



## Comparative Pattern of *Octopus vulgaris* Life Cycle with Environmental Parameters in the Northern Alboran Sea (Western Mediterranean Sea)

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### Abstract

*Octopus vulgaris* is a short living species with environmental adaptive plasticity and high fecundity. Its abundance can experience large fluctuations highly dependent on the recruitment success. Both, these abundance fluctuations and the reproductive season seem to be influenced by the variability of environmental conditions which can determine the beginning and the length of the spawning period, the existence of one or several spawning peaks and the length of both the embryonic and planktonic phases. Beside this inter annual variability, the availability of long time series of octopus landings and biological data can allow us to define a mean or average length for the different phases of the octopus life cycle. Time series for landings, biological and environmental data in the Alboran Sea are analyzed in the present work. Sexual maturity data are used to determine the average spawning season. The ratio of mature females in coastal waters and GSI indicate that spawning occurs during June, July and August. Temperature time series in the Alboran Sea are used to calculate the length of the embryonic and planktonic phases for *O. vulgaris*. According to our results, individuals spawned during late spring and summer would settle during September, October and November, incorporating to the fisheries some weeks later. These results from our simple model agree with landings time series which show maximum landings from October to January or February.

**Keywords:** *Octopus vulgaris*, life cycle, reproductive stages, spawning and settling, Cephalopods, environmental factors.

### Introduction

Cephalopod landings have considerably increased in the Mediterranean from mid twentieth century to the beginning of twenty first century (Pierce *et al.*, 2010), being octopus one of the species contributing to this increment. Additionally to the positive trend of octopus catches in Mediterranean fisheries, this species also exhibits important fluctuations. In order to understand the origin of these fluctuations, it has to be considered that *Octopus vulgaris* is a short lived species (1-2 years, Hastie *et al.*, 2009) with rapid growth and high fecundity. Therefore, Octopus abundance is linked to recruitment success which is highly dependent on environmental conditions (Sonderblohm, Pereira & Erzini, 2014; Boyle & Rodhouse, 2005) and, in some cases, to the combined effect of fishing and environmental variability (Quetglas *et al.*, 2013).

Several works have evidenced that octopus is a species with environmental adaptive plasticity (Lourenço, Moreno, Narciso, González & Pereira, 2012; Puerta, Hidalgo, González, Esteban & Quetglas, 2014). Environmental factors seem to modulate mainly the reproductive season and

therefore the whole life cycle of *Octopus vulgaris*. Rocha, Guerra, Prego and Piatkowski (1999) found that the hatching period in Galician waters was mainly at the end of spring and during summer, coinciding with the upwelling season which would favor prey availability. Lourenço *et al.* (2012) found that the spawning season in the Portuguese coast had two peaks in February-April and in June-July in the Northwest, while it occurred mainly in summer in the southern coast. These differences were attributed to the influence of the upwelling period in the northwestern coast and to more stable conditions in the southern one. Otero, González, Sieiro and Guerra (2007) reported that spawning happened in Galician waters during an extended period from December to September with a peak in spring. According to these authors the octopus reproductive strategy was based on the coincidence of the spawning period with the maximum upwelling intensity. Otero *et al.* (2008) also found that environmental factors such as chlorophyll concentration, Ekman transport, water temperature or zooplankton abundance were key factors modulating the whole life cycle of *O. vulgaris*. Sobrino, Juárez, Rey, Romero and Baro (2011) described a seasonal cycle for the octopus catches from the artisanal fleet

in the Gulf of Cadiz which was related to the life cycle of this species. According to these authors, maximum catches would occur in winter coinciding with the recruitment period.

Beside the importance of the spawning period, conditioned by environmental factors (Lourenço *et al.*, 2012; Otero *et al.*, 2007, 2008), the evolution of the abundance of *O. vulgaris* is also dependent on other parameters affecting the different phases of its life cycle. Both the duration of the embryonic and the paralarval or planktonic phases seem to be determined by the temperature of sea water (Katsanevakis & Verriopoulos, 2006). Furthermore, if the octopus catches are used as a proxy of its abundance, migratory movements should also be considered (Quetglas, Alemany, Carbonell, Merella & Sánchez, 1998; Bas, 1979; Mangold & Wirz, 1963).

Belcari, Cuccu, González, Srari and Vidoris (2002) analyzed data from trawling surveys in the Western Mediterranean during spring. *O. vulgaris* was distributed in the continental shelf to a maximum depth of 200m. The abundance of immature individuals was attributed to the migration of mature individuals to coastal waters. González, Barcala, Pérez-Gil, Carrasco and García-Martínez (2011) also pointed out that mature males were found all the year round being the reproductive season determined by the maturity of females. Both males and females migrate to coastal waters for breeding. Some weeks after settlement individuals incorporate to fisheries, normally in late autumn or winter. According to González *et al.* (2011), the reproductive cycle of *O. vulgaris* is not yet well known in Mediterranean waters. The purpose of the present work is to describe the octopus life cycle in the Alboran Sea (westernmost sector of the Mediterranean Sea). The evolution of the maturity stage of octopus and the most likely time for spawning will be determined from biological data from landings in some selected ports. The length of the embryonic and planktonic phases will be calculated from temperature time series obtained in the Alboran Sea in the frame of different monitoring programs. The combination of these results will be used to obtain the relative abundance of settled individuals. Considering that recruitment occurs a few weeks after settlement, these results will be compared with landings in the Alboran Sea, trying to close in this way the complete octopus life cycle.

## Data

### Fisheries and Biological Data

*Octopus vulgaris* landings and biological data were obtained from three different sources. The first one is made of monthly landings provided by the Organization and Regulation fund for fisheries and aquaculture products (FROM: Fondo de Regulación y Organización del Mercado de Productos de la pesca y cultivos marinos). This organization belongs to the Spanish Ministry for Agriculture and Fisheries. The

second one is made of landings data provided by the Junta de Andalucía Agriculture and Fisheries council (Consejería de Agricultura y Pesca y Desarrollo Rural) and the third one is made of biological data collected by the Spanish Institute for Oceanography (IEO: Instituto Español de Oceanografía) in the frame of the Spanish National Data Collection Program.

FROM data are monthly octopus landings for the following ports in the Western Mediterranean Sea: Estepona, Marbella, Fuengirola, Málaga, Vélez, Motril, Adra, Roquetas, Almería. These ports are located in the northern coast of the Alboran Sea. Their position is shown in Figure1, modified from Figure1 in Vargas-Yáñez *et al.* (2009). Available landings data from different gears are pooled and extend from 1987 to 2001. Information concerning the fishing effort was not available.

Junta de Andalucía data extend from 2001 to 2008. These data correspond to *O. vulgaris* monthly landings segregated by fishing gear (artisanal or trawling). The number of fishing days is available. Fishing days have been used as a measurement of the fishing effort and monthly landings per unit effort (LPUE) were obtained dividing the monthly landings in tones by the number of fishing days. These data correspond to the same ports considered in FROM data: Estepona, Marbella, Fuengirola, Málaga, Vélez, Motril, Adra, Roquetas, Almería (Figure1).

From 1999 to 2008, the Spanish Institute for Oceanography collected biological data from *O. vulgaris* landings. Individuals from landings in Fuengirola and Málaga port were purchased and then analyzed in the laboratory.

### Environmental Data

The Mediterranean Group for Climate Change from IEO (GCC, [www.ma.ieo.es/gcc](http://www.ma.ieo.es/gcc)) measures the temperature of sea water in Fuengirola beach on a daily basis. This time series has been averaged in order to construct a monthly temperature time series extending from 1987 to 2008. A network of oceanographic stations distributed along the Spanish Mediterranean continental shelf and slope is periodically visited in the frame of IEO project RADMED (López-Jurado *et al.*, 2015; Vargas-Yáñez *et al.*, 2012). Temperature profiles from the sea surface to the bottom are obtained for all the oceanographic stations. These stations are visited with a seasonal periodicity (four times per year). Three-monthly temperature time series at a coastal station in front of Cape Pino (close to Fuengirola, P1 in Figure1) have been used in this work.

## Methods

### Seasonal Cycles for Octopus Landings

For each port a time series of monthly landings from 1987 to 2008 was calculated. Data from the FROM and Junta de Andalucía were used together.

The final time series are made of FROM data from 1987 to 2000 and Junta de Andalucía data from 2001 to 2008. Figure 2 shows an example for Estepona port (westernmost sector of the analyzed area, Figure 1). The purpose of the present work is to analyze the average annual or seasonal cycle for octopus life. As a first step we calculate this average cycle for each of the nine ports already mentioned from Estepona to Almería. All the available data for each port and month of the year were considered. For instance, for the Estepona port, we considered all the landings data corresponding to January, all the data corresponding to February, etc. For each data group, the normality of data was checked by means of Chi-squared and Kolmogorov-Smirnov tests. For each port and month, a mean value was calculated and confidence intervals at the 95% confidence level were calculated assuming a t-student distribution for the mean (Zar, 1984).

Figure 2 shows an example of the followed procedure. Figure 2a is the time series of monthly landings for Estepona Port. Figure 2b is a zoom for some years. This figure shows that, although different years follow a similar pattern, each year has significant differences. Figure 2c is the averaged annual or seasonal cycle for octopus landings. Dashed lines are the 95% confidence intervals for the mean value corresponding to each month of the year. The average annual cycle of octopus landings is considered as an indication of the annual cycle of octopus abundance in the Alboran Sea. As the catches and landings could depend on the fishing effort instead of the abundance, LPUE should be used. Nevertheless, this would reduce considerably the length of our time series as fishing effort data previous to 2001 were not available. Following Vargas-Yáñez *et al.* (2009) the validity of landings data was checked analyzing the correlation between landings and LPUE.

### Seasonal Temperature Cycles

For the temperature time series a similar procedure was followed. Daily temperatures from Fuengirola beach were used to calculate an average annual cycle. The normality of temperature data was checked by chi-squared and Smirnov-Kolmogorov tests and the 95% confidence intervals for the means were obtained assuming a t-student distribution (Zar, 1984). In the case of Cape Pino oceanographic station, (P1 in Figure 1) temperature time series at the sea surface and at 25m depth were used. These time series are three-monthly (four data per year). In this case the average annual or seasonal cycle was obtained calculating a mean value for each season of the year.

### Seasonal Cycle for Biological Data

From 1999 to 2008, landings in Fuengirola and

Málaga ports were purchased and sampled by technicians from IEO. The sampling was carried out for the 12 months of the year and corresponds to landings from the artisanal fleet in Fuengirola port and from the trawling fleet in Málaga Port (Figure 1). A total of 642 individuals were sampled in Fuengirola port, corresponding to 330 males and 332 females. 1336 individuals were sampled in Málaga port, with 726 males and 609 females. The biological analysis included measurements of the dorsal mantle length in mm (DML), total weight in g (TW), sex determination and gonad weight (GW). Following Sánchez and Obarti (1993), Quetglas *et al.* (1998), the state of gonad maturity was determined establishing three states: I) Immature, II) maturing, III) mature (table 1). Gonad somatic index (GSI) was calculated using  $GSI = \frac{GW}{TW - GW} \cdot 100$  (Silva, Sobrino & Ramos, 2002).

The proportion of mature individuals or the values of GSI fluctuate. These fluctuations have both a monthly and an inter-annual variability. As we are interested in the average seasonal cycle, maturity data were grouped by months of the year. The proportion of mature individuals for each month of the year was estimated and confidence limits for the estimated proportion were calculated using a binomial distribution (Zar, 1984). The mean values of the GSI, DML and TW for each month of the year were estimated. In this case the data do not follow a normal distribution and confidence intervals at the 95% confidence level were estimated using a bootstrap method (Efron & Tibshirani, 1993).

3.4 Calculation of Embryonic and paralarval phase.

According to Katsanevakis and Verriopoulos (2006) the length of the octopus embryonic phase is given by the solution of equation:

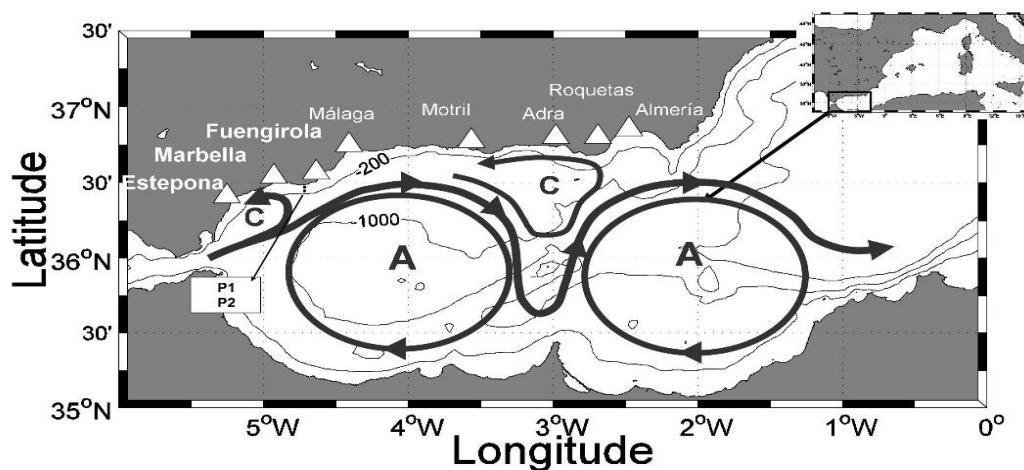
$$\int_{ts}^{th} \frac{1}{I(T)} dt = 1 \dots I(T) = \frac{532.2}{T - 8.763} \dots (1.1)$$

Being  $\frac{1}{I(T)}$  the instantaneous rate of development. T is the temperature at time t in °C, ts is the spawning time and th is the time for hatching.

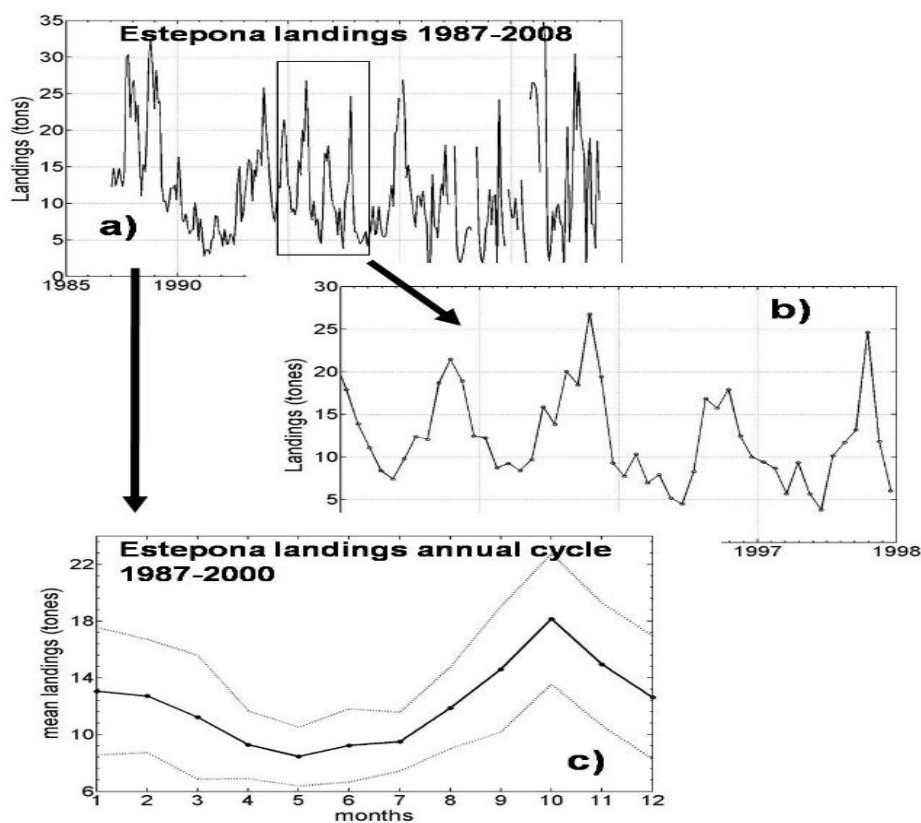
The length of the paralarval phase corresponds to the solution of equation:

$$\int_{th}^{tset} \frac{1}{P(T)} dt = 1 \dots P(T) = 157.5 - 5.008T \dots (1.2)$$

being tset the time when the individuals settle. The time interval in the present work, dt, is one day. Therefore, according to expressions (1.1) and (1.2), if



**Figure 1.** Alboran Sea in the Western Mediterranean. Dark arrows show the main surface circulation pattern. A stands for anticyclonic and C for cyclonic circulation. White triangles are the ports where landings data were obtained. Black dots marked with P1 and P2 show the position of two of the oceanographic stations belonging to RADMED monitoring program. P1 data are used in the present work.



**Figure 2.** Figure 2a is the time series of monthly octopus landings in Estepona port from 1987 to 2008. Figure 2b is a zoom showing the monthly landings for years 1994 to 1998. Fig. 2c is the average annual cycle of landings in Estepona port (solid line) and the 95% confidence intervals for the monthly means (dashed line).

**Table 1.** Maturity gonad stages (adapted from Sánchez and Obarti, 1993 in Quetglas et al, 1998)

Stage	Ovary	Spermatophoric Organ
Inmature (I)	Whitish, very small, no granulation signs	Transparent
Maturing (II)	Yellowish, granular structure	With white streaks
Mature (III)	Very large, plenty of eggs	With spermatophores

the spawning day is known and the daily temperature of sea water is known, it can be estimated the hatching day. In the same way, for a given hatching day, it can be calculated the day when paralarvae settle. The settlement day will also depend on the daily temperatures. The length of the embryonic and paralarval phases will be the sum of both quantities and will be a function of temperature and of the spawning day.

Once again we are not interested in the differences that can exist between different years, but on the average behavior. For this reason, expressions (1.1) and (1.2) were estimated using the average seasonal cycles of temperatures described in section 3.1. The seasonal cycle for Fuengirola beach was made of twelve values corresponding to the twelve months of the year. The temperature cycles estimated using the temperature at the sea surface and 25m depth in P1 station were made of four values corresponding to the four seasons of the year. In all the cases these annual cycles were linearly interpolated in order to obtain the 365 daily temperature values which are needed in expressions (1.1) and (1.2).

## Results

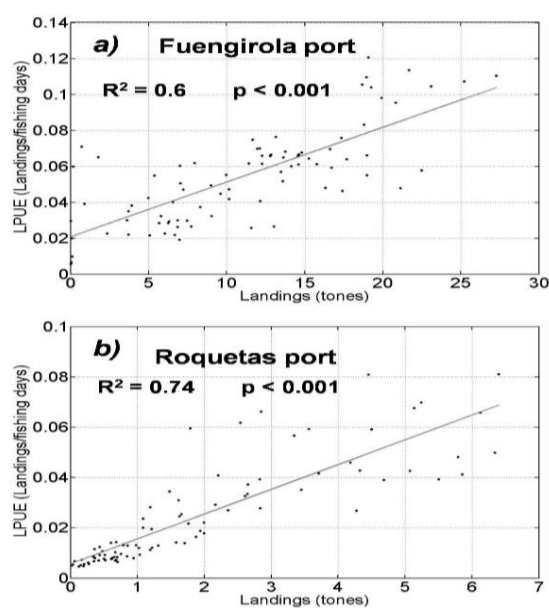
### Annual Cycles

Landings and LPUE were significantly correlated (Figure 3) supporting the use of the landings time series which have a longer extension. The seasonal cycle of annual landings is presented in figures 4 and 5. Figure 4 shows the annual cycle of octopus landings in the western sector of the Alboran Sea: Estepona, Marbella and Fuengirola ports. Months 1 to 12 correspond to months from January to

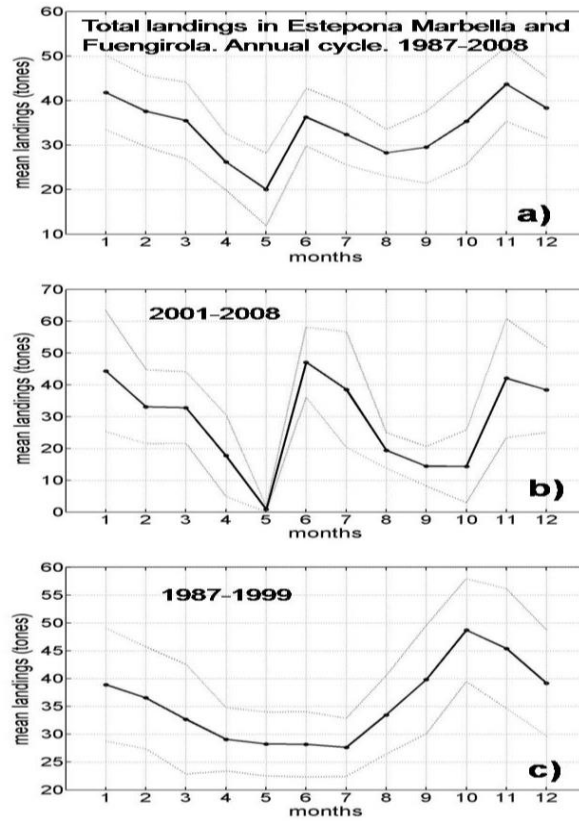
December. Figure 4a shows the annual cycle estimated from the complete time series from 1987 to 2008. Highest octopus landings occur at the end of the year, between October and December and a secondary maximum is observed in June, just after the minimum landings which are recorded in May. If only the 2001-2008 period is used for the calculation of the average annual cycle (Figure 4b), the results are very similar to those obtained using the complete time period. Nevertheless, if only the initial period is used, from 1987 to 2000, the secondary spring maximum disappears and maximum landings occur in October. The same analysis is presented for the eastern sector of the Alboran Sea: ports from Vélez to Almería. As in Figure 4, Figures 5a and 5b show the annual cycle estimated using the complete time series (Figure 5a) and the second part of the series (2001-2008, Figure 5b). Both figures show again that maximum landings correspond to the end of the year, from October to January with a secondary peak in June/July after a minimum in May. Nevertheless, when the annual cycle is calculated using the initial period (1987-2000), the spring/summer peak almost disappears.

Figure 6 shows the proportion of mature individuals and the GSI for males fished by the artisanal fleet (Figure 6a, clay pots), trawlers (Figure 6b), females from the artisanal fleet (Figure 6c), and females from trawlers (Figure 6d). Monthly mean sex ratio (males:females) are shown in 6e, 6f for both fishing gears. The presented results are mean values for each month of the year. The biological data used for calculations correspond to the period 1999-2008 and the 95% confidence intervals have been included in all the cases. Numbers in parenthesis are the number of available data used for the mean calculation.

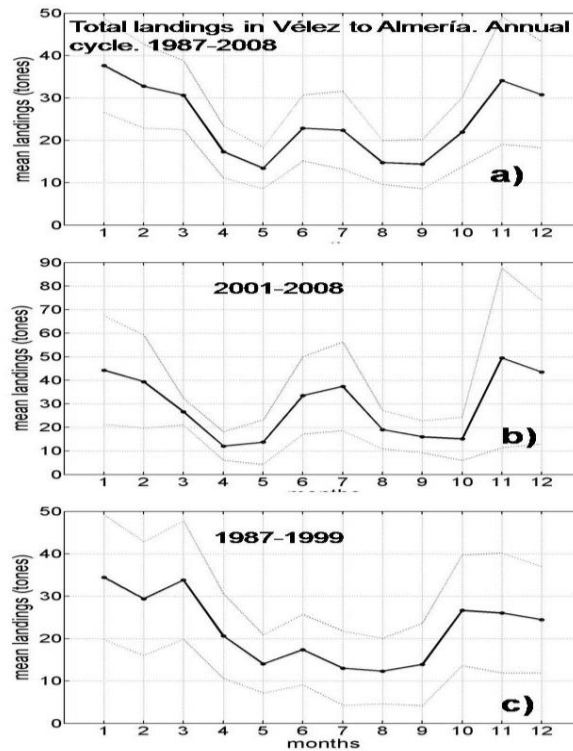
Almost all the males fished by clay pots



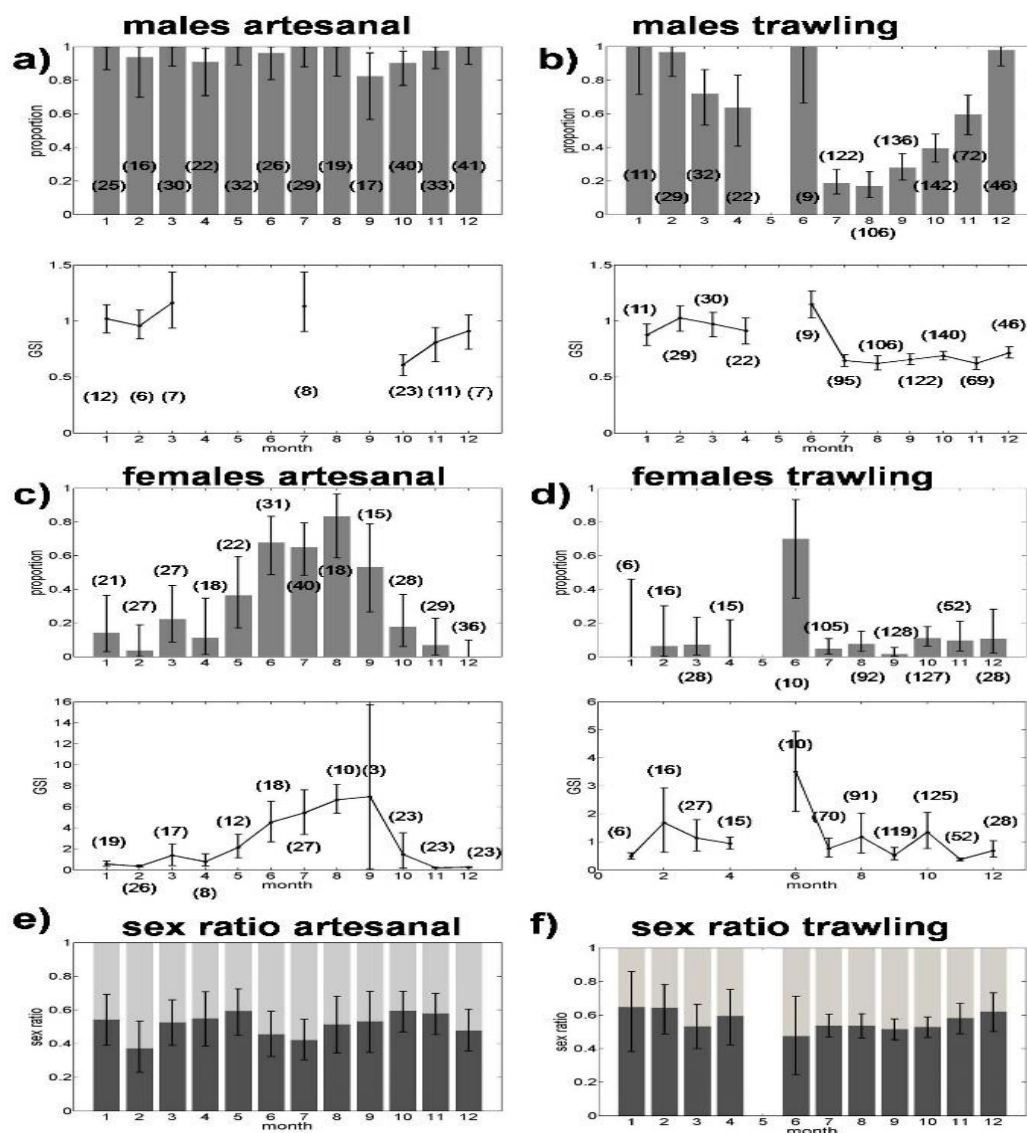
**Figure 3.** Figures 3a and b are the linear regression of Landings per Unit Effort on Landings in Fuengirola and Roquetas ports respectively. The explained variance ( $R^2$ ) is included in both cases.



**Figure 4.** Average annual cycle for landings in the western sector of the Alboran Sea: Estepona plus Marbella and Fuengirola landings. In figure 4a, all the data from 1987 to 2008 are used for the calculation of the monthly means. In Figure 4b only data from 2001 to 2008 are considered and in figure 4c only data from 1987 to 2000 are used.



**Figure 5.** The same as in figure 4, but for those ports in the eastern sector of the Alboran Sea, from Vélez to Almería.



**Figure 6.** For the four cases (Figures a,b,c and d), the upper plot shows the average proportion of mature individuals for each month of the year. The mean values for each month are calculated using time series of biological data from 2001 to 2008. The lower plots are the average GSI for each month of the year. 95% confidence intervals are included and the numbers in parenthesis are the numbers of data used. Figure 6a is for males from the artisanal fleet, 6b for males from the trawling fleet, 6c for females from the artisanal fleet and 6d for females from the trawling fleet. Figures 6e and 6f show the monthly mean sex-ratio for both fishing gear, darker part of the bar correspond to males proportion.

(artisanal fleet) were mature, as indicated by the proportion of mature individuals close to 1 during all the year. Contrary to this, males fished by trawlers would exhibit a clear annual cycle with significant differences along the year. Notice that no data are available for May in the trawling fleet. This is due to fishing regulation laws from 2000. If June data were not considered, a smooth cycle would be observed with maximum values in winter decreasing through spring to minimum values in spring/summer, and then again increasing in autumn. No clear cycle is observed for the GSI.

In the case of females fished by the artisanal fleet, both the proportion of mature females and the GSI show a very clear seasonal cycle. Both variables peak in late spring/summer, decreasing in autumn to minimum values in winter. For the case of females

from the trawling fleet, and if we discard the anomalous behavior in the month of June, most of the individuals are immature as shown by the low proportion of mature individuals and the low GSI values all the year round.

### Embryonic and Paralarval Phase

As *Octopus vulgaris* spawning occurs in coastal waters, the temperature conditions affecting, first to octopus eggs and then to paralarvae, are those of shallow waters close to the coast. Figure 7a shows the seasonal cycle of temperature for Fuengirola beach. These data have been interpolated and a temperature data per day is available. Temperatures have a maximum in August and values remain relatively high from July to September. Oceanographic station P1 is

in the continental shelf over a bottom depth of 30m. Temperature time series at the sea surface and at 25m depth, close to the sea bottom are considered (Figure 7a). Maximum values also correspond to August, although in this case the temperature drop through autumn is smoother. The use of different temperature annual cycles for the calculation of the embryonic and paralarval phases, provides an estimation of the uncertainty in the calculations.

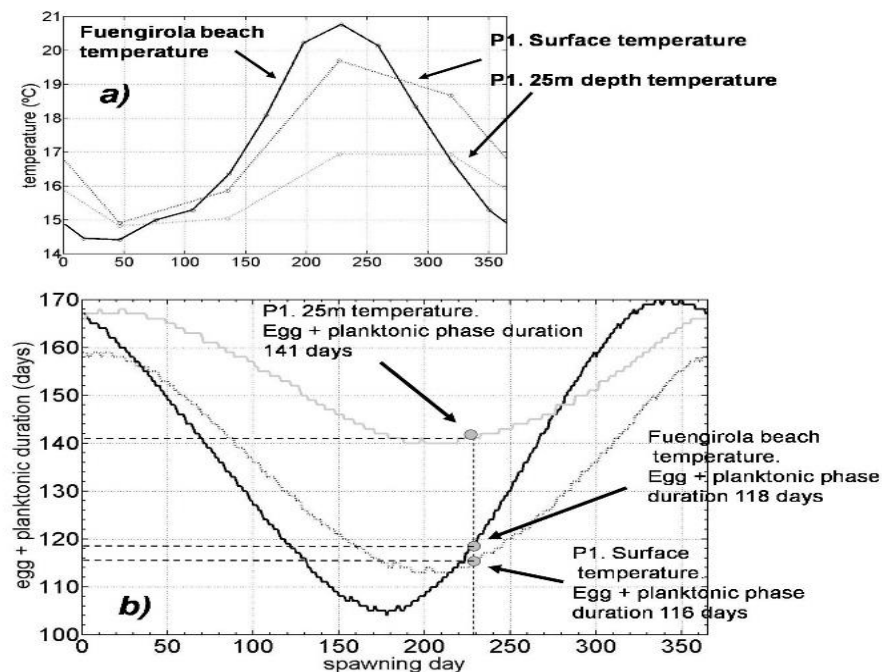
Figure 7b shows the duration of both phases (embryonic + planktonic) depending on the spawning day. In order to clarify the meaning of these figures, let's consider some examples. If eggs are spawned on day 1, that is, January first, paralarvae would settle around 170 days later if the temperature conditions were those in Fuengirola beach or 25m depth in P1 station (see black and grey lines intercept with y-axis). The duration of embryonic plus paralarval phases would be a little shorter if surface conditions in P1 were considered (around 160 days, dashed grey line). Figure 7b also shows the time from spawning to settlement for eggs spawned around day 230 (18<sup>th</sup> August). It would be 116, 118 and 141 days for temperature conditions in P1 station sea surface, Fuengirola beach, and 25m depth at P1 station respectively.

#### Seasonal Cycle for Settled Paralarvae

We considered that the number of spawned eggs

was proportional to the number of mature females. The procedure was as follows. First, all the biological data obtained by IEO from 1999 to 2008 are averaged by months of the year. Therefore, for each biological variable, twelve mean values were available representing the average biological conditions for an annual cycle. We then considered the number of females fished during each month of the year. Then we considered those females which were in a mature stage. Finally we divided the number of mature females for each month by the total number of mature females along the complete average year. This proportion was expressed as a percentage and we considered that the proportion of spawned eggs was the same. That is, if 25% of the mature females were found in July, we also considered that 25% of the eggs had been spawned in July. These data have been interpolated to obtain daily values of spawned eggs (normalized to 100). These data are represented by the grey line in Figure 8 where we have included two complete annual cycles.

Once we had the number of eggs spawned each day of the year, considering the temperature conditions during the following days, we calculated the number of paralarvae which will settle each day of the year. This result is also expressed as a percentage of the total number of settled paralarvae during the complete year (black line in figure 8). Figure 8 shows that, according to maturity data, the spawning should be maximum during June, July and August, and the



**Figure 7.** Figure 7a. Black solid line is the average temperature cycle for Fuengirola beach. Symbols correspond to the average monthly values and the solid line to the daily interpolated data. Dashed black line is the same for the average temperature cycle in the sea surface in Cape Pino 1 station (P1). Symbols correspond to the four seasonal means and the dashed line is for the daily interpolated values. Solid grey line is the same for the average annual cycle at 25m depth at P1 station. Figure 7b is the length of the embryonic plus paralarval (planktonic) phases as a function of the spawning day. Black solid line correspond to calculations using the temperature annual cycle in Fuengirola beach, dashed black line is for the temperature cycle at the sea surface in P1 station and the grey line is for the 25m depth temperature at P1 station.



number of settled paralarvae should be maximum in September, October and November.

## Discussion and Conclusions

In order to describe the life cycle of *Octopus vulgaris* in the northern Alboran Sea, we first focused on the reproduction of this species. The maturity stage of females fished by the artisanal fleet (clay pots) shows a very clear annual cycle. The proportion of mature females increases in spring (May) and reaches maximum values from June to September (Figure 6c). It is also from June to September when the GSI for females from the artisanal fleet is higher. This result suggests that the spawning season corresponds to late spring and summer. This spawning period would coincide with that observed by González *et al.* (2005) in Galician waters. Octopus spawning occurs in coastal waters, and that is the area where the artisanal fleet operates. If we consider the individuals from the trawling fleet, which operates over the outer part of the continental shelf (on depths ranging from 50 to 200m), it is observed that mature females represent a very low proportion all the year round and the proportion of mature males decrease considerably during summer months (July to September) increasing again from October (Figure 6b and 6d). In both Figures 6b and 6d, the month of June seems to be a value that does not fit with the general trend. Finally, those males obtained from the artisanal fleet (therefore in coastal waters) are almost always in a mature stage.

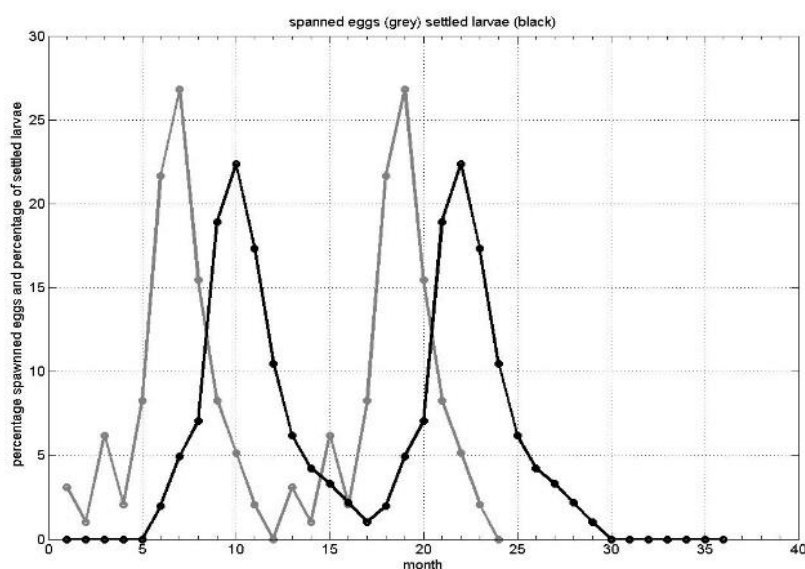
These results, mainly the decrease of mature males in trawling landings during summer months, and the increase of mature females in artisanal fleet landings, support the existence of a migration towards

coastal waters in spring/summer months. This result had already been suggested by several authors in the Mediterranean Sea (Quetglas *et al.*, 1998). Nevertheless, Moreno, Dos Santos, Piatkowski, Santos and Cabral (2009) found that the *O. vulgaris* benthonic phase was poorly known and the coastal migration observed in the Mediterranean could not occur in the Atlantic Iberian waters.

Once we accept that the spawning season is from late spring to the end of summer, we can estimate the duration of the embryonic and planktonic phases in the octopus life cycle. The exact knowledge of the temperature conditions during the embryonic and paralarval development introduces some uncertainty in these calculations. Nevertheless, the use of different temperature annual cycles such as those in Fuengirola beach or in P1 oceanographic station could provide a range of values or an estimation of the uncertainty of the length of this phase of octopus life cycle.

The embryonic and paralarval phases will depend on the spawning day and the annual cycle of water temperature. It is interesting to notice that the hatching phase of individuals spawned on May or beginning of June would last around 30-40 days. Therefore paralarval should be more abundant during summer months. This result is coincident with those in Salman, Katagan and Benli (2003) and in Lefkaditou, Papaconstantinou and Anastasopoulou (1999), who reported the presence of *O. vulgaris* paralarvae in the Aegean Sea during summer months.

The total length of the embryonic plus paralarval phase for eggs spawned on 1<sup>st</sup> June would last 108 days if the Fuengirola beach temperature is considered and 122, 148 days if the surface and 25m depth P1 temperature are used respectively. If the



**Figure 8.** Grey line is the proportion of eggs spawned for each month of the year. These proportions are averaged data from 2001 to 2008. The black line are the proportion of settled individuals for each month of the year. As these results represent an average annual cycle, two consecutive identical cycles are represented in order to make more clear its periodic character.

spawning occurs on 30<sup>th</sup> September, the embryonic-planktonic phase would last 142, 126 or 144 days for Fuengirola beach, P1 surface and P1 25m temperatures.

It is important to notice that the abundance of settled individuals will not only depend on the length of the embryonic-planktonic phase, but also on the way that spawning is distributed along the year. Eggs spawned at different times of the year can produce individuals settled at the same moment as they will be affected by different temperatures and the length of their embryonic-planktonic phases will be different. Katsanevakis and Verriopoulos (2006) considered different hypothetical spawning scenarios to estimate the density of individuals settled along the year. In the present work the spawning scenario is obtained from the analyzed maturity data. We calculate the percentage of mature females for each month of the year in relation to the total number of mature females fished along the year. These percentages are averaged values for the complete period of study (1999-2008). Grey line in Figure 8 shows these annual values for two consecutive years (notice that both years are exactly the same as we represent average cycles). We assume that for each month of the year, the percentage of spawned eggs relative to the total number along one year is the same as the percentage of mature females. Considering the length of the embryonic-planktonic phase as a function of the spawning day (Figure 7b) and the density of spawned eggs, we calculate the number of settled paralarvae for each day of the year (black line Figure 8). According to our results, the maximum density of settled individuals would occur from September to November, with a peak in October. Notice that González *et al.* (2005) also observed maxima abundances of Octopus paralarvae during October, while this is the month when individuals settle according to our model. The delay between results in González *et al.* (2005) and those from our model for the Alboran Sea could be associated to the lower temperatures in the Galician waters which produce a lower growth rate.

Individuals settled in September to November would become large enough to incorporate to fisheries a few weeks later (Katsanevakis & Verriopoulos, 2006). Therefore, the octopus landings annual cycle should be that represented by black line in Figure 8 with a few weeks or one month of delay. If we compare the results in Figure 8 with those in figures 4 and 5, we find quite a good agreement if figures 4c and 5c are considered. That is, according to our results, there is a spawning period from late spring to the end of summer which produces maximum abundances of octopus at the end of the year (October to January) with minimum values in spring/summer. In this way, the life cycle of *Octopus vulgaris* is closed with the description of maturity stages and the spawning period, the length of the embryonic and paralarval phases depending on the temperature cycle,

and the recruitment reflected in octopus landings. Nevertheless, if results in figures 4a, b and 5a, b were considered, the secondary abundance maximum in spring could not be explained by our simple model. It is interesting to notice that maturity data also showed a sudden increase of mature females and males from the trawling fleet in June which does not seem to fit with the rest of the annual cycle. If we exclude the second part of the time series and we only consider landings data from 1987 to 2000, the spring maximum disappears. In the case of maturity results, those data from the second part of the series cannot be excluded, as this sampling was only carried out from 1999 to 2008. Trawling fisheries were regulated after year 2000 and fisheries were banned for the month of May. We cannot be sure with the data at hand, but apparently this regulation seems to have an impact on the octopus population and could be the responsible for the spring abundance. As a summary, the data at hand and the simple model used show that *O. vulgaris* in the Alboran Sea has an extended spawning season from late spring to summer which would lead to recruitment and maximum abundances in late autumn and winter. Nevertheless the dynamics of this species is strongly affected by fisheries regulation and a secondary abundance maximum in June could be the result of banning in May. This result also suggests the need of introducing the effect of fisheries in our model in future works.

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