Bathymetric distribution and movements of red mullet *Mullus surmuletus*

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ABSTRACT: Using data from bottom-trawl surveys conducted each summer, winter and spring on the Cretan shelf from 1988 to 1991, we examined the bathymetric distribution of red mullet *Mullus surmuletus*. Additionally, we used data from 3 yr (1991 to 1993) of monthly sampling in the Iraklion Gulf. Depth, temperature and salinity data were combined with biological data on abundance, biomass, fish size, age, sex and maturity. The ranges of bottom depth, temperature and salinity over which red mullet is distributed were established. In general, fish size increased with bottom depth, and smaller individuals tended to be found in shallower and warmer water. Abundance increased in mid-shelf waters during spring, indicating a movement across the shelf towards deeper water. The latter seemed to be associated with spawning behavior. The factor controlling the timing of that movement to deep water seemed to be the maturity of individual fish.

KEY WORDS: Red mullet · Distribution · Depth selection · Temperature selection · Migration

INTRODUCTION

Knowledge of the distribution and movement of an exploited stock, particularly during its reproductive phase, is required for proper management of the resource (Mullen 1994, Wroblewski et al. 1995). However, studies on depth, temperature and salinity preferences of marine fishes are widely scattered in the literature and based on few observations (Scott 1982). This is especially true for demersal species on the Mediterranean continental shelf. Caddy (1993) hypothesized the existence of an offshore movement of older fish in several demersal species (e.g. sea breams, common pandora, mullets, etc.), possibly contributing to continuing high recruitment in many areas, as well as to stock recovery. The main problem in the study of these species is that the available data in the Mediterranean come from commercial fisheries, hence there is limited possibility for investigation of the relationships between biological and environmental parameters. Such investigations require long-term research surveys.

A general trend for larger fish to occur in deeper water has long been known, especially with respect to deep-sea fishes (Haedrich & Rowe 1977). The fishes of the inshore zone also seem to undertake an ontogenetic migration to deeper water but there is a paucity of studies on the phenomenon and its causes (Macpherson & Duarte 1991, Warburton & Blaber 1992, Blaber et al. 1995). However, there is disagreement as to the generality and the underlying cause of this phenomenon (Macpherson & Duarte 1991 and references therein, Swain 1993). More detailed studies on the causes of the ontogenetic movements have concentrated on long-lived species, especially cod and plaice (Harden Jones 1968), but similar investigations are lacking for short-lived species like red mullet. Stefanescu et al. (1992) noted that further study of this subject should center on the autoecology of each species, as the complexity of links established by a species with its environment will result in highly variable and specific adaptive responses in each case.

The red mullet *Mullus surmuletus* (L. 1758) is a common species on the Mediterranean shelf. It is distributed along the eastern Atlantic from the North Sea to the northern part of West Africa (Hureau 1986). In the

Mediterranean Sea, the red mullet is subject to intensive fishing (Stergiou 1990, Reñones et al. 1995).

Several aspects of red mullet biology have been studied, including feeding, reproduction, age and growth (see Reñones et al. 1995 and references therein), but information on its bathymetric distribution and movements is limited to depth ranges. Hureau (1986) reported that *Mullus surmuletus* inhabits depths less than 100 m and Macpherson & Duarte (1991) found a depth range of 12 to 182 m.

In the present study, we examine the seasonal changes in the distribution pattern of red mullet off the coast of Crete (eastern Mediterranean). Research survey data on distribution, abundance, biomass, size, age, sex and maturity of red mullet were compared with depth, temperature and salinity in order to elucidate factors (e.g. maturation) controlling the seasonal timing and direction of fish movement.

MATERIAL AND METHODS

Sampling. The seasonal distribution of red mullet at various depths and within various temperature ranges was studied using data from 3 yr 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 (August to early September), one in winter (December) and one in spring (late March to early April) of each year. Each survey comprised about 40 random, depth-stratified stations, in all areas of the shelf able to be trawled (Fig. 1). Three depth strata were selected (Tsimenides

et al. 1991): 26–70 m (stratum I), 71–150 m (stratum II) and 151–350 m (stratum III). Stratum I covered 25%, stratum II covered 24% and stratum III covered 51% of the total area. Stratum I spanned a substrate covered by algae (*Caulerpa prolifera*) and sea grass (*Posidonia oceanica* and *Halophila stipulacea*); the substrate of stratum II consisted mostly of mud, sand or detritus; and the substrate 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.

The duration of each haul ranged from 50 to 90 min at a towing speed of 1.8 to 3 knots, 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 (trawl with a cod-end bag liner of 22 mm stretched mesh-size) were used in the survey. The catch from each haul was identified to species, enumerated and weighed, and the bottom depth, water temperature and salinity were measured. 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 calculated as number of fish or biomass per square nautical mile (n mile^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.

Additionally, we used available data from 3 yr of monthly surveys (January 1991 to December 1993) on
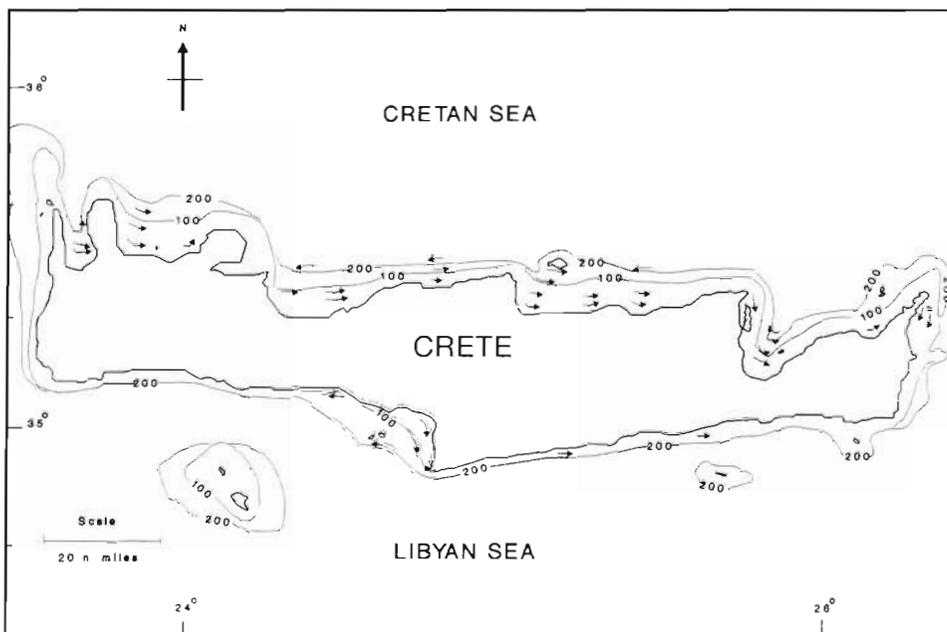

Fig. 1. Map of the sampled area indicating the 100 and 200 m isobaths as well as the position and direction of the hauls (arrows)

Table 1 *Mullus surmuletus*. Female and male maturity stages based on macroscopic examination of the gonads. Adapted from Macer (1974), Hilge (1977), N'Da & Deniel (1993)

Stage	Description
Females	
I Immature-resting	Ovaries small; less than one half of length of ventral cavity; pale pink to red. No granular appearance
II Developing	Ovaries becoming larger; one half of length of ventral cavity or more; pinkish or yellow. Granular appearance
III Late-developing to running	Ovaries very large; pale yellow or yellow. Transparent hyaline eggs
IV Spent	Ovaries flaccid; pink or red. Early stage of atresia visible in hyaline oocytes (white spots)
Males	
I Immature-resting	Testes very small; translucent or grey. Less than half of length of body cavity
II Developing	Testes becoming larger and white; more than half of length of body cavity. Lobed formation
III Late-developing to running	Testes very large and multilobed; creamy white or pinkish; free-flowing milt
IV Spent	Testes flaccid; possibility of a little residual milt

the shelf of the Iraklion Gulf (off central northern Crete). These data provided complementary and temporally more detailed information on changes in the depth distribution of red mullet. These additional data were from a total of 19 hauls for each month (at least 5 hauls at each station). Each monthly survey comprised a trawl at each of 3 stations (1 in each of the 3 strata) using the same gear and sampling method as in the seasonal surveys.

Biological sampling. During the 9 seasonal surveys, either all specimens or a random subsample of at least 100 individuals from each haul were measured and weighed. The following measurements were taken for each specimen: total length to the nearest mm, total and eviscerated mass to the nearest 0.1 g, and gonad mass to the nearest 0.1 mg. The sex and the macroscopic stage of maturity (Table 1) were also determined and a gonosomatic index calculated $\left(GSI = \dfrac{\text{gonad weight}}{\text{eviscerated body weight}} \times 100 \right)$. All data were transformed to number of individuals per n mile^2.

To study growth, scales were collected from all specimens during the first year of seasonal surveys, and from fish larger than 220 mm during subsequent surveys. Six scales from each specimen, taken from the region under the pectoral fin, were cleaned with water, placed on 0.3-mm-thick cellulose acetate plates and pressed at a temperature of 105°C for 3 min. Subsequently, the scales were removed and their imprints on the plates were examined using a binocular microscope. Annuli were identified using the standard criteria of Bagenal & Tech (1978), especially cutting-over of

circuli in the lateral field, close spacing of circuli followed by wider spacing in the anterior field, and consistency of these characteristics in at least 4 of the scales examined per fish.

Age classes were assigned according to number of scale annuli, marginal-increment spacing, month of collection, and size relative to the length frequency distribution (Ross 1988). We used May 1 as the birthdate, based on the results of the gonad study and on unpublished data from ichthyoplanktonic investigations in the same area. A total of 1526 specimens were aged and the von Bertalanffy growth curve (VBGC) was estimated as in Tserpes & Tsimenides (1995).

Growth curves for females and males were estimated separately and compared by analysis of residual sum of squares (Chen et al. 1992). Since the 2 VBGCs were not significantly different ($F = 0.015$, p > 0.05) data were pooled and the resulting curve was used for a deterministic aging of all fish caught, using the equation:

$$t = t_0 - \frac{1}{k}\ln\left(1 - \frac{L_t}{L_\infty}\right) \tag{1}$$

where L_t is total length at age t; L_∞ is asymptotic length; k is growth coefficient; t_0 is theoretical age at zero length (Hilborn & Walters 1992).

Data analysis. After logarithmic transformation (Middleton & Musick 1986, Stefanescu et al. 1992), means of abundance (ind. n mile^{-2}) and biomass (g n mile^{-2}) were calculated for each cruise (1) for each 50 m bottom-depth interval, and (2) per stratum (I, II, III). Furthermore, the seasonal distribution of the total abundance and biomass for each stratum or bottom-depth interval were calculated by weighting the mean values with the ratio of the surface area of the stratum or bottom-depth interval to the total area.

Analysis of variance showed no differences in abundance or biomass among the 3 surveys in the same season, nor among the 3 strata (I, II, III) in the same season (0.177 < p < 0.730; Bartlett's test, 0.101 < p < 0.562). 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.

A correlation analysis (Pearson's correlation coefficient) was performed to determine if there were any significant changes in abundance or biomass with bottom depth or water temperature. The same method 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', 'larger 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, minimum or maximum length (Middleton & Musick 1986, Macpherson & Duarte 1991, Stefanescu et al. 1992). The same 3 variables were used in correlation analysis with respect to temperature.

The distribution of different-sized fish was simplified, as follows: Lengths were converted to ages using Eq. (1). We examined relationships between red mullet density (ind. n mile^{-2}) and temperature or bottom depth using cumulative distribution functions (CDFs) following Perry & Smith (1994). The CDF (in %) for temperature (available temperature) or bottom depth (available depths), $f(t)$, was calculated for each season as follows:

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

and 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; L is the number of strata. The CDF for red mullet catch, $g(t)$, was calculated similarly:

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

and y_{hi} is the number of red mullet caught in tow i in stratum h. We calculated the red mullet CDF separately for each age 0 to 2 and for fish age 3 and older (Swain & Krammer 1995).

To examine seasonal variation in temperature or bottom depth selection by red mullet, we compared CDFs of temperature, $f(t)$, and red mullet catch, $g(t)$, in relation to temperature, as well as CDFs of bottom depth and red mullet catch in relation to bottom depth. We calculated

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

for each season and age group. S compares average available temperature or depth to the average temperature or depth selected by red mullet. Positive values of S indicated that the red mullet select high temperatures and depths within the ranges studied here. We used a Kolmogorov-Smirnov type of statistic to test the

significance of temperature and bottom depth selection. The test statistic D was defined $D = \max|f(t) - g(t)|$ (maximum absolute vertical distance) when $f(t)$ and $g(t)$ were the 2 functions compared at 0.2°C (CDFs of temperature) or 10 m (CDFs of depth) intervals. Significance was assessed using randomization tests (Perry & Smith 1994, Swain & Krammer 1995).

Standardized numbers of males and females in the 4 different maturity stages (Table 1), by age class, were used in the spring sampling to examine differences in maturity among strata. All statistical inferences were based on the 0.05 significance level.

RESULTS

Abundance and biomass

A total of 6280 individuals were analyzed. *Mullus surmuletus* was distributed between depths of 28 and 310 m, between temperatures of 13.6 and 23.8°C and between salinities of 38.12 and 39.75‰ (Table 2). Salinity showed very small variation and is not generally considered to affect the distribution of fishes on the

Table 2. Seasonal ranges of depth, temperature and salinity in which red mullet occurred in the period 1988 to 1991

	Min.	Max.	Range
Depth (m)			
Spring	28	300	272
Summer	28	273	245
Winter	28	310	282
Temperature (°C)			
Spring	14.5	17.3	2.8
Summer	14.4	23.8	9.4
Winter	13.6	17.8	4.2
Salinity (‰)			
Spring	38.65	39.05	0.4
Summer	38.12	39.75	1.63
Winter	38.66	39.23	0.57

Table 3. *Mullus surmuletus*. Correlation between red mullet abundance and biomass and depth and temperature

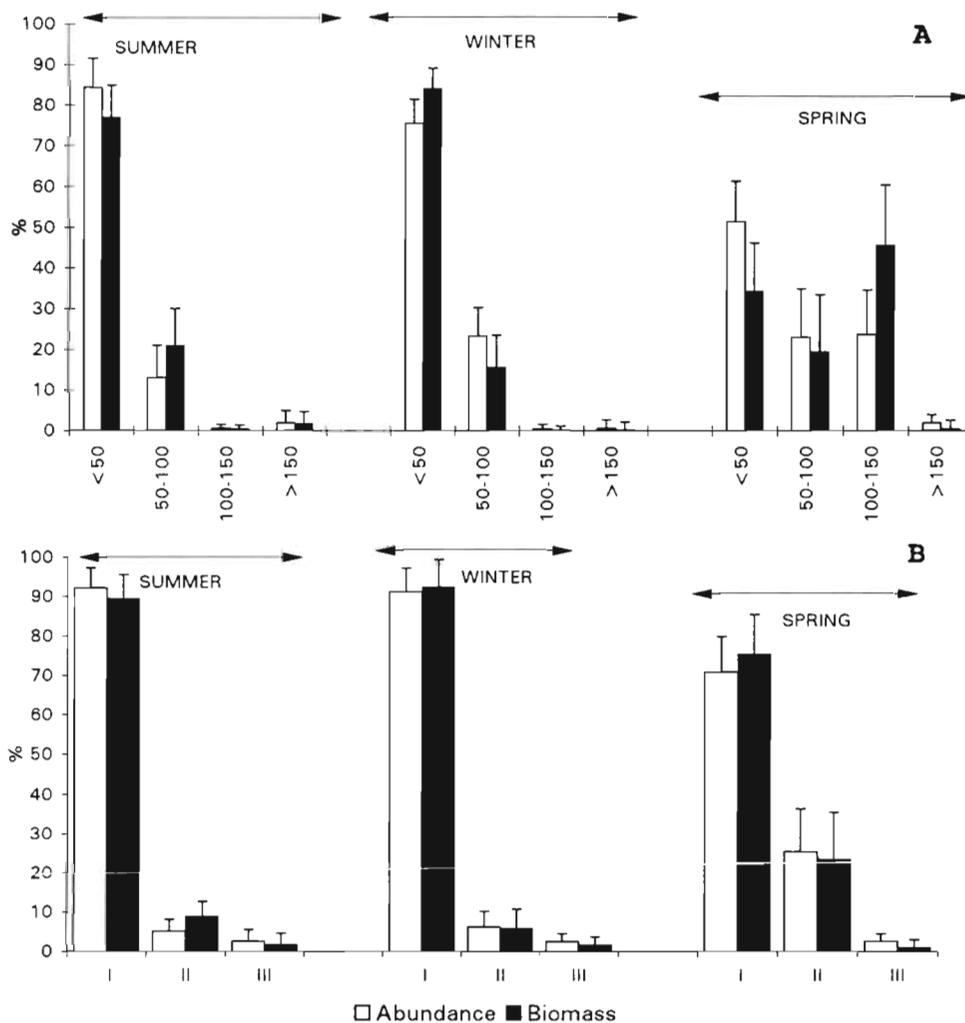|	Abundance		Biomass	
	r	p	r	p
Depth				
Spring	−0.490	0.000	−0.430	0.000
Summer	−0.591	0.000	−0.520	0.000
Winter	−0.679	0.000	−0.635	0.000
Temperature				
Spring	0.231	0.253	0.221	0.260
Summer	0.673	0.001	0.669	0.002
Winter	0.342	0.083	0.335	0.091

Fig. 2. *Mullus surmuletus.* Seasonal distribution by abundance and biomass (A) in 50 m depth intervals (m) and (B) in the 3 strata. I: stratum I (20–70 m); II: stratum II (71–150 m); III: stratum III (151–350 m)

Cretan shelf (Tsimenides et al. 1991). Abundance and biomass were significantly negatively correlated to bottom depth during all seasons and positively correlated to temperature during summer (Table 3). No significant correlations between abundance or biomass and temperature were observed during winter and spring. The lack of correlations could be mainly attributed to the small temperature variation during these seasons (Table 2).

Relative percentage of abundance and biomass by depth interval (Fig. 2) indicated that fish generally occurring in shallow waters increased their presence at mid-shelf depths (stratum II) during spring. A similar change was observed in the monthly collections in the Iraklion Gulf (Fig. 3). Fig. 3 shows that, after the aforementioned change in May, abundance and biomass remained low in stratum I and high in stratum II up to recruitment during July–August. Thus, the existence of a seasonal, depth-related movement is suggested.
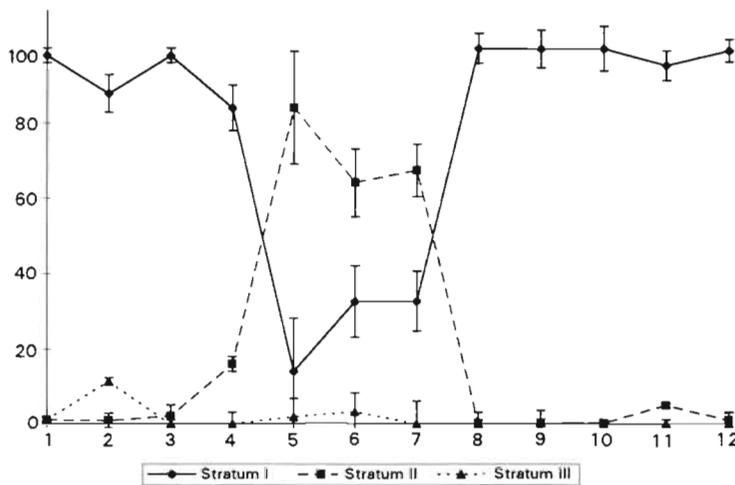

Fig. 3. *Mullus surmuletus.* Monthly distribution in the Iraklion Gulf, by abundance in the 3 strata (I, II, III). Months are numbered from January (1) to December (12)

Table 4. Correlation between mean, minimum and maximum total length (TL) of red mullet and depth and temperature

	Mean TL		Min. TL		Max. TL	
	r	p	r	p	r	p
Depth						
Spring	0.645	0.000	0.631	0.000	0.204	0.107
Summer	0.791	0.000	0.801	0.000	0.573	0.002
Winter	0.833	0.000	0.814	0.000	0.465	0.005
Temperature						
Spring	−0.215	0.108	−0.203	0.107	−0.198	0.125
Summer	−0.670	0.000	−0.651	0.000	−0.632	0.000
Winter	−0.601	0.000	−0.661	0.000	−0.354	0.082

Fish size

The relationships between mean total length (TL) and depth were significantly positive in all seasons (Table 4). The maximum TL of the samples increased with depth during summer and winter. Minimum TL of the samples increased with depth in all seasons. The relationship between mean TL and temperature was negative in summer and winter, but there was no significant correlation in spring. During summer, maximum length was negatively correlated with temperature. Length distribution by depth revealed that individuals larger than 155 mm, which is the length at first maturity (Reñones et al. 1995), were generally found in stratum II during summer and winter (Fig 4). The same was found for individuals larger than 165 mm in spring.

Age

The calculated VBGC is shown in Fig. 5. 0 yr old fish were found in shallow water, while 3+ yr old fish were found in deep water. 1 and 2 yr old fish selected intermediate bottom depths (Fig. 6). A randomization test based on the absolute maximum vertical distance between CDFs indicated significant shallow depth selection for the age 0 group during summer and winter and significant selection for greater depths for the age 3+ group during spring and summer (Table 5). Fish
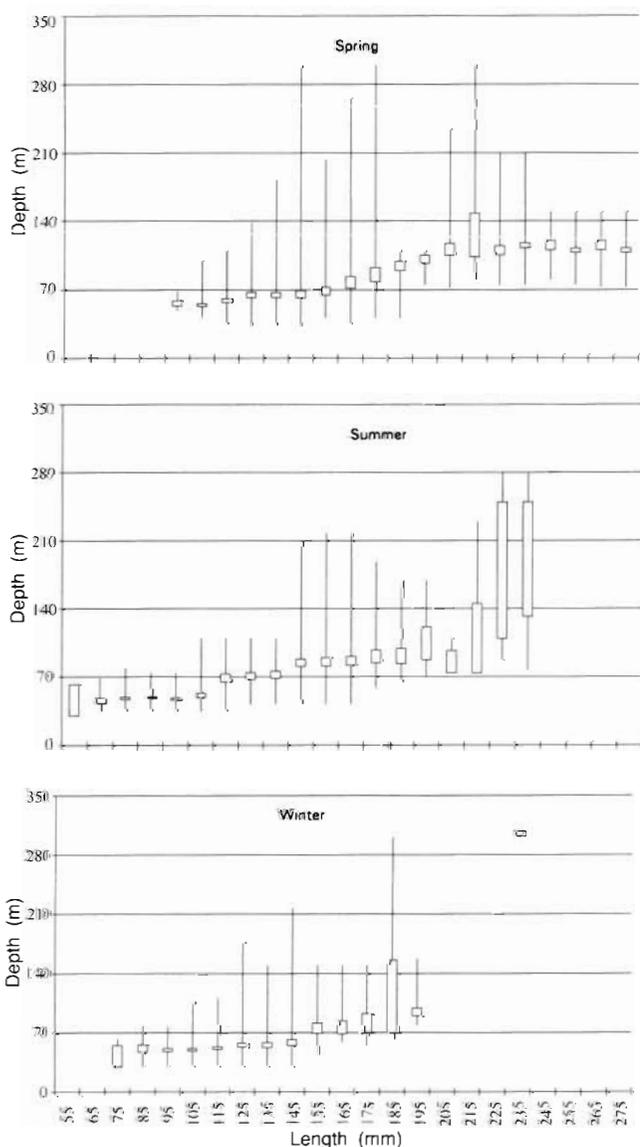

Fig. 4. *Mullus surmuletus*. Seasonal graph of fish total length vs depth. Rectangles represent 95% confidence intervals and lines represent corresponding ranges
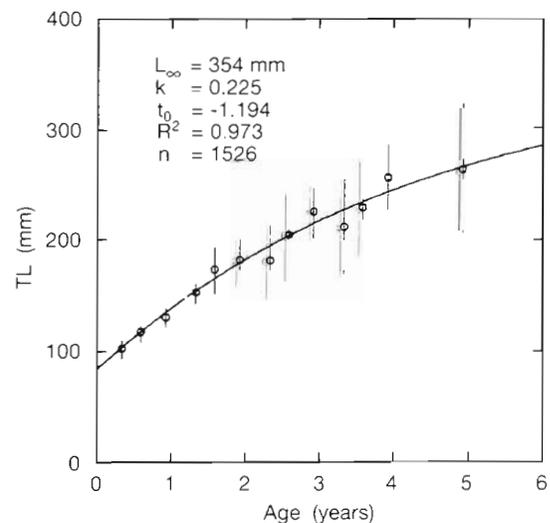

Fig. 5. *Mullus surmuletus*. The von Bertalanffy growth curve. Points correspond to the mean (±SE) values for each age. L_∞: asymptotic total length; k: growth coefficient; t_0: theoretical age at zero length; R^2: coefficient of determination; n: number of specimens
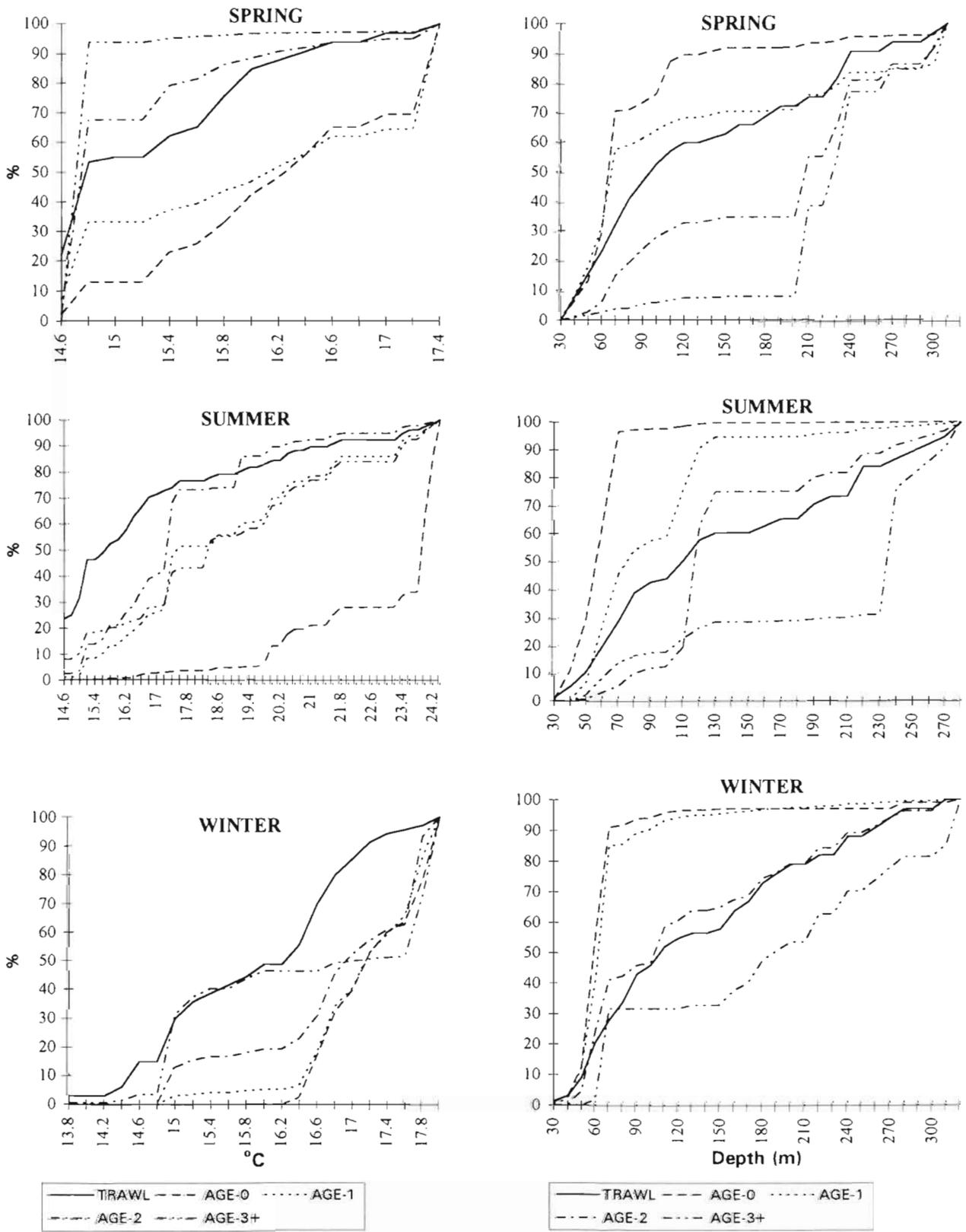
Fig. 6. *Mullus surmuletus*. Cumulative distribution function of red mullet catch in relation to available temperature and bottom depth

Table 5. Indexes of bottom depth and temperature selection by season. S: index of bottom depth or temperature selection; D: test statistic; p: probability of statistical significance of depth or temperature selection based on the randomization test described in the text

	Age 0	Age 1	Age 2	Age 3+
Depth				
Spring				
S	−455.13	−71.27	545.71	935.90
D	38.43	25.36	37.47	67.21
p	0.593	0.759	0.281	0.005
Summer				
S	−766.71	−439.78	47.10	640.06
D	67.67	34.43	31.42	52.91
p	0.015	0.291	0.714	0.004
Winter				
S	−668.41	−631.46	−66.55	482.11
D	62.88	56.95	13.09	26.82
p	0.049	0.089	0.982	0.764
Temperature				
Spring				
S	495.40	398.39	−68.01	−215.14
D	42.78	37.95	19.58	40.44
p	0.624	0.791	0.989	0.984
Summer				
S	3049.68	1010.42	387.70	1018.23
D	76.77	45.56	34.13	43.90
p	0.002	0.741	0.922	0.748
Winter				
S	654.83	607.65	457.93	287.18
D	53.25	51.93	39.35	44.047
p	0.005	0.003	0.150	0.198

older than 3 yr did not generally occur in shallow water (stratum I), which was dominated by young fish.

The temperature selection of red mullet showed a pattern consistent with the depth distribution pattern. Younger fish selected high temperatures within the ranges we studied here (Fig. 6). A randomization test indicated significant selection of the age 0 group for high temperatures during summer and winter and of the age 1 group, likewise, during winter (Table 5). A randomization test did not indicate any significant temperature selection in spring due to the small temperature variation with depth.

Maturity

All individuals collected during summer and winter were immature or resting (Stage I). During spring (late March to early April) most individuals were in early or late maturation (Stages II, III), but no spent individuals (Stage IV) were found, indicating that spawning takes place later in the season. Percentages of the different maturity stages by age group in shallow waters (stratum I) and in deeper waters (strata II and III) are shown in Fig. 7. Only a very small percentage of 0+ fish were in advanced maturation in stratum I, whereas most individuals were in an advanced maturity stage in strata II and III. This is also indicated by the GSI (Fig. 8). It seems, overall, that the movement to mid-shelf depths is associated with reproduction.
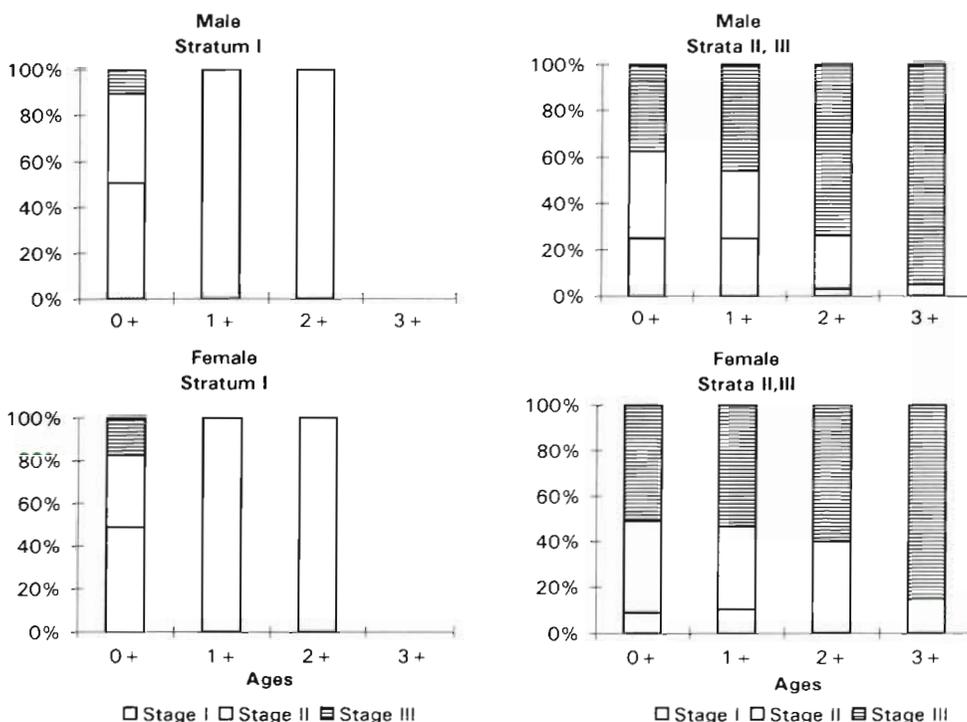

Fig. 7 Mullus surmuletus. Percentage of the maturity stage (see Table 1) by stratum, sex and age in spring; 0+: 0–0.99 yr olds; 1+: 1–1.99 yr olds; 2+: 2–2.99 yr olds; and 3+: fish older than 3 yr
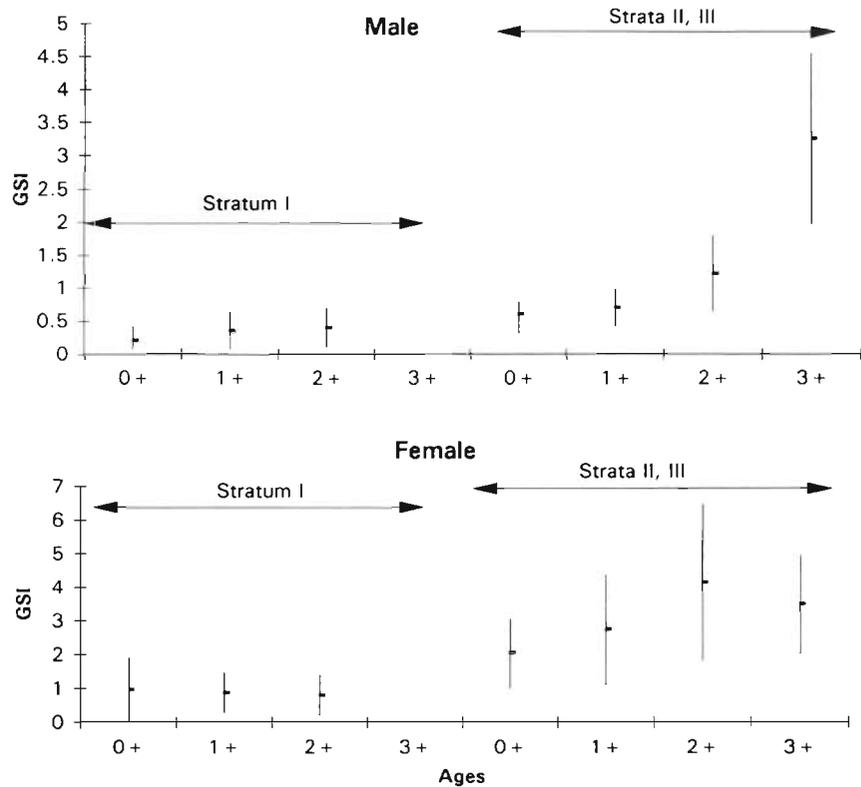
Fig. 8. *Mullus surmuletus*. Mean gonosomatic index (GSI), with 95% confidence intervals, by stratum, sex and age, in spring; age classes as in Fig. 7

DISCUSSION

There is a well-known general trend for size to increase with depth in most demersal fishes. The general nature of this size-depth 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 artifact, e.g. size-dependent catchability, or selective fishing pressure (Stefanescu et al. 1992). However, sampling artifacts are unlikely to account for this in our research survey data, because the sampling gear and methods were the same throughout the sampling, a reasoning previously followed by Snelgrove & Haedrich (1985). Additionally, selective fishing pressure is also unlikely to be the reason for this observation, since it is intensive throughout the sampling area (Tsimenides et al. 1991). A further question is whether the relationship reflects a progressive increase in fish size with increasing depth.

The phenomenon of older specimens being found at greater depths has sometimes been taken as a rule (Heinke's law), as in the case of plaice (Harden Jones 1968). The occurrence of smaller, younger individuals in shallower water and the movement towards deeper waters during ontogeny must involve a substantial advantage. It has been suggested that, by migrating to deeper waters, the adults could benefit from a reduced basal metabolic rate and increased life expectancy at lower temperature (Macpherson & Duarte 1991); there is also a density-dependent variation in bathymetric pattern (Swain 1993). Since, in the Mediterranean, the water temperature remains virtually constant below a depth of 160 to 200 m, Macpherson & Duarte (1991) suggested that this behavior represents an inherited evolutionary response and, therefore, has a genetic basis.

According to our results, *Mullus surmuletus* is among the species that show a positive relationship between mean length and depth. The analysis revealed that the smaller individuals tend to be found in shallower water during all seasons, whereas the larger fish tend to be found in deeper waters during summer and winter. In other words, smaller individuals tend to occupy warmer (high energy cost) shallower (high resource) grounds, and the older individuals colder, deeper grounds.

A change in the distribution of *Mullus surmuletus* occurs in spring just before spawning, which takes place during April–May (Reñones et al. 1995). This change is mainly attributable to a movement of individual fish from stratum I to stratum II. In addition, individuals in the final stages of gonadal maturation were generally absent from stratum I but abundant in strata II and III. Thus, final maturation seems to be accompanied by a movement of fish to deeper water.

In Crete, wind-driven currents flow in the coastal area in April–May (Tselepides et al. 1996). These currents may prevent larval dispersal away from the continental shelf. Furthermore, mullids have a pre-juvenile pelagic stage (Kendall et al. 1984, Watson 1996) which makes it advantageous to the mullids to settle in appropriate areas.

Stratum I is covered mainly by *Posidonia* and is the substrate where red mullet recruitment occurs (García-Rubies & Macpherson 1995). The trend of increasing mean length with depth in summer and winter is due primarily to recruitment during July–August and secondarily to the occurrence of larger fish in deeper water. The change in the distribution during spring could be attributed to the concentration of the immature specimens in shallow water and of fish approaching maturity in strata II and III. The vast movement from *Posidonia* beds to deeper water seems to be related to the final stage of gonad maturation, rather than directly to fish size. Individuals 1+ and 2+ yr old captured in stratum I seem to be the fish that had not reached maturity or that happened to be on the edge of stratum I. Alternatively, larger individuals may attain final maturation earlier than smaller ones and/or some individuals may spawn in stratum I. However, results of the monthly surveys (Fig. 3) support better the first hypothesis.

An ontogenetic movement (after maturation) to deeper water might have the advantage of reducing inter-specific competition (Warburton & Blaber 1992). Stratum I (*Posidonia* beds) is inhabited by a much greater number of species than the other strata (Tsimenides et al. 1991). It is the nursery ground of most Mediterranean demersal species (García-Rubies & Macpherson 1995). However, inter-specific competition in this stratum might be low as a result either of a temporary adjustment in the occupation of the shallow zone (Warburton & Blaber 1992, García-Rubies & Macpherson 1995) or of a shift in feeding habits (Labropoulou & Plaitis 1995, Labropoulou & Eleftheriou 1997). The movement of larger fish to greater depth could be a part of a strategy for better exploitation of the shallow zone by a greater number of species. Although no cannibalism has been reported, fish prey only made an important contribution to the diet of red mullet larger than 171 mm (Labropoulou et al. 1997). The latter are generally found in deep water (stratum II). Therefore, size-selective habitat use may also function as a defense against cannibalism on other conspecifics.

Intra-specific competition could also be relaxed by movement of larger fish to deeper water, e.g. by means of a bathymetric adjustment triggered by first maturity. Additionally, this timing results in the smaller, rapidly growing individuals inhabiting the shallow competitive stratum I for the minimum necessary time.

The movement of red mullet follows a definite pattern and could be considered as migration. The fish are spawned in stratum II, they are recruited in stratum I and subsequently return to the stratum in which they were born to reproduce. The following points may be made: (1) there seems to be a bathymetric rather than a geographical determination of the 'immature' and 'mature' segregation, so there is no 'homing'; (2) there was a short-distance rather than a long-distance movement; and (3) we found no evidence for any seasonal migration cycle. Nevertheless, this pattern seems to have an evolutionary origin, namely (1) a possible adaptive value in the tendency to dissociate the mature from immature individuals, and (2) a possible adaptive value of the timing of the 'evacuation' of the recruitment ground by older fish.

The same pattern of 'inter-depth' migration, related to reproduction, has been observed in deep-sea fishes (Middleton & Musick 1986). A difference is that the red mullet, instead of returning to shallow water after reproduction, continues dispersing into deeper waters. The absence of a correlation between maximum length and depth in the spring could be due to a movement from deep water to stratum II, but there was no clear evidence for that.

The stocks of red mullet in the Mediterranean Sea are considered to be heavily exploited (Caddy 1993). The existence of bathymetric movements in this species has ecological but also management implications. From a management perspective, it has generally been assumed that closure of trawl fisheries during the summer months (June to September) and in waters shallower than 50 m would be an effective means of increasing the biomass of fish available to the fisheries. Results of this study suggest that this management policy is successful in protecting the immature fraction of the population, but reproducing adults are fully vulnerable to overfishing, especially during spawning. This might cause a decrease in recruitment by decreasing the number of reproducing females.

Much of what fisheries management tries to achieve is aimed towards maintaining a sufficient biomass of reproductively active fish to replenish stocks (Roberts 1997). As pointed out by Stergiou & Pollard (1994), the multi-species, multi-gear nature of Greek fisheries (and of the Mediterranean fisheries in general) poses difficulties in designing and implementing protective measures. They suggest that the creation of marine harvest refugia may be potentially well applicable in the case of the Aegean Sea demersal fisheries. Such protected areas would allow a proportion of the stock to grow to a relatively large size at which overall fecundity is greatly increased.

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