Population dynamics of the jellyfish *Pelagia noctiluca* (Forsskål, 1775)

Alenka Malej1 & Matevž Malej2
1. Marine Biological Station Piran, Institute of Biology, University of Ljubljana, SLO-66350 Piran, I La 65, Slovenia
2. C. na Markiacev 17, SLO-66000 Koper, Slovenia

Abstract

Recurring massive appearances of different coelenterate species may cause considerable ecological as well as commercial impacts in affected areas, yet our knowledge of the population dynamics of these animals is poor.

We examined the seasonal occurrence, size structure, patterns of growth and mortality of the jellyfish *Pelagia noctiluca* (Saccomanella noctiluca, Scyphozoa) in the northern Adriatic Sea. The occurrence of mature specimens throughout the year and of ephyrae from April to December indicates a long spawning season, although size-frequency data suggest a peak spawning period from August to November. The growth curve fitted to a set of bell diameter-frequency data suggests that *P. noctiluca* reached the minimal size at which they may spawn in about 150 days. Mortality rates varied seasonally and showed a significant negative correlation with temperature.

The dynamics of the *P. noctiluca* population has been modelled by a modified Leslie matrix using size rather than age classes. The size-dependent matrices constructed also included the process of shrinkage, observed in many jellyfish species, and temporal changes incorporated for different seasons.

Keywords: population dynamics, jellyfish, *Pelagia noctiluca*, model.

Introduction

Sudden population increases and the mass occurrences of different jellyfish species have had a significant impact on human activities in various coastal areas (Cago & Schultz 1967, Anon. 1984, Aubert 1986) and play an important role in structuring pelagic food webs (Möller 1980, Lindahl & Henruth 1983, Peigembaun & Kelly 1984, Malej 1989). Despite the economical and ecological importance of medusae aggregations, little is known about factors which might be responsible for increasing jellyfish populations and terminating swarming.

*Pelagia noctiluca* (Forsskål, 1775), a warm-water holoplanktonic scyphomedusa (Russell 1970), often appears in high densities and shows very large population fluctuations. Typically the species shows a sudden increase in abundance from a virtually non-existent population, then it is very abundant for several years, followed by an abrupt decline without clear symptoms of distress. This phenomenon in the Mediterranean Sea can be traced back to the seventeenth century (Goy 1984). However, most of the essential data needed to explain and predict the population fluctuations are lacking, through recently much new information has been collected within the framework of the United Nations Environmental Programme MED POL – Phase II (Axiak & Civill 1989).

The purpose of this paper is to describe the population dynamics of *P. noctiluca* and provide estimates of growth and mortality rates. The dynamics of the *P. noctiluca* population in the northern Adriatic have been modelled through use of projection matrices and this model is then used to generate hypotheses (Grant 1989) about possible mechanisms that enable this species to reach and sustain high densities.

Material and methods

*P. noctiluca* were collected from the Gulf of Trieste (northern Adriatic Sea) from December 1984 to April 1986 approximately every 3-4 weeks. Medusae were captured either by oblique rows with a zooplankton net or individually with a dip net. *In situ* early growth to a size of 10 mm was followed from August to December 1985 and ephyrae sampled with a 200-μm mesh net approximately fortnightly.

The diameter of live *P. noctiluca* was measured to the nearest mm for bigger animals and 0.1 mm for ephyrae, within 2 h of sampling.

Bell diameter-frequency data through time were used to estimate growth parameters. The length-(bell-diameter)-frequency distribution was analysed using ELFAN (Electro Length Frequency Analysis; Pauly & David 1981). The growth curve was fitted using a seasonally oscillating von Bertalanffy growth formula:

\[ L_t = L_\infty [1 - e^{-K(t-t_0) + C(t-a)} \sin 2\pi (t-t_0)] \]

\( L_t \) = size at time \( t \)
\( L_\infty \) = asymptotic size (the mean size of an animal population would reach if they were allowed to grow indefinitely)
\( K \) = growth constant
\( C \) = amplitude of growth oscillation
\( t_0 \) = intercept at \( L = 0 \) (the age at which the size would be 0 if growth followed the curve throughout life)
\( t_p \) = starting point of seasonal oscillation.
A growth curve was fitted to the diameter-frequency data by an iterative process which varied the values of the parameters, and the program generated the best estimate for the growth parameters $K$, $C$, $t_p$, $t_0$.

The mortality rate was estimated using a simple mathematical model relating weight to mortality rate:

$$ M = \frac{W}{b} $$

$M$ = mortality rate
$W$ = average weight
$b$ = slope from the regression line of weight against bell diameter.

The dynamics of the *P. noctiluca* population has been modelled through the use of projection matrices. The form of the model used is:

$$ n_{x+1} = M \cdot n_x $$

$n_{x+1}$, $n_x$ are column vectors describing the population structure at time $x+1$ and $x$, respectively; $M$ is the matrix which determines the dynamics of the population.

Figure 1 shows a graphical presentation of the matrix model. The medusae were each assigned to one of five size classes: class 1, ephyrae (<1.0 cm diameter); class 2, immature medusae (1.0 < 3.5 cm); class 3, conditionally mature medusae (3.5 < 6.0 cm); class 4, mature (6.0 < 8.5 cm) and class 5 (>8.5 cm). During each time interval (one month) a specimen may either die (D) or survive; surviving individuals may grow (G) stay the same size (L) or shrink (S). The exceptions are survivors of class 1 which can only grow, survivors of class 2 which may grow or stay the same size but cannot shrink to ephyral size and class 5, which are assumed not to grow. It is also assumed that during one month an individual could neither grow or shrink by more than one size class. Recruits (R) to the smallest size class are contributed only by classes 3, 4 and 5 with an increasing proportion of reproducing individuals in larger size classes. The incorporation of demographic parameters such as regression or shrinkage (S) and loop (L) into the matrix reflects the ability of medusae to shrink and stop reproducing (Hamner & Jensen 1974, Larson 1987), recover from shrinking and return to sexual maturity.

$$ M = \begin{bmatrix} 0 & 0 & R_3 & R_4 & R_5 \\ G_1 & L_2 & S_{22} & 0 & 0 \\ 0 & G_2 & L_3 & S_{32} & 0 \\ 0 & 0 & G_3 & L_4 & S_{42} \\ 0 & 0 & 0 & G_5 & L_5 \end{bmatrix}, \quad n_x = \begin{bmatrix} n_{x1} \\ n_{x2} \\ n_{x3} \\ n_{x4} \\ n_{x5} \end{bmatrix}, \quad n_{x+1} = \begin{bmatrix} n_{x+11} \\ n_{x+12} \\ n_{x+13} \\ n_{x+14} \\ n_{x+15} \end{bmatrix}$$

Table 1 presents a projection matrix and corresponding column vectors. The elements along the top row of the matrix represent the recruits per time unit to size classes 3, 4 and 5; 1 and 2 do not reproduce (0). The elements along the sub-diagonal (G) represent the net growth into a larger size class, while the diagonal (L) describes the likelihood of an individual remaining in the same size class. Finally, the probabilities above the diagonal represent the shrinkage (S) as a contribution to the next, smaller size class. The size-specific mortality rate (D) is 1–sum of probabilities in each column: $1 - (G + L + S)$, means that an individual which neither grew to the next size class, remained the same size or shrank, died. Zeros mean that members of class 1 can only grow or die, class 2 may grow, remain the same size but do not shrink, and only classes 3, 4 and 5 reproduce.

**Results**

The diameter-frequency data arranged in 1-cm classes for 1985 are shown in Figure 2. Data are lacking for January–March as *P. noctiluca* were not caught although there were reports of small (<3 cm) but also larger (>5 cm bell diameter) specimens during January and March. Higher numbers of small-sized animals were found in the
population in June and December indicating that new recruits entered the population predominantly during autumn months and, to a lesser extent, in late spring. However, the fact that ephyrae were also found in other months (from April to December) indicates that some minor spawning is possible at other times of the year. Specimens having bell diameter >7 cm were recorded in April, July and during autumn, even though the largest animals (>8 cm) were found only in April.

The von Bertalanffy growth parameters estimated from these histograms are: $K = 0.003$, $C = 10$, and $t_r = 100$. These growth estimates suggest that *Pelagia noctiluca* reaches the minimal size at which it may spawn (~3.5 cm, Rottini et al. 1984) in about five months.

The mortality rates for 1-cm medusae ranged from 0.18 (14%) to 0.57 (43%) per month (0.6-2.0·10^{-3}·d^{-1}). The mortality rates varied seasonally and showed a negative correlation with temperature ($r^2 = 0.56$) and zooplankton carbon (Figure 3) as an estimate of the food availability ($r^2 = 0.34$). An expression describing the mortality rate as a function of temperature and zooplankton carbon was obtained:

$$M = 0.66 - 0.12T^{{\circ}C} - 0.007\text{ zooC} (\text{mg}·\text{m}^{-3})$$

The average survival rate (life expectancy) was estimated to be about nine months. Early growth from August to December 1985 is shown in Figure 4. It seems that either very little growth occurred during August–September or ephyrae suffered high mortality and were replaced by new offspring in September–October. The average growth rate from October to December (at temperatures from 11 to ~18°C) was $8.5·10^{-5}\text{ mm·d}^{-1}$; slightly higher rates were observed by Rottini Sandrini & Avian (1983) and Avian (1986) in laboratory conditions.
Most models of population dynamics using Leslie's matrix keep the matrix coefficients constant. Temporal changes were incorporated into our model by alternating matrices for different seasons, according to the present observations and measurements (Table 2) and using these coefficient values as a basic simulation case (standard run).

**Discussion and conclusions**

The reproduction of *P. noctiluca* has been shown to occur from April to December, with a peak in late summer and autumn; ephyrae growing to an average diameter of ~7 mm in December. Most probably the growth slowed down or even ceased during the winter due to low temperatures (<10°C). As during the spring the increased temperature and more abundant food accelerated growth, a part of this summer-autumn recruited group spawned even during late spring, while most of them seem to breed during late summer-autumn. The specimens having bell diameter around 6-7 cm would thus be about one year old. The growth rates obtained are less than have been reported for other gelatinous organisms (Larson 1986) and also *P. noctiluca* in laboratory conditions (Larson 1987).

The population model of *P. noctiluca* presented is based on a modified Leslie matrix using size rather than age (Hughes 1984). This model was used to examine the effects of earlier maturation (at a smaller size), variable reproduction, growth and mortality rates and the influence of shrinkage. The effect of maturation at a smaller size was tested because of the finding of Rottini et al. (1984), that specimens may be mature at a bell diameter of 3-4 cm in contrast to Franqueville's (1971) observations of mature specimens having a bell diameter >6 cm. The model was run for a range of coefficient values which might reasonably occur in the Mediterranean Sea. The results of the various runs of the simulation model indicate:

- the size at first reproduction significantly affected the population growth: if $R_s$ has been set to 0, a growth rate of a population was halved even if $R_s$ and $R_s$ were 1;
- variations of the growth rates within reasonable limits had little effect;
- an increase in the mortality term by only 5% in all size classes caused a marked reduction of the population, while even a larger increase of the mortality rate in a particular size class had a much less effect;
- the loop term had only a slight effect;
- the elimination of the shrinkage term caused a reduction of the population abundance of about 30% in one year.

A comparison of results from various model simulations suggests the importance of age (size) at first reproduction, i.e. earlier maturation which is probably enhanced in food-rich environment; and shrinkage, recovery and re-maturation occurring in conditions of pulsed food. These seem to be mechanisms which enable the increase and survival of the *P. noctiluca* population.

Considerable effects were produced by a slight increase of the mortality term which affects all sizes. This is more likely due to environmental influences operating at a larger scale than different predators which are preying upon particular size classes, and may therefore explain a sudden collapse of the population.

Using a simple predator-prey model, Legovic (1987) demonstrated the importance of the jellyfish food-source enrichment and the decrease of medusa mortality, of jellyfish competitors and/or predators in increasing the abundance of jellyfish.
The present results of field observations and the model of the population dynamics indicate the need to determine with more precision: the effects of age at first reproduction and rate of egg production, the process of shrinkage (degrowth) and recovery, and mortality rates, especially in relation to variable food regimes. These processes appear to have the greatest influence on population abundance.

Acknowledgements
This work was supported by a RS Slovenija grant and UNEP (Mediterranean Trust Fund).

References


Aubert, M., 1986. Problématique des méduses et risques sanitaires. – Nova Thalassia 8 (Suppl. 4): 137-140.


