

Culture and growth of the jellyfish Pelagia noctiluca in the laboratory

Martin K. S. Lilley, Martina Ferraris, Amanda Elineau, Léo Berline, Perrine Cuvilliers, Laurent Gilletta, Alain Thiéry, Gabriel Gorsky, Fabien Lombard

▶ **To cite this version:**

Martin K. S. Lilley, Martina Ferraris, Amanda Elineau, Léo Berline, Perrine Cuvilliers, et al.. Culture and growth of the jellyfish Pelagia noctiluca in the laboratory. Marine Ecology Progress Series, 2014, 510, pp.265-273. 10.3354/meps10854 . hal-03502778

HAL Id: hal-03502778
https://hal.science/hal-03502778

Submitted on 26 Dec 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Vol. 510: 265–273, 2014
doi: 10.3354/meps10854

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 9

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

FREE ACCESS

Culture and growth of the jellyfish *Pelagia noctiluca* in the laboratory

Martin K. S. Lilley[1,2,3], Martina Ferraris[3,4], Amanda Elineau[3,4], Léo Berline[3,4,5], Perrine Cuvilliers[3,4], Laurent Gilletta[6], Alain Thiéry[1], Gabriel Gorsky[3,4], Fabien Lombard[3,4,*]

[1]IMBE UMR CNRS 7263, Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix-Marseille Université, Avenue Louis Philibert, BP 67, 13545 Aix en Provence Cedex 04, France

[2]Institut Méditerranéen d'Océanologie (MIO), Aix-Marseille Université, UMR 7294, Campus de Luminy, 13288 Marseille Cedex 9, France

[3]Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire océanologique, 06230 Villefranche sur mer, France

[4]CNRS, UMR 7093, LOV, Observatoire océanologique, 06230 Villefranche sur mer, France

[5]Université du Sud Toulon-Var, Aix-Marseille Université, CNRS/INSU, IRD, Institut Mediterraneen d'Oceanologie (MIO), UM 110, 83957 La Garde Cedex, France

[6]CNRS, Sorbonne Universités, UPMC Univ Paris 06, Laboratoire de Biologie du Développement de Villefranche sur mer, Observatoire Océanographique, 06230 Villefranche sur mer, France

ABSTRACT: Four cohorts of the scyphozoan jellyfish *Pelagia noctiluca* were grown in the laboratory. For the first time, *P. noctiluca* was grown from eggs through to reproductive adults. The maximum life span in the laboratory was 17 mo. *Pelagia noctiluca* were first observed to release gametes at an umbrella diameter of 2.4 cm. Laboratory growth under steady feeding conditions showed initial growth followed by stagnation until dietary conditions were altered. A mismatch between the availability of optimal food and the presence of developmental stages may significantly increase the mortality rates of the young stages. Non-motile prey improved survival of ephyrae stages compared with zooplankton, but good survival and ephyrae growth were only obtained with a high-energy sea urchin egg diet. Maximal growth rates were up to 30% d^{-1} for young ephyrae and 1.5–4% d^{-1} for adults. Maximal growth rates were comparable between laboratory and *in situ* growth observations in the Ligurian Sea during 1969 and 2013. Combining observations would suggest that 230 d of continuous growth are required to reach the largest mean size observed in the wild (June 2013, mean ± SD = 15.6 ± 2.8 cm, range = 12–21 cm). We suggest that 90–120 d of continuous growth from planula larvae would yield reproductive individuals under ideal growing conditions. We discuss the daily prey abundances required by each individual to sustain basal metabolism and the observed growth rates.

KEY WORDS: Mauve stinger · Ligurian Sea · Mediterranean · Bloom · Life cycle · Mortality · Ephyra · Predation

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Found at frequently high abundances, the mauve stinger *Pelagia noctiluca* is a holoplanktonic scyphozoan jellyfish with a wide distribution. Populations occur in both the North and South Atlantic (Miller et al. 2012), as well as in all the major oceans (Mayer 1910). The species has a negative impact on tourism (Bernard et al. 2011) because of its painful stings (Maretic et al. 1991, Mariottini et al. 2008), on aquaculture by overwhelming fish farms and killing fish (Doyle et al. 2008, Delannoy et al. 2011), and potentially on the success of fish stocks such as tuna (Gordoa et al. 2013). In the Mediterranean Sea, *P. noc-*

*Corresponding author: lombard@obs-vlfr.fr

© Inter-Research 2014 · www.int-res.com

tiluca has been a recurrent problem for centuries (Goy et al. 1989). It has historically been observed to be present or absent for several consecutive years, with a periodicity of 10–12 yr (Goy et al. 1989, Kogovšek et al. 2010) attributed to climatic forcing. However, since 1994 this species has been present almost continuously in the Ligurian Sea, NW Mediterranean (Bernard et al. 2011, L. Berline & F. Lombard pers. obs.), suggesting a prolonged period of more favourable environmental conditions. *Pelagia noctiluca* is a holoplanktonic species, developing directly from planula larvae (Russell 1970, Rottini Sandrini & Avian 1983), and therefore cannot rely on polyps to survive through unfavourable conditions.

Pelagia noctiluca has been repeatedly studied because of its high abundances and impact on the human environment. Seasonal and spatial abundance estimates have been made (e.g. Bastian et al. 2011, Ferraris et al. 2012, Rosa et al. 2013), including localised predictions of blooms (Berline et al. 2013). The developmental stages have been well studied (Rottini Sandrini & Avian 1983, Avian 1986), along with gut contents and isotopic analyses (e.g. Giorgi et al. 1991, Malej et al. 1993, Sabatés et al. 2010), but the quantitative needs to sustain growth are still unknown.

Estimates of basal metabolic costs confirm that *P. noctiluca* is able to withstand periods of starvation (Larson 1987). Importantly though, the duration of the life cycle, the size at maturation and whether there are resting stages or adaptations to aid survival as a holoplanktonic species are all unknown. Likewise, the rate of growth has only been observed in short-term studies (Larson 1987, Malej & Malej 1992), while the energy requirements to sustain growth have not been quantified.

The objective of this study was to obtain reproductively viable *P. noctiluca* in the laboratory in order to estimate the duration of the life cycle and to compare growth rates between laboratory and *in situ* populations. We hypothesised that growth rates would allow a life cycle of approximately 1 yr, to allow a direct connection between successive generations.

MATERIALS AND METHODS

Jellyfish collection

Adult *Pelagia noctiluca* were collected individually from the sea surface using a hand net during night surveys in the Ligurian Sea (for details, see Ferraris et al. 2012) or by kayak in the bay of Villefranche-sur-Mer, France (43.696° N, 7.307° E). Fed *P. noctiluca* spawned daily, with fertilised eggs used to initiate new growth experiments. Gametes and ephyrae were transferred between culture containers using a 0.5 cm wide glass pipette. On one occasion, wild ephyrae were collected by plankton net (Regent net, 1 m diameter, 680 µm mesh size).

During 2013, all collected individuals were measured (bell diameter including lappets), sexed and weighed (wet weight, precision 0.1 g) on return to the laboratory. Mature male individuals have purple gonads with parallel transverse lines of tissue; female gonads are browner in colour, in a bunched, cauliflower-like form, and eggs are usually visible.

Experimental trials

Four cohorts of *P. noctiluca* were cultured in the laboratory and measured repeatedly to obtain growth rates for this species. One cohort was obtained from wild-caught young ephyrae of 5 mm in diameter, while the remaining larvae were obtained by mixing the gametes of fertile wild adult *P. noctiluca* and culturing the resulting planula larvae. All experiments were performed at 18°C using 1 µm filtered seawater in 5–15 l containers, depending on the organism size. Younger individuals required maintenance in suspension using motorised PVC paddles rotating at 6 rpm (Table 1). Individuals were fed *ad libitum* and as cohorts grew larger, larger prey items were offered, although selective ingestion and digestion were subject to individual variation. The prey offered was changed whenever growth within the experiment stagnated (Table 1). Non-motile prey items were offered initially in Runs 3 and 4 to improve survivorship.

Food organisms mostly originated from daily zooplankton samples collected every morning by oblique (50–0 m) net tows in the bay of Villefranche-sur-Mer, using nets with 50, 200 or 680 µm mesh. For organisms caught with the smallest mesh size (50 µm), only swimming zooplankton were used. Other natural prey sources offered to ephyrae were fragments of jellyfish bells (frozen *Cotylorhiza tuberculata*; fresh *Aurelia aurita* and *Leucothea multicornis*) and fresh *Paracentrotus lividus* sea urchin eggs (~90 µm in diameter). Artificial diets offered included freshly hatched brine shrimp nauplii (*Artemia* sp., some enriched with S. presso from Selco), frozen mysid shrimp, and a larval fish diet made up of fish and yeast extracts (50–100 or 100–200 µm Golden Pearls, Brine Shrimp Direct; see Table 1 for details).

Bell diameter was measured between opposite rhopalia (RD; cm), with the aboral surface upwards, from

Table 1. Experimental details of Runs 1–4 in the laboratory and wild populations sampled in 1968–1969 (Franqueville 1971) and 2013. Zooplankton offered to laboratory-grown juvenile *Pelagia noctiluca* was collected daily from the field with a vertically towed Regent net (1 m diameter, 680 µm), with 2 exceptions ([a],[b]). All animals were fed daily, but prey composition and assimilation efficiency were not recorded. Water was changed 2–3 times per week and individuals were measured every 1–2 wk. –: no data recorded

Run	Ephyrae source	Initial numbers	Start date (dd-mm-yy)	Duration (d)	Tank volume (l)	Tank stirring	Food offered
Laboratory growth							
1	Eggs (lab)	~1000	26-05-10	45	15	Yes	Mixed zooplankton (35–50 µm)[a]
		4	10-07-10	117	5	No	Mixed zooplankton (>200 µm)[b]
		4	04-11-10	64	5	No	Mixed zooplankton
		4	07-01-11	129	5	No	Mixed zooplankton + *Cotylorhiza tuberculata*
		4	16-05-11	148	5	No	Mixed zooplankton + enriched *Artemia* sp.
2	Ephyrae (field)	13	01-11-11	119	15	Yes	*Artemia* sp., *Aurelia aurita*, frozen mysid shrimp
3	Eggs (lab)	>1000	03-09-12	184	15	Yes	Golden Pearls
4	Eggs (lab)	>1000	29-03-13	46	15	Yes	*Paracentrotus lividus* eggs ~90 µm
		–	14-05-13	38	15	Yes	*Artemia* sp.
		–	21-06-13	26	15	Yes	Mixed zooplankton
		33	17-07-13	97	15	No	Mixed zooplankton
		24	22-10-13	10	15	No	Mixed zooplankton + *Leucothea multicornis*
		24	01-11-13	16	15	No	Mixed zooplankton
Field population (adults)							
–	Ligurian Sea (1968–1969)	–	01-12-68	274	–	–	–
–	Ligurian Sea (2013)	–	01-02-13	180	–	–	–

[a]A 0.5 m diameter net with 50 µm mesh was used; [b]a WP2 net with 200 µm mesh was used

calibrated microscope images (≤3 cm RD). Larger jellyfish were flattened in a Petri dish with a small amount of water, and bell diameter was measured with a ruler to the nearest millimetre. To transform our measured bell diameters between opposite rhopalia to the more commonly used bell diameter across the lappets (LD; cm), we used the following equation (M. Ferraris & M. K. S. Lilley unpubl. data):

$$LD = 1.29 \pm 1.0043\ RD^{0.93 \pm 0.0025} \quad (1)$$

where the numbers represent parameter estimates (±SE) (n = 200 individuals, size range 0.11–11.6 cm RD, $r^2 = 0.998$; data not shown).

Growth rate estimates

Growth rates were calculated from carbon weight (CW) using an equation of the relationship between CW and LD for adult *P. noctiluca* (M. Ferraris & M. K. S. Lilley unpubl. data):

$$CW = 0.24 \pm 0.098\ LD^{3.11 \pm 0.202} \quad (2)$$

where CW (mg) and LD (cm) were measured over a size range of 4–10 cm (data not shown) and numbers are parameter estimates (±SE). This equation overestimates carbon weights of the smallest individuals by 20–50% compared with Morand et al. (1987). However, using the equation of Morand et al. would overestimate adult carbon weights by 60%; therefore, the equation with the least error was chosen rather than switching equations at a specific size.

Instantaneous growth rates (µ; d^{-1}) were calculated between 2 observations using the change in carbon weight over consecutive time periods (t_1, t_2):

$$\mu = \ln(CW_2/CW_1)/(t_2 - t_1) \quad (3)$$

RESULTS

Varying rates of growth were obtained both between and within the 4 cohorts of young *Pelagia noctiluca*. Growth typically increased rapidly for a period before stagnating and, in many cases, shrinking slowly. Only once the prey offered were changed did medusa growth restart (Fig. 1A,D). Changes in carbon weight were predominantly positive, with greater instantaneous growth rates in the early stages of the life cycle (e.g. the smallest individuals; Fig. 2). Considering successful growth periods only, growth rates were 10–30% d^{-1} for ephyrae below

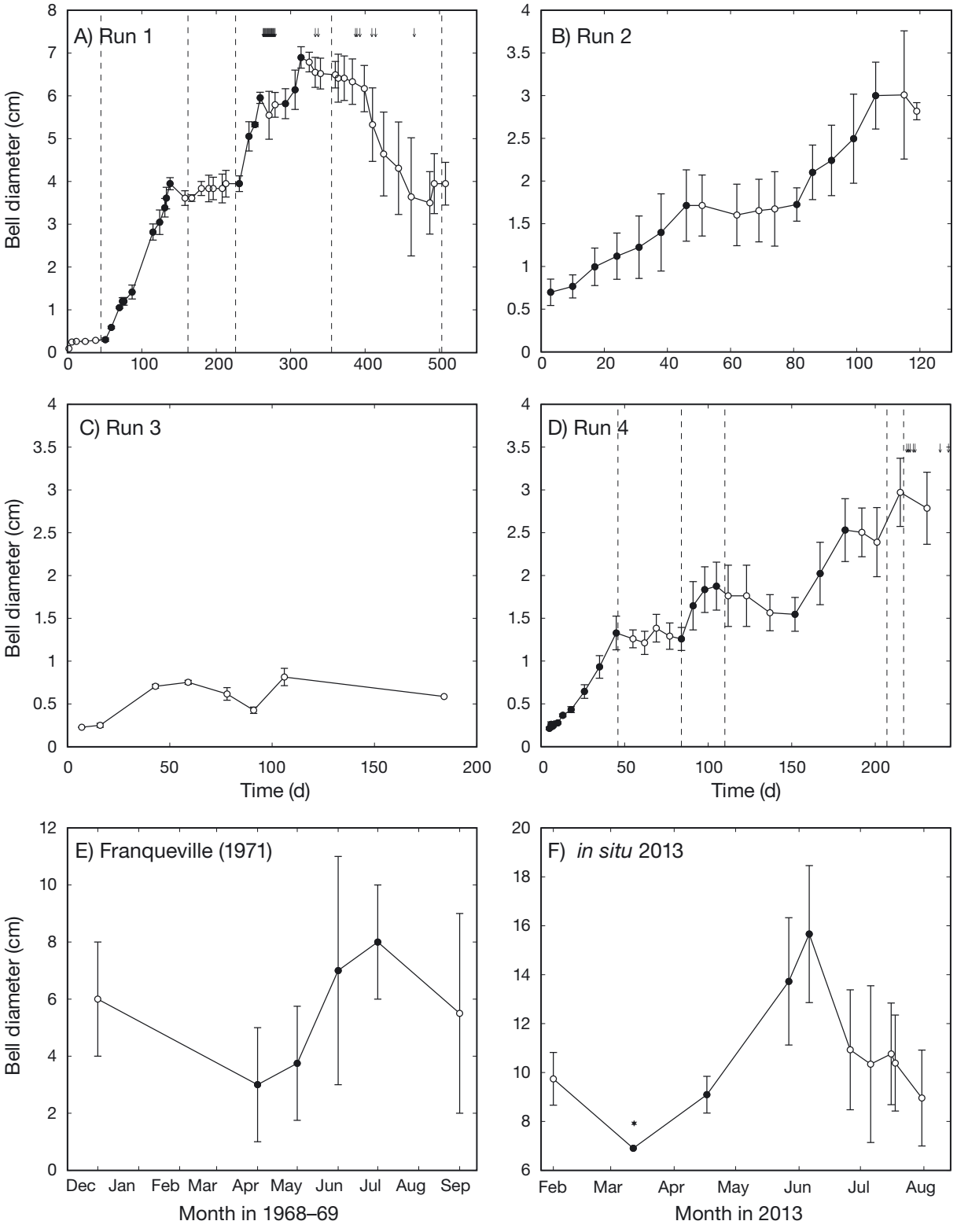


Fig. 1. (A–D) Growth observations (mean ± SD bell diameter over the lappets) of *Pelagia noctiluca* from the laboratory (Runs 1–4, respectively) and (E,F) *in situ* Ligurian Sea observations of population growth during (E) 1968–1969 (Franqueville 1971) and (F) 2013; (*) n = 1. Arrows represent observed spawning events (Run 1: Days 259–275, 329, 333, 383, 385, 389, 405, 410, 462; Run 4: Days 218–219, 221-222, 237, 242); dashed vertical lines show changes in feeding detailed in Table 1. Filled symbols are sequences of positive growth used in Fig. 3. Note different scales of *y*-axes

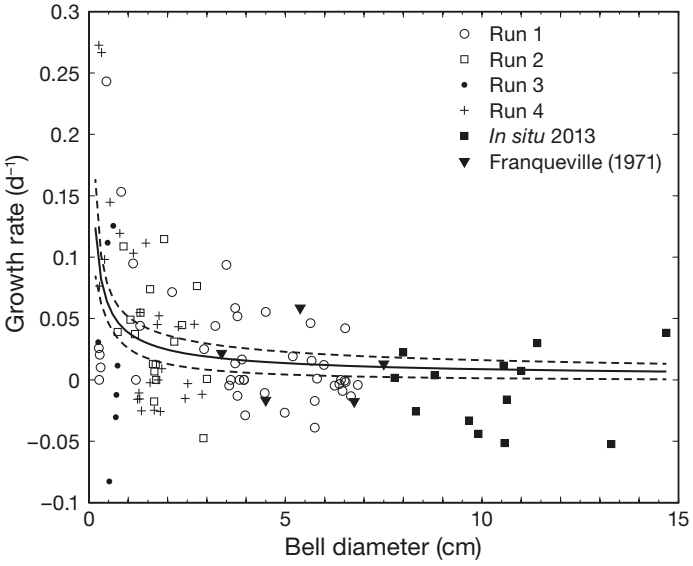


Fig. 2. Instantaneous growth rates (positive and negative) of *Pelagia noctiluca* from planula larvae to reproductive adults. This decrease in growth rate (μ; d^{-1}) with bell diameter (RD; cm) can be described using a power relationship (±SE) such that $\mu = 0.039 \pm 0.0065\ RD^{-0.65 \pm 0.13}$ ($r^2 = 0.25$, $F_{1,112} = 36.90$, $p < 0.0001$), solid line. Dashed lines represent 95% confidence limits

0.5 cm diameter, while adults (>5 cm) grew at 1.5–6% d^{-1}. Negative growth (shrinking) rarely exceeded 5% d^{-1}, with a slight trend for greater reductions by the biggest individuals. This decrease in growth rate with bell diameter was equally consistent between laboratory and *in situ* observations.

Development of oral arms and tentacles was observed at a size of approximately 1 cm in both Runs 1 and 4. These 2 cohorts also grew sufficiently for some individuals to become reproductively active adults, 7 to 8 mo after metamorphosing from eggs (Day 231, Run 1; Day 207, Run 4). Both sexes were observed to develop, but individuals in Run 1 grew to twice the diameter of those in Run 4 before they became reproductively active. Eggs were subsequently spawned on several occasions (denoted by arrows in Fig. 1) starting from Day 259 (4 Feb 2011) in Run 1 and Day 218 (2 Nov 2013) in Run 4. In both cases, eggs were viable and developed into planula larvae after the addition of adult male spawn. The number of eggs produced by each female was variable, reducing from 345 to 680 per spawn initially to 35 to 100 in later spawns during Run 1.

High mortality events affected several of the experimental runs, with the smallest ephyrae struggling to develop, particularly in Runs 1 and 3. Although survivorship was much better in Run 3 using a commercial particulate fish food, growth was minimal and stagnated. The best initial rate of growth and survivorship was obtained with a fresh, high-energy, non-motile prey (sea urchin eggs) in Run 4, with growth only stagnating when eggs became unavailable at the end of the sea urchin reproductive season. Throughout the experiments, the supplementation of gelatinous material (both frozen and fresh) to the prey offered was synchronous with enhanced growth and, in some cases, the development of gonads.

In situ observations

Regular field sampling of *P. noctiluca* during 2013 observed a growing population from mid-March (6.9 cm LD, n = 1) to the beginning of June (mean = 15.6 cm, range = 12–21 cm, n = 19; Fig. 1F), assuming the presence of a single population in the Ligurian Sea. Estimated growth was approximately 3% d^{-1}. During summer (June–August), the mean size of the population decreased sharply to approximately 9–10 cm diameter with the arrival of a new generation and shrinking or death of the largest individuals. Franqueville (1971) observed another *in situ* growth event in the same region (western Ligurian Sea) in 1969 (Fig. 1E) using an Isaac-Kidd midwater trawl for sampling. While sizes were generally smaller in 1969 than in 2013, the timing of growth was similar (April to July), with a decrease in size from July onwards. Mean size grew from 3 to 8 cm between April and July, thereby growing at approximately 3.4% d^{-1} (inverted triangles, Fig. 2).

DISCUSSION

Culturing *Pelagia noctiluca*

In the present study, *Pelagia noctiluca* was cultured for the first time for considerable periods in the laboratory and reproductive adults were successfully obtained (Runs 1 and 4). Previous studies observed mature adults in the wild at 3–6 cm bell diameter (Franqueville 1971, Rottini Sandrini & Avian 1991), which is in accordance with our laboratory results (2.5–5 cm bell diameter). Malej & Malej (1992) predicted maturity at 150 d of growth, which is in advance of our observed time scales of 218–260 d. Maturity and egg release were observed in both Runs 1 and 4 immediately after the introduction of abundant gelatinous prey to the diet. In addition, *P. noctiluca* has also been observed to consume the ctenophore *Mnemiopsis leidyi* when it was offered in

laboratory experiments (Tilves et al. 2013). Therefore, rather than a threshold size for gamete production, maturation of gonads may depend on an abundant source of prey, possibly of gelatinous origin. Salps and siphonophores are among the more numerous gelatinous prey available in the Ligurian Sea, typically blooming in spring (Licandro et al. 2010, Garcia-Comas et al. 2011), and may serve as a signal to synchronise the growth observed in populations of *P. noctiluca*.

High mortality of young ephyrae has been recorded previously for *P. noctiluca* (Malej & Malej 1992, Rosa et al. 2013), and we also observed this in Run 1. Repeated trials confirmed high mortality rates (~25% after 21 d; 85–100% after 60 d; data not shown) using fresh, small (~50–100 µm) zooplankton, independent of feeding frequency, ephyrae density and food density. Young ephyrae have been shown to use their lappets to collect prey items (Sullivan et al. 1997, Gordoa et al. 2013); therefore, motile prey may inhibit growth unless they are abundant or have slow escape responses. For example, we observed *Artemia* spp. nauplii frequently escaping from ephyrae on a number of occasions, which may explain the growth stagnation observed when *Artemia* spp. were the only food available. The ephyrae of *Aurelia labiata* were able to take up dissolved organic matter to increase their carbon content when otherwise starved (Skikne et al. 2009); however, it is unknown whether *P. noctiluca* is able to use this mechanism to mitigate against starvation. In the present study, only non-motile prey appeared to promote survival by the ephyrae stages, and the high-protein sea urchin eggs supported both growth and survival of ephyrae, until oral arms and tentacles were developed to assist in prey capture. At this developmental stage, ephyrae could feed successfully on fresh zooplankton and gradually on larger prey, improving growth. Unfortunately, ephyrae did not grow when offered the non-motile fish food in Run 3, although their survival was improved. It is not known whether the eggs (of fish or sea urchins) are a key part of the nutrition of *P. noctiluca*, but the ephyrae are certainly capable of ingesting fish eggs if they are captured (Gordoa et al. 2013), and sea urchin eggs resulted in growth during our study.

Our study did not produce jellyfish of a comparable size, within the laboratory environment, to those observed in the field (Fig. 1E,F). In the laboratory, individuals were confined in relatively small tanks, and were unable to undertake the large vertical migrations seen in the field (Franqueville 1971), both of which may have inhibited growth. Limited prey availability may also have restricted the maximum size of individuals if the basal metabolic costs for *P. noctiluca* (of 6.63–7.13% d^{-1}; M. K. S. Lilley et al. unpubl. data) were not met. Finally, conditions within the tanks may also have further inhibited growth when a stirring motion was in place, occasionally entangling organisms with long tentacles or oral arms, but these conditions were required to maintain vitality in young ephyrae; in addition, collisions with container walls may have increased the rate of nematocyst discharge and the need to renew tissue rather than growing.

We also assumed that the regular sampling of *in situ* animals was representative of a single simultaneously growing population, despite the knowledge of their presence in, and transport by, the Ligurian current (Ferraris et al. 2012, Berline et al. 2013). Nevertheless, the similarity between laboratory and *in situ* growth (Figs. 2 & 3) appears to confirm the hypothesis of a basin-scale population growing simultaneously.

Growth

Growth rates of *P. noctiluca* decreased with individual size under both laboratory and field conditions, varying from up to 30% d^{-1} weight increase for the youngest ephyral stages to approximately 1.5–6% d^{-1} for large individuals (>5 cm; Fig. 2).

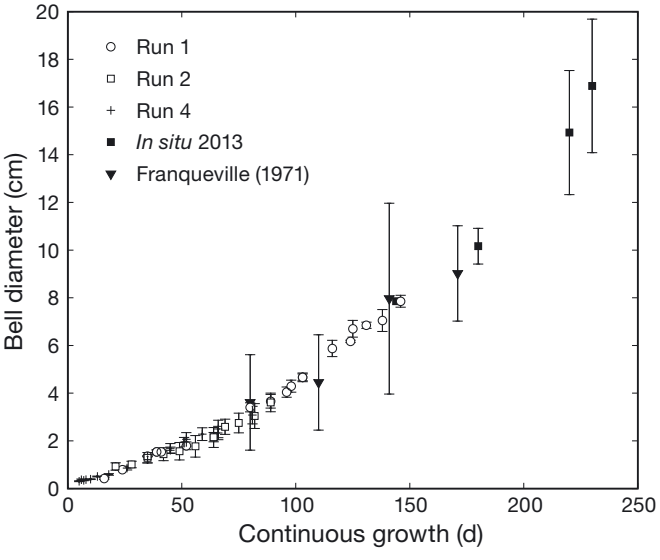


Fig. 3. Simulated growth curve between bell diameter (LD; cm, mean ± SD) and growing days, connecting only positive growth sequences (filled circles, Fig. 1) together and assuming a continuous sufficient food supply. Mean initial diameter was used to identify the starting point for each sequence

Decreases in growth rates with size have been widely observed in marine organisms, including copepods and jellyfish (e.g. Hirst et al. 2003). The range of growth rates observed is in agreement with that of other scyphozoan jellyfish (2–24 % d^{-1}; reviewed by Hirst et al. 2003), except for *Chrysaora quinquecirrha* ephyrae (≤70 % d^{-1}; Olesen et al. 1996). Comparing these with published data sets of *P. noctiluca*, our young ephyrae growth rates were slightly higher than the 7 % d^{-1} observed by Malej & Malej (0.5–7.5 mm; Malej & Malej 1992); the growth rates of larger individuals (2–11 % d^{-1}, 3–8 cm diameter) were comparable to those of similarly sized freshly collected animals (6–10 % d^{-1}; Larson 1987).

Successful periods of growth have previously been attributed to the seasonal influences of food availability and temperature (Malej & Malej 1992). In the Ligurian Sea, after negative winter growth, growth periods have been observed during spring (March–June/July) followed by a strong and abrupt decrease in the size of individuals during summer months (Fig. 1E,F). Previous studies also reported spring as favourable (Rosa et al. 2013) and the time when larger individuals were observed (Malej & Malej 1992). Laboratory individuals, grown at a fixed water temperature, also decreased in size during the summer period (Runs 1 and 4). These seasonal changes may be linked to the annual reduction in the plankton density after the spring bloom and, consequently, the food available, provided by from a regular plankton tow. Therefore, if the bloom period is weak or climatically shortened (Vandromme et al. 2011), growth may be inhibited and the probability of survival of the *P. noctiluca* population reduced, leading to the presence–absence periods observed in the past (Goy et al. 1989, Kogovšek et al. 2010).

Similar rates of growth were observed between laboratory-raised individuals and the *in situ* populations. This is surprising because *in situ* conditions are more variable (Béthoux et al. 1990), cooler in the winter and warmer in the summer, than laboratory temperatures. However, the vertical migration of *P. noctiluca* to the surface at night (Franqueville 1971, Ferraris et al. 2012) may mitigate the effect of temperature on growth costs. To allow for growth, a food source should provide more than 6.63–7.13 % d^{-1} of *P. noctiluca* body mass (M. K. S. Lilley et al. unpubl. data) to cover basal metabolic requirements. Additionally, growth rates of 6–10 cm sized *P. noctiluca* are approximately 3–4 % d^{-1}. Therefore, assuming an assimilation rate of 0.8 (Møller & Riisgård 2007), a *P. noctiluca* population would need to capture around 13 % of their own carbon weight per day to sustain the observed growth at a constant temperature of 18°C. If all material was assimilated, the carbon required daily for an 8 cm *P. noctiluca* would be equivalent to 31 salps (0.65 mgC for a 2 cm *Salpa fusiformis*; Madin & Deibel 1998), 828 doliolids (24 µgC for a *Dolioletta* sp.; Deibel 1985) or 5519 copepods (3.6 µgC for a 102 µm *Clausocalanus furcatus*; Mazzocchi & Paffenhöfer 1998). For a 6 cm medusa, only 40 % of these prey items would be required, or 200 % at 10 cm bell diameter. The metabolic requirements should increase exponentially with both jellyfish size and water temperature (Morand et al. 1987, Malej 1989), possibly explaining the minimal growth in the warmer summer months (Fig. 1E,F).

Life span

To our knowledge, the present study is the first to report the growth of *P. noctiluca* under laboratory conditions throughout the entire life cycle, from eggs to fertile reproductive individuals. Malej & Malej (1992) estimated the life span at approximately 1 yr, but our study would suggest that the survival could be much longer than this. By comparison, other scyphozoan species typically have medusa stages of 4–6 mo, and meroplanktonic hydrozoans weeks to months (Hosia & Båmstedt 2007, Pitt et al. 2013), with few species having an overwintering medusae stage. Holoplanktonic hydromedusae such as *Aglantha digitale* may persist year round with 1–6 generations in the year (reviewed by Hosia & Båmstedt 2007). Under laboratory conditions, we succeeded in maintaining some individuals for 17 mo in captivity (Fig. 1A) although they did not reach the size of adults observed offshore in this region, despite maturing and reproducing successfully. Since *P. noctiluca* can shrink in size (Larson 1987), and thereby minimise the effects of poor nutritional periods or starvation, it is important to consider what might happen under ideal growing conditions. Ten sequences of consecutive growth (n = 3–11 consecutive measurements) were identified from the available data (filled symbols, Fig. 1) and plotted together without the time delay caused by stagnation events (Fig. 3). The resulting figure gives an uninterrupted growth curve for *P. noctiluca* from eggs to large adults, assuming sufficient prey availability, space and therefore constant growth. Given that laboratory and wild growth rates were comparable, including in the years 1969 and 2013, we assume that the rates observed were equivalent to maximal growth rates, constrained by metabolic processes rather than food availability.

Assuming no stagnation or shrinkage, *P. noctiluca* would develop oral arms and tentacles (~1 cm) 50 d after hatching. The maturation of gonads and the first release of gametes could be predicted between Day 90 (2.5 cm) and 120 (5 cm), before that predicted by Malej & Malej (Malej & Malej 1992) in the Adriatic. The mean bell size of the largest individuals that we observed *in situ* (15.6 cm) would be reached after 230 d of continuous growth (Fig. 3), more than doubling in diameter in the final 86 d, as observed in 2013 (6.9–15.6 cm, Fig. 1F). Therefore, the life cycle could be completed in a single season with suitable food conditions. However, growth rates are rarely constant and 200–300 d were required under laboratory conditions to obtain reproductively active and viable medusae (Fig. 1A–D). Finally, the largest individuals, unless subjected to ideal growing conditions, will be over 1 yr old, the oldest individuals overlapping with subsequent year classes in a mixed population.

Acknowledgements. M.K.S.L., A.E. and F.L. were funded by l'Agence Nationale de la Recherche projects 'Ecogely' ANR-10-PDOC-005-01 and 'NanoDeconGels' ANR-12-EMMA-0008. M.F. was supported by a PhD fellowship under the project JELLYWATCH (Région Provence-Alpes-Côte d'Azur (France) and the FEDER EU fund). MEDAZUR I and II (Conseil Général Alpes Maritimes and Fondation d'Entreprise Crédit Agricole Provence Cote d'Azur) supported a postdoc fellowship to L.B. We thank the Association Alchimie Méditerranée (www.alchimie-mediterranee.fr) for logistical support with animal collection, especially Alain Garcia and Chantal Dumas. The Oceanographic Museum of Monaco provided aquarium space and assistance, with special help from Pierre Gilles, Angélique Sygut and the Aquarium team. Rebecca Helm and Maia Durozier provided assistance in the laboratory. Jean-Yves Carval and Jean-Luc Prévost supplied the fresh zooplankton daily. The suggestions of 3 anonymous reviewers greatly enhanced the manuscript.

LITERATURE CITED

Avian M (1986) Temperature influence on *in vitro* reproduction and development of *Pelagia noctiluca* (Forskål). Ital J Zool 53:385–391

Bastian T, Stokes D, Kelleher JE, Hays GC, Davenport J, Doyle TK (2011) Fisheries bycatch data provide insights into the distribution of the mauve stinger (*Pelagia noctiluca*) around Ireland. ICES J Mar Sci 68:436–443

Berline L, Zakardjian B, Molcard A, Ourmières Y, Guihou K (2013) Modeling jellyfish *Pelagia noctiluca* transport and stranding in the Ligurian Sea. Mar Pollut Bull 70:90–99

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

Béthoux JP, Gentili B, Raunet J, Tailliez D (1990) Warming trend in the western Mediterranean deep water. Nature 347:660–662

Deibel D (1985) Blooms of the pelagic tunicate, *Dolioletta gegenbauri*: are they associated with Gulf Stream frontal eddies? J Mar Res 43:211–236

Delannoy CMJ, Houghton JDR, Fleming NEC, Ferguson HW (2011) Mauve Stingers (*Pelagia noctiluca*) as carriers of the bacterial fish pathogen *Tenacibaculum maritimum*. Aquaculture 311:255–257

Doyle TK, De Haas H, Cotton D, Dorschel B and others (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. J Plankton Res 30:963–968

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

Franqueville C (1971) Macroplancton profond (invertébrés) de la Méditerranée nord-occidentale. Tethys 3:11–56

Garcia-Comas C, Stemmann L, Ibanez F, Berline L and others (2011) Zooplankton long-term changes in the NW Mediterranean Sea: decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes? J Mar Syst 87:216–226

Giorgi R, Avian M, De Olazabal S, Rottini Sandrini L (1991) Feeding of *Pelagia noctiluca* in open sea. MAP Tech Rep Ser 47:102–111

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

Goy J, Morand P, Etienne M (1989) Long term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea—prediction by climatic variables. Deep-Sea Res A 36:269–279

Hirst AG, Roff JC, Lampitt RS (2003) A synthesis of growth rates in marine epipelagic invertebrate zooplankton. Adv Mar Biol 44:1–142

Hosia A, Båmstedt U (2007) Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. Mar Ecol Prog Ser 351:113–127

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

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

Licandro P, Conway D, Yahia D, Fernandez de Puelles ML and others (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. Biol Lett 6:688–691

Madin L, Deibel D (1998) Feeding and energetics of Thaliacea. In: Bone Q (ed) The biology of pelagic Tunicates. Oxford University Press, Oxford, p 81–103

Malej A (1989) Respiration and excretion rates of *Pelagia noctiluca* (Semaeostomeae, Scyphozoa). Proceedings of the 21st EMBS Polish Academy of Sciences, Institute of Oceanology, Gdansk, p 107–113

Malej A, Malej M (1992) Population dynamics of the jellyfish *Pelagia noctiluca* (Forsskal, 1775). In: Colombo GA (ed) Proceedings of the 25th EMBS, Marine Eutrophication and Population Dynamics. Olsen & Olsen, Fredensborg, p 215–219

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

Maretic Z, Matic-Plantanida D, Ladavac J (1991) The bloom

of the jellyfish *Pelagia noctiluca* in the Mediterranean and Adriatic and its impact on human health. MAP Tech Rep Ser 47:260–267

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

Mayer AG (1910) Medusae of the world, Vol 3. Carnegie Institution of Washington, Washington, DC

Mazzocchi MG, Paffenhöfer GA (1998) First observations on the biology of *Clausocalanus furcatus* (Copepoda, Calanoida). J Plankton Res 20:331–342

Miller BJ, von der Heyden S, Gibbons MJ (2012) Significant population genetic structuring of the holoplanktonic scyphozoan *Pelagia noctiluca* in the Atlantic Ocean. Afr J Mar Sci 34:425–430

Møller LF, Riisgård HU (2007) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. Mar Ecol Prog Ser 346:167–177

Morand P, Carre C, Biggs DC (1987) Feeding and metabolism of the jellyfish *Pelagia noctiluca* (Scyphomedusae, Semaeostomae). J Plankton Res 9:651–665

Olesen NJ, Purcell JE, Stoecker DK (1996) Feeding and growth by ephyrae of scyphomedusae *Chrysaora quinquecirrha*. Mar Ecol Prog Ser 137:149–159

Pitt KA, Duarte CM, Lucas CH, Sutherland KR and others (2013) Jellyfish body plans provide allometric advantages beyond low carbon content. PLoS ONE 8:e72683

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

Rottini Sandrini L, Avian M (1983) Biological cycle of *Pelagia noctiluca*: morphological aspects of the development from planula to ephyra. Mar Biol 74:169–174

Rottini Sandrini L, Avian M (1991) Reproduction of *Pelagia noctiluca* in the central and northern Adriatic Sea. Hydrobiologia 216–217:197–202

Russell FS (1970) The medusae of the British Isles. Vol II—pelagic Scyphozoa. Cambridge University Press, Cambridge

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

Skikne SA, Sherlock RE, Robison BH (2009) Uptake of dissolved organic matter by ephyrae of two species of scyphomedusae. J Plankton Res 31:1563–1570

Sullivan B, Suchman C, Costello J (1997) Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. Mar Biol 130:213–222

Tilves U, Purcell JE, Marambio M, Canepa A, Olariaga A, Fuentes V (2013) Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea. J Plankton Res 35:218–224

Vandromme P, Stemmann L, Berline L, Gasparini S and others (2011) Inter-annual fluctuations of zooplankton communities in the Bay of Villefranche-sur-mer from 1995 to 2005 (Northern Ligurian Sea, France). Biogeosciences 8: 3143–3158

Submitted: November 18, 2013; Accepted: May 7, 2014

Proofs received from author(s): July 7, 2014