

## Feeding and metabolism of the jellyfish *Pelagia noctiluca* (scyphomedusae, semaestomae)

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**Abstract.** Laboratory experiments were carried out on the holoplanktonic scyphomedusa *Pelagia noctiluca*, which exhibits population explosions some years in the Mediterranean Sea. Feeding experiments performed on small, laboratory-reared medusae showed specific daily rations of 13 and 35% at 5 and 20 *Artemia* nauplii prey l<sup>-1</sup> respectively, while basal NH<sub>4</sub><sup>+</sup> excretion reached 3.9% (specific elemental metabolic rate) for adults at 22°C. These values appear to be consistent with those previously observed by several authors for other planktonic coelenterates. Assuming that such laboratory physiological rates are indicative of food requirements in natural environments, and given the high abundance of *P. noctiluca* observed regionally, we conclude that *P. noctiluca* can have a strong predatory impact in the Ligurian Sea (north-west Mediterranean), particularly during the summer and early fall.

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### Introduction

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Pelagic Cnidaria and Ctenophora, representing a diverse group of carnivorous gelatinous zooplankton, are often abundant in planktonic ecosystems (Longhurst, 1985), and some species have been reported to reach high densities over both time and space. For example, seasonal aggregations of ctenophores of the genera *Mnemiopsis* and *Pleurobrachia* (Fraser, 1970; Hirota, 1974; Reeve and Baker, 1975; Kremer and Nixon, 1976), siphonophores of the genera *Nanomia* and *Rhizophysa* (Rogers *et al.*, 1978; Purcell, 1981), hydromedusae of the genera *Tiaropsis*, *Rathkea* and *Phialidium* (Zelickman *et al.*, 1969; Huntley and Hobson, 1978) and scyphomedusae of the genera *Aurelia* and *Chrysaora* (Möller, 1980; Feigenbaum and Kelly, 1984) are well documented in the literature.

In the Ligurian Sea region of the north-west Mediterranean, the scyphomedusa *Pelagia noctiluca* (Forskål, 1775) frequently reaches very high numerical abundance. During the last three decades, for example, it was especially common during the years 1957-1959, 1969-1970 and 1982-1984. Moreover, the historical record documents population explosions dating back 100 years or more (Goy, 1984). When such 'infestations' are advected onshore by local winds or currents, they may severely impact local fisheries, and drive bathers from the water (UNEP, 1984).

Whereas the holoplanktonic life cycle of this semaestome is well known (e.g. Krohn, 1855; Delap, 1907; see also Russell, 1970; Rottini-Sandrini and Avian, 1983), quantitative physio-ecological studies of *P. noctiluca* have not been carried out.

The present report gives laboratory data on size-weight relationships of medusae, as well as estimates of individual daily rations and metabolic levels. From these laboratory data, we estimate and discuss the predatory impact of *P. noctiluca* in the Ligurian Sea, using data on predator-prey standing stocks collected in late summer and early fall 1984.



## Materials and methods

### *Laboratory rearing*

Adult medusae 4–10 cm in diameter were collected with a dip net in the Bay of Villefranche and offshore in the Ligurian Sea (43°N, 7°30'W) between June and December of 1984 and 1985. The medusae were maintained in the laboratory for periods ranging from a few hours to a few days, in a normal light–dark cycle and without aeration, either in small groups in 25-l flasks at a controlled temperature of 15°C, or *en masse* in 700-l tubs at uncontrolled room temperature varying from 21 to 25°C. These medusae were then used for laboratory studies of metabolism, starvation, hatching and larval development.

In addition, 60 ephyrae averaging 6 mm in diameter were collected on 19–20 June 1985 in the Bay of Villefranche, with a 680- $\mu$ m mesh plankton net. These were reared at first in 5-l beakers, at densities of  $\sim 3$  individuals  $l^{-1}$ . Temperature was controlled, remaining at 18–21°C, and the contents of each beaker were continually stirred at 10 revolutions  $min^{-1}$ . These ephyrae were fed twice a day with stage 1 and stage 2 *Artemia* nauplii hatched from commercially dried eggs from San Francisco Bay, California, with concentrations of nauplii reaching 100–150 individuals  $l^{-1}$ . In addition, natural populations of small size zooplankton collected by plankton tows in the Bay of Villefranche were added once or twice each week. Moribund plankters and other debris were removed every day, and every third day the ephyrae were transferred with a large-bore pipette to 5-l beakers containing clean water. Throughout the period of laboratory maintenance some healthy individual ephyrae were withdrawn from this rearing stock for analysis of C, H, N content, and for metabolism and feeding experiments. When the largest individuals had reached a diameter of 20 mm, the remaining specimens were transferred to a 25-l flask and fed until they reached a subadult diameter of 30–35 mm.

### *Size, volume and weight measurements*

All measurements correspond to the largest diameter of each medusa, including lappets. For small individuals (<35 mm), this measurement is easily obtained, since the lappets generally flatten when individuals are placed into a shallow Petri dish with a little water. While the lappets of larger individuals must be hand spread, we observed that a highly predictive relationship existed between the largest diameter measurement ( $D_1$ ) and 'routine' diameter measurements ( $D_2$ ) which were performed rapidly and without taking care to spread the lappets:  $D_1 = (1.20 \pm 0.03)D_2$  ( $n = 19$ ).

Small specimens were indirectly measured from lifesize photographs (Braconnot, 1985) to the nearest millimeter. Large individuals were placed on a ruler and measured alive, to the nearest 0.5 cm. For volume displacement measurements, live individuals were placed on blotting paper and then transferred to a graduated cylinder of the appropriate diameter.

To determine dry weight/carbon/nitrogen relationships (measured for small individuals only), specimens were fixed for a few seconds in Bouin's solution, rinsed three times in distilled water to remove surface salt, then dried for 1 week at 60°C, weighed and analyzed with a Perkin–Elmer model 240 CHN Analyzer.

*Feeding experiments*

Unbiased estimates of the daily ration and of the volume swept clear by macroplanktonic cnidaria are difficult to obtain from laboratory experiments because laboratory confinement of such large animals can modify their predatory behavior. Scyphomedusae with long tentacles are especially damaged by close confinement. Our observations indicate that container diameter must equal at least the maximum length of the tentacles, for only under such conditions will *P. noctiluca* swim actively around the walls of the aquarium with tentacles extended. We have found that 5-l beakers are quite convenient for specimens until they reach a size of ~22 mm diameter, and 25-l beakers seem adequate for individuals until they reach 30–35 mm.

Feeding of the experimental animals took place with moderate densities of prey (5–60 prey  $l^{-1}$ ), because we believe that medusae in the Ligurian Sea rarely encounter prey densities exceeding 10–100 prey  $l^{-1}$  (see Discussion). For small medusae (12–21 mm), experiments were run for 12 h ( $\pm 2$  h) with one individual per 5-l beaker filled with 'Millipore GF/A' (2–3  $\mu m$ ) filtered seawater.

Temperature was held constant at 21°C and the beakers were stirred slowly. Feeding rates are reported as the difference between the initial (25, 50, 100, 200 or 300) and remaining numbers of *Artemia* nauplii, divided by the duration of the experiment. The corresponding temporal mean density of prey was estimated as the geometric mean of initial and final density, where the final density never fell to <25% of the initial value. Such a calculation leads to a suitable estimation of the experiment temporal mean density of prey if we assume that predatory rate diminishes proportionally to the diminution of prey density during each experiment. Experiments were performed repetitively on the same individuals exposed to the same food concentrations. Photograms of the medusae were made every 4–7 days, and intermediate sizes were interpolated assuming linear growth for the period between two successive measurements.

For medium-size medusae (22–32 mm), four feeding experiments were run for 4–6 h in 25-l containers. Three individuals were used for each experiment. The resulting data were processed as described for small-size groups and were then integrated into the general feeding rate equation.

*Measurement of metabolism*

Measurements were performed on medusae caught in the Ligurian Sea or Bay of Villefranche and subsequently starved for 8 h–6 days. Such conditions do not apparently affect health and behavior of large jellyfish — well-known for their great capacity to be kept unfed for a long time without damage, except degrowth (Hamner and Jenssen, 1974). Nevertheless, starvation times were recorded to check for a possible effect on metabolic rate.

For simultaneous measurements of oxygen consumption and ammonium excretion, 13 medusae were transferred from holding tanks (700 l, 21°C) to 1-l, screw-cap glass jars filled with unfiltered seawater collected at the mouth of the bay. These were then incubated individually at the same temperature for 1–2 h after enclosure. Oxygen consumption and ammonium excretion were estimated by difference from a control jar without medusae, which never exhibited significant changes in  $O_2$  and  $NH_4^+$  concen-

tration. The concentration of dissolved oxygen was measured with a polarographic oxygen electrode (Orbisphere model 2604), while ammonium was measured spectrophotometrically by a modified phenolphthorite method (Solórzano, 1969; see also Biggs, 1977).

Ammonium excretion was also monitored as a function of time, to confirm linearity. For these measurements, one, two or three medusae of roughly the same size were kept for 3–5 h in 2–5-l parafilm-covered beakers filled with unfiltered seawater taken from the bay. Aliquots of 10 ml were withdrawn every 30 min for  $\text{NH}_4^+$  analysis by a Technicon II autoanalyzer and were corrected for any absorption of  $\text{NH}_4^+$  from laboratory air by concurrent measurement from a control beaker. Since the slope of the regression line of ammonium concentration as a function of time (the mean excretion rate) was in all cases quite linear, we have combined our endpoint and time-course data to calculate excretion as a function of biovolume and temperature.

Time-course analysis of  $\text{NH}_4^+$  excretion was also carried out on ephyrae from our laboratory rearing stock. These ephyrae were starved for 12 h and then placed in 200-ml beakers for 3–5 h at a density of 14–18 medusae per beaker.

## Results

### *Diameter–biomass relationships*

For nine ephyrae and small medusae, relationships between size and dry weight (DW), carbon (C) and nitrogen (N) weights are described by functional log–log regressions as found in Ricker (1973):

$$\ln \text{DW } (\mu\text{g}) = 3.55 \ln D_1 \text{ (mm)} - 1.0 \quad n = 9 \quad r^2 = 0.98 \quad (1)$$

$$\ln \text{C } (\mu\text{g}) = 2.96 \ln D_1 \text{ (mm)} - 1.96 \quad n = 9 \quad r^2 = 0.93 \quad (2)$$

$$\ln \text{N } (\mu\text{g}) = 2.99 \ln D_1 \text{ (mm)} - 3.4 \quad n = 9 \quad r^2 = 0.94 \quad (3)$$

Figure 1 presents data and adjusted relationships.

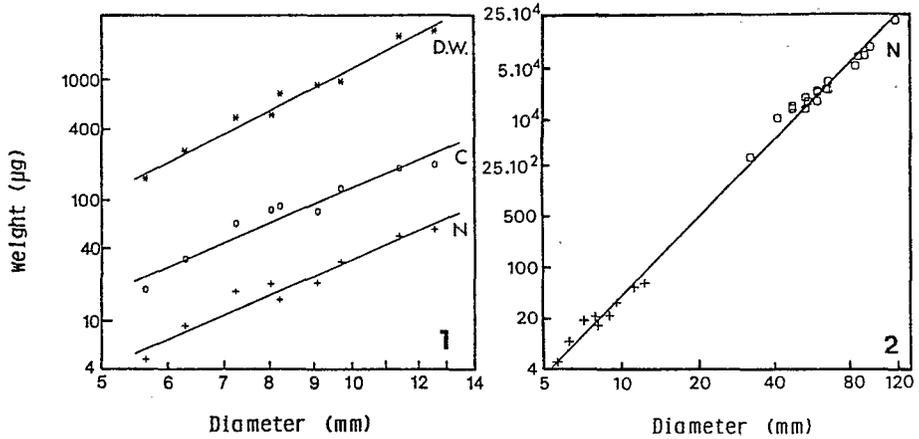
The mean C:DW, N:DW and C:N ratios equal 11.4% (SD = 2.5%), 2.9% (SD = 0.7%) and 4 (SD = 0.7) respectively.

For medium size and large specimens (33–120 mm,  $n = 19$ ), wet volume is proportional to the largest diameter ( $D_1$ ) cubed:

$$\ln \text{vol (cm}^3\text{)} = 3.02 \ln D_1 \text{ (mm)} - 9.4 \quad r^2 = 0.95 \quad (4)$$

Nitrogen content as a function of size in these medium size and large specimens was estimated indirectly, assuming a N:DW ratio of 2.9%, as measured for the small ones and a DW:WW ratio of 4% (literature values for Scyphomedusae include 4.1% for *Pelagia*, in Curl, 1962; 3.4–4.4% for non-Baltic *Aurelia*, in Russell, 1970; 3.62% for *Chrysaora*, in Shenker, 1985; 3.3–4.2% for three species, in Larson, 1985). The product of these two values leads to a direct ratio of 1.16 mg N cm<sup>-3</sup>, which is quite close to the value of 0.94 mg N cm<sup>-3</sup> computed from *P. noctiluca* protein data given by Bidigare and Biggs (1980), assuming a N/protein ratio of 0.16 (Ikeda, 1972).

Our direct and indirect estimates of nitrogen content of small and large specimens,



**Figs. 1 and 2.** Diameter-weight relationships. (1) Dry weight, C, H, N measurements data and adjusted functional logarithmic regressions for ephyrae-small medusae. (2) General (though approximate) diameter-nitrogen relationship, based both on small individuals nitrogen measurements data (+) and on wet volume measurements of adults, assuming a nitrogen content of  $1.16 \text{ mg cm}^{-3}$  (O) (see text).

respectively, are summarized in Figure 2. The general relationship between nitrogen content and diameter so defined is:

$$\ln N (\mu\text{g}) = 3.53 \ln D_1 (\text{mm}) - 4.5 \quad n = 28 \quad r^2 = 0.99 \quad (5)$$

### Feeding activity

The data from 153 feeding runs, relatively long-term experiments (4–14 h, most of them 10–14 h) carried out at  $21^\circ\text{C}$  using 20 medusae of size 12–32 mm, were processed by logarithmic multiple regression to yield feeding rate as a function of medusa size and the geometric mean density of the *Artemia* nauplii prey. The log transformed equation is:

$$\ln f (\text{prey h}^{-1}) = 2.16 \ln D_1 (\text{mm}) + 0.69 \ln C (\text{prey l}^{-1}) - 6 \quad (6a)$$

$n = 153 \quad r^2 = 0.81 \quad \text{Fisher } F\text{-test} = 325 \quad (P < 0.1\%)$

Such a logarithmic function corresponds to the more meaningful power function:

$$f = 25 \times 10^{-4} \cdot D_1^{2.16} \cdot C^{0.69} \quad (6b)$$

Data of two different size groups of small medusae ( $15 \pm 1 \text{ mm}$ ,  $20 \pm 2 \text{ mm}$ ) are plotted as Figure 3A,B. We recognize that local negative correlations between feeding rate and food density may arise as a consequence of the way mean food density was computed for the duration of an experiment. For example, if two experiments which began at a density of  $40 \text{ prey l}^{-1}$  fell respectively to 10 and  $22 \text{ prey l}^{-1}$ , the first will have a computed geometric mean density of  $20 \text{ prey l}^{-1}$ , while the latter will compute to  $28 \text{ prey l}^{-1}$ . Thus, for a same initial density, the greater predation rate will decep-

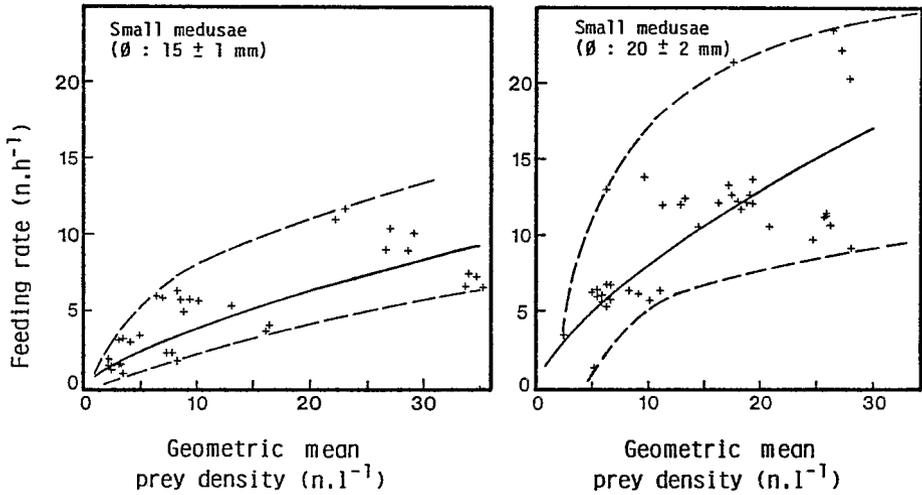


Fig. 3. Feeding rate of small medusae, diameter class (A, 15 ± 1 mm) and (B, 20 ± 2 mm). Other data are not presented. Continuous curves correspond to projection of the power form of the overall adjusted model (equation 6b) for the corresponding particular diameters (respectively 15 and 20 mm). Hand-fitted dotted lines join the three upper and lower points of each set of data.

tively correspond to the smaller geometric mean density. However, this drawback does not affect the display of a functional response pattern nor the model fitting overall data, though it probably increases residual variance. We think this way of expressing the average prey density is better than would result from standardizing predation rate by initial density, which leads to a systematic overestimation of the actual density and, therefore, an underestimation of the functional response.

Feeding activity can also be described in terms of clearance rate CR, which was indirectly computed from the general feeding rate equation (6a,b):

$$CR (l \text{ day}^{-1}) = [f (\text{prey h}^{-1}) / C (\text{prey l}^{-1})] \times 24$$

Since feeding rate is not linked linearly to prey density, clearance rate slowly decreases with increasing prey density. For example, clearance rate of a 14-mm medusae results in calculated values of 10.8 l day<sup>-1</sup> at 5 prey l<sup>-1</sup> and 6.2 l day<sup>-1</sup> at 30 prey l<sup>-1</sup>. The first one seems ecologically more likely, since it is representative of a high searching effort in a relatively poor environment, as would be the case in oceanic areas.

### Metabolism

The oxygen consumption and ammonium excretion rates at 21°C for 13 medium size medusae (9–28 cm<sup>3</sup>) that were starved for 5 days can be represented by the following equations:

$$\ln O_2 \text{ (ml h}^{-1}\text{)} = 0.95 \ln \text{ vol. (cm}^3\text{)} + 2.41 \quad r^2 = 0.71 \quad (7)$$

$$\ln NH_4^+ \text{ (}\mu\text{g-at NH}_4^+ \text{ h}^{-1}\text{)} = 0.90 \ln \text{ vol. (cm}^3\text{)} - 1.87 \quad r^2 = 0.77 \quad (8)$$

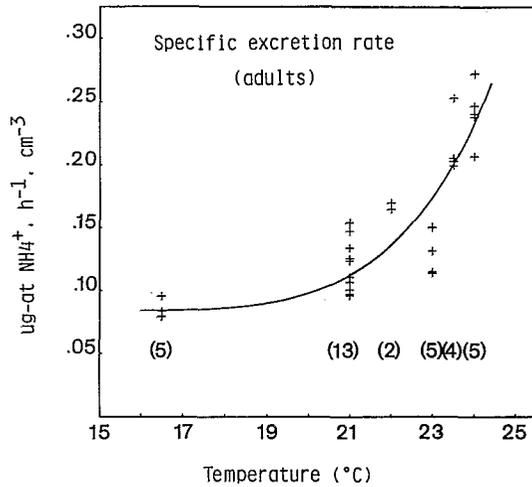


Fig. 4. Specific ammonium excretion rates of adult medusae at different temperatures. In brackets: number of experiments performed at each temperature. Curve corresponds to equation (10).

Computation of the average ratio of oxygen atoms (O) consumed to ammonium nitrogen atoms (N) excreted (see Harris, 1959) yields  $7.5 \pm 0.9$ , which indicates a protein-dominant catabolism (Ikeda, 1972). Assuming a respiratory coefficient of 0.8, this O:N ratio translates to a C:N ratio, by weight, of 2.55.

The  $\text{NH}_4^+$  excretion of 21 other *P. noctiluca* medusae ranging in volume from 10 to 118  $\text{cm}^3$  that were starved for 8 h–6 days after capture was measured both at 16.5°C and at 22–24°C. Pooling these data with that for the 13 medusae above yielded the following general multiple regression:

$$\ln \text{NH}_4^+ (\mu\text{g-at h}^{-1}) = 1.08 \ln \text{vol. (cm}^3) + 0.133T(^{\circ}\text{C}) - 5.08 \quad (9)$$

$r^2 = 0.93 \quad n = 34 \quad \text{Fisher } F\text{-test} = 221 \quad (P < 0.1\%)$

Correlation of multiple regression residuals with time after capture is low ( $r = -0.27$ ) and not significant (even for  $P = 10\%$ ). Thus, specific  $\text{NH}_4^+$  seems to be nearly constant for times ranging from a few hours to a few days of starvation.

Since the biovolume allometric coefficient (1.08) is not significantly different from 1.0 among these adult medusae (even for  $P = 10\%$ ,  $t$ -test), it is instructive to compute the mean specific excretion rate and then examine this as a function of temperature (Figure 5). This yielded the following empirical predictive relationship, using a non-linear least-squares algorithm (Glass, 1967):

$$\text{NH}_4^+ (\mu\text{g-at NH}_4^+ \text{ h}^{-1} \text{ cm}^{-3}) = 4.8 \times 10^{-7} (T-13)^{5.28} + 0.08 \quad (10)$$

This equation predicts a  $Q_{10}$  of 3.8 for  $\text{NH}_4^+$  excretion between 15 and 25°C.

One can independently estimate basal metabolic rates by measuring the individual volume decrease during starvation. Three specimens of volumes 45, 55 and 80  $\text{cm}^3$ ,

**Table I.** Element-specific daily rations on laboratory experiments for some planktonic carnivores.

Genus	T (°C)	Predator size	Prey density (Type of prey)	Element-specific rations (% day <sup>-1</sup> )	Authors	
<i>Mnemiopsis</i>	26	Every size	5 ( <i>Acartia tonsa</i> )	10	C	Reeve <i>et al.</i> (1978)
	26	Every size	20 ( <i>Acartia tonsa</i> )	40	C	Reeve <i>et al.</i> (1978)
<i>Pelagia</i>	21	14 mm	5 ( <i>Artemia</i> nauplii)	13	N	Present work
	21	89 µg N	20 ( <i>Artemia</i> nauplii)	35	N	Present work
<i>Sagitta</i>	21	9–17 mm	5 ( <i>Acartia tonsa</i> )	0.2–1	C	Reeve (1980)
	21	9–17 mm	20 ( <i>Acartia tonsa</i> )	2–10	C	Reeve (1980)
<i>Sphaeronectes</i>	13	44.5 µg N	5 (Copepods)	17	N	Purcell and Kremer (1983)
	13	44.5 µg N	20 (Copepods)	47	N	Purcell and Kremer (1983)

Values from Reeve *et al.* (1978) and Reeve (1980) are reported from their curves. For the 'theoretical' small *Pelagia*, both diameter and corresponding nitrogen weight (from equation 3) are indicated.

that were captured in December 1985, were maintained for 10 days in 'Millipore GF/A' (2–3 µm) filtered seawater at a temperature of 15°C. They shrank an average of 4.6% daily (SD = 0.2%) over this period. The corresponding daily loss of nitrogen by ammonium excretion, computed from equations (5) and (10), predicted a volume decrease of 2.4% day<sup>-1</sup>. The two estimates would agree more closely if we assume that additional nitrogen excretion may be contributed by organic nitrogen compounds not measured here.

The limited number of excretion experiments carried out with groups of ephyrae of 5–9 mm ( $n = 3$ ) yielded excretion rates ranging from  $1.8 \times 10^{-3}$  to  $7.1 \times 10^{-3}$  µg-at NH<sub>4</sub><sup>+</sup> h<sup>-1</sup> individual<sup>-1</sup> at 22°C. Using the ephyrae diameters and equation (3), we estimated the total nitrogen for the medusae in each experiment and computed the nitrogen-specific excretion to be  $384 \times 10^{-3}$  µg-at NH<sub>4</sub><sup>+</sup> h<sup>-1</sup> gN<sup>-1</sup> (SD = 100), corresponding to a 12.9% (SD = 3.3%) daily nitrogen turnover. By comparison, at this same temperature, equation (10) predicts that daily NH<sub>4</sub><sup>+</sup> excretion in adult medusae will average only 3.9% of the nitrogen content. Such a 3-fold difference for a 1–2 × 10<sup>3</sup>-fold increase in nitrogen body weight would correspond to a specific metabolic rate allometric coefficient close to 0.85 over the entire range of size.

## Discussion

### *Estimation of daily ration and clearance rate*

It is generally acknowledged that estimates of the feeding rates of almost all oceanic zooplankton vary with and reflect experimental methodology, and may be consistently underestimated by experiments carried out under laboratory conditions (Reeve, 1980). Nevertheless, we assume that experiments of relatively long-term duration which yield estimates of feeding rate which vary <2-fold at any given prey density, such as those illustrated in Figure 3A,B, may be adequate for the purpose of describing the general functional response.

Since there is no evidence for a minimum feeding threshold over the range of prey density investigated (Figure 3A,B), functional response was simply described by a

**Table II.** Clearance rate estimations from laboratory experiments for pelagic coelenterates.

Genus	Predator size (mm)	Prey density (ind. l <sup>-1</sup> ) (Type of prey)	Clearance rate (l day <sup>-1</sup> )	Authors
<i>Mnemiopsis</i>	Larval	5 ( <i>Acartia tonsa</i> )	1.2	Reeve <i>et al.</i> (1978)
	Adult	5 ( <i>Acartia tonsa</i> )	11	
<i>Eurhamphaea</i>	40	11–16 (Copepods)	12–36	Kremer <i>et al.</i> (1986)
<i>Phiallela</i>	8	<i>Artemia</i> sp. nauplii	1	Fulton and Wewar (1985)
<i>Aurelia</i>	12–14	5 (fish larvae)	6.7	Bailey and Batty (1983)
Pelagia	8 (extrapol.)	5 ( <i>Artemia</i> nauplii)	3.2	Present work
	14	5 ( <i>Artemia</i> nauplii)	10.8	Present work
	40 ( $D_2$ extrapol.)	5 ( <i>Artemia</i> nauplii)	165	Present work
<i>Chrysaora</i>	40 ( $D_2$ ?)	<i>Artemia</i> sp.	240	Felgenbaum and Kelly (1984)

Data from Bailey and Batty (1983) are calculated from their killing rate fitted curve. Existing and extrapolated diameters for *Pelagia* are chosen to allow comparisons with other species values.  $D_2$  (routine diameter, see text) is used for comparison with *Chrysaora* value of Felgenbaum and Kelly (1984), who give no description of the corresponding measurement method.

**Table III.** Nitrogen-specific ammonium excretion rates for pelagic coelenterates.

Genus	<i>T</i> (°C)	Mean experimental values (mg prot <sup>-1</sup> h <sup>-1</sup> )	Authors	Weight conversion <sup>a</sup>	Excretion (N-NH <sub>4</sub> % N day <sup>-1</sup> )
Pelagia	16.5	Equation (10)	Present work	2	2.4
	21	Equation (10)	Present work	2	3.3
	24	Equation (10)	Present work	2	6.7
Pelagia	26 ± 3	1.1 µg NH <sub>4</sub>	Biggs (1977)	1	12.8
Agalma	26 ± 3	0.7 µg NH <sub>4</sub>	Biggs (1976)	1	8.4
Sphaeronectes	13	<sup>b</sup>	Purcell and Kremer (1983)	<sup>b</sup>	3.5
Mnemiopsis	21.8	<sup>b</sup>	Kremer (1977)	<sup>b</sup>	8.4
Diverse tropical Ctenophores	25	<sup>b</sup>	Kremer <i>et al.</i> (1986)	<sup>b</sup>	4–10

<sup>a</sup>Weight conversion: 1, 1 mg protein = 0.16 mg N (Ikeda, 1974); 2, 1 cm<sup>3</sup> wet displacement volume — 1.16 mg N (see text).

<sup>b</sup>Daily turnover calculated directly by authors.

logarithmic (or power) function, which allow various curve forms. Fitting such a mathematical model to our data (equation 6a) exhibited a coefficient of 0.69 for the log prey – concentration effect. This value is significantly less than 1.0 ( $t$ -test:  $<0.1\%$ ) and so predicts progressive feeding satiation. Such a result has already been observed for *Aurelia* and may be characteristic of active predators (Bailey and Batty, 1983).

In other respects, a value of 2.16 for the log diameter effect, when divided by the general size – weight allometric coefficient ( $\sim 3-3.5$ , equations 1–5), yields a ratio ( $\sim 0.7-0.6$ )  $< 1$ , which reflects the dependence of specific ration on predator weight. This appears to be in agreement with the general concept of progressive reduction of both specific metabolic rate and growth rate with increasing size. However, we cannot exclude the possibility that predatory behavior was more restricted by experimental conditions in the large size individuals we investigated. Consequently, feeding rates predicted by equation (6a,b) for small size medusae may be more consistent than those for the largest ones.

From the feeding rate model (equation 6a,b), we can then estimate the specific nitrogen daily ration of a 'theoretical' small medusae (e.g. 14 mm in diameter), assuming a mean individual nitrogen weight of  $0.218 \mu\text{g}$  for San Francisco Bay stages 1–2 *Artemia* nauplii (Oppenheimer and Moreira, 1980). Values calculated for two prey densities (5 and 20 prey  $\text{l}^{-1}$ ) seem fairly representative of those estimated by other authors for various gelatinous carnivorous zooplankton of similar size (Table I), despite the differences between the prey used.

For small *P. noctiluca* (ephyrae and juvenile medusae  $< 15$  mm in diameter), we note that a comparison of daily ration and metabolic nitrogen expenditures at  $21-22^\circ\text{C}$  suggests an equilibrium or weakly positive nitrogen budget at a food concentration of 5 *Artemia* nauplii  $\text{l}^{-1}$ . However, that *Artemia* are not natural prey for *P. noctiluca* precludes any direct extrapolation to a field situation.

Clearance rates computed at low prey density (5 prey  $\text{l}^{-1}$ ) for different sizes of medusae are of the same order of magnitude as those found in the literature for predators of similar sizes (Table II). However, the overall data indicate that clearance rate steeply increased with increasing size and would probably be better scaled in terms of weight. Unfortunately, such data were not always furnished in previous studies.

#### *General metabolism and daily nitrogen turnover*

Several authors have characterized scyphomedusae as predators with relatively active metabolism (Kruger, 1968; Biggs, 1977). Our present data now allow such metabolism to be evaluated comparatively with that of other pelagic Cnidaria, in terms of mean daily rate of turnover of body nitrogen (Table III).

Although neither the methodological nor the biological conditions (e.g. nutritional state) were identical in these studies, these diverse pelagic Cnidaria and Ctenophora show a remarkably limited variability in daily nitrogen turnover rate. Clearly, the variability is even less when nitrogen turnover rate estimates are compared at a common temperature.

In other respects, the high estimated  $Q_{10}$  value (3.8) confirms the great sensitivity of metabolic rate to temperature among planktonic coelenterates, as reviewed by Larson (1985).

*Prey availability and daily ration in the Ligurian Sea*

In the Ligurian Sea, data gathered in surface waters by a high-speed continuous tub-Haï recorder, using 500- $\mu\text{m}$  mesh nets, document a mean concentration of 1.5 copepods  $\text{l}^{-1}$  in June (from Appendix 1 of Boucher *et al.*, 1987), the month generally coincident with the annual abundance peak of the closely epipelagic young stages of *P. noctiluca*. The mean nitrogen weight of those copepods, mainly *Clausocalanus* spp. *Oithona* spp., *Centropages* spp. copepodites IV–V and adults, would be close to 0.4–1  $\mu\text{g}$  nitrogen. On the other hand, one can suppose that a value of 10.8  $\text{l day}^{-1}$  given for 14-mm young medusae in Table II would indicate an actual *in situ* clearance rate range of 5–15  $\text{l day}^{-1}$ . Combining these values yields a daily nitrogen specific ration range of 3.3–25% for such a small *P. noctiluca*. These estimations, multiplying by a digestive efficiency of 0.8 (see review in Larson, 1985), should more or less allow maintenance, assuming a daily nitrogen usage of 10–15%. However, it is also well documented that a great deal of spatial heterogeneity exists, producing local concentrations of copepods one or more orders of magnitude greater than the regional average. Clearly, populations of small medusae located within such local aggregations of prey should be well fed and may show rapid growth.

In order to follow up these studies of near-surface distributions and to integrate them over the upper 200 m, we have sampled a transect of 12 stations running 2–54 km seaward into the Ligurian Sea from Cap Ferrat at the entrance of the Bay of Villefranche. One night each month in 1984–1985, oblique trawls 200–0 m were fished with an Omori net, while *P. noctiluca* density at the surface was estimated concurrently by direct observation. The greatest abundances of large *P. noctiluca* occurred in late summer to early fall. For example, on the night of 3 September 1984, a mean concentration of 5 adult medusae per 1500  $\text{m}^3$  were taken in the Omori net hauls, while 7 medusae per 100  $\text{m}^2$  were seen at the surface, at six successive stations 21–45 km off the southern French coast. Since the former density translates to  $\sim 0.6$  individuals  $\text{m}^{-2}$  in the upper 200 m, we estimate that  $\sim 10\%$  of the *P. noctiluca* population was visible at the surface at night.

Given that the average *P. noctiluca* medusa had a volume of 56  $\text{cm}^3$  (SD = 23;  $n = 54$ ) on the same date, these field data suggest a *P. noctiluca* population biomass of  $\sim 35 \text{ cm}^3 \text{ m}^{-2}$ . From equation (10), this translates to an average daily excretion of 79  $\mu\text{g-at NH}_4^+ \text{ m}^{-2}$ , assuming that these large *P. noctiluca* migrate vertically (Franqueville, 1970) and so spend about half their time below the thermocline at a temperature of 14°C, and half above it, at 21°C. If we now multiply this value by 1.5 (since non-ammonia nitrogen probably represents at least 30% of total nitrogen excretion by pelagic coelenterates — (see Biggs, 1976; Kremer, 1977, 1982; Purcell and Kremer, 1983) and by 1.25 (for non-assimilated food), we conclude that this population needed to ingest at least 2.1 mg nitrogen  $\text{day}^{-1} \text{ m}^{-2}$  for maintenance.

Mesoplankton ( $>200 \mu\text{m}$ ) biomass collected by vertical hauls, 200–0 m (daytime 31 August 1984) at four stations 23–43 km from the coast along the same radial averaged 297 mg ash-free dry weight  $\text{m}^{-2}$  (FRONTAL program, Durand, 1985). Applying a transform coefficient of 0.107 (Margalef and Vives, 1967) suggests that mesoplanktonic biomass averaged  $\sim 32$  mg nitrogen  $\text{m}^{-2}$ . Thus, the daily nitrogen requirement of this late summer–early fall *P. noctiluca* population probably corresponds

to ~6–7% of the regional average epipelagic mesoplankton biomass. While such calculations at first glance may imply that the mesoplankton ought to exhibit a rather high production/biomass ratio in order to support a *P. noctiluca* population, we recognize that the medusae may also exert direct predation on large micronekton (e.g. the euphausiid *Meganctiphanes norvegica* — G.Castello, personal communication; P.Morand, unpublished data), as well as on vertically migrating fauna. Moreover, that similar ( $\pm 2$ -fold) population densities of *P. noctiluca* persisted for at least 2 months was confirmed by previous (July 1984) and subsequent (October 1984) surveys along this transect line.

In conclusion, because of its relative abundance and large size, *P. noctiluca* appears to be an important predator in the Ligurian Sea planktonic system, similar to scyphomedusae *Aurelia*, *Cyanea* and *Chysaora* in neritic waters of the Baltic, Atlantic and North Sea (Möller, 1980; Lindahl and Hernroth, 1983; Feigenbaum and Kelly, 1984; Van der Veer and Oorthuysen, 1985). However, in contrast to the latter three species, *P. noctiluca* is an holoplanktonic form whose adult stage can be encountered throughout the year in the open sea. For this reason it should be a particularly key predator; it seems to displace (during population explosion years) other species of macroplanktonic carnivores, including the ctenophores *Leucothea multicornis* and *Cestum veneris* and the siphonophore *Hippopodius hippopus* (Morand and Dallot, 1985).

We suggest that a better understanding of the dynamics of such population explosions will hinge upon the clarification of two factors: (i) *P. noctiluca* generation time and reproduction as a function of temperature and (ii) *P. noctiluca* population fluctuations related to pluri-annual climatic and hydrological cycles. Some data are now beginning to be collected on the first point (Rottini-Sandrini *et al.*, 1985), and some hypotheses have been raised about the second one (Goy, 1984). However, the general scarcity of long-term quantitative population data requires that most insights will have to be made indirectly.

### Acknowledgements

We are grateful to Christiane Cellario and Isabelle Palazolli for assistance in excretion experiments and in analyzing the C, H, N samples. Michele Etienne kindly supplied us with mathematical and graphic software. This work could not have been carried out without the scientific advice and administrative help provided by Jacqueline Goy and Paul Nival. We thank Claudia Mills and Gabriel Gorsky for their comments on the manuscript. This research was supported by the Mediterranean United Nations Environment Program and by a grant from the French Technology and Research Ministry to P.M.

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Received on August 12, 1986; accepted on March 10, 1987

