Mediterranean Marine Science

Vol 18, No 1 (2017)

Growth and reproduction of the squid Illex coindetii Verany, 1839 in the central Mediterranean Sea

L. CERIOLA, N. MILONE

doi: [10.12681/mms.1682](https://doi.org/10.12681/mms.1682)

To cite this article:

CERIOLA, L., & MILONE, N. (2017). Growth and reproduction of the squid Illex coindetii Verany, 1839 in the central Mediterranean Sea. *Mediterranean Marine Science*, *18*(1), 107–120. https://doi.org/10.12681/mms.1682

Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.1682

Growth and reproduction of the squid *Illex coindetii* Verany, 1839 in the southern Adriatic Sea, central Mediterranean

L. CERIOLA[1] **and N. MILONE**[2]

[1] FAO MedSudMed, Viale delle Terme di Caracalla. 00153 Rome, Italy
[2] FAO AdriaMed, Viale delle Terme di Caracalla. 00153 Rome, Italy

Corresponding author: luca.ceriola@fao.org

Handling Editor: Stelios Katsanevakis

Received: 27 February 2016; Accepted: 3 January 2017; Published on line: 13 March 2017

Abstract

Life span, growth and cost of reproduction of *Illex coindetii* were examined for the first time in the southern Adriatic Sea, central Mediterranean. Age and growth were investigated through the reading of statoliths. The cost of reproduction was explored by studying the relative investment between somatic and gonad growth. The life span of *I. coindetii* was less than nine months in both sexes. Females (128-234 days) showed a longer life span than males (124-178 days). In both sexes the linear model best described the mantle length-at age data, while the exponential model provided the best fit for the total weight-at-age data. In terms of mantle length, females grew faster than males (the average growth rate was 1.33 mm day^{-1} in females and 1.00 mm day^{-1} in males). In terms of total weight, no significant differences were highlighted between the growth curves of males and females. Mantle length, total weight, mantle weight and fin weight increased up to the last maturity stage in both sexes. Immature and maturing individuals showed poorer body condition than mature counterparts in both sexes. Some evidence was found of a reproductive strategy that was more similar to a multiple-spawning than to a single-spawning species.

Keywords: Gonad maturity, growth, reproductive strategy, squid, statoliths analysis, Adriatic Sea.

Introduction

Squids traditionally accounts for the largest fraction (>70%) of world cephalopod capture production. Since 1996, squids landings have constantly exceeded 3 million tonnes and peaked in 2007 with about 4.3 million tonnes (about 4 million tonnes in 2012, FAO, 2014). Among squids, *Illex coindetii* (Verany 1837, Cephalopoda, Ommastrephidae) has considerable economic importance in specific areas of the Atlantic Ocean and of the Mediterranean Sea. In European Mediterranean countries such as Italy, Spain and Greece, cephalopods are high in local diets, total catch and trade (e.g. Sánchez *et al.*, 1998; Ceriola *et al.*, 2008; Arkhipkin *et al.*, 2015; Jereb *et al.*, 2015a). In the Adriatic Sea, central Mediterranean, *I. coindetii* is exploited by the fishing fleets of four countries, i.e. Albania, Croatia, Italy and Montenegro and its importance for their fisheries increased recently (Ceriola *et al.*, 2008; Arkhipkin *et al.*, 2015; Jereb *et al.*, 2015a).

Considerable work has been conducted to review current knowledge in cephalopod fisheries science, as well as to recommend future actions for scientists and cephalopod fishery managers (e.g. Pierce *et al.*, 2005; Payne *et al.*, 2006; Arkhipkin *et al.*, 2015; Jereb *et al.*, 2015b). The determination of age and growth is critical to understand the life history and reproductive strategy of harvested species, as well as to model the dynamics of their populations, both of which are essential for assessment and for fisheries management purposes. Accurate assessment and effective management depend on population models that incorporate life history parameters, such as proportion of sexual maturity at size and growth rate. Statolith analysis has proved to be one of the best tools for squid age and growth estimation in wild populations (Jackson, 1994; Arkhipkin, 2005; Villanueva *et al.*, 2007; Ceriola & Milone, 2008). Growth studies based on direct age estimation or studies on relative investment between somatic and gonad growth are poor or still lacking in many oceanic regions and in the Mediterranean Sea (Sánchez, 1995; Arkhipkin *et al.*, 2000; Arkhipkin & Roa-Ureta, 2005; Cavanna *et al.*, 2008).

I. coindetti has shown different life history characteristics in association with geographic distribution. Larger individual size, longer life span and a relatively lower growth rate were reported for *I. coindetii* in western Mediterranean and Galician waters with respect to the population in the central Mediterranean Sea, i.e. Sicily Channel (for review see e.g. Sánchez *et al.*, 1998; Jereb *et al.*, 2015a). However, its life history traits have not been described in all the distribution area yet. To date, no information on the life span, growth and reproductive strategy of the Adriatic population of *I. coindetii* and of squids in general has been provided. The aim of this paper is to describe, for the first time, the growth of *I. coindetii* (Cephalopoda, Ommastrephidae) in the south Adriatic Sea on the basis of statolith analysis. The paper also aims to provide the first evidence that, in this area, the species has similar individual growth and life span with respect to populations in the central Mediterranean Sea, but different compared to the western Mediterranean and Atlantic Ocean. A preliminary description of the reproductive strategy of *I. coindetii* in the southern Adriatic Sea is also provided in this paper.

Materials and Methods

Sampling and basic measurements

Samples of *I. coindetii* were collected on monthly basis in 2006 from March to July (main peak of reproduction, Ceriola *et al.*, 2006; Jereb *et al.*, 2015a) in the port of Molfetta, Italy. Samples were taken from commercial fishing vessels which operated on daily basis (one day = one fishing trip) in the southern Adriatic Sea, central Mediterranean Sea. All the specimens were measured and dissected fresh on the day of capture at the Department of Animal Production of the University of Bari (Italy). All the individuals were sexed and assigned to a maturity stage based on Lipinski's universal maturity scale (Lipinski, 1979). The maturity stages were treated both separately and grouped according to three functional stages, i.e. immature (stages 1 and 2), maturing (stages 3 and 4) and mature (including spent individuals). Total weight (TW), dorsal mantle length (ML), mantle weight (MW), fin weight (FW), stomach weight and digestive gland weight (DGW) were also measured. Gonad weight, as well as weights of other accessory sexual organs, were recorded for each animal. Accessory organs included testis and penis plus the spermatophoric complex (PSC) in males and ovary, oviducts, oviducal glands and nidamental glands in females. The ML and the nidamental gland length were taken at the nearest 0.1 mm. All the weights (wet weights) were taken at the nearest 0.01 g. Gonadosomatic indices (GSI) were calculated for males and females using the following equation: GSI = gonad weight / (total body weight – stomach weight) * 100, where gonad weight included testis or ovary weight. The relative weight of somatic and reproductive organs with respect to mantle length per specimens was also estimated.

The statoliths were removed from all specimens and stored dry after cleaning with distilled water (Ceriola & Milone, 2008). For each specimen, the presence of food in the stomach was recorded as an indication of feeding; no qualitative or quantitative measures of stomach contents are provided in this paper.

Statolith analysis and growth

The statoliths were mounted in Crystal Bond™ thermoplastic cement on a microscope slide in preparation for ageing. Statoliths were ground dry by hand on the posterior surface or, when necessary, on both the posterior and anterior surfaces along the longitudinal plane according to Ceriola & Milone (2008). To grind and polish statoliths, four lapping films with increasing grit were used in sequence: 30, 12, 3 and 0.05 µm grades. The coarsest lapping films (30 and 12 µm grades) were used for the main grinding. The remaining films (3 and 0.05 µm grades) were used to remove the scratches from the ground surfaces. Increments were counted using a Leica® high-power microscope (200-400 X) with polarized light connected to a computer monitor via a high-resolution video camera. According to previous studies on *I. coindetii*, each growth increment or ring (i.e. the sequence of a dark and light increments outside the natal ring) in the statolith section was assumed to represent one day's growth (Arkhipkin, 1996; González *et al.*, 1996; Sánchez *et al.*, 1998; Arkhipkin *et al.*, 2000; Arkhipkin & Roa-Ureta, 2005). Each statolith was counted twice. The average of the two counts was taken as the individual age in days. If the variation between the two counts was greater than 10%, a third count was taken and the average of all three counts was the estimated age in days.

The individual hatch date was back-calculated from age data: hatch date = sampling day – age in days. Based on the hatch date, all specimens were grouped into monthly cohorts. Growth curves were generated using size-at-age (TW or ML) data by sex and monthly cohort.

Several functions were fitted to the length- and weight-at-age data, including asymptotic and non-asymptotic models. The four parameters Schnute model re-parameterised according to Arkhipkin & Roa-Ureta (2005), Gompertz, linear, power and exponential models were tested to describe the form of growth of *I. coindetii* in the south Adriatic Sea (Arkhipkin, 1996; González *et al.*, 1996; Sánchez *et al.*, 1998; Arkhipkin *et al.*, 2000; Arkhipkin & Roa-Ureta, 2005).

The parameters of growth curves were estimated by minimising the sum of squares logarithms (SSQ):

$$SSQ = \sum_{\mathrm{i}=1}^{n} (lnOi - lnEi)^2$$

where O_i and E_i are respectively the observed and estimated values.

This approach was chosen based on the assumption that variation in age-at-size usually increases along with age, especially when total weight is considered (Quinn & Deriso, 1999).

The best model selection was based on the Akaike's information criterion (AIC). The AIC was estimated from sum of square (SSQ) function according to Burnham & Anderson (2002). In particular, the second-order AIC (AIC_c) was preferred, taking into account the small ratio between the sample size and the number of parameters to be estimated. The model with the smallest AIC_c value was selected as the best among the models tested (Haddon, 2001). According to Burnham & Anderson (2002), the AIC_c differences (Δ_i) were used to further verify if a model could explain the individual growth pattern. The AIC_c differences were computed over all candidate models as follows: $\Delta_i = AIC_{ci} - AIC_{cmin}$, where AIC_{ci} was the estimated AIC_c value for each candidate growth model *i* and AIC_{cmin} is the lowest AIC_c estimated. To quantify the plausibility of each model, given the data and the set of models, the Akaike weight (w_i) was estimated according to Burnham & Anderson (2002). The Akaike weight provides an effective way to scale and interpret the Δi values (Katsanevakis, 2006; Grueber *et al.*, 2011); it is considered as the weight of evidence in favour of model *i* being the best model currently of the available set of models.

A Student's *t*- test was used to test the significance of the differences between pairs of curves (e.g. Zar, 1984; González *et al.*, 1996; Triantafillos, 2004).

Relative growth rate (G, % of TW or ML day^{-1}) and absolute growth rate (AGR, g or mm day^{-1}) were calculated by 20-day age class as follows:

$$G = \frac{\ln R_2 - \ln R_1}{t_2 - t_2} * 100$$

$$AGR = \frac{R_2 - R_1}{t_2 - t_2}$$

where R_1 and R_2 are the body size (mantle length or total weight) respectively at the beginning (t_1) and at the end (t_2) of the time interval considered (20 days) (González *et al.*, 1996; Triantafillos, 2004). G and AGR for every length interval were compared by *t*-test.

Maturity and condition

To study the relative investment between somatic and gonad growth, the geometric mean regression (Model II) equations for ML-MW, ML-FW, ML-DGW, ML-gonad weight were calculated separately for males and females. From these equations, the residuals were estimated for each specimen and used as size-independent measure of tissue and somatic condition (Moltschaniwskyj & Semmens, 2000; García-Berthout, 2001; Green, 2001; Pecl, 2001; McGrath Steer & Jackson, 2004; Otero *et al.*, 2007; Ceriola & Jackson, 2010). The ML-gonad weight residuals were correlated with ML-FW residuals, ML-MW residuals, and ML-DGW residuals for each sex separately. This type of analysis can highlight possible trade-offs occurring between somatic and reproductive apparatus growth (Moltschaniwskyj & Semmens, 2000; Pecl, 2001; McGrath & Jackson, 2002; McGrath Steer & Jackson, 2004; Otero *et al.*, 2007; Ceriola & Jackson, 2010).

Results

Age and Growth

A total of 169 individuals were sampled from March to July 2006 (83 males, 80 females and 6 too small to be sexed) and they were all successfully aged (Table 1). Growth of *I. coindetii* was rapid and the life span was less than one year in both sexes. Females were generally larger (in ML) and lived relatively longer than males. Males were heavier than females at any size. Estimates of age ranged between 124 and 178 days for males and between 128 to 234 days for females. The back calculation of hatching date revealed continuous hatching from August to January, with an increase between November and December (Fig. 1).

Owing to the lack of any growth pattern in monthly cohorts (probably related to the small number of individuals), the age data were pooled together and only the distinction between sexes was considered in the analysis. There was a relatively small scatter in the ML-at-age plot, whilst the scatter was greater in the TW-at-age plot. The linear, power and exponential models described the size-at-age data relatively well (i.e. ML-at-age and TW-at-age) for both males and females. However, in both sexes the linear and exponential models provided the best fit for the ML- at-age and TW-at-age data respectively (Figs. 2 and 3; Tables 2 and 3).

Table 1. Descriptive statistics for *Illex coindetii* (March-July 2006). ML = dorsal mantle length; TW = total weight; s.d. = standard deviation

2006		**Males**	**Females**	**Unsexed**	**Total**
	N	83	80	6	169
ML (mm)	min	68	67	56	56
	max	156	210	71	210
	average	108.2	129.6	63.7	116.6
	s.d.	21.5	31.7	7.5	30.1
TW (g)	min	7.56	7.27	5.86	5.9
	max	170.7	235.0	8.8	235.0
	average	44.8	63.6	6.9	52.3
	s.d.	36.6	51.0	1.6	45.0
Age (days)	min	124	128	124	124
	max	178	234	134	234
	average	154.8	166.3	128.3	159.4
	s.d.	14.3	21.2	5.1	19.7

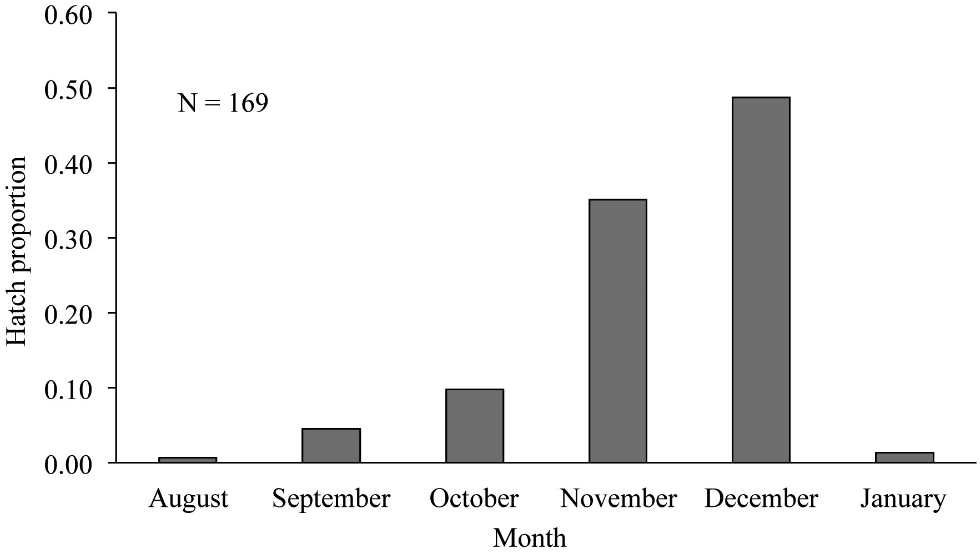

Fig. 1: Hatch date distribution of *Illex coindetii* from the south Adriatic Sea. N = number of specimens.

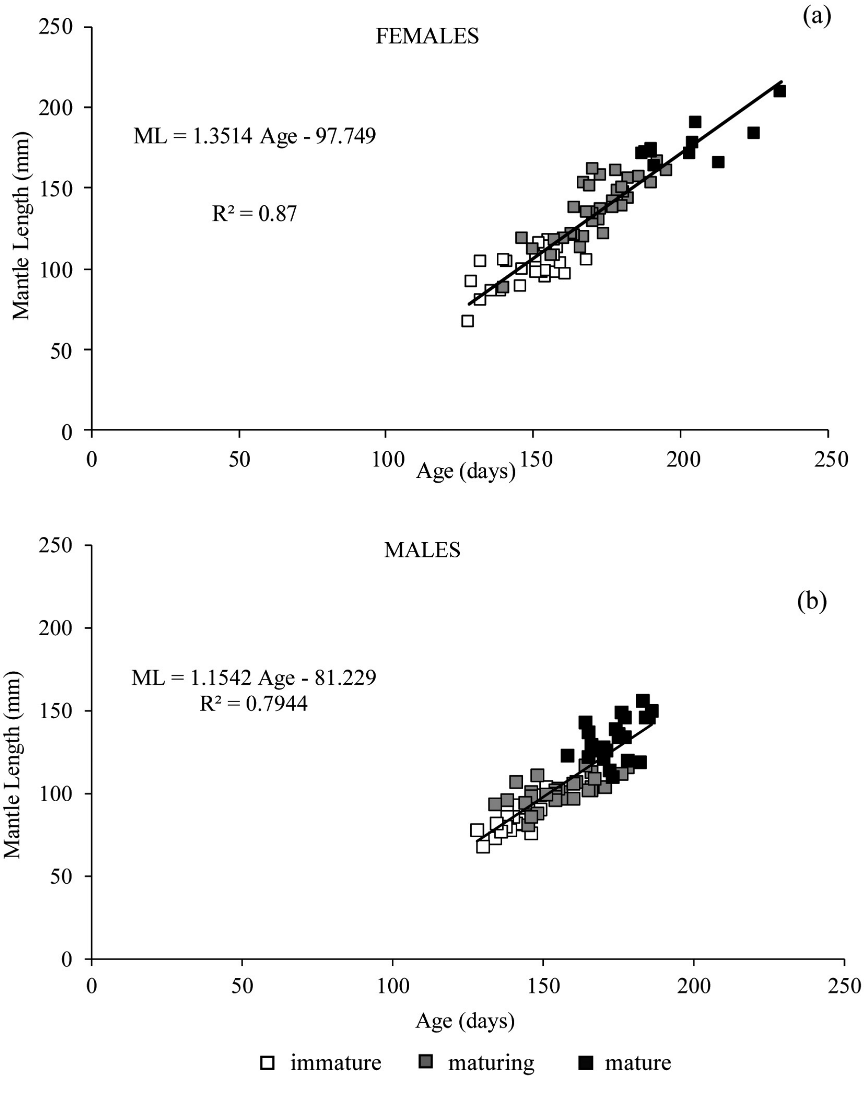

Fig. 2: Mantle length-at-age plots for immature (stages 1-2), maturing (stages 3-4) and mature (stages 5-6) female (a) and male (b) individuals of *Illex coindetii* from the south Adriatic Sea (March-June 2006).

G and AGR were generally greater in females than in males at all the age classes, with the exception of TW in the 160-179 day-old individuals (Fig. 4). In females, G decreased with age, with the greatest values (2.81% day^{-1} in ML and 6.99 % day^{-1} in TW) recorded in the 140-159 days age class. In terms of AGR, the greatest values for females were found in 160-179 days age class for ML (2.82 mm day^{-1}), and 200-219 days age class for TW (4.96 g day^{-1}). In males, G decreased in older individuals and peaked in the 160-179 days age class in both ML (1.96% day^{-1}) and TW (7.92% day^{-1}). The AGR in ML had the maximum (2.06 mm day^{-1}) in 160-179 days old specimens, but in TW it peaked (3.12 g day^{-1}) in 180-199 days age class.

Age-at-maturity was smaller in males than in females. The youngest mature male was 158 days old (123 mm ML). The youngest mature female was 187 days old (171 mm LM). The oldest immature male and females were 178 (116 mm ML) and 195 (160.5 mm ML) days old respectively.

Table 2. Parameter estimates and statistical response for the different models applied to the size-at-age data of *Illex coindetii* from the south Adriatic (March-July 2006). ML = dorsal mantle length; TW = total body weight; SE = standard error; CV = coefficient of variation. Bold underlined denotes the best model values.

Model	Parameter	Females ML			Females TW		
		Value	SE	CV	Value	SE	CV
	m_1	64.7	9.2	14.2	64.7	10.7	16.5
	μ	239.8	33.1	13.8	239.8	43.6	18.2
Schnute	g_1	-2.1E-03	-2.5E-04	12.1	-2.1E-03	-3.7E-04	18.1
	g_2	1.380	0.2	13.2	1.4	0.2	16.9
	m_∞	1122.1	218.8	19.5	1122.1	218.8	19.5
Gompertz	g_1	5.2E-03	7.3E-04	14.0	5.2E-03	1.1E-03	21.0
	γ	5.24	0.9	16.5	5.2	1.0	18.9
Exponential	m_0	19.540	3.8	19.4	***0.183***	***0.0***	***9.4***
	g_1	0.011	2.2E-03	20.2	***0.3E-02***	***2.2E-03***	***10.9***
Linear	***m_0***	***1.4***	***0.1***	9.5	1.5	0.3	19.9
	g_3	***-102.7***	***-10.3***	10.0	-202.0	-42.8	21.2
Power	m_0	2.3E-06	2.8E-07	11.9	2.3E-06	4.3E-07	18.6
	g_1	3.5	0.4	12.2	3.5	0.6	17.9

Model	Parameter	Males ML			Males TW		
		Value	SE	CV	Value	SE	CV
	m_1	85.0	14.1	16.6	7.0	1.1	16.4
	μ	230.9	37.2	16.1	149.9	19.8	13.2
Schnute	g_1	-4.4E-03	-7.6E-04	17.4	0.361	6.9E-02	19.2
	g_2	1.9	0.3	14.1	-7.7	-1.2	15.2
	m_∞	910.8	153.0	16.8	1.5E+06	2.0E+05	13.1
Gompertz	g_1	5.6E-03	8.5E-04	15.1	4.6E-03	6.8E-04	14.9
	γ	5.2	0.9	16.5	22.0	2.5	11.5
Exponential	m_0	15.7	2.4	15.1	***2.0E-02***	***0.0***	***10.1***
	g_1	1.2E-02	2.0E-03	16.2	***4.7E-02***	***5.2E-03***	***11.0***
Linear	***m_0***	***1.2***	***0.1***	***12.1***	1.2	0.2	17.3
	g_3	***91.9***	***11.9***	***12.9***	-148.9	-31.6	21.2
Power	m_0	1.8E-02	3.3E-03	18.3	2.8E-14	4.4E-15	15.7
	g_1	1.7	0.3	17.1	6.8	1.5	21.8

Table 3. Parameters for growth model selection for *Illex coindetii* from the south Adriatic (March-July 2006). N. parameters = number of parameters in the model; ML = dorsal mantle length; TW = total body weight; AIC_c = second order Akaike's information criterion; Δ_i = AIC_c difference; w_i = Akaike weight.

Sex	**Model**	**Schnute**	**Gompertz**	**Exponential**	**Linear**	**Power**
	N. parameters	**4**	**3**	**2**	**2**	**2**
FEMALES ML	AIC_c	-343.44	-340.9	-330.8	-374.7	-344.3
	Δ_i	31.3	33.8	43.9	0.0	30.4
	w_i	0.000	0.000	0.000	1.000	0.000
FEMALES TW	AIC_c	-181.34	-178.59	-187.71	-171.46	-116.64
	Δ_i	6.37	9.12	0.00	16.26	71.08
	w_i	0.736	0.186	0.073	0.005	0.000
MALES ML	AIC_c	-340.62	-357.47	-357.85	-360.88	-317.76
	Δ_i	20.3	3.4	3.0	0.0	43.1
	w_i	0.000	0.13	0.16	0.74	0.000
MALES TW	AIC_c	-155.76	-152.76	-161.18	-141.63	-112.57
	Δ_i	5.43	8.42	0.00	19.56	48.61
	w_i	0.093	0.049	0.736	0.000	0.000

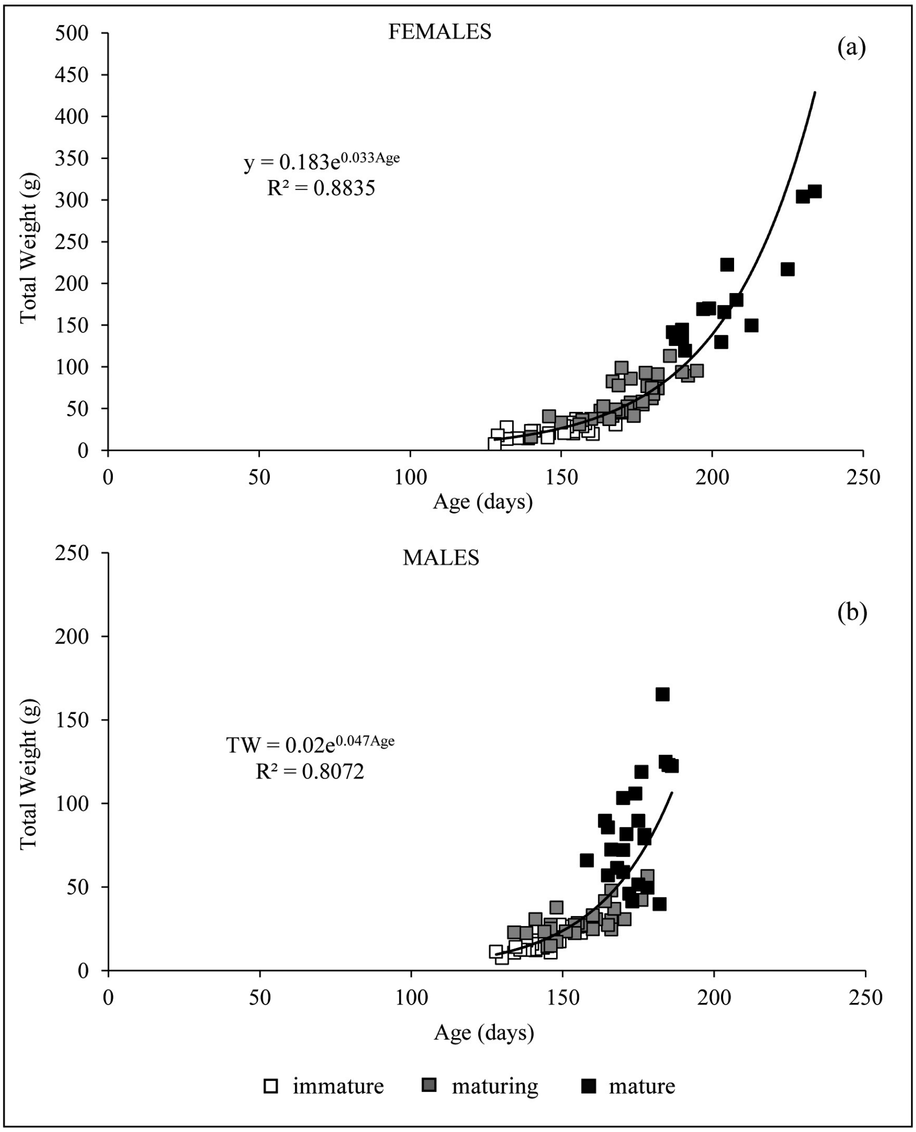

Fig. 3: Total weight-at-age plots for female (a) and male (b) individuals of *Illex coindetii* from the south Adriatic Sea (March-June 2006).

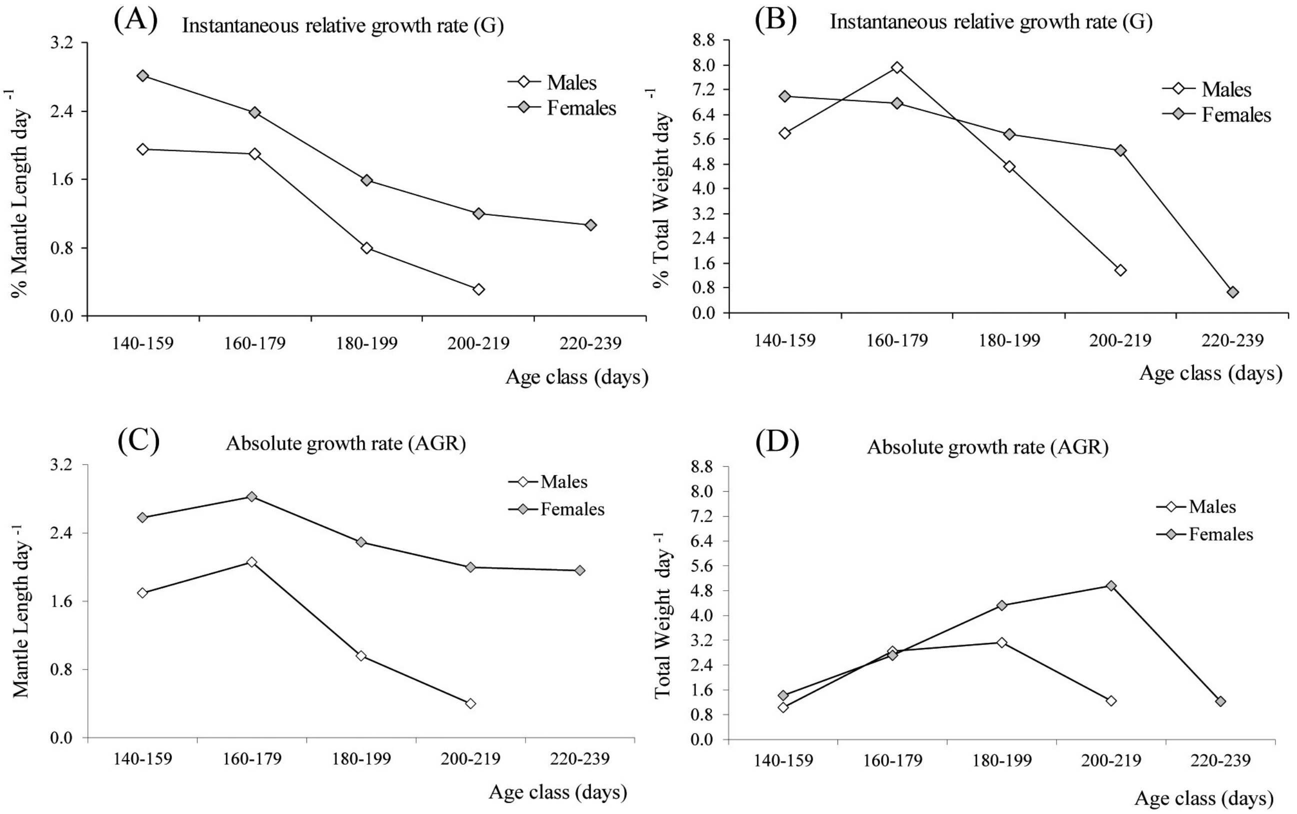

Fig. 4: Instantaneous relative growth rate G, % of TW or of ML day^{-1}(a, b) and Absolute Growth Rate AGR, g or mm day^{-1}(c, d) for male and female individuals of *Illex coindetii* from the south Adriatic Sea (March-June 2006).

Maturity and Condition

The mantle length, total weight and relative mantle weight and fin weight increased up to stage 6 animals in both sexes, even if in males growth from stages 5 and 6 was relatively low (Figs. 5, 6). The nidamental glands, ovary and oviduct relative weight increased up to stage 5 females but decreased in stage 6. Relative weight of oviducal glands increased up to the latest maturity stage. The relative ovary weight increased from stage 3 to stage 5 (with some ovaries exceeding 20 g absolute weight) and then dropped by 95 % from stage 5 to stage 6 animals. The absolute weight of the oviduct was relatively low in stages 3 and 4 (<1 g), but increased in stage 5 females (in some cases exceeding 3.5 g). The increase observed was due to the large number of eggs packed into the oviduct in all the stage 5 females. The absolute oviduct weight never exceeded the absolute ovary weight (maximum oviduct weight = 3.5 g, maximum ovary weight = 26.8 g in an animal of 190 mm DML). Digestive gland weight peaked in stage 4 individuals and dropped in stage 6 females.

In males, the relative weight of reproductive organs increased up to stage 5 and decreased in stage 6. The absolute testis weight exceeded 3g in stage 5 individuals and decreased of 93 % in stage 6. The PSC weight followed the same pattern with a decrease of 98 % from stage 5 to stage 6 individuals. The relative weight of the digestive gland increased up to stage 5 individuals and dropped in stage 6 males.

The GSI increased with maturation in both sexes. The greatest values were found in females, but GSI values never exceeded 15 % (Fig. 7). The mean GSI for mature females was 7.3 % with minimum and maximum values of 1.6 and 12.2 % respectively. In mature males the mean GSI was 4.1 %, with values ranging from 2.4 % to 5.1 %.

There was a significant linear relationship between gonad weight and body size in both sexes for maturing and mature individuals ($p < 0.01$, significance level tested according to Pearson's correlation coefficient) (Fig. 8). The geometric-mean (type II) regressions between ML and gonad, mantle, fin and digestive gland weight highlighted strong correlations between variables in both sexes except for the ML-DGW regression that was relatively weaker (Table 4) ($r^2 = 0.66$). There was no relationship between the ML-GW residuals and ML-MW, ML-FW, ML-DGW residuals (graphs not included). Accordingly, no trade-off between somatic organs, or digestive glands with gonad development was found. No evidence was observed that feeding ceased in maturing and mature individuals and food was found in stomachs at all the maturity stages, even if half of spent animals were found with empty stomachs. There was a positive relationship between ML-MW and ML-FW residuals in males ($n = 81$, $r = 0.55$, $p < 0.01$) and females ($n = 78$, $r = 0.72$, $p < 0.01$).

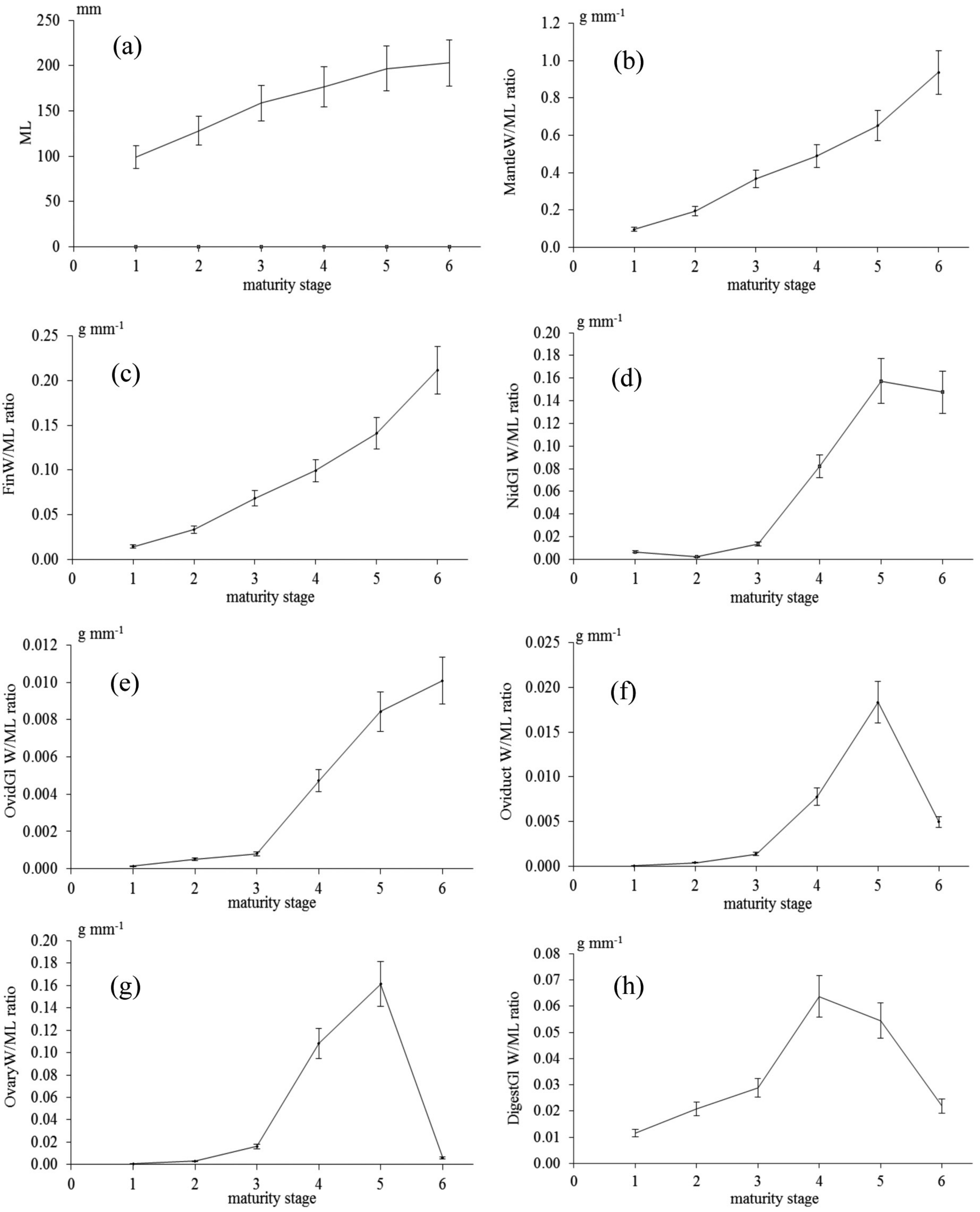

Fig. 5: Change in mean mantle length (a) and relative weight of selected organs with maturity stage for female individuals of *Illex coindetii* off the south Adriatic Sea: mantle (b); fin (c); nidamental gland (d); oviducal gland (e); oviduct (f); ovary (g); digestive gland (h). ML = dorsal mantle length; MantleW = mantle weigh; FinW = NidGl W = nidamental gland weight; OvidGl W = oviducal gland weight; Oviduct W = oviduct weight; OvaryW = ovary weight; DigestGlW = Digestive gland weight.

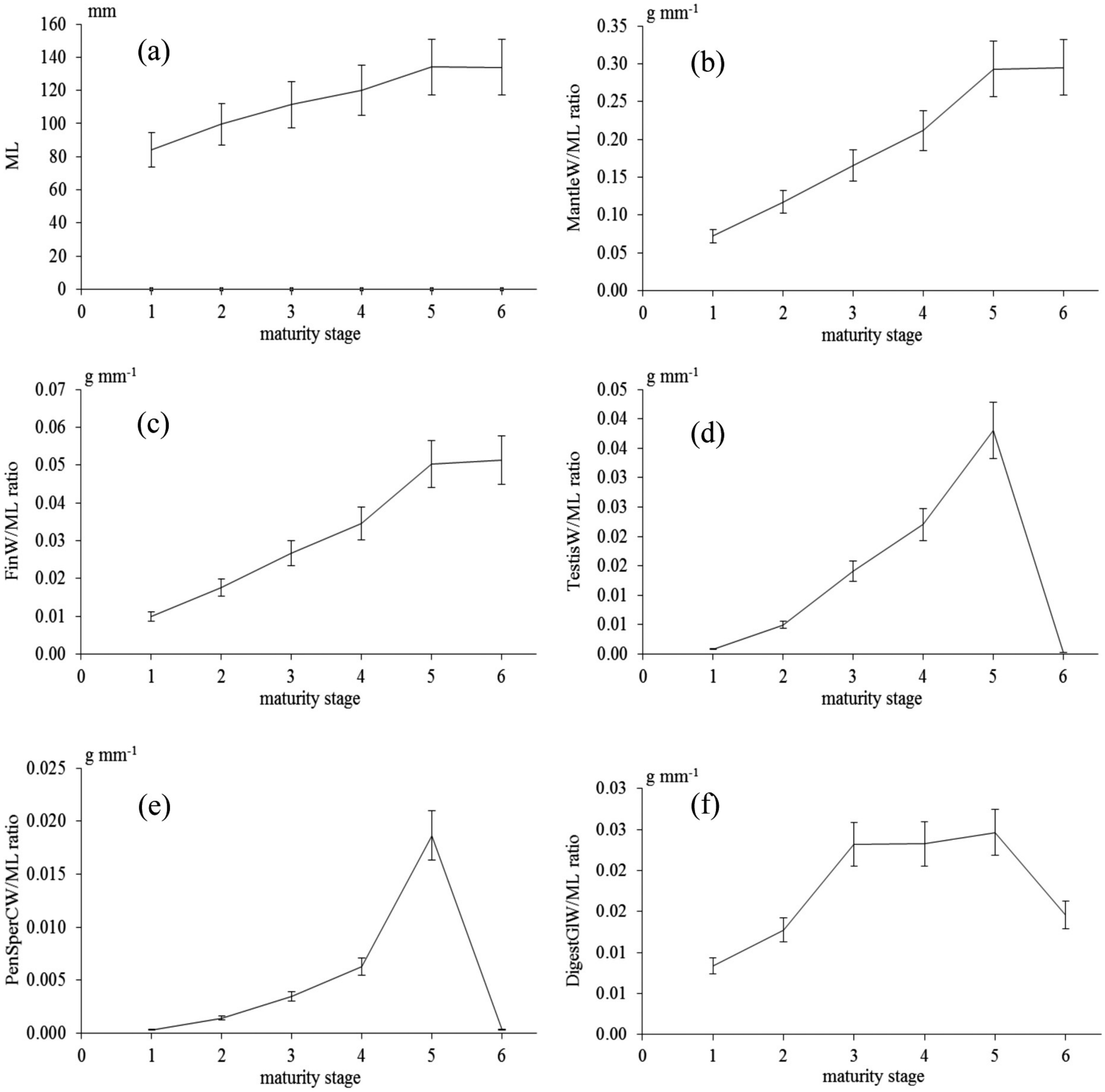

Fig. 6: Change in mean mantle length (a) and relative weight of selected organs with maturity stage for male individuals of *Illex coindetii* off the south Adriatic Sea: mantle (b); fin (c); testis (d); other sexual apparatus (e); digestive gland (f). ML = mantle length; MantleW = mantle weight; FinW = fin weight; TestisW = testis weight; PenSperCW = penis plus spermatophoric complex weight; DigestGlW = Digestive gland weight.

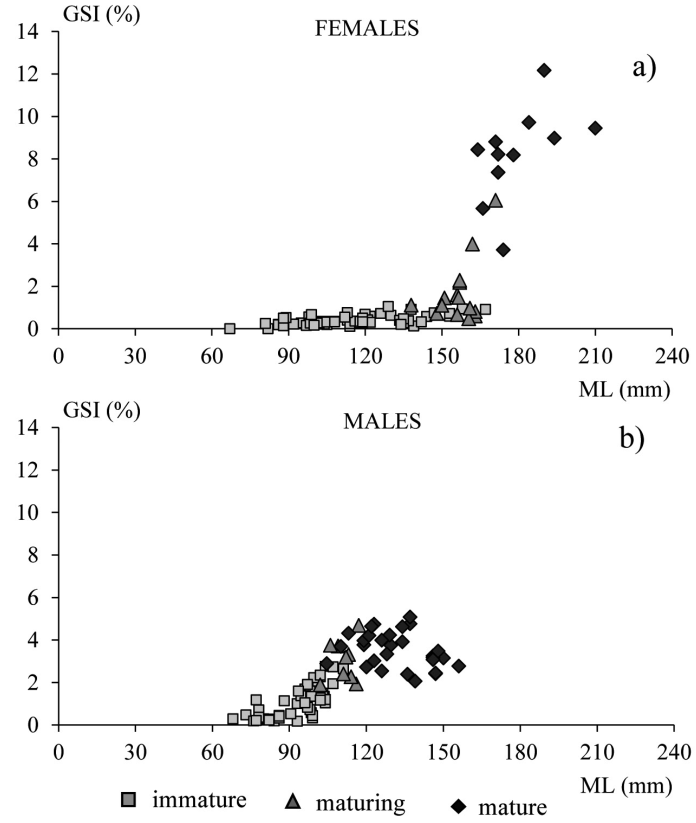

Fig. 7: Gonadosomatic index (GSI) values for mantle length and maturity stages for female (a) and male (b) individuals of *Illex coindetii* in the south Adriatic Sea.

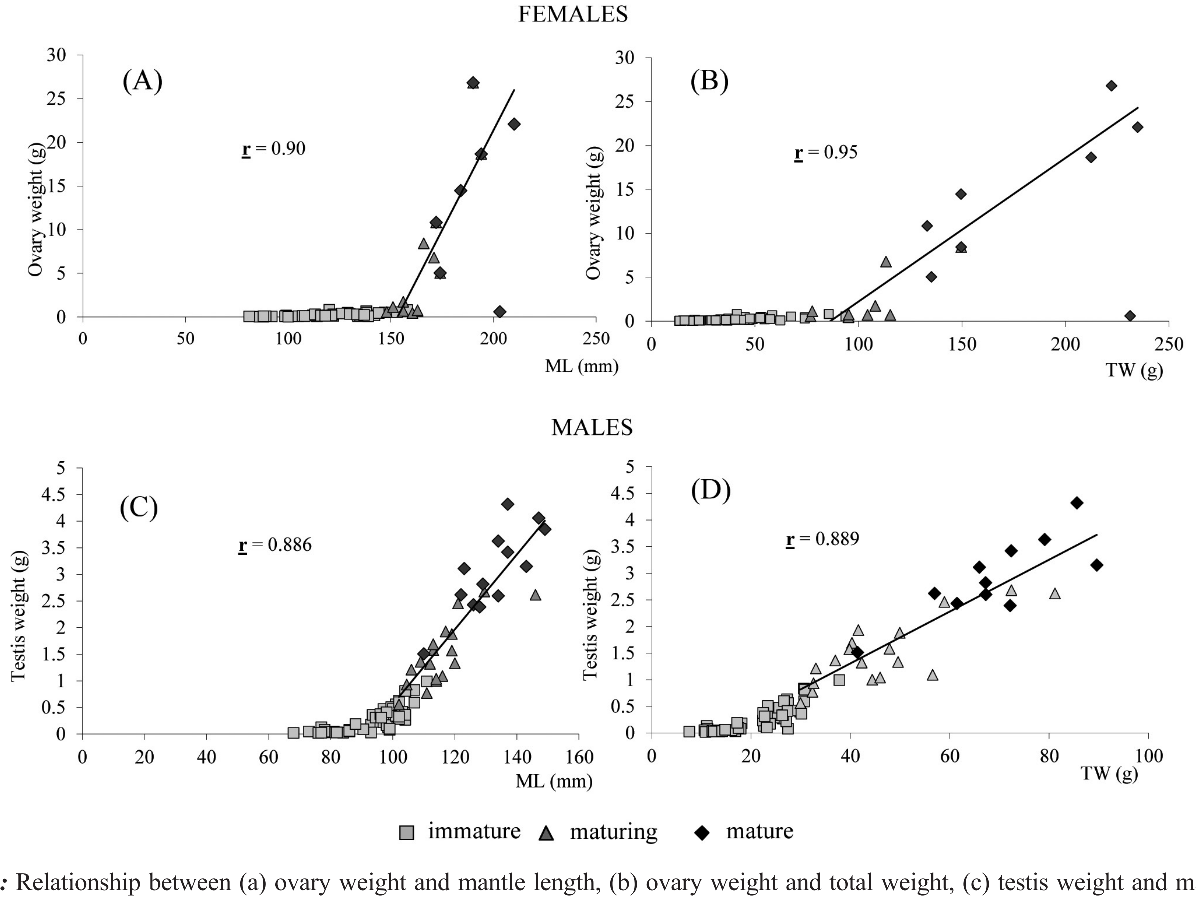

Fig. 8: Relationship between (a) ovary weight and mantle length, (b) ovary weight and total weight, (c) testis weight and mantle length and (d) testis weight and total weight for immature, maturing and mature individuals of *Illex coindetii*. Linear regression was tested for maturing and mature specimens only. r = Pearson's correlation coefficient (bold underlined **r**, denote significance at 0.01).

Table 4. Parameters of the geometric mean regressions between dorsal mantle length and the weights of the ovary (ML-OW), testits (ML-TstW), entire gonad apparatus (ML-GW), mantle (ML-MW), fins (ML-FW), and digestive gland (ML-DGW) for individuals of *Illex coindetii* in the Southern Adriatic (March-July 2006).

Linear regression	Females			
	Intercept	**Slope**	**Confidence interval**	**r^2**
ML - OW	-14.36	6.51	6.16-6.96	0.78
ML - GW	-15.34	7.15	6.83-7.5 5	0. 84
ML - MW	-4.55	2.77	2.71 -2.83	0.97
ML - FW	-6.58	3.36	3.31-3.43	0.97
ML - DGW	-6.60	3.32	3.15-3.51	0.82
	Males			
Linear regression	**a**	**B**	**Confidence interval**	**r^2**
ML - TstW	-15.59	7.54	7.14-8.14	0.75
ML - GW	-15.77	7.70	7.35-8.25	0.79
ML - MW	-4.90	2.95	2.93-3.05	0.97
FW- MW	-6.80	3.49	3.47-3.59	0.98
ML - DGW	-6.40	3.25	3.04-3.58	0.66

Discussion

Age and growth

This study provides the first description of the life history and growth of *Illex coindetii* in the Adriatic Sea contributing to the knowledge on the biology of this species. In a previous study on *I. coindetii*, Ceriola *et al.* (2006) found individual size and size-at-maturity smaller in the southern Adriatic Sea with respect to the Galician waters and Catalan Sea, but comparable to the Sicily Channel and central Tyrrhenian Sea (Jereb & Ragonese, 1995; González *et al.*, 1996; Sánchez *et al.*, 1998; Arkhipkin *et al.*, 2000; Gentiloni *et al.*, 2001). In further work on the south Adriatic *I. coindetii* population, a decrease in the average individual size from 1996 to 2004 was found, suggesting that this species was adapting to local "environmental" conditions by progressively shortening the life span and increasing growth rate (Ceriola *et al.*, 2007). This study confirms that *I. coindetii* in the southern Adriatic Sea has a comparable life span (< 9 months) to the Sicily Channel (Arkhipkin *et al.*, 2000), but lives less and grows faster than in the north western Mediterranean Sea (12-18 months, Sánchez, 1995) and in the Galician waters (13-15 months, González *et al.*, 1996). These findings agree with the positive relationship found between life span and latitude in oegopsin squids reported by Arkhipkin (2004). The recorded differences in life span are reflected in terms of individual size. In spite of the faster growth rate, *I. coindetii* in the Adriatic Sea is considerably smaller and matures earlier than in Galician waters (maximum size 390 mm ML for females and 279 mm ML for males) and in western Mediterranean areas (Sánchez *et al.*, 1998; Relini *et al.*, 1999; Arkhipkin *et al.*, 2000; Gentiloni *et al.*, 2001; Ceriola *et al.*, 2006). The local environmental conditions (including sea water temperature and fishery exploitation) and the high plasticity in growth and maturation are likely to be the main causes of the differences between the populations of *I. coindetii* described. Sea water surface temperature (SST) is generally lower during the spawning/hatching peak of *I. coindetii* (May-July period, for review see Sánchez *et al.*, 1998) in the Catalan Sea (2001-2007, SST range 18.3-19.4°C, average SST = 19.1°C) and Galician waters (2001-2007, SST range15.1-17.0°C, average SST = 15.9°C) with respect to the south Adriatic Sea (2001-2007, SST range 22.0-24.1°C, average SST = 22.6°C) (monthly data on the sea surface temperature through the POET interactive on-line system, http://podaac.jpl.nasa.gov). Warmer water generally induces a faster growth rate in squids and in *I. coindetii* leads to populations with a shorter life span and smaller adult size (Arkhipkin, 1996; González *et al.*, 1996; Sánchez *et al.*, 1998; Arkhipkin *et al.*, 2000; Ragonese *et al.*, 2002; Forsythe, 2004). Pecl & Jackson (2008) provided some evidences that warm-water squids would have smaller hatchlings with a shorter life span and smaller adult size even where there is an accelerated growth rate. In addition, the high fishing pressure characterising the Adriatic Sea (Mannini *et al.*, 2005) may have a role in affecting the individual size of *I. coindetii* in the Adriatic Sea (Murphy & Rodhouse, 1999; Gentiloni *et al.*, 2001; Ceriola *et al.*, 2006).

In terms of growth, the linear model for mantle length-at-age and the exponential model for total weight-at-age provided the best fit to the data. However, in none of the four cases considered (i.e. ML- TW-at age data for males and females) the best model was strongly supported as a 'clear winner' (with $w_i > 90\%$). In each case, there was at least one additional model that was also supported by the data. Linear growth for mantle length-at-age data was reported for *I. coindetii* in the Galician waters (González *et al.*, 1996) and in the Tyrrhenian Sea (Cavanna *et al.*, 2008). However, in Galician waters the power model best described the weight-at-age data (González *et al.*, 1996). Asymptotic functions were also used to describe growth in *I. coindetii* (Ragonese *et al.*, 2002; Arkhipkin & Roa-Ureta, 2005) and the identification of the form of growth in this species and in teuthoids in general is still an actively debated matter (e.g. Guerra *et al.*, 2010).

By comparing the growth between sexes, females *I. coindetii* generally showed faster growth rate and longer life span than males (González *et al.*, 1996; Sánchez *et al.*, 1998; Arkhipkin *et al.*, 2000). This feature was confirmed also in the southern Adriatic Sea in terms of ML-at-age, but was less evident in terms of TW-at-age. Moreover, weight of females increased faster towards the end of life. The morphometric changes occurring during the gonad maturation induce a positive length-weight relationship allometric in males and isometric in females (Belcari, 1996; Ceriola *et al.*, 2006). These changes are probably reflected in the size-at-age data and affect the growth in weight of old and mature individuals of the two sexes.

The back calculation of the hatch date revealed continuous spawning for *I. coindetii* in the south Adriatic during autumn and winter, with an increase between November and December. These findings, together with those reported by Ceriola *et al.* (2006) on the spawning of *I. coindetii* in the same region (i.e. continuous spawning in spring and summer with a considerable peak during spring), indicate year-round spawning with peaks in spring and late autumn. This behaviour confirms for the southern Adriatic Sea, a feature already described in other regions (for reviews see e.g. Relini *et al.*, 1999; Sánchez *et al.*, 1998; Arkhipkin *et al.*, 2015; Jereb *et al.*, 2015a). Taking into account the data on age-at-maturity of both sexes, the 'reproductive' period of *I. coindetii* (including maturation and spawning) covers approximately the final third of the entire life span, as already observed in previous works on this species (González & Guerra, 1996; González *et al.*, 1996).

Maturity and Condition

In agreement with the bias arising from the relatively low number of specimens sampled, only preliminary information on the reproductive strategy of *I. coindetii* in south Adriatic Sea is given. Jackson & Mladenov (1994) suggested that there is likely a continuum of reproductive strategies among cephalopods from single spawning to multiple spawning species. Rocha *et al.* (2001) described *I. coindetii* as an intermittent terminal spawning species, with behaviour more similar to a multiple than to a single spawning species. Although preliminary, the results of this study agree with the conclusions of Rocha *et al.* (2001). Males and females of *I. coindetii* displayed a regression in testis and ovary-oviduct weight in the latest maturity stage, whilst the growth of other somatic and, in females, reproductive organs continued. In mature females of terminal spawning squids, the oviduct/s exceeds the ovary weight before spawning and GSI values reach 50% (Harman *et al.*, 1989; Ikeda *et al.*, 1993; Moltschaniwskyj, 1995; Pecl, 2001; McGrath & Jackson, 2002; Jackson *et al.*, 2004). In *I. coindetii* specimens examined in this study, the oviduct weight never exceeded the ovary weight and GSI values were also relatively low in both sexes.

The increase in mantle, fin and gonad weight suggests that in *I. coindetii* there is no transfer of energy from the mantle or fins to support the maturation process (e.g. Moltschaniwskjy & Semmens, 2000; Semmens, 2002). Furthermore, the lack of correlation between digestive gland weight and gonad weight suggests that lipid reserves are not directly diverted from this organ to fuel the gonad maturation process. These preliminary results agree with the findings of Rosa *et al.* (2005) that *I. coindetii* takes energy for egg production directly from food. Overall, the information outlined in this study, although not conclusive, contributes to improving knowledge on the biology of *I. coindetii*, thus adding a further piece to the information necessary to plan management for multi-species demersal fisheries in the Adriatic Sea.

Acknowledgements

This study was part of the first author's PhD programme supported by Regione Puglia (Italy). Many thanks are due to Professor F. Toteda, to Professor G. Vonghia of the Department of Animal Production of the University of Bari and to Professor G. Marano of the Laboratory of Marine Biology of Bari for their support during the fieldwork that made the preparation of this paper possible. Statolith analysis was performed thanks to the kind hospitality of Professor G. De Metrio of the Department of Animal Health and Wellbeing of the University of Bari. Many thanks are also due to Ms Caroline Bennett (www.select.translations.com) for the proofreading. The authors would like to thank the two anonymous referees for their useful comments on the submitted draft of this paper.

References

Arkhipkin, A.I., 1996. Geographical variation in growth and maturation of the squid *Illex coindetii* (Oegopsida, Ommastrephidae) off the North-West African coast. *Journal of the Marine Biological Association of the United Kingdom*, 76, 1091-1106.

Arkhipkin, A.I., 2004. Diversity in growth and longevity in short-lived animals: squids of the suborded Oegopsina. *Marine and Freshwater Research*, 54, 341-355.

Arkhipkin, A.I., 2005. Statoliths as 'black boxes' (life recorders) in squids. *Marine and Freshwater Research*, 56, 573-583.

Arkhipkin, A.I., Jereb, P., Ragonese, S., 2000. Growth and maturation in two successive seasonal groups of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). *ICES Journal of Marine Sciences*, 57, 31-41.

Arkhipkin, A.I., Roa-Ureta, R., 2005. Identification of ontogenetic growth models for squids. *Marine and Freshwater Research*, 56, 371-386.

Arkhipkin, A.I., Rodhouse, P.G.K., Pierce, G.J., Sauer, W., Sakai, M. *et.al*., 2015. World squid fisheries. *Reviews in Fisheries Science & Aquaculture*, 1-161.

Belcari, P., 1996. Length-weight relationship in relation to sexual maturation *of Illex copindetii* (Cephalopoda: Ommastrephidae) in the Northern Tyrrhenian Sea (Western Mediterranean). *Scientia Marina*, 60 (2-3), 379-384.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference: A practical information-theoretic approach. Second ed. Springer, New York, 488 pp.

Cavanna, P., Lanteri, L., Beccorna, E., Relini, G., 2008. Growth of *Illex coindetii* (Verany, 1839) and *Todaropsis eblanae* (Ball, 1841) in the Ligurian Sea. *Biologia Marina Mediterranea*, 15, 320-321.

Ceriola, L., Milone, N., 2008. Cephalopods Age Determination by Statoliths Reading: a Technical Manual. Scientific Cooperation to Support Responsible Fisheries in the Adriatic Sea. *GCP/RER/010/ITA/TD-22. AdriaMed Technical Documents*, 22, 82 pp.

Ceriola, L., Jackson, G.D., 2010. Growth, hatch size and maturation in a southern population of the loliginid squid *Loliolus noctiluca*. *Journal of the Marine Biological Association of the United Kingdom*, 90, 755-767.

Ceriola, L., Ungaro, N., Toteda, F., 2006. Some information on the biology of *Illex coindetii* Verany, 1839 (Cephalopoda, Ommastrephidae) in the South-Western Adriatic Sea (Central Mediterranean). *Fisheries Research*, 82, 41-49.

Ceriola, L., Ungaro, N., Toteda, F., 2007. A "Traffic" Light approach for the assessment of the Broadtail shortfin squid *Illex coindetii* Verany, 1839 in the Southern Adriatic Sea (Central Mediterranean). *Reviews in Fish Biology and Fisheries*, 17, 145-157.

Ceriola, L., Accadia, P., Mannini, P., Massa, F., Milone, N. *et.al*., 2008. A bio-economic indicators suite for the appraisal of the demersal trawl fishery in the Southern Adriatic Sea (Central Mediterranean). *Fisheries Research*, 92, 255-267.

FAO, 2014. Fisheries and aquaculture software. FishStatJ (2.11.4) – A tool for fishery statistics analysis. FAO Fisheries and Aquaculture Department [online]. Rome, 2014. http://www.fao.org/fishery/statistics/software/fishstatj/en

Forsythe, J.W., 2004. Accounting for the effect of temperature on squids growth in nature: from hypothesis to practice. *Marine and Freshwater Research*, 55, 331-339.

García-Berthou, E., 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology*, 70, 708-711.

Gentiloni, P., Agnesi, S., Gargiulo, C., Belluscio, A., Ardizzone, G.D., 2001. Dati sulla distribuzione e biologia del cefalopode *Illex coindetii* (Verany, 1839) nel Mar Tireno Centrale. *Biologia Marina Mediterranea*, 8, 715-719.

González, Á.F., Castro, B.G., Guerra, Á., 1996. Age and Growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. *ICES Journal of Marine Sciences*, 53, 802-810.

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

Green, A.J., 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology*, 82, 1473-1483.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolution Biology*, 24, 699-711.

Guerra, Á., Allcock, L., Pereira, J., 2010. Cephalopod life history, ecology and fisheries: An introduction. *Fisheries Research*, 106, 117-124.

Haddon, M., 2001. Modeling and quantitative methods in fisheries. First ed. Chapman-Hall, Florida, 406pp.

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

Ikeda, I., Sakurai, Y., Shimazaki, K., 1993. Maturation process of the Japanese common squid *Todarodes pacificus* in captivity. 179-187. In: *Recent advances in cephalopod fishery biology.* Okutani, T., O'Dor, R.K., Kubodera, T. (Eds.). Tokai University Press, Tokyo.

Jackson, G.D., 1994. Application and future potential of statolith increment analysis in squids and sepioids. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 2612-2625.

Jackson, G.D., Mladenov, P.V., 1994. Terminal spawning in the deepwater squid *Moroteuthis igens* (Cephalopoda: Onychoteuthidae). *Journal of Zoology* (London), 234, 189-201.

Jackson, G.D., Semmens, J.M., Phillips, K.L., Jackson, C.H., 2004. Reproduction in the deepwater squid *Moroteuthis ingens*, what does it cost? *Marine Biology*, 145, 905–916.

Jereb, P., Ragonese, S., 1995. An outline on the biology of the squid *Illex coindetii* in the Sicilian Channel (Central Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, 75, 373-390.

Jereb, P., Koutsoubas, D., Belcari, P., Pierce, G.J., Villanueva, R. *et. al*., 2015a. *Illex coindetii*, in: Jereb, P., Allcock, A.L., Lefkaditou, E., Piatkowski, U., Hastie, L.C. *et.al*., 2015. (Eds.), Cephalopod biology and fisheries in Europe: II e. *ICES Cooperative Research Reports*, 303, 177-192.

Jereb, P., Allcock, A.L., Lefkaditou, E., Piatkowski, U., Hastie, L.C. *et. al.* (Eds.) 2015b. Cephalopod biology and fisheries in Europe: II. Species Accounts. ICES Cooperative Research Report No. 325. 360 pp.

Katsanevakis, S., 2006. Modelling fish growth: Model selection, multi-model inference and model selection uncertainty. *Fisheries Research*, 81, 229-235.

Lipinski, M., 1979. Universal maturity scale for the commercially important squids (Cephalopoda: Teuthoidae). The results of the maturity classification of the *Illex illecebrosus* (LeSeur, 1821) population for year 1973 - 77. ICNAF Research Document. 79/II/38.

Mannini, P., Massa, F., Milone, N., 2005. Adriatic Sea fisheries: outline of some main facts. Studies and Reviews. *FAO General Fishery Commission for the Mediterranean*, 78, 124-143.

McGrath, B.L., Jackson, G.D., 2002. Egg production in the arrow squid *Nototodarus gouldi* (Cephalopoda: Ommastrephidae), fast and furious or slow and steady? *Marine Biology*, 141, 699-706.

McGrath Steer, B.L., Jackson, G.D., 2004. Temporal shifts in the allocation of energy in the arrow squid, *Nototodarus gouldi*: sex-specific responses. *Marine Biology* 144, 1141-1149.

Moltschaniwskyj, N.A., 1995. Multiple spawning in the tropical squid *Photololigo* sp.: what is the cost in somatic growth? *Marine Biology*, 124, 127-135.

Moltschaniwskyj, N.A., Semmens, J., 2000. Limited use of stored energy reserves for reproduction by the tropical loliginid squid *Photololigo* sp. *Journal of Zoology (London)*, 251, 30-313.

Murphy, E.J., Rodhouse, P.G., 1999. Rapid selection effects in a short-lived semelparous squid species exposed to exploitation: inferences from the optimisation of life-history functions. *Evolutionary Ecology*, 13, 517–537.

Otero, J., González, Á.F., Sieiro, M.P., Guerra, Á., 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. *Fisheries Research*, 85, 122-129.

Payne, A.G., Agnew, D.J., Pierce, G.J., 2006. Trends and assessment of cephalopod fisheries. Proceedings of the CEPHSTOCK Cephalopod Assessment Workshop, Imperial College, London, United Kingdom, 30–31 August 2004. *Fisheries Research*, 78, 1-3.

Pecl, G., 2001. Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. *Marine Biology*, 138, 93-101.

Pecl, G.T., Jackson, G.D., 2008. The potential impacts of climate change on inshore squid: biology, ecology and fisheries. *Reviews in Fish Biology and Fisheries*, 18, 373-385.

Pierce, G.J., Portela, J.M., Robin, J.-P. (Eds.), 2005. Environmental effects on cephalopod life history and fisheries. *Aquatic Living Resources*, 18, 325-400.

Quinn, TJ II, Deriso, R., 1999. Quantitative fish dynamics. First ed. Oxford University Press, Oxford, 542 pp.

Ragonese, S., Jereb, P., Dawe, E., 2002. A comparison of growth performance across the squid genus *Illex* (Cephalopoda, Ommastrephidae) based on modelling weight-at-length and age data. *Journal of Shellfish Research*, 21 (2), 851-860.

Relini, G., Bertrand, J., Zamboni, A. (Eds), 1999. Synthesis of the knowledge on bottom fishery resources in Central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea*, 6, 715-720.

Rocha, F., Guerra, Á., González, Á.F., 2001. A review of reproductive strategies in cephalopods. *Biological Reviews*, 76, 291-304.

Rosa, R., Costa, P.R., Bandarra, N., Nunes, M.L., 2005. Changes in tissue biochemical composition and energy reserves associated with sexual maturation in the Ommastrephid squids *Illex coindetii* and *Todaropsis eblanae*. *Biological Bulletin*, 208, 100-113.

Sánchez, P., 1995. Age and growth of *Illex coindetii*. *ICES Marine Sciences Symposium*, 1994, 441-444.

Sánchez, P., González, Á.F., Jereb, P., Laptichovsky, V.V., Mangold, K. *et. al*., 1998. *Illex coindetii*, in: Rodhouse, P.G., Dawe, E.G., O'Dor, R.K. (Eds.), Squid recruitment dynamics: the commercial *Illex* species. FAO *Fisheries Technical Paper*, 376, Rome, FAO, pp. 59-76.

Semmens, J.M., 2002. Changes in the digestive gland of the loliginid squid *Sepioteuthis lessoniana* (Lesson 1830) associated with feeding. *Journal of Experimental Marine Biology and Ecology*, 274, 19-39.

Triantafillos, L., 2004. Effects of genetic and environmental factors on growth of southern calamari, *Sepioteuthis australis*, from southern Australia and Northern New Zealand. *Marine and Freshwater Research*, 55, 439-446.

Villanueva, R., Moltschaniwskyj, N.A., Bozzano, A., 2007. Abiotic influences on embryo growth: statoliths as experimental tools in the squid early life history. *Reviews in Fish Biology and Fisheries*, 17, 101-110.

Zar, J.H., 1984. Biostatistical Analysis. Prenitce-Hall: Englewood Cliffs, NJ. USA, 718 pp.