

Mediterranean Marine Science

Vol 12, No 2 (2011)



Fisheries and reproductive biology of *Octopus vulgaris* (Mollusca: Cephalopoda) in the Gulf of Alicante (Northwestern Mediterranean)

M. GONZALEZ, E. BARCALA, J.L. PEREZ-GIL, M.N. CARRASCO, M.C. GARCIA-MARTINEZ

doi: [10.12681/mms.38](https://doi.org/10.12681/mms.38)

To cite this article:

GONZALEZ, M., BARCALA, E., PEREZ-GIL, J., CARRASCO, M., & GARCIA-MARTINEZ, M. (2011). Fisheries and reproductive biology of *Octopus vulgaris* (Mollusca: Cephalopoda) in the Gulf of Alicante (Northwestern Mediterranean). *Mediterranean Marine Science*, 12(2), 369–389. <https://doi.org/10.12681/mms.38>

Fisheries and reproductive biology of *Octopus vulgaris* (Mollusca: Cephalopoda) in the Gulf of Alicante (Northwestern Mediterranean)

M. GONZÁLEZ¹, E. BARCALA², J.-L. PÉREZ-GIL¹, M.N. CARRASCO³
and M.C. GARCÍA-MARTÍNEZ¹

¹ Centro Oceanográfico de Málaga, Instituto Español de Oceanografía, Puerto Pesquero s/n, 29640 Fuengirola, Málaga, Spain

² Centro Oceanográfico de Murcia, Instituto Español de Oceanografía, Varadero 1, 30740 San Pedro del Pinatar, Murcia, Spain

³ Centro Oceanográfico de Tenerife, Instituto Español de Oceanografía, C/General Gutierrez 4, 38003 Santa Cruz de Tenerife, Canary Islands, Spain

Corresponding author: maria.gonzalez@ma.ieo.es

Received: 31 August 2010; Accepted: 19 May 2011; Published on line: 30 June 2011

Abstract

The common octopus *Octopus vulgaris* Cuvier, 1797 is the most fished cephalopod species along the Spanish coasts. Its catches fluctuate greatly due to the short life cycle of the species and to the annual variability of the recruitment pattern, strongly dependent on the environmental conditions affecting the eggs and paralarvae. This study examines the common octopus fishery, the catch composition, and the main features of the reproductive biology of this species in the Gulf of Alicante (Spanish Eastern coast, Western Mediterranean FAO division 37.1.1). The common octopus fishery was studied analysing the monthly landing and effort data by fishing gear from 1994 to 2005. Monthly samplings of the commercial *O. vulgaris* landings from trawlers and clay pots from January 2004 to December 2005 resulted in the measuring of 1833 specimens to enable analysis of the catch composition, and allowed the biological sampling of 1176 individuals to provide the reproductive parameters of the species in the study area. The length-weight relationship calculated for the species was $BW = 0.51 * DML^{2.87}$. The yearly sex ratios (males: females) were 1:1 (trawl, 2004), 1:0.74 (trawl, 2005), and 1:0.88 (clay pots, 2005). The size (dorsal mantle length, DML) at maturity of the species in the study area was 9.67 cm for males and 14.38 cm for females. The gonadosomatic index reached a peak between April and July for males and in July for females. The Fulton condition index was lower in both sexes between June and September, and for males in November-December, whereas for both sexes the values of the digestive gland index were at their maximum between June and December. The energy allocation between somatic and reproductive growth was investigated and the results suggested that the energy spent on reproduction mainly came from feeding, and not from energy stored in the mantle tissues or in the digestive gland.

Keywords: *Octopus vulgaris*; Fishery; Reproductive biology; Condition index; Reproductive energy allocation; Western Mediterranean.

Introduction

The common octopus, *Octopus vulgaris* Cuvier 1797, is the most fished octopus species in the world. While worldwide the greatest octopus fishery takes place in the Saharan Bank (off the northwest coast of Africa), other large fisheries exist along the European Atlantic coast and the Mediterranean Sea, as well as in the waters off Japan and Venezuela (GUERRA, 1997).

In the Mediterranean Sea *O. vulgaris* is the most important marketed cephalopod species, mainly fished by trawlers, but also captured with clay pots, trammel nets and other fishing gears (TSANGRIDIS *et al.*, 2002). In the Spanish Mediterranean *O. vulgaris* is also the most landed cephalopod species, averaging around 4000 t per year between 2000 and 2010 (Spanish regional statistics). Most of the catches are due to the fishing activities of coastal trawlers, although recently the artisanal fishing fleet has been increasingly targeting the catch of this species (FERNÁNDEZ & ESTEBAN, 2003). Despite its fishing relevance along the Spanish Mediterranean coast, the reproductive cycle of *O. vulgaris* is still little known in the area, even if the reproductive pattern is a key factor to explain -at least partially- the observed fluctuations of the octopus' abundance. In the Mediterranean area, *O. vulgaris* has been tackled by several studies focusing on different aspects: reproductive biology (MANGOLD-WIRZ, 1963; GUERRA, 1975; TIRADO-NARVÁEZ *et al.*, 2003); feeding behaviour (GUERRA, 1978); biometry (GUERRA & MANRIQUEZ, 1980); fisheries (TSANGRIDIS *et al.*, 2002); and both the fisheries and the biology of *O. vulgaris* (SÁNCHEZ & OBARTI, 1993; QUETGLAS *et al.*, 1998).

The life span of *O. vulgaris* seems to vary between 12 and 18 months (DOMAIN *et al.*,

2000; IGLESIAS *et al.*, 2004; KATSANEVAKIS & VERRIOPOULOS, 2006a). The duration of embryonic development depends on the temperature (CAVERIVIÈRE *et al.*, 1999; KATSANEVAKIS & VERRIOPOULOS, 2006a), and the juvenile and adult growth rate depends on temperature and food intake (GARCÍA GARCÍA & AGUADO GIMÉNEZ, 2002; KATSANEVAKIS & VERRIOPOULOS, 2006b). Males mature before females and, as mature males can be found throughout the year, the spawning season is mainly determined by the presence of a high proportion of mature females. ROCHA *et al.* (2001) define *O. vulgaris* as a simultaneous terminal spawning species with a reproductive model in which ovulation is synchronous and spawning takes place over a short period of time at the end of the animal's life. Due to its short life span, the abundance of *O. vulgaris* is believed to depend on recruitment strength, resulting in significant fluctuations of the interannual fishing yields and landings (BOYLE & RODHOUSE, 2005).

Sexual maturation and reproduction are the most energy-intensive periods of the cephalopod's life cycle (ROSA *et al.*, 2004a). The energy needed for reproduction may come from food intake or mobilization of previously stored reserves. Recent studies on the physiology of reproduction in *Octopus vulgaris* suggest that energy for reproduction could come from the diet (ROSA *et al.*, 2004a; for octopus females, OTERO *et al.*, 2007), although the results of OTERO *et al.* (2007) suggest that full maturity in males could be reached at the expense of the digestive gland.

Environmental variability seems to have an effect on cephalopod stock fluctuations (SOBRINO *et al.*, 2002; PIERCE *et al.*, 2008; VARGAS-YÁÑEZ *et al.*, 2009). In the study area, the shallowest waters (from 0 to 100 m)

over the continental shelf between Cabo de Palos (37° N) and Alicante (39° N) are under the influence of the thermohaline general current flowing southwestwards (Local Atlantic Waters, Atlantic modified waters usually colder and more saline than the original ones) and subject to the prevailing winds in the area (GIL, 1992). In the Western Mediterranean, the Spanish eastern coast and the Balearic Islands are the Spanish Mediterranean areas where the sea surface temperatures (SST) are the highest. In the study area there are no upwelling zones (VARGAS-Y ÁÑEZ *et al.*, 2010).

In this study we describe the reproductive cycle of *O. vulgaris* in the Gulf of Alicante (Spanish Eastern coast) and we assess

the impact of the reproductive pattern on the landings. We also estimate the main biological parameters, the spawning season, the size at maturity, the recruitment period, and the eventual effects of SST on the life span of the species in the study area. The allocation of the primary energy source for maturation is also analysed here.

Material and Methods

The study was carried out in the Spanish eastern coastal area located in the Gulf of Alicante (Western Mediterranean FAO division 37.1.1) where the fishing vessels landing at Santa Pola port operate (Fig. 1). In this area octopuses are caught by coastal

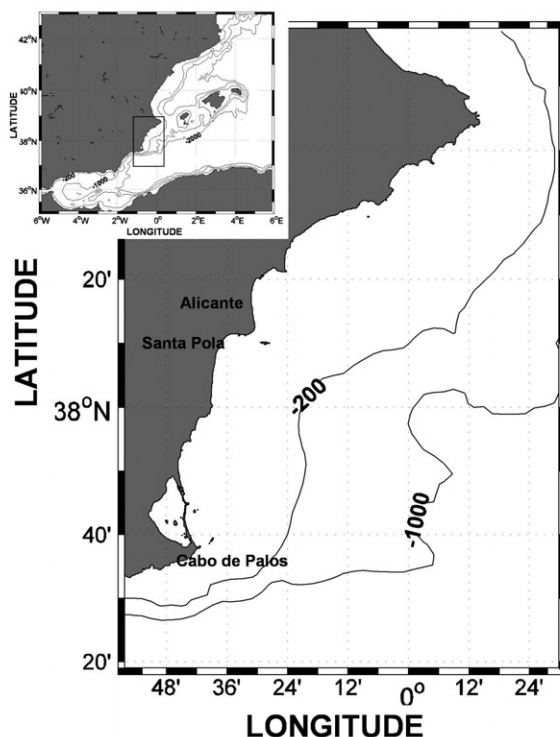


Fig. 1: Map of the area studied (Northwestern Mediterranean) showing the position of Santa Pola port (Spain).

trawlers fishing close to the coast (50-150 m depth), as well as by artisanal boats using trammel nets, gillnets and clay pots.

Fisheries data collection and analyses

Octopus landing and effort data were collected monthly by gear from 1994 to 2005. These data were provided by the Santa Pola Fishermen's Association. The number of fishing trips was chosen as the unit of fishing effort. To determine the exploitation scheme of the species in the area, the time-series of the landings per unit of effort (LPUE) and the dorsal mantle length (DML) range of individuals captured by gear were studied.

Between January 2004 and December 2005 the sizes (DML) of 1833 fresh specimens of *O. vulgaris* from commercial landings were measured on a monthly basis. During 2004, octopus DML measurements were taken only from trawler landings, whereas during 2005, DML records were both obtained from trawlers and clay pot landings. The measured specimens were selected by means of a random stratified sampling scheme (SPARRE & VENEMA, 1997, pp. 227-231) of commercial landings according to the catch composition and the spatio-temporal pattern of the fishing activity. A non-parametric analysis of variance ANOVA (Kruskal-Wallis) served to examine the interaction of the two gears based on DML data obtained in different months of 2005.

Sampling and analyses to determine biological parameters

A total of 1176 fresh *O. vulgaris* specimens selected for size sampling in 2004 (512 individuals) and 2005 (664 individuals) were also sampled for the following parameters: DML to the nearest mm, body weight (BW) and eviscerated body weight (EBW) to the nearest 0.1 g, sex and maturity stage according

to the three-stage maturity scale described by SÁNCHEZ & OBARTI (1993). A 2005 sub-sample of 551 specimens allowed the detailed observation of the reproductive organs and enabled the collection of the following data: gonad (ovary or testis) weight (GW), oviductal gland length (OGL), and Needham's complex weight (NCW). The digestive gland weight (DGW) was also recorded. Weights were rounded to the nearest 0.1 g and lengths to the nearest 0.1 mm.

Length-weight relationships

The length-weight relationships were calculated by linear regression, after decimal logarithmic transformation of the data (RICKER, 1973). For each species, the allometric exponent b was tested by a t -test to check if it was significantly different from 3, which corresponds to isometric growth. Comparisons between sexes were performed by analysis of covariance ANCOVA. The DML-BW relationship was calculated for 2004-2005 specimens ($n = 1162$).

Sex ratio

The sex-ratio (males:females) was calculated yearly and monthly by fishing gear (trawl and clay pot). Significant deviations from the 1:1 sex-ratio were tested with the Chi-square test.

Size at maturity

The size at maturity was estimated for each sex by calculating the percentages of mature individuals (stages II and III) per 1 cm size (DML) class. The size at maturity was defined as the size at which 50% of the individuals were mature, and it was estimated after fitting by the least squares method the relative length-frequency distribution of mature individuals to a logistic curve from the expression: $P_i = 1/\{1 + \exp[-(a + bDML_i)]\}$, where P_i represents the rel-

ative frequencies of mature individuals in size class DML_i , and a and b are the regression constants. Non-parametric bootstrap served to determine the uncertainty of these parameters. The fit was done following the maximum log-likelihood function using GLM with binomial errors. All calculations were made using the INBIO package in R (SAMPEDRO *et al.*, 2005).

Reproductive cycle

The reproductive cycle was defined by a combination of the monthly proportions of males and females in each maturity stage with the monthly variations of the monthly average values of the following maturity and condition indices by sex: gonadosomatic index (GSI): $GSI = GW/(BW-GW) \times 100$ (SILVA *et al.*, 2002), oviductal gland index (OGI): $OGI = OGL/BW \times 100$ (FERNÁNDEZ-NÚÑEZ *et al.*, 1996), and Needham's complex index (NcI): $NcI = NCW/BW \times 100$ (FERNÁNDEZ-NÚÑEZ *et al.*, 1996). Any differences in these indices between sexes and/or fishing gears were analysed with the Kruskal-Wallis test. Monthly frequencies of sexes and maturity stages obtained in the stratified sampling were raised to the monthly category landings of trawlers in 2004 and to the monthly category landings per gear (trawl and clay pot) in 2005.

Settlement

To identify the moment at which *O. vulgare* individuals begin their benthic life, the duration of embryonic and larval stages were calculated from hatching to settlement, according to the formulae in KATSANEVAKIS & VERRIOPOULOS (2006a). Monthly SST from 2003 to 2005 over the Santa Pola continental shelf were obtained from the NCEP (National Center for Environmental Prediction [Reanalysis Project, provided by NOAA-CIRES Climate Di-

agnostics Center, Boulder, Colorado, USA, <http://www.cdc.noaa.gov/>).

The model used relating the duration of embryonic development to temperature is $I(T) = 532.2/(T - 8.763)$. In this formula $I(T)$ gives the duration of the embryonic stage (days), as a function of temperature (T), while

$\frac{dt}{I(T)}$ is the fraction of total development

occurring in a short time interval dt . When

$\int_{t_s}^{t_s+I(t_s)} \frac{dt}{I(T)} = 1$, the embryonic development

is completed, where t_s is the spawning time and $t_s + I(t_s)$ is the eclosion time.

Similarly, planktonic stage duration $P(T)$ in relation to temperature is calculated from

$\int_{t_h}^{t_h+P(t_h)} \frac{dt}{I(T)} = 1$, where t_h is hatching time.

The model relating the duration of planktonic stage to temperature is $P(T) = 157.5 - 5.008T$, with $P(T)$ in days and T in °C.

Condition

The chosen indices calculated to study the condition of individuals were the digestive gland index (DGI): $DGI = DGW/BW \times 100$ (SILVA *et al.*, 2002) and the Fulton's condition index (K): $K = BW/DML^3 \times 100$ (RICKER, 1975). The relationship between these two indices was studied by Pearson's correlation.

Energy allocation

To examine the relationship between somatic and reproductive energy investment, three regressions were calculated (MCGRATH & JACKSON, 2002) using DML as the independent variable and the GW, EBW, and DGW as the dependent

variables. In each regression, the standardized residuals were calculated for each individual. As the three tissue weights (GW, EBW and DGW) were plotted against DML, the value of each residual gives an indication of the relative condition of each tissue (gonad, body, digestive gland) free of body-size bias (specimens with heavier tissues for their length have positive residual values).

To ascertain whether individuals with higher gonad condition had poorer somatic condition, the GW-DML residuals were correlated separately with each of the EBW-DML and DGW-DML residuals (MCGRATH & JACKSON, 2002).

Results

Average size and length-weight relationships

Neither the average DML (males 121.72 ± 1.64 mm; females 124.25 ± 1.44 mm) nor the average BW (males 755.56 ± 43.01 mm; females 791.48 ± 35.17 mm) showed any significant differences between sexes (Kruskal-Wallis, $\chi^2 = 1.90$, $p = 0.169$ and $\chi^2 = 1.79$, $p = 0.181$).

The length-weight relationships were as follows:

Both sexes pooled: $BW = 0.51 \pm 1.07 \times DML^{2.87 \pm 0.03}$ ($n = 1160$; $r^2 = 0.89$; $p < 0.00001$).

Males: $BW = 0.43 \pm 1.10 \times DML^{2.95 \pm 0.04}$ ($n = 628$; $r^2 = 0.89$; $p < 0.00001$).

Females: $BW = 0.55 \pm 1.10 \times DML^{2.84 \pm 0.04}$ ($n = 518$; $r^2 = 0.89$; $p < 0.00001$).

There were no significant differences between sexes (ANCOVA, $F = 1.79$, $p = 0.268$). When sexes were pooled the species showed negative allometric growth. ($t = 98.25$, $p < 0.05$).

Sex ratio

From January 2004 to December 2005,

628 males and 520 females were sampled. The sex-ratio in bottom trawl catches was 1:1 during 2004 ($\chi^2 = 0.80$, $p = 0.371$), 1:1 in clay pot catches for 2005 (sex ratio = 1:0.88; $\chi^2 = 0.458$, $p = 0.420$), whereas males dominated in 2005 trawl catches (sex ratio 1:0.74; $\chi^2 = 13.067$, $p < 0.001$).

The study of the sex ratio by month has shown significant differences between sexes in May 2004 (1:0.36, $Z = 3.9$, $p = 0.0001$), November 2004 (1:0.51, $Z = 3.0$, $p = 0.0027$) and in September and October 2005 (males:females 1:0.54, $Z = 2.83$, $p = 0.0046$ and 1:0.47, $Z = 4.78$, $p = 0.00001$, respectively).

Size at maturity

The smallest mature female caught had a size of 8.7 cm DML and weighed 458 g, whereas the smallest mature male measured 6.5 cm DML and 89.7 g. The DML at maturity (DML50%) was 9.67 cm for males ($a = 8.073$, $b = 0.835$, $r = 0.45$) and 14.38 cm for females ($a = 10.897$, $b = 0.758$, $r = 0.95$) (Fig. 2).

Reproductive cycle

Figure 3 shows the monthly evolution of the maturity stages for males and females during 2004 and 2005. Even when specimens in the three maturity stages were caught throughout all the year, most of the fished males were mature (85.5%), while the majority of the females were immature (64.6%).

Significant differences were found between the proportion of mature specimens of both sexes pooled caught by trawlers and clay pots in the studied period ($\chi^2 = 39.31$, $p = 0.0001$).

The mature males were more frequent in the catches between February and July, as corroborated by the peaks observed for the GSI and the NCI (Figs 4 and 5). For fe-

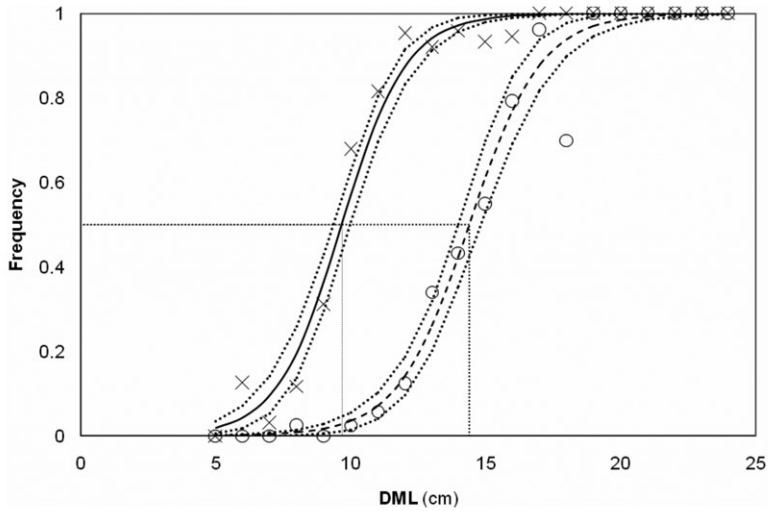


Fig. 2: Maturity ogive corresponding to DML (cm) for male (solid line) and female (broken line) *Octopus vulgaris* and associated 95% confidence intervals.

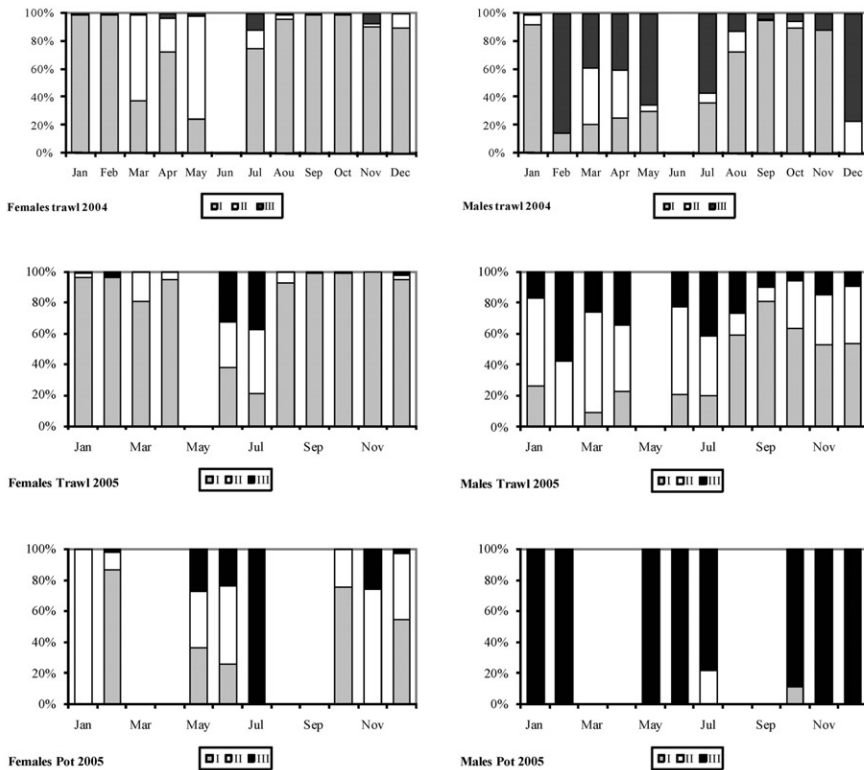


Fig. 3: Monthly percentages of each maturity stage in female and male *Octopus vulgaris*.

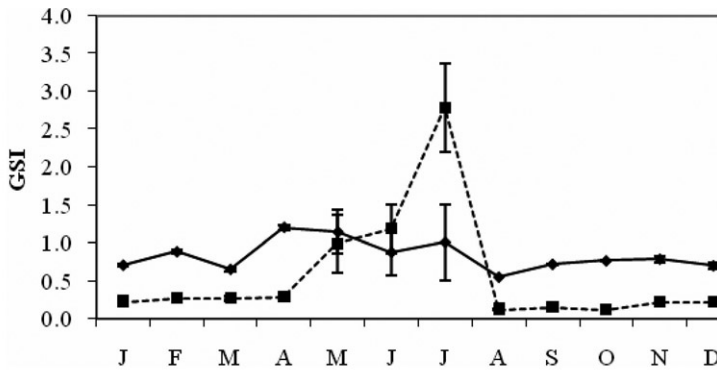


Fig. 4: Gonadosomatic index (GSI) in males (solid line) and females (broken line) *Octopus vulgaris*. Bars: standard error.

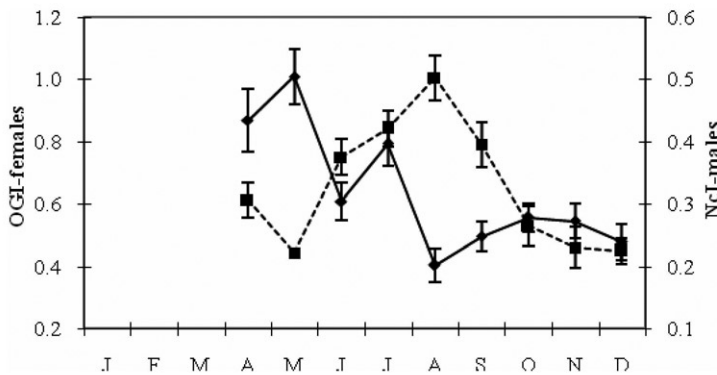


Fig. 5: Monthly changes in Needham's complex index (NcI) and the oviductal gland index (OGI) in males (solid line) and females (broken line) *Octopus vulgaris*. Bars: standard error.

males, the GSI peaked from May to July, just when mature individuals appear in the landings of both fishing gears examined (Fig. 3), whereas the OGI was higher from June to September (Figs 4 and 5). The GSI were significantly higher for males than for females during most of the year: January-April (Kruskal-Wallis, $\chi^2 = 97.14$, $p < 0.0001$); August-December (Kruskal-Wallis, $\chi^2 = 132.98$, $p < 0.0001$). Nevertheless, in spring and early summer (May-July) the GSI of the females

was much higher than the GSI of the males (Fig. 4).

Settlement

Figure 6 shows the seasonal cycle of SST over the Santa Pola continental shelf, the duration of the embryonic development and the paralarvae phase, as well as the period between spawning and settlement (embryonic plus paralarvae stage). Considering the occurrence of the spawning peak from 1st to

31st July, the length of the embryonic plus paralarvae stages should range between 79 and 87 days. The hatching would thus occur between days 221 and 248, corresponding to 9th August and 5th September respectively, and settlement between days 261 and 296, corresponding to 18th September and 23th October, respectively.

Condition

A moderate correlation between males (Fig. 7A) and females (Fig. 7B) was found for K, which followed the same trend throughout the year ($r^2 = 0.522$, $P > 0.10$, $n = 11$), showing lower values in both sexes between June and September and, only for males, between November and December.

K did not show significant differences between maturity stages of females, but those differences were significant for males (Kruskal-Wallis, $\chi^2 = 47.69$, $p < 0.0001$), where K increased as they reached maturity.

A high correlation was found in the DGI between males (Fig. 7A) and females (Fig. 7B) [$r^2 = 0.930$, $P > 0.001$, $n = 11$]. For both sexes, DGI peaked between June and December. The lowest values were recorded during the colder months of the year (January-May).

Figure 7 showed that K and DGI evolved inversely throughout the year and presented a negative correlation (males: $r^2 = -0.464$; females: $r^2 = -0.374$). From autumn to the

beginning of spring, K was high and DGI was low, whereas in spring and summer K reached minimum values and DGI maximum values. For females, GSI (Fig. 4) and DGI (Fig. 7B) followed the same trend (peaking in summer), whereas for males, GSI (Fig. 4) peaked in spring.

Energy allocation

For males and females, the regressions of DML on EBW and DGW showed strong relationships, with coefficients of determination (r^2) above 0.82 (Table 1). The regression of DML on GW showed in both sexes a moderate relationship, with r^2 between 0.70 for females and 0.78 for males (Table 1). No significant correlation was found between the GW-DML residuals and the EBW-DML residuals in females ($r^2 = 0.099$, $P > 0.05$, $n = 164$), indicating that, for females, the changes in the condition of the gonad were not related to changes in the body condition (Fig. 8C). Nevertheless, correlation between GW-DML residuals and between DGW-DML residuals (Fig. 8D) was positive for females ($r^2 = 0.198$, $P < 0.05$, $n = 164$), suggesting that the increase in the condition of the gonad was not made at the expense of the digestive gland reserves. For males, positive and significant correlations were also found between the GW-DML residuals and the EBW-DML residuals ($r^2 = 0.656$, $P < 0.05$, $n = 303$) [Fig. 8A] or

Table 1
Geometric-mean regression statistics for dorsal mantle length with the body weight, gonad weight and digestive gland weight in males and females.

| Sex | Variable | Slope | 95% confidence intervals | Intercept | r^2 |
|--------|-------------------------|-------|--------------------------|-----------|-------|
| Male | Eviscerated Body weight | 3.103 | 2.978-3.228 | -8.541 | 0.89 |
| | Gonad weight | 4.148 | 3.901-4.395 | -18.366 | 0.78 |
| | Digestive gland weight | 2.636 | 2.496-2.776 | -9.450 | 0.82 |
| Female | Eviscerated Body weight | 2.986 | 2.839-3.134 | -8.019 | 0.91 |
| | Gonad weight | 2.977 | 2.676-3.279 | -12.496 | 0.70 |
| | Digestive gland weight | 2.794 | 2.630-2.957 | -10.067 | 0.87 |

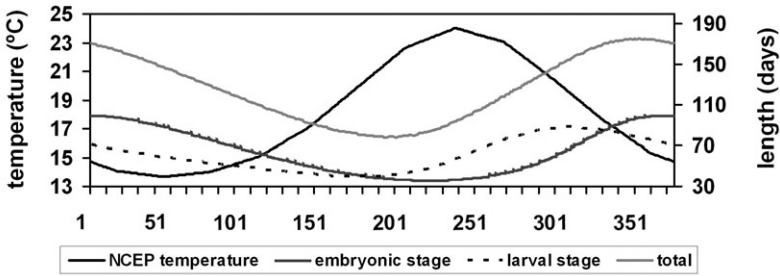


Fig. 6: The dark grey line is the length (in days) of embryonic development as a function of the spawning day (bottom axis). The broken line represents the larval phase (from hatching to settlement). The light grey line is the addition of both thick black and broken lines. The black line is the average sea surface temperature (SST) (2003-2005) of the Santa Pola shelf.

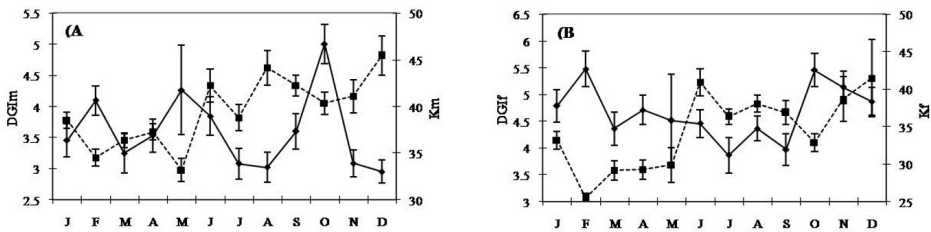


Fig. 7: Monthly changes of the Fulton condition index (K, solid line) and digestive gland index (DGI, broken line) in males (A) and females (B).

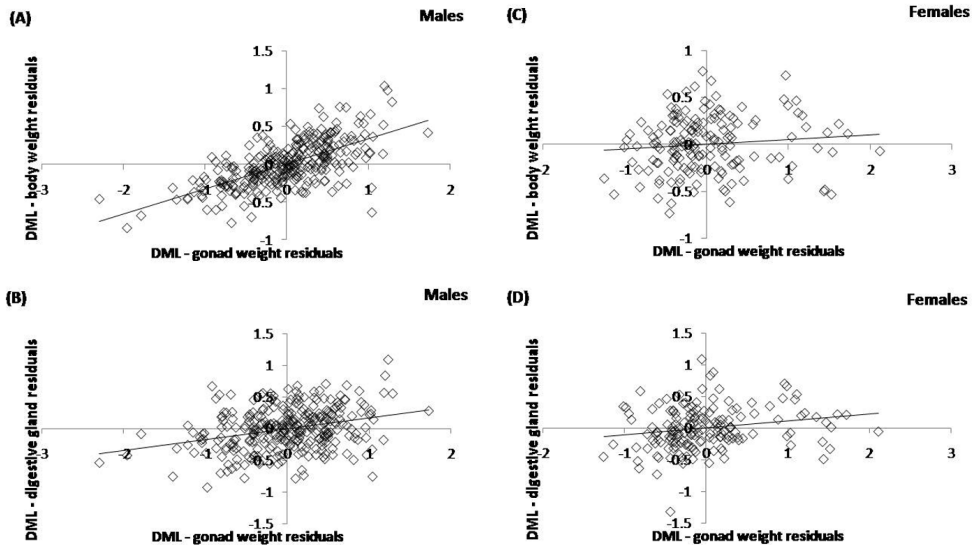


Fig. 8: Residuals from the GW-DML regression with BW-DML residuals and DGW-DML residuals, in males and females. Positive values represent heavier structures than those predicted by the model and negative values indicate structures lighter than the predicted ones.

DGW-DML residuals ($r^2 = 0.302$, $P < 0.05$, $n = 303$) [Fig. 8B], indicating that the growth of the gonad was not made at the expense of the mantle tissues or the digestive gland reserves.

Fishery patterns

O. vulgaris is caught by trawlers fishing close to the coast (50-150 m depth), as well as by artisanal boats (Fig. 9). The trawl fleet

accounts for 90% of the octopus landings, whereas the remaining 10% is due to different types of artisanal fishing. Most of the artisanal landings are due to trammel nets (for mullet and cuttlefish), ‘plasticeras’ (local name for a type of gillnet), and ‘alca-truces’ (local name for clay pots) (Fig. 10). They are all bottom fishing gears set between 0 to 50 m depth (FERNÁNDEZ & ESTEBAN, 2003). Clay pots are exclu-

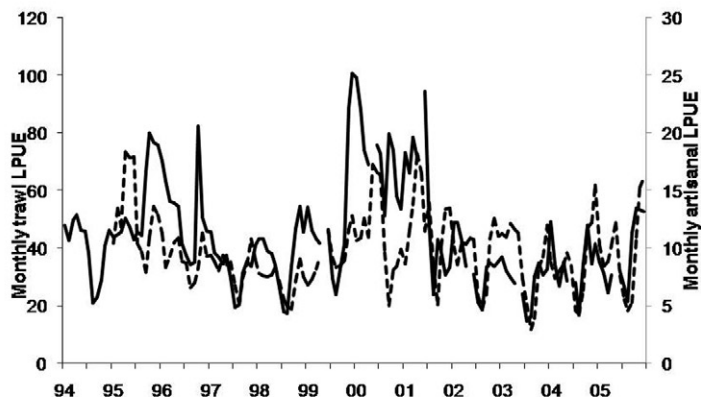


Fig. 9: Monthly evolution of the *Octopus vulgaris* LPUE (kg/trip) in Santa Pola port. Solid line: trawl; broken line: artisanal.

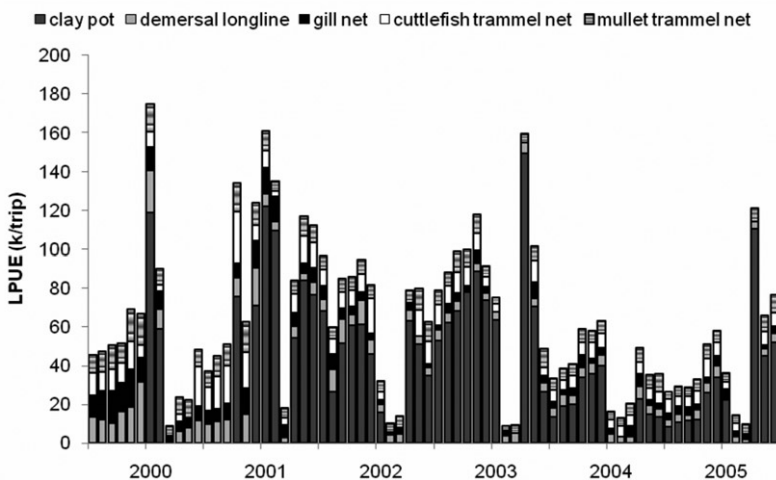


Fig. 10: LPUE (kg/ trip) of *Octopus vulgaris* by type of artisanal gear in Santa Pola port.

sively used for catching octopuses, while trawl and trammel nets are multi-specific fishing gears. Pots are checked every 4-6 days.

Marked seasonal fluctuations were observed in the octopus landings (Fig. 11). The landings of the trawl fleet decreased gradually from January to August, increasing again from September to January. The landings of the artisanal fleet increased from January to May, following thereafter the same pattern as the trawl catches (decreasing until September and increasing until the end of the year). Lack of data from trawl landings in May-June was due to a trawling ban in the area.

The mean DML of the octopuses caught by trawlers in 2004 and 2005 did not show any differences, while the mean DML of the octopuses caught by clay pots and trawlers in 2005 showed a statistical difference indicating that clay pots exploited larger sizes than trawlers (Table 2).

The average size of the landed specimens varied throughout the year (Kruskal-Wallis, $\chi^2 = 163.90$, $p < 0.0001$). The smallest specimens were recruited to the trawlers' fishing grounds in autumn and the size increased gradually until the spring-summer peak, which was followed by the disappearance of the large specimens in September (Fig. 12).

Discussion

Reproduction and life history

As a rule the sex ratio has been 1:1, as reported for the common octopus in the Balearic Islands (QUETGLAS *et al.*, 1998), the Gulf of Cádiz (SILVA *et al.*, 2002; RODRÍGUEZ-RÚA *et al.*, 2005), and along the Galician coastline (OTERO *et al.*, 2007). In this study, the sex ratio showed a significant predominance of males in the trawl landings of May 2004, maybe because the females had moved to shallower zones for spawning. Males also predominated in the autumn 2004 and autumn 2005 landings, probably due to the great female post-spawning mortality during this period (HERNÁNDEZ-GARCÍA *et al.*, 2002).

The BW at maturity corresponding to the DML at maturity (14.38 cm) obtained in this study using our BW-DML relationship for the female octopus of the Spanish Mediterranean area is 1067.57 g. This BW at maturity is smaller than the same value obtained for *O. vulgaris* in areas close to the Atlantic Ocean: 1250 g in the Gulf of Cádiz (RODRÍGUEZ-RÚA *et al.*, 2005) or 2023 g (SILVA *et al.*, 2002); 2400 g in Santa Luzia (waters off southern Portugal); 1750 g in Cascais (Portugal) [CARVALHO & SOUSA REIS, 2003]; 1784.3 g in Galician waters (Northeastern Atlantic) [OTERO *et al.*,

Table 2
Maximum, minimum and mean length of *Octopus vulgaris* per gear.

| | Bottom trawl 2004 | Bottom trawl 2005 | Clay pots 2005 | Total |
|---------------|-------------------|-------------------|----------------|-------|
| Max DML (mm) | 245 | 320 | 230 | 245 |
| Min DML (mm) | 50 | 50 | 70 | 50 |
| Mean DML (mm) | 98.75 | 97.99* | 145.33* | 98.65 |
| SD | 26.78 | 26.75 | 29.54 | 27.06 |
| number | 424 | 1128 | 281 | 1833 |

*: Significant difference (Kruskal Wallis, $\chi^2 = 136.90$, $p < 0.001$)

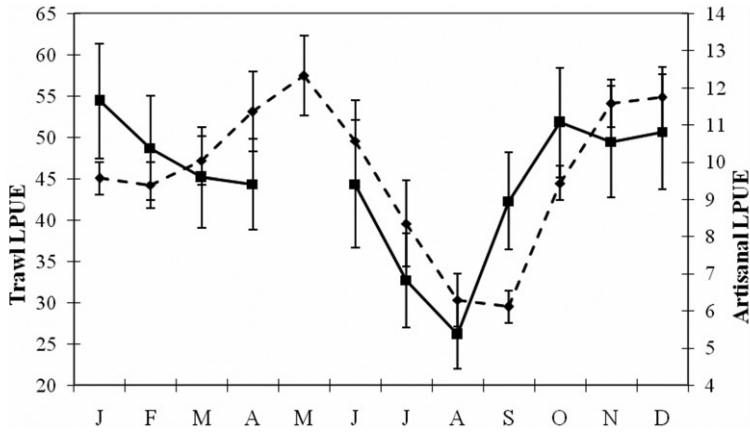


Fig. 11: LPUE (kg/ trip) of *Octopus vulgaris* by type of artisanal gear in Santa Pola port.

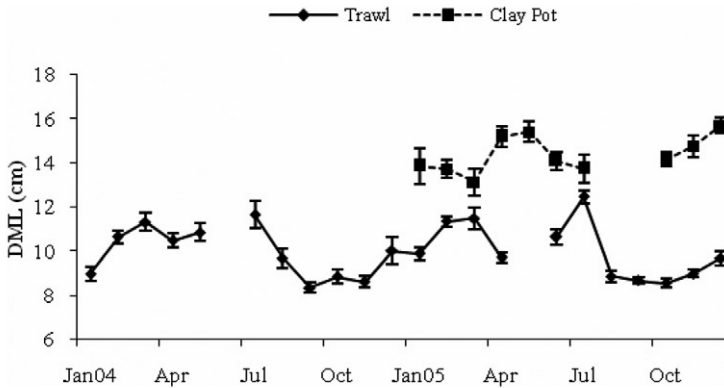


Fig. 12: Mean dorsal mantle lengths (DML) and standard error (bars) of the *Octopus vulgaris* caught by trawl (solid line) and clay pots (broken line) from January 2004 to December 2005.

2007]. These results could indicate the existence of a gradient making a decrease in the size at maturity as the species penetrates into the Mediterranean. Unfortunately, we have not found any relevant estimates of the size at maturity of *O. vulgaris* in different regions of the Mediterranean Sea. Only MANGOLD & BOLETZKY (1973) mentioned that ‘the usual weight at the time

of reproduction in females is over 1 kg’ and MANGOLD (1983) stated: ‘In the Mediterranean, females of *O. vulgaris* spawn at an average size of 1000-1500 g’. Despite the similarity of these results, we must keep in mind that females of *O. vulgaris* become sexually mature at very different sizes, no matter if the animals come from different areas or from the same population, primarily

depending on light, temperature and feeding (MANGOLD, 1983).

In females the reproductive indices analysed (GSI and OGI) increased with sexual maturation. Maximum values of the indices occur when reproductive activity is at its highest. In males, the testis and the Needham sac (acting as a reservoir for spermatophores before mating), increase in weight before the beginning of the spawning season for females. The size at maturity also showed that males reached sexual maturity much earlier than females, as occurs in other Mediterranean areas (GUERRA, 1975; MANGOLD, 1983), or in the Gulf of Cádiz (SILVA *et al.*, 2002). Hence, males mature before females, and can transfer their spermatophores to females even before females are mature (MANGOLD, 1983). In the Gulf of Alicante, mature males occurred throughout the year, as in other areas of the Mediterranean (MANGOLD & BOLETZKY, 1973) and in the Gulf of Cádiz (SILVA *et al.*, 2002, RODRÍGUEZ-RÚA *et al.*, 2005). The spawning season is thus determined based on the maturity of the females. *O. vulgaris* females can store the spermatophores inside their oviductal glands for some time before fertilization and spawning, and this could be one of the explanations for the earlier maturation of males, as this strategy would guarantee the presence of fully mature males able to mate with maturing or subsequently spawning females (FERNÁNDEZ-NÚÑEZ *et al.*, 1996).

In the study area, the spawning takes place from May to July, a shorter period than the reproductive period observed in different areas of the Mediterranean and in areas close to the Atlantic (Table 3). MANGOLD (1983), KATSANEVAKIS & VERRIOPOULOS (2006b), SILVA *et al.* (2002), and CARVALHO & SOUSA REIS (2003) describe two spawning peaks, a main one in

late winter-spring and a secondary peak during late autumn that did not appear in our area. Our results showed a single spawning peak in July. RODRIGUEZ-RUA *et al.* (2005) in the Gulf of Cádiz and FERNÁNDEZ-NÚÑEZ *et al.* (1996) in the Saharan Bank also observed a single spawning peak in summer, followed by minimum values of reproductive indices in autumn, probably related to the decreasing percentage of females in pre-spawning and spawning stages and post-spawning mortality (FERNÁNDEZ-NÚÑEZ *et al.* 1996).

The duration of the common octopus' embryonic development (MANGOLD & BOLETZKY, 1973, MANGOLD, 1983; CAVERIVIÈRE *et al.*, 1999) and of the planktonic stage is highly dependent on temperature. Depending on the day of the year in which spawning occurs, eggs and paralarvae would face different temperature conditions. KATSANEVAKIS & VERRIOPOULOS (2006a) provided equations to calculate the duration of embryonic development and of the planktonic stage for any given spawning day and using daily SST values, and we used these formulae to calculate the duration of embryonic development and the moment of hatching and settlement. Octopus eggs and paralarvae will remain in the water column during the summer, when the high temperatures enable a very fast development.

In addition, feeding studies carried out on natural populations have revealed that small planktonic crustaceans contribute to a major portion of the diets of such cephalopod stages (VECCHIONE, 1987; PASSARELLA & HOPKINS, 1991). The water column seasonal cycle in temperate areas shows a spring phytoplankton bloom, followed by a zooplankton peak in summer, and the decrease of zooplankton due to predation in autumn (VALIELA, 1995, pp. 467-

Table 3
Reproductive period of *Octopus vulgaris* zones adjacent to the study area.

| Author | Area | Reproductive period |
|-------------------------------------|-------------------|--------------------------|
| MANGOLD-WIRZ (1963) | NW Mediterranean | March to October |
| MANGOLD & BOLETZKY (1973) | NW Mediterranean | March to October |
| SÁNCHEZ AND OBARTI (1993) | NW Mediterranean | January to July |
| RODRÍGUEZ-RUA <i>et al.</i> (2005) | Gulf of Cádiz | April to October |
| OTERO <i>et al.</i> (2007) | Galician waters | December to September |
| KATSANEVAKIS & VERRIOPOULOS (2006b) | NE Mediterranean | Winter-Spring and Autumn |
| SILVA <i>et al.</i> (2002) | Gulf of Cádiz | Winter-Spring and Autumn |
| CARVALHO & SOUSA-REIS (2003) | Portuguese waters | Winter-Spring and Autumn |

476). As common octopus paralarvae are planktonic and carnivorous, the abundance of zooplankton in summer will ensure the presence of enough appropriate food for those paralarvae.

The settlement would take place in late summer-early autumn, and several weeks later juveniles would be recruited to the fishery, giving rise to the increase of landings in October and November. VARGAS-YÁÑEZ *et al.*, 2009 calculated the spawning period of *O. vulgaris* in the northern Alboran Sea (Southwestern Mediterranean) using the KATSANEVAKIS & VERRIOPOULOS (2006a) formulae. Summer spawning explained the autumn increment of trawler landings in the area well, which is in agreement with the results of our study.

The length-weight relationships were similar to those reported for octopuses caught by trawlers in adjacent areas (GUERRA & MANRÍQUEZ, 1980; QUETGLAS *et al.*, 1998; IDRISSE *et al.*, 2006), showing higher values of the allometric exponent than those reported in studies based on octopuses caught by traps (SÁNCHEZ & OBARTI, 1993; SILVA *et al.*, 2002; OTERO *et al.*, 2007). Length-weight relationship parameters are dependent on the range of da-

ta used (MOREY *et al.*, 2003). When the individuals used in the calculation are larger (i.e. clay pots individuals), the allometric exponent trends to be smaller. No differences between sexes were found in other areas.

Condition and energy allocation

In females the reproductive indices analysed evolved in a similar way to the DGI during the spawning season, while the K evolved inversely. Thus, the gonad, the oviductal gland and the digestive gland increase in size with sexual maturation, while muscular weight decreases. As for females, in males the digestive gland increases and muscular weight decreases during the same period, suggesting that maturity could be partially reached at the expense of the mantle (muscular) tissues. However, when relationships between gonad and storage tissues were tested, the results showed that neither sex of *O. vulgaris* showed any obvious decreases in relative mantle or digestive gland mass during maturation and gonadal development, thus not providing any evidence of somatic growth ceasing due to energy allocated to reproductive investment (MCGRATH & JACKSON, 2002). The fact that the diges-

tive gland increased during the spawning season indicates that the energy stored in it is not used for reproduction. ROSA *et al.* (2004a) found that the digestive gland of *O. vulgaris* and *O. defilippi* continued accumulating substantial energy reserves throughout the whole period of sexual maturation, with no evidence for the use of either the digestive gland or mantle tissues to supply the energy for the gonads. *O. vulgaris* could increase its ingestion rate in order to supply the energetic demand and the nutrients that the development of the gonads implies, which is supported by ROSA *et al.* (2004a), and occurs in other octopuses: *O. defilippi* (ROSA *et al.*, 2004a), *Eledone cirrosa* and *E. moschata* (ROSA *et al.*, 2004b). OTERO *et al.* (2007) obtained similar results for females, but in males the DGI decreased with maturation and individuals with higher gonad investment also had a poorer condition. OTERO *et al.* (2007) proposed two explanations for this fact: the digestive gland helps the males to attain maturity or the digestive gland loses weight due to the cessation of eating during its last weeks of life. Our findings did not show any decreasing of DGI, on the contrary, the EBW and DGI increase with maturation. This could indicate that male octopuses in better somatic condition and with better relative condition of the digestive gland tend to have a higher level of reproductive investment. The difference with the results of OTERO *et al.*, (2007) is probably due to a lack of males in their last weeks of life in our study.

Octopus fishery

Regarding the sales volume, Santa Pola is one of the major ports on the Spanish Mediterranean coast, acting as a focal point for the landings of fishing vessels from other ports operating in the area (GARCÍA-RODRÍGUEZ, 2003). This port has an ex-

tensive and powerful fleet using different types of gears, although most of the units are trawlers.

Trawling has been shown to account for the majority of the octopus catches (90%), due to the dominance of trawlers in Santa Pola fleet. Nevertheless, in other Mediterranean ports (SÁNCHEZ & OBARTI, 1993; TSANGRIDIS *et al.*, 2002) the octopus caught by different types of artisanal gears account for 30% - 50% of total landings. The biology of *O. vulgaris*, a coastal species seeking shelter in cavities, in conjunction with its high market price have led to the development of specialized artisanal fishing gears specifically targeting this species (TSANGRIDIS *et al.*, 2002).

The variability observed in the landings reflects the life cycle of the species. Trawler landings showed inter-annual variations reflecting the intrinsic fluctuations of the species abundance, as the catches of the multi-specific trawl fleet, not specifically targeting the common octopus, can be considered as good estimators of the abundance (SOBRINO *et al.*, 2002). The landings of the artisanal fleet also followed the same trend, with landing peaks observable for both fleets in 1995-96 and 2000-01. These oscillations of common octopus abundance might be related to the variability of environmental conditions affecting development in the early life stages of the species, therefore influencing the success or failure of *O. vulgaris* recruitment (BOYLE & BOLETZKY, 1996; FAURE *et al.*, 2000; SOBRINO *et al.*, 2002; BOYLE & RODHOUSE, 2005; VARGAS-YÁÑEZ *et al.*, 2009).

The landings also showed a marked seasonality, as a consequence of the species life cycle. During the first months of the year we observed a decrease in the octopus landings of the trawl fleet and an increase in the octopus landings of the artisanal fleet, domi-

nated by mature individuals and thus indicating that octopus migrate towards shallower (coastal) waters for spawning, as pointed out by MANGOLD-WIRZ (1963) in the Catalanian Sea (Northwestern Mediterranean). From May to September we noted a decrease in the landings of both types of gear. During this period, octopus migration continues towards coastal waters and the breeding animals start to die after the hatching of the eggs (females) or after mating (males) (MANGOLD & BOLETZKY, 1973; MANGOLD, 1983; QUETGLAS *et al.*, 1998). Both trawl and artisanal landings increased during autumn, due to the recruitment to the fishery of a new generation of individuals and their subsequent fast growth. The marked seasonality of the landings and its relationship with the life cycle of the octopus has been observed by various authors in the Northwestern Mediterranean (MANGOLD-WIRZ, 1963; GUERRA, 1975; SÁNCHEZ & OBARTI, 1993; QUETGLAS *et al.*, 1998; TSANGRIDIS *et al.*, 2002). In fact, as the successive generations hardly overlap, the reproductive cycle determines the temporal variation in the species abundance. The progression of the average size of the specimens caught in 2004 and 2005 confirms this hypothesis. Specimens increased in size during winter and spring, with the largest individuals disappearing from landings in August, while small immature ones are recruited in the catches, mainly during autumn. The recruitment of new specimens to the fishery takes place later than that observed off the Catalanian coasts of Spain, where it takes place in July (GUERRA, 1975).

Trawlers and clay pots exploit different fractions of the population. Trawl gear is not very selective and captures octopuses of all sizes, with major incidence on the small sizes, whereas clay pots capture mainly large

octopuses. TSANGRIDIS *et al.* (2002) found a similar pattern in the fishery of the Catalanian Sea (Northwestern Mediterranean). The clay pots are used in shallower waters, where the adults that have moved to the coast to spawn are predominant, while the trawlers work at depths greater than 50 m, where the immature specimens predominate (QUETGLAS *et al.*, 1998). In addition, a strong size selection seems to exist for the clay pots, since the large pots catch larger specimens than the small pots (JUÁREZ *et al.*, 2008).

Females need rocky substrates where they can lay eggs (MANGOLD-WIRZ, 1963). For this reason we could expect higher catches of females in the clay pots during the spawning period. However, the clay pots do not catch a greater proportion of females, most probably due to the fact that females need a period of adaptation to the new environment before undertaking spawning (KALLIANOTIS *et al.*, 2001), which would not be possible due to the relatively frequent checking of the traps in our study area (every 4-6 days).

In general the results obtained in this study are consistent with the reproductive biology of *O. vulgaris* described in the Mediterranean and adjacent Atlantic areas: the main spawning season in spring-summer is responsible for the main recruitment season in autumn. This life cycle is reflected in the catches obtained by both trawlers and clay pots. Nevertheless, further work is needed to complete the whole picture that would include the rest of the artisanal fleet, and to study possible interactions between the different gears that catch *O. vulgaris*.

Acknowledgements

We are grateful to Javier Delgado, Antonio Esteban and Jose Antonio Martínez

Madrid¹, from the Centro Oceanográfico de Murcia, for their assistance during the samplings, and we thank Toni Romero for his help with fishing market sampling. We also wish to thank the three anonymous referees, whose comments were of a great help in improving the manuscript. This work was carried out with the financial assistance of the Commission of the European Communities under the DG Fish Data Collection Regulation. Environmental data have been collected under RADMED project, funded by the Instituto Español de Oceanografía.

References

- BOYLE, P. & BOLETZKY, S.V., 1996. Cephalopod population: definition and dynamics. *Philosophical Transactions of the Royal Society, London*, 351 (1343): 985-1002.
- BOYLE, P. & ROADHOUSE, P., 2005. *Cephalopods: Ecology and Fisheries*. Blackwell Publishing, Oxford, 452 pp.
- CARVALHO, J.M.N. & SOUSA REIS, C., 2003. Contributions to knowledge on the maturation and fertility of the common octopus *Octopus vulgaris* Cuvier, 1797 on the Portuguese coast. *Boletín del Instituto Español de Oceanografía*, 19 (1-4): 473-481.
- CAVERIVIÈRE, A., DOMAIN, F. & DIALLO, A. 1999. Observations on the influence of temperature on the length of embryonic development in *Octopus vulgaris* (Senegal). *Aquatic Living Resources*, 12 (2): 151-154.
- DOMAIN, F., JOUFFRE, D., & CAVERIVIÈRE, A., 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. *Journal of the Marine Biological Association of the UK*, 80: 699-705.
- FAURE, V., INEJIH, C.A., DEMARCO, H. & CURY, P., 2000. The importance of retention processes in upwelling areas for recruitment of *Octopus vulgaris*: the example of the Arguin Bank (Mauritania). *Fisheries Oceanography*, 9 (4): 343-355.
- FERNÁNDEZ, A. & ESTEBAN, A., 2003. *La pesquería artesanal de Santa Pola (sureste de la península Ibérica). Descripción y actividad en el periodo 1992-2000*. Informes Técnicos del Instituto Español de Oceanografía 181, 49 pp.
- FERNÁNDEZ-NUÑEZ, M.M., HERNÁNDEZ-GONZÁLEZ, C.L., RAYA, C.P. & BALGUERÍAS, E., 1996. *Reproductive biology of octopus Octopus vulgaris Cuvier, 1797 from north-western African coast (21°N-26°N)*. ICES Shellfish Committee CM/K, 15, 19 pp.
- GARCÍA GARCÍA, B. & AGUADO JIMÉNEZ, F., 2002. Influence of diet on on-growing and nutrient utilization in the common octopus (*Octopus vulgaris*). *Aquaculture*, 211 (1-4): 171-182.
- GARCÍA-RODRÍGUEZ, M., 2003. Characterisation and standardisation of a red shrimp, *Aristeus antennatus* (Risso, 1816), fishery of the Alicante gulf (SE Spain). *Scientia Marina*, 67 (1): 63-74
- GIL, J., 1992. *Hidrografía de la plataforma continental Mediterránea española y Golfo de León (Octubre-Noviembre 1990)*. Informes Técnicos del Instituto Español de Oceanografía 133, 37 pp.
- GUERRA, A., 1975. Determinación de las diferentes fases del desarrollo sexual de *Octopus vulgaris* Lam. mediante un índice de madurez. *Investigación Pes-*

¹ José Antonio Martínez Madrid died in November 2006. In memoriam.

- quera, 39 (2): 397-416.
- GUERRA, A., 1978. Sobre la alimentación y el comportamiento alimentario de *Octopus vulgaris*. *Investigación Pesquera*, 42 (2): 351-364.
- GUERRA, A., 1997. *Octopus vulgaris*: Review of the World fishery. p. 91-97. In: Lang, M.A. & Hochberg, F.G. (Eds), *Proceedings of the Workshop on the Fishery and Market Potential of Octopus in California*. Smithsonian Institution, Washington, DC.
- GUERRA, A. & MANRIQUEZ, M., 1980. Parámetros biométricos de *Octopus vulgaris*. *Investigación Pesquera*, 44 (1): 177-198.
- HERNÁNDEZ-GARCÍA, V., HERNÁNDEZ-LÓPEZ, J.L. & CASTRO-HERNÁNDEZ, J.J., 2002. On the reproduction of *Octopus vulgaris* off the coast of the Canary Islands. *Fisheries Research*, 57: 197-203.
- IDRISSI, F.H., KOUETA, N., IDHALLA, M., BELGHYTI, D. & BENCHERIFI, S., 2006. Les modalités du cycle sexuel du pulpe *Octopus vulgaris* du sud marroccain (Tantan, Boujdour). *Comptes Rendus Biologies*, 329: 902-911.
- IGLESIAS, J., OTERO, J.J., MOXICA, C., FUENTES, L. & SÁNCHEZ, F.J., 2004. The complete life cycle of the Octopus (*Octopus vulgaris*, Cuvier) under culture conditions: paralarval rearing using *Artemia* and *Zoeas*, and first data on juvenile growth up to eight months of age. *Aquaculture International*, 12: 481-487.
- JUÁREZ, A., REY, J., ROMERO, Z., SOBRINO, I., BARO, J. *et al.*, 2008. Estudio de las pesquerías de alcatruces dirigidas al pulpo (*Octopus vulgaris*) en el litoral andaluz español. In: *XV Simposio Ibérico de Estudios de Biología Marina, 9-13 de Setembro 2008*, Funchal, Madeira, Portugal.
- KALLIANOTIS, A., VIDORIS, P. & KOKKINAKIS, A., 2001. Common octopus (*Octopus vulgaris*, Cuvier 1797) coastal fishery, during the peak of species reproduction. *Rapports de la Commission Internationale de la Mer Méditerranée*, 36: 279.
- KATSANEVAKIS, S. & VERRIOPOULOS, G., 2006a. Modelling the effect of temperature on hatching and settlement patterns of meroplanktonic organisms: the case of the octopus. *Scientia Marina*, 70 (4): 699-708.
- KATSANEVAKIS, S. & VERRIOPOULOS, G., 2006b. Seasonal population dynamics of *Octopus vulgaris* in eastern Mediterranean. *ICES Journal of Marine Science*, 63: 151-160.
- MANGOLD-WIRZ, K., 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie et Milieu*, (Suppl. 13): 1-285.
- MANGOLD, K., 1983. *Octopus vulgaris*. p. 335-364. In: P.R. BOYLE (Ed), *Cephalopods Life Cycles. Species Account, Vol. 1*. Academic Press, London.
- MANGOLD, K. & BOLETZKY, S.V., 1973. New data on reproductive biology and growth of *Octopus vulgaris*. *Marine Biology*, 19: 7-12.
- MCGRATH, B.L. & JACKSON, G.D., 2002. Egg production in the arrow squid *Nototodarus gouldi* (Cephalopoda: Omsatrephidae), fast and furious or slow steady? *Marine Biology*, 141: 699-706.
- MOREY, G., MORANTA, J., MASSUTÍ, E., GRAU, A., LINDE, M. *et al.*, 2003. Weight-length relationships of littoral to lower slope fishes from the western Mediterranean. *Fisheries Research*, 62: 89-96.
- OTERO, J., GONZÁLEZ, A.F., SIEIRO, M.P. & GUERRA, A., 2007. Repro-

- ductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. *Fisheries Research*, 85: 122-129.
- PASSARELLA, K.P. & HOPKINS, T.L., 1991. Species compositions and food habits of the micronektonic cephalopod assemblage in the Eastern Gulf of Mexico. *Bulletin of Marine Science*, 49: 638-659.
- PIERCE, G.J., VALAVANIS, V.D., GUERRA, A., JEREB, P., ORSIRELINI, L. *et al*, 2008. A review of cephalopod-environment interactions in European Seas. *Hydrobiologia*, 612: 49-70.
- QUETGLAS, A., ALEMANY, F., CARBONELL, A., MERELLA, P. & SÁNCHEZ, P., 1998. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, Western Mediterranean). *Fisheries Research*, 36: 237-249.
- RICKER, W.E., 1973. Linear regressions in fishery research. *Journal of the Fisheries Research Board of Canada*, 30: 409-434.
- RICKER, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin. Fisheries Research Board of Canada*, 191: 1-382.
- ROCHA, F., GUERRA, A. & GONZÁLEZ, A.F., 2001. A review of reproductive strategies in cephalopods. *Biological Reviews*, 76: 291-304.
- RODRÍGUEZ-RÚA, A., POZUELO, I., PRADO, M.A., GÓMEZ, M.J. & BRUZÓN, M.A., 2005. The gametogenic cycle of *Octopus vulgaris* (Mollusca: Cephalopoda) as observed on the Atlantic coast of Andalusia (south of Spain). *Marine Biology*, 147: 927-933.
- ROSA, R., COSTA, P.R. & NUNES, M.L., 2004a. Effect of sexual maturation on the tissue biochemical composition of *Octopus vulgaris* and *O. defilippi* (Mollusca: Cephalopoda). *Marine Biology*, 145: 563-574.
- ROSA, R., COSTA, P.R., PEREIRA, J. & NUNES, M.L., 2004b. Biochemical dynamics of spermatogenesis and oogenesis in *Eledone cirrhosa* and *Eledone moschata* (Cephalopoda: Octopoda). *Comparative Biochemistry and Physiology - Part B: Biochemistry and Molecular Biology*, 139: 299-310.
- SÁNCHEZ, P. & OBARTI, R., 1993. The biology and fishery of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean coast. p. 477-487. In: *Recent advances in cephalopod fisheries biology: contributed papers to 1991 CIAC International Symposium and proceedings of the Workshop on Age, Growth and Population Structure*. T. Okutani, R.K. O'Dor, & T. Kubodera (Eds), Tokai University Press.
- SAMPEDRO, P., SAINZA, M. & TRUJILLO, V., 2005. A simple tool to calculate biological parameters' uncertainty. Working Document. p. 12. In: *Workshop on Sampling Design for Fisheries Data (WKSDFD)*, Pasajes, Spain.
- SILVA, L., SOBRINO, I. & RAMOS, F., 2002. Reproductive biology of the common octopus, *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopodidae) in the Gulf of Cádiz (SW Spain). *Bulletin of Marine Science*, 71 (2): 837-850.
- SOBRINO, I., SILVA, L., BELLIDO, J.M. & RAMOS, F., 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cádiz (SW Spain). *Bulletin of Marine Science*, 71 (2): 851-865.
- SPARRE, P. & VENEMA, S.C., 1997. *Introducción a la evaluación de recursos pesqueros tropicales. Parte I: Manual*. FAO Documento Técnico de Pesca. N° 306.1, Rev. 2. Roma. 420 pp.

- TIRADO NARVÁEZ, C., RODRÍGUEZ DE LA RÚA FRANCH, A., BRUZÓN GALLEGO, M.A., LÓPEZ LINARES, J.I. SALAS CASANOVA, C. *et al.*, 2003. *La reproducción del pulpo (Octopus vulgaris) y el choco (Sepia officinalis) en la costa andaluza*. Junta de Andalucía, Sevilla, 159 pp.
- TSANGRIDIS, A., SANCHEZ, P. & IOANNIDOU, D., 2002. Exploitation patterns of *Octopus vulgaris* in two Mediterranean areas. *Scientia Marina*, 66 (1): 59-68.
- VALIELA, I., 1995. *Marine Ecological Processes*. Springer-Verlag, New York, 686 pp.
- VARGAS-YÁÑEZ, M., GARCÍA-MARTÍNEZ, M., MOYA-RUIZ, F., TEL, E., PARRILLA, G. *et al.*, 2010. *Cambio climático en el Mediterráneo español. Segunda edición actualizada. Temas de Oceanografía 3*. Instituto Español de Oceanografía. Ministerio de Ciencia e Innovación, Madrid, 176 pp.
- VARGAS-YÁÑEZ, M., MOYA, F., GARCÍA-MARTÍNEZ, M., REY, J., GONZÁLEZ, M. *et al.*, 2009. Relationships between *Octopus vulgaris* landings and environmental factors in the northern Alboran Sea (Southwestern Mediterranean). *Fisheries Research*, 99: 159-167.
- VECCHIONE, M., 1987. Juvenil ecology. p. 61-84. In: P.R. BOYLE (Ed), *Cephalopod Life Cycles. Comparative Reviews*, Vol. 2. Academic Press, London.