

Seasonal population dynamics of *Octopus vulgaris* in the eastern Mediterranean

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The population density of *Octopus vulgaris* was measured by visual census with scuba diving in coastal areas in Greece (eastern Mediterranean). A time-variant, stage-classified, matrix population model was developed to interpret the seasonal variation of octopus stage densities and to estimate several life cycle parameters. An annual and a semi-annual periodic cycle were found in the stage densities. A main peak of benthic settlement was observed during summer and a secondary, irregular one during late autumn. Two spawning peaks were estimated, a main one during late winter – spring and a secondary one during late summer – early autumn. More than 50% of the just-settled individuals will eventually die after 3 months. Mortality rate declines as individuals grow larger, reaches a minimum approximately 6 months after settlement and then grows again probably because of terminal spawning. The life expectancy of recently-settled individuals (<50g) during their summer peak is approximately 5 months. The life-span of the common octopus is estimated to be between 12 and 15 months. The octopuses' mean specific growth rates (\pm s.d.) in their natural environment were $1.61 \pm 0.30 \text{ d}^{-1}$ for 50-200 g individuals and $1.19 \pm 0.31 \text{ d}^{-1}$ for 200-500 g individuals.

Key words: abundance, cephalopod, growth, matrix population model, mortality, octopus, population dynamics, seasonal variation, settlement, spawning

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Introduction

There is a significant worldwide commercial interest in cephalopods for human consumption. World catches of cephalopods have increased steadily throughout the last 50 years with annual landings increasing from 0.5 million tons in 1950 to over 3.3 million tons in 2001 (FAO, 2003). Specifically, *Octopus vulgaris* (common octopus) is an important species for the artisanal as well as industrial fisheries of many countries and commands high prices throughout its distributional range. It is captured by trawls, pots, traps, lures, hook-and-lines, fyke-nets, set-nets, spears etc. *O. vulgaris*' annual landings increased from 3.7 thousand tons in 1950 to over 100 thousand tons in the mid '70s and then gradually declined to slightly over 50 thousand tons in 2001 (FAO, 2003).

Due to the significance of the common octopus fishery and the declining trend in landings during the last decades, there is increasing interest in managing and conserving common octopus stocks. Currently, octopus stocks in Greece are not assessed and managed. There is no management organization and except from a low legal fishing limit of 500 g no other actions have been taken for the sustainability of the stocks. A good understanding of life cycle processes and the variation of vital rates is necessary for sustainable management of stocks. Demographic models are essential tools in that direction.

The distribution and abundance of *Octopus vulgaris* have been investigated in the main fishing areas of the species mainly by trawl surveys (Guerra, 1981; Quetglas *et al.*, 1998; Belcari *et al.*, 2002) but also by pot and trap surveys (Whitaker *et al.*, 1991; Sanchez and Obarti, 1993; Hernandez-Garcia *et al.*, 1998; 2002). The catching efficiency of these fishing gears is highly size-selective for octopuses and also varies according to the season, the time of the day, the maturity stage, the type of substrate and the type of natural dens (Katsanevakis and Verriopoulos, 2004a).

In this study, the abundance of common octopus was surveyed by visual census and a size-structured, time-variant, matrix population model was developed to interpret the temporal variance of the octopus population. Using the model, several life cycle parameters, necessary for developing a conservation policy, were estimated.

Methods

The population density of *Octopus vulgaris* was measured by visual census with scuba diving. All surveys were conducted in coastal areas and on soft sediment in Greece (Eastern Mediterranean). The dives were made at 14 fixed 1600 m² transects (50 x 32 m) at 7 different sites, which were visited monthly, in coastal waters and at depths from 5 to 25 m (Table 1, Fig. 1). It was found in an earlier study (Katsanevakis and Verriopoulos, 2004b) that in these sites there are average or high octopus densities, in relation to the average octopus densities in Greek coastal areas and on soft sediment (Katsanevakis, 2004). Early trials indicated that smaller transects yielded too many zero values and larger transects were unfeasible due to violation of no decompression dive limits. The depth range of each transect (maximum-minimum depth) was less than 5 m. Density measurements lasted from July 2001 till September 2003.

During each dive the researcher recorded all the octopuses present in the transect and classified them, by sight, into one of the following size classes (or stages): class 1 (<50 g), class 2 [50 g, 200 g], class 3 [200 g, 500 g], class 4 (>500 g). To reduce the classification error the authors practiced initially on more than 70 specimens that were used at the lab for other purposes and before the onset of this survey 5 test dives (in other sites) were made where, after classifying 23 animals, the diver collected them and weighted them on shore. 18 out of 23 were classified correctly (78%) and the other 5 were classified into neighboring classes. This error was considered acceptable for the needs of the survey. The exact methodology applied for defining transects and counting octopuses is given in detail in Katsanevakis and Verriopoulos (2004a). Octopuses were never observed to leave their den due to the presence of the diver or due to the applied procedure, so disturbance is assumed to be insignificant. No octopus samples were taken, so as not to affect the local population. The estimation of octopus density by visual census in soft sediment areas is quite accurate and certainly much better than by fishing surveys (Katsanevakis, 2004; Katsanevakis and Verriopoulos, 2004a; 2004b), as on soft sediment the dens of octopuses are very conspicuous and is almost impossible to miss an octopus (except for very small sizes).

For each stage (=size class) and for each month, the mean density of the 14 transects was calculated and taken as that month's density. Fourier analysis was conducted on the time series of the 4 stage densities, using STATISTICA v5.5 software (StatSoft, Inc). Prior to conducting Fourier Analysis, each data set was detrended, padded with 10 zeros (so that the length of the data set was an integral multiple of 12) and 15% tapered (Bloomfield, 1976) to reduce frequency leakage. The spectral density, for each stage time series, was calculated by smoothing the periodogram values via Hamming weighted average transformation (Blackman and Tukey, 1958), with a window width of 3.

Many aspects of the population dynamics of *O. vulgaris* were further investigated with Matrix Population Models (Caswell, 2001), with the aid of MATLAB v5.2 software (The MathWorks, Inc). The complete stage-classified life cycle graph (Caswell, 2001) of *O. vulgaris* is given in Fig. 2a. During a projection time interval, an individual in stage k may survive and grow to stage $k+1$ with probability G_k , or may survive and remain in stage k with probability P_k . Individuals reproduce, with fertility F_k , producing new individuals in the smallest class (eggs). Egg and paralarva densities were not measured in this study and have never been estimated for octopus in any study. Thus, it was necessary to exclude these stages from the analysis as well as the fertilities F_k . To counteract the effect of this removal on the other stages, parameter N_1 was added to the life cycle graph representing individuals that enter size class 1 during the projection interval, and a modified stage-classified life cycle was created (Fig. 2b). Because of this modification, we only carried out transient analysis of the *O. vulgaris* population and no inferences on the population growth rate or ergodicity were made, as there was no link in the model between mature stages (3 and 4) and subsequent recruitment at N_1 (no stock-recruitment effect was modeled).

Seasonal variation of the model parameters (P_k , G_k , N_1) is significant and they may not be considered time-invariant. As the model parameters change significantly during a time period of one month, using monthly projection intervals would induce a large error in the estimation of the parameters. Thus, to estimate the time-variant model, three additional density values were linearly interpolated between any two observed monthly stage densities, thus creating 4 new stage time series S_k (one for each stage k) with projection intervals $\frac{1}{4}$ of a month. The intervals Δt_i were defined to include 8 successive density values, thus 7 projection intervals ($\Delta t_i = 7 \cdot \frac{1}{4} = \frac{7}{4}$ months). Δt_{i+1} included the density values of Δt_i after removing the first value and adding as final term the next value in the density time series S_k . For example, Δt_1 included the observed densities on July 2001, three linearly interpolated values between July 2001 and August 2001, the observed densities on August 2001 and three more values linearly interpolated between August 2001 and September 2001, thus a total of eight values. Δt_2 included three linearly interpolated values between July 2001 and August 2001, the observed densities on August 2001, three linearly interpolated values between August 2001 and September 2001 and the observed densities on September 2001, and so on. As the field data cover a 27-month time interval, there are 98 intervals Δt_i , so $i_{\max}=98$.

Wood's quadratic programming method (Wood, 1997; Caswell, 2001) was implemented sequentially on the intervals Δt_i , thus on time series of 8 population density vectors $\mathbf{n}_i(t)=[n_{i1}(t) \ n_{i2}(t) \ n_{i3}(t) \ n_{i4}(t)]^T$, where $n_{ik}(t)$ is the density of stage k at time t of interval Δt_i , $t=1, \dots, 8$ and superscript 'T' denotes the transpose of vector $\mathbf{n}_i(t)$. Specifically, observing the modified stage-classified life cycle graph (Fig. 2b) we deduce that

$$\begin{cases} n_{i1}(t+1) = P_{i1} \cdot n_{i1}(t) + N_{i1} \\ n_{i2}(t+1) = G_{i1} \cdot n_{i1}(t) + P_{i2} \cdot n_{i2}(t) \\ n_{i3}(t+1) = G_{i2} \cdot n_{i2}(t) + P_{i3} \cdot n_{i3}(t) \\ n_{i4}(t+1) = G_{i3} \cdot n_{i3}(t) + P_{i4} \cdot n_{i4}(t) \end{cases} \quad t = 1, \dots, 7$$

which can be expressed in matrix form

$$\mathbf{n}_i(t+1) = \mathbf{K}_i(t) \cdot \mathbf{p}_i$$

where:

$$\mathbf{p}_i = (P_{i1} \quad G_{i1} \quad P_{i2} \quad G_{i2} \quad P_{i3} \quad G_{i3} \quad P_{i4} \quad N_{i1})^T$$

$$\mathbf{K}_i(t) = \begin{bmatrix} n_{i1}(t) & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & n_{i1}(t) & n_{i2}(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & n_{i2}(t) & n_{i3}(t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & n_{i3}(t) & n_{i4}(t) & 0 \end{bmatrix}$$

Defining

$$\mathbf{z}_i = \begin{pmatrix} \mathbf{n}_i(2) \\ \mathbf{n}_i(3) \\ \vdots \\ \mathbf{n}_i(8) \end{pmatrix} \quad \text{and} \quad \mathbf{M}_i = \begin{pmatrix} \mathbf{K}_i(1) \\ \mathbf{K}_i(2) \\ \vdots \\ \mathbf{K}_i(7) \end{pmatrix}$$

then, for each interval Δt_i

$$\mathbf{z}_i = \mathbf{M}_i \cdot \mathbf{p}_i$$

The vector \mathbf{z}_i and the matrix \mathbf{M}_i are observed quantities. To estimate the parameters in \mathbf{p}_i , the sum of squared deviations between \mathbf{z}_i and $\mathbf{M}_i \mathbf{p}_i$ is minimized:

$$\text{minimize} \|\mathbf{z}_i - \mathbf{M}_i \cdot \mathbf{p}_i\|^2$$

This is equivalent to (Caswell, 2001):

$$\text{minimize} \left(\frac{\mathbf{p}_i^T \cdot \mathbf{G}_i \cdot \mathbf{p}_i}{2} + \mathbf{f}_i^T \cdot \mathbf{p}_i \right), \quad \mathbf{G}_i = \mathbf{M}_i^T \cdot \mathbf{M}_i, \quad \mathbf{f}_i = -\mathbf{M}_i^T \cdot \mathbf{z}_i$$

Parameters P_k, G_k, N_l should be nonnegative and additionally P_k, G_k represent independent probabilities of the fate of an individual in stage k , so their sum cannot exceed 1 ($P_k + G_k \leq 1, k=1,2,3$ and $P_4 \leq 1$). These constraints are expressed in matrix form as:

$$\mathbf{C} \cdot \mathbf{p}_i \leq \mathbf{b}$$

with

$$\mathbf{C} = \begin{bmatrix} -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 \\ 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}, \quad \mathbf{b} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \\ 1 \\ 1 \\ 1 \end{bmatrix}$$

Hence, the complete specification of the quadratic programming problem is:

$$\begin{cases} \text{minimize} & \left(\frac{\mathbf{p}_i^T \cdot \mathbf{G}_i \cdot \mathbf{p}_i}{2} + \mathbf{f}_i^T \cdot \mathbf{p}_i \right) \\ \text{subject to} & \mathbf{C} \cdot \mathbf{p}_i \leq \mathbf{b} \end{cases}$$

This problem is solved by MATLAB, using the routine ‘qp’. The solution \mathbf{p}_i is considered to be valid at the central point of interval Δt_i . Solving the quadratic programming problem for all Δt_i subsequently, a time series of vector \mathbf{p} was created.

The transition matrix (Caswell, 2001), valid at the central point of Δt_i , is $\mathbf{T}_i = (t_{nk}^i)$:

$$\mathbf{T}_i = \begin{bmatrix} P_{i1} & 0 & 0 & 0 \\ G_{i1} & P_{i2} & 0 & 0 \\ 0 & G_{i2} & P_{i3} & 0 \\ 0 & 0 & G_{i3} & P_{i4} \end{bmatrix}$$

The resulting projection model is a linear, time-variant system of difference equations, expressed in matrix form:

$$\mathbf{n}(i+1) = \mathbf{T}_i \cdot \mathbf{n}(i) + [\mathbf{N}_{i1} \quad \mathbf{0} \quad \mathbf{0} \quad \mathbf{0}]^T \quad [\text{Eq.1}]$$

The probability of death for stage k , during a projection interval at time i , was denoted m_{ik} and is

$$m_{ik} = 1 - \sum_n t_{nk}^i \quad [\text{Eq.2}]$$

The following matrix is defined as the fundamental matrix of the chain $\mathbf{T}_i, \mathbf{T}_{i+1}, \mathbf{T}_{i+2}, \dots$, starting at time i :

$$\mathbf{F}_i = \mathbf{I} + \mathbf{T}_i + \sum_{n=1}^{\infty} \prod_{m=1}^n \mathbf{T}_{i+m} \cdots \mathbf{T}_{i+1} \cdot \mathbf{T}_i \quad [\text{Eq.3}]$$

The infinite series in the above relationship was approximated by a finite series whose last term has a norm smaller than 0.01. If to accomplish that accuracy, i should be greater than the maximum i with available data ($i_{\max}=98$), the time series of \mathbf{T}_i was projected further assuming a 12 month periodicity (=48 projection intervals) according to the relationship $\mathbf{T}_i = \mathbf{T}_{i-48}$ (for every $i > 98$). The elements (f_{nk}) of the fundamental matrix \mathbf{F} are the expected values of the number of visits to transient state n before death, given that the individual starts in stage k . If the time to death, starting in transient stage

k , is denoted η_k , then the mean value of η_k , which is the life expectancy, is the sum of column k of the fundamental matrix \mathbf{F} (Caswell, 2001); thus, for the time interval Δt_i , where $\mathbf{e}^T = (1 \ 1 \ 1 \ 1)$,

$$(\bar{\eta}_{i1} \ \bar{\eta}_{i2} \ \bar{\eta}_{i3} \ \bar{\eta}_{i4}) = \mathbf{e}^T \cdot \mathbf{F}_i \quad [\text{Eq.4}]$$

The specific growth rate (SGR) was calculated with the use of the formula:

$$SGR = 100 \cdot \frac{\ln W_f - \ln W_i}{t_{i \rightarrow f}} \quad [\text{Eq.5}]$$

where W_f and W_i are the final and initial weight respectively, during a time interval $t_{i \rightarrow f}$. The upper limit of the stage k was used as W_f , the lower limit of the same stage as W_i and the mean duration of the stage as $t_{i \rightarrow f}$. The mean duration of the stage is the mean time an individual needs to pass from the lower size limit of the stage to the upper one. SGR was calculated only for stages 2 and 3, since only these stages have definite size limits: [50 g, 200 g] for stage 2 and [200 g, 500 g] for stage 3. The mean duration of stage k could be taken as the k diagonal element of the fundamental matrix \mathbf{F} (the expected value of the number of visits to transient state k before death, given that the individual starts in state k). But, in this way, individuals that never reach the upper size limit of the stage (due to mortality) cause an underestimation of the mean stage duration. To correct this underestimation a new matrix \mathbf{F}^* was used, which comes from (Eq.3) after replacing P_{ik} with $(1-G_{ik})$ for $k=1,2,3$ in every \mathbf{T}_i . By this way, zero mortality is assumed and the final stage is the only absorbing state. Then the mean duration of stage k was taken as the k diagonal element of matrix \mathbf{F}^* .

Results

The observed mean monthly stage densities are presented in Fig. 3. The time series of the 4 stage densities were processed using Fourier Analysis to explore cyclical patterns of data. Two main peaks appear in all four spectral density graphs (Fig. 4), at periods of 12 and 6 months. The 12 month peak is the most significant peak for stages 1, 2 and 3, while at stage 4 the two peaks are approximately equal. Thus, there are cyclical patterns in the densities of the size classes of *O. vulgaris* with annual and semi-annual periodicity. To verify that the periodicity found by the Fourier analysis is significant, we tested the distribution of periodogram values against the exponential distribution (Kolmogorov-Smirnov d statistic), which would occur in case of no significant periodicity. In all four cases the distribution of periodogram values was significantly different ($p < 0.001$) from the exponential distribution ($d_1=0.47$, $d_2=0.47$, $d_3=0.44$, $d_4=0.38$, for the four stages respectively) (Zar, 1996).

The Fourier series approximation of the stage densities time series was calculated, keeping only the annual (period 12) and semi-annual (period 6) cosine and sine terms (Fig. 5). We observe a main peak of stage 1 density during mid-July, followed by a peak of stage 2 density during late July – early August and successive peaks of stages 3 and 4 densities during late August and December respectively. Secondary density peaks appear during January for the first 3 stages and at the end of May for stage 4.

The time series of the matrix population model parameters (elements of vector \mathbf{p}) were smoothed using a 13-point weighted moving average filter (Fig. 6), in order to bring out the major patterns and de-emphasize minor fluctuations. The weights of the moving average filter were $w_0=w_1=1.0/8.8$, $w_2=0.9/8.8$, $w_3=0.8/8.8$, $w_4=0.6/8.8$, $w_5=0.4/8.8$ and $w_6=0.2/8.8$, where the index accounts for the distance from the central point.

N_1 expresses the density of young octopuses that have just entered stage 1, so it is a good approximation of the benthic settlement of octopus paralarva. A main settlement peak was observed during summer (Fig. 6), which in 2002 began to develop in May and in 2003 began to develop in April. A secondary settlement peak was observed during late autumn, which was more significant in 2001 and minor in 2002. These peaks were followed by stage 1 peaks, then by stage 2 peaks and so on (Figs 3 and 5). The succession of density peaks is more apparent following the main summer benthic settlement, while the secondary settlement peak seems unstable and it is difficult to track it through the following stages. Two different cohorts are formed this way annually, which mix and create complicated density patterns. The larger the size class the more complicated the density pattern (Figs 3 and 5).

Stage probabilities of death during a projection interval m_k (stage mortality rates) were calculated using Eq. 2 (Fig. 7). Fourier analysis was conducted on stage mortality rate time series (detrended and 15% tapered). The spectral density of m_1 had two peaks at periods of 6 and 12 months, of m_2 had two peaks at periods of 4 months and 12 months, of m_3 had no peak and of m_4 one peak at a period of 6 months. During the main benthic settlement peak (late spring – summer) m_1 is minimum, favoring the survival and development of the new cohort. Mortality of stage 4 (m_4) has a semi-annual periodicity with one peak during late winter – early spring and one during late summer – early autumn. As *O. vulgaris* is a terminal spawner, these maximum mortality periods probably indicate two main spawning seasons, followed by octopus death.

To evaluate the fate of an octopus settled either during the main or during the secondary settlement peak, an initial population density vector $\mathbf{n}_i = [1 \ 0 \ 0 \ 0]^T$ was successively left multiplied by the transition matrices $\mathbf{T}_i, \mathbf{T}_{i+1}, \mathbf{T}_{i+2}, \dots$. After each multiplication, the new population density vector expressed the projected stage synthesis of the population. The index i was chosen to correspond either to the main or to the secondary settlement peak ($i = 43$ and $i = 15$ respectively). The fate of an instantaneous settlement episode during the two peaks is presented in Fig. 8. When settled during the main period, after the stage 1 peak, 15 days pass for the stage 2 peak, 61 days for the stage 3 peak and 213 days for the stage 4 peak. Over 50% of the individuals entering stage 1 will eventually die after 3 months. Total mortality rates were calculated as the first differences of the ‘Total’ data of Fig. 8 and are presented in Fig. 9. The mortality rate declines, as individuals grow larger, reaches a minimum approximately 5 to 6 months after settlement and then grows again probably because of terminal spawning. The life expectancy of individuals that at time i entered stage k , was calculated with Eq. 4 for the first year of the study (Fig. 10).

The SGR of stages 2 and 3 was calculated using Eq. 5 (Fig. 11). The mean SGR over the first year of the study was calculated and was (\pm stand. dev.): $\text{SGR}_2 = 1.61 \pm 0.30 \text{ d}^{-1}$ for stage 2 and $\text{SGR}_3 = 1.19 \pm 0.31 \text{ d}^{-1}$ for stage 3.

With initial vector $\mathbf{n}_1 = [0.312 \ 1.062 \ 0.472 \ 0.326]$ (observed at the central point of interval Δt_1) and sequential projection using the matrix model (with the smoothed P_i 's and G_i 's but the unsmoothed N_1 as initially estimated), a stage-structured population density time series was calculated and compared with the observed one (Fig. 12). Although the parameters P_i and G_i were intensely smoothed with a 13-point weighted moving average filter, the model fits the observed data very well during the first year ($R^2=0.95$) and adequately over the whole time range of observed data ($R^2=0.77$).

Discussion

Two main benthic settlement periods were found for *O. vulgaris*, a main one during late spring – summer and a secondary one during late autumn. Furthermore, stage 4 mortality had a semi-annual periodicity with 2 peaks, one during late winter – early spring and one during late summer – early autumn, probably related to spawning and hatching. These mortality peaks occur just before the settlement peaks, strengthening the argument of two main spawning periods during the year in the eastern Mediterranean. Taking into account the length of embryonic development and planktonic life in relation to the time of the year (Katsanevakis, 2004) we estimate that for the summer main settlement peak, a spawning peak during late winter – spring should occur, while for the late autumn settlement peak, a spawning peak during August – September should occur. Both spawning seasons coincide with the aforementioned mortality peaks.

Spawning all year around with two main seasons, one from January to July with a peak in April and one in October – November has been estimated off the coast of the Canary Islands (Hernández-García *et al.*, 2002). Off the Azores, Gonçalves (1991) reported two spawning peaks, a main one in September and a secondary one in May. Two spawning peaks in spring and autumn were also reported by Hatanaka (1979) for the northwest coast of Africa. On the Spanish Mediterranean coast, Sánchez and Obarti (1993) argue that there is one main reproduction period lasting from January to July, although mature females were also found in autumn, but not regularly. Such an irregularity in the secondary settlement peak during late autumn was also found in this study, with the secondary peak in autumn of 2002 being almost negligible. It seems possible that the secondary settlement peak is irregular and quite dependable on annual environmental variation.

Close examination of the fate of individuals (Fig. 8) settled during the summer peak (end of June), clearly reveals that the maximum of stage 4 density will occur approximately 210 days later (end of January). The graph of total density declines steeply later on, for about two months, indicating that the corresponding spawning period is during February – March. At this time of the year, octopus eggs need about 2-3 months to hatch and 1-2 months to settle (Katsanevakis, 2004). Thus, settlement will occur during June-July. In this way an exact 12-month cycle is completing. So, the summer settlement peak creates annual periodicity and, therefore, is stable and repetitive. As for the fate of individuals settled during the late autumn peak (end of November), it is evident that the maximum of stage 4 density will occur approximately 180 days later (end of May) and the corresponding spawning peak will be during June, July and early August. During this period, embryonic development is completed in about one month and settlement will occur during August, September and October (Katsanevakis, 2004). In this case, the time interval between the late autumn benthic settlement and the next settlement is less than a year (10-11 months), so there is no annual periodicity; this is a possible explanation of the irregularity of the secondary settlement peak.

According to the aforementioned reasoning and assuming that spent individuals will survive for 2-3 more months, the life-span of the common octopus, would be between 12 and 15 months. Hernández-López *et al.* (2001) estimated a lifespan of 12-13 months for *O. vulgaris* in the Canary Island waters, by counting the number of concentric rings on the upper beaks of 275 octopuses (this method, though, was validated only for the paralarval stage). Several hypotheses have been made about longer-lived individuals (Mangold, 1983) but they are not substantiated. Nevertheless, the majority of octopuses that will manage to spawn should expect to live 12-15 months and a longer life-span, if possible, would be exceptional in eastern Mediterranean

coastal areas. Of course, at deeper sites with lower temperatures, hence slower development and maturation, a longer life might be possible. However, octopus densities decline with depth and are mostly restricted below 100m depth with maximum densities in areas shallower than 50m (Belcari *et al.*, 2002). Hence, the environmental conditions of our study are close to the ‘average environment’ encountered by an octopus.

The specific growth rates for stage 2 were higher than for stage 3, as expected. The mean relative daily growth rate during the first 50 days of benthic life of reared individuals was 10.6% as measured by Itami *et al.* (1963). Short-term relative growth rates of small animals reported by Nixon (1966) averaged about 4%. Animals maintained at 20°C, ranging from 100 to 1000g, had growth rates of 1.14 to 5.08% (Mangold and Boletzky, 1973). The estimated field daily growth rates of this study (mean, relative to the initial stage weight) were 3.5% for stage 2 and 1.9% for stage 3, with maximum rates of 4.8% for stage 2 and 2.9% for stage 3. Field growth rates were of similar magnitude as laboratory values but lower than the maximum growth rates that cultured animals reached when fed *ad libitum*. This indicates that *O. vulgaris* in its natural environment in the eastern Mediterranean does not fully utilize its potential for growth.

Compared to trawl or pot and trap surveys, a visual census has many benefits (Katsanevakis and Verriopoulos, 2004a) and stage-specific densities are measured more accurately. An underestimation of stage 1 densities is possible, since very small octopuses (<10g) are difficult to spot visually. The consequence of such an underestimation would be: (1) an underestimation of stage 1 duration, and (2) a positive time shift of function N_1 , which means that the real settlement peaks might be a couple of weeks earlier than those estimated.

A complete matrix population model would require the knowledge of fertilities as well as egg and paralarva densities. The paralarva density (and in particular its seasonal variation) has not been estimated (in any published work), as there are many difficulties in sampling and in converting paralarva catches into densities. Estimation of egg production in the field is also difficult, because eggs are laid inside the den and tended by the female till they are hatched. It is difficult to spot eggs by visual census too, as they may be deep inside the den or completely covered by the female’s body. A thorough search for eggs in a den would cause, in most cases, serious disturbance to the octopus and possible desertion of the den, which was contrary to our minimum disturbance policy adopted to achieve unbiased density measurements. Transportation of paralarvae by currents is significant and no dynamic equilibrium may be assumed at a restricted site (as was done for benthic stages) but rather more complicated multiregional models should be used. For these reasons, this study was limited to transient analysis of part of the population, ignoring egg and paralarva stages as well as fertilities.

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Table 1. Sites and transects of octopus density measurements

| Site | Coordinates | Transect Depth Range (m) |
|--------------|-----------------------|-------------------------------------|
| Mikro Amoni | 37°50'12"N 23°07'36"E | 15-20 |
| Mikro Amoni | 37°50'12"N 23°07'36"E | 10-15 |
| Megalo Amoni | 37°50'00"N 23°08'12"E | 20-25 |
| Megalo Amoni | 37°50'00"N 23°08'12"E | 10-15 |
| Sideronas | 37°50'48"N 23°02'24"E | 20-25 |
| Sideronas | 37°50'48"N 23°02'24"E | 5-10 |
| Lychnari | 37°50'36"N 23°04'00"E | 15-20 |
| Frangolimano | 37°50'24"N 23°06'48"E | 20-25 |
| Frangolimano | 37°50'24"N 23°06'48"E | 10-15 |
| Loumbarda | 37°49'00"N 23°50'12"E | 10-15 |
| Kitries | 36°55'00"N 23°07'30"E | 20-25 |
| Kitries | 36°55'00"N 23°07'30"E | 15-20 |
| Kitries | 36°55'00"N 23°07'30"E | 10-15 |
| Kitries | 36°55'00"N 23°07'30"E | 5-10 |

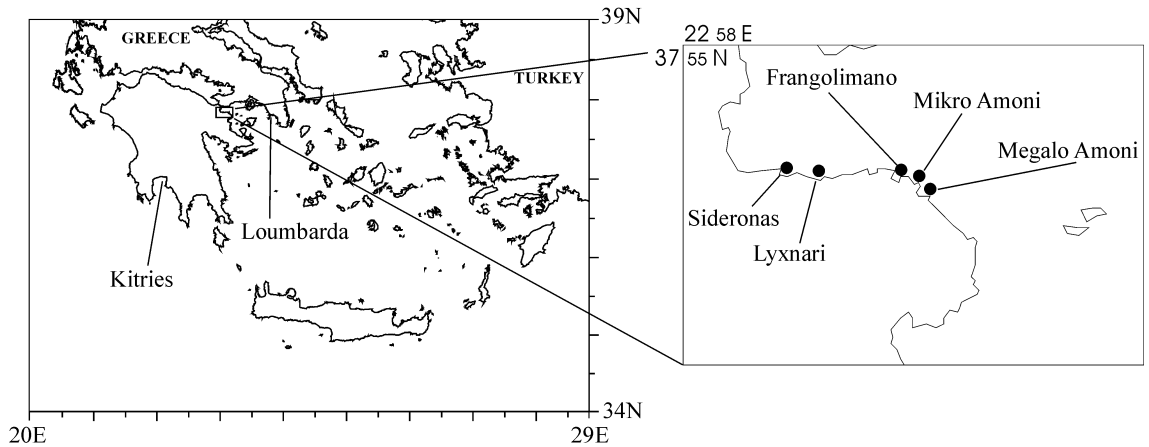


Figure 1. Map with the locations of the sites of the survey.

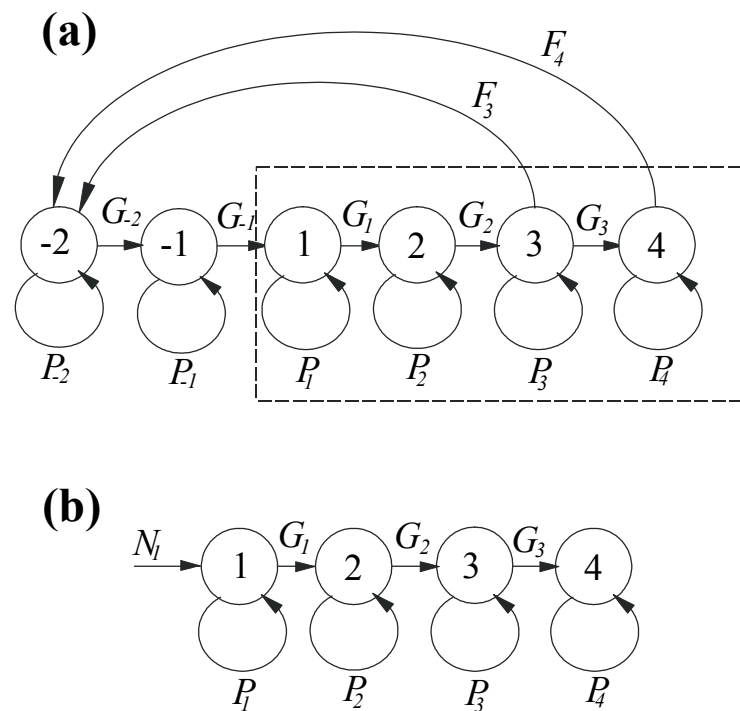


Figure 2. (a) Complete stage-classified life cycle graph of *O. vulgaris*. (b) Modified stage-classified life cycle graph of *O. vulgaris*. '-2' stands for egg stage and '-1' for paralarva stage. Stages 1-4 correspond to size classes 1-4. For each stage k , G_k is the probability that an individual will survive and grow to stage $k+1$, P_k is the probability that an individual will survive and remain in stage k and F_k is the corresponding fertility.

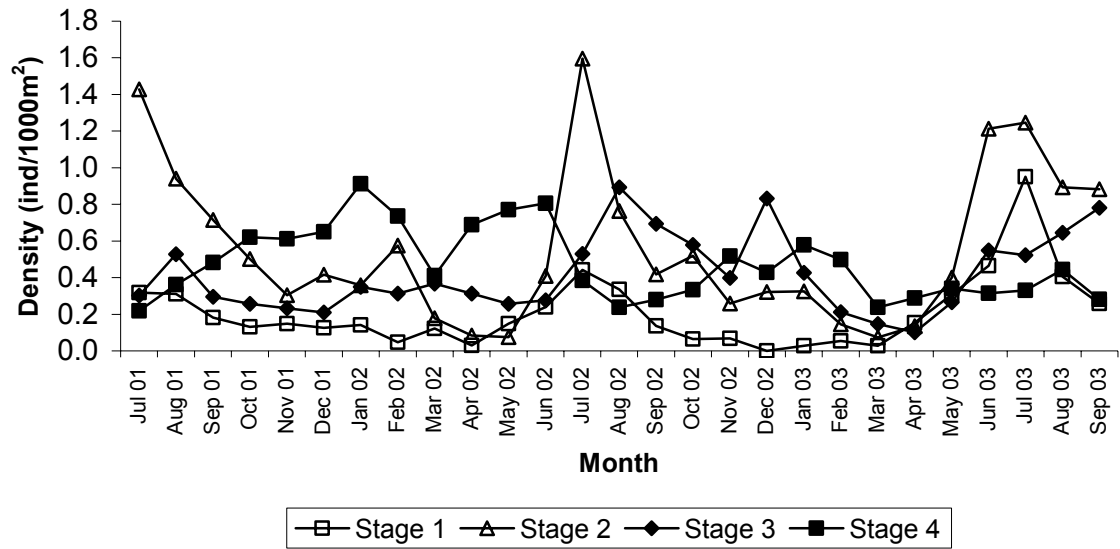


Figure 3. Monthly variation of stage-specific octopus densities, measured as individuals per 1000m² (ind/1000m²) from July 2001 till September 2003. Each density value is the mean of the estimated densities of the 14 transects.

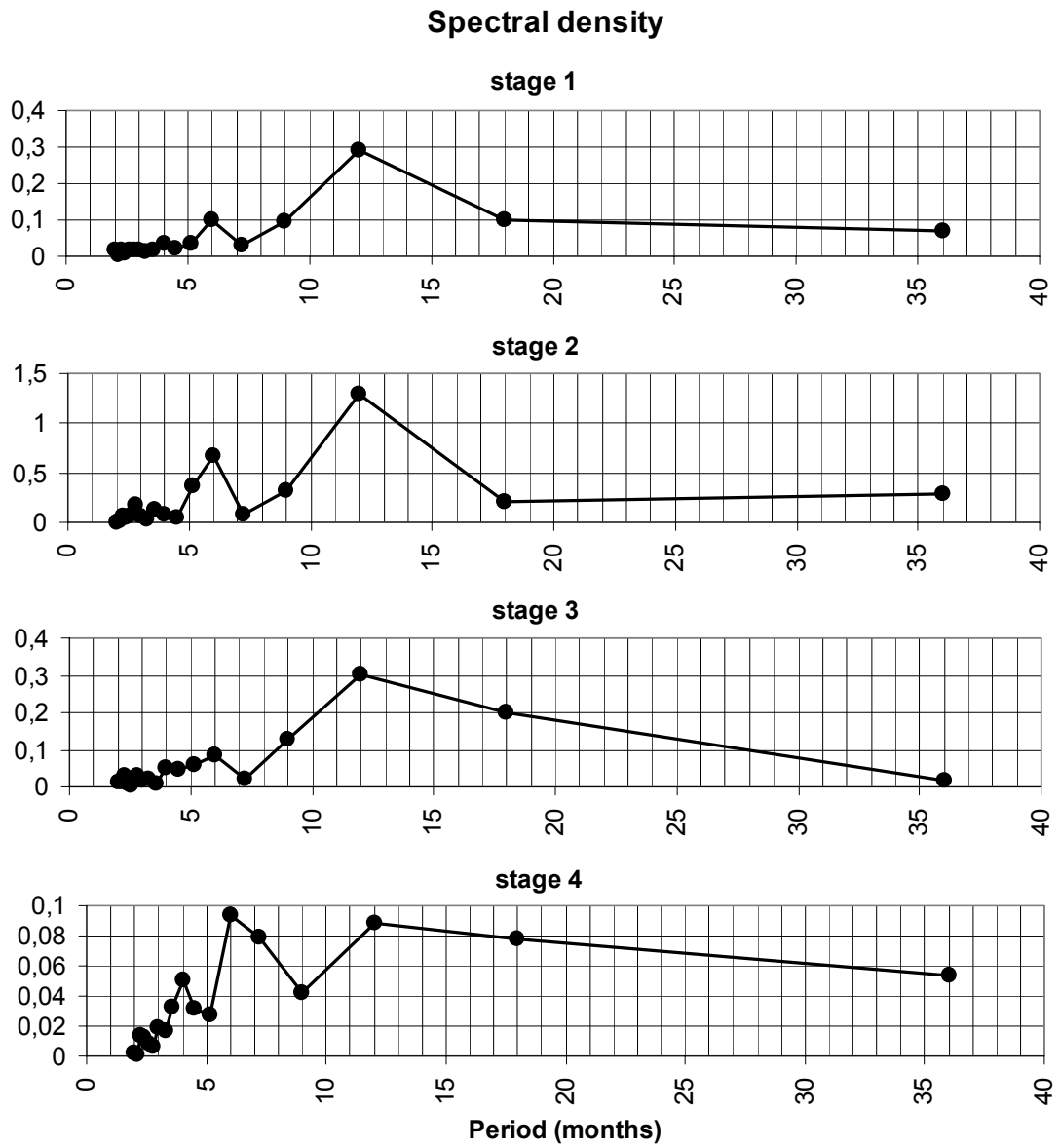


Figure 4. Spectral densities of the time series of each stage density.

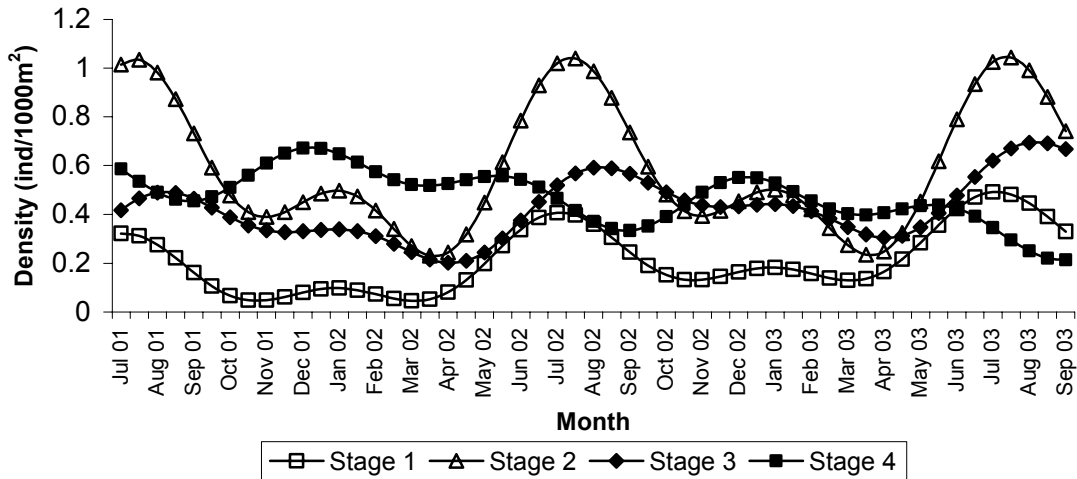


Figure 5. Fourier series approximation of the stage densities time series, keeping only the terms with periods 12 and 6 (for annual and semi-annual periodicity).

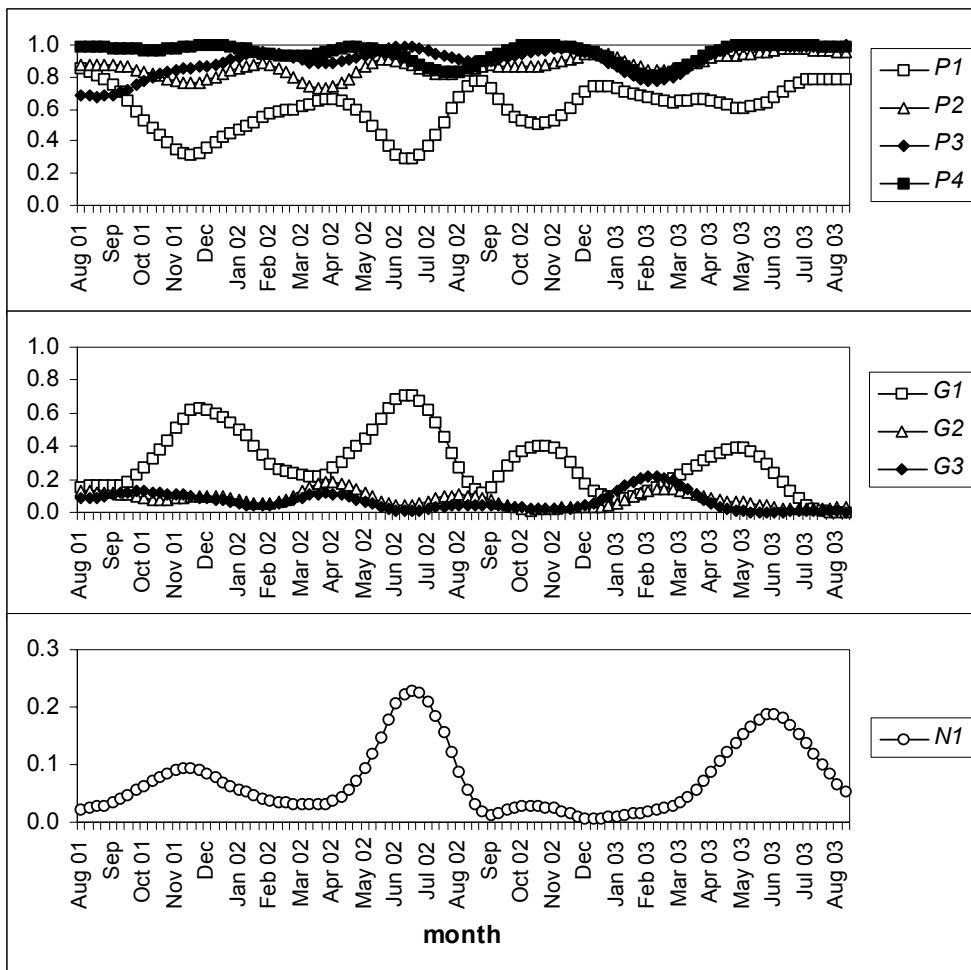


Figure 6. Smoothed matrix population model parameters P_k , G_k and N_1 . P_k is the probability that an octopus will survive and remain in stage k , G_k is the probability that it will survive and grow to stage $k+1$, and N_1 represents the density of individuals entering stage 1 during a projection interval. As the parameter values each time correspond to the central point of Δt , the time range of these graphs is narrower than the time range of the observations.

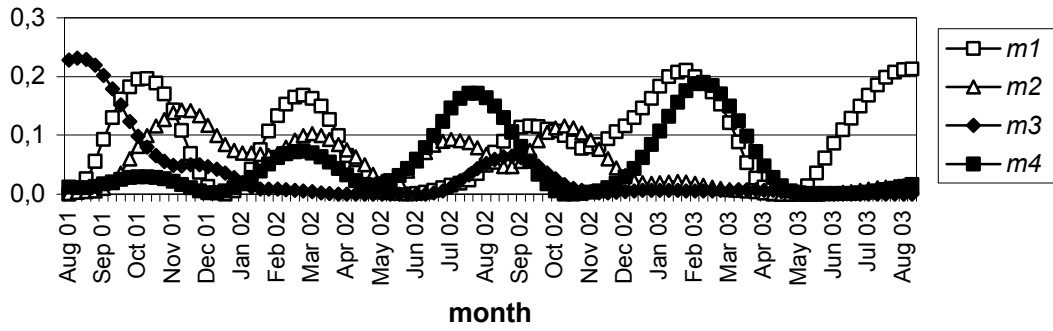


Figure 7. Stage probabilities of death m_k .

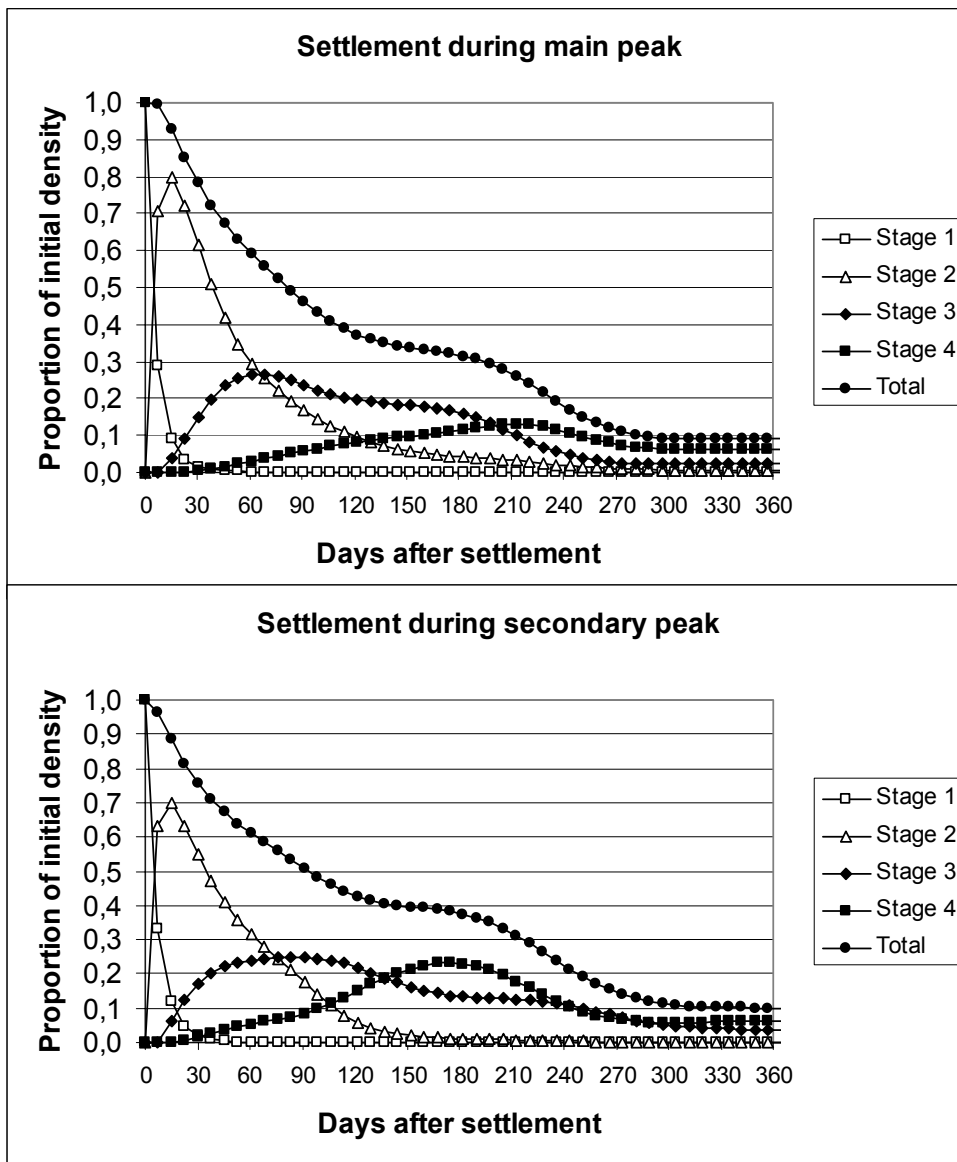


Figure 8. The fate of individuals settled during the main or the secondary settlement peak periods.

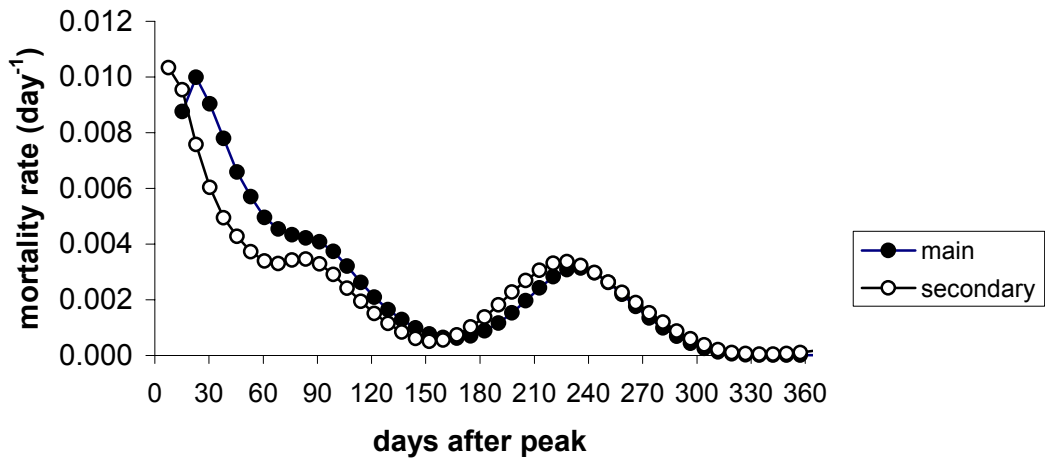


Figure 9. The mortality rates of octopuses settled during the main or the secondary settlement peak periods.

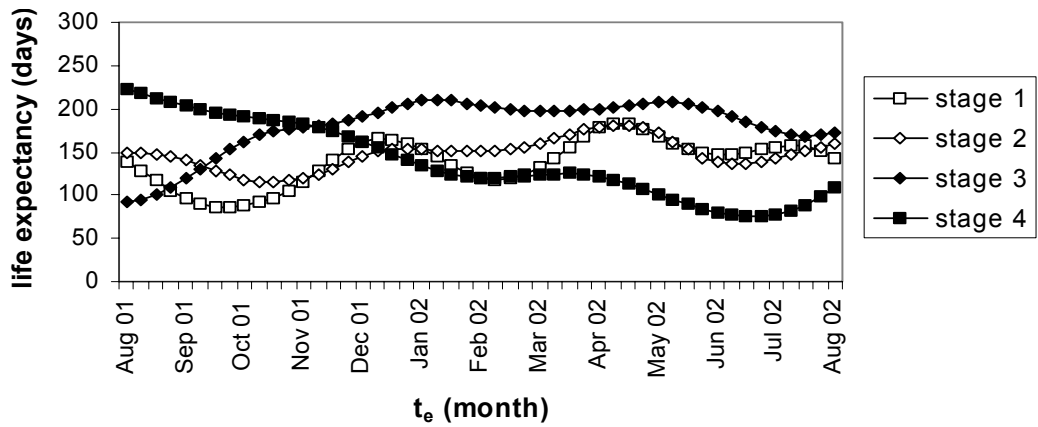


Figure 10. Life expectancy of individuals that entered stage k , at time t_e .

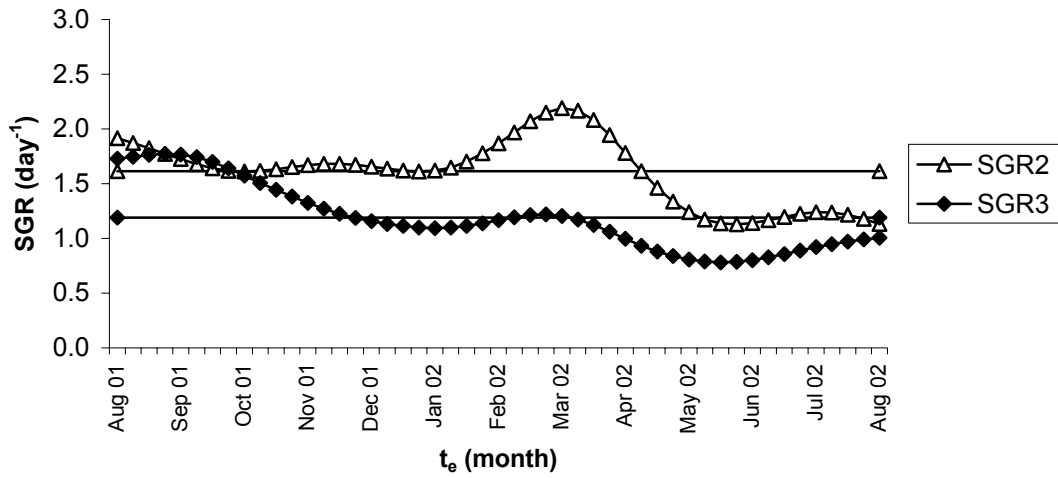


Figure 11. Specific growth rates (SGR) of individuals that entered stage k , at time t_e , calculated as a mean during their presence in stage k . The annual means of SGR are given as straight horizontal lines.

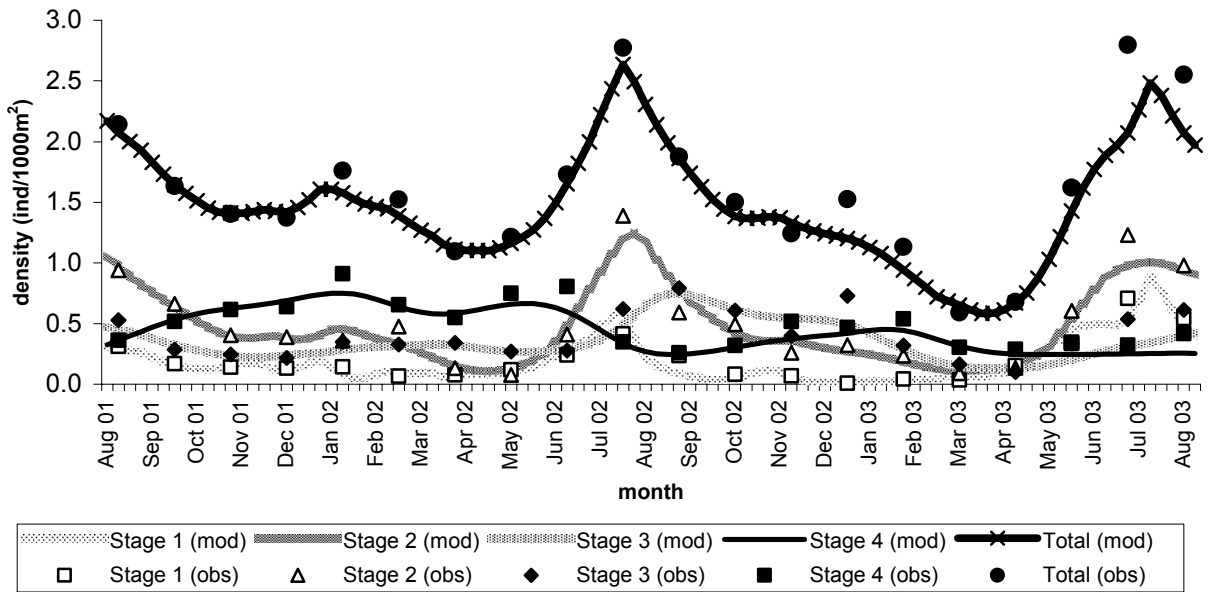


Figure 12. Model predictions, starting from an initial density vector n_1 equal to the observed vector at that time, vs observed densities. Lines represent model estimations and markers represent observed data.