A COMPARISON OF THE FISHERY BIOLOGY OF THREE *ILLEX COINDETII* VÉRANY, 1839 (CEPHALOPODA: OMMASTREPHIDAE) POPULATIONS FROM THE EUROPEAN ATLANTIC AND MEDITERRANEAN WATERS

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ABSTRACT

Three populations of the short-finned squid *Illex coindetii* were simultaneously sampled and studied from the Southern Celtic Sea and Bay of Biscay, Portuguese waters and Greek Seas, during a EU funded project (FAIR CT 1520). Dorsal mantle length (DML) ranged from 24 mm to 360 mm and body weight (BW) from 2.4 g to 1630 g. Modal progression analysis (MPA) indicated a female life span of 13–18 mo and in male life span of 11 mo. Length-weight relationship was found to be positively allometric for males and negatively allometric for females in all three populations. Sex ratio did not differ significantly from 1:1 over the entire sampling period. Differences among the three populations were observed for the following life-cycle parameters: (1) males from the Portuguese waters had significantly different length-weight slopes from those from the remainder areas; (2) size at full recruitment was determined at 110 mm in females from the Portuguese waters whereas in females from the Southern Celtic Seas and Bay of Biscay and from the Greek Seas was 170 mm; (3) female recruitment peaks were recorded only during autumn in samples from the Southern Celtic Sea and Bay of Biscay while in those from the Portuguese waters and the Greek Seas the recruitment peaks were recorded at various seasons; (4) maturing and mature males were found abundantly over the entire sampling period in the samples from the Southern Celtic Sea and Bay of Biscay and the Greek Seas whereas in those from the Portuguese waters maturing and mature males were at higher percentages than immature ones only during spring and summer; peaks of the Gonadosomatic index, calculated for mature females from the Southern Celtic Sea and Bay of Biscay, were scored from February to April of 1998 and 1999 and during September of 1998 while in the samples from the Greek waters during April and August 1998 and during January and May 1999; (5) L50 (mantle length at which 50% of the individuals are mature) values estimated for both females and males from the three studied areas were gradually decreased from the North Atlantic to the Mediterranean; (6) length data suggest that females from the Greek Seas potentially mature at two modal sizes while those from the remainder areas show only one modal size at maturity. Environmental variables (sea surface temperature and chlorophyll-*a* concentration) were correlated with some of the biological indices of the *I. coindetii* populations. Finally, results on biological indices of the *I. coindetii* are compared with those calculated for its congeneric species *I. illecebrosus*, *I. argentinus* as well as with another European ommastrephid species *Todaropsis eblanae*.

The ecological importance of ommastrephid squids has been recently summarized in a number of papers (e.g., Mangold, 1983; Lordan et al., 1998). Ommastrephids are characterized by high food intake and high conversion rates (Mangold, 1983) thus increasing rates of energy transformation and accumulating high quality protein, available to higher consumers. Consequently, terms such as 'ecosystem accelerators' and 'ecosystem enzymes' can fully explain the essential role they play in the oceanic system.

Many of the ommastrephid species are caught in considerable quantities in different areas of the world oceans (Roper et al., 1984). The great expansion in commercial exploitation of the ommastrephids and particularly those distributed in the western Atlantic, i.e., *Illex illecebrosus* and *I. argentinus*, over the last two decades, resulted in large-scale investigations of various biological parameters of these squid which have been presented in a number of published papers and reviews (e.g., O'Dor, 1983; Rodhouse and Hatfield, 1990; Arkhipkin, 1993; Laptikhovsky and Nigmatullin, 1993).

The broadtail short-finned squid *Illex coindetii* Vérany, 1839, is an amphi-Atlantic ommastrephid species, widely distributed on both sides of the Atlantic and the Mediterranean (e.g., Roper et al., 1984; Mangold and Boletzky, 1987; Sánchez et al., 1998). Its systematic position, within the family Ommastrephidae, has been well established (Mangold et al., 1969).

Fisheries, life cycle and population dynamics of *I. coindetii* have recently drawn the attention of various authors, working in many areas of its geographical range: Eastern Atlantic (Nigmatullin and Vovk, 1972; González et al. 1994, 1996, Arkhipkin, 1996, González and Guerra, 1996, Lordan et al., 1998); Western and Central Mediterranean Sea (Mangold-Wirz, 1963, Sánchez 1984, 1995, Tursi and D'Onghia, 1992; Jereb and Ragonese, 1995; Belcari, 1996, Arkhipkin et al., 2000); Eastern Mediterranean Sea (D'Onghia et al., 1996; Salman et al., 1997). Sánchez et al. (1998) who summarized the previous knowledge on the biological characteristics and fisheries of the species in the Mediterranean and the eastern Atlantic reported short life span, continuous recruitment and spawning, fast growth and high mortality, which are biological attributes characterizing r-strategist species (Pauly, 1984). During the last decade the species has been commercially exploited in many areas of the Northeastern Atlantic and the Mediterranean (Mangold and Boletzky, 1987; Gonzalez et al., 1994; Gonzalez and Guerra, 1996).

However, information either on the population biology or the fisheries of the *I. coindetii* is still scarce and far from being considered complete, since data from large areas, e.g., Eastern Mediterranean, are rarely reported. Furthermore, comparative analysis of biological parameters derived from populations of *I. coindetii*, simultaneously studied, on a European scale (NE Atlantic and Mediterranean) has never been attempted. The objectives of the present study are: (1) to provide information on the biological attributes of *I. coindetii* from areas in the Northeastern Atlantic and the Mediterranean where information on the species is very limited; (2) to correlate the resulting biological attributes with the environmental variables (sea surface temperature and chlorophyll-*a* concentration).

Material and Methods

Study Areas and Sampling.—Samples of *I. coindetii* were collected on a monthly basis from three different areas in the Northeastern Atlantic (Southern Celtic Sea and Bay of Biscay – ICES Divisions VIIH, VIIIA and Portuguese waters –ICES Sub-area IX) and the Eastern Mediterranean (Greek Seas) over the period 1997–1999. Sampling started on a monthly basis during February 1997 in the Portuguese waters, during May 1997 in the Greek Seas and during November 1997 in the Southern Celtic Sea and Bay of Biscay, and was completed during June 1999 in all areas. Samples from the Southern Celtic Sea and Bay of Biscay were caught primarily by fish and Norway lobster trawlers (minimum cod-end mesh size, stretched: 65 mm) and were obtained from commercial French markets; those from the Portuguese waters were obtained from research cruises by means of a trawl-net (cod-end mesh size of 20 mm); samples from the Greek Seas were caught by trawlers and were obtained from commercial markets for the period October–-May and research

sampling by means of a trawl-net (cod-end mesh size of 26 mm) for the rest of the year (June to September is the closed season for commercial trawlers). A total of 18 samples were taken from the Southern Celtic Sea and Bay of Biscay, 13 samples from the Portuguese waters and 16 samples from the Greek Seas. Standardized LPUE (landings per unit effort, kg h^{-1}) values were calculated from all sampling areas where both fishing hours and fishing power were taken into account.

DATA ANALYSIS.—Body weight (BW) and dorsal mantle length (DML) were taken from fresh (stored on ice) animals. Additionally, ovary and testis were weighed. The maturity stage for each individual was recorded, using the scale (stages I–V) proposed by Lipinski (1979).

Monthly length frequencies were analysed using the Bhattacharya (1967) method with the software package FiSAT. Gonadosomatic index (GSI) was adapted from Pierce at al. (1994). Recruitment size was determined as proposed in Pierce et al. (1994) and recruitment index (RI) was adapted from Cochran (1977). Equations of the form BW = aDML^b, where a and b are constants of the regression, were fitted by transforming the data into logarithms and deriving the regression line by the least square method (Trippel and Harvey, 1991). Comparison of slopes of the regressions between males and females were made using the method proposed by Campell and Madden (1990). All mature individuals (stages IV, V) were analysed to determine the mantle length at which 50% of the individuals were mature (L50 value). A standard logistic curve (Trippel and Harvey, 1991) was fitted to the relative frequency distribution for length classes. Sex ratio was calculated for each month and significant deviations from 1:1 were observed using the c^2 test.

Finally, Spearman's rank correlation coefficient was used to test for any significant relationship between the biological indices and the SST and Chlorophyll-*a* (Chl-*a*) values. The SST values from all studied areas were derived by processing of AVHRR (Advanced Very High Resolution Radiometer) data, as obtained by DLR (German Aerospace Agency). Chl-*a* values were calculated by weekly SeaWIFs imagery for the Greek Seas only.

RESULTS

FISHERIES.—Ommastrephids are caught as a by-catch of other fisheries in all three sampled areas. High inter-annual variability characterizes the ommastrephid landings throughout the sampling areas.

In France, *I. coindetii* from the Southern Celtic Sea and Bay of Biscay is sold in the market along with *Todaropsis eblanae*. Ratio values in total numbers of these species averaged 2 *Illex*: 1 *Todaropsis* during the period 1997–1998. Mixed landings of the previously mentioned species are also reported from the Portuguese fish market. Although the two ommastrephid species may be sold together in the Greek market, the percentage of the latter species is estimated to be negligible (perhaps less than 1% of the total yearly landings).

Monthly LPUE values from the three sampling areas are shown in Figure 1. In the Southern Celtic Sea and Bay of Biscay LPUE values averaged 6.2 kg h^{-1} with minimum, maximum and standard deviation of 0.9, 11.6 and 3.4, respectively. The corresponding values from the Portuguese waters and the Greek Seas are: 2.9, 0.7, 20.4 and 3.9 by 1.0, 0.5, 1.7 and 0.3. In the Southern Celtic Sea and Bay of Biscay, LPUE values were increasing from February to May and then were decreasing till September 1997. From October 1997 were again increasing till January 1998 and remained in high level till June 1998. In the Portuguese waters, LPUE values peaked in January, March, April and December 1997 and January and April 1998 and remained in relatively low levels the rest of the sampling period. The lowest LPUE values were obtained from the Greek Seas. In this area LPUE values were almost invariable for the entire sampling period, with maxima repetitively scored during October, and from March to May.
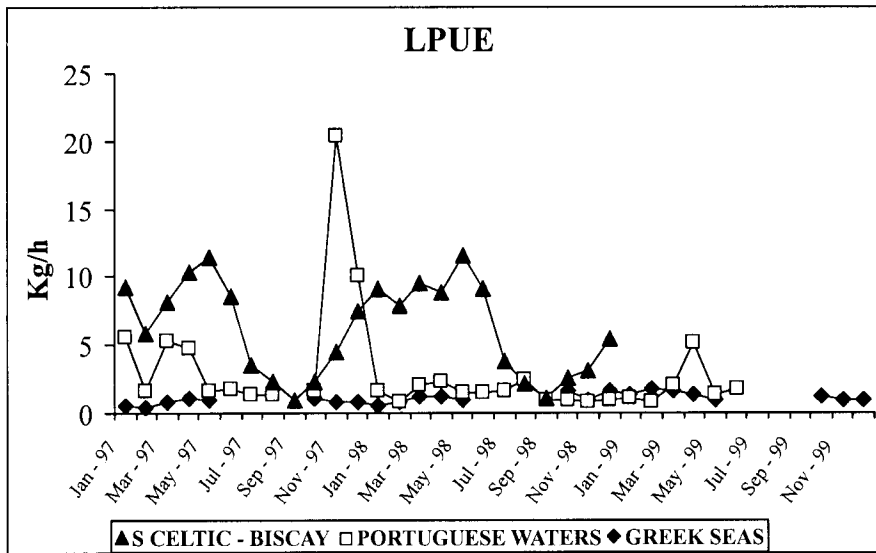
Figure 1. Monthly LPUE values of *Illex coindetii* in the three sampling areas.

SIZE.—Average body size, for both females and males, tended to increase over the first and second trimester in samples from Southern Celtic Sea and Bay of Biscay, and over the second and third trimester in samples from Greek Seas and Portuguese waters. Minimum, maximum, and average length and weight values measured in females and males from the three studied areas are shown in Table 1. Average size, in both sexes, is gradually decreasing from the Northeastern Atlantic to Mediterranean waters.

GROWTH RATES.—Modal progression analysis indicates the presence of two to four cohorts in females, in most of the months when sampling took place in the Southern Celtic Sea and Bay of Biscay and the Greek Seas, while from two to five cohorts in those sampled from Portuguese waters. In the case of males, the analysis suggests one to three cohorts in the samples from the Southern Celtic Sea and Bay of Biscay and the Greek Seas, and one to four cohorts in the samples from the Portuguese waters. The subjective growth rate, as resulted from the tentative links between modes in successive months, and the estimated life span of the species in the studied areas are given in Table 2. For the males sampled in the Portuguese waters it was almost impossible to link modes in successive months.

LENGTH-WEIGHT RELATIONSHIP.—Regressions were significant for the total of the females and males. Slopes and intercepts by sex and studied area are given in Table 1.

Female length-weight regression slopes were significantly different from male slopes in all sampling areas. Over the entire sampling period, only males from Portuguese waters had significantly different slopes from those caught in the remainder areas.

In all sampling areas, *I. coindetii* length-weight relationship, as calculated for the entire sampling period, is positively allometric (b > 3) in males and negatively allometric (b < 3) in females.

RECRUITMENT.—Females are fully recruited in the size of 170 mm in samples from the Southern Celtic Sea and Bay of Biscay and from Greek Seas while for female samples from the Portuguese waters this size drops to 110 mm. Size at which males are fully recruited is 150 mm, throughout all areas sampled (Table 1).

Table 1. Comparison of the biological indices of the three *Illex coindetii* populations as calculated over the entire sampling period. F: females; M: males; CB: Southern Celtic Sea and Bay of Biscay; GS: Greek Seas; PW: Portuguese waters; min: minimum value; max: maximum value; avg: average value; DML: dorsal mantle length; BW: total body weight; L-W: length weight regression; r^2: coefficient of determination; size recr.: size at full recruitment; n: number of individuals.

Sex	Indicies	CB	GS	PW
Female	min DML (mm)	80	35	24
	max DML (mm)	360	352	286
	avg DML (mm)	207	143	167
	min BW (g)	32	2.5	3
	max BW (g)	1,325	1,630	600
	avg BW (g)	302.3	108.8	117
	L-W intersept	0.0001	0.00007	0.00008
	L-W slope	2.76	2.83	2.76
	r^2	0.89	0.92	0.92
	size recr. (mm)	170	170	110
	n	769	630	1,812
Male	min DML (mm)	70	42	47
	max DML (mm)	240	182	217
	avg DML (mm)	174	123	142
	min BW (g)	39	2.4	4
	max BW (g)	606	222	341
	avg BW (g)	227.5	92.5	103.6
	L-W intercept	0.0002	0.00001	0.000008
	L-W slope	3.17	3.25	3.3
	r^2	0.82	0.9	0.91
	size recr. (mm)	150	150	150
	n	847	845	2,375

Following the plots of the percentages of recruits (females and males, stage I) over the sampling period (Fig. 2), two autumnal recruitment peaks, during 1997 and 1998 were recorded for the female squids in samples from the Southern Celtic Sea and Bay of Biscay, while male recruits showed very low percentages throughout the entire period. Female recruits were recorded in high percentages from the Greek Seas during winter and spring 1998 and during autumn 1998 and winter 1999. For males from the Greek Seas recruitment peaks were observed during winter and spring 1998 and during winter 1999. Finally, in the samples from Portuguese waters, recruitment percentages were high for both females and males during winter and summer of 1997 and autumn 1998.

MATURATION.—The higher percentages in mature males and the earlier occurrence of mature males in relation to females is a common feature in the short-finned squid populations in all three sampled areas (Fig. 2). Another common observation was the absence of spent males and the low percentage of maturing animals (maturity stage III, 6.8 % of the total number of the individuals sampled).

Immature females (stages I and II) are found at higher percentages during the first and fourth trimester while maturing and mature (stage III and stages IV and V, respectively) are mostly found during the second and third trimester in the samples from all the studied areas. Maturing and mature males were found to be abundant during the entire sampling period in samples from the Southern Celtic Sea and Bay of Biscay and from the Greek Seas, while in those from the Portuguese waters only during the second and third trimes-

Table 2. Comparison of the growth rate and life-span of the *Illex coindetii* reported in the literature and the results of this study.

Method	Growth rate		Life-span		Area	Reference
	Females	Males	Females	Males		
Direct ageing	1.55	1.78	6-7	6-7	Sicilian Channel	Arkhipkin et al., 2000
Direct ageing	0.72	0.84	13	15	Galician waters	González et al., 1996
Direct ageing	1.11	-	12	12	Eastern Atlantic	Sánchez et al., 1998
Direct ageing	0.44	-	18	18	Western Mediterranean	Sánchez et al., 1998
Direct ageing	-	-	8	6	Sierra Leone	Arkhipkin, 1996
Direct ageing	-	-	10	8	Western Sahara	Arkhipkin, 1996
Monitoring of cohorts	0.39–0.43	0.33– 0.34	24	12– 20	Western Mediterranean	Mangold-Wirz, 1963
Monitoring of cohorts	0.47	0.38	17.7	16.6	Catalan Sea	Sánchez, 1984
MPA	0.32–0.45	0.32– 0.45	14-16	14-16	Sicilian Channel	Jereb and Ragonese, 1995
MPA	0.67	0.73	18	11	S. Celtic Sea - Bay of Biscay	This study
MPA	0.82	0.84	15	10	Greek Seas	This study
MPA	0.92	-	13	-	Portuguese waters	This study

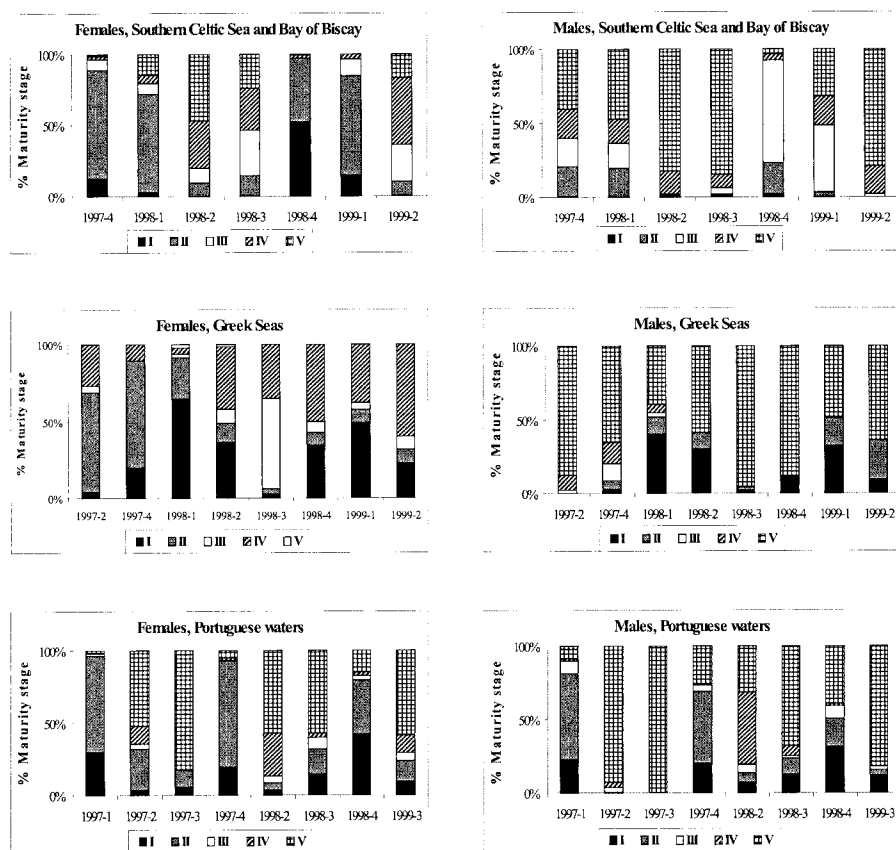Average growth rate in mm· d⁻¹; Life-span in months

Figure 2. Percentage of the maturity stages of female and male short-finned squids, by trimester.

ter. It should be noted that maturing males were found at high percentages only during the fourth trimester of 1998 and first of 1999, in the samples from the Southern Celtic Sea and Bay of Biscay, while in the remainder sampling areas maturing males were always in low percentages.

In the mature females from the Southern Celtic Sea and Bay of Biscay peaks of GSI values were scored during February to April of 1998 and 1999 and during September 1998 (Fig. 3). Peaks of mature females GSI values in the samples from the Greek Seas were recorded during April and August 1998 and during January and May 1999. Mature male GSI values were almost invariable for almost the entire sampling period in both of these areas, with slightly raised values in February and June 1998 and March 1999 in the samples from the Southern Celtic Sea and the Bay of Biscay and, with also slightly raised values during February to May 1999 in the samples from the Greek Seas. Values, as well as peaks of GSI derived from all animals follow those derived from mature animals with a few exceptions only.

Males and females showed increasing maturity with size, in all studied areas (Fig. 4). In Portuguese waters, very few females occurred above 250 mm and among those a small percentage was not mature animals. Females from the Greek Seas showed a different
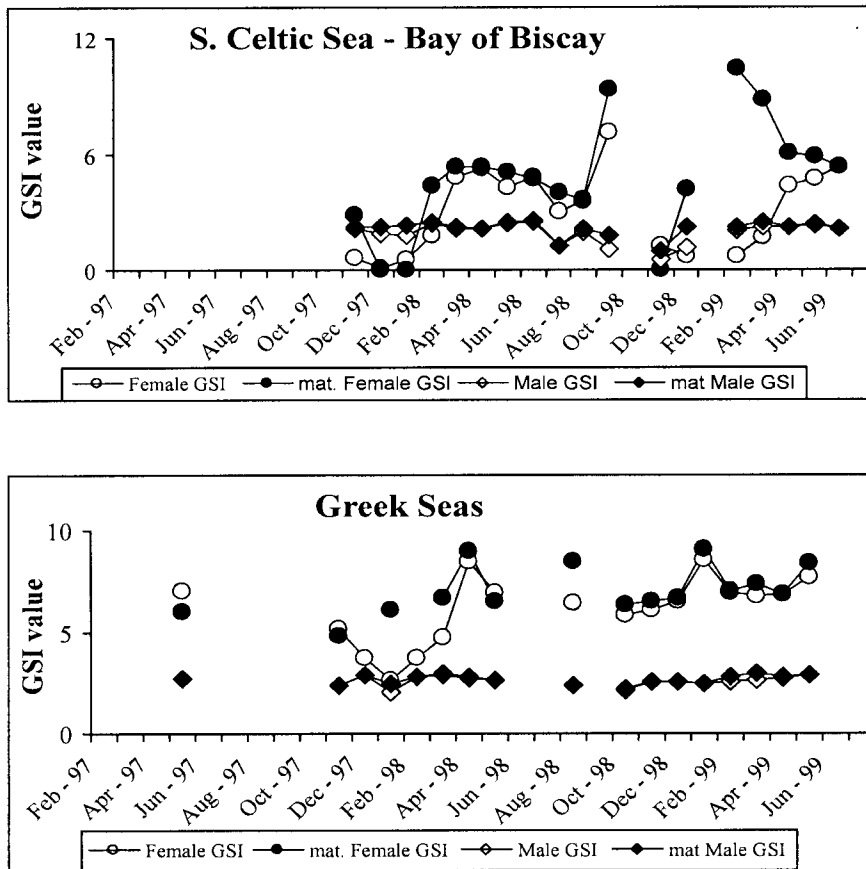
Figure 3. Monthly GSI values for females and males.

pattern: at 170 mm, more than 69% of females were mature, but at 200 mm, only 47% of females were mature; at >210 mm, 100% of females were mature. These data may suggest that females from Greek Seas mature at two different modal sizes: first mode size at maturity is estimated at 140 mm and second between 190 and 360 mm. Nevertheless, the small number of animals after the inflexion point (6.4% of mature animals) and the fact that the animals were not directly aged during the present study do not permit any further analysis (e.g., Collins et al., 1995).

Fitting the standard logistic function, the L50 for females from the Southern Celtic Sea and Bay of Biscay was estimated as high as 248 mm, for those from the Greek Seas 179 mm, and from the Portuguese waters 181 mm. For the males the L50 values were 153 mm, 113 mm and 129 mm, respectively (Fig. 4). A comparison of the L50 values estimated from areas along the Eastern Atlantic and the Mediterranean is given in Table 3.

In the three sampled areas, gonad weight averaged 5.37% of the BW for females and 2.28% of BW for males.

SEX RATIO.—There were more months where the sex ratio was significantly different from the expected 1:1 in the samples taken from the Southern Celtic Sea and Bay of Biscay than in samples taken from Greek Seas and Portuguese waters (Table 4). No sig-
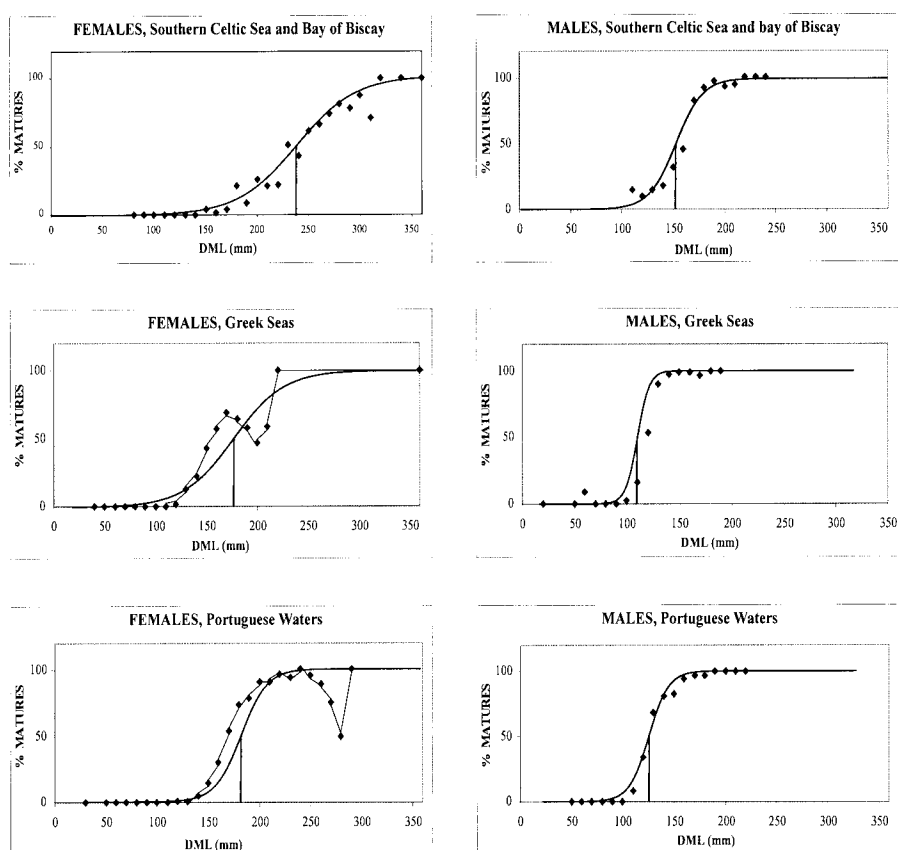
Figure 4. Cumulative percentage of mature females and males against length. Standard logistic curves are fitted for the estimation of the L50 values (straight lines).

nificant differences were observed in the total female and male numbers over the entire sampling period, in all areas.

In the Southern Celtic Sea and Bay of Biscay, males were predominant in four months out of the eighteen of the sampling period, while females were predominant in three. In all of these cases, sex ratio was close to 1.5–2:1 except in September 1998 where the ratio rose to 4:1 females to males. In the Greek Seas, males only were found in significantly higher numbers than females, in four months. Sex ratio was 2–2.5:1. Finally, in the Portuguese waters, male numbers were significantly higher than female numbers in three months (ratio range, 1–3.9:1), while the opposite case occurred only once (2 : 1).

CORRELATION WITH ENVIRONMENTAL VARIABLES.—Values of Spearman's rank correlation coefficient (r) performed between biological indices, and average SST values (and Chl-*a*, for the Greek Seas only), as calculated by month and by trimester within each area, are shown in Table 5.

Both length and weight were found to be negatively correlated (though weakly) with SST monthly values in the samples taken from the Southern Celtic Sea and Bay of Biscay. When female individuals only were considered, gonado-somatic index of mature animals was also negatively correlated with SST average values. When biological indices were

Table 3. Comparison of the L50 values for females and males as calculated from areas along the Eastern Atlantic and the Mediterranean.

Area	L50 Value (mm)		Reference
	Females	Males	
S Celtic Sea – Bay of Biscay	248	153	This study
Northwestern Africa	208	160	Hernández-García and Castro, 1995
Galician waters	184	128	González and Guerra, 1996
Portuguese waters	191	129	This study
Western Mediterranean	150	120	Sánchez et al., 1998
Sicilian Channel	150	120	Jereb and Ragonese, 1995
Greek Seas	179	113	This study

calculated over trimester intervals, male gonado-somatic index (as calculated for matured animals), maximum length, maximum weight, and regression slope were strongly but negatively correlated, with SST values.

Similar results have been furnished by the samples from Portuguese waters, with the addition of the positive and strong correlation of the recruitment index with the SST values as calculated by trimester. No significant correlation was found when the life-cycle indices were estimated on a monthly basis.

The reverse correlation was revealed from the samples from the Greek Seas: SST values were positively correlated with length and weight of males and negatively correlated

Table 4. Results of chi-square test performed on monthly sex ratio values. Y-M: year-month; nF: number of female individuals; nM: number of male individuals; Significance level: *: $P < 0.05$; **: $P < 0.01$; NS: $P > 0.05$.

S. Celtic Sea - Biscay				Greek Seas				Portuguese Waters			
Y-M	nF	nM	c^2	Y-M	nF	nM	c^2	Y– M	nF	nM	c^2
1997–11	59	49	0.85	1997–5	26	42	5.53**	1997–2	552	527	0.05
1997–12	81	85	0.05	1997–11	11	17	4.59*	1997–5	105	147	2.77
1998–1	91	102	0.32	1997–12	9	18	11.11**	1997–6	101	163	5.51
1998–2	44	52	0.69	1998–1	17	13	1.77	1997–7	17	26	4.38*
1998–3	38	43	0.38	1998–2	22	30	2.36	1997–10	206	197	0.04
1998–4	27	55	11.65**	1998–3	69	76	0.23	1997–11	32	34	0.09
1998–5	39	40	0.16	1998–4	23	26	0.37	1998–4	35	44	1.29
1998–6	25	35	2.77	1998–5	46	66	3.18	1998–5	96	119	1.14
1998–7	14	31	14.27**	1998–8	67	166	18.05**	1998–6	281	375	2.05
1998–8	15	12	1.23	1998–10	23	33	3.18	1998–7	92	101	0.21
1998–9	12	3	36.00**	1998–11	69	85	1.07	1998–8	28	14	11.11**
1998–11	12	24	11.11**	1998–12	35	29	0.87	1998–10	124	115	0.14
1998–12	89	83	0.12	1999–1	30	37	1.09	1998–11	21	34	5.58**
1999–2	50	59	0.68	1999–2	51	63	1.1	1999–6	122	479	35.28**
1999–3	53	89	6.42**	1999–3	57	71	1.19				
1999–4	32	32	0	1999–4	18	24	2.04				
1999–5	47	26	8.27**	1999–5	57	49	0.56				
1999–6	41	27	4.23**								

Table 5. Correlation (Spearman's coefficient) between SST and Chla-a values and biological indices, calculated by month and by trimester, for the samples from the three studied areas. RI: recruitment index; Spawning: proportion of the mature animals; GSI all: gonadosomatic index calculated for all animals; GSI mat: gonadosomatic index calculated for mature animals only; min: minimum value; max: maximum value; avg: average value; rng: range of values; mat: mature animals; DML.: dorsal mantle length; BW: total body weight; slope: regression length-weight slope. (significance level: *: P < 0.05; **: P < 0.01; NS: P > 0.05).

| | | S. Celtic Sea - Bay of Biscay | | | | Portuguese waters | | | | Greek seas | | | | | | | |
| | | Month SST avg | | Trimester SST avg | | Month SST avg | | Trimester SST avg | | Month SST avg | | CHL-a avg | | Trimester SST avg | | CHL-a rng | |
Sex	Indicies	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
F	RI	0.28	0.25	0.19	0.67	-0.12	0.66	0.78*	0.02	-0.55**	0.01	0.02	0.44	0.56	0.4	-0.78*	0.03
	Spawning	-0.23	0.34	0.09	0.84	-0.05	0.85	-0.69*	0.05	0.26	0.31	-0.32	0.22	0.01	0.81	0.5	0.25
	GSI all	-0.19	0.42	-0.16	0.72	-	-	-	-	0.08	0.92	-0.16	0.56	-0.28	0.72	0.14	0.75
	GSI mat	-0.48**	0.04	-0.09	0.84	-	-	-	-	-0.11	0.61	0.26	0.32	-0.4	0.9	0.1	0.81
	min DML mat	-0.41	0.08	-0.44	0.31	0.25	0.38	0.33	0.41	0.21	0.34	0.14	0.59	-0.46	0.52	0.5	0.25
	min DML	-0.34	0.15	0.05	0.9	0.3	0.29	-0.63	0.09	0.29	0.42	0.16	0.54	0.03	0.89	0.5	0.25
	max DML	-0.45*	0.05	-0.3	0.5	-0.23	0.41	-0.41	0.3	0.57**	0.01	-0.4	0.11	-0.33	0.92	0.32	0.48
	avg DML	-0.48*	0.03	-0.52	0.22	0.03	0.89	-0.71*	0.04	0.67**	0.002	-0.37	0.15	-0.33	0.81	0.39	0.38
	min BW	-0.1	0.68	0.3	0.5	0.28	0.32	-0.4	0.31	0.28	0.38	0.14	0.59	0.16	0.87	0.28	0.53
	max BW	-0.49*	0.03	-0.45	0.31	-0.14	0.61	0.35	0.38	0.49*	0.03	-0.65**	0.006	-0.15	0.82	0	1
	avg BW	-0.45*	0.05	0.03	0.93	0.07	0.79	-0.71*	0.04	0.66**	0.002	-0.44	0.08	-0.41	0.73	0.67	0.09
	slope	-	-	-0.16	0.1	-	-	-0.74*	0.03	-	-	-	-	-0.06	0.91	0.32	0.48
M	RI	0.43	0.06	0.59	0.15	-0.19	0.51	0.83**	0.01	-0.44	0.08	0.32	0.21	-0.75**	0.01	0.71	0.07
	Spawning	0.28	0.22	0.07	0.87	-0.01	0.95	-0.45	0.26	0.4	0.38	-0.39	0.12	0.26	0.62	-0.92**	0.002
	GSI all	-0.11	0.62	-0.61	0.14	-	-	-	-	-0.28	0.45	0.12	0.64	-0.36	0.31	0.57	0.18
	GSI mat	-0.22	0.35	-0.88**	0.008	-	-	-	-	-0.56	0.22	0.44	0.08	-0.38	0.42	0.67	0.09
	min DML mat	-0.35	0.13	-0.55	0.2	-0.06	0.82	0.33	0.41	-0.09	0.92	0.12	0.63	-0.26	0.75	0.21	0.64
	min DML	-0.07	0.75	-0.18	0.68	0.31	0.27	-0.28	0.49	0.11	0.66	0.05	0.85	-0.03	0.91	-0.1	0.85
	max DML	-0.58**	0.008	-0.87**	0.01	-0.03	0.89	0.09	0.82	0.29	0.37	-0.33	0.2	0.51	0.18	-0.39	0.38
	avg DML	-0.46*	0.04	-0.55	0.19	0.03	0.89	-0.71*	0.04	0.62	0.09	-0.32	0.22	0.71*	0.05	-0.85**	0.01
	min BW	0.32	0.16	-0.08	0.86	0.42	0.12	-0.43	0.27	0.18	0.56	-0.09	0.71	0.05	0.91	-0.28	0.53
	max BW	-0.6**	0.005	-0.81**	0.02	-0.05	0.85	-0.33	0.41	0.38	0.25	-0.41	0.11	0.45	0.37	-0.14	0.75
	avg BW	-0.2	0.04	-0.16	0.72	0.02	0.93	-0.76*	0.02	0.67**	0.002	-0.53*	0.03	0.65	0.45	-0.92**	0.002
	slope	-	-	-0.88**	0.008	-	-	-0.28	0.49	-	-	-	-	-0.21	0.62	0.39	0.38

with recruitment index. Monthly average Chl-*a* values were found to be negatively correlated with female maximum weight values only. Male recruitment, spawning, length and weight, and female recruitment index were found to be negatively correlated with the range of Chl-*a* values, calculated on a trimester basis.

Discussion

The high spatial and inter-annual variation in ommastrephid landings along with the mixed landings primarily of the species *I. coindetii* and *T. eblanae* are two of the characteristics of the ommastrephid fisheries throughout the Mediterranean and the Eastern Atlantic (e.g., Stergiou, 1989; Sánchez et al., 1998). The only observable pattern in landings was recorded in the Southern Celtic Sea and Bay of Biscay where raised values were observed during winter and spring. Highly variable annual catches have also been recorded for *I. illecebrosus* in the Canadian waters (Amaratunga et al., 1978; Dawe, 1988) and for *I. argentinus* off the Argentine exclusive economic zone (Arkhipkin, 1993).

Based on the relevant literature (cited below) of the species from the European Atlantic and Mediterranean waters, the size of *I. coindetii* reaches 379 mm and 1630 g. The highest female DML and BW values were recorded from the Galician waters (González and Guerra, 1996) and from the Greek Seas (this study). Maximum male DML and BW values were recorded from Galician waters and Southern Celtic Sea and Bay of Biscay (320 mm by 606 g; Sánchez et al., 1998, and present study, respectively). The low percentage of females from the Portuguese waters with DML > 250 mm cannot be attributed to the low number of animals sampled (over 4000) but, rather, to the population structure in this particular area. Similar results have been reported from a population of the species studied in the Sicilian Channel of the Mediterranean (Jereb and Ragonose, 1995). The previously mentioned maximum size values are comparable with those reported for the congeneric species distributed on the other side of the Atlantic: *I. illecebrosus* (Amaratunga et al., 1978; Laptikhovsky and Nigmatullin, 1993) and *I. argentinus* (Nesis, 1987; Arkhipkin and Laptikhovsky, 1994), but larger than those reported for the *T. eblanae* populations (González et al., 1994; Hastie et al., 1994) studied in the European waters.

A comparison between available information on growth rate and life span of *I. coindetii* populations studied in the Eastern Atlantic and the Mediterranean and the results of the present study are presented in Table 2. Growth rates may well range from 0.33–1.78 mm d^{-1} and life span from 0.5–2 yrs, depending on the studied area and on the method performed. Results derived by MPA, during the present study, suggest faster growth than the previous estimations, and are comparable with those derived by direct ageing of populations from the Galician waters and Western Mediterranean (González et al., 1996; Sánchez, 1995; Sánchez et al., 1998) although the major disadvantage of the indirect (MPA) method is that the multi-cohort structure of squid populations, combined with the simultaneous presence of different ontogenetic stages, mask natural modes and do not allow MPA to resolve them entirely and detect their appearance in certain time intervals (Caddy, 1991; Pierce et al., 1994). Additionally, the presence of female immature (González et al., 1996) and maturing (this study) outliers indicates an even greater maximum age of the species from that already reported in the literature. Studies in *I. illecebrosus* (e.g., Dawe, 1988; Coehlo et al., 1994) and in *I. argentinus* (e.g., Rodhouse and Hatfield, 1990; Laptikhovsky and Nigmatullin, 1993; Arkhipkin and Laptikhovsky, 1994) suggest a 1-yr life span. Fi-

nally, Hastie et al. (1994) found a life span of 1–2 yrs for both sexes of *T. eblanae* in populations from the Scottish coastal waters.

The existence of positive allometry in mature males and negative allometry in females in the length-weight relationship has been considered as indicative of the general morphological and functional characteristics not only of the species *I. coindetii* (Sánchez et al., 1998) but of the entire family Ommastrephidae (Forsythe and van Heukelem, 1987). This has been consistently reported from studies along the Mediterranean and the Northeastern Atlantic (e.g., González et al. 1994, 1996; Sánchez et al., 1998) with two exceptions: (a) in the Tyrrhenian Sea (Belcari, 1996), where female length-weight slope found to be isometric; (b) in the Northwestern Spain, where the slope was found to be higher than three but still lower than the corresponding one for males (Sánchez et al., 1998). Positive allometric growth in the case of males may be interpreted as greater strength in the arms which increases the effectiveness of copulation, while in the case of females negative allometric growth may be explained by the large variability of ovary mass in mature individuals and, consequently, the size at which full maturity is reached. However, positively allometric length-weight relationship was observed for both sexes of *I. illecebrosus* populations studied in the Newfoundland and the eastern Canadian waters (Amaratunga et al., 1978; Dawe, 1988). In the *T. eblanae* populations studied from the Scottish and Galician waters (González et al., 1994; Hastie et al., 1994), slopes were consistently lower than three for both sexes, with male slope significantly higher than female slope only in the latter population.

The consistent appearance of recruits throughout the year is a feature commonly shared in all sampling areas. However, peaks of recruitment events show spatial and inter-annual variation. The low percentages of male recruits from the Southern Celtic Sea and Bay of Biscay can most probably be explained by the selectivity of the gear used. There is a pronounced seasonality in female recruits in the samples from Southern Celtic Sea and Bay of Biscay and in those from the Portuguese waters, over the entire sampling period: most of the recruits appear in autumn and winter. In the samples from the Greek Seas female recruits may remain in high percentages during the autumn, winter and spring. It is not surprising, however, that the pronounced seasonality in recruits appears in the edges of the Northern part of the geographical distribution of the species. The difference in size at full recruitment between females from the Portuguese waters and those from the remainder areas may be also attributed to different gear selectivity. Continuous recruitment throughout the year has also been observed in populations of *I. illecebrosus* from the Newfoundland waters (Dawe and Beck, 1997) while in populations of *T. eblanae*, recruitment occurs from winter to summer in the Scottish waters (Hastie et al., 1994) and from autumn to spring in the Galician waters (González et al., 1994).

Results of this study as well as those from the literature (e.g., Mangold-Wirz, 1963; Jereb and Ragonese, 1995; González and Guerra, 1996; Sánchez et al., 1998) point to some maturation features, commonly shared in all areas studied: (1) wide size range of mature animals; (2) males appear to mature at smaller size than females; (3) lack of spent (maturity stage VI) males; (4) extended spawning period covering the whole year with greater reproductive activity during particular seasons, depending on the studied area, but usually spring and summer. From the above maturation features a, b and d are also commonly occurring in the studied populations of *I. argentinus, I. illecebrosus* and *T. eblanae* (e.g., O'Dor, 1983; Rodhouse and Hatfiled, 1990; Laptikhovsky and Nigmatullin, 1993; Arkhipkin and Laptikhovsky, 1994; Hastie et al., 1994). Extended spawning through-

out the year (point d) has been interpreted as an adaptation, which is critical for the survival of the populations of *I. illecebrosus* since it ensures the interaction of migratory and non-migratory life history strategies (Coehlo et al., 1994). Absence of spent animals (point c) has been reported from populations of *I. illecebrosus* from the Canadian Atlantic waters (O'Dor, 1983) and *T. eblanae* from Scottish waters (Hastie et al., 1994). Conversely, spent females have been recorded from *I. argentinus* populations (Laptikhovsky and Nigmatullin, 1993). The most plausible explanation for the absence of spent males is that they continue to produce spermatophores until death (Jereb and Ragonese, 1995). Low percentages of maturing animals suggest the very fast transition from the immature to the mature stage according to González and Guerra (1996). Although a certain degree of bias caused by the different seasonal sampling in the studied areas is expected, high percentages of maturing and mature animals show similar seasonal pattern in the female samples from the Southern Celtic Sea and Bay of Biscay and from the Portuguese waters, while no single pattern was found over the entire sampling season in the female samples from the Greek Seas. Females from the Greek Seas show a more flexible spawning peak activity, potentially subjected to the influence of the environmental variables. The latter is further strengthened by the correlations between spawning and environmental variables. Variability in spawning peaks has also been documented for the species *T. eblanae* in which mature animals are abundantly occurring during summer and autumn in the Scottish waters (Hastie et al., 1994), during winter and spring in Galician waters (González et al., 1994) and during autumn in the Mediterranean (Mangold-Wirz, 1963). In *I. argentinus*, spawning peaks have been consistently reported during winter (Laptikhovsky and Nigmatullin, 1993; Arkhipkin and Laptikhovsky, 1994), while in *I. illecebrosus* populations from the Canadian Atlantic waters major spawning peaks are occurring during winter and summer and minor spawning peaks during spring. In the latter species, the resulting overlap-spawning season has been interpreted as critical for the maintenance of the population as it ensures the gene flow between summer and winter breeding components.

The use of Gonado-Somatic index (GSI) for the determination of the spawning period was found to be much more efficient for females than for males. This is probably caused by the fact that females spent much more energy for their reproductive output than males. In the Tyrrhennian Sea for example, as much as 16% of the total BW was invested in female gonads and accessory organs while in males this investment was almost threefold lower (Belcari, 1996).

Taking into account the L50 values for both sexes calculated from this study and the corresponding ones from the literature (González and Guerra, 1996; Jereb and Ragonese, 1995), a west-east gradient of decreasing values, in *I. coindetii* populations from the Atlantic to the Eastern Mediterranean, appears: higher L50 values were calculated for populations from the most distal areas in the Atlantic, Southern Celtic Sea and Bay of Biscay and Northwestern Africa; intermediate values from the Atlantic areas proximal to the Mediterranean: Portuguese waters and Galician waters; lower values from the Mediterranean, Sicilian Channel and Greek Seas. Geographical north-south gradient in decreasing L50 values has been reported for the species *I. illecebrosus* studied in the Canadian Atlantic waters (Coehlo and O'Dor, 1993). In the latter study, the L50 values varied markedly from year to year.

The potential of two mode sizes at maturity in females has never been reported for *I. coindetii* although a narrow inflexion appears in the data presented by González and Guerra (1996: 109) from Galician waters. However, in European waters, two clear size

modes at maturity have been observed for both males and females of the loliginid species *Loligo forbesi* from Scottish and Spanish waters (Boyle et al., 1995; Guerra and Rocha, 1994). These findings have been interpreted as indicative of either two different growth cohorts at breeding or mixing of two populations from different centers of origin (Boyle et al., 1995). In the present study, the existence of one or potentially two (Greek Seas) mode sizes at maturity may suggest two reproductive strategies of the species along the Atlantic and the Mediterranean.

Female and male numbers were not significantly different over the entire sampling period. However, this is not the case when sex ratio is calculated over trimester and monthly intervals. Significant monthly deviations of sex ratio from 1:1 do not follow any repetitive pattern over the samples taken from the three areas. Therefore, all of the deviations which occurred could be attributed only to sampling error and/or occasional variations in population structure as suggested by Sánchez et al. (1998) for *I. coiindetii* and by Moreno et al. (1994) for the loliginid squids *L. forbesi* and *L. vulgaris*. Sex ratios close to 1:1 have also been reported from the Sicilian Channel (Jereb and Ragonese, 1995), Catalonian Sea and Western Africa (Sánchez et al., 1998), while significant deviations in sex ratio were recorded only from the Galician waters (González and Guerra, 1996) and the Ionian Sea (Tursi and D'Onghia, 1992). Sex ratio calculated from populations of *T. eblanae* from the European waters was close to 1:1. However, in populations of *I. illecebrosus* from the Canadian Atlantic waters sex ratio appeared either to be close to 1:1 for long periods of the year (Amaratunga, 1978; Lange and Sissenwine, 1983) or to vary significantly from one population to another (O'Dor, 1983).

Two main conclusions may be derived from the results of the correlation of the environmental variables with the biological indices of the species: (1) both temperature and food availability, which were represented only by SST values and Chl-*a* in surface water during this study, are important factors in the cephalopod life-cycle. The significance of temperature and food availability for the growth rate, spawning season, reproductive peaks, maturation rates, recruitment, and other biological characteristics not only for this species but also for its congeners have been pointed out by various authors (e.g., Forsythe and van Heukelem, 1987; Mangold, 1987; Dawe, 1988; Nigmatullin, 1989; Coelho and O'Dor, 1993; Forsythe, 1993); (2) different correlation patterns in the areas sampled also suggest high levels of environmentally driven flexibility of the life cycle of the *I. coindetii* (e.g., Forsythe and van Heukelem, 1987; González et al., 1994). Large variations in landings (e.g., Sánchez et al., 1998) could be also attributed to the previously-mentioned flexibility of the species.

Further detailed studies of the life-history, and particularly the influence of oceanographic variables, are required before sustainable management can be undertaken.

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