Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae)

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Ripe egg dimensions in the squid genus *Illex* are close to the minimum for cephalopods. The average diameter varies significantly depending on species (0.77–0.82 mm in *I. coindetii*, 0.75–0.88 mm in *I. illecebrosus*, and 0.96–1.04 mm in *I. argentinus*), on geographical distribution intraspecifically, e.g. *I. argentinus* (0.96–0.97 mm in the shelf groups and 1.04 mm in the slope oceanic group), and between pre-spawning and spawning females of the summer-spawning shelf group of *I. argentinus* (0.97 and 0.92 mm, respectively). The potential fecundity (PF), defined as total oocyte stock both in the ovary and oviducts, depends on mantle length (ML) in each species. It varies from 90 000 (ML = 150–160 mm) to 800 000 (ML = 230–250 mm) in *I. coindetii*, from 200 000 to 630 000 (ML = 220–280 mm) in *I. illecebrosus*, and from 75 000 (ML = 150–170 mm) to 1 200 000 (ML = 360–380 mm) in *I. argentinus*. It is possible to estimate the actual value of PF shortly before vitellogenesis begins and up to a start of spawning, when the diameter of the smallest oocytes exceeds 0.05 mm. The summer-spawning shelf females of *I. argentinus* release about of 70% of PF. Their spawning is intermittent and ripe egg production decreases over time with only a 50% replacement of the initial stock of vitelline oocytes and a decreasing volume of eggs at each release. Feeding activity decreases and the mantle wall and internal organs shrink once spawning commences. In spent animals, a degeneration of both vitelline and protoplasmic oocytes occurs. The squids genus *Illex* is one of typical r-strategists among the cephalopods.

Key words: egg size, *Illex*, potential fecundity, r-strategist.

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Introduction

Squids of the genus *Illex* are one of the most important cephalopods to be commercially exploited, representing about 30% of the world cephalopod catch and yielding up to 500 000–700 000 tonnes year⁻¹, mainly of the species *I. argentinus*. In spite of this, there are few data on potential and actual fecundity of the *Illex* species. There are, however, abundant data on egg number in the female oviducts (Mangold-Wirz, 1963; Schuldt, 1979; Brunetti *et al.*, 1991), on egg number in egg masses (Boletzky *et al.*, 1973; O'Dor *et al.*, 1980), and on fecundity estimation based on total counts of vitelline oocytes both in the ovary and oviducts (Kliuchnik and Zasyapkina, 1972; Durward *et al.*, 1978; Coelho *et al.*, 1982; Rodhouse and Hatfield, 1990). None of these methods takes into account the total number of oocytes that females produce, nor the asynchronous nature of vitellogenesis or intermittent spawning. These data are not, therefore, strictly comparable and may not reflect the actual value of fecundity. This situation

is, however, characteristic for all cephalopods (Mangold, 1987).

This paper presents fecundity estimations and describes the process of egg release in *Illex* using methods developed during investigations on 18 ommastrephid squid species (Nigmatullin and Laptikhovsky, in press). The primary subject of the study was *I. argentinus*, the species for which most data are available. For this species, the comparative analysis of both egg size and fecundity was carried out separately to follow three ecological groups (Nigmatullin *et al.*, in prep.). Both the summer-spawning shelf group and winter-spawning shelf group inhabit subtropical and temperate shelf waters throughout the year and differ by season of spawning and adult size. The winter-spawning slope-oceanic group presumably spawns in the waters of the continental slope. The larvae and early juveniles are carried southward by the Brazil current and the juveniles grow in the sub-Antarctic oceanic waters of the Argentina Basin. Afterwards, they feed in sub-Antarctic shelf waters of the Falkland and south Argentina shelves, where

Figure 1. Geographical distribution of *Illex* species: (1) *I. argentinus*, (2) *I. coindetii*, and (3) *I. illecebrosus*. Sampling areas are marked by circles.

productivity is high; during maturation, the animals gradually migrate northward along the slope to the spawning grounds.

Materials and methods

The following were collected: 114 reproductive systems of *I. argentinus* females [dorsal mantle length (ML) 60–380 mm] of all levels of sexual maturity from the Patagonian shelf and slope (42–46°S, 1982–1990); 20 mature and 1 physiologically maturing specimens of *I. coindetii* (ML: 150–250 mm) from the west Africa shelf (7–26°N, 1969–1988), and three physiologically maturing *I. illecebrosus* (ML: 222–277 mm) from the USA coast (30°N, 1977). Species ranges and sampling places are presented below (Fig. 1). The ML and wet body weight (BW) were measured, presence or absence of traces of copulation were determined, and maturity condition was identified using the Nigmatullin (1989) scale but with the following simplified combined stages that were adopted for our present purposes:

1. Immature (stages 1 and 2): all gonad oocytes are at different phases of protoplasmic growth.
2. Physiological maturation (stages 3 and 4): the most advanced gonad oocytes are at different stages of intercalary and trophoplasmic growth; mature eggs are absent in the oviducts.
3. Beginning of functional maturation (stages 5–1): small number of mature eggs present in the oviducts (<20% of ovary volume); as a rule, the females have not copulated.
4. Advanced functional maturation, pre-spawning (stages 5–2 and 5–3): oviducts are full of mature eggs; females have not copulated or (rarely) with 1–2 fresh bunches of spermantangues; the body and all internal organs are in normal condition as at preceding stages.
5. Functionally mature, spawning (stage 6): numerous bunches of spermantangues are attached to the mantle wall, some of them being exhausted; the ovary is small as at the beginning of physiological maturation; the oviduct fullness is as at functional maturation; the nidamental glands become grey; the mantle wall becomes thinner; the liver shrinks; the body becomes more slender and the fin more acute.

6. Spent (stage 7): ovary is small as in immature animals; oocyte degeneration begins and abundant mucus production in the gonad occurs; in the most advanced animals, ovulated eggs remained intact only in the ovary; numerous bunches of the exhausted spermatangues are present; degeneration of the gill lamellae begins; degeneration of the other body parts is extreme.

In *I. argentinus* the summer-spawning shelf group was represented by 15 pre-spawning (ML=173–246 mm), 13 spawning (ML=177–277 mm), and three spent (ML=207–216 mm) females. The winter-spawning shelf group was represented by one juvenile (ML=60 mm), 21 animals at physiological and beginning of functional maturation (ML=210–286 mm), and 19 pre-spawning (ML=210–306 mm) females. The winter-spawning slope-oceanic group was represented by 11 immature (ML=199–240 mm), 17 physiologically maturing and at the beginning of functional maturation (ML=260–370 mm), 12 pre-spawning (ML=300–380 mm), and two spawning (ML=343–366 mm) animals.

Reproductive systems were stored in 6–8% formaldehyde. The ovaries, nidamental glands, and oviducts (oviducal glands, mature eggs, and oviducal envelopes) were weighed after fixation. Due to the effect of preservation, the eggs when measured were not always perfectly symmetrical and, following Clarke (1934) to obviate any selection of the longest or shortest diameter, the micrometer was placed in a horizontal position in the eyepiece and the diameter parallel to the graduation on the micrometer measured. This average egg diameter was estimated on 50 eggs, excluding animals with badly deformed eggs. In some oocytes with a regular ovoid form, longer and shorter diameters were measured. Oviducal egg number was estimated from counts on three 200-mg samples. To estimate oocyte number in the ovary, three 30-mg samples were taken: from the ovary surface, from the ovary core, and from an intermediate layer. Four oocyte stages were distinguished: protoplasmic, intercalary period, vitelline, and ripe eggs (the intercalary period oocytes are the cells with follicular folds penetrated into cytoplasm, but still without yolk accumulation (Burukovsky *et al.*, 1977). A comparative analysis did not reveal any differences in oocyte abundance or in size distribution in relation to the sample localization. Oocytes <0.05 mm in diameter were absent in advanced immature, maturing, pre-spawning, spawning, and spent animals, because oocyte production ceases prior the onset of vitellogenesis. The number of oocytes remains constant after the end of the immature stage until spawning begins (Laptikhovsky and Nigmatullin, 1992). The total number of oocytes in the reproductive systems of both physiologically and functionally maturing pre-spawning females, therefore, was considered to be the total oocyte production during ontogeny.

Potential fecundity (PF) was calculated as the sum of total oocyte number in the gonad and egg number in the oviducts. Relative fecundity (RF) was estimated as the ratio of PF to BW. An index of potential reproductive investment (PRI) was calculated as the product of RF and the weight of an individual ripe egg. This estimates the potential reproductive investment of an individual female aggregated over the whole spawning season. In squids, the PRI is more convenient for this purpose than the gonad-somatic index. It is caused by the asynchronous vitellogenesis that provides the multiple accumulation of eggs in the oviducts and long-term intermittent spawning. Moreover, the PRI is a good index for the interspecific comparison of reproductive investment. The stock of vitelline oocytes was calculated as the sum of the oviducal egg numbers and the number of vitelline oocytes in the ovary. The actual fecundity realized was estimated from the difference between the average values of PF in pre-spawning, spawning, and spent females. The results are used to outline the ontogeny of a single generation, considering changes in mantle, fins, arms, and internal organs (liver, gills, reproductive system), and presence and number of old and fresh traces of copulation.

Results

Illex argentinus

Mantle length of adult females falls in range 150–420 mm. The life span is 1 year. Maturation of females occurs over a wide age range (6–10 months) and they attain functional maturity at 7–11 months (Arkhipkin, 1990; Arkhipkin and Shcherbich, 1991). Spawning occurs throughout the year with a peak in winter. There are several intraspecific groups of uncertain taxonomic status (see Introduction) which are separated on the basis of spawning season, feeding, and spawning biotopes, and the size of mature squid (Brunetti, 1988; Nigmatullin, 1989; Nigmatullin *et al.*, in prep.).

Ripe eggs are ovoid: 0.75–0.85 × 1–1.2 mm. Both average egg diameter (ED) and egg weight (EW) in the total sample slightly increase with female size from 0.86 to 1.09 mm and 0.34 to 0.50 mg, respectively, according to the following equations:

$$ED = 0.556 ML^{0.0998} \quad (r = 0.42)$$

$$EW = 0.253 BW^{0.0773} \quad (r = 0.55).$$

These low values of correlation coefficients are caused mainly by ecosystem-specific egg size and weight (Table 1, 2). The larger winter-spawning shelf females produce eggs of the same size as the smaller summer-spawning shelf animals, in contrast to the winter-spawning slope-oceanic group whose eggs are of larger dimensions than either shelf-spawning groups. No correlation exists between ML of female and egg diameter within any group: $r = 0.006$,

Table 1. Reproductive features in the pre-spawning females of different groups of *I. argentinus* and *I. coindetii*.

	<i>I. argentinus</i> spawning groups			<i>I. coindetii</i> geographic regions	
	Summer shelf	Winter shelf	Winter slope-oceanic	7–11° N	20–26° N
ML (mm)	208 173–246 (S.D. = 25.1)	262 210–306 (S.D. = 27.3)	353 300–380 (S.D. = 21.4)	164 150–180 (S.D. = 12)	223 172–250 (S.D. = 26)
N (sp.)	16	24	13	6	9
ED (mm)	0.97 0.88–1.07 (S.D. = 0.09)	0.96 0.91–1.08 (S.D. = 0.04)	1.04 0.95–1.09 (S.D. = 0.05)	0.77 0.73–0.80 (S.D. = 0.03)	0.82 0.77–0.93 (S.D. = 0.06)
EW (mg)	0.38 0.32–0.46 (S.D. = 0.09)	0.41 0.32–0.48 (S.D. = 0.04)	0.43 0.35–0.52 (S.D. = 0.05)	0.21 0.17–0.24 (S.D. = 0.03)	0.30 0.23–0.41 (S.D. = 0.06)
PF (10 ³)	155 74–524 (S.D. = 125)	273 102–702 (S.D. = 129)	762 480–1247 (S.D. = 218)	123 87–184 (S.D. = 46)	453 281–778 (S.D. = 160)
RF (10 ³)	795 462–1383 (S.D. = 232)	654 428–1036 (S.D. = 178)	707 575–952 (S.D. = 149)	1264 891–2019 (S.D. = 426)	1778 1006–2686 (S.D. = 587)
PRI	0.30 0.16–0.55 (S.D. = 0.11)	0.25 0.17–0.41 (S.D. = 0.07)	0.28 0.13–0.46 (S.D. = 0.1)	0.26 0.18–0.34 (S.D. = 0.07)	0.51 0.25–0.67 (S.D. = 0.14)

ED, egg diameter; EW, egg weight; PF, potential fecundity; RF, relative fecundity; PRI, potential reproductive investment.

Table 2. Difference in egg size (average diameter) and egg mass between seasonal spawning groups of *Illex argentinus* (values of t-criteria: egg size/egg mass).

	Spawning groups			
	Summer shelf		Winter shelf	Winter slope-oceanic
	Pre-spawning	Spawning	Pre-spawning	Pre-spawning
Summer shelf				
Pre-spawning		3.567 2.083	1.060 1.242	2.207 3.023
Spawning	3.567 2.083		2.833 3.528	6.485 4.275
Winter shelf				
Spawning	1.060 1.242	2.833 3.528		2.241 2.436
Winter slope-oceanic				
Spawning	2.207 3.023	6.485 4.275	2.241 2.436	

0.142 and -0.089 for summer- and both winter-spawning shelf, and slope-oceanic females. For egg weight the corresponding coefficients are $r = 0.29$, 0.32 , and -0.14 , respectively. Moreover, egg dimensions may change during the spawning season. Thus, in spawning of summer shelf females, egg size and weight decrease to

0.87 – 0.98 mm (mean 0.92 , S.D. = 0.032) and 0.30 – 0.41 mg (mean 0.36 , S.D. = 0.04), respectively.

PF (thousands) increases in pre-spawning females with ML and BW from $75\,000$ – $100\,000$ (ML: 170 – 180 mm) to $800\,000$ – $1\,200\,000$ (ML: 350 – 380 mm) (Fig. 2) according to the following equations:

Figure 2. Potential fecundity of females of the genus *Illex*. Functionally maturing, pre-spawning females are marked by points; spawning by crosses; and spent by triangles.

For females at physiological maturation (ML = 210–370 mm)

$$PF = \exp(2.685 + 0.0112 ML) (r = 0.93)$$

$$PF = \exp(5.011 + 0.00158 BW) (r = 0.87).$$

For pre-spawning females (ML = 173–380 mm)

$$PF = \exp(2.244 + 0.0122 ML) (r = 0.93)$$

$$PF = \exp(4.588 + 0.00184 BW) (r = 0.93).$$

For spawning females (ML = 177–366 mm):

$$PF = \exp(1.932 + 0.0118 ML) (r = 0.93)$$

$$PF = \exp(4.210 + 0.00184 BW) (r = 0.92).$$

These equations describe PF over the whole ML range, not taking into account the intraspecific groups. Within each of these groups, there is a positive allometric growth of PF in relation to ML, which does not differ in any group and may be expressed by an equation:

$$PF = \exp(A) \times ML^B,$$

where for summer-spawning shelf squids $A = -12.05$ (S.D. = 4.77), $B = 3.13$ (S.D. = 0.86); for winter-spawning shelf squids $A = -12.21$ (S.D. = 4.98), $B = 3.20$ (S.D. = 0.85); and for winter-spawning slope-oceanic squids $A = -11.70$ (S.D. = 4.54), $B = 3.10$ (S.D. = 0.85).

Estimation of fecundity in females at physiological maturation is the most convenient for comparison of squid species with different reproductive strategies. The

Table 3. Comparison of reproductive features in females of summer shelf-spawning group of *I. argentinus* during spawning.

	Pre-spawning	Advanced spawning	Spent
Number	6	2	3
ML (cm)	173–192 (186) S.D. = 6.9	177 and 187	207–216 (210) S.D. = 4.9
BW (g)	102–135 (115) S.D. = 17.6	67 and 83	111–179 (147) S.D. = 34.1
PF (10^3)	82–148 (100) S.D. = 26.0	35 and 43	2–15 (10) S.D. = 7.1
OE (10^3)	6–38 (20) S.D. = 11.5	2.6 and 2.7	0.4–3.8 (1.9) S.D. = 1.7
OVO (10^3)	13–29 (21) S.D. = 6.9	12 and 18	0.7–7.6 (3.7) S.D. = 3.7
OIO (10^3)	11–46 (21) S.D. = 14.6	9 and 13	0–4.8 (2.5) S.D. = 2.4
OPO (10^3)	22–80 (42) S.D. = 23.7	10 and 12	0–2.8 (2.3) S.D. = 2.3

OE, oviducal egg number; OVO, vitelline oocyte number in ovary; OIO, number of intercalary period oocytes in ovary; OPO, protoplasmic oocyte number in ovary.

winter-spawning slope-oceanic group possesses maximal PF, the summer spawners, minimal PF. The RF and PRI are similar in all groups and do not differ statistically (Table 1).

A comparison of the PF in pre-spawning, spawning, and spent females of the summer shelf-spawning group that spawned in January and February 1984 on the edge of shelf in 45–47°S allows an estimate of the realized fecundity. Following the regressions between PF and ML we assume that the average PF of spawning animals is 25–30% lower than in pre-spawning females of similar size with possible insignificant linear growth taken into account. In the most advanced spawning (pre-spent) females the PF is 55–65% lower than the initial PF (Table 3). In the most advanced spent female (ML = 216 mm) only 1472 eggs remained in the oviducts and about 660 oocytes in the ovary (about 510 vitelline oocytes at different stages of the resorption and 110 intact ovulated eggs), corresponding to more than a 90% decrease of PF. However, we suppose that this decrease was mainly caused by clearly visible oocyte degeneration. In two other spent females only a few thousand oocytes (including the protoplasmic ones) were present due to this degeneration after spawning, which was accompanied by the appearance of mucus in the ovary.

Thus, females presumably realized some 60–70% of initial PF during the spawning period.

The number of oocytes in the oviducts of functionally maturing pre-spawning animals increases with female

Figure 3. Schematic diagram of the multiple spawning pattern in *Illex* (potential fecundity decrease owing to oocyte degeneration is marked by points).

size from 20 000–30 000 (ML = 160–170 mm) to 200 000 (ML = 320–350 mm). This value is 30–55% of realized fecundity (that is, 20–30% of PF). Oviducts attain their maximal fullness prior to first egg laying: 25 000–40 000 eggs are contained in the summer-spawning females with ML = 190–240 mm; this value decreases during spawning to 8000–12 000 eggs and further to 2000–5000 eggs in the animals that spawn latest. The actual number of vitelline oocytes in pre-spawning females is some 50–70% of realized fecundity. It may be shown by a comparison of data on animals of similar size presumably belonging to one ontogenetic line (Table 3). The oviducal eggs are gradually replenished during the spawning period, so that there is a continuous repeated accumulation of eggs in the oviducts followed by multiple egg layings.

On the basis of our data we propose that in the single reproductive season of each female there are several periods of active spawning, interrupted by periods of egg accumulation in the oviducts. During each period of active spawning, females lay one or several egg masses. The number of eggs in subsequent egg layings decreases from 30–55% of realized fecundity in the first spawning, to 12%–5% at the end of spawning (Fig. 3).

At spawning, females decrease their feeding activity and, as a result, lose 40% of total body weight, including weight decreases in the mantle of 40–50%, fins of 30–40%, and both arms and tentacles of 30%. The mantle decreases to half its original thickness and the liver shrinks to about 60–70% of initial mass. Ovary weight (initial weight is 4.4–10.1%, average 6.3% of BW) decreases by a factor of two in spawning animals (Table 4) up to a factor of 5–10 in spent ones. Then, in spent females, during oocyte resorption accompanied by mucus production, gonad weight falls to 5–15% of the initial value. Both nidamental and oviducal gland weight decreases by 40–50% and oviduct weight by a factor of 5–10. The fins become more acute and elongated, body form extends and becomes arrow-like as described for *I. oxygonius* (Roper *et al.*, 1969). The females die shortly afterwards.

Illex coindeti

The life cycle off the west African coast is 1 year. Spawning occurs on the shelf year-round. The ML of adult

Table 4. The variations both of the body and internal organ dimensions in spawning of *Illex argentinus*.

Feature	Functionally maturing pre-spawning females	Spawning females
Number	5	4
Mantle length (mm)	222 213–231	218 215–220
Body weight (g)	200 172–252	131 114–140
Mantle weight (g)	55 33–68	30 25–34
Fin weight (g)	16.5 15–18	12 10.2–13.2
Arms and tentacles weight (g)	37.8 31–47	27 25.6–30.6
Liver weight (g)	11.9 5.7–17.6	4.7 4.2–5.0
Ovary weight (g)	11.9 7.6–16.3	5.8 3.1–7.9
Oviduct weight (g)	13.7 10.5–22.7	2.5 1.4–4.0
Oviducal gland weight (g)	1.1 0.7–1.7	0.6 0.5–0.7
Nidamental gland weight (g)	15.8 10.0–26.6	11.2 9.9–13.5
Mantle thickness (mm)	4	2
Relation of fin length to fin width	0.87 0.82–0.96	0.98 0.95–1.01

females is 97–310 mm (our data) at an age of 190–270 days (Arkhipkin, 1989). Recent data do not reveal any clearly visible intraspecific group. The minimum and maximum ML of adults are quite similar over the species range along the west African coast (our data).

Ripe eggs are ovoid, their size (at 20–26°N) being 0.7–0.75 × 0.9–1.0 mm. The average diameter and weight are lower in small females from 7–11°N than in large animals from 20–26°N (Table 1). However, we are not able to discuss possible geographic variations in egg dimensions, owing to the different ML of animals in our particular samples from 7–11°N and 20–26°N.

The equations describing the egg diameter (ED) and egg weight (EW) increase with ML and BW in the total sample are as follows:

$$ED = 0.343 ML^{0.161} (r = 0.45)$$

$$EW = 0.061 BW^{0.274} (r = 0.72).$$

The PF increases (Fig. 2) from 80 000–180 000 (ML: 155–180 mm) to 500 000–800 000 (ML: 240–250 mm) according to the following equations:

$$PF = \exp(2.292 + 0.162 ML) (r = 0.80)$$

$$PF = \exp(4.336 + 0.00604 BW) (r = 0.86).$$

The RF is nearly similar in animals from both regions (Table 1) and does not differ statistically ($t = 1.808$). Higher values of PRI in larger females from colder waters ($t = 3.603$) are caused by the presence of larger eggs. Due to differences of PF between pre-spawning and spawning females with ML = 165–180 mm (Fig. 2), those spawning lay at least 40% of PF, possibly more (no advanced spawning or spent females were examined). The egg mass of a female with a body weight of 253 g (equivalent to a ML of 210–230 mm from the ML/BW relation) contained about 50 000–100 000 eggs (Boletzky *et al.*, 1973). This suggests that spawning is intermittent.

Illex illecebrosus

In this species the life cycle is 1 year and spawning is year-round, with a winter peak. The ML of adult females is 190–340 mm. There are two seasonal spawning groups: a minor summer group and dominant autumn–winter group (O'Dor, 1983; Froerman, 1985; Hatanaka *et al.*, 1985).

The size of the ovoid ripe eggs is $0.9\text{--}0.6 \times 1.0\text{--}0.8$ mm (O'Dor, 1983) and the mean wet weight is 0.24 mg (Durward *et al.*, 1978). Estimation of fecundity for a female with BW 400 g was approximately 400 000 (Durward *et al.*, 1978). Our data show that gonads of three physiologically maturing females with ML = 222, 224, and 277 mm contained 200 000, 300 000, and 630 000 oocytes, respectively, corresponding to a PRI of some 0.20–0.34%. At spawning, females lay several egg masses of different size (O'Dor *et al.*, 1980) the first of which contains up to 100 000 eggs (O'Dor and Balch, 1985). In this species at least two, and perhaps several, egg masses may be released in one night (O'Dor *et al.*, 1980), demonstrating the potential for laying more than one egg mass in a given period of active spawning.

Discussion

Our data and methods allow us to compare both egg dimensions and PF between the three *Illex* species and between intraspecific groups of *I. argentinus*, and to describe some of the features of the actual fecundity realized. In each species, reproduction probably varies with population density, size structure of adults, region, and seasonal spawning group. This restricts the possibilities of interspecific comparisons, owing to the limitations of our data, and the absence of appropriate investigations that have been carried out on other cephalopod taxa using comparable methods.

Egg size

Egg size in *Illex* is close to the minimum given for cephalopods (Mangold, 1987), i.e. in ommastrephids (Nigmatullin and Laptikhovsky, in press). Other shelf and slope ommastrephids, such as *Todaropsis* and *Todarodinae* (*Todarodes*, *Martialia*, *Nototodaros*), have ripe eggs with an average diameter of 1.0–2.2 mm (mostly 1.2–1.6 mm). The single exception – *T. pacificus* – which is an ecological “sibling” of *Illex* (Nigmatullin, 1977, 1979; Hatanaka *et al.*, 1985) has an egg diameter of $0.77\text{--}0.80 \times 0.90\text{--}0.92$ (Okutani, 1983). Because the genus *Illex* is the most primitive among Ommastrephidae (Nigmatullin, 1979), we suppose that small eggs are primitive for this family. The more highly evolved oceanic ommastrephids (*Ornithoteuthis* and Ommastrephinae – *Dosidicus*, *Onmmastrephes*, *Sthenoteuthis*, *Eucleoteuthis*, *Hyaloteuthis*) have an egg diameter of 0.7–1.0 mm (mostly 0.75–0.85 mm), i.e. they probably have retained a primitive egg type, while an evolution of shelf and slope ommastrephids took the form of an egg size increase (Nigmatullin and Laptikhovsky, in press).

Egg size in *Illex* is rather labile. It varies among different species, as well as for different intraspecific forms, for animals in distinct physiological condition (pre-spawning and spawning) and probably (in *I. coindetii*) for animals of different size (Tables 1, 5). The smallest eggs have been discovered in *I. coindetii* and *I. illecebrosus*, the larger ones in summer- and winter-spawning shelf groups, and the largest in winter-spawning slope-oceanic groups of *Illex argentinus*. In different seasonal spawning groups of *I. argentinus* egg size does not depend on animal size, but varies with the type of ecosystem. Thus, both summer- and winter-spawning shelf squids that complete their life histories in the subtropical and temperate shelf ecosystems in different seasons, and have different sizes of adults, nevertheless produce eggs of the same size. Egg size in the winter-spawning slope-oceanic group, which spends part of its life cycle in the oceanic and shelf sub-Antarctic ecosystems, statistically differs from the other two (Tables 1, 2). Thus, the observed differences in egg size probably reflect ecosystem peculiarities.

Fecundity

All *Illex* species have comparable PF values (Tables 1, 5). The relationship between PF and ML has been considered for two species and in both cases there was positive correlation. Unfortunately, we could not compare our results with other squid families owing to the absence of comparable data. Among 18 ommastrephids species belonging to all genera of the family that have been studied by the same methods (Nigmatullin and Laptikhovsky, in press), the PF and RF in *Illex* are similar to PF and RF of shelf and slope species but lower than oceanic species by a factor

Table 5. Comparative data on reproductive features of three *Illex* species of ML = 210–246 mm.

Feature	<i>I. argentinus</i> * (winter-spawning shelf group)	<i>I. coindetii</i> *	<i>I. illecebrosus</i>
Mantle length (mm)	235 210–246 (S.D. = 13)	232 218–244	22.2 and 24.4
Number	7	6	2
Egg dimensions (mm)	0.8–0.9 × 1.0–1.1	0.7–0.75 × 0.9–1.0	0.69–0.76 × 1.09–1.63†
Egg average diameter (mm)	0.96 0.91–1.00 (S.D. = 0.04)	0.81 0.77–0.84 (S.D. = 0.03)	0.75–0.88† 0.67–0.75‡
Egg wet weight (mg)	0.40 0.37–0.42 (S.D. = 0.02)	0.28 0.23–0.34 (S.D. = 0.03)	0.24‡
PF (thousands)§	182 102–269 (S.D. = 69)	509 320–780 (S.D. = 162)	200 and 300
RF (egg g ⁻¹)§	707 462–894 (S.D. = 186)	1676 1006–2690 (S.D. = 515)	1200 and 1370
Yolk oocyte number (thousands)	75 47–122 (S.D. = 29)	136 78–200 (S.D. = 44)	
PRI	0.28 0.19–0.34 (S.D. = 0.06)	0.45 0.25–0.67 (S.D. = 0.07)	0.29 and 0.34

*Our data for reproductive systems preserved in 6–8% formaldehyde.

†Data from frozen samples (Dawe and Drew, 1981).

‡Data from samples preserved in Bouin's fluid (Coelho *et al.*, 1982).

§Data for pre-spawning females of *I. argentinus* and *I. coindetii* and for maturing (3–4 m s.) *I. illecebrosus*.

two–seven times (animals of similar size being taken into account).

I. coindetii has a higher RF than *I. argentinus* at similar body dimensions, but produces smaller eggs of lesser mass (Tables 1, 5). Differences in RF and PRI between both shelf summer- and winter-spawning groups of *I. argentinus*, on the one hand, and *I. coindetii* from north-west African waters on the other hand (all of them have comparable size distribution of adults and inhabit shelf ecosystems) may be hypothetically explained mainly by differences in larval and juvenile mortality caused by local features of the surface-water circulation, ecosystem structure, and temperature (tropical versus subtropical). Reproductive output may depend on features of the biotope, such as food resources, predator pressure, and temperature. The last factor influences metabolic rate and hence resource allocation to egg production.

Regulation of individual fecundity probably takes place during three ontogenetic phases: the juvenile stage, when the growth rate determines body and (correspondingly) gonad size; during the maturation period, when food supply influences yolk accumulation in the eggs; and

during spawning, when environmental conditions may extend or shorten the individual spawning period so affecting the actual value of realized fecundity.

Spawning

It is likely that there is a multiple "descending" type of spawning in all three species, i.e. a decreasing number of eggs at each release, as described here for the summer shelf-spawning group of *I. argentinus* (Fig. 3). However, it is possible that large squids, mainly winter slope-spawners, may differ in some respects. After the end of the first period of egg accumulation in the oviducts, copulation with a male (or males) takes place and the first egg mass or several egg masses are laid containing 30%, or more, of the realized fecundity. Subsequently, copulation occurs each time an egg mass is spawned (Nigmatullin, 1989; Laptikhovsky and Nigmatullin, 1992). Up to the first spawning, energy and nutrients for gonad development and vitellogenesis are derived from the food (Hatfield *et al.*, 1992; Rodhouse and Hatfield, 1992). After

the first spawning, feeding intensity declines, then ceases, and body tissues are increasingly drawn upon for metabolism (Table 4). The body shape becomes more acute, giving rise to the body form that was originally described as *Illex oxygonius*. The first specimens of this supposed species was from the geographical range of *I. illecebrosus*. Later specimens have been caught in the areas of *I. coindetii* and *I. argentinus* (Roper *et al.*, 1984; Nigmatullin, 1989). In the case of the spawning of *Illex argentinus* there is clear, gradual change of body shape from the "argentinus" form to the "oxygonius" form (Nigmatullin, 1989; our data). It is therefore evident that *I. oxygonius* consists of spawning and spent specimens of the three *Illex* species, *argentinus*, *coindetii*, and *illecebrosus*. In spent animals degeneration of different organs occurs; in the ovary this process spreads both to protoplasmic and vitelline oocytes. Post-spawning oocyte degeneration has not hitherto been described in cephalopods, but it was shown in fishes by Sakun and Svirsky (1992).

In other squid species there is a comparable "descending" type of spawning with 50% replenishment of the yolk oocyte stock of pre-spawning squids, as shown for *Loligo pealei* (Hixon, 1980). This type of spawning is intermediate between the short-duration type in *Loligo opalescence*, *L. plei*, and *Lolliguncula brevis* (fecundity up to 15 000) and the long-duration intermittent type with production of multiple egg masses of similar size as in *Sthenoteuthis* and *Thysanoteuthis* (fecundity up to 15–20 million). In the first group the replenishment of the stock of vitelline oocyte during spawning is insignificant (Hixon, 1980; Mangold, 1987), while in the second group replenishment is very important and may exceed by a factor of 7–10 times the number of vitelline eggs in pre-spawning females (Arkhipkin *et al.*, 1983; Harman *et al.*, 1989; Nigmatullin *et al.*, 1991; Nigmatullin and Laptikhovskiy, in press).

Reproductive strategy

Comparing our results and data from the literature (Boletzky, 1986; Mangold, 1987, 1989; Arkhipkin, 1992) on the basis of *r* and *K* selection, we conclude that *Illex* is one of the most *r*-oriented squid species after most of the Enoploteuthidae (Arkhipkin and Murzov, 1990) and other small-sized cephalopods whose life spans are about 6 months or less and whose eggs are of small dimensions. All variations of the reproductive features in *Illex* occur within the *r* part of the *r*–*K* continuum of cephalopods. Among Ommastrephidae, *Illex* and *T. pacificus* occupy the intermediate position between more *r*-oriented oceanic *Ornithoteuthis* and *Ommastrephinae* and more *K*-oriented *Todaropsis* and *Todarodinae* (Nigmatullin and Laptikhovskiy, in press). *I. coindetii* of west African waters is most *r*-oriented among species of this genus (Table 5); in addition to other parameters, some of the females of this species may mature at an age of 6 months (Arkhipkin,

1989); *I. illecebrosus* is probably less *r*-oriented and *I. argentinus* relatively more a *K*-strategist. The PF has a positive allometric growth to ML, but the adaptive role of the differences in PF between different-sized animals of intraspecific groups of *I. argentinus* is not clear. Therefore, the possibility of using PF for a comparison of the reproductive strategies within this species is now doubtful. Thus, if we exclude PF, in *I. argentinus* the summer- and winter-spawning shelf groups are more *r*-oriented than the winter-spawning slope-oceanic group. The reproductive features of the winter squids are quite similar to *Todarodes* and *Nototodarus*, revealing in the slope *Illex* the same evolutionary tendency to *K*-strategy as in the slope ommastrephids.

Generally, for *Illex* the following explanation may be given. Females that spawn in warmer waters reach a smaller size, produce smaller eggs, and have a lower fecundity than females that spawn in relatively cold waters. At the same time, the ecosystem features and respective ecological niches of different populations influencing mortality introduce significant corrections in these relationships. The complicated structure of the tropical ecosystems, with high diversity of predators, determines the need for a fecundity increase in *I. coindetii* together with a simultaneous decrease of egg size. In the low temperature conditions of cold seasons or high latitudes metabolic rate is lower, food supply is better, and the females can reach greater size and allocate more energy to reproduction (so leading to a PF increase) and, moreover, to yolk accumulation in the oocytes (and a greater egg size).

General conclusions

On the basis of our results and other data on *Illex* biology (O'Dor, 1983; Froerman, 1985; Brunetti, 1988), we can describe the main characteristics of *Illex* reproduction. Copulation occurs just before egg laying; there is no seminal receptacle so sperm storage is impossible. The spermatophores are attached inside the mantle cavity near the openings of the oviducts. At any one time, the number of ripe eggs in the female is much lower than the realized fecundity, but there is moderate replenishment of the stock of vitelline oocytes during maturation and a "descending" type of spawning. Fecundity is moderate and the number of eggs per egg mass decreases at each spawning. Feeding ceases and spawning is accompanied by degeneration of both internal organs and the mantle. Spawning is year-round with one seasonal peak. Sympatric and allopatric seasonally spawning groups exist. Male and female feeding grounds coincide. The *Illex* species are monocyclic with a 1-year life span and equal longevity in both sexes. Successful recruitment depends mainly on features of the water circulation in the vicinity of the spawning grounds so that there are large interannual

fluctuations in abundance (up to several orders of magnitude). *Illex* is one of typical r-strategists among the cephalopods.

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