Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea

UXUE TILVES1*, JENNIFER E. PURCELL2, MACARENA MARAMBIO1, ANTONIO CANEPA1, ALEJANDRO OLARIAGA1 AND VERÓNICA FUENTES1

1INSTITUT DE CIENCIES DEL MAR, CSIC, P. MARÍTIM DE LA BARCELONETA, 37-49 08003 BARCELONA, SPAIN AND 2SHANNON POINT MARINE CENTER, WESTERN WASHINGTON UNIVERSITY, 1900 SHANNON POINT ROAD, ANACORTES, WA 98221, USA

*CORRESPONDING AUTHOR: tilves@icm.csic.es

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The invasive ctenophore *Mnemiopsis leidyi*, which now may be established in the NW Mediterranean, is a voracious predator of zooplankton and ichthyoplankton. *Pelagia noctiluca*, an abundant scyphomedusa there, eats other gelatinous species. We measured predation, digestion and escape when different sizes of medusae fed on ctenophores. Clearance rates increased with predator size and ingestion rates increased with prey concentration. Digestion times were longer when medusae were smaller than the ctenophores. All large ctenophores escaped from the medusae, but small ctenophores were ingested completely. *Pelagia noctiluca* is potentially an important predator of *M. leidyi* that may help control populations of this ctenophore.

KEYWORDS: jellyfish; invasive; escape; functional response; feeding rates

The invasive ctenophore *Mnemiopsis leidyi* was reported for the first time along the entire Catalan coast (Spain), in the northwestern Mediterranean Sea in the summer of 2009 (Fuentes et al., 2009). Its reappearance in large numbers in subsequent years suggests its potential establishment (Marambio et al., unpublished data). This ctenophore species has invaded all European seas (reviewed in Costello et al., 2012) and it is known for
negative effects on the invaded ecosystems, including reduction and changed composition of the zooplankton, and collapse of fisheries (Shiganova, 1998; Shiganova and Bulgakova, 2000; Roohi et al., 2010; Riisgård et al., 2011). *Mnemiopsis leidyi* has had devastating effects especially where no native predators were present, such as in the Black and Caspian seas (Purcell et al., 2001).

Predators control the ctenophores to some degree in native environments (Purcell et al., 2001); in fact *M. leidyi* was controlled in the Black Sea (reviewed in Costello et al., 2012) when *Beroe ovata* was accidentally introduced. Moreover, Shiganova and Malej (Shiganova and Malej, 2009) suggested possible predatory control of *M. leidyi* by *Beroe* spp. in the northern Adriatic Sea. In this context, predators and their potential to control *M. leidyi* populations in the Mediterranean Sea are of particular interest. In addition to *Beroe* spp., some scyphomedusae consume *M. leidyi*, including *Chrysaora quinquecirrha* in the USA (Purcell and Cowan, 1995; Kreps et al., 1997) and *Cyanea capillata* in the North Sea (Hosia and Titelman, 2011).

The scyphozoan *Pelagia noctiluca* is a potential predator of ctenophores. This jellyfish is abundant in the northwestern Mediterranean (Sabatés et al., 2010) and is an opportunistic predator that consumes a wide variety of prey, including gelatinous species (Malej, 1989; Sabatés et al., 2010). It occurs widely in the open ocean and often is reported in high numbers in coastal areas (Doyle et al., 2008; Licandro et al., 2010). Our objective was to evaluate the predation potential of *P. noctiluca* on *M. leidyi*. We measured feeding and digestion rates of ephyrae, juvenile and adult medusae feeding on ctenophores in the laboratory and videotaped interactions between medusae and ctenophores to quantify the frequency of escape.

*Pelagia noctiluca* jellyfish were collected off the northeastern Spanish coast during September–December 2010 in plastic bags or buckets to minimize damage and reduce capture stress. Adult medusae released gametes in experimental aquaria at the Institut de Ciències del Mar (ICM-CSIC) in Barcelona, Spain, where ephyrae and juveniles were raised. Specimens of *Mnemiopsis leidyi* were gently collected in jars from the Ebro River Delta. Immediately after collection, specimens were transferred to 25-L plastic containers filled with ambient seawater and transported to the laboratory.

Specimens were kept 1 week before the experiments in 200-L flow-through tanks with natural filtered seawater (temperature: 20°C ± 0.5, salinity: 37.8). These conditions were maintained during the experiments. *Pelagia noctiluca* medusae were fed daily with frozen crustaceans and fresh jellyfish, either *Aurelia aurita* or *Rhizostoma pulmo*. *Mnemiopsis leidyi* individuals were fed *Artemia salina* nauplii. Medusae were kept without food for 24 h before the experiments.

To estimate the feeding rates of *P. noctiluca*, individual medusae of different sizes and stages were incubated with different concentrations of *M. leidyi* (Table I). Experiments with adult and juvenile medusae were conducted in 100-L flow-through tanks with a water flow of ~300 L h⁻¹. The ctenophore length (oral–aboral axis including the lobes) was measured before each experiment; the bell diameter of *P. noctiluca* was measured after each experiment to minimize stress to the animals. Medusae were allowed 1 h to acclimatize until the tentacles were completely extended before incubations; then the ctenophores were added to the experimental tanks. *Pelagia noctiluca* ephyrae and *M. leidyi* larvae were incubated together in 1.4-L bottles that were placed in a plankton wheel to keep the organisms in suspension. After incubation, the number of remaining ctenophores was recorded. Controls ensured that the ctenophores disappeared only due to the predation by the ephyrae. New animals were used in each incubation. The

### Table I: Experimental conditions for Pelagia noctiluca medusae feeding on Mnemiopsis leidyi ctenophores

<table>
<thead>
<tr>
<th>Experiment type</th>
<th>Medusa diameter (mm)</th>
<th>Ctenophore length (mm)</th>
<th>Prey container⁻¹</th>
<th>Replicates</th>
<th>Incubation time</th>
<th>Tank volume (L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>40–55</td>
<td>8–16</td>
<td>3,5,7,10,15</td>
<td>3,3,4,3,3</td>
<td>30 min</td>
<td>100</td>
</tr>
<tr>
<td>Feeding</td>
<td>20–25</td>
<td>8–12</td>
<td>7,10,15,20,30</td>
<td>3</td>
<td>30 min</td>
<td>100</td>
</tr>
<tr>
<td>Feeding</td>
<td>3.8–4.2</td>
<td>1–3</td>
<td>5,7,15</td>
<td>3</td>
<td>2 h</td>
<td>1.4</td>
</tr>
<tr>
<td>Digestion</td>
<td>32–35</td>
<td>30–36</td>
<td>1</td>
<td>3</td>
<td>Until complete</td>
<td>100</td>
</tr>
<tr>
<td>Digestion</td>
<td>32–35</td>
<td>40–49</td>
<td>1</td>
<td>3</td>
<td>Until complete</td>
<td>100</td>
</tr>
<tr>
<td>Digestion</td>
<td>40–47</td>
<td>30–36</td>
<td>1</td>
<td>3</td>
<td>Until complete</td>
<td>100</td>
</tr>
<tr>
<td>Digestion</td>
<td>40–47</td>
<td>40–49</td>
<td>1</td>
<td>3</td>
<td>Until complete</td>
<td>100</td>
</tr>
<tr>
<td>Digestion</td>
<td>50–56</td>
<td>30–36</td>
<td>1</td>
<td>3</td>
<td>Until complete</td>
<td>100</td>
</tr>
<tr>
<td>Digestion</td>
<td>50–56</td>
<td>40–49</td>
<td>1</td>
<td>3</td>
<td>Until complete</td>
<td>100</td>
</tr>
<tr>
<td>Behaviour</td>
<td>51–62</td>
<td>42–50</td>
<td>6</td>
<td>6</td>
<td>4 h</td>
<td>200</td>
</tr>
</tbody>
</table>

One predator was in each container "adults"; 3j"juveniles"; "ephyrae; "larvae, "lobate stage."
incubation times were short (30 min) to prevent severe reduction of the prey available. During all incubations, fewer than 40% of the prey were consumed.

Feeding was calculated as the clearance rate (CR) according to the equation of Purcell and Cowan (Purcell and Cowan, 1995) (CR: the volume of water filtered in L medusa$^{-1}$ h$^{-1}$):

$$CR = \frac{V}{(n \times t)} \times \ln \left( \frac{C_0}{C_t} \right),$$

where $V$ is the container volume (L), $n$ is the number of predators (medusae), $t$ is the incubation time (h), and $C_0$ and $C_t$ are the number of prey (ctenophores) at the beginning and at the end of the incubation, respectively.

The ingestion rate (IR, defined as: number of prey eaten medusa$^{-1}$ h$^{-1}$) was calculated according to the equation of MOller and Riisgård (MOller and Riisgård, 2007):

$$IR = CR \times C_m,$$

where $C_m$ is the geometric mean of the prey concentration during the incubation and was calculated from the equation

$$C_m = \exp \left[ \frac{\ln(C_0 + C_1)}{2} \right].$$

Digestion times (DTs) of 18 $P$. noctiluca of different sizes feeding on $M$. leidyi were measured (Table I). Each measurement began when one ctenophore was put into the oral arms of one $P$. noctiluca. Predator and prey conditions were visually checked every 15 min and DT was defined as when no prey tissue could be seen inside the medusa.

Interactions between $P$. noctiluca and $M$. leidyi were observed by videotaping (Table I). Encounters between medusae and ctenophores were recorded with a Prosilica GE 4900C (Allied Vision Technologies) CCD high-resolution camera at a frequency of one picture every 10 s with the focal distance held constant. “Encounters” were defined as when a ctenophore touched the medusa tentacles or oral arms. The encounters were grouped as “short encounters” (<20 s) and “long encounters” (>20 s), even if the prey later escaped.

For analyses of the CR and IR of $P$. noctiluca feeding on $M$. leidyi, the data were processed according to functional response (FR) models. Data were fitted to different models based on the best likelihood (highest $R^2$ value), according to Holling (Holling, 1959; Gentelman et al., 2003).

Two analyses of DT data were performed: (i) to test the effects of predator and prey sizes on the DT separately, data were rank transformed to pass normality and homoscedasticity assumptions and linear regressions then fitted; (ii) untransformed data were analysed in three groups to test if the relative sizes of the predator and the prey affected the DT. The groups were: predator $>$ prey (medusa bell diameter was at least 5 mm greater than ctenophore length); predator $<$ prey (size difference was 2–3 mm); and predator $<$ prey (medusa bell diameter was at least 10 mm less than ctenophore length). No homoscedasticity of the data required the use of Kruskal–Wallis and Wilcoxon rank-sum tests.

All analyses were performed using the R 2.15 software (R Development Core Team, 2012). Data are given as mean ± standard deviation.

CR and IR of $P$. noctiluca were significantly related to prey concentration ($F_{1,34} = 34.6; P < 0.0001$) (Fig. 1A–F). Individual CR of all sizes of $P$. noctiluca ranged from 0.4 ± 0.1 to 103.2 ± 32.6 L medusa$^{-1}$ h$^{-1}$. We analysed the CR and IR separately for $P$. noctiluca of different sizes.

The slope of the regression between CR of adults and prey concentration was not significantly different from 0 (Fig. 1A). IR increased with increasing ctenophore concentration (1.6–11.5 prey medusa$^{-1}$ h$^{-1}$, Fig. 1D). Adult $P$. noctiluca ate more when more prey were available, and no saturation point was observed (functional response Type I; Holling, 1959), as observed for $C$. capillata medusae feeding on $M$. leidyi (Hosia and Titelman, 2011). Data were fitted by the use of linear models.

The CR of juveniles ranged between 38 and 80 L medusa$^{-1}$ h$^{-1}$. The CR increased over the lower prey concentrations, but decreased at the highest two prey densities (Fig. 1B). The IR increased with ctenophore concentration and ranged from 3.6 to 10.1 prey medusa$^{-1}$ h$^{-1}$. Juvenile $P$. noctiluca ate more when more prey were available. No clear saturation point was detected with the concentrations of prey used, but the best fit was the negative exponential model corresponding to a functional response Type II (Fig. 1B CR and E IR).

Ephyrae showed a Type II functional response and the best fit was the Michaelis–Menten model (Fig. 1C and F). The CR decreased with increasing prey concentration from 0.5 to 0.3 L medusa$^{-1}$ h$^{-1}$ and the IR increased from 1.8 to 3.4 prey medusa$^{-1}$ h$^{-1}$ (Fig. 1C–F). The CR of $P$. noctiluca ephyrae were higher than those of $C$. quinquecirrha ephyrae <4 mm (0.03 L h$^{-1}$) (Olesen et al., 1996); in our $P$. noctiluca experiments, the containers were larger, the ephyrae generally larger and the
ctenophore densities lower, all of which could have contributed to the higher CR for that species.

Medusa size was an important factor affecting the individual CRs ($F_{1,41} = 94.53; P < 0.0001$) with ephyrae of 4.1 mm diameter clearing $0.4 \pm 0.1 \text{ L h}^{-1}$ juveniles of 20–25 mm diameter clearing $62.1 \pm 19.9 \text{ L h}^{-1}$ and medusae of 40–45 mm diameter clearing $103.2 \pm 32.6 \text{ L h}^{-1}$. The CR for *P. noctiluca* adults were higher
than those for other scyphomedusan species eating *M. leidyi* (Table II), even though the other predators (*C. capillata* 75 mm; *C. quinquicauda* 81 mm) were larger than *P. noctiluca* medusae (45 mm) and their containers were larger than in our study.

The relatively small container size in our experiments may have affected the feeding rates, which may be consistently underestimated in experiments conducted in containers (Purcell, 2009). Purcell and Cowan (Purcell and Cowan, 1995) obtained a lower CR in 1000-L than in 3200-L mesocosms (Table I). Our experiments were conducted in flow-through tanks; however, the possible efficacy of water circulation in reducing container size effects on feeding is untested.

Ctenophore size was significantly correlated with the DT ($R^2 = 0.24$, $t = 2.246$, $P$-value = 0.039). Regardless of the predator’s size, DT increased with larger prey (Fig. 2A). In contrast, medusa size did not significantly affect the DT, although an inverse trend was observed ($R^2 = 0.071$, $t = -1.105$, $P = 0.29$). Although the DT were not significantly different among all relative-size groups of predators and prey ($P = 0.762$), the DTs of the groups “predator > prey” and “predator < prey” were significantly different ($P = 0.027$), with the DT being longer when the predator is smaller than the prey (Fig. 2B).

A total of 838 encounters between large ctenophores (45.6 ± 4.6 mm) and *P. noctiluca*, resulting in 375 “short encounters” and 463 “long encounters” were videotaped. The ctenophores escaped in 100% of the encounters, which is comparable with results for *C. quinquicauda* (97.2%; Kreps *et al.*, 1997) and for *C. capillata* (90.8%; Hosia and Titelman, 2011). Subsequent “short encounters” also resulted in escape. When a ctenophore adhered to an oral arm or tentacle, it displayed escape behaviour, consisting of rotation along the oral-aboral axis and change in the swimming direction; pieces of tissue left attached to the medusa’s oral arms or tentacles (Supplementary data, Fig. S1) subsequently were ingested by the medusa, as seen in previous studies (Purcell and Cowan, 1995; Kreps *et al.*, 1997; Hosia and Titelman, 2011). Thus, the ctenophores were damaged and partly consumed. After losing several parts of tissue, the ability to change their swimming direction was reduced. Damage was reflected by an increased frequency of “long encounters” during the incubations; “long encounters” constituted 43.1% of the encounters, during the first hour, but 70.6% in the last hour. *M. leidyi* has a remarkable capacity to regenerate lost tissue and damaged ctenophores healed quickly (Coonfield, 1936; Purcell and Cowan, 1995). These abilities enhance the survival of *M. leidyi*. Even though repeated encounters could affect its health, the ctenophore was never ingested, showing the high ability of large ctenophores to escape.

Behaviour of *P. noctiluca* and DTs also influenced the CR and the IR. Observations during the feeding experiments, in which the ctenophores were smaller than during videotaping, showed that small ctenophores (19 ± 8 mm) did not escape from the medusae. Small ctenophores were transported from the tentacles or oral arms to the manubrium, where they were enveloped and could not escape; pieces of tissue attached to the predator’s oral arms also were ingested (Supplementary data, Fig. S2A–C). Parts of the ctenophores were visible inside the medusa’s umbrella, with the ciliated comb rows visible longest (Supplementary data, Fig. S2C). When the DT was short, the medusae could feed more without becoming saturated in high prey densities. In each capture and ingestion event, the ctenophore was considerably smaller than the medusa, as in other studies (Purcell and Cowan, 1995; Kreps *et al.*, 1997; Hosia and Titelman, 2011).

Many species of gelatinous zooplankton are eaten by other gelatinous species (Purcell, 1991). Although several studies have been conducted to study these interactions, few were with *P. noctiluca* as the predator (Malej, 1989) and few with *M. leidyi* as the prey (Purcell and

### Table II: Experimentally measured clearance rates of scyphomedusae (*Chrysaora quinquecirrha, Chrysaora capillata, Pelagia noctiluca*) feeding on Mnemiopsis leidyi

<table>
<thead>
<tr>
<th>Predator and diameter (mm)</th>
<th>Prey length (mm)</th>
<th>Prey L$^{-1}$</th>
<th>Clearance (L ind$^{-1}$ h$^{-1}$)</th>
<th>Container volume (L)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. noctiluca</em> Adult 40–55</td>
<td>8–16</td>
<td>0.0053–0.0421</td>
<td>40 ± 11</td>
<td>380</td>
<td>This study</td>
</tr>
<tr>
<td><em>P. noctiluca</em> Juvenile 20–25</td>
<td>8–12</td>
<td>0.074 ± 0.0025</td>
<td>29 ± 27</td>
<td>1000</td>
<td>(Purcell and Cowan, 1995)</td>
</tr>
<tr>
<td><em>P. noctiluca</em> Ephyra 3.8–4.2</td>
<td>1–3</td>
<td>1.5 ± 4; 1.6 ± 0.4</td>
<td>10–40</td>
<td>0.03</td>
<td>(Purcell and Cowan, 1995)</td>
</tr>
<tr>
<td><em>P. noctiluca</em> Ephyra 3.8–4.2</td>
<td>1–3</td>
<td>5–15</td>
<td>0.4</td>
<td>1.4</td>
<td>This study</td>
</tr>
<tr>
<td><em>C. capillata</em> Adult 75 ± 13</td>
<td>28.7 ± 55</td>
<td>0.0003 ± 0.0032</td>
<td>69.5 ± 55</td>
<td>3200</td>
<td>(Purcell and Cowan, 1995)</td>
</tr>
<tr>
<td><em>C. quinquicauda</em> Adult 81 ± 15</td>
<td>14.1 ± 58 mL</td>
<td>0.008 ± 0.0032</td>
<td>80 ± 55</td>
<td>3200</td>
<td>(Purcell and Cowan, 1995)</td>
</tr>
<tr>
<td><em>C. quinquicauda</em> Adult 75 ± 21</td>
<td>10.5 ± 44 mL</td>
<td>0.0074 ± 0.0025</td>
<td>29 ± 27</td>
<td>1000</td>
<td>(Purcell and Cowan, 1995)</td>
</tr>
<tr>
<td><em>C. quinquicauda</em> Ephyra &lt; 4</td>
<td>1.5 ± 4; 1.6 ± 0.4</td>
<td>10–40</td>
<td>0.03</td>
<td>0.5–1</td>
<td>(Olesen <em>et al.</em>, 1996)</td>
</tr>
<tr>
<td><em>M. leidyi</em></td>
<td>97.2% (Kreps <em>et al.</em>, 1997)</td>
<td><em>C. capillata</em> (90.8%; Hosia and Titelman, 2011)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Cowan, 1995; Olesen et al., 1996; Kreps et al., 1997; Hosia and Titelman, 2011). Our study is the first on Pelagia noctiluca feeding on Mnemiopsis leidyi. Different feeding and digestion rates and type of functional response were obtained depending on the developmental stage of P. noctiluca.

We conclude that P. noctiluca is a potential predator of M. leidyi and may be important in reducing the impact of the ctenophore when they co-occur in time and space. Both species form blooms in the NW Mediterranean (Fuentes et al., 2010; Bernard et al., 2011). Moreover, the predation effect would be stronger when this predator is bigger than the prey. M. leidyi and P. noctiluca adults have been occasionally reported together on the Mediterranean Spanish coast, in Denia (Alicante) (Fuentes et al., 2010; M. Acevedo, ICM, Barcelona, personal communication) and in the Mar Menor lagoon (V. L. Fuentes, ICM, Barcelona, personal communication). More studies on the distribution of these species in the NW Mediterranean are needed to understand the effect of P. noctiluca on M. leidyi populations.

**SUPPLEMENTARY DATA**

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

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