Reproductive biology of jumbo squid *Dosidicus gigas* in relation to environmental variability of the northern Humboldt Current System

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ABSTRACT: *Dosidicus gigas* is a monocyclic ommastrephid squid and is an important component of its ecosystems in the Eastern Pacific Ocean. The species shows variable reproductive characteristics; among these are 3 spatially separated groups of size-at-maturity. Biological data from the industrial fisheries of the Peruvian Humboldt Current System (HCS) from 1991 to 2007 were analyzed. Changes in reproduction patterns allow jumbo squid to cope with productivity changes in their environment. In the HCS, low productivity is related to warm water masses prevailing during warm periods, and high productivity is found for cool water masses during cool periods. Three general features related to reproduction enabling the squid to adjust to changes have been identified: (1) variable size-at-maturity, (2) temporal decoupling of male and female formation of reproductive tissue in order to temporally distribute the required energy and (3) changing sex-ratios. Smaller sizes-at-maturity are found in warm water masses, specimens maturing at larger sizes in cool water masses. Females mature at the end of their life which leads to a j-shaped increase in maturity when plotted against mantle length, while males mature at a medium size which results in an s-shaped form of maturation. The 3 groups of size-at-maturity proposed in earlier studies may not actually exist, and may only be an observational artifact from a continuous change in size-at-maturity between 2 extremes.

KEY WORDS: *Dosidicus gigas* · Cephalopoda · Reproductive patterns · Interannual variability · Size-at-maturity · Energy availability · Peru

INTRODUCTION

The jumbo squid *Dosidicus gigas* d'Orbigny 1835 is found in pelagic waters off the coasts of the highly variable Eastern Pacific Ocean (EPO) in both hemispheres. This ommastrephid cephalopod has access to a wide range of prey sizes and trophic levels during its short life (Nigmatullin et al. 2001, Markaida 2006a); together with its abundance, this makes it a key predator in its ecosystem (Field et al. 2007, Rosas-Luis et al. 2008). *D. gigas* is a monocyclic species (Rocha et al. 2001), i.e. it dies after its first reproductive cycle. Thus, its final size is related to its size-at-maturity. During the reproductive cycle, female jumbo squids undergo multiple spawnings of 10 to 14 spawning batches. With 32

million eggs or more, it has the highest fecundity of all cephalopods, and fecundity is directly related to size (Nigmatullin & Markaida 2009). Females, even when immature, can store male sperm in buccal spermathecae after copulation (Nesis 1983). This pattern is found in many cephalopods, increasing reproductive flexibility and helping to secure population survival in variable environmental conditions (Boyle & Rodhouse 2005). With very few short-time exceptions (Markaida & Sosa-Nishizaki 2001), the sex ratio of jumbo squid has been found to be in favor of females, ranging from a female:male ratio of 1:1 to 24:1 (Table 1).

Since the turn of the millennium, different stocks of *Dosidicus gigas* have shown changes in distribution (Zeidberg & Robison 2007, Keyl et al. 2008), reproduc-

tive biology (Markaida 2006b, Argüelles et al. 2008), as well as population structure in general (Bazzino et al. 2007). Analyzing size-at-maturity of females of the Peruvian exclusive economic zone only, a transition period lasting from 1999 to 2000 was identified that separates a period of small mature females in the 1990s from the period of large mature females in the 2000s (Argüelles et al. 2008). At the same time, landings of jumbo squid have greatly increased (IMARPE unpubl. data: see also FAO ftp://ftp.fao.org/FI/STAT/summary/ a1e.pdf). Temporal variation in size-at-maturity has also been observed in the northern hemisphere, although in a different form; here jumbo squid generally matured at large sizes (at least since the late 1980s), and only during the El Niño event of 1997/1998 did size-at-maturity drop to sizes similar to those found in Peru during the early 1990s (Markaida 2006b, Bazzino et al. 2007). However, small specimens were also reported from Mexican waters in the 1970s and the 1980s (Table 1).

The northern Humboldt current system (HCS) shows high variability in abiotic and associated biotic conditions. Water temperature, salinity and ecosystem productivity are coupled to water masses that change their extent according to global climate conditions and events like El Niño (EN) and La Niña (LN) as well as large-scale regime shifts (Morón & Sarmiento 1999, Morón 2000, Tomczak & Godfrey 2005). Cool water masses are generally assumed to be more productive than warmer ones (e.g. Ayón et al. 2008a,b). Observed changes in size-at-maturity of *Dosidicus gigas* have been proposed to be a phenotypic response to changes in its physical and biotic environment (Nesis 1970, 1983, Keyl et al. 2008) or have a genetic origin (Nesis 1970, 1983). The work of Nesis is based on partially un-published data from Russian scientific cruises in the 1960s to 1980s. It proposes 3 different groups of size-at-maturity that are thought to be found in different zones of the distribution area: the small group in the tropical region, the medium-sized group throughout the whole distribution area, and the large group in the distribution limits in both hemispheres (Nesis 1970, 1983, Nigmatullin et al. 2001).

Shifts in reproductive biology according to oceanographic conditions (such as size-at-maturity, female:male ratio and portion of mated females; Table 1), have already been documented (but not specified) in the 1970s and 1980s for *Dosidicus gigas* from the Gulf of California (GoC) and the Northern Mexican Pacific (Sato 1976, Ehrhardt et al. 1982, 1983; all cited in Markaida & Sosa-Nishizaki 2001).

This work aims to identify and understand changes in the reproductive characteristics of *Dosidicus gigas* in relation to changing environmental conditions. It analyses data from nearly 2 decades that covers the

strong LN of 1996 and the strong EN of 1997/1998, as well as the shift from warm to cool conditions in 2000. The energetic implications of changes in size-at-maturity and other reproductive related strategies are discussed. A simple model for energy allocation is put forward to explain the relation between size-at-maturity and cool and warm periods. The present work continues and amplifies the study of Tafur et al. (2001).

MATERIALS AND METHODS

The study area is the Peruvian exclusive economic zone (EEZ), the northern part of the Humboldt Current System (HCS, Fig. 1) where the coastal and the oceanic branch of the north and west flowing Humboldt Currents are counteracting the equatorial undercurrent (Tomczak & Godfrey 2005). The stable year-round wind-driven upwelling cells along the coast of Peru make this ecosystem one of the most productive in the world (Ayón et al. 2008b).
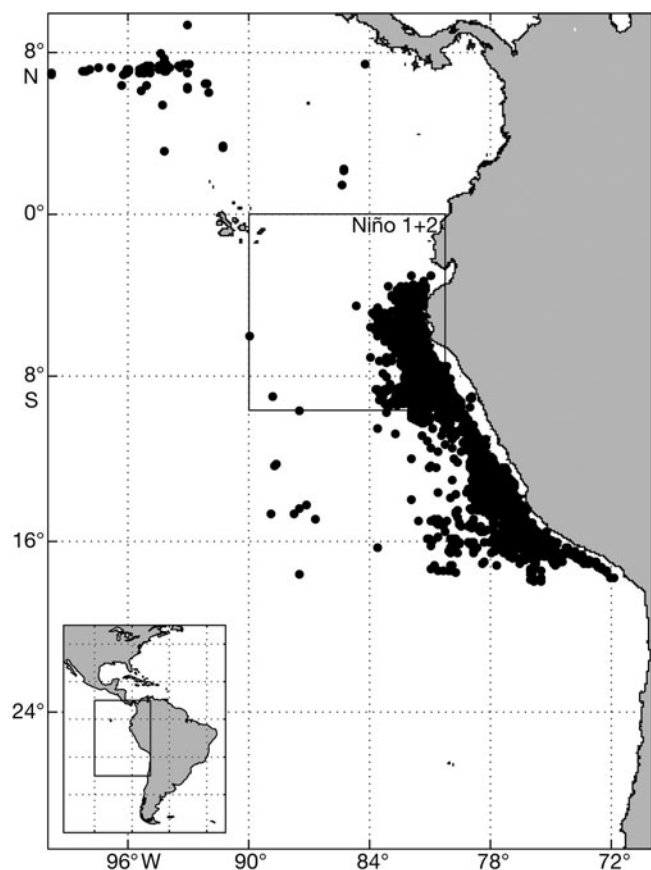

Fig. 1. Sample locations. The area north of the equator was sampled from August to December 1996 (n = 1612); samples west of 85° were taken in June 2000 (n = 215) and April 2005 (n = 19); the square is the Niño 1+2 monitoring area

Table 1. *Dosidicus gigas*. Reproduction parameters in the Eastern Pacific Ocean; GoC: Gulf of California, HCS: Humboldt Current System; EEZ: Exclusive Economic Zone; BC: Baja California Peninsula; sampling period: year, or month & year, or season & year; W: winter, SPR: spring

Sampling period	Location	Size-at-maturity (mm)	Female:male ratio	Source	Comments
1968	HCS	♀ >400 ♂ <250	Mean 2:1	Nesis (1970)	Size dependent female:male ratio
1971	GoC Pacific, off BC	♀ 200[a] 200 to 480[a]	1.5 to 5.2:1	Sato (1976)	5 diff. (sub-)populations according to oceanogr. cond.
–	East of Peru-Chile trench	♀ 400 to 600[b]	–	Shevtsov (1970)[c]	
1980	GoC, Pacific off BC	♀ 350 to 400 ♂ 180 to 250	–	Erhardt et al. (1982, 1983, 1986[d])	Reproductive cycle changes according to oceanogr. cond.
5 to 9/81 6/1981	GoC	♀ 300[e] ♀ 200 to 400[a]	1.5 to 3:1 1.82:1	Ramírez & Klett-Traulsen (1985)	Fisheries captures or scientific sampling, 90% mature
11 & 12/ 1989	Peru	♀ 150 to 470[a] ♂ 170 to 450[a]	7.34:1	Rubio & Salazar (1992)	
1989/90	GoC	500 to 700[a]	1 to 24:1, Mean 6:1	Morán-Angulo (1990)[d]	
3/1990	GoC	♀ 660 to 800[a] ♂ 550 to 730[a]	7.62:1	Sánchez (2003, 1996)[d]	65% mature 85% mature
1991	GoC	300 to 750[a]	2.6:1	Guerrero-Escobedo et al. (1992)[d]	
5 & 6/1996	GoC	♀ 420 ♂ 510	3.3 to 14.3:1 Mean 5:1	Hernández-Herrera et al. (1996)	
1991 to 1995	Peru EEZ	–	~2 to 8:1 Mean 2.85:1	Tafur et al. (2001)	
W 93 SPR 93	Central Chile	–	9:1 3:1	Chong et al. (2005)	
W 93 SPR 93	Central Chile	♀ 890[f] ♀ 470, ♂ 471[f]	12.4:1 2.5:1	González & Chong (2006)	Total 3.8:1
1995/96 1996 1996/97	Guaymas Sta. Rosalia Guaymas	♀ 420, 760[e] ♂ 600, 680[e]	1.1 to 4.9:1 Mean 2.3:1	Markaida & Sosa-Nishizaki (2001)	
5/1999 9/1999	GoC Pacific off BC	♀ 310 to 458 ? 322 to 429	2.3:1 1.21	Markaida (2006b)	Total 2.21
2001	West of Peruvian EEZ	♀ 327 ♂ 228	2.52:1	Ye & Chen (2007)	
2001/02	GoC	♀ 740	4:1	Díaz-Uribe et al. (2006)	
2001/02	Sta. Rosalía, GoC	♂ 720	1:3 to 9:1	Martínez-Aguilar et al. (2004)	
S 03/04 W 03	Central-South Chile	♀ >710[g] ♂ >660[g]	Min. 1.3:1 Max. 4.5:1	Ibáñez & Cubillos (2007)	Coastal Oceanic
2003 2004	Sta. Rosalía, GoC	♀ 770, ♂ 570[e] ♀ 690, ♂ 590[e]	1.45:1 1.72:1	Bazzino et al. (2007)	
W 05	Central-South Chile	♀ 763, ♂ 796[f]	1.25:1	Ulloa et al. (2006)	By-catch of hake trawl fishery

[a]Total sampled mode; [b]only immature; [c]cited in Nesis (1983); [d]cited in Markaida & Sosa-Nishizaki 2001; [e]ML$_{50\%}$; [f]mean of mode of mature specimens; [g]mode of mature specimens

Data used in this study were collected by onboard technical observers on behalf of the Instituto del Mar del Perú (IMARPE – Peruvian Institute of the Sea) during the operations of the international jigging fleet in the Peruvian EEZ from 1991 to 2007. The resulting biological database, with data on more than 145 000 specimens, contains information on individual mantle length (ML), sex and reproduction-related variables. Ten females and 10 males were sampled from the catch during each fishing operation. Mantle lengths, gonadal lengths, and nidamental gland lengths were taken to either the closest 1 mm or 0.5 cm. Not all measurements were taken or are available in all cases. Individual maturity was determined by a simple visual system (Tafur & Rabí 1997); this consists of 4 stages discriminated by size and color of the gonads (stage I: immature specimens, stage II: maturing ones and stage III: mature individuals. Stage IV contains only the spawned females.

Two reproduction-related measures were used to assess the stage of maturity of the population: (1) size-at-maturity of the population is defined as the mean size of all mature individuals (ML_{mean}), and (2) the size of massive maturity ($ML_{50\%}$) that is defined as the ML where 50 % of all individuals are mature (stages III and IV). Both were calculated by biological semester for females and males separately. Austral winter is from April to September, austral summer from October to March. A simple additive model, assuming 1 to 3 Gaussian cohorts, was adjusted to the semestral length-frequency distributions (with length classes of 30 mm) to test if the population distribution was homogenous or consisted of separated groups. $ML_{50\%}$ was calculated for each group from 1 semester by adjusting the sigmoidal model:

$$\%\text{mature} = \frac{1}{1+e^{-(a+b\cdot ML)}} \qquad (1)$$

to the relative number of mature individuals (stages III and IV) in each size class (Tafur et al. 2001). The relative frequency of mature individuals in each length class is represented by %mature; ML and *a* and *b* are the parameters that describe the function. $ML_{50\%}$ then is estimated as:

$$ML_{50\%} = -\frac{a}{b} \qquad (2)$$

To be able to compare the semestral reproduction related series to sea surface temperature (SST), the Niño 1+2 SST-anomalies series were transformed from the original monthly time increment to a semestral one; this was done by filtering the original series with a 6-point running mean and using the values of the 4th and the 10th month of each year.

The length-based nidamental gland index (Tafur et al. 2001) acts as a proximal indicator for the individual maturity of females, and was used and extended to calculate a similar index for males using testicle length in relation to the mantle length. The maturity index (MI) was calculated for each individual as the percentage of nidamental gland length and testis length to ML for females and males, respectively.

To identify reproduction and spawning periods, the monthly mean MI for small and large individuals, the monthly proportions of mature individuals for females and males, and the percentage of copulated females were calculated. Females were considered as having copulated if spermatophores were found in their buccal mass or if they had swollen spermathecae that contained remnants of spermatophores. The monthly mean MI was calculated separately for small and large individuals to highlight spawning peaks, as it is assumed that the larger individuals of a population are generally those that are or will mature. To highlight changes in size-at-maturity in different years, the limit between the 2 groups was defined for each month by calculating the mean ML of all mature specimens (maturity stages III and IV for females; III in the case of males) of that month and subtracting one standard deviation. All individuals with ML above the limit were designated as large; those with ML below the limit as small. The MI for large and small individuals was estimated from these monthly means.

The monthly female:male sex ratio was calculated using data available from over 4.3 million individuals from 1996 to 2007.

RESULTS

Size-at-maturity (ML_{mean}) and size of massive maturity ($ML_{50\%}$) changed considerably during the period investigated (Fig. 2A,B), during which time total fisheries landings in the Peruvian EEZ increased rapidly, from nearly zero in 1991 to a maximum of over 230 000 t in 2006. More than 1 group each with a characteristic $ML_{50\%}$ was identified in the early 1990s, as well as 2000 and 2001 (Fig. 2A). After a reduction in the period from 1993 to 1999, $ML_{50\%}$ after 2000 returned to similar values as the higher $ML_{50\%}$ groups from the years 1991 and 1992. The other group that matured at smaller sizes in 1991 and 1992 was of similar size to the $ML_{50\%}$ of the years 1993 to 1999. After the 1990s (ML_{mean} ~300 mm), ML_{mean} rose to >800 mm (males) and ~900 mm (females) over a transition period from winter 1999 to summer 2001. The inhomogeneous population structure found in some semesters for $ML_{50\%}$ was not observed.

Female $ML_{50\%}$ and ML_{mean} in nearly all semesters was above that of males. Although the absolute difference between ML_{mean} of females and males increased in the 2000s, the differences between the sexes relative to body size decreased from 15.4 % in the 1990s to
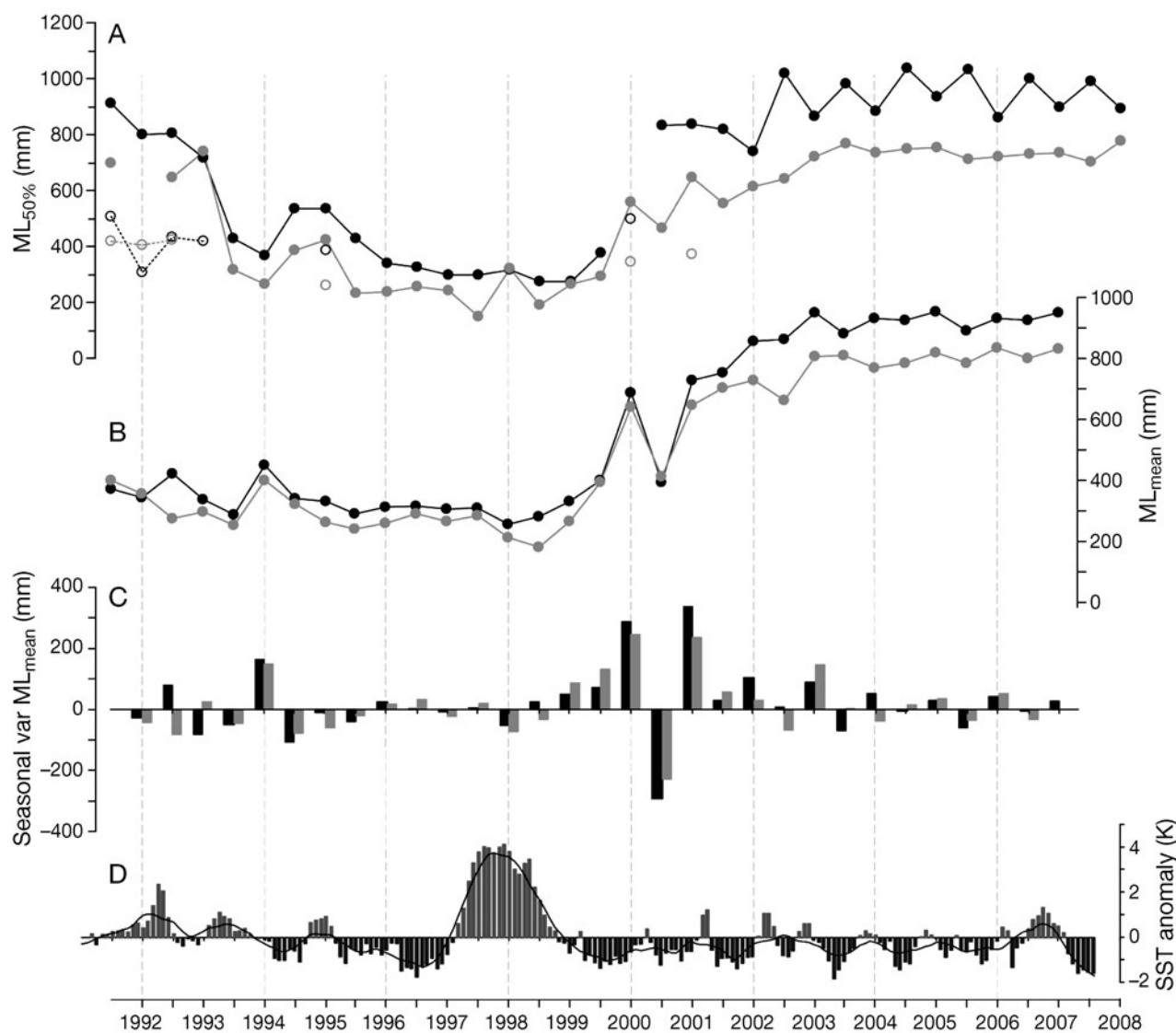
Fig. 2. *Dosidicus gigas.* Semestral variation in size of massive maturity ($ML_{50\%}$) and size-at-maturity (ML_{mean}) of females (black) and males (grey) in the Peruvian EEZ in comparison to environmental variability; (A) $ML_{50\%}$ for females and males; open circles = smaller group in years with more than one group of $ML_{50\%}$; (B) absolute values of ML_{mean} for females and males; (C) variation of ML_{mean} between subsequent semesters for both sexes; (D) SST-anomalies of the Niño 1+2-box with 11 mo centered running mean (line)

13.6% during the 2000s. During the transition period, the differences between the ML_{mean} of females and males were close to zero (Fig. 2B).

Highest inter-seasonal variation of ML_{mean}, both positive and negative (Fig. 2C), can be observed after the EN-event of 1997/1998 and the moderate EN of 1991/1992. Direct cross-correlation analyses of the ML_{mean} series (Fig. 2B) and the intra-seasonal variation of size-at-maturity (Fig. 2C) with the SST anomalies of the Niño 1+2-box (Fig. 2D) did not yield significant correlations between the series with any lag. However, when using absolute values of the variation of ML_{mean} and the SST-anomalies series, high significant correla-

tions (up to r = 0.8, p < 0.05) were found for lags from 4 to 7 and 4 to 6 semesters for females and males, respectively (Fig. 3). This translates to a delay of about 2 to 3 yr in the biological response to environmental variability, i.e. EN events are followed 2 to 3 yr later by a change of size-at-maturity. For the $ML_{50\%}$ series that contains missing values no clear relation to environmental series was found irrespective of lag.

The individual values of the maturity index (MI) by sex versus mantle length support the difference between the 1990s and 2000s, and the transition time from 1999 to 2001 (Figs. 4 & 5). The increase in size-at-maturity seems less clear as might be supposed from
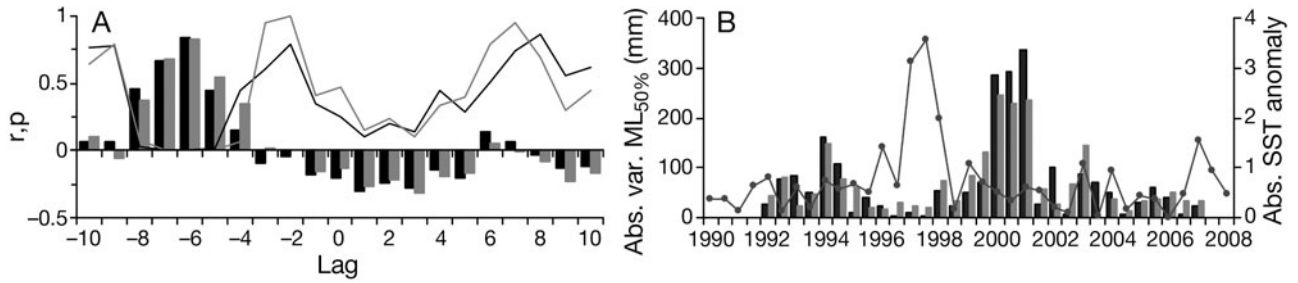
Fig. 3. *Dosidicus gigas.* Relationship between size-at-maturity and SST. Females: black; males: grey. (A) cross-correlations between the absolute series shown in (B); bars: correlation coefficient r; lines: p-level; (B) absolute series of semestral variations of $ML_{50\%}$ of females and males (bars) and the mean semestral SST-anomalies of the Niño 1+2-series (line with filled circles; every 6th point of a 6 pt. running mean of the original data to obtain a half-annual series relatable to the biological series) used for cross correlations
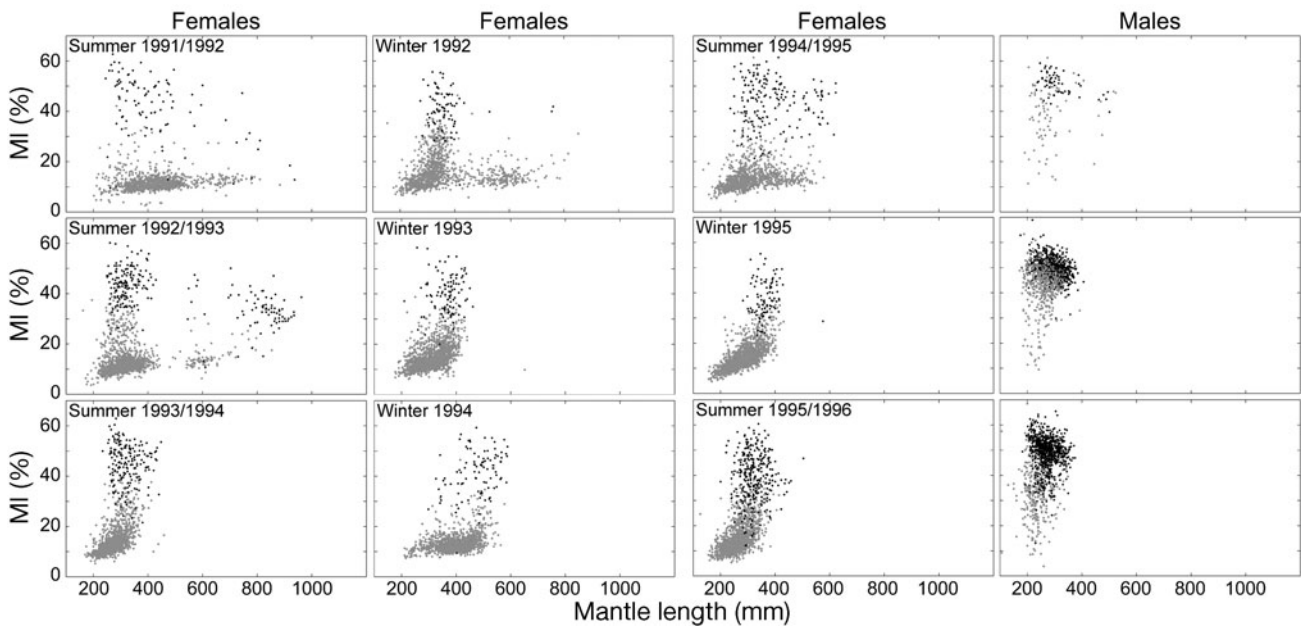
Fig. 4. *Dosidicus gigas.* Individual maturity index (MI) for females and males by season (1991 to 1996); grey points = immature specimens (stages I & II); black points = mature specimens (stages III & IV). Note: from 1991 to 1994 MI data for males are missing

the ML_{mean} series (Fig. 2B). In 1991/1992, 1992/1993, 1994/1995, and from 2000 to 2002, more than 1 group of size-at-maturity can be observed.

After 1999, individuals started to become larger, and distinct maturing processes for males and females can be noticed (Fig. 5). While females grow continuously in body size without increasing the relative length of their nidamental glands until close to maximum size, males start to mature at a size of about half their maximum size. After a combined growth of gonadal and somatic tissue (i.e. increase in testicle length and ML) further relative gonadal increase is stopped, and then only somatic growth takes place until the final body size is reached. While the gonadosomatic growth in females can therefore be seen as j-shaped, leading to

death soon after maturation without further body growth, male gonadosomatic growth follows an s-shaped function that allows them to live on and grow in body size after complete maturation.

The monthly mean MI (Fig. 6) not only shows a clear difference between small and large specimens, but also between sexes. The MI of the small females is constant during the whole study period, and the MI values

Fig. 5. *Dosidicus gigas.* Maturity index (MI) for individual females and males by season 1996 to 2007; grey points = immature specimens (stages I & II); black points = mature specimens (stages III & IV). Note: no data from summer 1997/1998 to summer 1998/1999
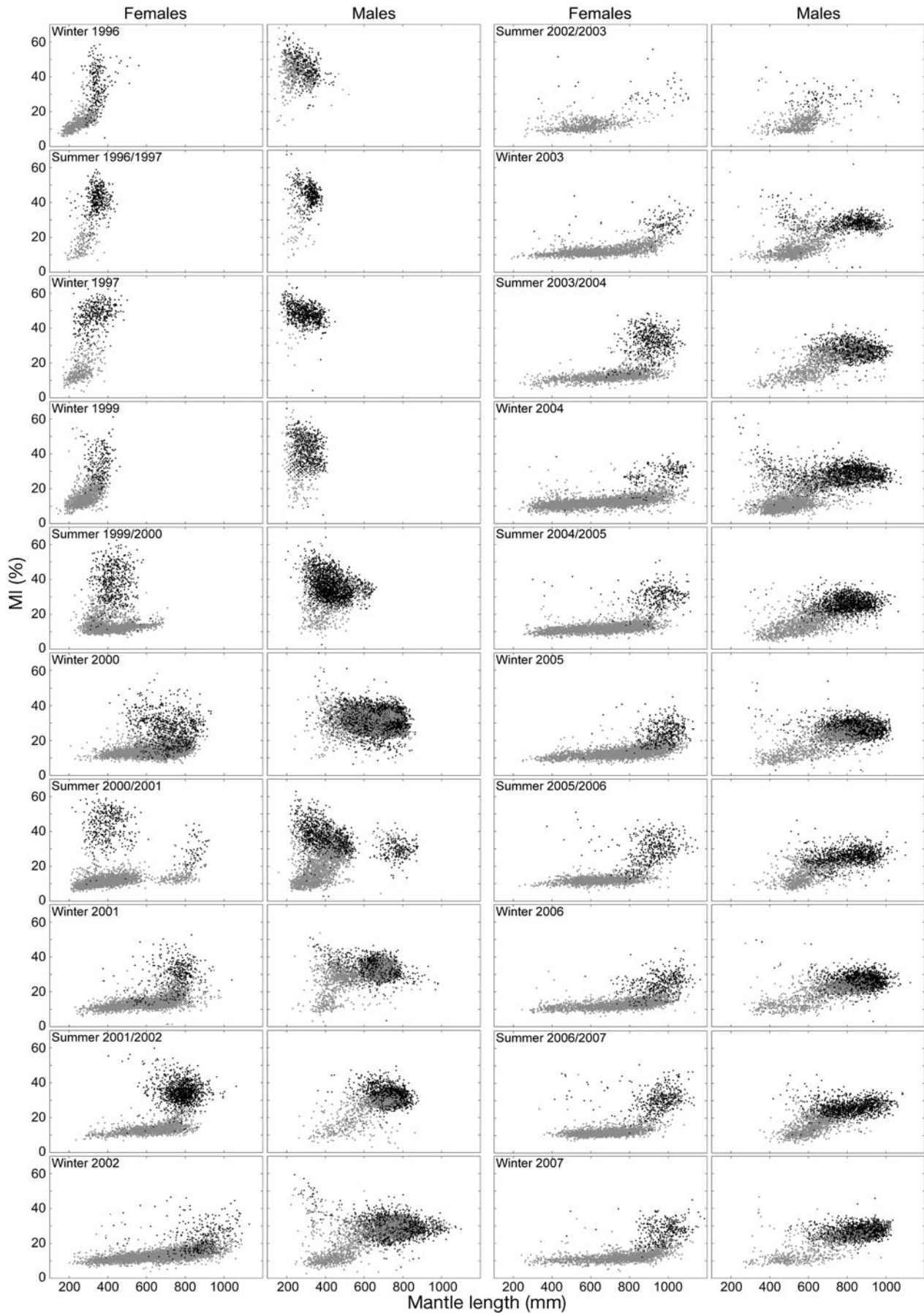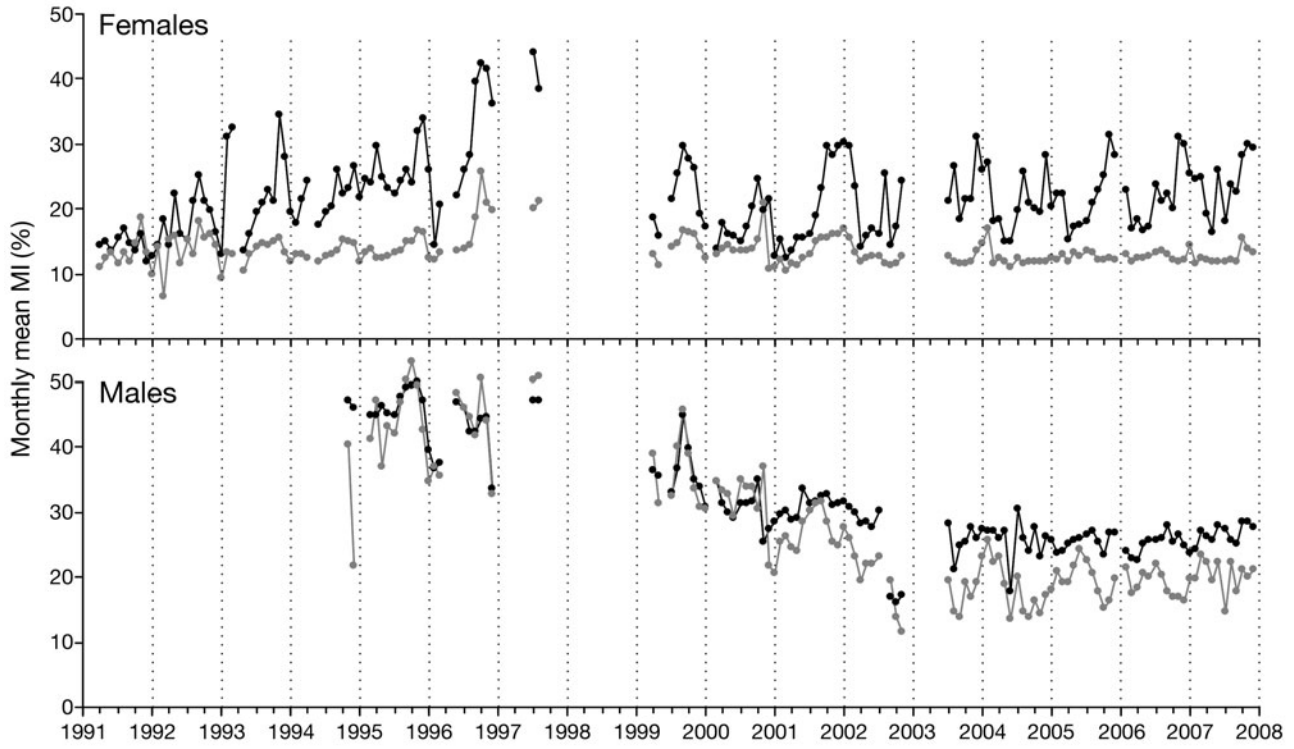
Fig. 6. *Dosidicus gigas*. Monthly mean values of the maturity index (MI) by sex for small (grey) and big (black) individuals

of the large individuals show periodic or semi-periodic peaks as well as a continuous increase of mean MI in the early 1990s (Fig. 6, upper panel). Main peaks occur around the end of most years. For males (Fig. 6, lower panel), periodic peaks are found in both the large and

the small specimens; the small peaks show more marked and more regular peaks, which can be expected in this form as males show the s-shape gonadosomatic or mid-life maturation (i.e. the large male specimens have already passed through maturation,
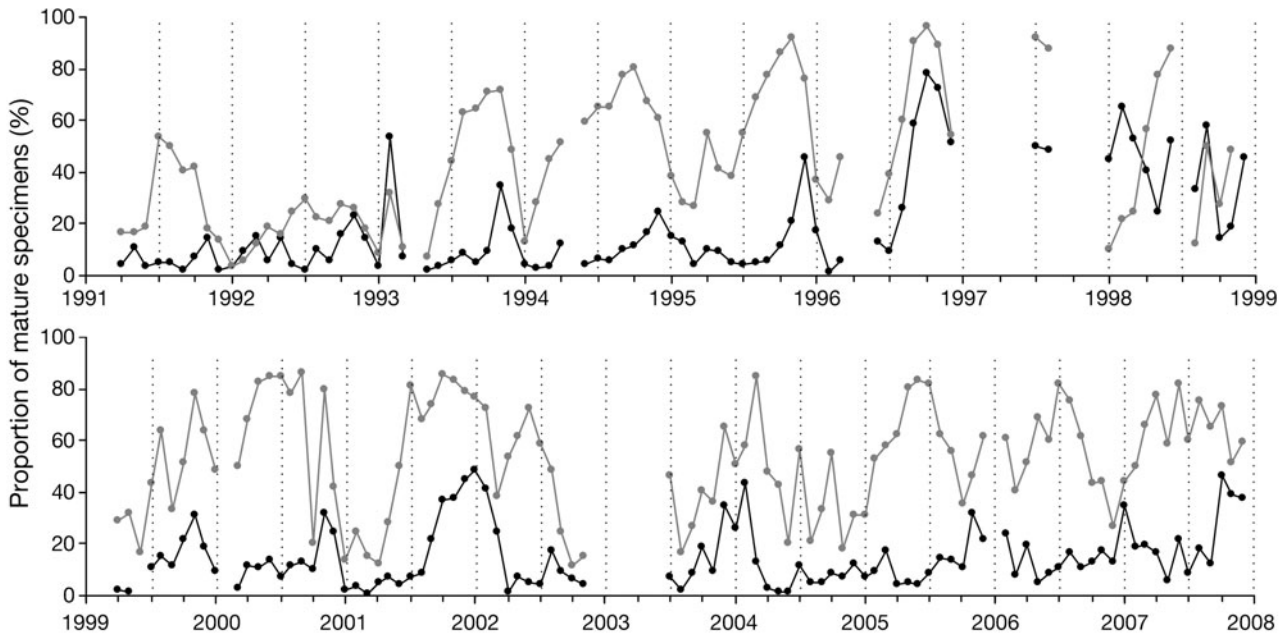

Fig. 7. *Dosidicus gigas*. Monthly percentages of mature females (black) and males (grey) in the population
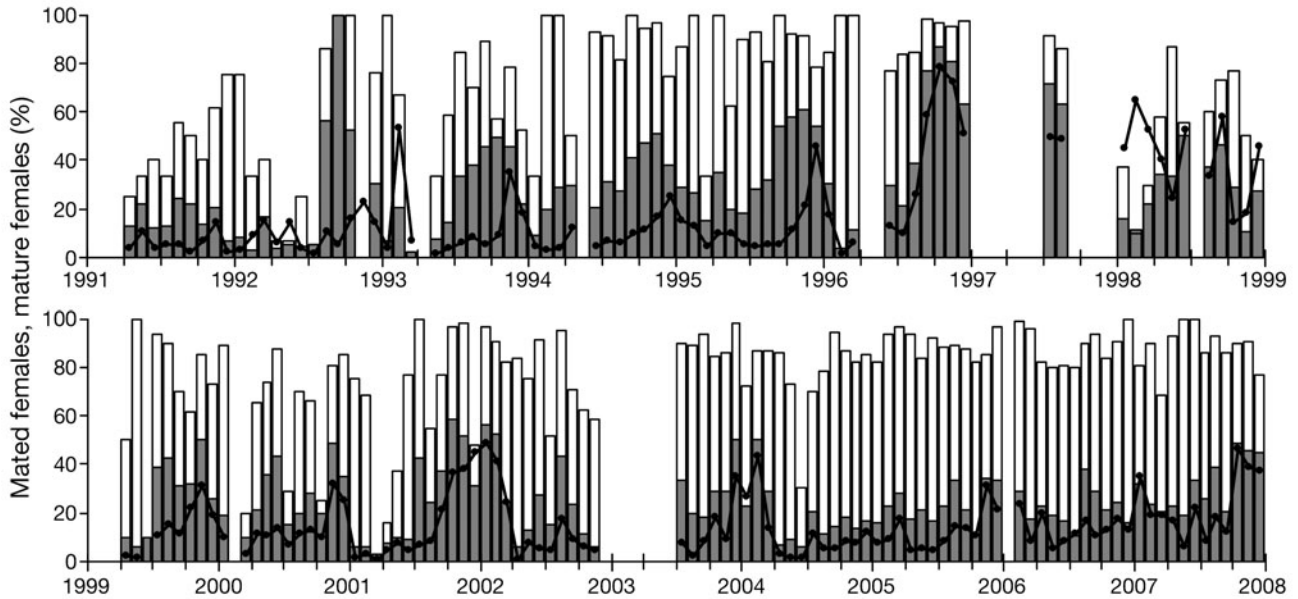
Fig. 8. *Dosidicus gigas*. Monthly percentages of mated females (grey bars) among all females and (white bars) among mature females; black line percentage of mature females

and from then on increase their gonad size only relative to body size). The series of both groups of males in total show a constant decrease in mean MI until 2004, with a steady phase afterwards. A steady phase of the mean MI of the males during the early 1990s, during which females increased their monthly mean MI, can only be presumed as no data is available for males during the first years.

Differences between sexes can be noticed in the proportion of mature specimens in the population (Fig. 7). Mature males generally have a higher proportion in the male part of the population than the mature females in the female part. Marked main reproduction peaks occur at the end of the year (i.e. austral spring) until 2004, but become less clear and more frequent afterwards. Females in particular after that year show an elevated maturity baseline, with smaller peaks that less clearly show the annual periodicity observed in previous years. It is noticeable that the highest proportion of mature females was found in 1996 during the LN event preceding the very strong EN of 1997/1998. The reproductive peaks of males are generally wider than those of the females, resulting in a relatively high constant overall percentage of mature males in the population, broken up by short periods with lower percentages of mature males after the maturity peaks of the females.

With the exception of some periods (1991 to 1993, 1998 and 2000/2001),

the fraction of mature females that have mated (white bars in Fig. 8) exceeds 90% of the mature part of the population in most months. The fraction of all mated females in the entire population usually still reached between 20 and 50% (grey bars in Fig. 8). Percentage of mated females usually increased or peaked with the onset of austral summer in October, although this pattern was less marked after 2002. The percentage of mated females (grey bars in Fig. 8) is related to male maturity (exponential function, $r^2 = 0.44$, $p < 0.01$; Fig. 7).

Monthly sex ratios (females:males) are also highly variable (Fig. 9). In the 1990s and until ~2002, the ratio on average was ~3:1 in favor of females. After 2002, a slow decrease of the sex-ratio to ~2:1 has been observed. Ratios between 6.55:1 and 0.24:1 were observed until 2002, while afterwards they changed to values between 3.86:1 and 1.09:1. Similar ratios, and even higher ones, have been reported before, as has the high temporal variation of the ratio (see Table 1).
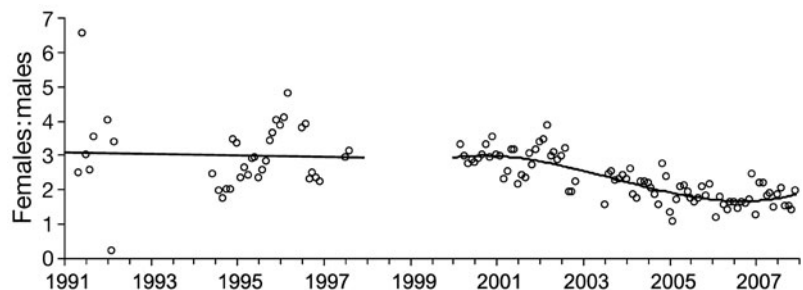

Fig. 9. *Dosidicus gigas*. Monthly sex ratios females:males

DISCUSSION

The results of the analysis of mean monthly MI and relative occurrence of mature individuals (Figs. 6 to 8) give strong evidence that the main reproduction period of Peruvian jumbo squid is austral spring. This is consistent with previous findings (Tafur & Rabí 1997, Tafur et al. 2001).

A strong shift of size-at-maturity of *Dosidicus gigas* in Peruvian waters was observed for both sexes, similar to that reported before for females (Argüelles et al. 2008); it took place after the very strong climate event combination of the 1996 La Niña (LN) and the 1997 to 1998 El Niño (EN). After this 'system reset' (Bakun & Broad 2003), a cool regime was especially noticeable in the study area (see Niño 1+2-box in Fig. 1 and the integrated SST anomalies series of this area in Fig. 2D). Environmental conditions have been hypothesized to be important for changes in size-at-maturity of *D. gigas* (Keyl et al. 2008).

It is assumed that the onset of maturation in cephalopods is controlled mainly by temperature and nutrition, and that higher temperatures and low food availability result in maturation at smaller sizes (Mangold 1987). From an energetic point of view, the individuals maturing at small sizes benefit over the larger ones as they can put less energy in somatic and reproductive tissue before spawning. Specimens that mature at small sizes were found in less productive warm water masses (Keyl et al. 2008). In the HCS, temperature and nutrition availability are related: the warm water masses that dominate the system during warm periods are less productive than the cooler waters that prevail during cool periods (Ayón et al. 2008a,b, Swartzman et al. 2008). Additionally, the species dominance of the ecosystems of the HCS changes with water masses (Chavez et al. 2003, Gutiérrez et al. 2007, Tam et al. 2008, Taylor et al. 2008). If it is understood that the Niño 1+2-series is the mean SST of all water masses in this area, it can easily be seen that negative anomalies correspond to the prevalence of cool waters while positive ones correspond to warmer waters. The temporally changing maturation patterns found here (Fig. 2A,B) must then be related to different water masses and point out that the variable reproductive patterns of *Dosidicus gigas* via trophic links are the result of spatial variability of oceanographic factors.

The results of the cross-correlation between the absolute series of monthly variation of ML_{mean} and SST anomalies indicate that changes in size-at-maturity are related to disturbance of the ecosystem (Fig. 3). Lifespan of jumbo squid in the past has mostly been assumed to be no more than 12 to 18 mo (Masuda et al. 1998, Argüelles et al. 2001, Nigmatullin et al. 2001). The lag of 2 to 3 yr between strong environmental vari-

ability (EV) and the biological response then translates to an inter-generational lag to the impact of changes in environmental conditions. More recent data from the industrial fishery in the Peruvian EEZ showed lifespan to be highly variable, ranging from ~12 up to 32 mo, and only loosely related to the terminal size of a cohort (Keyl et al. unpubl.). There, lifespan of over 2 yr was found for all cohorts hatched in the period of the high environmental variability from 1996 to 1999. If it is true that lifespan was actually higher than found before, then the observed lag of 2 to 3 yr would describe an intra-generational response to environmental conditions (i.e. a shift in environmental conditions directly and instantaneously affects individual life history traits, or at least those related to maturation processes). This would also make the genetic origin of the changes, as proposed by Nesis (1983), improbable. It has to be noted that these shifts, as with all others found here, occurred during a period of increasing fishing pressure and landings (IMARPE, unpubl. data).

The effect of the 'system reset' was noticed in larger specimens after both strong EN events that occurred during the study period, but after the 1997/1998 EN the environment of the northern HCS entered into a cool phase (Fig. 2D). This phase seems to have stabilized the change from the small to the large size-at-maturity that was triggered by the EN 'reset' as proposed by Keyl et al. (2008). The similar, but weaker, changes in size-at-maturity of *Dosidicus gigas* that have been observed with a similar temporal lag after the weaker EN of 1992/1993 support this point of view. After the occurrence of a few cohorts with increased size-at-maturity without a similar cool phase to that observed in the 2000s, the size-at-maturity in the mid 1990s dropped again (Fig. 3 and F. Keyl et al. unpubl.) to small sizes that prevailed in the HCS since at least the end of the 1980s (Rubio & Salazar 1992). The fact that only individuals maturing at large sizes have been found in the cooler southern HCS off Chile up until now (González & Chong 2006, Ulloa et al. 2006, Ibáñez & Cubillos 2007) further strengthens the hypothesis that size-at-maturity is coupled to water masses, i.e. temperature and nutrient conditions.

Temporal shifts in size-at-maturity also occurred in Mexican waters. In the GoC, a shift to smaller sizes was described during and after the 1997/1998 EN (Markaida 2006b). Sizes of jumbo squid inside the GoC in the 1970s and early 1980s were generally less than 400 mm, and slightly larger off the west coast of the Baja California (see Table 1). Around 1980/1981, small and large size-at-maturity (different modes with ML of up to 750 mm) can be retrieved from Ehrhardt et al. (1982, 1983) and Ramírez & Klett-Traulsen (1985). However, these changes occurred before the 1982/1983 EN. Jumbo squid abundance was very low during

most of the 1980s, and the fishery existed on the subsistence level only (Nevárez-Martínez et al. 2000, Markaida 2001); as a consequence no data is available for nearly the whole decade. The first studies at the end of the 1980s found sizes of up to 800 mm, indicating increased size-at-maturity (see Table 1). Changes in size-at-maturity or subpopulational groups with different size-at-maturity have been reported for other cephalopods: e.g. the purpleback squid *Sthenoteuthis oualaniensis* in the Arabian Sea (Shulman et al. 2002), and the cuttlefish *Sepia officinalis* in the English Channel (Dunn 1999).

It has to be doubted if 3 separate but overlapping size-at-maturity groups in spatially distinct areas of the EPO exist (Nesis 1983, Nigmatullin et al. 2001). Results of the present work show temporal shifts in size-at-maturity instead of a spatial separation, as do those of Markaida (2006b) for Mexican and Argüelles et al. (2008) for Peruvian jumbo squid; in all 3 cases spatiality has not been addressed explicitly. The changes in size-at-maturity found here in ML_{mean}, $ML_{50\%}$ and MI (Figs. 2, 4 & 5) suggest a more continuous alteration of size-at-maturity between 2 extremes (Fig. 10), supposedly in response to abiotic conditions that impact the productivity of the ecosystem (see above). However, a step is apparent and indicated by separate regression lines in Fig. 10. It could either suggest an incomplete covering of all possible sizes-at-maturity, or indicate the existence of 2 groups of size-at-maturity. Until now no data has been presented that clearly show the 3 groups of size-at-maturity of Nesis (1970, 1983) and Nigmatullin et al. (2001). The author of the first study himself doubted the separation of the 2 larger groups which would result in the 2 separate groups of size-of-maturity, and these 2 groups were reproduced here. The step could also be the result of incomplete coverage of the entire range of sizes-at-maturity existent.

The overlap of mature and immature individuals (black and grey points in Figs. 4 & 5) in one cloud of data points is especially marked in some years (1995 and beginning of the 2000s) for males. In the case of the females the overlap is visible but less marked. The overlap indicates the difficulty in assessing maturity with the visual system. The reason for this overlap in the different visual stages of maturity may be the multiple spawning behavior of jumbo squid (Rocha et al. 2001, Nigmatullin & Markaida 2009), as has been described in more detail by Staaf et al. (2008): they assume that the method of classifying the stages of maturity cannot reproduce the repeated spawning batches seen, as apparently little or no eggs remain in the oviduct after each spawning event. Females, although fully mature, may be mistaken as maturing or immature. Until now, it has not been established if and how development of multiple spermatophores occurs in males of *Dosidicus gigas*, but it is possible that the system that is used here for males has a similar limitation in this sense. However, the length-based maturity index used here (MI) may already reduce this problem: it has the advantage over the more commonly used weight-based indices in that it classifies the maturity of females relatively independently of oviduct fullness (which changes due to repeated spawning batches).

Female jumbo squids are larger than males (Markaida & Sosa-Nishizaki 2001), and this type of sexual dimorphism is a general pattern in all oegopsid squids (O'Dor 1998); the higher size-at-maturity of females found here in nearly all semesters reflects this. The exceptions (Fig. 2A,B) may be due to small and large size-at-maturity being present in those semesters, as they happened in the early 1990s and during 2000/2001.

Semestral graphs of individual MI after 2000 (Fig. 5) display different somatic and gonadal growth patterns for the 2 sexes. They can be described as j-shaped in the case of the females, leading to death soon after reproduction, and as s-shaped for the males, allowing them to continue growth after the onset of reproduction (Figs. 5 & 11A). As a result, the terminal size of males is clearly higher than their size of maximal maturity (i.e. maximal testis and nidamental gland length), while the size of maximal maturity of females is close to their terminal size. Another, much more important, effect of this different maturation process is the temporal separation of the maturation of males and females (Figs. 7 & 8), allowing each sex to mature without ele-
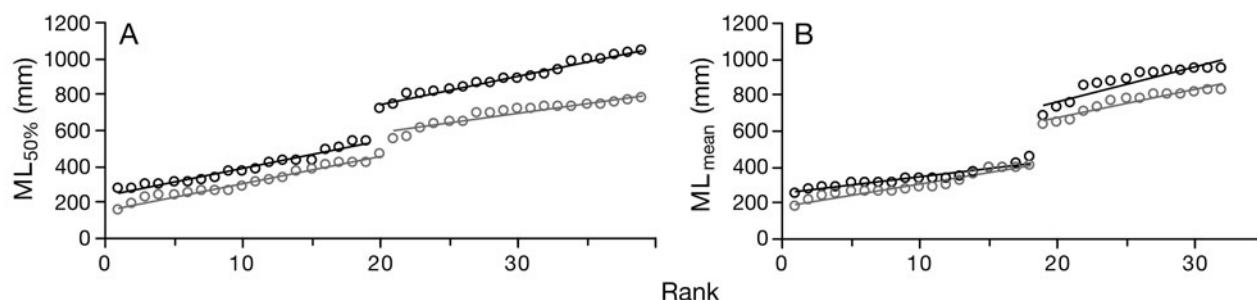

Fig. 10. *Dosidicus gigas*. Size-ranked semestral values of (A) $ML_{50\%}$ and (B) ML_{mean}; black: females, grey: males
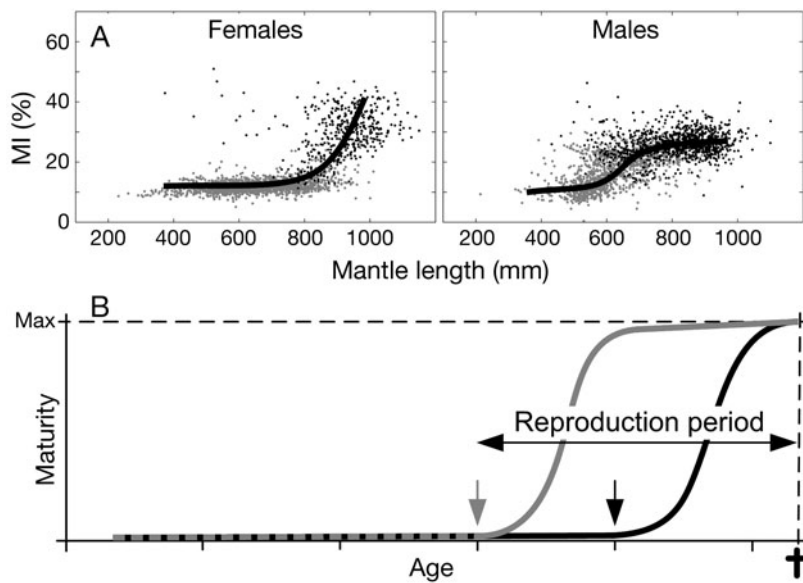
Fig. 11. *Dosidicus gigas*. Decoupled reproduction periods of females and males; (A) j- and s-shaped maturation progress of females and males respectively; example from summer 2005/2006; grey points = immature specimens (stages I & II); black points = mature specimens (stages III & IV); (B) temporally distinct maturation of (black line) females and (grey line) males

vated intra-specific competition for resources with the other sex (Fig. 11B). As that immature females can store spermatophores in their buccal membrane (Nigmatullin & Markaida 2009), it allows *Dosidicus gigas* to efficiently extend its reproductive period. Similar temporal decoupling of male and female maturation processes have been reported for general species of octopus (Forsythe 1993), *Illex illecebrosus* (O'Dor & Dawe 1998), and the *Sepia officinalis* population of the English Channel (Dunn 1999). The mating of immature females also explains the lag between increased female mating and maturation, especially visible from 1993 to 1995 (Fig. 8).

Gonadal growth consumes energy, and 3 principal sources (or a combination of these) may be assumed to make up this energy demand: (1) additional food intake, (2) less migration and (3) reduced (or even zero or negative) somatic growth rates and maintenance of somatic tissue (i.e. standard metabolism). Cephalopods in general (Rodhouse & Nigmatullin 1996), and also *Dosidicus gigas* (Markaida & Sosa-Nishizaki 2003), are described as ferocious predators that must have a high energy demand due to high somatic growth rates. Thus, it can be assumed that any increase in the already high feeding rate is difficult. Nevertheless, it has been suggested that the more demersal *Loligo gahi* may increase its ingestion rate during maturation to meet the higher energy demand (Ibáñez et al. 2005). For *D. gigas*, feeding activity continues during the maturation and spawning phase without drop off

(Markaida et al. 2004, Nigmatullin & Markaida 2009). With respect to migration behavior, the second possible source of energy saving for gonadal tissue growth, little is known regarding *D. gigas*. Both unaltered and reduced migration has been described for cephalopods as a means of saving energy for maturation without decreasing growth rates (Wells & Clarke 1996). Knowledge on the third potential source of energy saving, reduced somatic growth, is similarly limited. Reduced somatic growth after the onset of gonad production was proposed for the myopsid squid *Alloteuthis subulata* (Rodhouse et al. 1988). No direct study exists on growth of *D. gigas*, but it has been assumed that growth during maturation continues with the same rate as before (Markaida et al. 2004).

The highest oviduct weight found in this study was 2043 g for a female of 920 mm ML and 31.1 kg. Assuming 10 to 14 spawning batches (Nigmatullin & Markaida 2009) and complete evacuation of the oviduct during each batch (Staaf et al. 2008), the summed gonad weight of this female could total 28.6 kg, i.e. nearly its overall weight. Assuming a 40% conversion rate, much higher than that of Wells & Clarke (1996) for the ommastrephid *Illex illecebrosus*, the formation of this tissue alone would require a food intake (or its energetic equivalent) of at least 71.52 kg (600 to 715 g daily for the 100 to 120 d reproductive period used by Nigmatulin & Markaida 2009); a part of this amount must already be allocated to the primary formation of the oocytes during the immature part of life. Considering that a similar amount of energy is additionally put into the maturation of the nidamental glands during the mature stage of life (Nigmatullin & Markaida 2009), we assume that the sum of 10 to 14 oviduct masses roughly represents the energy needed for reproduction during the spawning period. The ~5 kg of somatic tissue build-up proposed during maturing and mature life stages (Markaida et al. 2004) requires another 12.4 kg of food intake (assuming the same conversion efficiency). As potential fecundity and weight of the spawning batches is directly related to the size of the female (Nigmatullin & Markaida 2009), smaller specimens need to invest relatively more and absolutely less ingested energy into reproduction (Keyl et al. 2008).

Assuming that the 3 above-mentioned sources of energy play a role in meeting the costs of maturation, and that male investment in reproduction is signifi-
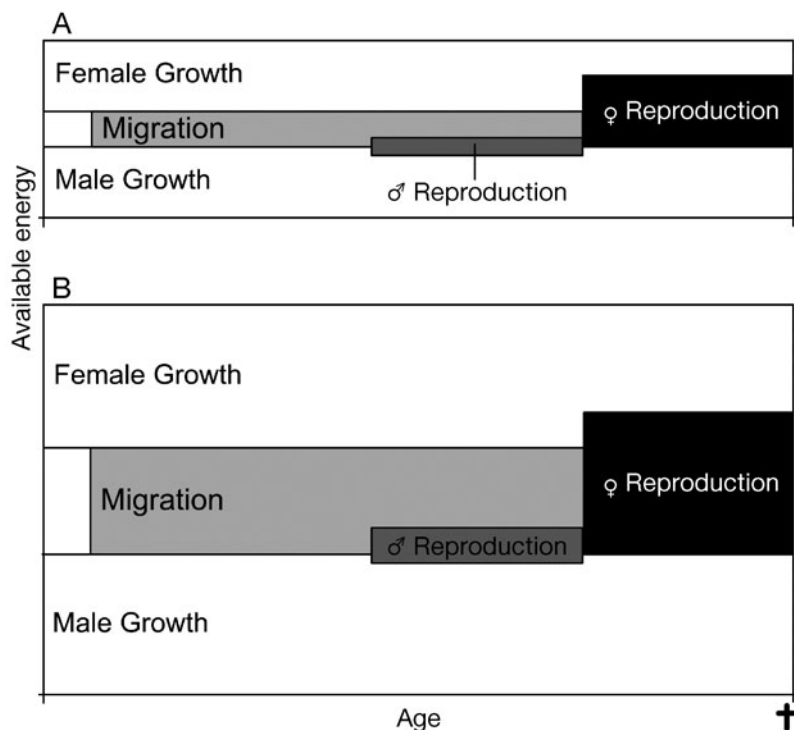
Fig. 12. *Dosidicus gigas*. Scheme of hypothetical allocation of available energy to males and females; (A) during low production periods resulting in small specimens and (B) for high production periods resulting in large specimens

cantly lower than that of females, an energy allocation scheme as shown in Fig. 12 could result. This oversimplified, and certainly questionable, scheme explains larger sizes, higher absolute reproductive output and expanded energy available for migration during the cooler, nutrient rich periods. Parts of the energy needed for gonadal growth is reallocated from energy that is used for somatic growth before maturation. Such a reallocation of energy must result in temporally reduced growth after the onset of maturation and, as males and females show distinct maturation processes, should also result in dissimilar growth curves for the 2 sexes. According to the length-frequency data of Peruvian *Dosidicus gigas*, some of the larger cohorts show reduced growth rates in their last period of life.

The monthly female:male ratio and its variation (Fig. 9) are in the range found by other studies in the whole distribution area (listed in Table 1). The shift to a lower female:male ratio, noticeable after 2001, is also interesting from an energetic point of view. After all, males do not directly contribute to reproduction; there is intra-specific competition for resources for the females, the actively reproducing part of the population. The reason that males exist is the very same why sexual reproduction in general exists: to foment genetic diversification, allowing species to adapt to changes in their environment. The mixed paternity of the progeny of 1 female reported for some cephalopods

(Boyle & Rodhouse 2005) may at least be seen as a measure to reduce the amount of energy 'lost' in the non-reproductive part of the population (i.e. the males) without losing too much opportunity to genetically diversify in every generation. The reduced female:male sex ratio (i.e. more males per females and a higher energy demand per progeny) found in the 2000s corresponds to the cool and more productive period in the Peruvian part of the HCS. However, so far no further support exists for this hypothesis.

The present work analyzed maturation and reproduction of jumbo squid in relation to their size and large-scale environmental conditions. It remains unclear how these processes chronologically and spatially develop. We believe that jumbo squid, with its extremely plastic reproduction patterns in relation to variability of its environment, may act as a model organism to understand less extreme patterns of other marine and non-marine species that are more difficult to detect.

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