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RESEARCH ARTICLE

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Population biology and life strategies of *Chlorophthalmus agassizii* Bonaparte, 1840 (Pisces: Osteichthyes) in the Mediterranean Sea

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Abstract The population biology and life strategies of *Chlorophthalmus agassizii* were studied in the Ionian Sea (eastern–central Mediterranean) using the data collected during the experimental trawl surveys carried out from 1995 to 2000. Depth-related trends of both density and size were found. With depth the former decreased while the latter increased. A typical bigger–deeper phenomenon was detected: young-of-the-year individuals occur on the shelf during autumn–winter months and move towards bathyal bottoms as they grow. The sampled population was made up of several size–age groups. The maximum age of 8 years was identified by means of otolith readings. The Von Bertalanffy growth parameters were estimated from the age–length key ($L_\infty = 189.04 \pm 5.401$ mm; $k = 0.24 \pm 0.021$; $t_o = -1.20 \pm 0.132$; $\phi' = 3.94$) and modal progression analysis ($L_\infty = 218.33 \pm 18.397$ mm; $k = 0.164 \pm 0.028$; $t_o = -1.694 \pm 0.171$; $\phi' = 3.89$). Reproduction of this monoecious fish was observed during summer–early autumn. Considering the female portion of the gonad, the size at attainment of 50% maturity was 115 mm TL. The corresponding age is within the third year of life. The simultaneous occurrence of oocytes in different development stages was shown in the ovary. Both the asynchronous ovary and oocyte size distribution indicate that *C. agassizii* spawns more than once during a reproductive season (batch spawner). Functional fecundity (on average 3,018 hydrated oocytes) was between 37 and 69% of the absolute fecundity and increased significantly with the individual size. Since adult specimens are mostly distributed on the slope, eggs and larvae develop in epipelagic waters and migrate in-shore where juvenile forms recruit on the shelf. Juveniles migrate ontogenetically towards deeper bottoms and after 2–3 years start to reproduce annually within a life span greater than 10 years.

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Introduction

The shortnose greeneye, *Chlorophthalmus agassizii* Bonaparte, 1840, is a demersal species distributed on the continental shelf and upper slope of the Atlantic Ocean, both western and eastern, and Mediterranean Sea (Whitehead et al. 1984). It is a monoecious fish with epipelagic development (Mead et al. 1964). Juvenile stages were first described through individuals collected off New England and in the Mediterranean (Sanzo 1915; Taning 1918; Mead et al. 1964). Adults have schooling and sedentary habits on muddy bottoms where they can be quite abundant (Whitehead et al. 1984).

In the Mediterranean, data on the distribution of *C. agassizii* between the continental shelf and the upper slope have been collected during several studies on demersal resources carried out in the last two decades (Relini et al. 1999). In this basin the shortnose greeneye is caught as a by-catch species during trawl fishing but its commercial utilization changes in different areas (Fisher et al. 1987). There are some Mediterranean areas, such as the Tyrrhenian Sea, Sardinian Sea and Sicily Channel, where *C. agassizii* is among the most abundant fishes in the upper slope, providing biomass values even greater than those of the most abundant commercial fishes (Relini et al. 1999). In the eastern Ionian Sea, *C. agassizii* has been caught with average yields of up to 50 kg/h of trawling, being among the dominant species in the epi-bathyal fish assemblage (Politou et al. 2003; Mytilineou et al. 2004).

Despite the abundance of *C. agassizii* in the Mediterranean Sea there are no comprehensive studies on its population biology. Observations on the light organ and reproductive cycle have been carried out by De Domenico et al. (1990) and Follesa et al. (2004) with attempts to identify growth and diet carried out by Specchi et al. (1995) and Kabasakal (1999), respectively. Recently, the feeding habits of *C. agassizii* related to size and seasons have been investigated in the central–western Mediterranean (Cabiddu et al. 2005).

Therefore, the objective of this study is to present an outline of the population biology and life strategies of *C. agassizii* in the Mediterranean Sea, providing a specific contribution to the knowledge of its demographic structure, age, growth and reproductive biology.

Materials and methods

Sampling

Data used in this study were collected during 17 experimental bottom trawl surveys carried out in the Ionian Sea (eastern–central Mediterranean) from June 1995 to September 2000 as part of four study projects: DEEP-FISHERIES (Gordon 1999); GRUND (Relini 1998); MEDITS (Bertrand et al. 2002) and INTERREG II Italy–Greece (Politou et al. 2003). Samples from the first three study projects regarded the western Ionian, along the Italian coasts (between Cape Otranto and Cape Passero), while those from INTERREG II concerned the eastern Ionian Sea, along the Greek coasts (between Kerkira Island and northern Zakinthos) (Fig. 1).

A commercial motor powered vessel, equipped with an otter trawl net, with stretched mesh of 40 mm in the codend, was hired for the DEEP-FISHERIES, GRUND and INTERREG II cruises. However, during the DEEP-FISHERIES surveys a cover with a stretched mesh of 20 mm was employed on the codend (D'Onghia et al. 2003). During the MEDITS surveys a specially designed net with a stretched mesh of 20 mm in the codend was used (Bertrand et al. 2002). The horizontal and vertical opening of the two types of nets, measured with the SCANMAR acoustic system, depended on depth, wire length, towing speed, etc. (Fiorentini et al. 1994, 1999). The sampling design adopted in each survey was depth stratified. The depths examined were between 10 and 700 m during GRUND and MEDITS while these were between 250 and 750 m during DEEP-FISHERIES and between 300 and 900 m during INTERREG II. The hauls were carried out from dawn to dusk. Haul duration ranged from 0.5 to 3 h according to the cruise. However, the number of sampled specimens was standardized to Km^2 for subsequent numerical processing. The vessel speed, measured using GPS, was maintained at 2.5–3.0 knots. The cruise, date, number of sampling hours, depth range and number of specimens concerning each cruise are reported in Table 1.

Data collection and processing

Data collected during DEEP-FISHERIES (pooled data of 288 sampling hours) and MEDITS (pooled data of 240 sampling hours), although concerning different depth ranges, were used to investigate the depth trends in density and size of *C. agassizii* in the western Ionian Sea. Using the number of individuals caught in each haul swept area, the density was computed as Number/Km^2. The change in density and size with depth was tested by regression analysis. For these analyses the log transformation of the density and the median value of the sizes were adopted in order to minimize the negative effect caused by the extreme values and asymmetric distributions.

The population structure was investigated for each cruise carried out in the western Ionian Sea during DEEP-FISHERIES and MEDITS. With this aim, the total length (TL) was taken to the nearest millimeter on the sampled specimens. The modal components in the length–frequency distributions were separated by means of the Bhattacharya method as reported in the FiSAT program (Gayanilo et al. 1995). Each representative component with a separation index (SI) greater than 2 was assumed to be a single cohort. Differences between observed and expected length–frequency distributions were evaluated by means of the χ^2 test.

Concerning age and growth, both *sagittae* were removed from 300 specimens collected during the GRUND survey (September–October 1998). Otoliths were placed in a black dish with glycerine (30%) and alcohol (70%) to improve reading. An opaque and translucent zone deposition pattern was considered as an annual event (Morales-Nin et al. 1996). Otoliths were read on the major axis of the proximal surface (longitudinal plane) at least twice independently by two readers. If agreement was not reached, the otoliths in question were excluded from the growth estimations. The number of annual rings was conventionally designated as 1, 2, 3, 4,..., *n*. The growth parameters of the Von Bertalanffy equation were estimated by means of the age–length key obtained from the otolith readings. Validation of the growth pattern was carried out by means of modal progression analysis. Length-at-age from Von Bertalanffy parameters obtained by this method and otolith readings were compared by means of the *t*-test. The Von Bertalanffy equations obtained by the two methods were compared through the growth performance index (ϕ') (Munro and Pauly 1983).

The data used to study the reproductive biology of *C. agassizii* were collected during INTERREG II. The maturity stage of the ovaries was recorded macroscopically in 10,991 individuals. In particular, according to Fishelson and Galil (2001) who analyzed the gonad

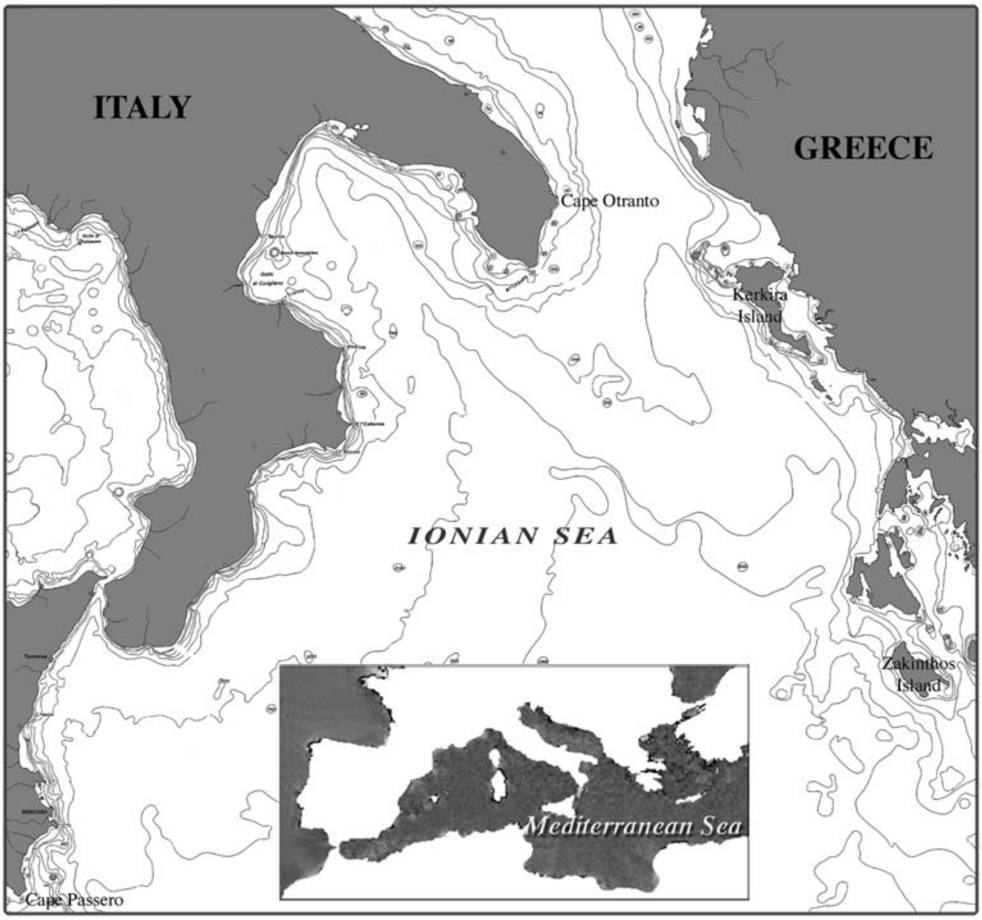

Fig. 1 Map of the northern Ionian Sea

structure of the monoecious fish *Bathypterois mediterraneus* belonging to the same family (Chlorophthalmidae), the features of the female portion of the gonad in terms of size, shape, thickness and color were used to classify four main maturity stages: (I) immature (very small size, thin and ribbon-like translucent ovary); (II) maturing (thicker, whitish-pink ovary with small visible oocytes); (III) mature (ovary with maximum thickness and weight full of oocytes of different sizes, many of which hydrated); (IV) spent (opaque and flaccid ovary, no oocyte clusters are visible with the naked eye). In each stage, the ovary was the most evident component of the *ovotestis* while the testis appeared as a colorless filament varying in thickness, the maturity stage of which was never discriminated macroscopically. In order to confirm macroscopic staging, histological analysis was carried out on a sub-sample of gonads (42) collected in each cruise. They were fixed in Bouin's solution and then

Table 1 List of the cruises, date, number of sampling hours, depth range and number of *C. agassizii* specimens collected in the Ionian Sea

Cruises	Date	Number of sampling hours	Depth range (m)	Number of specimens
MEDITS	June 1995	60	10–700	1,866
DEEP-FISHERIES	April 1996	36	250–750	1,888
MEDITS	June 1996	60	10–700	676
DEEP-FISHERIES	July 1996	36	250–750	395
DEEP-FISHERIES	October 1996	36	250–750	4,829
DEEP-FISHERIES	February 1997	36	250–750	2,577
DEEP-FISHERIES	May 1997	36	250–750	1,240
MEDITS	June 1997	60	10–700	2,780
DEEP-FISHERIES	July 1997	36	250–750	1,710
DEEP-FISHERIES	December 1997	36	250–750	5,251
DEEP-FISHERIES	March 1998	36	250–750	2,157
MEDITS	May 1998	60	10–700	2,272
GRUND	Sept–Oct 1998	74	10–700	2,292
INTERREG II	Sept–Oct 1999	49	300–900	37,259
INTERREG II	April 2000	49	300–900	33,529
INTERREG II	July 2000	37	300–900	19,705
INTERREG II	September 2000	37	300–900	6,297

dehydrated in an ascending ethanol series and embedded in paraffin wax (melting point = 56°C). Serial sections of 7 μm thickness were cut and stained with Mayer's hematoxylin–eosin (West 1990).

Considering only the female portion of the gonads and the pooled data for July and September 2000, the size at first maturity (size at which 50% of the fish in the population had mature ovaries) was computed through the logistic curve, showing the percentage of mature specimens by size class.

On a sub-sample of mature individuals (12) collected in September 2000, ovaries were manually dissected to free the oocytes from the ovarian *stroma*. Oocytes were counted and their diameters were measured with an ocular micrometer under a stereoscope. Due to the fact that oocytes are rarely perfectly spherical in shape, the random diameter was measured (West 1990). The size distribution of over 70,000 oocytes was calculated. Absolute and functional fecundity were estimated (Kartas and Quignard 1984). The former was assessed by the number of eggs > 0.1 mm and the latter by the number of hydrated oocytes (Hunter and Goldberg 1980; Jons and Miranda 1997). The relationship between functional fecundity, the total length and body weight of the specimens was assessed using linear regression. The gonad weight and index were not considered in the reproduction analyses since the male portion could affect the results.

Results

Distribution pattern and population structure

C. agassizii was collected between depths of 95 and 670 m in the western Ionian Sea and between 307 and 840 m in the eastern Ionian. In the former area, during the DEEP-FISHERIES and MEDITS surveys, a significant decrease in the density and increase in size with depth were shown (Fig. 2).

The size distributions of *C. agassizii* sampled in the western Ionian Sea are shown in Figure 3. The smallest and largest specimens measured 38 and 189 mm TL, respectively. Although a multi-modal structure was observed in most of the cruises, generally the first two modal classes were found to be the most abundant and were generally well separated from the following classes. The smallest specimens were collected during autumn–winter months. The results of the Bhattacharya

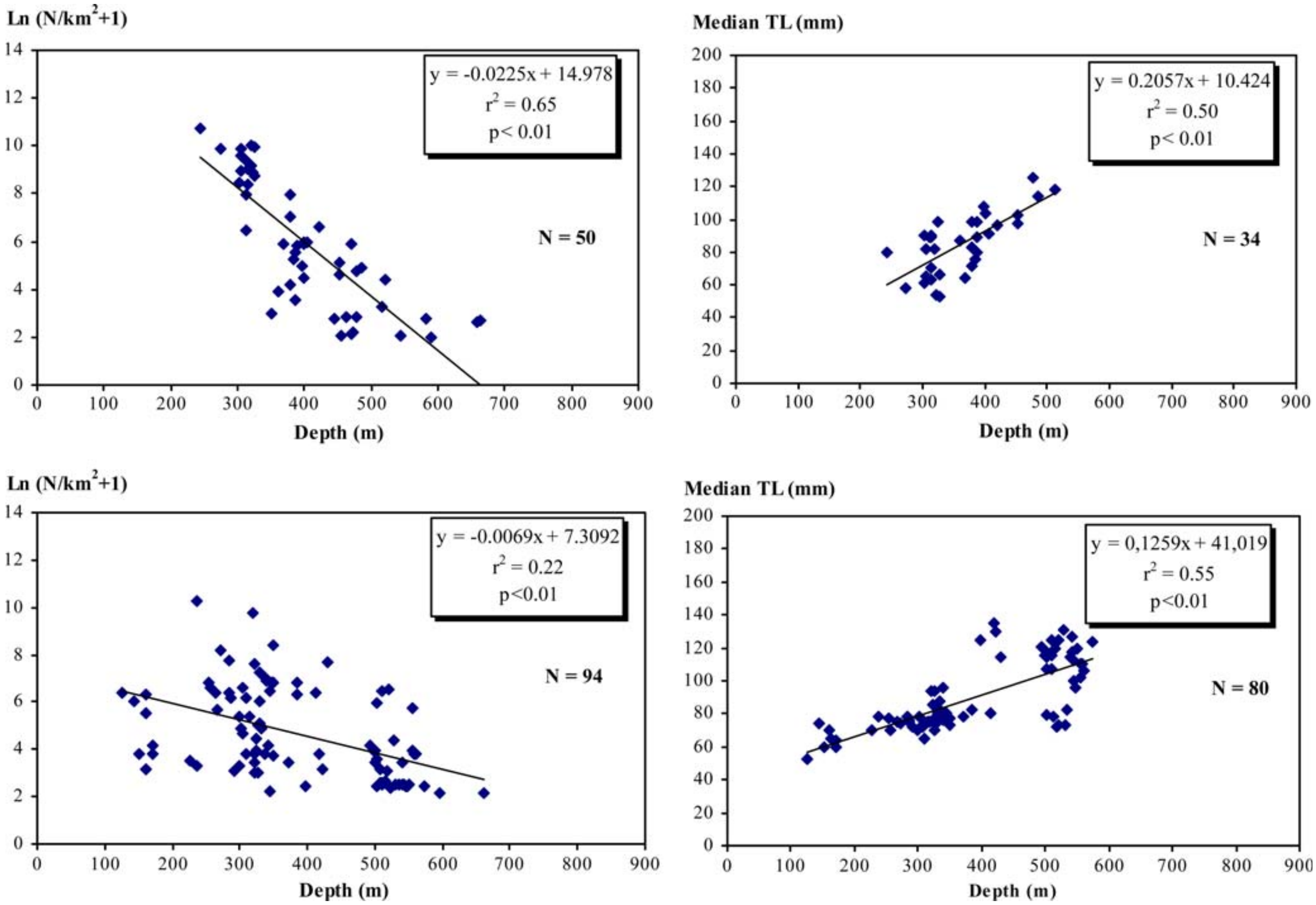

Fig. 2 Scatter plot of the density and median size of each haul by depth, with regression line and parameters, in *C. agassizii* caught in the western Ionian Sea during the DEEP-FISHERIES surveys (above) and MEDITS surveys (below). *N* number of hauls in which density and median size were computed

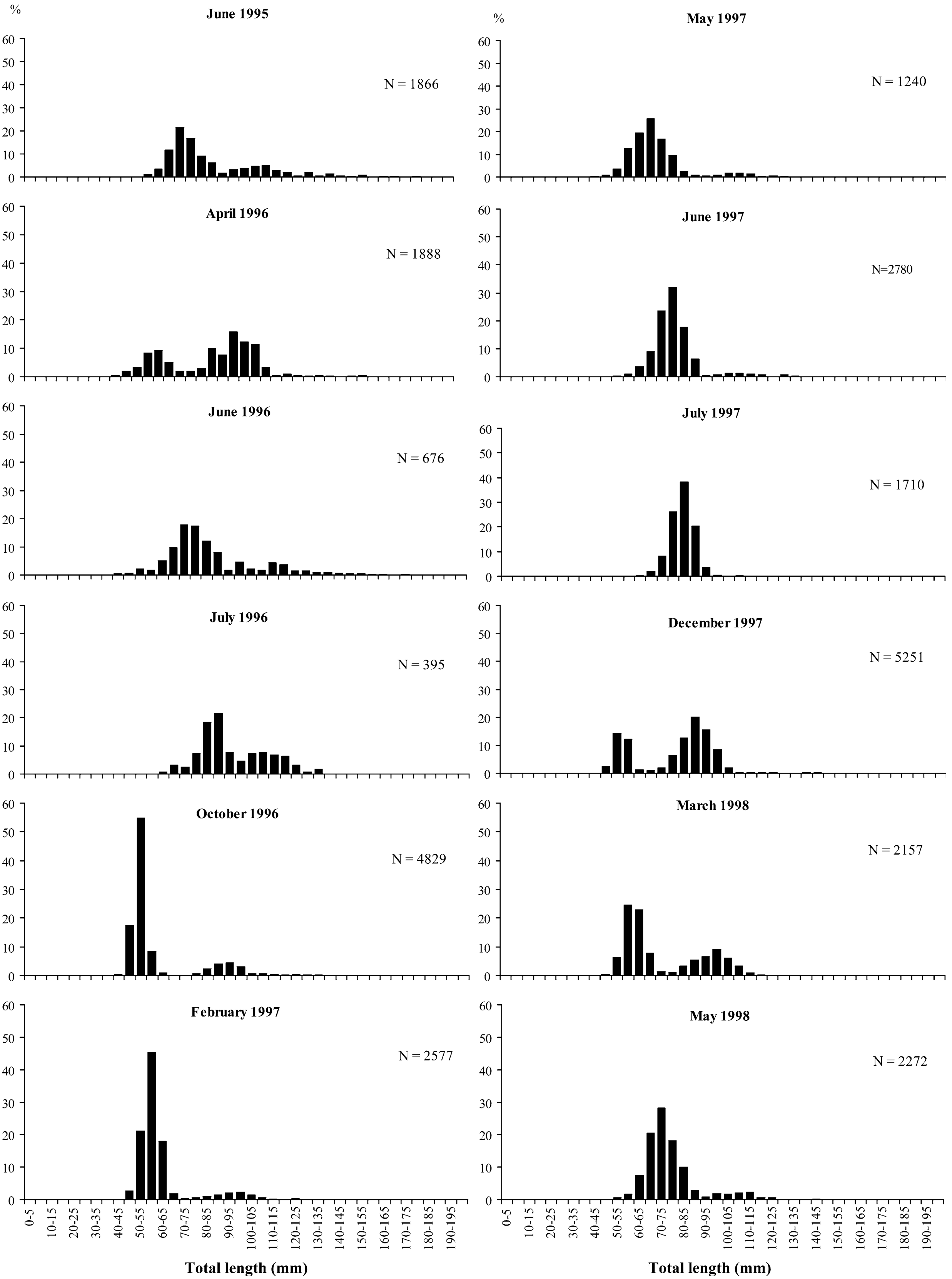

Fig. 3 Length–frequency distribution of *C. agassizii* caught in the western Ionian Sea

method are reported in Table 2. From two to six size groups were identified in the length–frequency distributions of the sampled population. The groups were generally well defined (SI > 2) even though those of the greater individuals were scarcely represented. This is one of the causes that produced significant differences between observed and expected size distributions. However, no statistical differences ($\chi^2 <$ critical value; $p > 0.05$) were shown during June 1996, July 1996 and March 1998.

Age and growth

Although the proportion of the small specimens changed greatly during the study period as a whole, the pattern in the recruitment and in the progression of the first two modes was consistent over the years (Table 2, Fig. 3). In particular, the specimens belonging to the first mode in April 1996 (64.15 ± 5.39 mm) reached a mean size of 86.82 ± 4.42 mm in July 1996. The recruits of 54.44 ± 3.2 mm caught in October 1996 grew to a mean size of 83.48 ± 4.16 mm in July 1997. The recruits of 57.10 ± 3.87 mm collected in December 1997 reached a mean size of 74.05 ± 4.58 mm in May 1998. Although the progression of the second modal component was less evident, the same trend was shown during the study period. The individuals of 76.52 ± 7.68 mm collected in June 1995 reached a size of 104.1 ± 7.18 mm in April 1996. Those of 91.88 ± 6.69 mm caught in October 1996 reached a size of 98.25 ± 7.29 mm in February 1997 and that of 105.16 ± 6.71 in May 1997; individuals of 83.48 ± 4.16 mm caught in July 1997 grew to a mean size of 97.56 ± 7.82 mm in March 1998.

Otoliths of *C. agassizii* are approximately ellipsoidal in shape and are rather thin in the margin. They exhibit alternating opaque and translucent rings. Several thin and not clearly distinct translucent zones were shown around the otolith primordius during the first year of life. The last one of these was generally best developed and distinguished as a complete hyaline zone. The age–length key obtained from 232 otoliths is reported in Table 3. The greatest fraction of otoliths discarded (68 in total) was within the age classes older than 5 years in which the rings in the margin were less distinguishable from each other. The maximum age recorded was 8 years. Apart from the fifth and sixth age classes, a decreasing growth rate with age was shown in the sample. The greatest variability in the length-at-age was shown in the second and third age classes.

The computation of Von Bertalanffy growth parameters using the age–length key gave the following results:

Parameter	Estimate	Standard error
L_∞(mm)	189.04	5.401
k(year)	0.24	0.021
t_o	−1.20	0.132

Table 2 Modal classes separated by means of Bhattacharya method in the length–frequency distributions of *C. agassizii* collected in the western Ionian Sea

Modal class	June 1995				April 1996				June 1996				July 1996			
	Mean	SD	*N*	SI	Mean	SD	*N*	SI	Mean	SD	*N*	SI	Mean	SD	*N*	SI
1	76.52	7.68	500	–	64.15	5.39	97	–	55.15	5.57	30	–	86.82	4.42	178	–
2	112.69	4.51	125	5.93	104.10	7.18	218	6.36	77.09	6.76	260	3.56	115.36	4.83	62	6.17
3	131.63	5.75	36	3.69	130.51	4.30	16	4.60	98.24	5.83	43	3.36				
4	145.56	4.05	16	2.84					118.84	5.56	71	3.62				
5	162.12	3.22	13	4.55					135.52	3.95	14	3.51				
6	187.50	3.37	5	7.69												

Modal class	October 1996				February 1997				May 1997				June 1997			
	Mean	SD	*N*	SI	Mean	SD	*N*	SI	Mean	SD	*N*	SI	Mean	SD	*N*	SI
1	54.44	3.20	751	–	58.90	4.25	573	–	69.62	7.32	660	–	77.61	5.90	616	–
2	91.88	6.69	231	7.57	98.25	7.29	107	6.82	105.16	6.71	77	5.07	108.82	5.41	28	5.52
3	126.06	3.97	14	6.41	112.18	2.04	4	2.98					129.91	4.67	16	4.19
4	141.49	4.00	6	3.87									145.00	4.18	2	3.41
5																

Modal class	July 1997				December 1997				March 1998				May 1998			
	Mean	SD	*N*	SI	Mean	SD	*N*	SI	Mean	SD	*N*	SI	Mean	SD	*N*	SI
1	83.48	4.16	861	–	57.10	3.87	519	–	62.42	4.80	891	–	74.05	4.58	475	–
2	106.36	4.07	6	5.56	77.74	3.84	83	5.36	97.56	7.82	402	5.57	109.07	7.56	104	5.77
3					90.91	6.72	891	2.49					145.00	7.72	5	4.70
4					122.04	5.71	14	5.01								
5					142.44	3.57	9	4.39								

(*SD* = standard deviation; *N* = number of individuals; *SI* = separation index)

Table 3 Age–length key of *C. agassizii* caught in the western Ionian Sea

TL (mm)	Age (year)								
	0	1	2	3	4	5	6	7	8
45 – 50	2								
50 – 55	4								
55 – 60	8								
60 – 65	2								
65 – 70		1							
70 – 75		12	1						
75 – 80		10							
80 – 85		11	2						
85 – 90		7	2						
90 – 95		7	13						
95 – 100		3	16						
100 – 105		2	16						
105 – 110			10						
110 – 115			9						
115 – 120			6	3					
120 – 125			8	5					
125 – 130				2	12				
130 – 135					20				
135 – 140					8				
140 – 145					3	1			
145 – 150					1	8			
150 – 155					1		6		
155 – 160							2		
160 – 165							4	1	
165 – 170									3
N	16	53	83	10	45	9	12	1	3
Mean	54.8	81.8	102.6	120.2	132.8	145.8	156.1	164.0	168.7
SD	3.62	8.84	10.44	3.88	5.92	1.92	4.89	–	1.15
Min	47.0	67.0	74.0	115.0	125.0	142.0	150.0	–	168.0
Max	61.0	103.0	123.0	125.0	152.0	148.0	164.0	–	170.0
Growth rate	–	27.02	20.78	17.59	12.62	12.96	10.31	7.92	4.67

The modal progression analysis throughout the size groups identified in the length frequency distributions produced the following estimate of the Von Bertalanffy growth parameters:

Parameter	Estimate	Standard error
L_∞(mm)	218.33	18.397
k(year)	0.164	0.028
t_o	−1.694	0.171

The growth performance index (ϕ') estimated for the Von Bertalanffy growth parameters obtained from otolith readings and length–frequency analysis were 3.94 and 3.89, respectively. No significant differences were detected in the length-at-age between the two methods ($p > 0.05$).

Reproduction

The specimens collected in the eastern Ionian Sea during the INTERREG II surveys had sizes between 45 and 192 mm TL. The percentages of their ovary maturity stages from macroscopic analysis are reported in Table 4. Immature (stage I), maturing (stage II) and mature (stage III) ovaries were observed in all surveys. However, immature gonads represented the bulk of the samples during April, when only a low percentage of specimens was maturing (7.44%), starting from the size of 90 mm TL, and mature (1.12%), from the size of 130 mm TL. The greatest percentages of mature specimens were shown during July and September 2000 starting from the size of 84 mm TL. However, the size at attainment of 50% maturity was 115 mm TL (Fig. 4). Spent ovaries were only observed during September–October 1999.

Table 4 Total number (N) of individuals examined by season and relative percentages of the ovary maturity stages computed for *C. agassizii* collected in the eastern Ionian Sea

	N	stage I	stage II	stage III	stage IV
September–October 1999	4,179	58.86	27.74	11.37	2.03
April 2000	3470	91.38	7.44	1.12	0.00
July 2000	2164	25.26	56.03	18.69	0.00
September 2000	1178	35.68	17.40	46.46	0.00

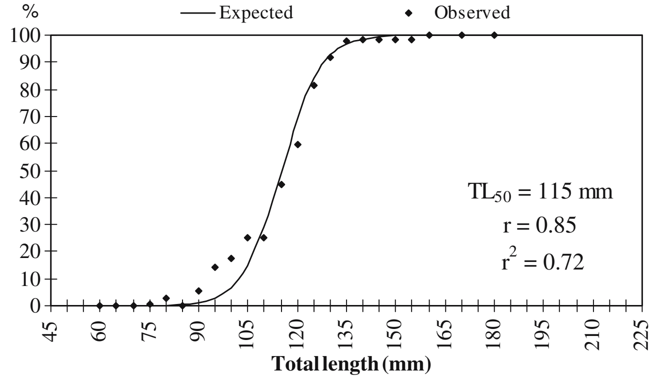

Fig. 4 Expected and observed percentage of mature specimens, related to the size, and size at first maturity of *C. agassizii* sampled in the eastern Ionian Sea

Histological analysis in all samples revealed the presence of ovotestis, in which both male and female tissues occurred simultaneously and were clearly separated into two zones by the connective tissue (Fig. 5).

The ovary showed the presence of oocytes in different developmental stages at the same time. On the basis of the oocyte stages, five different ovarian developmental phases were distinguished:

1) *Immature ovary*. The immature ovary showed mainly pre-vitellogenic oocytes ranging from 15 to 150 μm and few oocytes (diameter 150–250 μm) containing lipid droplets.
2) *Resting (inactive) ovary* (Fig. 6A). The pre-vitellogenic ovary contained a greater number of lipid stage oocytes, some of them showed atretic phenomena.
3) *Maturing (growing) ovary* (Fig. 6B). This ovary showed pre-vitellogenic oocytes as well as early vitellogenic oocytes (diameter 250–300 μm) characterized by the appearance of acidophilic yolk globules.
4) *Gravidic (mature) ovary* (Fig. 6C). The ovary contained pre-vitellogenic, early vitellogenic, advanced vitellogenic (diameter 350–450 μm), hydrated oocytes (diameter 450–850 μm) and post-ovulatory follicles.
5) *Spent (regressive) ovary* (Fig. 6D). The ovaries were characterized by pre-vitellogenic oocytes, some of them were atretic, post-ovulatory follicles and lacunose interstitial tissues. Testis tissue consisted of a convoluted seminiferous tubule. The wall of the seminiferous tubule was formed by several types of cysts, each consisting of synchronously developing germ cells. Mature spermatozoa were accumulated in the tubule lumen after the breakdown of the cysts.

Fecundity

The fecundity was measured in 12 specimens with mature ovaries and sizes between 99 and 179 mm TL. The absolute fecundity ranged from 1,499 to 15,730 oocytes (mean value = 5,421 ± 3,855 oocytes) while the functional fecundity was between 569 and 7,428 oocytes (mean value = 3,018 ± 2,006 oocytes). The functional fecundity was between 37 and 69% of the absolute fecundity and increased significantly with individual total length ($FF = 44.57TL - 2873$, $r^2 = 0.36$, $p < 0.05$) and individual body weight ($FF = 105.42BW + 1003$, $r^2 = 0.40$, $p < 0.05$).

The oocyte diameter distribution showed a bimodal trend more skewed to the right in September than in July (Fig. 7). Pre-vitellogenic and vitellogenic oocytes in different development stages belonged to the first mode while hydrated oocytes made up the second mode. Although, the diameter of the oocytes increased according to their development stage, high variability was shown in each stage.

Discussion and conclusions

The distribution of *C. agassizii* in the Ionian Sea showed a clear depth-related trend: its density decreased significantly with depth while its size increased. The highest densities recorded on the shelf and shelf edge were mostly due to the young-of-the-year and juveniles which move towards deeper bottoms as they grow. This depth-related trend appears to conform to the "bigger–deeper" phenomenon (Polloni et al. 1979) and indicates ontogenetic migrations towards deep waters as shown in many shelf and slope species in the western Mediterranean (Macpherson and Duarte 1991). According to a

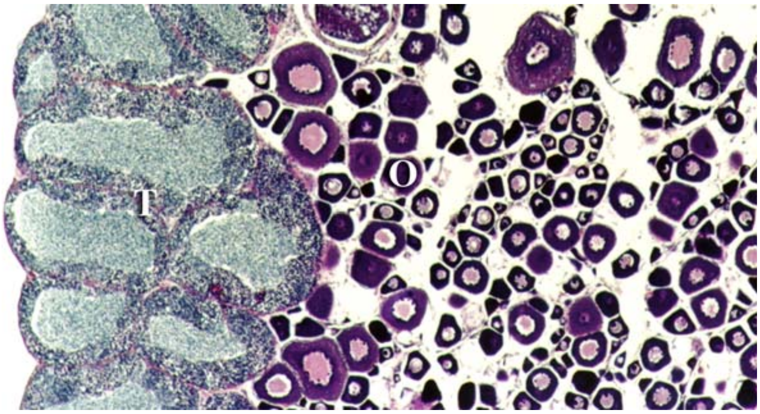

Fig. 5 Male (*T*) and female (*O*) portions of the gonad in *C. agassizii*

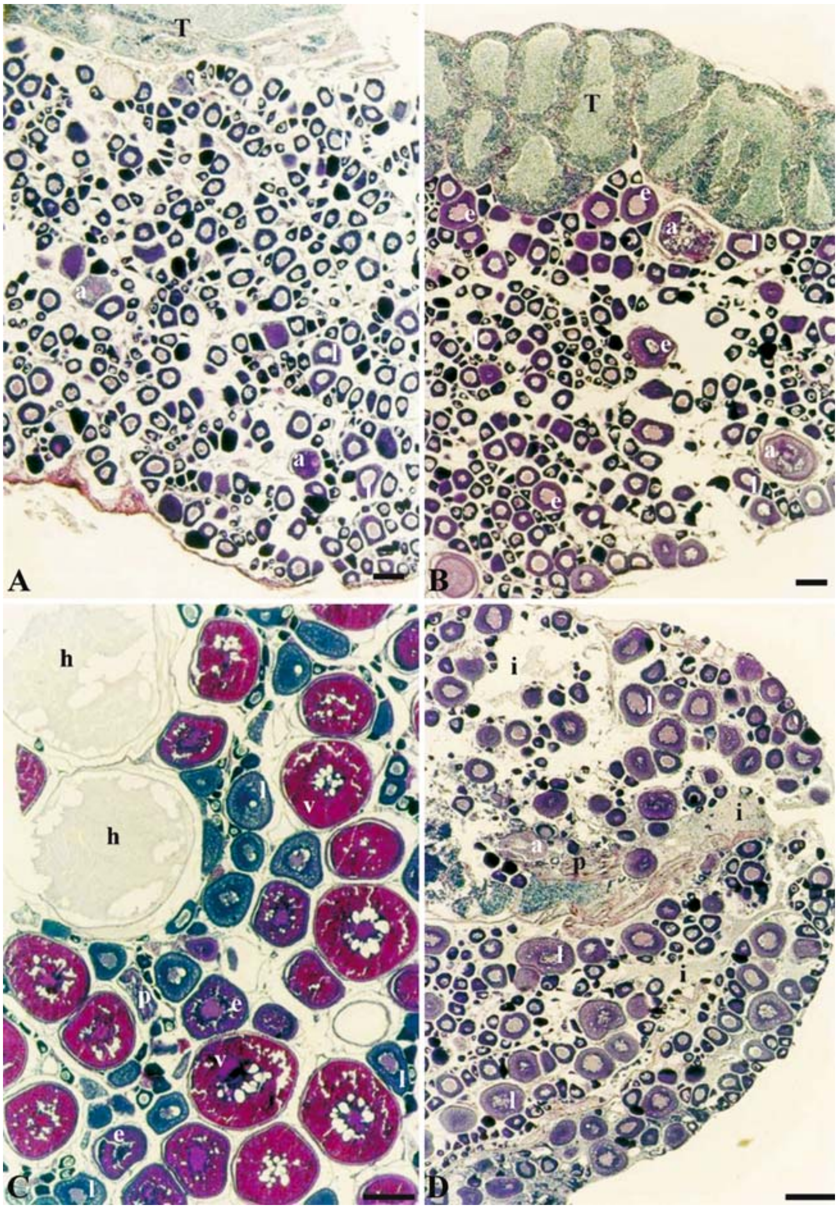

Fig. 6 Light micrographs showing different ovarian developmental phases in *Chlorophthalmus agassizii*. (**A**) Resting ovary. (**B**) Maturing ovary. (**C**) Gravidic ovary. (**D**) Spent ovary. Haematoxylin–eosin staining (bar = 200 μm). *a*, atretic oocyte; *e*, early vitellogenic oocyte; *h*, hydrated oocyte; *i*, lacunose interstitial tissue; *l*, lipid stage oocyte; p, post-ovulatory follicle; *T*, testis; *v*, late vitellogenic oocyte

common pattern in teleosts (Cushing 1976; Gordon 1979; Macpherson and Duarte 1991) and previous observations on *C. agassizii* (Sanzo 1915; Taning 1918; Mead et al. 1964; Costa 1999), in the Ionian Sea the early life stages of this fish develop in warmer waters while adults are mostly distributed in a colder habitat with a fairly constant temperature (13–14°C) (Malanotte-Rizzoli et al. 1997). The former live in an environment where food supply is greater than that where the latter are distributed (Danovaro et al. 1999; Cartes et al. 2002).

Despite the high changes in the individual numbers sampled throughout the surveys, the modes in the size distribution were consistent over the years. The recruitment peak of *C. agassizii* in the Ionian Sea occurs as a discrete phenomenon during autumn–winter months. A high correspondence in the growth pattern was shown between the modal progression analysis and otolith readings, suggesting that the former can validate the latter, at least for the first years. In fact, due to the superimposition of the lengths in the size–age classes older than the third, the length–frequency distribution analysis rarely revealed a complete correspondence between modal components and age classes. Thus, from the third size–age class onwards the growth process becomes less clear in the length–frequency distributions. A more complete coverage of the age distribution in the sampled population was obtained through otolith readings, although the maximum age read on the otoliths (eight years for a mean size of 168.7 mm TL) is most probably less than that present in the population (maximum size of 192 mm TL). In fact, the greatest individuals are distributed at greater depths than those investigated in the western Ionian Sea.

The age–length key obtained in this study shows a greater growth rate than that reported by Specchi et al.

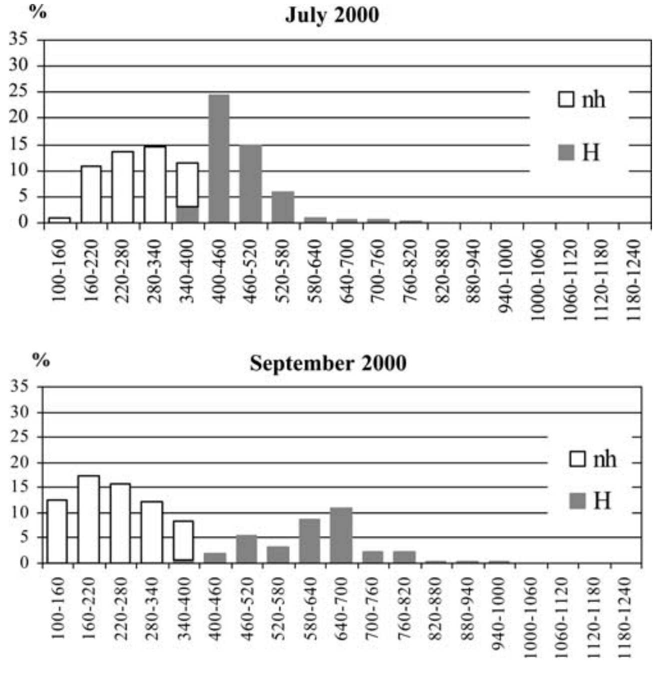

Fig. 7 Size frequency distribution of diameters for non-hydrated (*nh*) and hydrated (*H*) oocytes in *C. agassizii*

(1995), even though these authors provided results only for the first three age classes. Considering the maximum size collected in the sampled population, a longevity greater than 10 years appears to be realistic for this "shelf-slope" fish of relatively small size and living in the relatively warmer deep-water of the Mediterranean. A higher growth rate and a lesser longevity were detected in *C. agassizii* than in *Bathypterois mediterraneus*, a teleost fish belonging to the same family (Chlorophthalmidae) but living on the lower slope (Morales-Nin et al. 1996; D'Onghia et al. 2004). In fact, when closely related species are compared, those living at the greatest depths show the slowest growth rates and greatest longevity (Gage and Tyler 1991).

Otolith readings in *C. agassizii* provided an indication of seasonal growth both in juveniles and adults. Temperature cycles, spawning and changes in feeding patterns are considered the main factors influencing ring formation (Massutí et al. 1995 and references therein). Concerning temperature, during its life cycle the shortnose greeneye dwells both in waters subject to seasonal variations of this parameter and in waters with a fairly constant temperature. Thus, excluding the influence of spawning, since seasonal growth was shown even in immature individuals, the periodicity of ring formation might be mostly related to seasonal fluctuations in feeding patterns, as shown in other deep-water fish (e.g. Childress et al. 1980; Mauchline and Gordon 1984). Indeed, Cabiddu et al. (2005) reported that the diet of *C. agassizii* consists mainly of copepods and euphasiids and it is mostly influenced by the size and, to a lesser extent, by the season in relation to the different availability of food resources. In the oligotrophic Mediterranean waters the seasonal food availability, not only in surface waters but also on the slope, is due to the annual peaks of primary production occurring during spring and autumn (Dugdale and Wilkerson 1988; Danovaro et al. 1999; Cartes et al. 2002).

Seasonal reproduction in deep-sea species also seems to be mainly regulated by food availability (Gage and Tyler 1991). A seasonal reproductive pattern is known in Mediterranean fish species, such as *Phycis blennoides* and *Hoplostethus mediterraneus*, distributed in the same depth range as *C. agassizii* (e.g. D'Onghia et al. 1998; Matarrese et al. 1998; Rotllant et al. 2002 and references therein). Indeed, *C. agassizii* in the Ionian Sea displays a seasonal synchronized reproduction with spawning occurring between July and September as recently shown in the central–western Mediterranean (Follesa et al. 2004). According to these authors, the simultaneous presence of oocytes in different development stages in the mature ovary (asynchronous ovary) together with the oocyte size distribution trend would indicate that eggs can be spawned more than once during the reproductive season and thus *C. agassizii* can be considered as a multi-spawner fish (batch spawner). Wallace and Selman (1981) reported that in ovaries with at least two size groups of oocytes, the larger group is spawned in more than one batch during the reproductive season.

Deep-water fish belonging to the order Iniomi (Scopeliformes) are known as simultaneous hermaphrodites (Mead et al. 1964; Fishelson and Galil 2001) and some of them are batch spawners (Merrett and Haedrich 1997). Batch spawning helps larvae to coincide with their food supply (Marshall 1971). The fact that the shortnose greeneye is a hermaphrodite although it lives in abundant shoals might be related to the phylogenetic constraints which affect reproduction more than environmental adaptations (Grassle 1994; Haedrich 1996). The smallest mature specimen and the size at attainment of 50% maturity shown in the Ionian Sea, would indicate that reproduction can start in the second year of life but become prominent for the population in the third year of life.

Concerning fecundity, this varies within species with spawning time, latitude and location, as well as individual and egg size (Ware 1975; Mann et al. 1984; Merrett and Haedrich 1997). Fecundity in *C. agassizii* varied greatly among the specimens examined: the bigger the specimens, greater was the fecundity. However, it was in the range of Aulopiformes fishes reported by Merrett and Haedrich (1997). Mead et al. (1964) reported a fecundity of 4,500 eggs for *Bathypterois quadrifilis* and 900 eggs for *Ipnops murrayi*, indicating that the deep-sea Iniomi produce a relatively small number of eggs. Fishelson and Galil (2001) counted 2,000–2,400 eggs in a clutch from *Bathypterois mediterraneus*. The relatively low fecundity recorded in the shortnose greeneye may be offset by its batch spawning and iteroparity (Miller 1979) as well as by its simultaneous hermaphroditism in high-density shoals. In this latter respect, one compensatory effect of high-density in a population is reduced fecundity (Begon et al. 1986).

With regard to the egg size, this increases with body size and decreases with increasing temperature (Chambers 1997). Furthermore, the egg size is inversely correlated to the number produced (Duarte and Alcaraz 1989). Most of the species which spawn small eggs (< 2 mm) have pelagic development (Ware 1975; Duarte and Alcaraz 1989; Merrett and Haedrich 1997). Indeed, pelagic development is known in *C. agassizii* (Mead et al. 1964). Sanzo (1915) collected larval forms with sizes between 7.86 and 30 mm in the waters of the Strait of Messina. He reported that Facciolà found a larvae of 40 mm in the same waters. Taning (1918) sampled young stages during the *Dana* expedition. In the Strait of Messina, Costa (1999) collected a larval form of 24 mm at 50 cm under the surface during November. The type of eggs (size and hydration) recorded in this study conforms to a pelagic larval phase. Pelagic environment plays a fundamental role in the success of offspring (Cushing 1976; Gordon 1979). *C. agassizii* seems to be subject to casual fluctuations in the environment well displayed by the variable abundance in the recruitment. Indeed, in temperate waters recruitment seems to be more strongly affected by the abiotic factors of the ecosystem (Cushing 1982).

In summary, *C. agassizii* seems to adopt life strategies in which both phylogenetic constraints and environmental adaptations act on its life cycle under variable conditions, from the shelf to the slope and between pelagic and demersal habitats. Recruitment of *C. agassizii* occurs as a discrete phenomenon during early autumn and is the consequence of synchronous spawning during summer–early autumn. The spawners produce a relatively small number of eggs that are shed more than once during the reproductive season. Pelagic development of the early life stages occurs in warmer surface waters with a greater food supply. After the pelagic phase, the juvenile forms adopt a demersal habit and can be collected on the shelf. Thus, they carry out ontogenetic migration towards deeper bottoms. The growth rate appears to be relatively slow and decreases with the age. The population consists of several size–age groups. Individuals reach sexual maturity within the third year of life and start to reproduce annually, exhibiting batch spawning during the reproductive season and iteroparity over a life span greater than 10 years.

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