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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

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 &

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* (Scombri-

dae) 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 × $\log_{10}$L − 0.620 × $\log_{10}$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

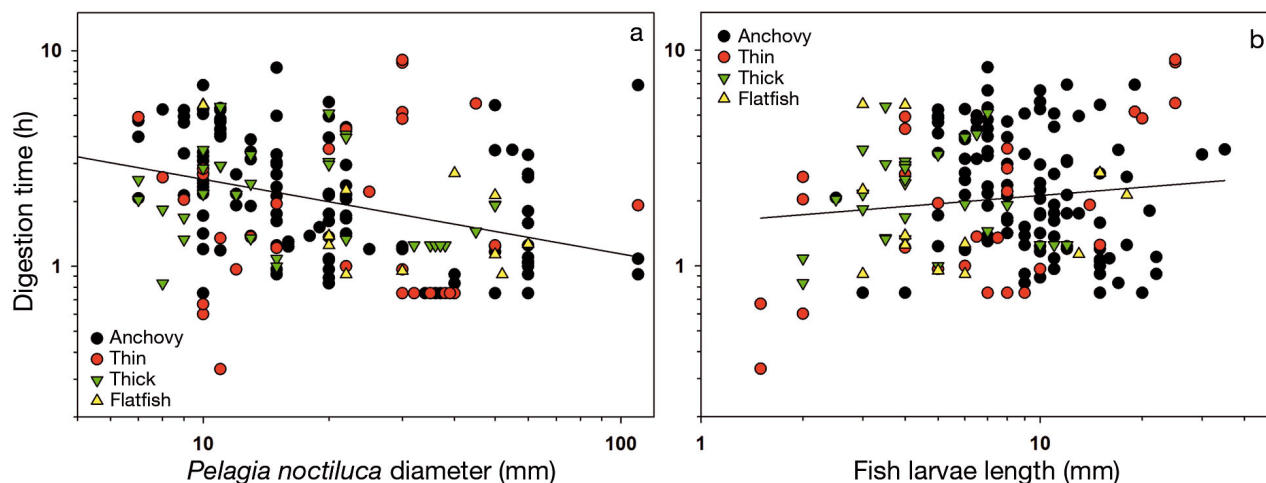| ——— Jellyfish ——— Diameter (D, mm)	n	T (°C)	Prey length (L, mm)	DT (h)	Error (%)	Regression statistics	RT (h)
Medusae 48.6 ± 20.6 (25–110)	63	22.7 ± 1.3 (20.2–25.5)	**Fish larvae** 14.1 ± 6.5 (5–30.0)	2.1 ± 2.2 (0.8–8.3)	13.3 ± 12.5 (0–50)	$R^2 = 0.425$ $F_{3,59} = 14.55$; p < 0.001 $\log_{10}$D $t = -0.79$; 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 × $\log_{10}$L	0.9 ± 0.8 (0.3–5.8)
Ephyrae 13.4 ± 5.2 (4–22)	107	23.4 ± 0.9 (20.7–24.4)	**Fish larvae** 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 × $\log_{10}$L − 0.379 × $\log_{10}$D	1.2 ± 0.2 (0.2–5.8)
Medusae 42.2 ± 11.4 (15 – 60)	30	22.2 ± 1.4 (19.6–23.7)	**Salps** 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 × T + 0.087 × L	1.8 ± 1.1 (0.2–5.0)
Ephyrae 10.4 ± 0.6 (10–11)	5	23.4 ± 1.3 (21.6–25.2)	**Salps** 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 11.8 ± 0.6 (7–22)	51	23.9 ± 0.7 (22.3–25.0)	**1 copepod** 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 17.0 ± 3.6 (13–20)	4	23	**2–4 copepods** 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 ——— | | T (°C) | Fish larvae | DT (h) | Error (%) | RT (h) |
Diameter (mm)	n		length (mm)			
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)	(0.2–5.8)
			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)
			Scombrid, sciaenid, 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)	(0.2–3.2)

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

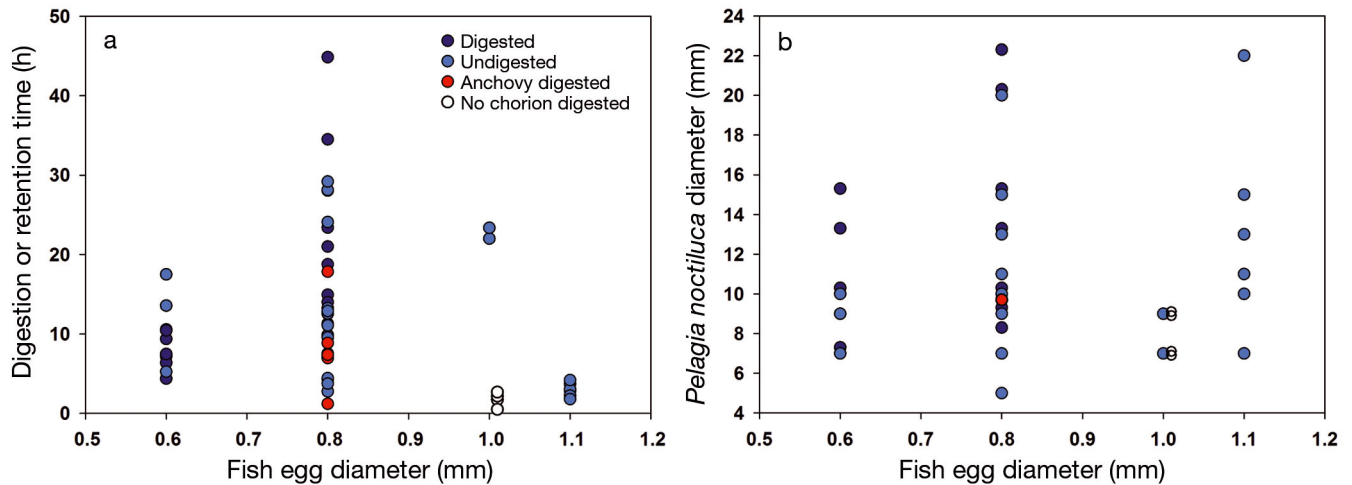| Fish egg diameter (mm)	Digested eggs					Undigested eggs		
	Ephyra (mm)	n	DT (h)	RT (h)	Error (%)	Ephyra (mm)	n	Retention (h)
0.6 [75%]	9.9 ± 3.1 (7–15)	9	8.2 ± 2.2 (4.3–10.6)	6.1 ± 2.1 (3.2–9.5)	15.8 ± 2.2 (13–20)	8.7 ± 1.5 (7–10)	3	12.1 ± 6.3 (5.2–17.5)
0.8 [45.2%]	12.1 ± 4.3 (8–22)	14	17.4 ± 12.0 (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 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 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)	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 20 sm 7–22 13	*A. mitchilli* eggs (1–2)	~1.0	24	DT 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
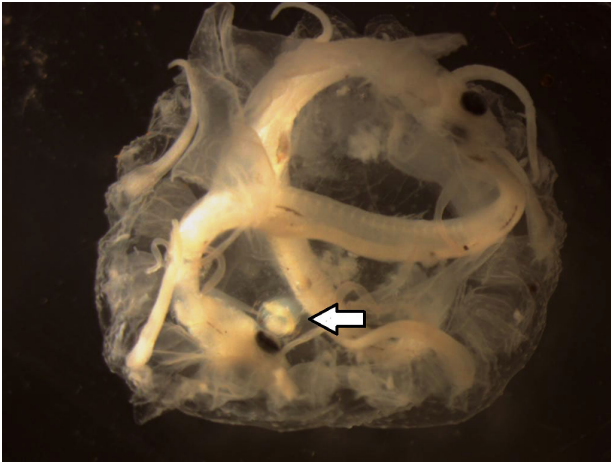
Fig. 3. *Pelagia noctiluca* ephyra collected from the surface at night and immediately preserved on 4 July 2011. The ephyra contained 2 anchovy larvae (~10 mm long) and 1 unidentified fish egg (0.9 mm diameter; indicated by arrow). Ephyra preserved diameter is 7 mm

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 tran-

sect 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
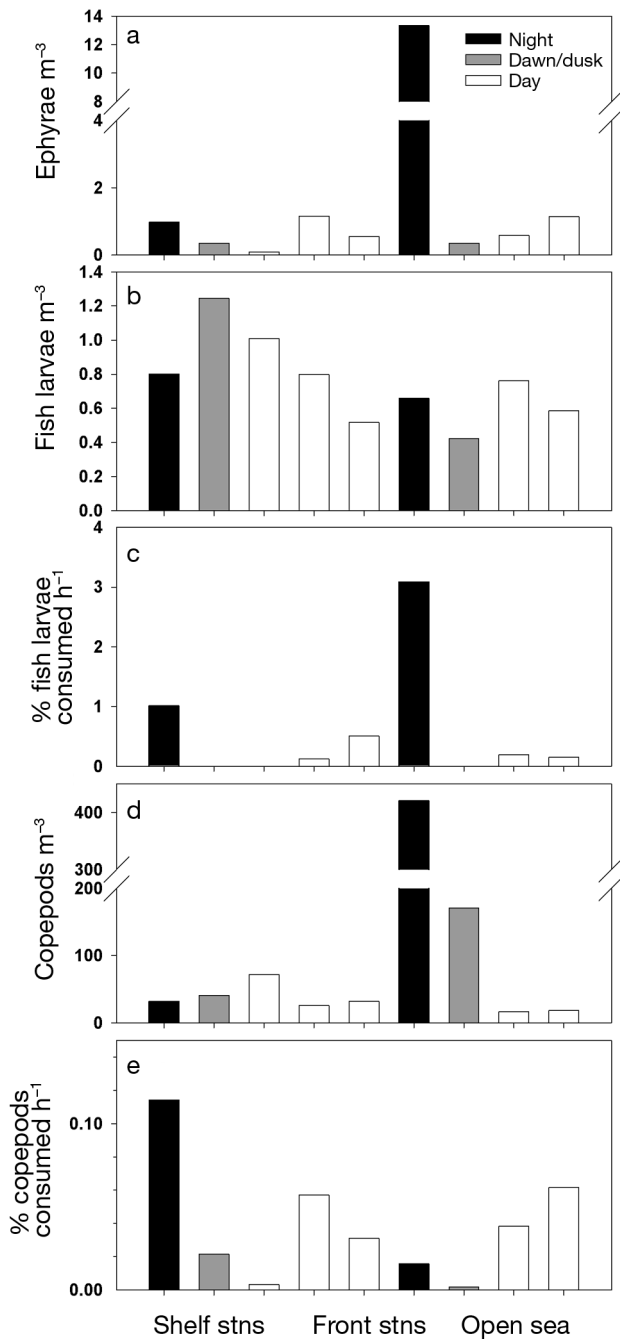
Fig. 4. Abundances and predation effects of *Pelagia nocti-luca* ephyrae on fish larvae and copepods according to sta-tion (stn) and time of day in the northwestern Mediterranean Sea during 18 to 23 June 1995. Three stations each were over the shelf, at a shelf-break front, or in the open sea along a 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

Table 6. Estimated potential predation effects (% prey con-sumed 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

the ephyrae only at night (22:00 h) on the Shelf, when we estimated that 1.2% h⁻¹ could have been con-sumed. 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).

Estimated potential predation effects by *P. noctiluca* ephyrae on copepods were much lower than on fish larvae (Fig. 4). Although copepods were very abun-dant 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 cope-pods at each station ranged from 0.30 to 0.42% d⁻¹; Table 6). The predation effects of ephyrae on cope-pods were much lower (≤0.42% d⁻¹) than on fish lar-vae (≤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 preda-tion effects on fish larvae by *P. noctiluca*. First, we believe that the net sampling damaged the ephyrae and reduced their apparent feeding. That was indi-cated 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 sur-face 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. noc-tiluca* was underestimated with these net samples.

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

densities on the Shelf (0–0.03 m⁻³), fish larval densi-ties 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

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 con-
sidered 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 con-
ducted only in near-surface waters, whereas concen-
trations 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 stud-
ied in only a few locations, primarily in Irish waters
(Doyle et al. 2008, Bastian et al. 2011) and the Medi-
terranean Sea, this species is found in tropical to tem-
perate oceans around the world (Kramp 1961). Stud-
ies 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 ichthyo-
plankton and mesozooplankton and increasing detri-
mental effects on fish populations.

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