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Oocyte development, fecundity and spawning strategy of large sized jumbo squid *Dosidicus gigas* (Oegopsida: Ommastrephinae)

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Ovaries of 39 large jumbo squid Dosidicus gigas *(415–875 mm mantle length (ML)) of different stages of maturity from the Gulf of California and Nicaragua were analysed. Oocyte development is asynchronous during female ontogenesis, with predominance (>85–90%) of small protoplasmic oocytes 0.1–0.2 mm in diameter for all stages of female maturity. Potential fecundity (PF) is determined at late immature stage II with average values around 18–21 million oocytes. The maximum PF estimated, 32 million oocytes, is so far the largest recorded for any cephalopod. PF is closely related to female size. Nicaraguan females, of smaller size (415–720 mm ML), show lower fecundity (5–15 million oocytes). Eggs were analysed in oviducts of mature females (540–875 mm ML), 7 from the Gulf of California and three females from Nicaragua. Eggs measured 0.9 × 1.1 mm in diameter and weighed 0.45 mg on average. The oviducts of the largest female (875 mm ML) held 1.2 million eggs, representing 4.6% of PF and no more than 14% of all vitelline oocyte stock of that squid. Variability in oviduct filling is very high and unrelated to ovary weight. However, a strong correlation was found between oviduct fullness and nidamental glands development. These observations suggest that spawning is extended and intermittent. A female spawns no less than half of the initial PF, and the minimal number of spawning activity events (egg batches) is roughly estimated at 8–12. During this terminal spawning stage females continue actively feeding and grow between egg-mass laying periods.*

Keywords: jumbo squid *Dosidicus gigas*, reproductive biology, oocyte, egg size, fecundity, spawning

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INTRODUCTION

Coleoid cephalopods are monocyclic invertebrates that have developed a wide array of reproductive strategies showing a high adaptive flexibility. Current efforts have classified this set of variable reproductive strategies, some only recently described (Hanlon & Messenger, 1996; Nesis, 1996; Rocha *et al.*, 2001; Nigmatullin, 2002; Boyle & Rodhouse, 2005).

The jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) is the largest ommastrephid squid, endemic to the eastern Pacific from California to central Chile over the continental slope and open waters. It is the most primitive and least oceanic representative of the subfamily Ommastrephinae. Jumbo squid shows a very complex population structure with three size reproductive groups, differing in adult squid mantle length (ML). The large-sized group females mature at 550–650 to 1000–1200 mm ML and inhabit the northern and southern periphery of the species range (Nigmatullin *et al.*, 2001). This form supports a fishery in the Gulf of California originating in 1995 (Markaida & Sosa-Nishizaki, 2001), with mean annual catches of 75 thousand tonnes (t) since then. In the last 5 years this group has formed a significant part of the southern hemisphere fishery, with catches in 2005 of 290 thousand t in both Peru and Chile. Jumbo squid lead the cephalopod landing records since 2004 with an annual worldwide total catch of over 750 thousand t (FAO, 2007).

The fishery biology of jumbo squid has been intensively studied in recent years, but studies on the female reproductive biology on an individual level are lacking. Nesis (1971, 1983) reported a fecundity range from 100,000 to more than 600,000 eggs for the medium-sized form (350–560 mm ML) of female jumbo squid from South American waters. This estimate was correctly written in the abstract and corresponding table, although it was mistakenly reported as an order of magnitude larger in the text (Nesis, 1971, p. 114). The same error is found in the original Russian paper (Nesis, 1970). Ehrhardt *et al.* (1983) ambiguously cited Nesis (1971) with these erroneous numbers (1 million to more than 6 million eggs). Earlier reviews on squid fecundity (Voss, 1983; Mangold, 1987; Boyle, 1990) considered this erroneous estimate as an original figure by Ehrhardt *et al.* (1983) for the jumbo squid from the Gulf of California.

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In fact, Nesis (1971, 1983) counted only eggs in the oviducts and maturing vitelline oocytes (diameter ~0.8–1 mm) in the ovary. He described mature eggs as amber-yellow, slightly oval, 0.9–1.1 mm in length and weighing on average 0.57 mg. He recognized that his fecundity figure would be an underestimate if the maturation of oocytes was not simultaneous.

Lately it has been found that oceanic ommastrephids (subfamily Ommastrephinae) show the highest potential fecundity among cephalopods with peculiarities in their reproductive strategy such as group asynchronous ovulation, multiple spawning and somatic growth between egg batches (Harman *et al.*, 1989; Nigmatullin & Laptikhovsky, 1994; Rocha *et al.*, 2001; Nigmatullin, 2002; Laptikhovsky & Nigmatullin, 2005). Counting oocytes with diameter >0.05 mm in female jumbo squid 150–720 mm ML collected in 1980–1989 from open waters off Nicaragua, equatorial areas and Peru, yielded an estimated potential fecundity of 0.3–13 million eggs (Nigmatullin & Laptikhovsky, 1994). However, these features have never been described in detail for jumbo squid before. The aim of this paper is to describe full oocyte development, ripe egg size variability and different aspects of potential fecundity and its realization during spawning of the large-sized maturing group of jumbo squid.

MATERIALS AND METHODS

Reproductive systems of 39 females of the large form of jumbo squid of different stages of maturity were analysed. Twenty-nine were collected in the Guaymas Basin, Gulf of California, between 1995 and 1997 (Markaida & Sosa-Nishizaki, 2001) and ten females were taken over the continental slope in Nicaraguan waters during 1988–1989 (Table 1). Dorsal ML was measured to the nearest millimetre, and body weight (BW) to the nearest 15 g with a commercial scale. Stages of maturity were assigned according to Nigmatullin (1989) (Table 2). The complete reproductive system was stored in 6–8% buffered formaldehyde. Ovary, nidamental glands and oviductal complexes were weighed to the nearest 0.1 g.

Three subsamples of 1–5 mg were analysed from each part of the ovary (anterior, medial and posterior) of females from II to IV maturity stages. For seven mature (stage V) females of the Gulf of California, five to six subsamples of approximately 15–30 mg each from the aforementioned parts of the ovary were analysed. Each subsample was weighed and then observed in a Bogorov chamber under a binocular microscope (×8–56). All oocytes in the subsample were counted and classified in the six morphological groups described by Laptikhovsky & Nigmatullin (1992) and Nigmatullin *et al.* (1995) (Table 3). The major axis of 150 to 250 randomly selected oocytes of each subsample was measured to the nearest 0.01 mm for 13 squid of different maturity stages from the Gulf of California.

Eggs from the oviducts of 9 mature (stage V) females were analysed (Table 1). Egg number was estimated as the mean egg count between 3 to 6 subsamples of 30–60 mg from different oviduct parts: anterior, medial and posterior. Eggs are oval and thus the shortest and longest diameters, of 3 subsamples of 50 eggs each, from the anterior part of the oviducts of each squid were measured to the nearest 0.05 mm. In addition the casual diameter was measured obviating any selection of the longest or shortest diameter. The micrometer was placed in a horizontal position in the eye-piece and the diameter parallel to the graduation on the micrometer was measured to the nearest 0.1 mm in 3–6 subsamples of 50 eggs from different parts of the oviduct (Laptikhovsky & Nigmatullin, 1993, 1999, 2005).

Potential fecundity (PF) was calculated as the sum of total oocytes (>0.05 mm in diameter) in the ovary and ripe eggs in the oviducts. Relative fecundity (RF) was estimated as the ratio of PF to BW (g). Oviductal load (OL) is the number of eggs in the oviducts. Coefficient of yolk oocytes (%YO) is the number of vitelline oocytes (groups IV, V and VI) in the ovary as a percentage of the total oocyte number in the ovary. Coefficient of vitelline oocytes (%CVO) was calculated as the ratio of the sum of vitelline oocytes in the ovary and eggs in the oviduct to the PF. An index of potential reproductive investment (PRI) was calculated as the product of RF and the weight of an individual ripe egg (Laptikhovsky & Nigmatullin, 1993; Nigmatullin & Laptikhovsky, 1994).

Additionally, the weight of the components of the reproductive system (ovary; both oviductal complexes, OCW; and both nidamental glands, NGW) of 72 mature females (stage of maturity V) from the Gulf of California was taken with an accuracy of 0.1 g (data from Markaida & Sosa-Nishizaki, 2001). The percentage of oviduct fullness (%OF) was calculated for 51 of these females as follows. The maximum value of OCW for all squid in each 25 mm ML interval were taken, and a linear regression was applied to them, without transformation, to estimate the maximum OCW for the ML of any mature female. Subsequently the percentage of oviduct fullness was calculated as the % of each OCW to that maximum weight predicted by the regression for its size (Harman *et al.*, 1989). The nidamental gland thickness index (NGTI) was calculated as the relationship between the weight, in grams, and length, in mm, of the average of both nidamental glands (modified from Rasero *et al.*, 1995).

To assess the feeding behaviour of mature females, data of stomach fullness index (FI) and stomach fullness weight index (FWI) for 340 females collected in the Guaymas Basin in 1995–1997 were considered (Markaida & Sosa-Nishizaki, 2003). FI is based in a subjective, visual scale, while FWI is the percentage of stomach contents weight related to squid BW. Differences between females of different maturity stage, I to V according to Lipiński & Underhill (1995), by stomach preservation method (in formalin or frozen) for these indices were tested using a Kruskal–Wallis non-parametric ANOVA.

RESULTS

Oocyte development

Oocyte group and size distribution in the ovary was unimodal at all maturity stages, with protoplasmic oocytes (groups I and II) predominating in all ovaries. They represent about 90% of total oocyte stock in the ovary (Figures 1–3). No oogonia or oocytes <0.05 mm in diameter were found.

Group I oocytes prevail during maturity stage I and the beginning of stage II (Figure 1). During stage II, oocyte group II dominates (60–70%). In stage III, oocytes preparing to vitellogenesis (group III) comprise up to 2% of all oocytes (Figures 1 & 3). Vitelline oocytes (group IV) first appear in early mature females (stage IV). The number of oocytes of group III increases to 8.6–36%, while vitelline oocytes (YO) range from 0.8–1.8% (Figure 3; Table 1). No oocytes with expulsing follicle or ripe

Table 1. Means of potential fecundity (PF, in millions), relative fecundity (RF), coefficient of viteline oocytes (%CVO), coefficient of yolk oocytes in ovary to total oocyte number in ovary (%YO), oviductal load (OL, in thousands) and index of potential reproductive investment (PRI) of large size maturing *Dosidicus gigas* females from the Gulf of California and Nicaragua (*) waters.

Stage of maturity	ML, mm	Weight, g	Ovary, g	Oviducts, g	PF	RF	%YO	%CVO	OL	PRI
V	875	23175	361.0	540.3	25.790	1112	9.7	13.9	1197	0.49
	855	19000	263.1	197.7	23.157	1218	4.2	5.8	395	0.60
	826	18675	260.5	13.1	25.887	1386	5.3	5.4	26	0.69
	746	15075	269.8	212.5	14.782	980	9.3	12.6	531	0.40
	720*	14060	130.5	125.1	15.331	1090	2.4	4.0	255	0.47
	710	11975	188.1	23.1	32.475	2711	2.6	2.8	50	1.26
	696	10300	163.2	62.2	15.862	1540	7.2	8.1	148	0.64
	670	8650	138.6	96.1	11.529	1332	8.4	10.1	213	0.59
	660*	8500	122.5	116.5	5.128	603	2.1	7.8	299	0.20
IV	707	14500	94.3		16.258		1.8	1.8		
	674	10700	52.0		19.419		0.8	0.8		
III	750	12450	47.0		21.363					
	712	12425	48.8		20.333					
	710	13050	50.2		22.818					
	664	7625	28.2		17.647					
	652	9100	25.1		17.928					
	633	8850	37.5		23.437					
	580	6100	17.8		17.260					
	572	5250	16.1		16.100					
	492	2775	10.5		12.366					
	460*	2450	7.8		5.260					
	446	2300	7.2		11.546					
II	696	11050	27.6		23.000					
	695	8450	16.7		13.916					
	640	6650	19.8		19.010					
	635	7400	23.0		15.133					
	620	7350	16.7		14.521					
	591	6200	26.2		17.466					
	552	5225	9.0		10.000					
	491	2175	8.9		8.900					
	479	2125	14.1		12.819					
	432*	2200	7.9		6.300					
	431*	2340	8.0		7.300					
	430*	2280	7.8		10.530					
	422	1175	8.0		10.952					
	420*	1850	5.1		7.300					
	420*	1780	8.1		6.750					
	416*	1810	7.0		7.500					
	415*	1760	7.6		6.500					

eggs were found in these two females (Figures 1 & 3). In mature females (stage V), vitelline oocytes represent an average of 5.7% of the total intraovaric oocytes, and never more than 10% (Table 1). Mature oocytes (groups V and VI) in the ovary are always rare (0.1–0.5%; Figures 1–3). Oocytes of group V are the largest at 1–1.2 mm, because they are covered by the follicular layer. Resorbed oocytes were not observed and no oocyte resorption is evident.

Oocyte frequency distribution among the six morphological groups significantly differed between the subsamples taken from the three different regions of the ovary (anterior, medial and posterior) in mature females from the Gulf of California (χ^2 test, df $= 17$, $P < 0.001$ in all cases). However no tendency was observed in oocyte development regarding ovary regions (Figure 2).

Egg size

Ripe eggs are pinkish or crimson. Egg shortest diameter in the oviducts of females from the Gulf of California averaged 0.87–0.91 mm and the longest ranged between 1.06 and 1.11 mm (Figure 4). The casual diameter means ranged between 0.94 and 1 mm. Egg weight means ranged between 0.4 and 0.5 mg, with an average of 2350 ± 313 eggs by gram of oviduct (Table 4).

Egg size variability can be very high in the same female. There were significant intraindividual differences in oocyte size (shortest and longest diameters) among subsamples taken from three squid (ANOVA, $P < 0.05$; Table 4). There were highly significant differences between the shortest and longest diameters among all analysed squid from the Gulf of California (ANOVA, $P < 0.001$; Table 4). However, there was no correlation between the sizes of these females and the average size of the shortest or of the longest diameter of their eggs ($P > 0.05$; Table 4).

Potential fecundity

The total number of oocytes in the ovaries and oviducts of studied females ranged from 5.2 million in the maturing

Table 2. Maturity stages of the reproductive system of female ommastrephid squids (modified from Nigmatullin, 1989). Most developed oocytes (MDO) in the ovary (O) and development of oviducts (OV), oviductal glands (OG) and nidamental glands (NG) were taken as diagnostic.

Stage of maturity	Functional features	Oocyte development[1]	Reproductive system development
I	Formation of ovary and accessory organs	Formation of oocytes. Previtellogenesis (PV)	O, OV and NG filamentous and transparent
II	Reproductive system development	MDO are in third phase of PV, 'simple follicle'	All organs semitransparent. O grey and conical. OV flat. NG stripe like
III	Beginning of ovary maturation	MDO are in the phase of complicated follicle with fold formation	O grey-whitish, granular. OV visible. OG grey-whitish. NG lancelate, opaque-grey, later grey
IV	Physiological maturation	MDO are vitellogenic or ripe egg. Many yolk oocytes in ovary (>0.2% all)	O enlarged and granulose. No ripe eggs inside OV. OG white and elastic. NG fusiform, grey-whitish
V	Functional maturity. Mature and spawn	MDO are ripe eggs	O large and yellow. Ripe eggs in oviducts. NG fusiform, milky. Maximum size, excretions of secretive drops
VI	Near end of spawning	Same	O reduced. NG grey-whitish, reduced and flaccid
VII	Premortal spent condition	Same	O destroyed. NG grey and diminishing

[1] Oocyte morphological groups related to each development phase are listed in Table 3.

female of 460 mm ML to 32 million in a mature female of 710 mm ML (Table 1). A comparison of the PF between immature, maturing and mature animals showed that PF is defined at least at the beginning of stage II. Three immature (stage II) females already had fecundities of 17–23 million oocytes (Table 1). All oocytes may be easily counted in these squid in the late immature stage. The average ±SD PF by stage of maturity for large females from the Gulf of California are: stage II (420–696 mm ML), 15.0 ± 4.6 million; stage III (446–750 mm ML), 18.1 ± 5.0 million; stage IV (674–707 mm ML), 16.6 ± 1.0 million; stage V (670–875 mm ML), 20.9 ± 8.8 million. Larger variances among females of stage V are due to the fact that some eggs have been deposited. There are significant differences in PF values among females of all (II–V) maturity stages (Kruskal–Wallis non-parametric ANOVA, $H = 10$, $df = 3$, $P < 0.05$). The post-hoc Tukey test demonstrated that PF for stage of maturity (V) is larger than stage (II) ($P < 0.05$). Lack of differences among stages III–V strongly suggests that PF is determined at an early stage of maturity. Immature females from Nicaragua had a significantly lower potential fecundity (7.4 ± 1.4 million) than those from the Gulf of California (15.0 ± 4.6 million: Table 1; Figure 5A) (Mann–Whitney *U*-test, $U = 3.22$, $P < 0.01$).

Potential fecundity increased with squid dimensions (Figure 5A) and according to the equations given in Table 5 for females of different maturity stages. In all cases the fecundity is characterized by a negative allometry, both in ML ($b < 3$) and in weight ($b < 1$). The mean relative fecundity was 1330 ± 583 eggs/g for mature females (V), ranging between means of 603 and 2711 eggs/g. Relative fecundity is not related to BW in mature females (V) (Figure 5B).

The coefficient of vitelline oocytes (%CVO) on average represented 7.8 ± 3.7% of the total oocytes in mature females (V), with a range of 2.8–13.9% (Table 1). The relationship between the total number of the vitelline oocytes in the ovary and the ML of mature females (IV–V) (Figure 5C) was significant. PRI averaged 0.59 ± 0.29 with a range of 0.2–1.26 (Table 1). This index did not correlate with squid BW ($r = 0.001$, $N = 9$, $P > 0.05$).

Oviduct filling

The oviducts of the large-size females contain an average of 346 ± 356 thousand eggs, although the large observed variability is due to different degrees of their fullness. The lowest figures probably reflect situations of beginning of the filling or the end of the emptying of the oviducts after a spawning activity event. The maximum number, 1.2 million

Table 3. Squid oocyte morphological groups found in female *Dosidicus gigas* (modified from Laptikhovsky & Nigmatullin, 1992; Nigmatullin *et al.*, 1995) and their correspondence with the phases of oocyte development (Burukovsky *et al.*, 1977).

Oocyte group	Oocyte diameter, mm	Oocyte morphology	Oocyte development phase
I	0.05–0.1	Polygonal, with a large and oval large central nucleus	Second phase of previtellogenesis (PV), 'primary follicle'
II	0.1–0.3	Oval or globate shaped oocytes, increased cytoplasm volume	Third phase of PV, 'simple follicle'
III	0.2–0.7	Leaf-like, dark oocytes, with numerous shallow longitudinal grooves in the surface. Nucleus not visible	Phases of 'complicated follicle'. Formation of follicular folds, preparing for vitellogenesis (VG)
IV	0.4–1.2	Nearly spherical shape. Covered with reticulate grooves. Dark colour	First and second phases of VG, 'vacuolization and yolk accumulation'
V	1–1.2	Rounded and yellow, reticulate grooves almost disappeared	Third phase of VG, 'expulsion of follicle folds'
VI	1–1.1	Oval and amber-yellow, with smooth surface	Fourth phase of VG, 'ovulated ripe egg'

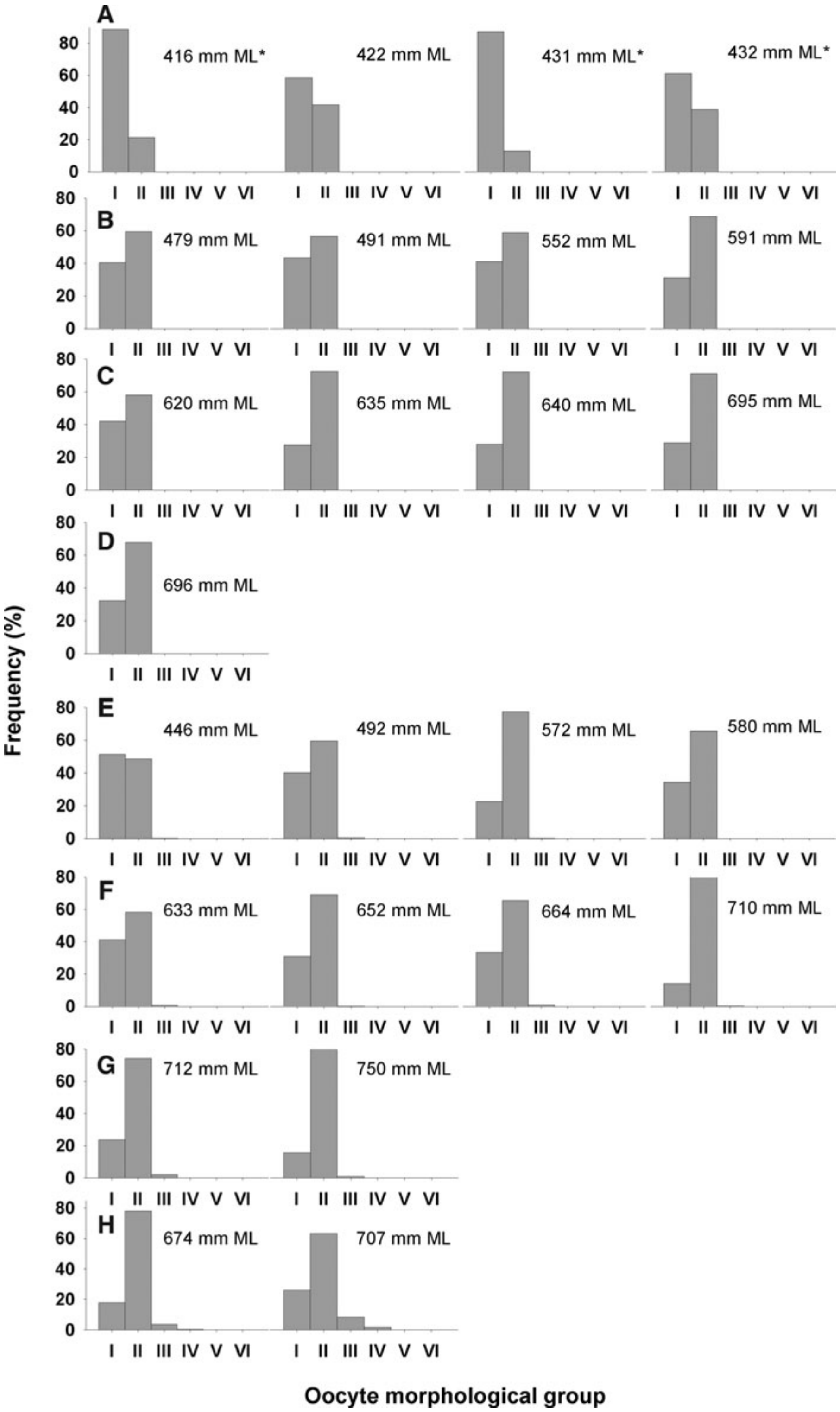

Fig. 1. Frequency distribution of oocyte morphological groups in the ovaries of *Dosidicus gigas* females, related in Table 1. (A, B, C & D) stage of maturity II; (E, F & G) stage III; and (H) stage IV. All individuals are from the Gulf of California, except * from Nicaragua. Stage V females are shown in Figure 2.

eggs (4.6% PF), was observed in the largest female considered in this study, whose totally full oviducts together weighed 540 g (Table 1). Oviductal load represented only 2.27 ± 2% PF in mature females (V) on average, with a maximum of 5.8%. The relationship with squid size (Figure 5D) was not significant.

Relations among the reproductive organs

The relationship between the maximum OCW and the ML was significant (Figure 6A; $P < 0.05$). However, the variability in %OF was very high; there was no correlation between this percentage and squid size (Figure 6B). %OF

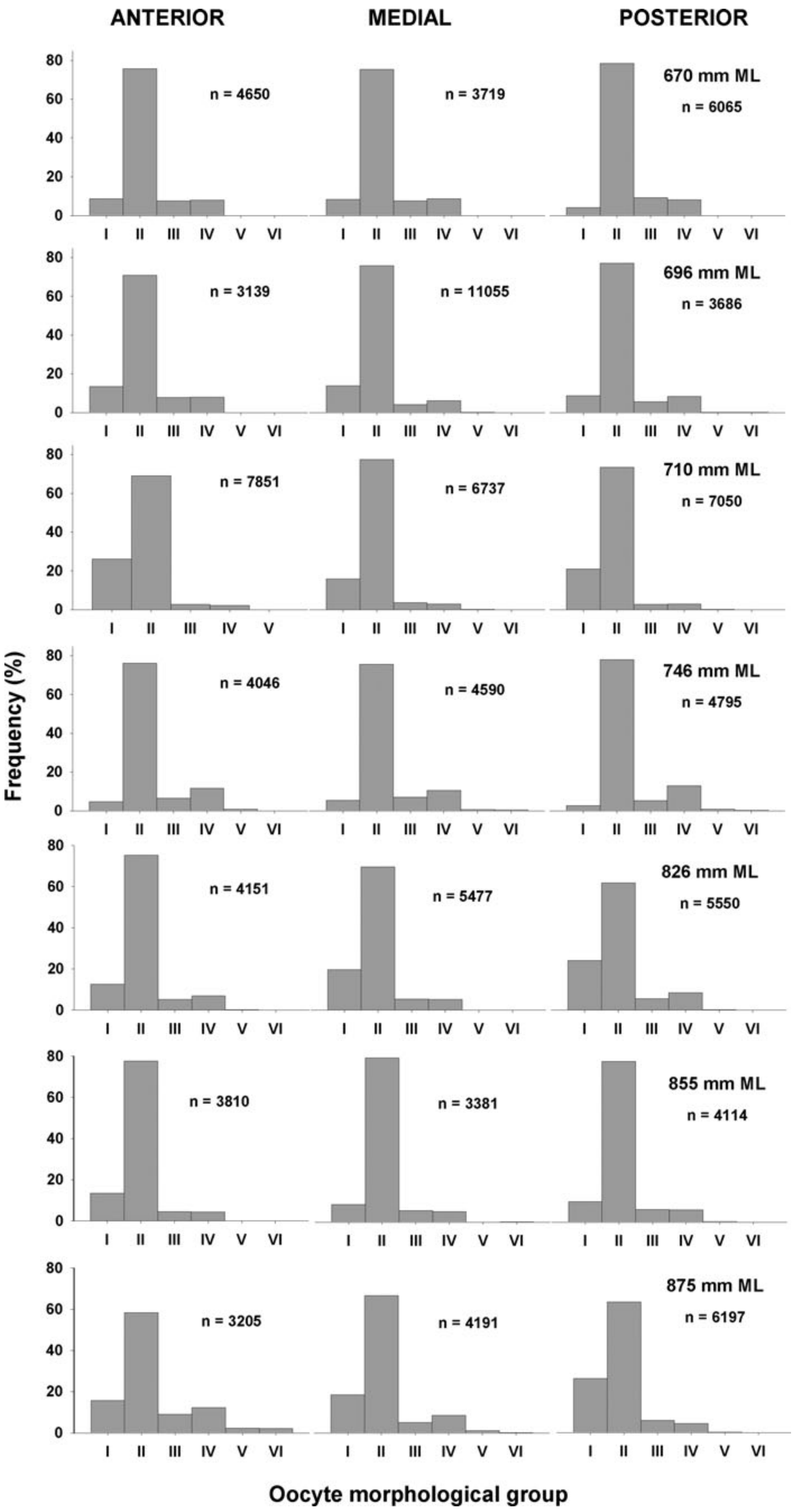

Fig. 2. Frequency distribution of oocyte morphological groups in the different regions of the ovary (anterior, medial and posterior) of mature females (stage V) of *Dosidicus gigas* from the Gulf of California, as related in Table 1. n, observed oocyte number.

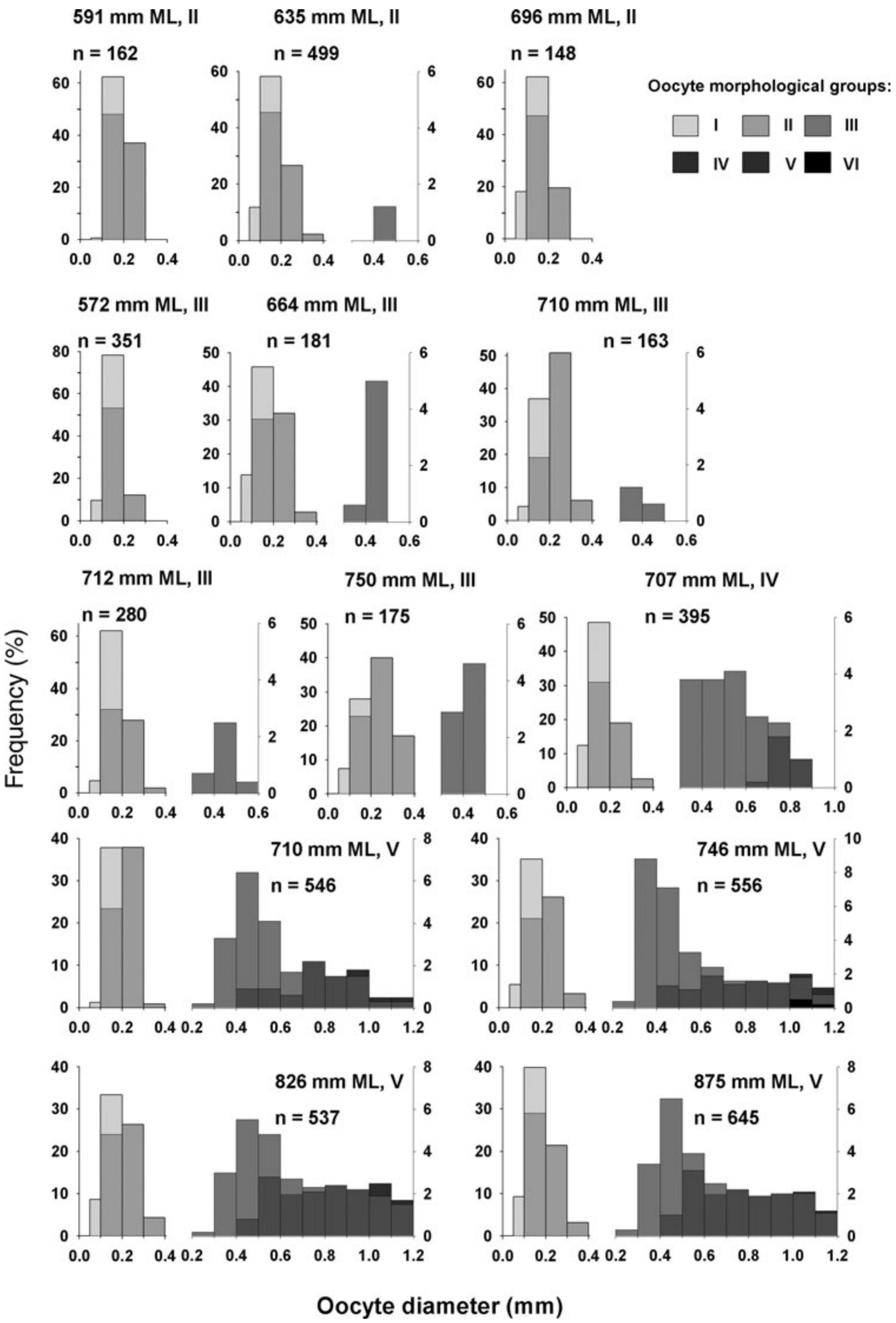

Fig. 3. Size–frequency distribution of oocyte morphological groups found in the ovary of 13 *Dosidicus gigas* females from the Gulf of California of different stages of maturity, as related in Table 1. Frequency axis for oocyte size-groups III–VI is shown at right. n, observed oocyte number.

averaged 46 ± 30% and only 11% of females showed fullness ≥80%.

The relationship between the ovary weight and OCW was weak, although highly significant for mature females, as well for the relationship with the NGW (Figure 6C, D). The correlation between the PF and OL was not significant for mature squid (Table 1; $r = 0.22$, N = 9, $P = 0.53$). However, the relationship between the OCW and NGW was high and significant, as well as the relationship between the OCW and the NGTI (Figure 6E, F).

Feeding activity during spawning period

Means of FI by maturity stage ranged 1.2–2.2. They did not show any differences between all maturity stages considered, even testing for stomach samples by formaldehyde and frozen preservation methods together (Kruskal–Wallis non-parametric ANOVA, $H = 4.81$, df = 4, $P > 0.05$). FWI values were low, with means by maturity stage ranging 0.01–0.35% of squid body weight. They showed no differences between females of all different maturity stages for formalin

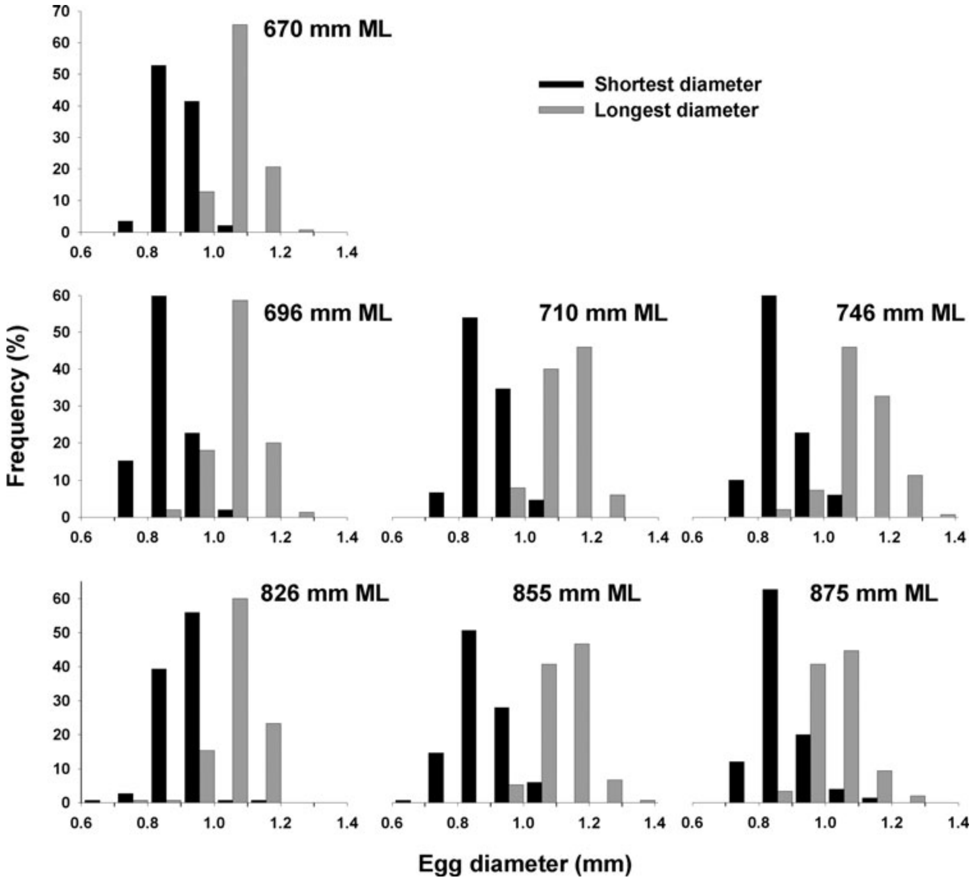

Fig. 4. Size–frequency distribution of shortest and longest diameters of the eggs found in the oviducts of mature *Dosidicus gigas* females (stage V) from the Gulf of California, as related in Table 4.

preserved stomachs (Kruskal–Wallis non-parametric ANOVA, $H = 2.67$, $df = 4$ $P > 0.05$). Among frozen stomachs, largest FWI values were found in stage V females ($H = 14.10$, $df = 3$, $P < 0.01$).

DISCUSSION

Oocyte morphological groups correspond to consecutive phases of oocyte development already described by histological validation in large *D. gigas* females (Díaz-Uribe *et al.*, 2006). The development of the oocytes of the jumbo squid is clearly asynchronous, reflected by the predominance of small protoplasmic oocytes in all maturity stages, including mature and spawning ones. The same has been documented for other ommastrephid squid (Burukovsky *et al.*, 1977; Harman *et al.*, 1989; Nigmatullin & Laptikhovsky, 1994, 1999). Thus a mature female shows all stages of oocyte development in the ovary (Burukovsky *et al.*, 1977), while protoplasmic oocytes of about 0.2 mm prevail in the ovary through all the ontogenetic stages, after maturity stage I. However, oogonia and oocytes <0.05 mm were absent from advanced immature stages, reflecting the end of egg production before vitellogenesis and indicating a monocyclic life style, as shown in other ommastrephids (Burukovsky *et al.*, 1977; Coelho, 1990; Laptikhovsky & Nigmatullin, 1993, 1999). On the other hand, scarcity of mature oocytes in the ovary reflects their rapid passage to the oviducts (Nigmatullin *et al.*, 1995). Given the asynchronous character of oocyte development and egg maturation, potential fecundity should be estimated from the total number of oocytes (Nigmatullin, 2002). Fecundity estimates based only on the number of vitelline oocytes and ripe eggs (Nesis, 1970, 1971, 1983) underestimate the real fecundity, since they represent no more than 14% PF at any given moment.

The large-size maturing group of jumbo squid presents the maximum values of potential fecundity (up to 32 million eggs) known for any cephalopod, previously assigned to the large form of *Sthenoteuthis oualaniensis* with 22 million eggs (Nigmatullin & Laptikhovsky, 1994). High productivity in the eastern Pacific waters allows rapid somatic growth to a very large ML in adults. Coupled with highly variable inter-annual conditions and conservation of small egg size, this can result in a very high fecundity in the large-sized group of jumbo squid. High fecundities of more oceanic ommastrephids (*Sthenoteuthis* and *Ommastrephes*) with the same small egg sizes are related to the unpredictability of their habitat (Nigmatullin & Laptikhovsky, 1994). Thus the most important factors contributing to the high PF of *D. gigas* are large female size and small egg size, close to the smallest of any cephalopod (Mangold, 1987). Females of the Gulf of California attain larger fecundity than females from Nicaragua because they reach a larger size. Nicaraguan mature females of the large-sized group range between 550 and 700 mm ML (Nigmatullin, unpublished data), while females from the Gulf of California mature at 750 mm ML (Markaida & Sosa-Nishizaki, 2001). The largest jumbo squid females, known to reach 120 cm ML and 58–65 kg BW off

Table 4. Mean measures of the diameters and mean weights of the eggs from the oviducts of 11 mature (stage V) females of *Dosidicus gigas* related in Table 1. For the shortest and longest diameters, 3 subsamples of N = 50 in each case. Significant differences between subsamples of the same female and between females are denoted. For the casual diameters N = 160–325. For the weight of eggs N = 6.

ML, mm	Shortest diameter, mm				Longest diameter, mm				Casual diameter, mm	Mean egg weight, mg
	Mean ± SD	Min.	Max.	*P*	Mean ± SD	Min.	Max.	*P*	Mean ± SD	
Gulf of California										
875	0.88 ± 0.06	0.72	1.17		1.03 ± 0.07	0.87	1.25		1.00 ± 0.07	0.440
855	0.89 ± 0.07	0.70	1.05		1.11 ± 0.06	0.95	1.32			0.496
826	0.91 ± 0.05	0.68	1.16		1.06 ± 0.06	0.76	1.20	*	0.94 ± 0.06	0.497
746	0.89 ± 0.06	0.72	1.10	**	1.10 ± 0.08	0.85	1.35	*	0.99 ± 0.08	0.405
710	0.89 ± 0.05	0.76	1.04		1.10 ± 0.07	0.92	1.28	*	0.95 ± 0.09	0.464
696	0.87 ± 0.06	0.75	1.10		1.06 ± 0.06	0.87	1.25		0.96 ± 0.08	0.415
670	0.90 ± 0.05	0.77	1.05		1.06 ± 0.05	0.92	1.25		0.94 ± 0.06	0.445
	ANOVA between females									
	$F_{6,1033} = 6.51$			***	$F_{6,1033} = 29.1$			***		
	Correlation between ML and egg diameter									
	$r = 0.08$, N = 7			n.s.	$r = 0.14$, N = 7			n.s.		
Nicaragua									Mean (range)	
720									0.9 (0.8–1.0)	0.427
660									0.86 (0.8–1.0)	0.331

Significant differences: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; Min., minimum; Max., maximum; n.s., not significant.

Peru (Clarke & Paliza, 2000) may show a much higher fecundity. PF calculated for those maximum dimensions from equations for females in Table 5 yield an estimation of around 42–50 million eggs.

Actual (realized) fecundity (AF, as part of the PF that will be spawned) in jumbo squid is unknown, due to the lack of specimens of spent females with which to estimate remaining non-spawned eggs and oocytes. AF has been estimated in few ommastrephid squid (*Illex* and *Todarodes*) ranging 60–80% (Nigmatullin & Laptikhovsky, 1999). Minimum AF of partially spent *Sthenoteuthis pteropus* was calculated at 35–50% (Laptikhovsky & Nigmatullin, 2005). A rough figure of AF for ommastrephids may be 50–70% PF of pre-spawning females (ranging from minimum to realistic values). Taking a conservative mean PF estimate for large jumbo squid females of 20 million eggs (mean PF for mature stage V females), this would give an AF of 10–14 million eggs.

Jumbo squid egg size is similar to the rest of the Ommastrephinae, with 0.7–1 mm diameter and egg weight of 0.2–0.24 mg. The lack of correlation between egg dimensions and squid size are found in other ommastrephid species (Laptikhovsky & Nigmatullin, 1993, 2005; Nigmatullin & Laptikhovsky, 1994, 1999).

A great individual variability exists in many, if not in all, the parameters related to fecundity. Large differences in the PF of jumbo squid from the same area have been found. This fact may be a reflection of the variability of the habitat, which directly affects the growth and development at early stages, when the potential fecundity is determined. Another reason for this fact could be the significant individual variability of genetic factors that control the fecundity level (Futuyma, 1986).

A large variability in the oviductal egg size has been also found. The nature of these differences may rely on the varying lengths of time that samples were stored in formalin. This fact precludes comparison of egg size between different localities. In addition, formalin causes eggs to be not symmetrical (Laptikhovsky & Nigmatullin, 1993). In many cases eggs had a polyhedral shape, preventing an accurate measurement of their diameter. A suitable solution to this problem in the future relies on the measurement of fresh, not fixed eggs.

Oviducts are organs of multiple accumulations, storage and discharging of eggs, necessary for the asynchronous character of vitellogenesis, that leads to intermittent spawning, and to realize a high PF (Burukovsky *et al.*, 1977; Nigmatullin & Laptikhovsky, 1994). In jumbo squid the oviducts of non-spawning females cannot store more than 5% PF. Thus, to complete the actual fecundity, even if it only represents 50–70% of the PF (see above), oviducts should be filled and evacuated several times (Harman *et al.*, 1989; Nigmatullin & Laptikhovsky, 1994; Rasero *et al.*, 1995). During an individual spawning season other oocytes begin the vitellogenesis process given the asynchronous oocyte stock development, and the amount of vitelline oocytes is being continually renewed (Laptikhovsky & Nigmatullin, 1993, 2005). Jumbo squid, as the rest of ommastrephids, is a monocyclic organism with intermittent spawning (Harman *et al.*, 1989; Nigmatullin & Laptikhovsky, 1994). As found for other ommastrephids, indirect evidence of intermittent spawning in jumbo squid females include: a high positive relationship between the weight of oviductal eggs and

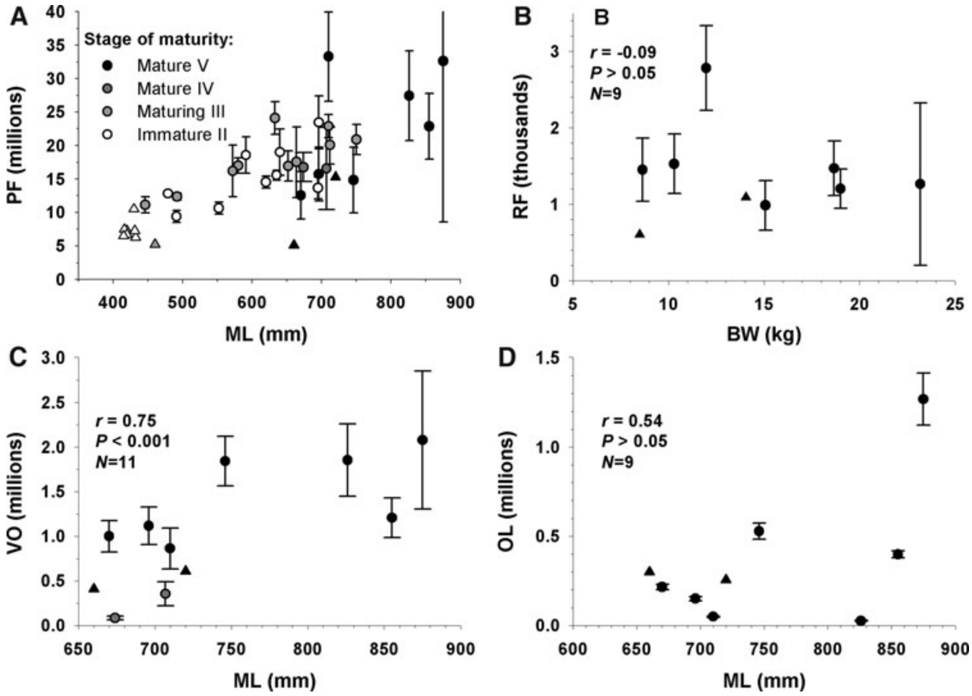

Fig. 5. Relationship between the fecundity and the size of large *Dosidicus gigas* females. (A) Relationship between the mantle length (ML) and the potential fecundity (PF) of all females; (B) relationship among body weight (BW) and the relative fecundity (RF) of mature V females; (C) all vitelline oocytes (VO) in the ovary of females (IV–V); and (D) oviductal load (OL) of mature (V) females. Circles, squid from the Gulf of California (mean ± SD); triangles, squid from Nicaraguan waters (mean).

nidamental gland weight (Young & Hixon in Mangold, 1987); nidamental gland thickness index (Rasero *et al.*, 1995); low correlation among ovary and nidamental glands weights (Young & Hixon in Mangold, 1987); and a wide range in the oviduct fullness (Young & Hixon in Mangold, 1987) without any relationship with squid size (Harman *et al.*, 1989; González & Guerra, 1996).

The single, terminal spawning stage in ommastrephids is composed of periods of spawning activity (egg laying events and egg batches; Rocha *et al.*, 2001) interspersed with periods of egg accumulation in the oviducts (Harman *et al.*, 1989; Laptikhovsky & Nigmatullin, 1993, 2005). The number of eggs spawned in each event (laying one or several egg masses) is determined by the size of the oviducts, which in turn are determined by the size of the female squid (Burukovsky *et al.*, 1977; Mangold, 1987). Maximum oviductal load for jumbo squid in this study was estimated at 1.2 million eggs. Observations of female ommastrephids (*Illex* and *Todarodes*) kept in captivity suggest that not all oviductal eggs are released at once (Durward *et al.*, 1980; Bower &

Table 5. Relationships between potential fecundity (PF, in thousands) and mantle length (ML, in mm) and body weight (BW, in g) for *Dosidicus gigas* females of different maturing stages.

Relationship	a		b		r^2	N	
	Estimate	SE	Estimate	SE			
All females							
$PF = a\,ML^b$	0.775[1]	1.16	1.539	0.2289	0.60	39	
$PF = a\,BW^b$	345.9[1]	206.1	0.4286	0.06487	0.60	39	
Females from the Gulf of California							
$PF = \exp(a + b\,ML)$	8.4163	0.2348	0.0020	3.57×10^{-4}	0.54	29	
$PF = \exp(a + b\,BW)$	9.3409	0.082	4.19×10^{-5}	7.73×10^{-6}	0.52	29	
Immature females (stage II)							
$PF = \exp(a + b\,ML)$	7.5745	0.2611	3.3×10^{-3}	4.9×10^{-4}	0.74	17	
$PF = a\,BW^b$	209.890[1]	149.493	0.4886	0.0829	0.71	17	
Maturing females (stage III)							
$PF = a\,ML^b$	0.6645[1]	1.5519	1.5816	0.3608	0.73	11	
$PF = a\,BW^b$	289.09[1]	233.52	0.4608	0.0892	0.79	11	
Mature females (stage V)							
$PF = \exp(a + b\,ML)$	6.3291	1.4818	0.0045[1]	0.0019	0.43	9	n.s.
$PF = \exp(a + b\,BW)$	8.70163	0.47490	7.1466×10^{-5} [1]	3.132×10^{-5}	0.42	9	n.s.

[1] Parameter statistically not significant; n.s., regression not significant.

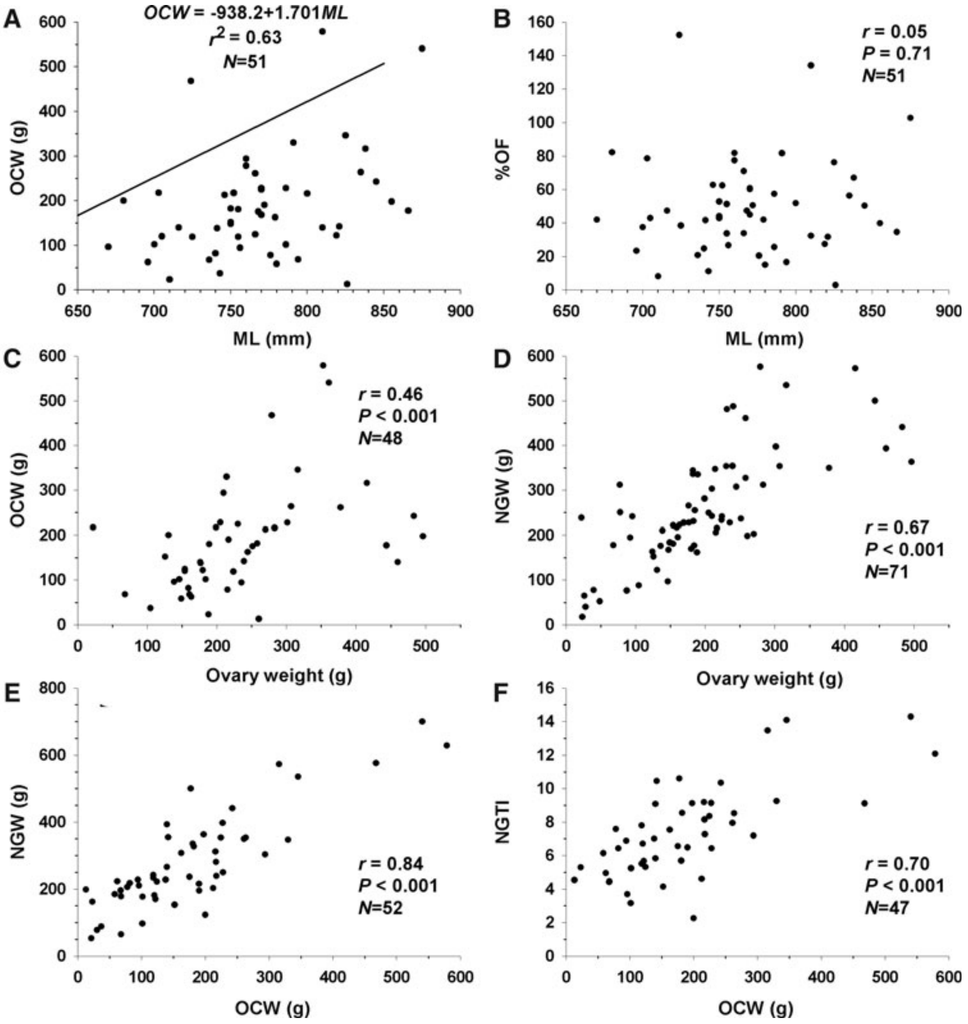

Fig. 6. Relationships among the reproductive organs of mature (stage V) large *Dosidicus gigas* females from the Gulf of California: relationship among the ML and (A) both oviductal complex weight (OCW) (the regression calculated from the maximum values each 25 mm ML is shown); (B) the coefficient of oviductal fullness (%OF); relationship among the weight of the ovary and (C) the OCW; (D) both nidamental glands weight (NGW); relationship among the OCW and (E) the NGW; and (F) the index of nidamental gland thickness (NGTI).

Sakurai, 1996), although medium-size female *D. gigas* spawning in captivity showed empty oviducts (Staaf *et al*., 2008). Our observations (Ch. Nigmatullin) on the oviductal load in spawning females of this family suggest that around 80% of all oviductal eggs are released during a period of spawning activity. Thus in the case of large-sized jumbo squid around 1 million eggs could be spawned in each of these events. This fall in the range of egg number (0.6 to 2 million) estimated for the single *D. gigas* egg mass has been found in nature so far (Staaf *et al*., 2008). In oceanic ommastrephids (subfamily Ommastrephinae) it is thought that the number of realized eggs in each successive spawning event is quasi-equal (Nigmatullin & Laptikhovsky, 1994, 1999).

A rough estimation of periods of individual spawning activity can be made based on available data for estimated age at maturity and maximum age. Large-sized females in the Gulf of California attain maturity and start spawning at the age of about 12 months and 730 mm ML, while maximum ages for mature females of 810–866 mm ML have been estimated at 15 months (Markaida *et al*., 2004). These older females showed good condition of somatic and reproductive organs, without signs of final degenerative changes, being far from spent (Markaida & Sosa-Nishizaki, 2001; U. Markaida, personal observation). Thus, these females may continue to spawn for at least one month more. The duration of their individual complete spawning stage may last about 100–120 days (3–4 months). Considering an actual fecundity of 10–14 millions eggs and that a million eggs are spawned in each event (see above), actual fecundity must be realized during 10–14 egg-laying events (batches). The interlude period in which egg accumulates in the oviducts again, between two periods of spawning activity, may last from 8 to 12 days, on average 10 days.

During these interlude periods jumbo squid females actively feed. Stomach fullness indices suggest that feeding intensity in mature females does not decrease. Large mature jumbo squid are commonly caught jigging in the Gulf of California (Markaida & Sosa-Nishizaki, 2001), an indication that they were actively hunting. Moreover between 8 and 10% of mature females (>800 mm ML) showed evidence of recent cannibalism (although artificial) in their stomachs (Markaida & Sosa-Nishizaki, 2003). Feeding supplies the energy needed for an active and routine metabolism, and generative (active vitellogenesis) and somatic growth (Harman *et al.*, 1989). According to growth equations calculated by Markaida *et al.* (2004), they could gain at least 115 mm (15%) ML and 5200 g (41%) in body weight during a spawning stage of 3–4 months. Thus feeding of adult females between egg batches is a characteristic feature of the oceanic type of ommastrephid spawning strategy (Nigmatullin & Laptikhovsky, 1994; Laptikhovsky & Nigmatullin, 2005; Nigmatullin, 2007).

The r_m index is a measure of the maximum production of a population with exponential growth (Parsons *et al.*, 1977). Supposing that the actual fecundity is 50–80% of the potential fecundity (see above) and the longevity of the four largest females of this study averaged 13 months (Markaida *et al.*, 2004), monthly r_m would range from 1.21–1.29. These values are close to *Sthenoteuthis* (1.2–1.3) and bigger than those for neritic ommastrephid subfamilies (0.9–1.15) (Nigmatullin & Laptikhovsky, 1999).

In jumbo squid the relation between copulation and egg spawning is unknown. Females start copulating while immature and keep copulating until maturity because fresh spermatangia have been found in the buccal mass during all those maturity stages (Markaida & Sosa-Nishizaki, 2001). The buccal membrane holds 125–225 seminal receptacles with special glands secreting products for sperm immobilization and nourishment (Ch.M. Nigmatullin, personal observation) where viable sperm is kept during a very long time after copulation (Hanlon & Messenger, 1996).

In general the large-sized group of *D. gigas* can be considered a typical representative of the oceanic reproductive strategy, despite their nerito-oceanic range and close association with shelf waters (Nigmatullin & Laptikhovsky, 1994, 1999; Nigmatullin *et al.*, 2001). This strategy is characterized by the most evident r-strategy features: small eggs, very high potential and, probably, actual fecundity. A long intermittent spawning stage is composed of 10–14 cycles of egg laying events (egg batches) intercalated with periods of active feeding and somatic growth in which eggs accumulate in oviducts. It is in contrast to the offshore spawning strategy shown by neritic and nerito-oceanic ommastrephids (i.e. *Illex*, *Todaropsis* and *Todarodes*) with large eggs size (1.0 to 1.6–2.4 mm) and a moderate fecundity. Females of these squid cease to feed after the start of the spawning stage and thus the number of spawned eggs in each subsequent egg-laying event decreases (Laptikhovsky & Nigmatullin, 1993; Nigmatullin & Laptikhovsky, 1999; Nigmatullin, 2007).

The oceanic reproductive pattern, along with a large body size, is very similar to reproductive strategy of oceanic scombroid fish, and particularly for tuna of the genus *Thunnus*. Despite large body size, these fish also show basic *r*-strategist reproductive characteristics such as asynchronous oocyte development, relatively small eggs (0.9–1.3 mm), high actual fecundity (1–11 million), protracted multiple batch spawning with active feeding and high rates of somatic growth, at least for their first and second years of life (Alekseyev & Alekseyeva, 1981; Schaefer, 2001). It is important to stress that these similar reproductive strategies in jumbo squid and tuna are formed on a different basis: monocyclia with life cycle within one year in squid, and polycyclia with a long 5–10 years life cycle in tuna. The similarity of the main reproductive traits in ommastrephid squid and tuna fish is an example of a typical functional homoplasy (Futuyma, 1986, p. 295). It is based on the convergent evolution by both groups during their development toward an oceanic realm from an initial shelf-slope zone (Parin, 1970, Nigmatullin, 2007). The convergent formation of this adaptive strategy has mainly been determined by a high level of unpredictable habitat in the oceanic realm.

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REFERENCES

Alekseyev F.E. and Alekseyeva E.I. (1981) Some aspects of the reproductive biology of oceanic and neritic tuna (Scombridae) in the tropical Atlantic. *Journal of Ichthyology* 21, 52–64.

Bower J.B. and Sakurai Y. (1996) Laboratory observations on *Todarodes pacificus* (Cephalopoda: Ommastrephidae) egg masses. *American Malacological Bulletin* 13, 65–71.

Boyle P.R. (1990) Cephalopod biology in the fisheries context. *Fisheries Research* 8, 303–321.

Boyle P.R. and Rodhouse P.G. (2005) *Cephalopods: ecology and fisheries.* Oxford: Blackwell Science Ltd.

Burukovsky R.N., Zuev G.V., Nigmatullin Ch.M. and Tsymbal M.A. (1977) Methodological principles for developing of the reproductive system maturity scales for female squids with reference to *Sthenoteuthis pteropus* (Cephalopoda, Ommastrephidae). *Zoologicheskii Zhurnal* 56, 1781–1791. [In Russian with English summary.] Translated by the Language Services Branch, NMFS, NOAA, US Department of Commerce: 13 pp.

Clarke R. and Paliza O. (2000) The Humboldt current squid *Dosidicus gigas* (Orbigny, 1835). *Revista de Biología Marina y Oceanografía* 35, 1–39.

Coelho M.L. (1990) Gametogenesis in the squid *Illex illecebrosus*. *Journal of Cephalopod Biology* 1, 75–90.

Díaz-Uribe J.G., Hernández-Herrera A., Morales-Bojórquez E., Martínez-Aguilar S., Suárez-Higuera M.C. and Hernández-López A. (2006) Histological validation of the gonadal maturation stages of female jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *Ciencias Marinas* 32, 23–31.

Durward R.D., Vessey E., O'Dor R.K. and Amaratunga T. (1980) Aspects of maturation, mating, spawning, and larval development of *Illex illecebrosus* relevant to field studies. *International Convention of the Northwest Atlantic Fisheries Selected Papers* 6, 7–14.

Ehrhardt N.M., Jacquemin P.S., García F., González G., López J.M., Ortiz J. and Solís A. (1983) On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. In J.F. Caddy (ed.) *Advances in assessment of world cephalopod resources.* Rome: FAO Fisheries Technical Paper no. 231, 306–339.

FAO (2007) *FAO yearbook of fishery statistics for 2005*. Volume 100/1. FAO: Rome. 539 pp.

Futuyma D.J. (1986) *Evolutionary biology*. 2nd edition. Sunderland, MA: Sinauer Associates.

González A.F. and Guerra A. (1996) Reproductive biology of the short-finned squid *Illex coindetii* (Cephalopoda, Ommastrephidae) of the Northeastern Atlantic. *Sarsia* 81, 107–118.

Hanlon R.T. and Messenger J.B. (1996) *Cephalopod behaviour.* Cambridge: Cambridge University Press.

Harman R.F., Young R.E., Reid S.B., Mangold K.M., Suzuki T. and Hixon R.F. (1989) Evidence of multiple spawning in the tropical oceanic squid *Stenoteuthis oualaniensis* (Teuthoidea: Ommastrephidae). *Marine Biology* 101, 513–519.

Laptikhovsky V.V. and Nigmatullin Ch.M. (1992) Características reproductivas de machos y hembras del calamar (*Illex argentinus*). *Frente Marítimo*, 12(A), 23–37. [In Spanish with English summary.]

Laptikhovsky V.V. and Nigmatullin Ch.M. (1993) Egg size, fecundity and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *International Council for the Exploration of the Sea Journal of Marine Science* 50, 393–403.

Laptikhovsky V.V. and Nigmatullin Ch.M. (1999) Egg size and fecundity in females of the subfamilies Todaropsinae and Todarodinae (Cephalopoda: Ommastrephidae). *Journal of the Marine Biological Association of the United Kingdom* 79, 569–570.

Laptikhovsky V.V. and Nigmatullin Ch.M. (2005) Female reproductive biology of the orange-back squid, *Sthenoteuthis pteropus* (Steenstrup) (Ommastrephidae: Oegopsidae) in the eastern tropical Atlantic. *Scientia Marina* 69, 383–390.

Lipiński M.R. and Underhill L.G. (1995) Sexual maturation in squid: quantum or continuum? *South African Journal of Marine Science* 15, 207–223.

Mangold K. (1987) Reproduction. In Boyle P.R. (ed.) *Cephalopod life cycles*, volume II. London: Academic Press, pp. 157–200.

Markaida U. and Sosa-Nishizaki O. (2001) Reproductive biology of jumbo squid *Dosidicus gigas* in the Gulf of California, 1995–1997. *Fisheries Research* 54, 63–82.

Markaida U. and Sosa-Nishizaki O. (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the United Kingdom* 83, 507–522.

Markaida U., Quiñonez-Velazquez C. and Sosa-Nishizaki O. (2004) Age, growth and maturation of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Fisheries Research* 66, 31–47.

Nesis K.N. (1970) The biology of the giant squid of Peru and Chile, *Dosidicus gigas*. *Okeanologiya* 10, 140–152. [In Russian with English summary.]

Nesis K.N. (1971) The biology of the giant squid of Peru and Chile, *Dosidicus gigas*. *Oceanology* 10, 108–118. [Translated from *Okeanologiya*.]

Nesis K.N. (1983) *Dosidicus gigas*. In Boyle P.R. (ed.) *Cephalopod life cycles*, volume I. *Species accounts*. London: Academic Press, pp. 215–231.

Nesis K.N. (1996) Mating, spawning and death in oceanic cephalopods: a review. *Ruthenica* 6, 23–64.

Nigmatullin Ch.M. (1989) Las especies del calamar mas abundantes del Atlántico sudoeste y sinopsis sobre la ecología del calamar (*Illex argentinus*). *Frente Marítimo* 5A, 71–81. [In Spanish with English summary.]

Nigmatullin Ch.M. (2002) Ovary development, potential and actual fecundity and oocyte resorption in coleoid cephalopods: a review. *Berliner Paläobiologische Abhandlungen* 1, 82–84.

Nigmatullin Ch.M. (2007) Brief review on evolutionary and ecological aspects of biology of squids family Ommastrephidae (Cephalopoda: Teuthida). *Proceedings of the Kazan State University. Series Natural Sciences* 149, 182–193. [In Russian with English summary.]

Nigmatullin Ch.M. and Laptikhovsky V.V. (1994) Reproductive strategies in the squids of the family Ommastrephidae (preliminary report). *Ruthenica* 4, 79–82.

Nigmatullin Ch.M. and Laptikhovsky V.V. (1999) Reproductive biology in females of the subfamilies Todaropsinae and Todarodinae (Cephalopoda: Ommastrephidae). *Ruthenica* 9, 63–75.

Nigmatullin Ch.M., Arkhipkin A.I. and Sabirov R.M. (1995) Age, growth and reproductive biology of diamond-shaped squid *Thysanoteuthis rhombus* (Oegopsida: Thysanoteuthidae). *Marine Ecology Progress Series* 124, 73–87.

Nigmatullin Ch.M., Nesis K.N. and Arkhipkin A.I. (2001) A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fisheries Research* 54, 9–19.

Parin N.V. (1970) *Ichthyofauna of the epipelagic zone*. Moscow: Nauka Publisher, 272 p. Translated to English by Israel Program for Scientific Translations, Jerusalem. US Department of Commerce Clearinghouse for Federal Scientific and Technical Information, Springfield, Virginia, 154 pp.

Parsons T.R., Takahashi M. and Hargrave B. (1977) *Biological oceanographic processes*. 3rd edition. Oxford: Pergamon Press.

Rasero M., Gonzalez A.F. and Guerra A. (1995) Spawning pattern and fecundity of the ommastrephid squid *Todaropsis eblanae* in Northeastern Atlantic waters. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM 1995/K:9, 18 pp.

Rocha F., Guerra A. and González A.F. (2001) A review of the reproductive strategies in cephalopods. *Biological Reviews* 76, 291–304.

Schaefer K.M. (2001) Reproductive biology of tunas. In Block B.A. and Stevens E.D. (eds.) *Tuna: physiology, ecology and evolution.* San Diego: Academic Press, pp. 225–270. [Fish Physiology Series, no. 19.]

Staaf D.J., Camarillo-Coop S., Haddock S.H.D., Nyack A.C., Payne J., Ramirez-Rojo R., Salinas-Zavala C.A., Seibel B.A., Trueblood L., Widmer C. and Gilly W.F. (2008) Natural egg mass deposition by the Humboldt squid (*Dosidicus gigas*) in the Gulf of California and characteristics of hatchlings and paralarvae. *Journal of the Marine Biological Association of the United Kingdom* 88, 759–770.

and

Voss G.L. (1983) A review of cephalopod fisheries biology. *Memoirs of the National Museum of Victoria* 44, 229–241.

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