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Environmental influences on age and size at maturity of *Loligo vulgaris*

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Abstract – Age and size-at-maturity of *Loligo vulgaris* from Portuguese waters were evaluated in order to explain its complex population structure, which is strongly influenced by continuous spawning. Age was obtained by increment counting in statoliths. Maturity ogives by age group indicated that males mature one month earlier (at 277 days) than females (at 298 days). Females mature at a $ML_{50\%}$ of 17.6 cm, while males mature at smaller sizes. The later, however, showed a high degree of complexity in the size at maturity with evidence of two size at maturity groups. In both sexes, maturity was ultimately found to be primarily dependent on size rather than age. The effect of hatching season on age-at-maturity, size-at-maturity and reproductive investment was analysed by comparing two groups of squid hatched under distinct environmental conditions, namely the temperature during the first 3 months of life, the cold cohort (CC), hatching between December and March and the warm cohort (WC), hatching between May and September. Significant differences were found between cohorts on age-at-maturity, size-at-maturity and reproductive investment, giving indication of the environmental influences on sexual maturity. CC squid mature ca. 2 months later in life than WC squid and at a significantly larger size. The reproductive investment as measured by GSI was higher in the WC squid. Much of the variability in age and size-at-maturity of females in the population was due to differences between cohorts but this was not the case for males.

Key words: Squid / Maturation / Age / Size / *Loligo vulgaris* / Environmental influence

Résumé – Influences environnementales sur l'âge et la taille à la maturité sexuelle de *Loligo vulgaris*. L'âge et la taille à la maturité de *Loligo vulgaris* des côtes portugaises ont été étudiées pour expliquer une structure de population complexe, fortement influencée par une période de ponte continue. L'âge est déterminé à partir du dénombrement des stries des statolithes. Les courbes de maturité sexuelle, estimées par groupe d'âge, montrent que les mâles acquièrent leur maturité plus jeunes que les femelles (277 jours contre 298 respectivement). Les femelles sont matures à une taille de 17,6 cm ($ML_{50\%}$ – longueur du manteau de 50 % d'entre elles) alors que les mâles sont matures à des tailles inférieures. Ces derniers, cependant, ont montré une relation complexe entre taille et maturité avec deux groupes de tailles d'animaux matures. Pour les deux sexes, la maturité sexuelle semble davantage dépendre de la taille que de l'âge. L'influence de la période d'éclosion, sur l'âge ou la taille à la maturité, et l'investissement reproductif, ont été recherchés en comparant deux groupes de calmars, éclos dans des conditions de température distinctes, durant leurs 3 premiers mois de vie. La cohorte d'eaux froides (CF) naît entre décembre et mars et celle d'eaux tièdes (CT) naît entre mai et septembre. Des différences significatives dans l'âge et la taille à la maturité et l'investissement reproductif ont été constatées. Les calmars CF atteignent leur maturité sexuelle à une taille significativement plus grande et plus tardivement (2 mois plus tard) que les calmars CT. L'investissement reproductif, mesuré par l'indice gonado-somatique, est supérieur pour les calmars d'eaux tièdes. La majeure partie de la variation, de l'âge et la taille à la maturité des femelles dans la population, est due à des différences entre les cohortes ; ce qui n'est pas le cas pour les mâles.

1 Introduction

Loligo vulgaris Lamarck 1798 is the most abundant and commercially important loliginid squid in Portuguese waters. It is a short lived species, males attaining larger sizes and females undergoing "partial ovulation", i.e. there are oocytes at various stages of development in the ovaries and egg-laying occurs in separate batches during the spawning period (Melo and Sauer 1999). Energy for reproduction is probably obtained directly from ingested food rather than stored reserves. In many cephalopod species, this was hypothesized because the composition of energy storage organs is not significantly changed with maturity (e.g. Ho et al. 2004).

In north-west Portuguese waters *L. vulgaris* presents a complex population structure strongly influenced by year round spawning (Moreno et al. 1994; Moreno et al. 2002). The extended spawning season and the marked environmental seasonality in this geographic area mean that squid hatched in

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distinct seasons will be exposed to different influences during their life cycle, which will affect growth and maturation rates in different ways. It was already observed that *L. vulgaris* living under different water temperature regimes display high variability in reproductive and growth parameters (Moreno et al. 2002).

Growth estimates in *L. vulgaris* have revealed high variability in size at a given age, and significant differences between growth rates of seasonal groups (Arkhipkin 1995; Bettencourt et al. 1996; Raya et al. 1999; Rocha and Guerra 1999). If there is a specific minimal size before maturation could take place, regardless of age, as observed in *Lolliguncula brevis* by Jackson et al. (1997), differences in age-at-maturity between seasonal groups, due to different growth rates, are also to be expected. On the other hand, it has been shown experimentally for animals in captivity that temperature, photoperiod, and food availability directly influence maturation rates (Mangold 1987). Therefore, distinct environmental conditions are likely to result in differences between seasonal groups.

This study aims to describe age- and size-at-maturity in *L. vulgaris* from north-west Portuguese waters and to analyse these parameters, as well as the reproductive investment, in two groups of squid hatched in distinct periods of the year. Squid were grouped based on the average temperature experienced during the first three months after hatching, the cold cohort (CC) and the warm cohort (WC), given the assumption that temperature at an early life stage has a major impact on growth rates and adult size (Forsythe 2004). Besides temperature, each of those cohorts was obviously subjected to other distinct environmental conditions considered relevant to maturation processes, such as varying photoperiod and food supply. The differences in age- and size-at-maturity and reproductive investment between cohorts and the environmental influences on sexual maturation are discussed.

2 Materials and methods

2.1 Biological sampling

Specimens of *L. vulgaris* landed in ports on the North-West Portuguese coast, between January 1993 and December 1994 were collected monthly from the commercial fishery. Additional samples were collected from survey cruises and from the commercial fishery between February 1995 and March 2000. All samples were kept frozen for up to one month and thawed overnight before examination in the laboratory. Specimens were sexed and measures were obtained of the dorsal mantle length (ML), body weight (BW), the combined testis and Needham complex weight (TNC) in males, and the combined ovary and oviducal complex weight (OOC) and OOC plus combined nidamental and accessory nidamental glands weight (OOCN), in females. A maturity stage was assigned on a scale ranging from 1 to 5 (Boyle and Ngoile 1993).

2.2 Age readings

Statoliths were extracted and a transverse section of each obtained by grinding on both sides for age readings. In each statolith the total number of increments was counted from the nucleus to the tip of the rostrum. Readings were made using an image analysis system linked to a light microscope. The total number of increments was assumed to represent the age of the animal in days, based on the assumption that increment deposition in the statoliths has a daily rhythm, which was previously validated for paralarvae of *L. vulgaris* (Villanueva 2000), juveniles and adults of the sub-species *L. vulgaris reynaudii* (Lipinski et al. 1998) and adults of other loliginid species (e.g. *Sepioteuthis lessoniana*, Jackson et al. 1993; *Lolliguncula brevis*, Jackson et al. 1997). Statoliths were discarded if less than 80% of the reading trajectory was readable. Two or more independent readings were performed in 10% of the statoliths. The coefficient of variation ($CV = 100$ sd/mean) between independent readings indicated a high precision in ageing (mean $CV = 3.2\%$). No relationship was observed between mean age and precision in ageing (linear regression, $r^2 = 0.002$, $n = 50$). A total of 436 specimens were successfully aged (194 females, 23 unknown sex, 219 males).

2.3 Data analysis

Maturity ogives were estimated by fitting the logistic model $\mathrm{Y} = 1 / (1 + \exp(-a - b\mathrm{X}))$, to the proportion of mature squid (Y) by age or size class (X). Parameters a and b were calculated by non-linear estimation. The age and size at which 50% of females or males were mature, respectively $t_{50\%}$ and $\mathrm{ML}_{50\%}$, were derived as $-a/b$. The effect of sex and hatching cohort on age- and size-at-maturity was tested by comparing, between data-sets, the best fitted values of the parameters a and b of the maturity ogives using an F-test.

Hatching dates were back-calculated as the capture date minus the age in days. The temperature to which each specimen was exposed was determined as the average of the sea surface temperature (SST) during the first three months of life (i.e. the month of hatching plus the two following months). Hatching cohorts based on temperature were defined as follows: cold cohort CC ($n = 124$; 28.4% of total sample) comprising squid that experienced average SST below 15 °C during the first 3 months of their life (i.e. hatching in December to March, depending on annual variation in SST); warm cohort WC ($n = 153$; 35.1% of total sample) comprising squid that experienced average SST above 17 °C during the first 3 months of life (i.e. hatchings in May to September, depending on annual variation in Sea Surface Temperature). Average SST was computed from weekly data for North-West Portuguese waters (38.5 to 41.5°N and 8.5 to 9.5°W) extracted from the Integrated Global Ocean Services System – Meteorological Center "IGOSS nmc" database (Reynolds and Smith 1994).

The relationships between the weight of reproductive organs (OOC and TNC) and ML or age were assessed by Spearman rank order correlations. Mean OOC and TNC by age group (t) were estimated for each cohort and maturation rates (mr) calculated as $mr = \mathrm{OOC}_2 - \mathrm{OOC}_1/t_2 - t_1$ or $mr = \mathrm{TNC}_2 - \mathrm{TNC}_1/t_2 - t_1$.

Gonadosomatic indices (GSI) were computed for each male and female at maturity stages 2 to 5, as $\mathrm{GSI} = \mathrm{OOC}/(\mathrm{BW} - \mathrm{OOC})100$ or $\mathrm{GSI} = \mathrm{TNC}/(\mathrm{BW} - \mathrm{TNC})100$.

The effect of hatching cohort on maturation was analyzed by comparing the mean GSI, OOC, OOCN and TNC using

ANCOVA, with ML as the covariate, since reproductive organ weight was highly dependent on the size of specimens. These analyses were performed only on mature specimens (stages 4 and 5), to minimize the effect of differences in the proportion of maturing vs. mature squid between cohorts.

3 Results

3.1 Age and size at maturity

Sex could be identified macroscopically in squid from 4 months old (121 days). The beginning of gonad maturation (maturity stage 2) was observed from 5 months in males and 6 months in females (Fig. 1). Minimum age observed at maturity in males was 5 months. In less than one month from the beginning of the maturation process, specimens of either sex can be fully mature. Spawning took place at a mean age of 10 months (298 days) and males reached maturity at a mean age of 9 months (277 days). Variability in the maturity cycle was high in both sexes, with standard deviations of 1−1.5 months in squid in maturity stages 1 to 4 and up to 1 month in squid in maturity stage 5. About 92% of females and 86% of males were mature before the age of 1 year.

Maturity ogives were estimated for each sex by age group (Fig. 2a) and size class (Fig. 2b). Maturity ogives by age group provided a good fit to the observed data, explaining 94.1% and 93.7% of the variance in maturity of females and males, respectively.

Males matured *ca.* 1 month earlier than females and at a smaller size. Maturity ogives were found to be significantly different between sexes in relation to age group ($F_{2,18} = 4.69$, $p < 0.01$) and size class ($F_{2,34} = 7.32$, $p < 0.01$). The $t_{50\%}$ was estimated to be 7.6 months for males and 8.7 months for females.

The smallest mature female measured 15 cm (8 months) and the smallest mature male measured 8 cm (5 months). The ML$_{50\%}$ of females was estimated to be 17.6 cm.

Size-at-maturity in males showed a high degree of complexity, with high proportions of small mature males and low proportions of mature males in some of the larger size classes. The ML$_{50\%}$ of males was estimated to be 15.3 cm, but the adjusted maturity ogive by size class explained only 82.7% of the variance in maturity and estimated excessively high proportions of mature squid for the smaller size classes.

3.2 Maturity cycle by cohort

The effect of hatching season on age- and size-at-maturity was analysed by comparing two groups of squid hatched in distinct periods of the year, the cold cohort (CC) and the warm cohort (WC). Minimum age-at-maturity in the CC (8.5 months in females and 6.8 months in males) was higher than the average value for the whole population. The spawning season in this cohort was between September and January (mainly in autumn), with a peak in December (Fig. 3). Males reach maturity between July and February, the majority in October and November.

Minimum age-at-maturity in the WC (7.3 months in females and 5.5 months in males) was lower than the average and near the minimum of the whole population. The spawning season in this cohort was between January and July (mainly in spring), with a peak in April (Fig. 3). Males reach maturity throughout the year, the majority between December and April.

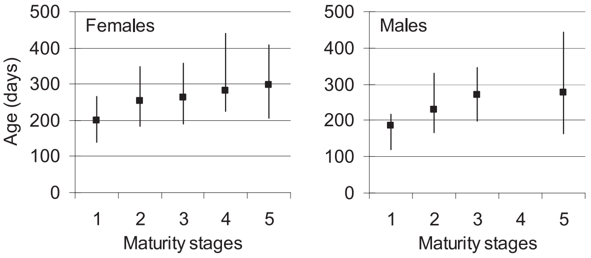

Fig. 1. Minimum and maximum age (lines) and mean age (dots) by maturity stage in female and male. Maturity stage 4 males were disregarded ($n = 3$).

A significant influence of hatching cohort on age-at-maturity, as assessed by comparing the cohort's maturity ogives, was found in females ($F_{2,10} = 153.7$, $p < 0.001$) and males ($F_{2,14} = 8.88$, $p < 0.01$), indicating that CC squid mature later in life than WC squid. Females of the CC mature at $t_{50\%} = 9.5$ months and females of the WC mature at $t_{50\%} = 7.3$ months (Fig. 4). Males of the CC mature at $t_{50\%} = 8.4$ months and males of the WC mature at $t_{50\%} = 6.2$ months. As for females, minimum age-at-maturity was greater in CC males (6.8 months) than in WC males (5.5 months). The variability in age-at-maturity was lower within cohorts than for the whole population in females but not in males.

Differences in size-at-maturity were also observed between cohorts. ML$_{50\%}$ was 19.1 cm and 15.6 cm in females of the CC and WC, respectively (Fig. 5).

Size-at-maturity in males was lower than in females, ML$_{50\%}$ = 14.1 cm in the CC and ML$_{50\%}$ = 12.0 cm in the WC. The variation in size-at-maturity of males was especially high and the fit of a maturity ogive to data on maturity by size class, for males of each cohort, was considered poor ($r^2 = 0.70$ to 0.79). In both cohorts high proportions of small mature males were observed as well as low proportions of mature males in some of the larger size classes. The high variability for the whole population and the co-existence of groups of small and big mature animals was not explained by differences between cohorts ($F_{2,27} = 0.483$, $p > 0.05$), two sizes-at-maturity still being present in each cohort. Fitting a single maturity ogive to the size-at-maturity data for both male cohorts combined gave a more satisfactory fit.

In maturity ogives by size class a better fitting of was observed when splitting females by cohorts, indicating the underlying significant differences in the size-at-maturity between cohorts. In fact, the comparison between maturity ogives fitted to each cohort indicated that WC females mature at significantly smaller sizes than those of CC ($F_{2.19} = 40.51$, $p < 0.001$).

3.3 Reproductive investment with age

As maturation started earlier in WC females, differences in mean gonad weight (OOC) and GSI with age in relation

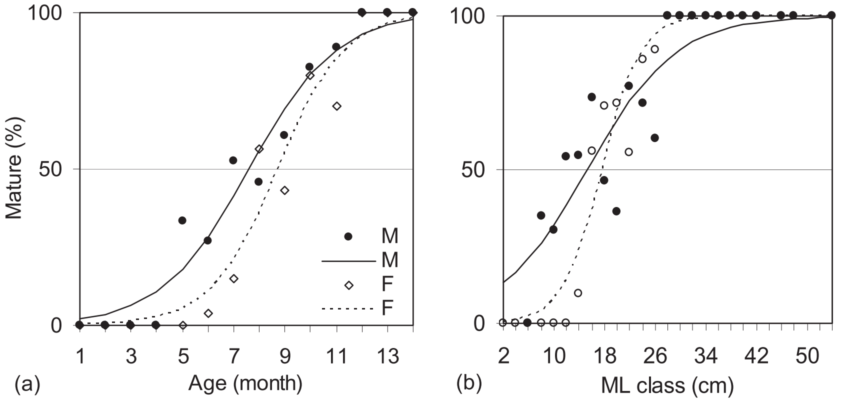

Fig. 2. Percentage mature by age group (a) or ML class (b) and estimated maturity ogives for females and males. $t_{50\%}$ or ML$_{50\%}$ are the estimated age or ML at which 50% of females (F) or males (M) are mature.

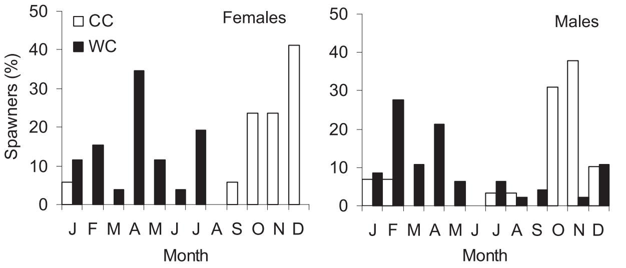

Fig. 3. Percentage of female or male spawners by month from the total spawners in the cold cohort (CC) and in the warm cohort (WC).

to CC females were apparent from 7 months old (Figs. 6a,b). Within WC females the highest increase in OOC, i.e. the maturation rate (mr), occurred earlier (6 to 8 months) than within CC females (9 to 11 months). In both cohorts the highest mr were observed close to the respective $t_{50\%}$ and, by this age, the mr was much higher in the CC than in the WC (Fig. 6a, Table 1), i.e. close to the main spawning time of each cohort the increase in gonad weight was faster in the CC.

The reproductive investment in the WC females, revealed by GSI, increased with age and was highest at 9 months old (Fig. 6b). In the CC females, GSI also increased with age and was highest at 10 months old. However, GSI was much higher at every age in WC females than in CC females.

The variation of OOCN with age (Fig. 7) showed similar trends and differences between cohorts as that of the OOC.

In males of both cohorts, the monthly increase in TNC (*mr*) was highest between 10 and 11 months. In the WC a high mr also occurred between 6 and 7 months, which resulted in mean TNC values between 7 and 10 months slightly larger than those in the CC males (Table 1, Fig. 8a). GSI was greater in the WC males up to 8 months of age, and similar in both cohorts beyond that age (Fig. 8b).

The combined ovary and oviducal complex weight (OOC) was better correlated with size (R = 0.858) than age (R = 0.493) of females. The increase in the combined testis and Needham complex weight (TNC) was also better correlated with increasing size (R = 0.828) than age (R = 0.700) of males.

Table 1. *Loligo vulgaris*: maturation rates (g month^{-1}) of different age groups in females and males of the cold cohort (CC) and the warm cohort (WC).

Age group (month)	Females		Males	
	CC	WC	CC	WC
6–7	-	11.9	0.0	3.7
7–8	0.8	15.3	0.8	0.0
8–9	11.3	8.7	1.4	1.7
9–10	33.2	5.9	2.5	2.2
10–11	27.5	-	7.7	3.9
11–12	-	-	-	1.5

The results of the ANCOVA tests indicated a significant influence of hatching cohort on the reproductive investment in each sex, as the mean GSI of mature squid of the WC was significantly greater than that of the CC (Table 2). The mean TNC in the WC mature males was also significantly higher than that of the CC. However, no significant differences were found between cohorts in mean OOC and OOCN of mature females.

4 Discussion

4.1 Age and size at maturity

In analyzing age and size-at-maturity data it appears that a complex combination of factors may influence the exact shape of growth and maturation curves. Significant differences were observed in maturity ogives between sexes, highlighting the important differences in the maturation process that exist between males and females. In males, reproductive investment is lower and maturity is reached earlier and at a smaller size, while in females reproductive investment is higher and maturity is reached at older ages and bigger sizes. The fact that males mature at a smaller size than females has been observed across the geographic distribution of this species (Baddyr 1991; Coelho et al. 1994; Guerra and Rocha 1994; Moreno et al. 1994). The earlier maturation of males in Portuguese waters explains their seasonal maturity peak, which is around

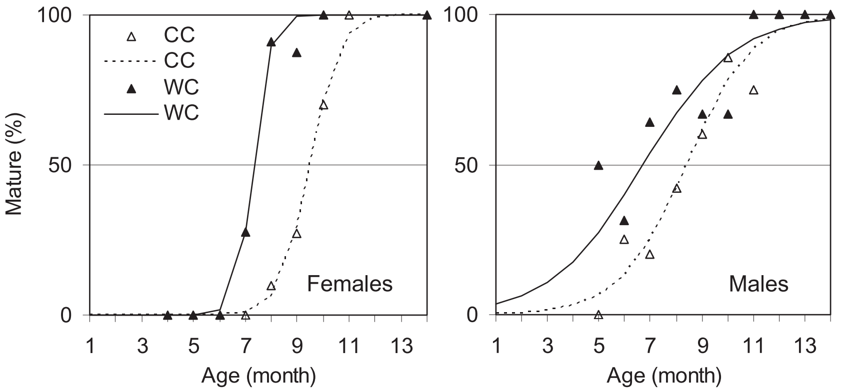

Fig. 4. Percentage of mature females and males by age group and estimated maturity ogives for the cold cohort (CC) and the warm cohort (WC).

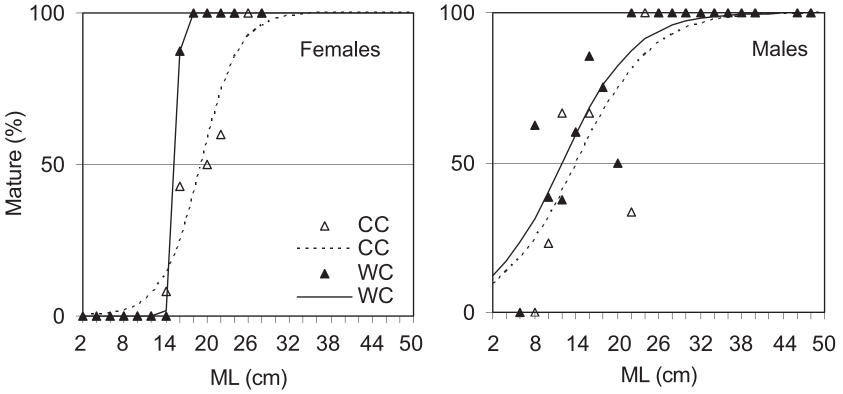

Fig. 5. Percentage of mature females and males by size class and estimated maturity ogives for the cold cohort (CC) and the warm cohort (WC).

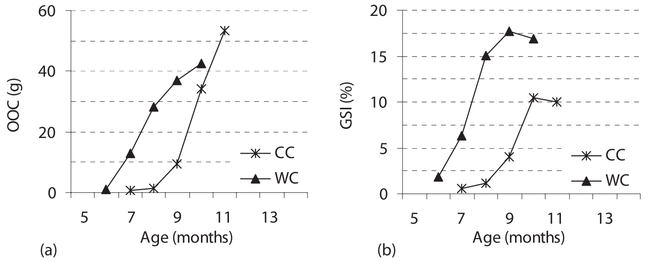

Fig. 6. Female: mean combined ovary and oviducal complex weight (OOC) by age group (a) and mean gonadosomatic index (GSI) by age group (b) in females of the cold cohort (CC) and the warm cohort (WC).

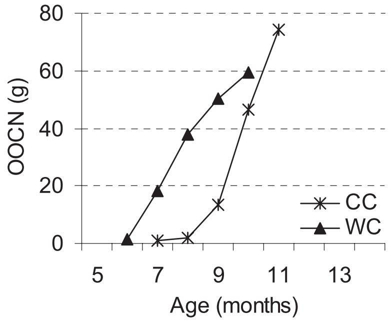

Fig. 7. Female: mean combined ovary and oviducal complex weight plus combined nidamental and accessory glands weight (OOCN) by age group in females of the cold cohort (CC) and the warm cohort (WC).

one month before that of females, as observed in several *L. vulgaris* and *L. forbesi* populations of the NE Atlantic (Collins et al. 1997; Moreno et al. 2002).

A higher complexity in size-at-maturity than in age-at-maturity was found, especially in males, suggesting that in the case of Portuguese squid there are groups of animals with distinct growth rates, and that there may be different cohorts that are subjected to different environmental conditions as the animals grow. Temperature appears to be a determining factor for somatic growth, at least in an early phase (Grist and des Clers 1999; Forsythe 2004). Therefore, cohorts of animals that hatched at different temperature regimes have different somatic growth rates, reaching different sizes prior to the onset of maturation. However, because there is always a coupling between different environmental factors, temperature does not necessarily explain all the variability in growth and consequently in age- and size-at-maturity. Sexual maturation, like growth, may be promoted by exposure to relatively high average water temperature, a favourable feeding regime (Richard 1966; Rodhouse and Hatfield 1990), or combinations of these or of these and other factors. It has been shown that the maturation rate is very responsive to changes in temperature (Jackson et al. 1997) and that there is a decelerating effect of long days (Mangold 1987), the two factors having an effect on the age of spawning. In our case the CC individuals, that hatched in colder water, were exposed to an increasing photoperiod,

Table 2. Influence of hatching cohort; cold cohort (CC), warm cohort (WC): gonadosomatic indices (GSI, %), mean combined ovary and oviducal complex weight (OOC, g), mean combined OOC weight plus accessory and nidamental glands weight (OOCN, g), mean combined testis and Needham complex weight (TNC, g), mean mantle length (ML, cm), ANCOVA, ML as the covariate.

		CC	WC	Mean square effect	*df* error	Mean square error	*F*	*p*
Females	GSI	12.2	17.0	211	40	48	4.4	**0.042**
	OOC	40.1	37.3	459	40	120	3.8	0.058
	OOCN	55.3	51.0	830	40	205	4.0	0.051
	ML	23.0	20.6					
Males	GSI	3.4	3.9	10	70	1	13.0	**0.001**
	TNC	5.5	8.1	35	70	6	6.1	**0.016**
	ML	19.3	21.7					

Significant differences between cohorts marked in bold.

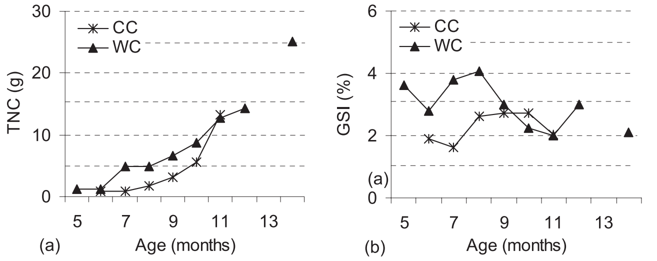

Fig. 8. Male: mean combined testis and Needham complex weight (TNC) by age group (a) and mean gonadosomatic index (GSI) by age group (b) in males of the cold cohort (CC) and the warm cohort (WC).

which was the highest (13 to 15 hours of light) when squid had achieved the minimum age of maturation (5–6 months), and increasing food availability (higher in summer). These environmental factors together would contribute to the delayed maturation observed in this cohort, as lower temperatures experienced early in life decrease growth rates and, consequently, minimum size for maturity is reached later in life. At this time, maturation will be further delayed in the majority of the cohort by a long photoperiod and high food supply. On the other hand, in the WC age-at-maturity was lower. The faster growth induced by higher temperatures enables this cohort to attain the minimum size for maturity earlier (ca. one month). This cohort then faces favourable environmental conditions and the majority of individuals quickly reach maturity. It has also been shown that, among a seasonal group of *Illex coindetii*, under lower temperature and longer photoperiod, maturation started at older ages (less 20–40 days) than in another group, under the opposite environmental regime (Arkhipkin et al. 2000). In *Loligo chinensis* and *Lolliguncula brevis* differences were also found in age-at-maturity between seasonal groups, and were thought to be related to differences in growth rates and the minimum size to reach maturity (Jackson 1993; Jackson et al. 1997).

The differences in age-at-maturity between cohorts resulted in a relatively short period between the main spawning peaks of each (December and April). It has been said that a certain degree of life cycle synchronization is achieved by an environmental induction of maturation (Moreno et al. 2002), possibly following temperature and photoperiod cues. These spawning cues will induce a rapid maturation in a given period of the year, if the minimum size threshold has been reached. From the recognisable onset of maturation, the process takes place at a very rapid rate and within less than a month full maturation is reached. This may allow the animal to take immediate advantage of favourable environmental conditions, switching from somatic to reproductive growth within a short time. The lowest sizes-at-maturity were observed during the main spawning seasons, and a significant negative correlation was found between seasonal trends of proportion mature and size-at-maturity (Moreno et al. 2002). This seems to indicate that at favourable spawning times most animals that have reached the minimum size threshold will begin the maturation process (as in the WC). Otherwise, they will delay maturation and continue the somatic development until the next environmental spawning cue (as in the CC).

In males, variability in age- and size-at-maturity could not be accounted for by assigning them to a temperature cohort. Other authors have shown distinct sizes-at-maturity for *L. vulgaris* and *L. forbesi* (Guerra and Rocha 1994; Moreno et al. 1994; Pierce et al. 1994), probably as a result of a "guard-sneaker" breeding strategy, as observed in *L. vulgaris reynaudii* (Sauer et al. 1997) or *L. pealei* (Hanlon 1998). Males seem to display complex breeding strategies, perhaps derived from endogenous stimuli. These breeding strategies may help to maintain the genetic homogeneity of the population by co-occurring and interbreeding with different female cohorts.

4.2 Reproductive investment

Some of the characteristics of the brood, such as the number and quality of the eggs and sperm cells, and its relation to the reproductive investment, may be determined by the interval of time between reaching the minimum size for maturity and experiencing the cues (environmental or otherwise) that determine adequate breeding conditions.

The late maturing CC females experience favourable environmental conditions, namely high food supply and temperature, before and during the main spawning period (summer and autumn, respectively), which enables enough energy storage to be used for fast maturation rates even during their spawning peak in December, when temperatures are lower. The WC females spawn mainly during or soon after the adverse winter months; thus a lower amount of energy will probably be available to allocate for gonad maturation, as revealed by their lower maturity rates. On the other hand, the reproductive investment as indicated by GSI was significantly higher in the WC than in the CC females. This fact highlights the differences in the relative reproductive investment and is more closely related with the differences in the age- and size-at-maturity between cohorts, since the absolute reproductive investment (i.e. the weight of the reproductive system) did not differ significantly between them. In *Sepioteuthis lessoniana* (Jackson and Moltschaniwskyj 2002) and *Idiosepius pygmaeus* (Jackson and Choat 1992; Jackson 1993) the absolute reproductive investment (i.e. total mass of the ovary) was greater in the late maturing females. In any case, the differences in GSI between cohorts show that, at all ages, the amount of energy allocated for gonad growth in relation to body mass was higher in the WC females. In *Sepioteuthis lessoniana,* it was also observed that the "hot" strategy squid invested a greater proportion of their total mass in reproduction than the "cool" strategy squid (Jackson and Moltschaniwskyj 2002).

In the CC females, the energy for reproduction was probably mainly derived from ingested food rather than body reserves. In this strategy, there is an increase of an individual's ability to capitalise on favourable environmental conditions by rapidly converting food to fuel sexual maturation and somatic growth (Ho et al. 2004), favouring large size mature animals and longer life spans. On the other hand, in the WC, part of the energy must be re-allocated for reproduction at some cost to somatic growth. A decline in relative mass of the mantle during reproductive maturation was seen in *Illex argentinus* (Hatfield et al. 1992) and *Photololigo* sp. (Moltschaniwskyj and Semmens 2000), and a decline in growth rates was seen in *Photololigo* sp. (Moltschaniwskyj 1995).

In males of the WC both relative reproductive investment (GSI) and absolute reproductive investment (i.e. the total mass of the reproductive system) were higher than in the CC, demonstrating that temperature, photoperiod and perhaps other environmental factors are not the only important factors in maturation.

4.3 Implications for management

Back-calculated dates of hatching suggest that hatching, and therefore spawning, occurs all year round in *L. vulgaris*, assuring exposure of squid to all seasonal extremes. Given that growth, maturation and potentially also life span, are dependent on environmental factors that have a great seasonal variability in Portuguese coastal waters, it is not unexpected that we find a highly variable and fluctuating population structure. This has important implications for population modelling and fisheries management (Dawe and Beck 1997; Pecl 2004). There being a recognized plasticity in both age and size-at-maturity, an influence of those in the characteristics of the next generation and a fishery-induced differential mortality-at-length and mortality-at-age could induce a strong selection for early age of maturation. This could in the medium to long-term affect the yield from the fishery and in the long-term the sustainable management of the stocks may be placed at great risk (Murphy and Rodhouse 1999). A question that arises from this study is whether the different reproductive strategies, which result in small mature females and large mature females with gonads of similar size, have any implications in their fecundity. Directed fecundity studies are needed in order to investigate this aspect, since potential differences in fecundity between cohorts would have major implications for the options available to manage this important resource.

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