissecting microscope to determine whether the prey could be recognized as a fish larva. This experiment was conducted twice (18 and 25 July 2013) with 3 species of larvae: anchovy *Engraulis encrasicolus* (Engraulidae), round sardinella *Sardinella aurita* (Clupidae), and bullet tuna *Auxis rochei* (Scombridae) that had been collected during the previous night using a Bongo net (60 cm diameter, 300 and 500 µm meshes) from nearby coastal waters. These results were compared to the digestion observations made on board ship. Medusae in which the larvae could no longer be seen were also included in the analysis of digestion time.

P. noctiluca ephyrae and post-ephyrae with small oral arms and tentacles (hereafter, all referred to as 'ephyrae,' with a diameter ≤22 mm) were collected in short surface hauls with a Neuston net (1.5 m^2 mouth, 1 mm mesh). Undamaged ephyrae were kept individually in 25 to 350 ml glass bowls or beakers in which they could swim freely, with container size increasing with specimen size. A fish egg, larva, or zooplankter held with forceps and put in contact with each ephyra was ingested quickly. This time of ingestion was recorded, and each ephyra was checked under magnification of a dissecting microscope at 5 to 60 min intervals, with prey requiring prolonged digestion (fish eggs) being checked at the longer intervals. DT, RT, and % error were determined as described for medusae. Ephyral diameter was measured to the nearest 1 mm with calipers under a dissecting microscope. We used multiple linear regressions to test whether DT was related to T, *P. noctiluca* diameter, or prey size (largest dimension). Regressions were made only when sufficient data were available. When data did not meet assumptions of normality and constant variance, we used $\log_{10}$ transformation before statistical analysis. One-way ANOVA was used to test for differences in digestion times among fish larval taxa and among fish egg diameters. Digested and undigested eggs were tested for differences in ephyral sizes and egg sizes with *t*-tests. When those data failed to meet assumptions after transformation, we used a non-parametric *t*-test (Mann-Whitney rank sum test). All data were presented as mean ± SD.

Table 1. Numbers of single fish larvae recognizable in *Pelagia noctiluca* medusae following digestion and preservation at intervals of 15 to 90 min. Results are shown as the number recognizable/number tested. Number of larvae digested = number tested − number recognizable. '0' indicates that all larvae were completely digested. Temperature = 21.3°C. Species were anchovy *Engraulis encrasicolus*, round sardinella *Sardinella aurita*, bullet tuna *Auxis rochei*. NT: not tested

Species	Larval length (mm)	Time interval (min) 15	30	45	60	90
Anchovy & round sardinella	7–9	6/6	6/6	2/11	0/9	NT
Bullet tuna	9–11	NT	3/3	3/3	3/3	0/6

RESULTS

To test when larvae digested by medusae (35.7 ± 2.1 mm diameter) could not be recognized as fish larvae with microscopic examination, we examined the gut contents of medusae preserved at intervals, as described above (Table 1). All larvae were easily recognizable after 15 and 30 min. The long, thin anchovy and round sardinella larvae could not be

recognized as fish larvae after 45 or 60 min. The larger bullet tuna larvae could still be recognized in the gut contents after 45 or 60 min, but not after 90 min of digestion. Based on these results, we removed digestion data for 5 anchovy larvae >10 mm long that could not be seen within swimming medusae on board ship after 30 min.

DTs of *Pelagia noctiluca* medusae and ephyrae fed 1 fish larva averaged 2.5 to 3.0 h (Table 2). DTs of all medusae and ephyrae combined were significantly related to ephyral diameter (D) and larval length (L), but not to T (R^2 = 0.258, $F_{3,205}$ = 24.23, p < 0.001; $\log_{10}$D t = −8.33; p < 0.001; $\log_{10}$L t = 6.23; p < 0.001; T t = 0.66; p = 0.513; $\log_{10}DT = 0.334 + 0.562 \times \log_{10}L - 0.620 \times \log_{10}D$). DT of combined medusae and ephyrae increased with larval length and decreased with the diameter of *P. noctiluca* (Fig. 1). Because our methods differed for medusae (>22 mm diameter) and ephyrae (≤22 mm), we considered the 2 groups separately in further analyses.

DTs of both ephyrae and medusae were significantly related to diameter and larval length; DTs were shorter for smaller larvae and larger *P. noctiluca*. DTs for fish larvae were not significantly related to T. Similar results were obtained for a multiple regression using larval dry mass (DM) instead of length; however, the relationship with DM (R^2 = 0.288, $F_{3,102}$ = 13.74, p < 0.001, $\log_{10}$ DM t = 3.85; p < 0.001) was not as strong as with length (Table 2). The DTs for ephyrae differed significantly ($F_{5,101}$ = 346.36, p < 0.001) among different types of larvae (Table 3); pairwise comparisons of the DT of anchovy versus all

Table 2. Digestion time (DT) and recognition time (RT) for *Pelagia noctiluca* given single fish larvae, salps, and copepods unless noted otherwise. Errors (% of DT) and multiple regression statistics are also given. Salps given to medusae were *Salpa fusiformis*; those given to ephyrae were *Thalia democratica*. Data are presented means ± SD, with ranges in parentheses. T: temperature; NS: not significant; NT: not tested

Jellyfish Diameter (D, mm)	n	T (°C)	Prey length (L, mm)	DT (h)	Error (%)	Regression statistics	RT (h)
Medusae			**Fish larvae**				
48.6 ± 20.6 (25–110)	63	22.7 ± 1.3 (20.2–25.5)	14.1 ± 6.5 (5–30.0)	2.1 ± 2.2 (0.8–8.3)	13.3 ± 12.5 (0–50)	R^2 = 0.425 $F_{3,59}$ = 14.55; p < 0.001 $\log_{10}$D t = −0.79; p = 0.432 NS $\log_{10}$L t = 6.41; p < 0.001 T t = −1.04; p = 0.300 NS $\log_{10}DT = 0.024 + 1.061 \times \log_{10}L$	0.9 ± 0.8 (0.3–5.8)
Ephyrae			**Fish larvae**				
13.4 ± 5.2 (4–22)	107	23.4 ± 0.9 (20.7–24.4)	5.9 ± 2.6 (1.5–13.0)	3.0 ± 1.7 (0.3–8.3)	20.6 ± 25.2 (0–50)	R^2 = 0.319 $F_{3,103}$ = 15.89; p < 0.001 $\log_{10}$D t = −2.73; p = 0.007 $\log_{10}$L t = 5.71; p < 0.001 T t = −1.37; p = 0.172 NS $\log_{10}DT = 1.213 + 0.662 \times \log_{10}L - 0.379 \times \log_{10}D$	1.2 ± 0.2 (0.2–5.8)
Medusae			**Salps**				
42.2 ± 11.4 (15 – 60)	30	22.2 ± 1.4 (19.6–23.7)	21.3 ± 12.0 (1.5–40.0)	2.0 ± 1.8 (0.4–6.9)	7.7 ± 9.0 (0–35)	R^2 = 0.766 $F_{3,103}$ = 27.23; p < 0.001 D t = 0.66; p = 0.515 NS L t = 4.26; p < 0.001 T t = −2.87; p = 0.008 $DT = 12.217 - 0.519 \times T + 0.087 \times L$	1.8 ± 1.1 (0.2–5.0)
Ephyrae			**Salps**				
10.4 ± 0.6 (10–11)	5	23.4 ± 1.3 (21.6–25.2)	5.6 ± 2.6 (4.0–10.0)	3.2 ± 2.1 (1.0–5.7)	16.2 ± 8.8 (5–29)	NT	1.8 ± 1.4 (0.4–4.0)
Ephyrae			**1 copepod**				
11.8 ± 0.6 (7–22)	51	23.9 ± 0.7 (22.3–25.0)	1.3 ± 0.3 (1.0–2.0)	4.1 ± 1.3 (1.2–7.8)	10.2 ± 5.3 (0–29)	R^2 = 0.131 $F_{3,44}$ = 2.20; p = 0.101 NS D t = −1.66; p = 0.105 NS L t = 1.20; p = 0.235 NS T t = −1.10; p = 0. 276 NS	2.2 ± 1.2 (0.7–5.0)
Ephyrae			**2–4 copepods**				
17.0 ± 3.6 (13–20)	4	23	1.1	4.1 ± 0.5 (3.4–4.7)	11.4 ± 5.2 (7–20)	NT	1.8 ± 0. 4 (1.3–2.1)

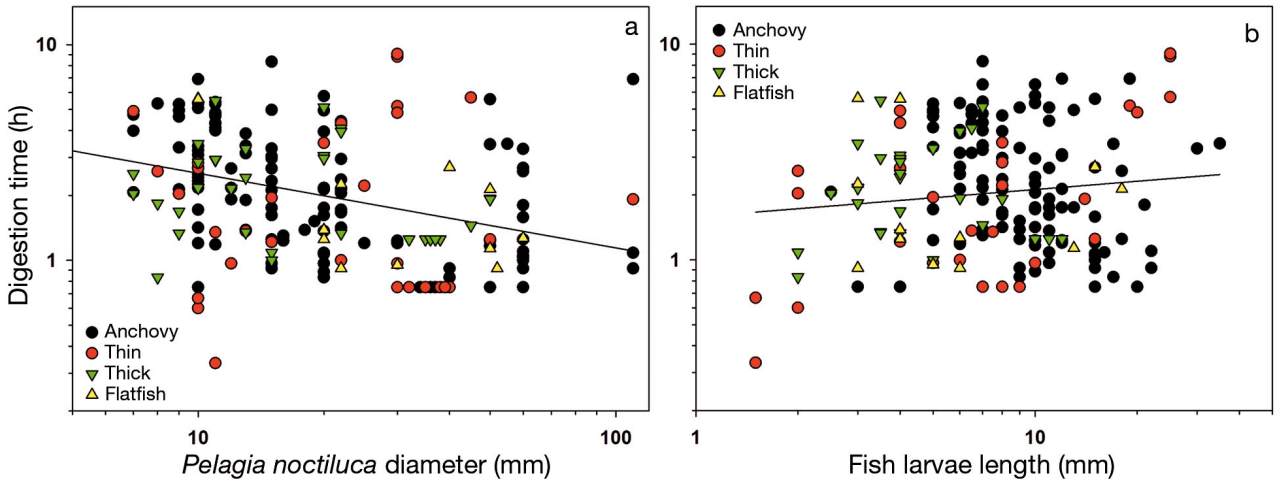

Fig. 1. Digestion times of *Pelagia noctiluca* medusae and ephyrae of fish larvae by type: anchovy *Engraulis encrasicolus*, thin larvae (sardinellas, gobies), thick larvae (carangids, sciaenids, serranids, scombrids), and flatfish *Aroglossus laterna* with respect to (a) *P. noctiluca* diameter, and (b) fish larvae length. Trend lines are best fit linear regressions for all larvae. See Table 2 for multiple regression equations

Table 3. *Pelagia noctiluca* ephyrae digestion time (DT) and recognition time (RT) of single fish larvae by taxon. Errors (% of DT) are also given. Prey were anchovy *Engraulis encrasicolus*, serranid *Serranus cabrilla*, round sardinella *Sardinella aurita*, mackerel *Trachurus mediterraneus*, myctophid *Ceratoscopelus maderensis*, flatfish *Aroglossus laterna*, and unidentified gobies, sciaenids, and carangids. Data are presented as means ± SD, with ranges in parentheses. T: temperature

Jellyfish Diameter (mm)	n	T (°C)	Fish larvae length (mm)	DT (h)	Error (%)	RT (h)
Ephyrae			**Anchovy**			
12.9 ± 5.0 (4–22)	64	23.1 ± 0.9 (20.7–24.4)	7.3 ± 2.4 (2.5–13.0)	3.5 ± 1.7 (0.8–8.3)	13.0 ± 10.2 (0–50)	1.3 ± 0.8 (0.2–5.8)
			Serranid			
13.2 ± 0.6 (9–13)	6	24.2 ± 0.2 (23.7–24.4)	3.8 ± 0.11 (3.5–4.0)	2.7 ± 1.5 (1.3–2.6)	17.8 ± 6.9 (0–24)	1.8 ± 0.3 (1.4–2.2)
			Round sardinella			
13.3 ± 4.2 (10–22)	7	23.7 ± 0.2 (23.3–24.4)	6.0 ± 1.4 (4.0–8.0)	1.7 ± 0.8 (1.0–2.8)	10.8 ± 7.9 (9–24)	0.8 ± 0.4 (0.4–1.5)
			Goby			
9.8 ± 2.8 (8–15)	6	24.1 ± 0.5 (23.5–24.4)	2.2 ± 0.9 (1.5–4.0)	1.2 ± 0.9 (0.5–2.7)	35.0 ± 18.2 (6–50)	0.6 ± 0.3 (0.3–1.1)
			Scombrid, sciaenid, carangid			
13.5 ± 5.5 (7–22)	24	23.9 ± 0.8 (21.1–24.4)	3.6 ± 1.5 (1.5–7.0)	2.2 ± 1.2 (0.3–5.1)	22.0 ± 17.9 (0–50)	1.2 ± 0.6 (0.4–2.5)
			Flatfish			
17.3 ± 5.8 (10–22)	6	23.8 ± 0.7 (23.0–24.4)	3.5 ± 0.6 (3.0–4.0)	2.8 ± 2.2 (0.9–5.6)	14.9 ± 19.0 (0–50)	1.3 ± 1.2 (0.2–3.2)

other types of larvae were significantly different (Holm-Sidak method, t = 18.12 to 29.63, $p < 0.001$), and DTs of goby larvae also differed significantly from DTs of serranid and flatfish larvae (t = 3.08 and 2.80, respectively, $p < 0.01$). Thus, long, thin larvae (anchovies, sardinellas, gobies) were digested more rapidly than short, thick larvae (scombrids, carangids, serranids, flatfish; Fig. 1). The lengths of time that they were recognizable as fish larvae in the guts (RTs) were approximately half of the DTs for both medusae and ephyrae.

Fish eggs were digested more slowly (1.2–44.8 h) than fish larvae by *P. noctiluca* ephyrae (Table 4, Fig. 2). About half of all eggs tested (29 of 56) were egested undigested after many hours, but interestingly, all anchovy eggs were digested. The sizes of ephyrae that had not digested eggs did not differ from those that had (t-test, t_{51} = 1.445, p = 0.155);

Table 4. *Pelagia noctiluca* ephyrae digestion time (DT) and recognition time (RT) of single fish eggs by diameter. Eggs 0.8 mm in diameter are presented in 2 groups (anchovy and those other than anchovy). Retention times are for undigested eggs that were egested. Errors (% of DT) are also given. Temperatures were 23.4 ± 0.5°C (22.3–25.2°C). Data are presented as means ± SD, with ranges in parentheses. Percentages of each egg size digested are in square brackets. Errors reflect digested and undigested eggs; NA: not applicable

Fish egg diameter (mm)	Digested eggs					Undigested eggs		
	Ephyra (mm)	n	DT (h)	RT (h)	Error (%)	Ephyra (mm)	n	Retention (h)
0.6 [75%]	9.9 ± 3.1 (7–15)	9	8.2 ± 2.2 (4.3–10.6)	6.1 ± 2.1 (3.2–9.5)	15.8 ± 2.2 (13–20)	8.7 ± 1.5 (7–10)	3	12.1 ± 6.3 (5.2–17.5)
0.8 [45.2%]	12.1 ± 4.3 (8–22)	14	17.4 ± 12.0 (3.8–44.8)	14.8 ± 13.0 (2.3–43.0)	19.0 ± 18.8 (6–50)	9.8 ± 3.7 (5–20)	17	12.6 ± 7.9 (2.8–29.2)
0.8 anchovy [100%]	9.7 ± 0.5 (9–10)	6	8.5 ± 5.4 (1.2–17.8)	6.3 ± 3.1 (4.5–12.5)	19.8 ± 6.2 (15–30)	NA	0	NA
1.0 [0%]	8.0 ± 1.0 (7–9)	0	NA	NA	NA	8.0 ± 1.4 (7–9)	2	22.7 ± 1.0 (22.0–23.4)
1.1 [0%]	13.3 ± 6.5 (7–20)	0	NA	NA	NA	15.0 ± 5.1 (10–22)	6	3.0 ± 0.9 (1.8–4.2)

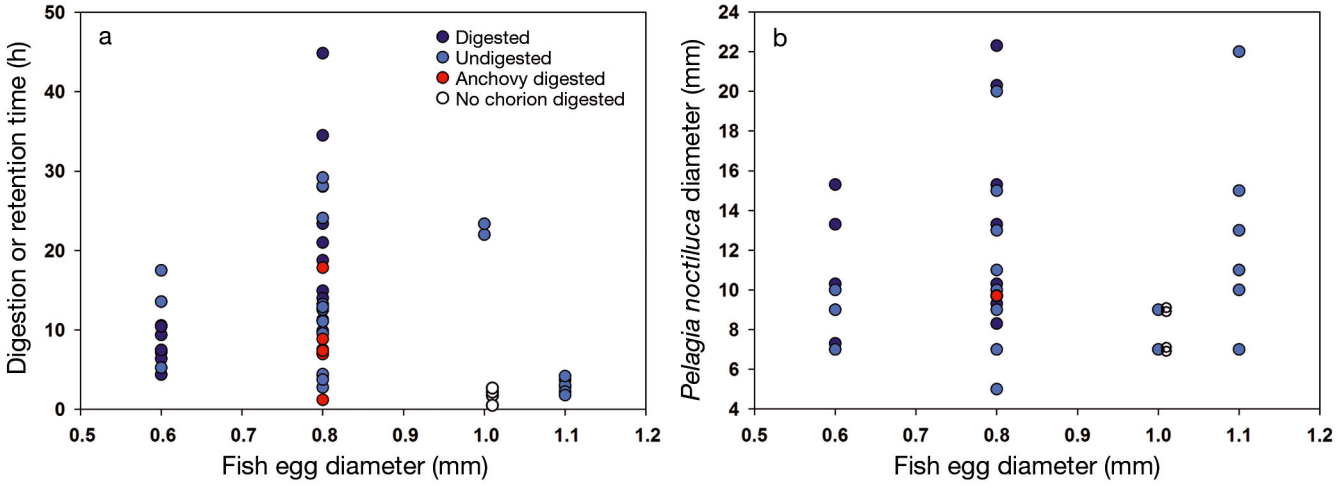

Fig. 2. (a) *Pelagia noctiluca* ephyral digestion and retention times of fish eggs with respect to egg diameter. Time (h) that eggs were inside ephyrae. (b) Size of ephyrae compared to size of digested and undigested eggs. In (b), ephyral diameters for digested eggs were offset by +0.3 mm and only 1 point is shown for anchovy (of 6 at 9–10 mm) to enable them to be better seen

thus, small ephyral size did not explain why some eggs were not digested. Similarly, egg sizes did not differ between those digested or undigested (Mann-Whitney U = 296.50, p = 0.194) although no 1.0 or 1.1 mm eggs were digested. To test whether eggs would be digested without the chorion, it was dissected from 4 of the 1 mm eggs, which otherwise were not digested by ephyrae. These embryos were digested rapidly by the ephyrae (1.78 ± 0.46 h; Fig. 2), suggesting that the chorion protected the eggs from digestion. DTs of eggs differed significantly by diameter ($F_{3,29}$ = 5.68, p = 0.003), with 0.8 mm eggs requiring longer to digest than all others. One 3 mm diameter egg was digested in 22.4 h by a 22 mm ephyra. Neither DTs nor RTs of undigested eggs were significantly related to ephyral size, T, or egg size ($F_{3,28}$ = 1.071, p = 0.377 and $F_{3,22}$ = 0.622, p = 0.608, respectively). RT of digested fish eggs were 75–85% of the DT for ephyrae, and RT of undigested eggs were 100% of retention times.

DT and RT of copepods could only be measured for ephyrae (Table 2). DTs of single copepods by ephyrae averaged 4 h and were not significantly related to prey or ephyral size, or T. We gave 2 to 4 copepods only to 4 ephyrae, but average digestion time remained ~4 h. RTs of copepods were about half of the DTs for ephyrae.

Salps were very abundant and were eaten by medusae in 2011 (J. E. Purcell pers. obs.). DTs of large salps *Salpa fusiformis* by medusae averaged 2 h and

were significantly related to salp length and temperature (Table 2). The few salps *Thalia democratica* small enough to be ingested by ephyrae were digested in ~3 h.

P. noctiluca eats a variety of zooplankton, but digestion times previously were unavailable. DTs of euphausiids (n = 10, 10–20 mm TL) by medusae averaged 5.0 ± 2.4 h. *Velella velella* colonies were eaten by medusae *in situ* (V. L. Fuentes et al. pers. obs.). DTs of 15 and 26 mm long colonies by 2 medusae were ~3.7 h, and those of 1 to 3 mm long colonies by 4 ephyrae were ~5.3 h. The chitin sail of *V. velella* was still recognizable after egestion. The nectophores of 2 polygastric colonies of the siphonophore *Muggiaea atlantica* were egested with their firm mesoglea intact from medusae after 5.0 and 6.5 h. Cladocerans (*Penilia* sp. and *Podon* sp.) were digested by ephyrae in 3.0 ± 1.7 h (n = 17). DTs of euphausiid furcilia larvae (n = 13, 3–11 mm TL) for ephyrae averaged 5.0 ± 0.9 h. DTs by ephyrae were short for 2 appendicularians (<1 h) and 1 chaetognath (1–2 h). Coiled pteropods (n = 3, 0.5 mm), whose shells were recognizable until egestion, were digested in ~4 h by ephyrae. RTs of the crustaceans were 45 to 65% of DTs. RTs of shelled pteropods and the cnidarians were 100% of DT.

DISCUSSION

Digestion and recognition times

Gut contents of gelatinous predators in combination with DT can be used to determine *in situ* predation rates (prey consumed predator^{-1} time^{-1}), and in combination with population densities of the predators and prey, they can be used to estimate predation effects (% prey consumed time^{-1}). Even though *Pelagia noctiluca* blooms in tropical to temperate oceans around the world (Kramp 1961), few studies exist on DT. Gordoa et al. (2013) mentioned 18 ± 5 h as the DT of bluefin tuna *Thunnus thynnus* eggs by 'burst feeding' *P. noctiluca* ephyrae. We also only know the DT for *P. noctiluca* medusae consuming *Mnemiopsis leidyi* ctenophores (Tilves et al. 2012).

Martinussen & Båmstedt (2001) comprehensively summarized earlier studies on DTs of fish larvae, fish eggs, and zooplankton by gelatinous predators. The DTs of fish larvae in our study were similar to those in other studies that included larvae and medusae of comparable sizes, even when the temperatures were 10°C lower (Table 5). Few DTs were available for fish eggs, and no other studies used ephyrae and eggs. DT of anchovy eggs by *Chrysaora quinquecirrha* medusae (3.7–5.2 h, mean 4 h) and *Stomolophus meleagris* (3 h) were within the range for *P. noctiluca* ephyrae (1.2–17 h, mean 8.5 h), but shorter on average. DTs of ~1 mm copepods by *P. noctiluca* ephyrae were similar to those of other species of comparable sizes even at temperatures that were 10°C lower (Table 5). Our results are also comparable to other species digesting cladocerans and appendicularians. The cladoceran *Evadne* sp. was digested by *Aurelia aurita* ephyrae in 3.4 h at 4–5°C (Sullivan et al. 1997). Digestion of appendicularians was very rapid by hydromedusae (<2 h; Larson 1987b) and by *S. meleagris* at 28–30°C (1.5 h; Larson 1991). We are unaware of other DTs for gelatinous predators of salps, pteropods, or stages of euphausiids other than eggs or nauplii (see Martinussen & Båmstedt 2001).

Our estimates of DT and RT in *P. noctiluca* were constrained by the numbers and sizes of medusae available and the relatively narrow range of ambient seawater temperature. Too few medusae were present to allow repeated microscopic analysis to follow digestion over time, which could have damaged the specimens, or to preserve them for gut analysis to confirm complete digestion or recognition. *P. noctiluca* inhabits a wide range of temperatures from deep waters at <14°C to the surface at >26°C in the Mediterranean Sea. Therefore, DT and RT should be measured over that range of temperatures, which large medusae traverse on daily vertical migrations. Because we followed prey items in swimming medusae, 2 problems resulted. First, the end-point of digestion was usually very subjective. Second, we were unable to measure digestion of small prey (copepods, most fish larvae, and fish eggs) by medusae; therefore, additional experiments need to be conducted in which digestion of prey can be monitored more precisely. Our study was also limited by monitoring digestion of single prey items. Because of their small size, ephyrae may not catch several prey items concurrently (but see Fig. 3); however, medusae usually contain numerous prey (J. E. Purcell & U. Tilves pers. obs.), which affected DT measured for small *A. aurita* (Martinussen & Båmstedt 2001, Fitz-George-Balfour et al. 2013).

The lack of digestion of about 50% of the fish eggs by ephyrae raised interesting questions. Although small ephyral size did not explain that phenomenon (Fig. 2b), we could not measure digestion of fish eggs by medusae because we could not visually follow such small prey inside them. As ephyrae grew, the number and length of the digestive filaments in the gastric pouches increased (J. E. Purcell pers. obs.).

Table 5. Selected studies reporting digestion times (DT) for medusae and ctenophores eating fish larvae or eggs and copepods. The percentages of the standing stocks consumed and percentages of prey in the gut contents also reported if available. If more than 1 prey item was digested, the numbers are given in parentheses. T: temperature; NG: not given; lg: large; sm: small; n: number

Predator species	Diameter (mm)	n	Prey Type (n)	Prey Size (mm)	T (°C)	DT (h)	Notes	Standing stock eaten (% d^{-1})	(% of prey)	Reference
			Fish larvae							
Aequorea victoria	49–68	204	*Clupea harengus pallasi* larvae (1–15)	9–14	8–12	1.6–5.2	DT increased with prey size and number, decreased with T	0.8–73	0–97	Purcell (1989), Purcell & Arai (2001)
Aurelia aurita	20–75	10	*C. harengus* larvae	11	9.5	3.9 ± 0.5		NG	NG	Martinussen & Båmstedt (1999)
A. aurita	3–25[a]	40[a]	*Pleuronectes americanus* larvae	NG	7	2.3 ± 1.0		~1[a,c]	<2[a,c]	Sullivan et al. (1994)
Chrysaora quinquecirrha	NG	7	*Anchoa mitchilli* larvae (1–9)	3	26	1.1 ± 0.5		29 ± 14	0–8.8	Purcell et al. (1994)
Pelagia noctiluca	4–110	175	*Engraulis encrasicolus* & other larvae	1.5–30	20–25	0.7–8.3	DT decreased with jelly size, increased with larval size	1.2–13.4	0–13.6	This study; Sabatés et al. (2010)
			Fish eggs							
Cyanea capillata	~2–100	~35	Fish eggs	NG	NG 20–25[b]	5.3		0.1–3.8	14.3	Fancett (1988), Fancett & Jenkins (1988)
Pseudorhiza haeckeli	~5–100	~35	Fish eggs	NG	NG 20–25[b]	3.3		0.1–2.4	40.8	Fancett (1988), Fancett & Jenkins (1988)
Stomolophus meleagris	15–100	165	Fish eggs	0.6–0.8	28–30	3		NG	<1	Larson (1991)
C. quinquecirrha	23–44	16	*A. mitchilli* eggs (9–52)	~1.0	26	3.7–5.2 3.9 ± 0.8	DT independent of egg numbers and medusa size	14 ± 4	0.1–90	Purcell et al. (1994)
P. noctiluca	7–22	29	*E. encrasicolus* & unident. eggs	0.6–3	23–25	1.2–44.8	DT independent of ephyra and egg sizes and T	NG	NG	This study
Mnemiopsis leidyi	lg 50–75 sm 7–22	20 13	*A. mitchilli* eggs (1–2)	~1.0	24	lg 0.6 ± 0.1 sm 1.0 ± 0.4	DT	0–36 9 ± 14	NG NG	Purcell et al. (1994)
			Copepods							
C. capillata	~2–100	~35	Copepods	NG	NG 20–25[b]	1.7	DT	0.1–1.6[d]	10.7	Fancett (1988), Fancett & Jenkins (1988)
P. haeckeli	~5–100	~35	Copepods	NG	NG 20–25[b]	1.7	DT	0.2–4.8[d]	32.8	Fancett (1988), Fancett & Jenkins (1988)
S. meleagris	15–100	165	Calanoids	0.3–1.5	28–30	1.5	DT	NG	4.3	Larson (1991)
A. aurita	4.5–13.5	24	*Pseudocalanus elongatus*	1.4	9.5	3.7 ± 1.7	DT	NG	NG	Martinussen & Båmstedt (1999)
A. aurita	8.7–13	6	*Temora longicornis*	1	9.5	3.2 ± 0.9	DT	NG	NG	Martinussen & Båmstedt (1999)
A. aurita	4.3–54	39	*Calanus finmarchicus*	2.3	9.5	1.5–7.7 5.2 ± 2.0	DT decreased with medusa size	NG	NG	Martinussen & Båmstedt (1999)
A. aurita	3–25 mm[a]	40[a]	*Acartia hudsonica*	NG	7	2.3 ± 1.0	DT	<25[a,c]	0–70	Sullivan et al. (1994)
C. quinquecirrha	25–126	16	*Acartia tonsa* (3–631)	1	20–27	1.1–6.2 3.5 ± 1.1	DT decreased with T	1–94	55–71	Purcell (1992)
P. noctiluca	7–22	53	Calanoids	1–2	22.3–25	1.2–7.8 4.1 ± 1.3	DT independent of ephyral and prey size and T	<0.1–3	43–86	This study
M. mccradyi = leidyi	NG	39	*Acartia tonsa*	1	25–27	1	DT	12–82[c] 34 ± 28[c]	13[c]	Larson (1988)

[a]In mesocosm; [b]estimated from Port Phillip Bay summer water temperature; [c]calculated from data in paper; [d]laboratory feeding estimates

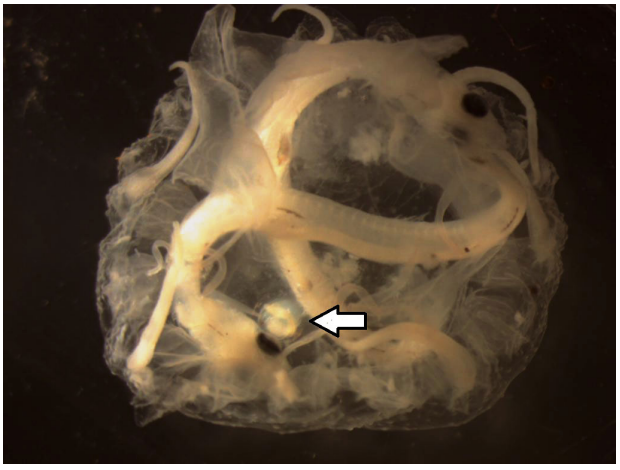

Fig. 3. *Pelagia noctiluca* ephyra collected from the surface at night and immediately preserved on 4 July 2011. The ephyra contained 2 anchovy larvae (~10 mm long) and 1 unidentified fish egg (0.9 mm diameter; indicated by arrow). Ephyra preserved diameter is 7 mm

The ephyrae collected by Sabatés et al. (2010) did not contain any fish eggs, although they were available for consumption (A. Sabatés pers. obs.). Therefore, we do not know whether *P. noctiluca* medusae >22 mm would digest all fish eggs.

On the other hand, the fish eggs may be resistant to digestion. Baltic cod *Gadus morhua callariasadus* eggs were rejected by *M. leidyi* ctenophores; ctenophores that had ingested eggs subsequently ejected 12 of 14 eggs undigested after 2 h at 22°C and 3 d at 7°C (Jaspers et al. 2011). Plaice *Pleuronectes platessa* eggs similarly were ingested, but were egested undigested 'after some hours' by *Bolinopsis infundibulum* ctenophores (Gamble 1977). Most (98–99%) bivalve veligers were not digested or killed by *C. quinquecirrha* medusae (Purcell et al. 1991). 'Passing alive' of pelagic larvae of benthic invertebrates through their predators has been described previously (Mileikovsky 1974), but we could find no further information about fish eggs. Unfortunately, we were unable to determine whether the eggs had been killed by the ephyrae or remained viable.

Potential predation effects by *Pelagia noctiluca* on fish larvae and copepods

The DT and RT of *P. noctiluca* are valuable instruments for estimating predation on prey populations *in situ*. We, therefore, chose a study conducted in the Catalan Sea (Sabatés et al. 2010) to illustrate this method and problems we encountered. In the Sabatés et al. (2010) study, sampling was conducted on a transect perpendicular to the coast at 3 stations (Shelf: over the shelf; Front: over the slope at a shelf-break front; Open Sea: in the open sea) during 18 to 23 June 1995. Sampling was repeated 3 times at each station, and temperature was measured at each station with a CTD. Zooplankton, jellyfish, and fish larvae were sampled by oblique tows of a 60 cm diameter bongo net with a flowmeter and 500 m mesh from near-bottom (70–80 m) to the surface over the shelf or from 200 m to the surface at the front and in the open sea (≥1000 m depth). The duration of the tows ranged from 6 min at shallow shelf stations to 23 min at the front and open sea stations. Net samples were fixed in a 5% formaldehyde–seawater solution. *P. noctiluca* ephyrae (≤12 mm diameter), and fish larvae were counted and identified to the lowest possible taxonomic level from whole preserved samples aided by a dissecting microscope. All copepods were counted from 1/256 to 1/32 aliquots obtained with a plankton splitter. The gut contents of all ephyrae in the samples were identified, counted, and measured; only partly digested prey were included to ensure that the prey items had not been captured while in the net.

Although Sabatés et al. (2010) presented average predation by location (Shelf, Front, Open Sea), we calculated feeding at each of the 3 stations per location. Individual feeding rates of *P. noctiluca* ephyrae on fish larvae and copepods were calculated from the numbers of each prey type in the gut contents at each station divided by the DT of 107 fish larvae or 53 copepods at the mean surface water temperature in 1995 (20.4°C), as calculated from mean prey sizes and regression equations in Table 2. Individual feeding rates were multiplied by ephyral densities and divided by prey densities at each station to estimate the effects of the ephyrae on the prey populations (% prey standing stock consumed h^{-1}). To estimate the potential daily predation at each location, we assumed that feeding and digestion were continuous over the 8 h periods represented by the samples at each location (day, dawn/dusk, night) and multiplied the hourly rates by 8 and then summed the 3 stations.

Estimates of potential predation by ephyrae on fish larvae were highly variable among the 9 stations (Fig. 4). Ephyrae were much more abundant (13.4 m^{-3}) at the Front at night (01:00 h) than at other stations (<1 m^{-3}). The incidences of feeding (ephyrae with prey) at the Front were only 6 to 13%, probably reflecting damage to the ephyrae and loss of prey in the 200 m depth tows. Fish larvae were of average abundance at that station, and the highest levels of predation (3.7% of the larvae h^{-1}) occurred there at night (Fig. 4). Although ephyrae were found at low

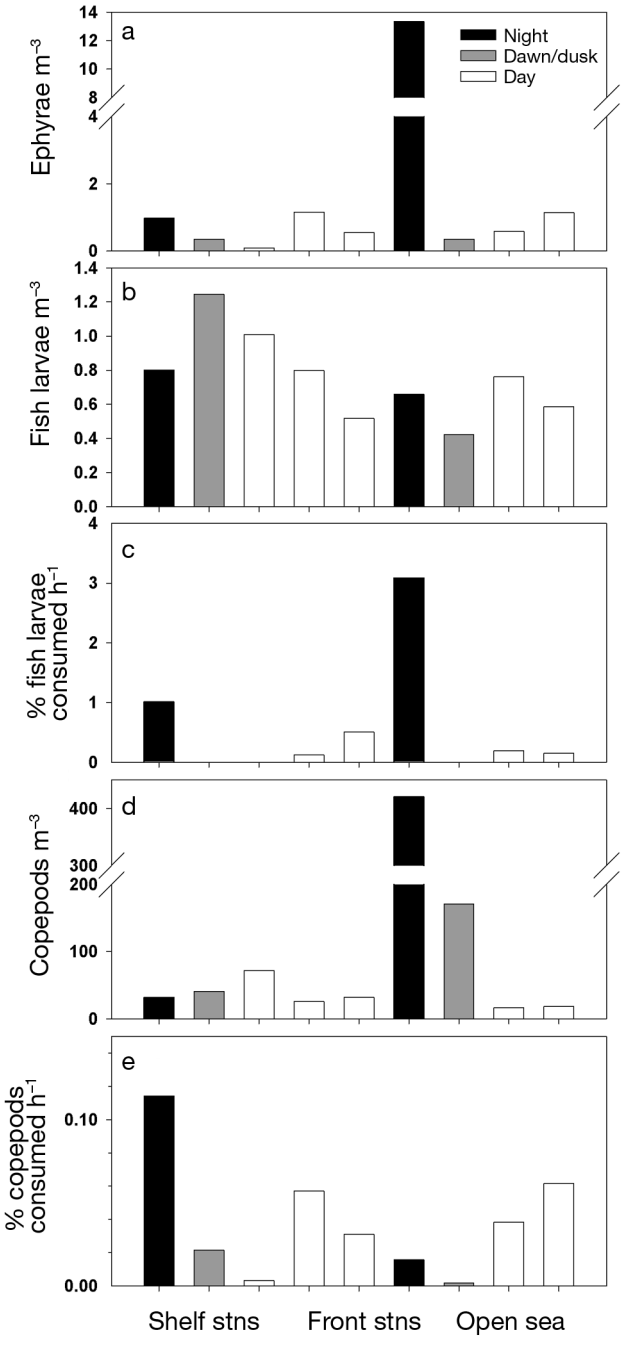

Fig. 4. Abundances and predation effects of *Pelagia noctiluca* ephyrae on fish larvae and copepods according to station (stn) and time of day in the northwestern Mediterranean Sea during 18 to 23 June 1995. Three stations each were over the shelf, at a shelf-break front, or in the open sea along a transect perpendicular to the coast. (a) Ephyrae densities, (b) fish larvae densities, (c) predation effects on fish larvae, (d) copepod densities, and (d) predation effects on copepods

densities on the Shelf (0–0.03 m^{-3}), fish larval densities were highest there (0.8–1.2 m^{-3}), and feeding incidences were high (14–33%) where tows were from only 70 to 80 m depth. Fish larvae were found in the ephyrae only at night (22:00 h) on the Shelf, when we estimated that 1.2% h^{-1} could have been consumed. In the Open Sea, ephyral densities, feeding incidences (9–10% in 200 m tows), and predation effects were low (0–0.7% h^{-1}; Fig. 4). Daily potential predation effects on fish larvae at each location ranged from 1.2 to 13.4% d^{-1}; Table 6).

Table 6. Estimated potential predation effects (% prey consumed d^{-1}) of *Pelagia noctiluca* ephyrae on fish larvae and copepods in the northwest Mediterranean Sea in June 1995

Prey type	Location	Prey in guts (n)	Ephyrae examined (n)	Prey consumed (% d^{-1})
Fish larvae	Shelf	2	145	3.6
	Front	26	4400	13.4
	Open sea	5	1135	1.2
Copepods	Shelf	18	145	0.42
	Front	110	4400	0.31
	Open sea	48	1135	0.31

Estimated potential predation effects by *P. noctiluca* ephyrae on copepods were much lower than on fish larvae (Fig. 4). Although copepods were very abundant at the Front station at night, the estimated potential predation effect was low (0.05% h^{-1}) because of the low feeding incidence. The highest predation effect (0.11% h^{-1}) was at night on the shelf, again probably because of the high feeding incidence (25%). The daily potential predation effects on copepods at each station ranged from 0.30 to 0.42% d^{-1}; Table 6). The predation effects of ephyrae on copepods were much lower (≤0.42% d^{-1}) than on fish larvae (≤13.4% d^{-1}) due to the 50- to 500-fold greater densities of copepods.

Even though the sampling methods of Sabatés et al. (2010) were standard for fisheries oceanography, they illustrated some problems for estimating predation effects on fish larvae by *P. noctiluca*. First, we believe that the net sampling damaged the ephyrae and reduced their apparent feeding. That was indicated by the higher feeding incidence on the shallow shelf where tows were half as deep as at the other stations. This likelihood also was clearly illustrated by the gut contents of ephyrae dipped from the surface in 2011 to 2012 (Fig. 3), which contained fish eggs and more fish larvae than in 1995. Additionally, the 60 cm diameter net was too small to adequately sample the larger medusae. Thus, feeding by *P. noctiluca* was underestimated with these net samples.

Other biases in the predation estimates resulted because the oblique tows of Sabatés et al. (2010) obscured the diel vertical migration patterns of *P. noc-*

tiluca and their prey. The medusae are known to migrate near to the surface at night (Ferraris et al. 2012), and the ephyrae move near the surface during the night (Gordoa et al. 2013; V. L. Fuentes et al. pers. obs.). Anchovy larvae also migrate towards the surface at night (Sabatés et al. 2008). Thus, the oblique net tows in 1995 did not reflect the fine-scale patterns of overlap of ephyrae and larvae over 24 h, which were not known, but may have extended the duration of overlap. The variable sampling times at the different stations in 1995 also made predation estimates difficult to compare. If we had used RT instead of DT to calculate predation effects, the effects would have been approximately doubled. We consider the predation estimates presented here to be rough approximations.

Thus, our recommendations for use of the gut-content method to estimate gelatinous predator consumption of ichthyoplankton and mesozooplankton are as follows:

- Collect specimens for gut contents individually, not in plankton nets, and preserve them immediately.
- Collect gut-content specimens from all appropriate depths, not only at the surface.
- Appropriate sampling methods should be chosen with consideration of the depth distribution patterns of predator and prey species during day and night.
- Use ambient temperature to measure digestion and recognition times.
- Different digestion methods may be best depending on predator and prey characteristics (e.g. Purcell et al. 1991, FitzGeorge-Balfour et al. 2013).
- The duration between ingestion and when prey can still be recognized in microscopic gut-content analysis (RT) is the most appropriate measure for use in feeding estimates using gut contents.
- Use data for ephyral size and ichthyoplankton species and size consumed for greatest accuracy.
- Determine densities, depths, and size distributions of the gelatinous species and their prey to estimate predation effects (% prey standing stock consumed d^{-1}).

Effects of gelatinous zooplankton as predators and competitors of fish

Surprisingly few studies have addressed consumption of fish eggs and larvae by gelatinous predators *in situ*. Whenever such studies were conducted, the predation effects were substantial (reviewed by Purcell 1985, Purcell & Arai 2001). Ichthyoplankton often constitutes large proportions of prey found in the gut contents (Table 5). *P. noctiluca* ephyrae and medusae could be important predators of fish eggs and larvae. Larson (1987a) stated that fish eggs were the most numerous prey items in 50 medusae, with as many as 10 eggs $medusa^{-1}$. Sabatés et al. (2010) found that fish larvae represented ~12% of the prey items in ephyral gut contents in the spring. Fish larvae and eggs represented 0.2 and 1.1%, respectively, of the prey in medusae collected throughout a year (Rosa et al. 2013). Gelatinous predators have been demonstrated to reduce populations of fish larvae (Purcell & Grover 1990).

Gelatinous predators consume a variety of fish species in the plankton, including commercially valuable species. The siphonophore *Rhizophysa eysenhardti* consumed fish larvae in 5 families (Purcell 1981). The scyphomedusae *Cyanea capillata* and *Pseudorhiza haeckeli* consumed 4 kinds of larvae and eggs (Fancett 1988). *S. meleagris* consumed 4 kinds of eggs (Larson 1991). Similarly, the large hydromedusan *Aequorea victoria* consumed larvae of at least 10 species of fishes and eggs of at least 3 species (Purcell 1989). Eight species of larvae were eaten by *P. noctiluca* ephyrae (Sabatés et al. 2010). Additional studies conducted since the reviews by Purcell (1985) and Purcell & Arai (2001) have shown that the cubomedusae *Chironex fleckeri*, *Tamoya haplonema*, and *Chiropsalmus quadrumanus* eat fish (Carrette et al. 2002, Nogueira Júnior & Haddad 2008). Young fish and fish eggs represented 5.2 and 1.2%, respectively, of the prey items in the pleustonic hydrozoan *Velella velella* (Purcell et al. 2012). Thus, the potential effects of gelatinous predators on fish are great.

Mesozooplankters are the main components of the diets of many fish and pelagic cnidarians and ctenophores, and dietary overlaps have been shown (Purcell & Grover 1990, Purcell & Sturdevant 2001, Brodeur et al. 2008). The small percentages of the copepod standing stocks consumed by *P. noctiluca* ephyrae may seem unimportant, but the combined predation of the suite of gelatinous predators (Fuentes et al. 2010, Sabatés et al. 2010, Canepa et al. 2014) removes food that otherwise could be consumed by fish. Studies of *in situ* predation by gelatinous species eating mesozooplankton are more numerous than studies on ichthyoplankton (e.g. Larson 1987b, 1988, Purcell 1997, 2009). Predation effects on mesozooplankton, primarily copepods, vary greatly depending on the abundance of the predators (summarized by Purcell & Arai 2001). Competition for prey requires that prey are limiting, and when abundant, pelagic cnidarians and ctenophores can reduce copepod populations (e.g. Purcell & Decker 2005).

We believe that existing evidence of gelatinous species as important predators of ichthyoplankton

and mesozooplankton covers only a small fraction of the extent of their predation. Past studies have considered only a few of the >1400 species of gelatinous predators that inhabit all depths of estuaries and oceans (Purcell et al. 2007). The studies were conducted only in near-surface waters, whereas concentrations of ichthyoplankton, mesozooplankton, and predators often occur at sub-surface hydrographic discontinuities (clines) (Graham et al. 2001, Purcell et al. 2014). The studies have also been limited spatially and temporally. Although *P. noctiluca* has been studied in only a few locations, primarily in Irish waters (Doyle et al. 2008, Bastian et al. 2011) and the Mediterranean Sea, this species is found in tropical to temperate oceans around the world (Kramp 1961). Studies suggest that blooms of *P. noctiluca* and other species have increased in frequency and duration in the Mediterranean Sea (Daly Yahia et al. 2010, Kogovšek et al. 2010, Licandro et al. 2010, Bernard et al. 2011). If cnidarian and ctenophore populations increase around the world, as evidence from some locations suggests (Brotz et al. 2012, Condon et al. 2013), there could be increasing predation on ichthyoplankton and mesozooplankton and increasing detrimental effects on fish populations.

Acknowledgements. We greatly appreciate the assistance of the crew of the RV 'García del Cid' and all the participants during the cruises. This study was supported by the project MAR-CTM2010-18874. V.L.F. was funded by a JAE-DOC contract of CSIC co-financed by the FSE (European Social Fund).

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Submitted: November 18, 2013; Accepted: March 17, 2014 *Proofs received from author(s): May 9, 2014*

[Publications]

- **Uxue Tilves, Jennifer E. Purcell, Verónica L. Fuentes, Anna Torrents, Maria Pascual, Vanesa Raya, Josep-Maria Gili, Ana Sabatés**. *Natural diet and predation impacts of Pelagia noctiluca on fish eggs and larvae in the NW Mediterranean. Journal of Plankton Research*, Volume 38, Issue 5, September/October 2016, Pages 1243–1254. https://doi.org/10.1093/plankt/fbw059

This article, at pages 163 to 174 of the thesis, is available at the editor's web

https://academic.oup.com/plankt/article/38/5/1243/2452771

- **Uxue Tilves, Verónica L. Fuentes, Giacomo Milisenda, Christopher C. Parrish, Salvatrice Vizzini, Ana Sabatés** *Trophic interactions of the jellyfish Pelagia noctiluca in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition.* Marine Ecology Progress Series, vol. 591: 101–116, 2018. https://doi.org/10.3354/meps12332

This article, at pages 175 to 204 of the thesis is available at the editor's web

https://www.int-res.com/abstracts/meps/v591/p101-116/

- **Uxue Tilves, Ana Sabatés, Mercedes Blázquez, Vanesa Raya, Verónica L. Fuentes.** *Associations between fish and jellyfish in the NW Mediterranean.* Marine Biology (2018) 165:127. https://doi.org/10.1007/s00227-018-3381-4

This article, at pages 163 to 174 of the thesis, is available at the editor's web
https://link.springer.com/article/10.1007%2Fs00227-018-3381-4