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Age, growth and bathymetric distribution of red pandora (*Pagellus erythrinus*) on the Cretan shelf (eastern Mediterranean)

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Data from bottom trawl surveys conducted each summer, winter and spring on the Cretan shelf from 1988 to 1991, were used to study the age, growth, maturity and bathymetric distribution of red pandora (*Pagellus erythrinus*). The good agreement of back-calculated and observed lengths-at-age with length frequencies and the marginal increment analysis, supported the annual nature of scale marks. A comparison of available growth data from the Mediterranean and the Atlantic revealed higher lengths-at-age for red pandora in the north-western Mediterranean and the Atlantic than in the central and eastern Mediterranean. The auximetric analysis, i.e. the double logarithmic plot of the parameter K of the von Bertalanffy growth function vs asymptotic length ($L\infty$), showed a strong negative relationship for the central and eastern Mediterranean data set, implying a common 'growth space' for the populations in these areas. Lengths-at-maturity were lower on the Cretan shelf than in the Atlantic. These differences were attributed to the synergistic combination of trophic and thermal conditions.

Depth, temperature and salinity data were combined with biological data on abundance, fish size, age and maturity. In general, mean size increased with bottom depth because smaller individuals tended to be found in shallower and warmer waters. Individuals having reached first maturity were mainly distributed in the periphery of the algal/angiosperm meadows (60–80 m). All detailed studies of the bathymetric distribution and movements of shelf-dwelling demersal species (*Mullus barbatus*, *Mullus surmuletus*, *Lepidotrigla cavillone* and *Pagellus erythrinus*) in the Mediterranean show that these species are characterized by a spring–summer spawning season, a high concentration of spawning adults at mid-shelf depths, and nursery grounds located in the vegetated shallows. This multispecies pattern might have an adaptive function with both ecological and management implications.

INTRODUCTION

The multispecies nature of demersal fisheries in the Mediterranean poses serious problems to single species management (Caddy, 1993; Stergiou et al., 1997). It is considered fundamental that demersal fishes be categorized into groups of species sharing similar biological characteristics for the implementation of management measures (Caddy, 1993). Such groupings should be based on a detailed knowledge of species distribution and growth patterns, lengths at maturity and trophic level. Under the more general framework of multispecies approaches to the study of fish populations, an important ecological consideration would be whether such groups have an intrinsic adaptive function, reflecting common adaptations of species to the marine environment (Somarakis et al., 2000).

Knowledge of the distribution and movements of the exploited stocks is essential for the proper management of the resources (Machias et al., 1998; Mullen, 1994). It is important for management to identify 'sensitive areas', or 'critical habitats', such as spatially restricted spawning and/or nursery grounds (Caddy, 1998). Depth, temperature and salinity preferences of most marine fish are generally poorly known and relevant information is widely scattered in the literature, being mainly based on limited observations. This is especially true for demersal species on the Mediterranean continental shelves where available data come mainly from commercial fisheries, hence there is limited possibility for investigation of the relationships between biological and environmental parameters (Machias et al., 1998).

There is a general trend for larger fish to occur in deeper waters and the fish of the inshore zone usually seem to undertake an ontogenetic migration to deeper water. However, there is a paucity of studies on the phenomenon and disagreement on its causes and generality (Haedrich & Rowe, 1977; Labropoulou et al., 1999; Machias et al., 1998; Macpherson & Duarte, 1991; Stefanescu et al., 1992).

Red pandora, *Pagellus erythrinus* (L., 1758), is a highly valued demersal species distributed in the Mediterranean, Black Sea and along the European and African coasts of the Atlantic, from Angola to Norway (Fisher et al., 1987). It is a protogynous hermaphrodite and a multiple spawner characterized by a protracted late-spring to late-summer spawning period (Girardin, 1981; Pajuelo & Lorenzo, 1998; and references therein). Age and growth of the species have been studied in the western Mediterranean (Castellon coast: Larraneta, 1967; Gulf of Lions:

Girardin, 1981), the eastern Mediterranean (Ionian Sea: Papaconstantinou et al., 1988) and the Atlantic Ocean (Canary islands: Pajuelo & Lorenzo, 1998). There are also many other reports of less detailed studies all along the Mediterranean coasts. One objective of the present study was the estimation of the age and growth of red pandora on the Cretan shelf and the comparison of all available growth data. The second objective was to analyse the bathymetric distribution and movements of the species, which are largely unknown. The results of this analysis are compared to those of other Mediterranean, demersal, shelf-dwelling species in an effort to identify common multispecies patterns.

MATERIALS AND METHODS

Trawl sampling

The seasonal distribution of red pandora at various depths and within various temperature ranges was studied using data from three years of seasonal sampling. Seasonal bottom-trawl surveys were carried out on the Cretan shelf from August 1988 to April 1991. Specifically, one survey was conducted in summer (late July to September), winter (November to December) and spring (March to May) of each year (Table 1). Each survey comprised about 40 depth-stratified random stations, in all trawlable areas of the shelf (Figure 1). Three depth strata were selected (Tsimenides et al., 1991): 26–70 m (stratum I), 71–150 m (stratum II) and 15–350 m (stratum III). Stratum I covered 25%, stratum II covered 24% and stratum III 51% of the total survey area. Stratum I spanned a substratum covered by algae (*Caulerpa prolifera*) and sea grass (*Posidonia oceanica* and *Halophila stipulacea*); the substratum of stratum II consisted mostly of mud, sand or detritus, and the substratum of stratum III was covered for the most part by crinoids (mostly *Leptometra phalangium*). All tows were carried out approximately in parallel with the 100 or 200 m isobaths during daytime. No tows were taken in water deeper than 350 m.

Table 1. *Cretan shelf (eastern Mediterranean). Cruise dates of the demersal fish surveys.*

Cruise	Date
1	03 Aug–11 Aug 1988
2	29 Nov–15 Dec 1988
3	04 Apr–03 May 1989
4	27 Aug–30 Sep 1989
5	11 Nov–21 Dec 1989
6	20 Mar–27 Mar 1990
7	20 Jul–09 Aug 1990
8	05 Dec–17 Dec 1990
9	24 Apr–23 May 1991

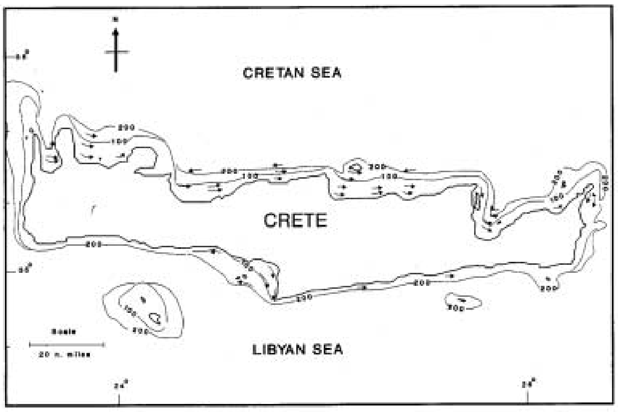

Figure 1. Map of the sampled area indicating the 100 and 200 m isobaths, as well as the position and direction of the hauls (arrows).

The duration of each haul ranged from 50 to 90 min at a towing speed of 1.8 to 3 kn, depending on the depth and nature of the bottom. Gear selectivity was assumed to be constant because the same vessel (RV 'Philia') and fishing gear were used in the survey (Tsimenides et al., 1991). The catch from each haul was identified to species level, enumerated and weighted, and the bottom depth, water temperature and salinity were recorded. The door spread of the trawl net was calculated for each haul based on the method of Carrothers (1980). Total area swept was calculated by multiplying the door spread by the vessel speed and the fishing time. Fish abundance was expressed as number of fish or biomass per square nautical mile (n.m.^{2}). The depth of tow was determined by means of an echo-sounder (average depth of tow was used). Bottom temperature and salinity were measured using a SEA–BIRD CTD unit. Length frequencies were measured onboard during all cruises.

Biological measurements

All red pandoras caught during the first three cruises were frozen-transferred to the laboratory where individuals were measured to the nearest mm for fork (FL) and total length (TL), and sexed. Total weight and gonad weight were measured to the nearest 0.01 g and 0.1 mg respectively. Gonadal development was assessed macroscopically, using a four stage key adapted from Larraneta (1953) and Machias et al. (1998): I, immature or resting; II, developing; III, late-developing to running; IV, spent. The size at which 50% of fish were mature (size at maturity, L_{50}) was determined from the relationship between percentage (P) of mature fish (stage II–IV) at length class L. This relationship, widely used for maturity studies (Stergiou et al., 1996) is described by the logistic function:

$$P = [\exp(v_1 + v_2 \times L)]/[1 + \exp(v_1 + v_2 \times L)] \qquad (1)$$

and the value L_{50}, L_{25}, L_{75} can be estimated from the expressions:

$$L_{50} = -v_1/v_2,$$

$$L_{25} = [-\ln(3) - v_1]/v_2$$

$$L_{75} = [\ln(3) - v_1]/v_2$$

The proportion of mature fish for each 10-mm length class was calculated by sex and v_1, v_2 were calculated using Fryer's (1991) algorithm by maximizing the log-likelihood, ln(L) (Petrakis & Stergiou, 1997). A test for over-dispersion was obtained by estimating the deviance statistic Δ and comparing it to a χ^2 distribution on N-2 degrees of freedom (Petrakis & Stergiou, 1997). The data are over-dispersed if $\Delta > \chi^2$.

The standard errors and the 95% confidence intervals of the estimated value of L_{50} were calculated following procedures described in Petrakis & Stergiou (1997).

Age and growth

Scales and otoliths were removed from a representative sample of fish for subsequent age determinations. In total, 1190 individuals were used (Table 2). They were mainly caught in cruises 1, 2 and 3 (1988–1989, Table 1). Additional samples of large fish (>150 mm) were obtained during the last cruise (April–May 1991, Table 1) because large fish were generally rare in the samples of the first year.

Scales were used for age determinations since the macrostructure of unsectioned otoliths was unclear (see also Girardin, 1981; Larraneta, 1967). Scales and scale marks of red pandora have been described in much detail (Girardin, 1981; Larraneta, 1967). They are generally clear, linearly and closely related to fish length and easily interpretable.

The scales were removed from the left side below the lateral line near the tip of the pectoral fin, and stored dry. Six scales from each fish were cleaned with water, placed on a 0.3 mm thick cellulose acetate plastic plate and pressed at a temperature of 90°C for two minutes. The prepared plates with the prints of the scales were examined under a binocular microscope.

Scales were interpreted by use of standard criteria (Bagenal & Tesch, 1978). Annual marks were distinct in both the anterior and lateral scale fields and displaced cutting-over of circuli in one or both lateral fields. Annuli were clearest in the anterior field, were closely spaced circuli were followed by wider spacing beyond the edge of the annulus. Non-annual marks, when occurring, were usually unclear or missing in one or more fields and often lacked cutting-over. Annuli were apparent in all scales examined per fish, whereas accessory marks usually were not.

The scales were examined independently by each of the authors. When readings of the same fish were different, the scales were considered unreadable (10% of the examined scales, Table 2).

Annuli and scale sizes were measured on one representative scale along the longest axis from the focus to the right of the anterior field. We used marginal increment analysis and length frequency comparisons to establish approximate time and frequency of mark formation. The marginal increment ratio was calculated for each specimen according to the formula:

$$MI = (S - R_i)/\text{mean}\ (R_{i+1} - R_i) \qquad (2)$$

where S = scale radius; R_i = radius at the most recent annulus (i = I, II, III, ...); and mean $(R_{i+1} - R_i)$ = average width of the i-th+1 scale increment calculated from all fish. The marginal increment ratio used here ranges from 0 to >1, and allows comparisons and pooling of marginal increment data of different fish ages.

Age-classes were assigned based on the number of scale annuli, marginal increment spacing, month collected and size comparison to length frequencies. June was used as the birthdate, when fish of a particular age were assigned to the next age-class. Red pandora spawn from spring to late summer (Girardin, 1981; Mytilineou, 1989). The evolution of the gonadosomatic index (GSI) of fish collected in

Table 2. Pagellus erythrinus. *The sample used in the growth analysis.*

			Annuli							
Length	N	Aged	0	I	II	III	IV	V	VI	VII
50	5	5	5							
60	9	9	9							
70	23	23	23							
80	42	40	37	3						
90	97	96	80	16						
100	92	92	52	40						
110	64	55	15	40						
120	139	125	3	119	3					
130	174	159		140	19					
140	173	138		43	94	1				
150	161	135		11	112	12				
160	82	74		3	59	12				
170	60	55			25	30				
180	25	22			1	17	4			
190	19	19				10	7	2		
200	14	13				2	6	5		
210	7	7						6	1	
220	1	1								1
230	3	2								2
Total	1190	1070	224	415	313	84	17	13	1	3

N, number of specimens used in scale ageing; Aged, number of fish for which ageing was possible; I, a single annulus is present on the scale; II, two annuli present, etc.

Iraklion Bay (northern Crete) during other trawl samplings in spring–summer 1991 (Table 3), indicated higher GSI values in late May–mid June justifying our use of 1 June as the peak spawning-birth date (Moreau, 1987).

Back-calculated lengths at annulus formation were derived by the use of Lee's method (Bagenal & Tesch, 1978), which is a modified version of the direct proportion formula:

$$L_i - c = (R_i/S)/(L - c) \tag{3}$$

where $L_i = FL$ when the annulus i was formed; $L = FL$ at time of capture; $c =$ intercept on length axis from linear regression of length on scale radius; $R_i =$ distance from scale focus to annulus I; and $S =$ scale radius.

Estimates of theoretical growth in length were obtained by fitting the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938) to the mean observed length-at-age data. The VBGF is expressed as

$$L_t = L\infty(1 - \exp(-K(t - t_0))) \tag{4}$$

in which L_t is length-at-age, $L\infty$ is the asymptotic length, K is Brody growth coefficient, and t_0 is the age at which length is zero. Growth parameters were estimated iteratively using the Simplex minimization algorithm (Wilkinson, 1988). Mean data were used in order to assign equal weight to all observations.

Growth curves for females and males were estimated separately and compared by analysis of the residual sum of squares (Chen et al., 1992). The two curves were not significantly different ($P > 0.05$). Similarly, the FL-on-S relationships and the back calculated lengths-at-annuli formation were not statistically different between sexes ($P > 0.05$), hence, age data of different sexes were pooled.

Available growth data for red pandora from different parts of the Mediterranean Sea and the Atlantic Ocean were re-analysed to account for differences in methodologies and data quality and subsequently compared. The estimated VBGF growth parameters of the different stocks were used to construct an auximetric plot, i.e. a double logarithmic plot of the parameter K vs asymptotic length ($L\infty$). When the regression of $\log_{10}K$ on $\log_{10}L\infty$ is restricted to stocks with similar growth performance, the slope equals -2 (Pauly et al., 1998; Stergiou, 2000).

Bathymetric distribution and movements

Analysis of variance of the log-transformed abundance or biomass values showed no significant differences either among the three surveys in the same season, nor among the same stratum of the three surveys in the same season ($0.074 < P < 0.564$, Bartlet test: $0.087 < P < 0.765$). For each season, results and conclusions were similar and independent of whether survey-specific or pooled data were used. Hence, only the latter are presented here.

Correlation analysis (Pearson correlation coefficient) was used to test the hypothesis that fish size is depth-dependent. Fish size was also tested for any significant correlations with temperature. Geometric mean was preferred for calculation of the mean fish size of each sample, because the arithmetic mean is susceptible to the influence of a few large specimens and does not represent accurately the mode in fish size at a given station (Stefanescu et al., 1992). To test the hypotheses 'fish size is depth-dependent', 'bigger individuals tend to be found in deeper water' and 'smaller fish tend to be found in shallow water', correlation analysis was performed between depth and mean, maximum or minimum FL (Machias et al., 1998; Macpherson & Duarte, 1991; Stefanescu et al., 1992). The same three variables were used in correlation analysis with respect to temperature.

The bathymetric distribution of different-sized fish was simplified as follows: lengths were converted to ages using the estimated von Bertalanffy growth equation (Machias et al., 1998). Relationships between density (fish n.m.$^{-2}$) and temperature or bottom depth were examined by use of cumulative distribution functions (CDFs; Perry & Smith, 1994). The CDF (%) for temperature (available temperature) or bottom depth (available depths), f(t), was calculated for each season as follows:

$$f(t) = 100\frac{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}I}{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}} \quad \text{where } I = \begin{cases} 1, \text{if } x_{hi} < t \\ 0 \; otherwise \end{cases} \tag{5}$$

where t is a level of temperature or bottom depth, A_h is the area of stratum h, n_h is the number of tows in stratum h, x_{hi} is the bottom temperature or depth of tow i in stratum h and L is the number of strata. The CDF for red pandora catch, g(t), was calculated similarly:

$$g(t) = 100\frac{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}y_{hi}I}{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}y_{hi}} \quad \text{where } I = \begin{cases} 1, \text{if } x_{hi} < t \\ 0 \; otherwise \end{cases} \tag{6}$$

where y_{hi} is the number of red pandora caught in tow i in stratum h. Cumulative distribution functions were produced separately for each age. Subsequently, we calculated:

Table 3. *The evolution of the gonadosomatic index (GSI) of fish collected in Iraklion Bay (northern Crete) during trawl samplings in spring–summer 1991 (unpublished data).*

Date	N	Length range (mm)	GSI (%)	SE
02 Apr	7	150–193	1.76	0.348
25 Apr	4	140–152	3.87	1.775
21 May	16	143–187	4.49	0.748
13 Jun	10	156–188	4.47	1.149
13 Jul	5	151–160	3.74	0.706

N, number of specimens; SE, standard error.

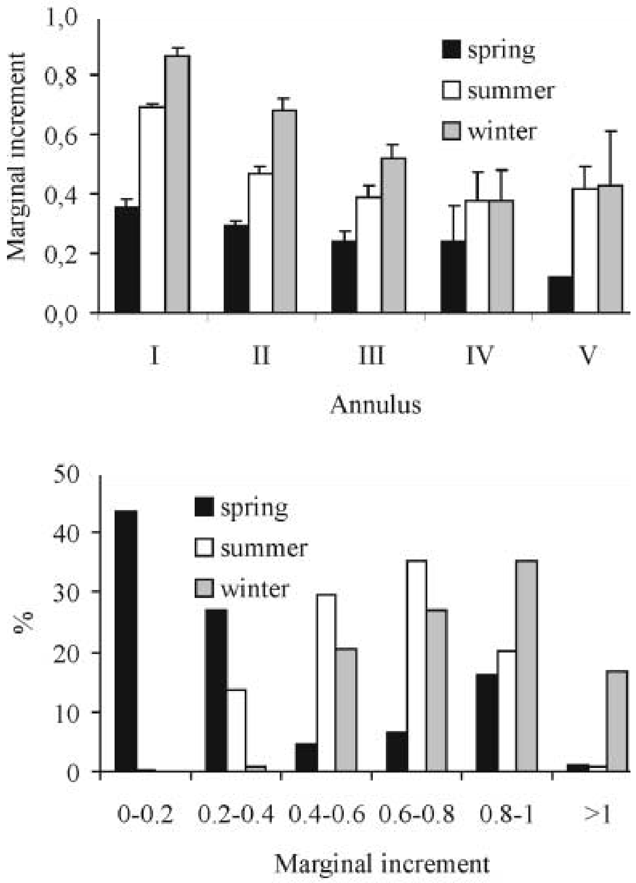

Figure 2. Marginal increment analysis. (A) Means and standard errors (bars) of marginal increment (MI) following annulus I, II, III, IV and V in spring, summer and winter; (B) frequency distribution (%) of marginal increment values in spring, summer and winter.

$$S = \sum_{t=1}^{t} [\, f(t) - g(t)] \qquad (7)$$

for each season and age group. S compares average available temperature or depth to the average temperature or depth selected by red pandora. Positive values of S indicated that fish select temperatures and depths greater than the available and vice versa. A Kolmogorov–Smirnov type of statistic was used to test the significance of temperature and bottom depth selection. The test statistic D was the maximum absolute vertical distance between f(t) and g(t) with the two functions compared at 0.2°C (CDFs of temperature) or 10 m (CDFs of depth). Significance was assessed using randomization tests (Perry & Smith, 1994; Swain & Krammer, 1995).

RESULTS

Annuli formation

Marginal increment (MI) data indicated that one annulus was formed per year. Minimum mean marginal scale increments were displayed in spring for age 1–5 fish (Figure 2A), suggesting annulus formation near that period. The seasonal pattern in mean marginal increment was less clear for ages greater that four because sample sizes were small. The frequency distributions of MI values for the seasonal samples (Figure 2B), showed a bimodal pattern for the spring sample. This was due to most fish having a scale annuli situated near the margin of the scale and a smaller group of specimens having large MI values (but higher FL than fish of the same annuli number but low MI). The latter group, were most likely fish that had not yet formed their last annuli.

Whereas different annuli are not formed synchronously and there might be large inter- and intra-age class variability in the timing of their formation, it might be suggested that most specimens form an annual mark in their scales around April.

Mean FL at capture and back-calculated to time of annulus formation for assigned ages (Table 4) closely agreed with length frequencies (see below), which supported annual mark validity. Additionally, a strong linear relationship (r^2=0.96) between scale size (S, mm) and fish length (FL, mm) was found: FL=8.97+38.56(S).

Length frequencies (Figure 3)

Young-of-the-year were represented in the samples as early as August–September. The age-0 fish in December (30–110 mm) were easily followed from winter to spring (time of first annulus formation) through late summer, when they were assigned to age 1. Age class designations were generally complicated by greatly overlapping sizes for fish older than one year. However, a strong year-class in 1988 (indicated with an arrow in Figure 3) was followed

Table 4. Pagellus erithrinus. *Mean back calculated fork lengths at annulus formation.*

	Backcalculated lengths at annulus formation						
Annuli	I	II	III	IV	V	VI	VII
I	92.19						
II	90.91	138.55					
III	91.85	140.14	162.30				
IV	95.05	144.49	167.24	184.07			
V	97.18	146.58	167.23	182.60	195.81		
VI	102.04	146.82	167.40	185.47	197.12	209.58	
VII	107.59	146.73	165.51	189.00	201.52	212.48	220.30
Weighted mean	91.88	139.41	163.68	183.98	196.89	211.75	220.30

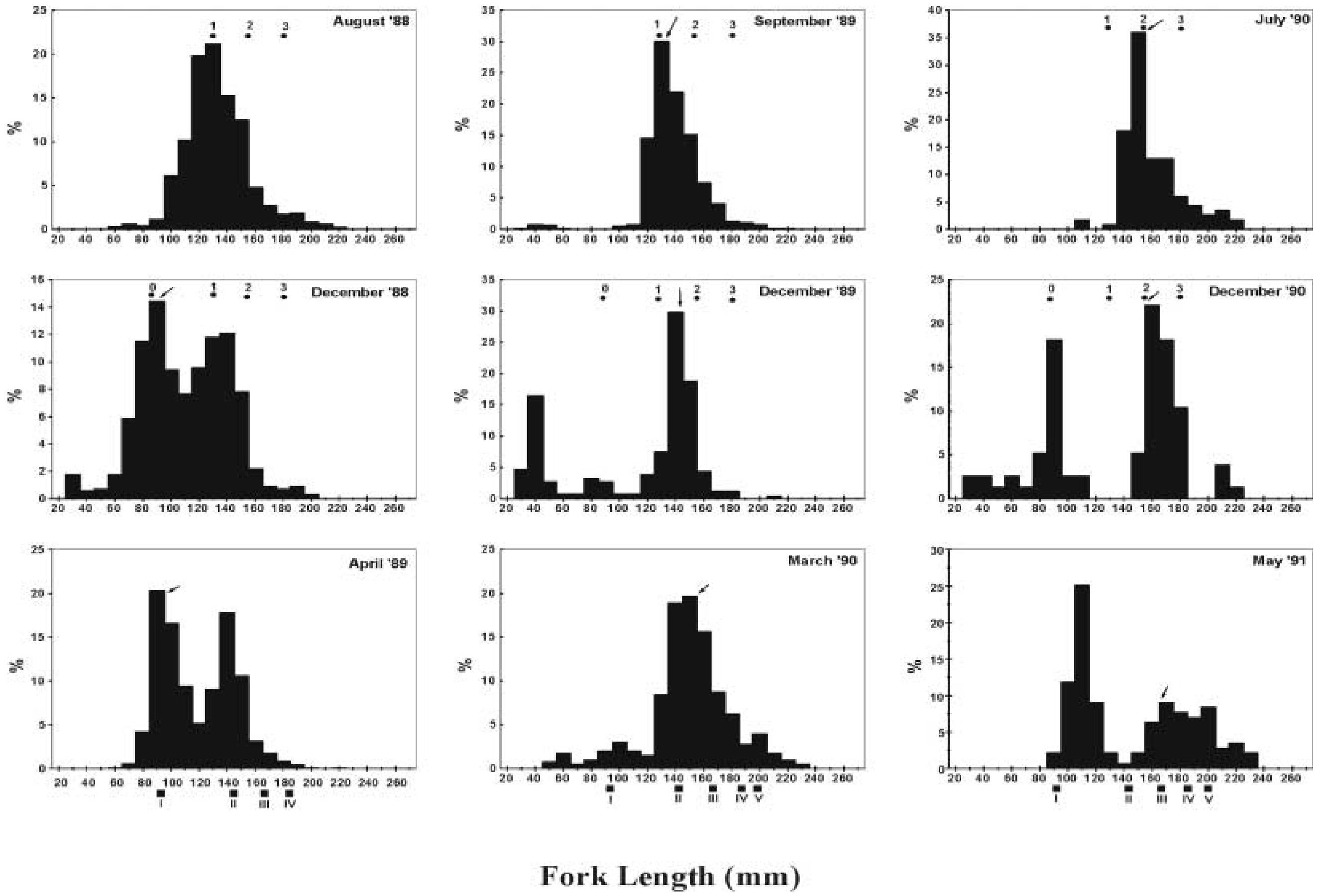

Figure 3. Seasonal length-frequencies of red pandora on the Cretan shelf (1998–1991). Solid dots indicate observed mean lengths at age and solid squares back-calculated mean fork lengths from scale ageing data. Zero and Arabic numerals designate age-classes and Roman numerals designate annulus number. The arrow indicates the strong 1988 year-class.

by a very weak year-class in 1989, which allowed the tracking of the year-class of 1988 up to May 1991, i.e. the time of formation of annulus III. Mean observed lengths calculated from aged fish agreed closely with length frequency modes (Figure 3). Mean back-calculated fork lengths at annulus formation (Table 4; Figure 3) generally corresponded to appropriate length-frequency modes during the period of annulus formation (spring).

Growth

Mean back-calculated lengths at age indicated rapid growth in the first year, slower growth in the second year and a sharp decline in growth during the subsequent years (Table 4). The estimated von Bertalanffy growth curve for red pandora is shown in Figure 4. Standard errors of L, K and t_0 were 9.437, 0.048 and 0.220 respectively. Back-calculated lengths at age were very close to predicted length assuming annulus formation at age 0.8, 1.8, 2.8, etc.

The VBGF parameters of red pandora from different parts of the Mediterranean Sea and the Atlantic Ocean are summarized in Table 5. Despite differences in methodology and data quality, available data showed that growth of *Pagellus erythrinus* was generally similar in all areas of the eastern and central Mediterranean. In the western Mediterranean (Castellon coasts and Gulf of Lions) and the Atlantic (Canary Islands), the growth pattern was substantially different (Figure 5A). The auximetric plot (Figure 5B) revealed that the relationship between K and L∞ was not significant ($P>0.1$) when

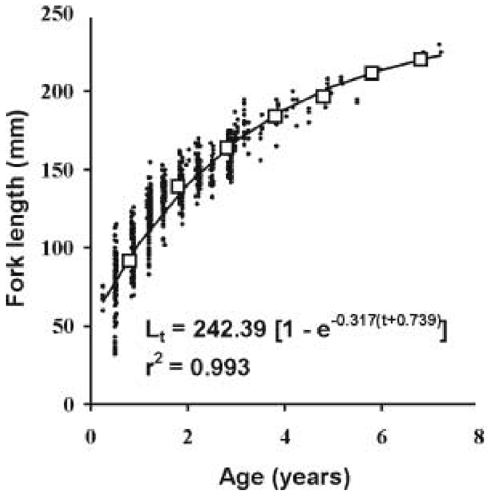

Figure 4. von Bertalanffy growth curve for red pandora on the Cretan shelf. Solid dots represent individual fish. Open squares are back-calculated mean lengths at annulus formation (assumed to take place two months before the assigned birth-date (see text for details)).

Table 5. Pagellus erythrinus. *von Bertalanffy growth parameters estimated for different regions of the Mediterranean Sea and the Atlantic Ocean.*

Region	Gear	Ageing	L∞	K	t_0	Reference
Canary Islands	Traps—Longlines	Otolith sections	418	0.205	−0.550	Pajuelo & Lorenzo (1998)
Castellon	Trawls	Scales	517	0.136	−1.120	Larraneta (1967)
Gulf of Lions[3]	Trawls	Scales	465	0.255	−0.039	Girardin (1981)
Archipelago Toscano[1]	Trawls	Otoliths	270	0.239	−1.573	Matta (1958)
Sicilian Channel	Trawls	Otoliths	367	0.164	−1.249	Andaloro & Giarrita (1985)
Tunisia	Trawls		358	0.137	−1.631	Ghorbel (1996)
Ionian Sea[2,4]	Trawls	Scales	302	0.199	−1.444	Papaconstantinou et al. (1988)
Saronikos Gulf (Aegean Sea)[2,4]	Trawls	Scales	355	0.156	−1.787	Vassilopoulou et al. (1986)
Evoikos Gulf (Aegean Sea)[2,4]	Trawls	Otoliths	364	0.142	−2.383	Mytilineou (1989)
Crete[4]	Trawls	Scales	278	0.317	−0.739	Present study
Cyprus	Trawls	Otoliths	300	0.203	−1.623	Livadas (1989)

[1], the VBGF was estimated from mean observed lengths-at-age given by the author; [2], the VBGF was re-estimated from mean back-calculated lengths-at-annulus formation given by the authors; [3], fork lengths (FL) were converted to total lengths (TL) using equation given by the authors; [4], FLs were converted to TLs using the equation: TL(mm) = −3.36 + 1.18 FL(mm), $r^2 = 0.998$ (calculated in the present study).

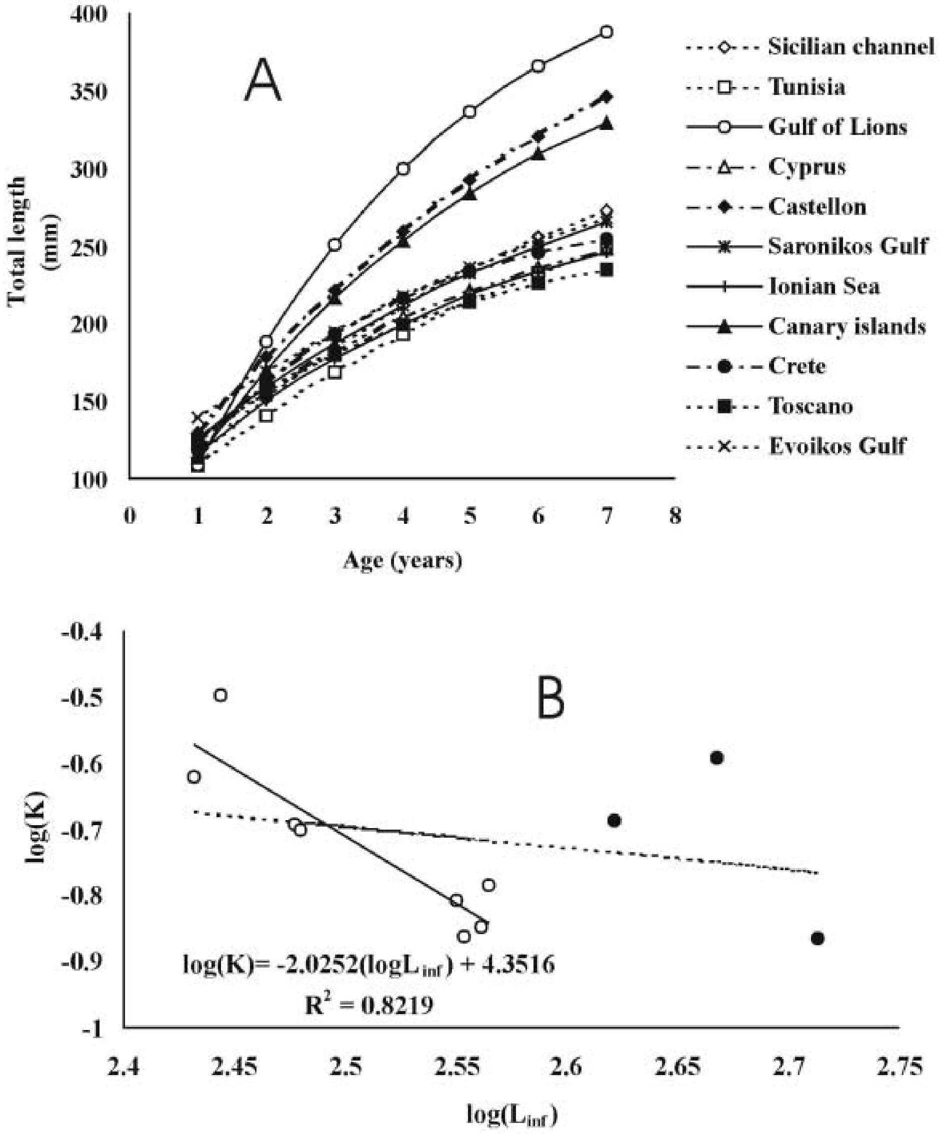

Figure 5. (A) Plot of VBGFs for red Pandora in different regions of the Mediterranean and the Atlantic (see Table 5); (B) relationship between the von Bertalanffy K and L∞ parameters (auximetric plot). Open cycles, estimates for the central and the eastern Mediterranean; black cycles, estimates for the western Mediterranean and the Atlantic; solid line, fitted least-squares linear equation for the eastern and central Mediterranean values (the equation is given in the graph, $P = 0.001$); broken line, fitted linear equation for all values (the relationship is not significant, $P > 0.05$).

values from all regions were pooled in the analysis. However, the relationship was significantly negative for the central and eastern Mediterranean populations, with a slope of −2.

Maturity and sex ratio

The sex ratio (Figure 6) was female-biased and macroscopically identified bisexual gonads were occurring up to the length of 180 mm. All specimens larger than 210 mm were males.

With the exception of fish larger than 200 mm, less than 50% of fish were mature (macroscopic stages II–III) in smaller length classes during late summer (August 1988). In spring (April–May 1989) all fish larger than 155 mm were mature. Thus, late summer is situated at the end of the annual spawning period (see also Girardin, 1981; Larraneta, 1967; Pajuelo & Lorenzo, 1998; Papaconstantinou et al., 1988), whereas, the period April–May is at the beginning of the spawning period (see also Table 3).

Lengths at first maturity were estimated from the spring samples. First maturation occurred within 130–150 mm (age 1+ and 2+). The L_{50} of males was higher than that of females, at 142 and 134 mm respectively (Table 6).

Distribution

Pagellus erythrinus was found between depths of 26 and 177 m, temperatures of 14.5 and 24.2°C and salinities of 38.10 and 39.76 psu (Table 7). Its presence in stratum III

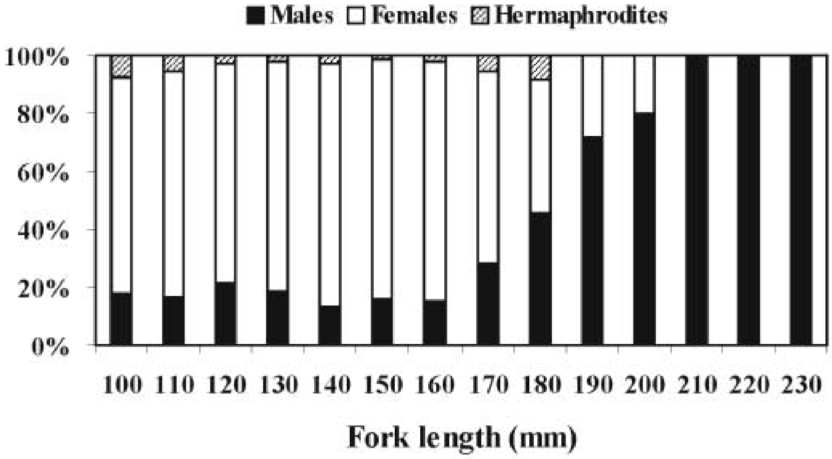

Figure 6. *Pagellus erythrinus*. Percentages of macroscopically determined male, female and hermaphodite fish by 10-mm length classes.

Table 6. *Estimated parameters for the size at maturity, L_{50}.*

Parameter estimates	Males	Females
v_1	−23.406	−27.021
v_2	0.165	0.202
SE v_1	3.136	2.926
SE v_2	0.022	0.021
L_{50}	142.07	133.99
CI L_{50}	138.9–145.0	132.3–135.5
L_{25}	135.41	128.55
L_{75}	148.74	139.44
Δ	12.610	1.763
df	9	9
χ^2	16.919	16.919
r^2	0.882	0.897

SE, standard error; CI, 95% confidence intervals; Δ, deviance statistic; df, degrees of freedom. All lengths are FL in mm.

Table 7. *Seasonal ranges of depth, temperature and salinity in which red pandora occurred, 1988–1991.*

	Minimum	Maximum	Range
Depth (m)			
Spring	26	177	151
Summer	28	176	148
Winter	28	156	128
Temperature (°C)			
Spring	14.5	17.3	2.8
Summer	14.5	24.2	9.7
Winter	15.5	17.8	2.3
Salinity (psu)			
Spring	38.66	39.06	0.40
Summer	38.13	39.76	1.63
Winter	38.66	38.99	0.34

Table 8. Pagellus erythrinus. *Pearson correlation coefficients between mean, minimum and maximum fork length (FL) and depth, temperature.* P *values in parentheses.*

	Minimum FL	Maximum FL	Mean FL
Depth			
Spring	0.748 (0.003)	0.102 (0.864)	0.585 (0.036)
Summer	0.578 (0.003)	−0.012 (0.864)	0.491 (0.046)
Winter	0.520 (0.002)	0.294 (0.053)	0.542 (0.001)
Temperature			
Spring	−0.207 (0.220)	0.105 (0.637)	−0.075 (0.667)
Summer	−0.659 (0.000)	−0.030 (0.841)	−0.545 (0.000)
Winter	−0.330 (0.090)	0.041 (0.837)	−0.226 (0.266)

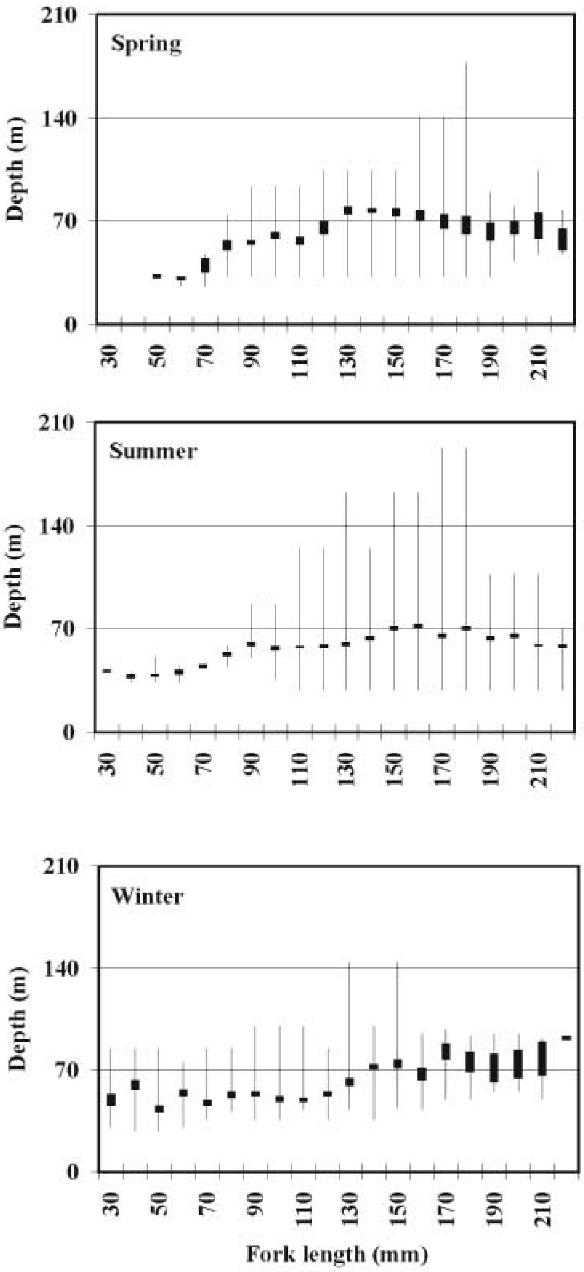

Figure 7. *Pagellus erythrinus.* Seasonal graph of fork length vs depth. Rectangles represent the 95% confidence intervals and the lines represent the corresponding ranges.

Table 9. Pagellus erythrinus. *Indices of bottom depth and temperature selection by season.*

	Age 0	Age 1	Age 2	Age 3+
Depth				
Spring				
D	33.68	26.10	27.70	28.70
S	−107.75	9.40	13.74	−37.83
P	0.020	0.395	0.331	0.142
Summer				
D	30.80	13.90	11.10	17.30
S	−124.95	−28.09	−6.71	−56.04
P	0.040	0.756	0.912	0.415
Winter				
D	38.51	25.50	15.40	20.55
S	−194.68	−120.18	−48.34	9.75
P	0.043	0.120	0.612	0.532
Temperature				
Spring				
D	36.29	29.84	29.59	32.41
S	189.29	136.53	134.65	157.87
P	0.010	0.233	0.254	0.080
Summer				
D	35.42	23.13	20.30	26.55
S	700.86	286.11	193.64	405.20
P	0.030	0.261	0.463	0.110
Winter				
D	37.76	37.38	33.35	33.83
S	187.15	184.12	135.22	95.54
P	0.003	0.005	0.002	0.052

D, test statistic; S, index of bottom depth or temperature selection; P, probability of statistical significance of depth or temperature selection based on the randomization test described in the text.

(>150 m) was very rare. Bottom salinity showed very small variation and is not generally considered to affect the distribution of fishes on the Cretan shelf (Tsimenides et al., 1991).

The relationships between mean FL and depth were significantly positive in all seasons (Table 8). Maximum FL was not correlated with depth but minimum FL was positively correlated. The relationship between FL and temperature was not significant, except for mean and minimum length in summer, i.e. during the season of maximum temperature variation (Table 7).

The length distribution by depth (Figure 7) indicated that small individuals (<130 mm) were mainly present in stratum I (<70 m), whereas bigger individuals occupied both stratum I and II. In spring, individuals of 120–150 mm FL were mainly found in stratum II.

The randomization tests based on the maximum vertical distance between CDFs showed the significant association of the age-0 fish with the shallow and warm waters during all seasons (Table 9; Figure 8). Other age groups did not show any significant depth selection, except that they were most abundant at higher bottom temperatures during winter (late November–December).

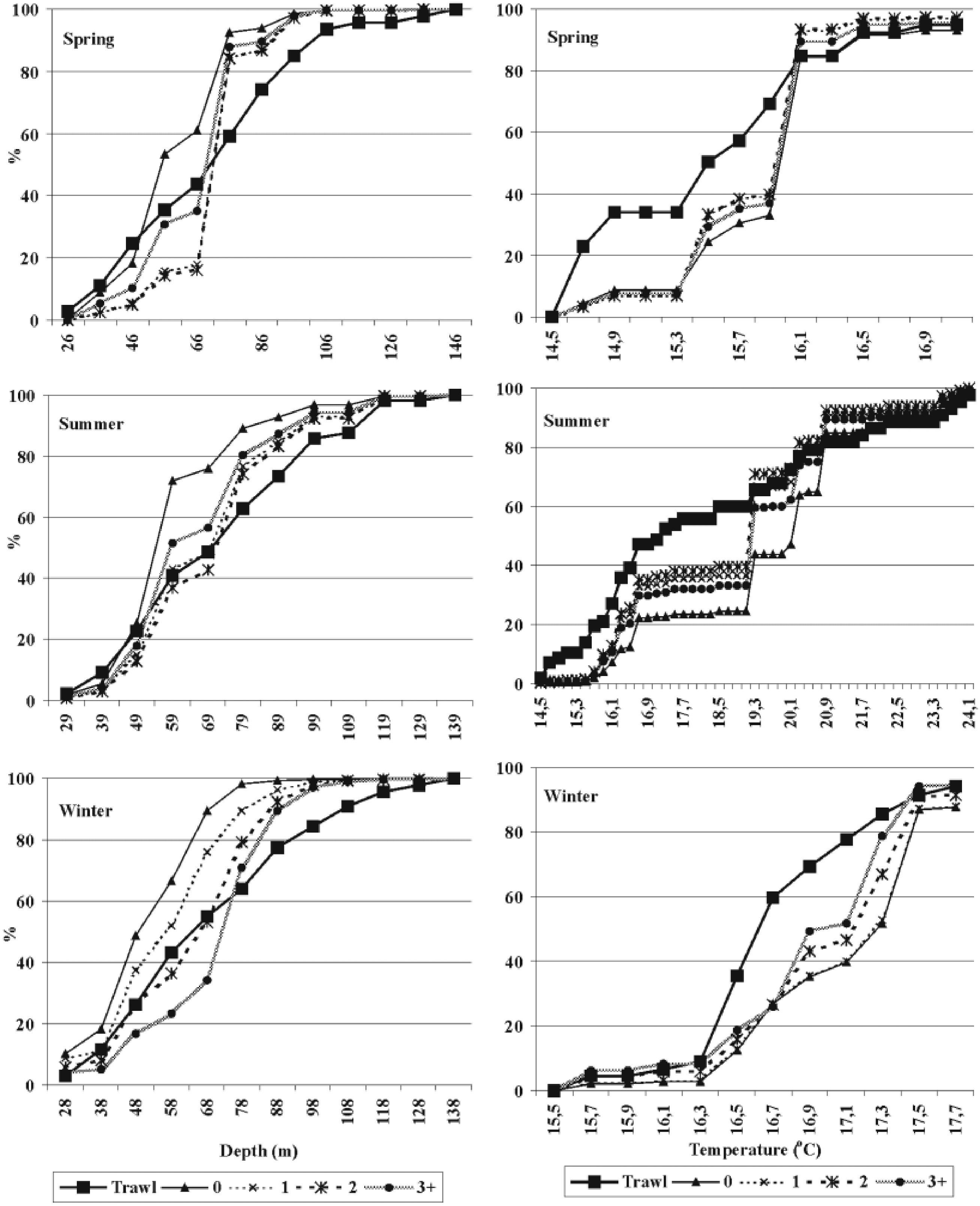

Figure 8. *Pagellus erythrinus*. Cumulative distribution function of bottom depth, temperature and red pandora catch in relation to the available values of the parameters.

DISCUSSION

Age and growth

Growth of fishes in the eastern Mediterranean is generally slow, maturity is reached at low lengths and spawning seasons are extended, resulting in large size variation in juvenile and adult fish (Stergiou et al., 1997). Hence, age class designations are generally complicated by greatly overlapping sizes for fish older than one year.

In the present study, the good agreement of back-calculated and observed lengths-at-age with length frequencies supported the annual nature of scale marks of the eastern Mediterranean red pandora. The alternation of strong and weak year-classes facilitated the comparison up to the period of third annulus formation. The annual nature of the annuli I–V was further supported by the results of the marginal increment analysis (Figure 2). Spring was the season of annuli formation and back-calculated lengths-at-age agreed closely with the VBGF predicted lengths (Figure 4), considering that peak annuli formation occurs two months before the assumed peak spawning period (June).

The comparison of VBGF parameters of red pandora from different parts of the Mediterranean Sea and the Atlantic Ocean showed that growth of *Pagellus erythrinus* was generally similar in all areas of the eastern and central Mediterranean. In the western Mediterranean and the Atlantic, the growth pattern was substantially different. The auximetric plot revealed that the relationship between $\log_{10}K$ and $\log_{10}L\infty$ was not significant when values from all regions were used in the analysis. However, the relationship was significantly negative for the central and eastern Mediterranean populations, with a slope of 2, i.e. equal to the value that Pauly has empirically estimated for a large data set (Pauly et al., 1998; and references therein). Hence, the populations of the western Mediterranean and the Atlantic belong to a different 'growth space' than populations of the central and eastern Mediterranean (Pauly et al., 1998; Stergiou, 2000).

Stergiou et al. (1997) has pointed out that the well-known phenomenon of 'dwarfism', i.e. smaller body sizes characterizing benthic invertebrates species in the eastern Mediterranean, might also be true of marine fishes. Indeed, the Mediterranean Sea is characterized by a west–east gradient in nutrient deficiency, which is especially pronounced in the eastern Mediterranean and reflected in the phytoplankton and benthic communities, which depend on sinking organic material. Macrofauna biomass is impressively lower in the eastern than in the north-western Mediterranean and the Atlantic (Karakassis & Eleuftheriou, 1997, 1998). The combination of extremely low food availability and higher temperatures may lead to significantly lower lengths-at-age, asymptotic sizes and age/length at 50% maturity (Stergiou, 1993, 1999, 2000; Stergiou et al., 1997). Our estimates of lengths at first maturity (Table 6) are substantially lower than those calculated for the Atlantic (L_{50}=174 mm for females and 232 for males; Pajuelo & Lorenzo, 1998). Despite the lack of any other estimates of lengths at first maturity (most other reproductive studies are rather observational), we may expect that lower lengths-at-age of the eastern Mediterranean red pandoras are generally coupled with lower size-at-maturity.

Bathymetric distribution

There is a well-known general trend for size to increase with depth in most demersal fishes. The general nature of this depth–size relationship could derive from migratory or diffusive movements to deeper water during ontogeny (Cushing, 1975). The preponderance of the positive size–depth relationships in fish species may reflect a fundamental aspect of fish life history or it could be the result of sampling artefact, e.g. size-dependent catchability, or selective fishing pressure (Stefanescu et al., 1992). However, sampling artefacts are unlikely to account for this in our research survey data (Machias et al., 1998). A further question is whether the relationship reflects a progressive increase in fish size with increasing depth.

Our analysis showed that red pandora exhibits a positive relationship between mean length and depth (Table 8). This relationship was due to the association of 0-group fish with the vegetated shallows, whereas bigger fish did not exhibit any significant depth selection (Table 9; Figure 8). Consequently, the relationship between minimum fish size and depth was significant which was not the case between maximum fish size and depth. However, most fish having reached first maturity (>130 mm) tended to occur at depths between 60 and 80 m, i.e. in the periphery of the algal/angiosperm meadows (Figure 7).

The bathymetric distribution and movements of Mediterranean shelf-dwelling demersal species have been analysed in detail for Mullidae, *Mullus surmuletus* (Machias et al., 1998) and *Mullus barbatus* (unpublished data; Caddy, 1998, p. 15), and in the large-scaled gurnard, *Lepidotrigla cavillone* (Colloca et al., 1997). All these co-occurring species (including red pandora) are characterized by a spring–summer spawning season, a high concentration of spawning adults at mid-shelf depths (60–100 m) and nursery grounds located in the vegetated shallow waters. The multispecies character of this distribution and reproductive pattern might have an adaptive function, with both ecological and management implications.

From an ecological perspective, it might be possible that factors affecting the advection of early life history stages from the mid-shelf spawning grounds to the inner-shelf nursery grounds are common among species, hence shelf-dwelling demersal species with a spring/summer spawning season and mid-shelf spawning grounds might exhibit synchronous variations in year-class strength.

From a management perspective, the recognition of similar biological characteristics is of prime importance for the implementation of management measures (Caddy, 1993).

In Hellenic waters, it has generally been assumed that closure of trawl fisheries during the summer months (June–September) and in waters shallower than 50 m would be an effective means of increasing the biomass of fish available to the fisheries (Stergiou et al., 1997). Available data for several demersal species suggest that this management policy has succeeded for protecting the immature fraction of the population, but reproducing adults are vulnerable to over-fishing, especially during the maturation/spawning period. This might affect a decrease in recruitment by decreasing the number of reproducing females. Stergiou & Pollard (1994) suggest that the creation of marine harvest refugia (i.e. no-take zones) may be potentially applicable in the case of the demersal fisheries in the eastern Mediterranean. Such protected areas would allow a proportion of the stock to grow at a relatively large size at which overall fecundity is greatly increased.

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