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Reproductive strategies in macrourid fish: seasonality or not?

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ABSTRACT: Macrourid fish are abundantly found on the continental slope of the Ionian Sea (eastern Central Mediterranean), but the knowledge on their biology is still rather scanty. The reproductive stragegy of *Hymenocephalus italicus*, *Nezumia sclerorhynchus* and *Coelorhynchus coelorhynchus* was studied through data collected during 8 seasonal trawl surveys carried out between April 1996 and March 1998. Ripe females of *H. italicus* and *N. sclerorhynchus* were found all year round, with a small increase during summer and autumn in the former and without any seasonal component in the latter. Few ripe females of *C. coelorhynchus* were collected over the study period, with the exception of October 1996 when an increase was recorded, indicating that autumn could be included in the breeding season of this grenadier. The many different sizes of eggs and postovulatory follicles found in the ovaries indicate that all 3 species reproduce serially as multiple batch spawners. Maximum egg sizes were 1.5 mm in *H. italicus* and *N. sclerorhynchus* and 1.6 mm in *C. coelorhynchus*. The highest gonadosomatic index values were found in *H. italicus*, and the lowest in *C. coelorhynchus*. All 3 species seem to delay reproduction. The size at first maturity (50% of the population) was 27 mm pre-anal length in *H. italicus*, 37 mm in *N. sclerorhynchus* and 61 mm in *C. coelorhynchus*. Aseasonal continuous spawning can be assumed for *N. sclerorhynchus* while the low frequency of the early maturity stages in *H. italicus* makes it difficult to state whether or not this macrourid spawns throughout the year without a seasonal component. Further study is necessary to define the reproductive cycle of *C. coelorhynchus*.

KEY WORDS: Biology · Reproduction · Macrourids · Mediterranean

INTRODUCTION

Although the physico-chemical stability of the deep sea long led scientists to consider many organisms as continuous year-round spawners (Orton 1920), deep-sea fish are now recognized to have seasonal reproduction cycles. Several studies carried out in the Atlantic reported that in the context of a physically constant environment the reproductive cycles of deep-sea fish could be synchronised with the surface primary production linked to the seasonal thermocline, so that developing pelagic eggs float upwards and larvae are produced in food-rich waters. Moreover, the reproductive cycles of deep-sea fish could be linked with the consequent secondary production through vertical migration of the mesopelagic fauna (e.g. Mead et al. 1964, Marshall 1965, Marshall & Merrett 1977, Gordon 1979a,b, Hureau et al. 1979, Gage & Tyler 1991).

Gage & Tyler (1991) reported that one problem in understanding seasonality in deep-sea fish reproduction is that the spawning season is not synchronous between species and thus cannot necessarily be related to the spring plankton bloom, unless the young stages are able to feed on secondary production. As these authors stated, the scarce and geographically dispersed data are not adequate to define a general pattern of reproductive biology in deep-sea species. In fact, in the North-East Atlantic, both continuity and seasonality have been observed in the reproduction of different species (e.g. Merrett 1987).

Although day-by-day research provides new data reviewing and updating previous work, several gaps remain in the study of deep-sea species, most of them

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linked to sampling difficulties and to limited knowledge of the deep-sea environment. In the last decade the increasing studies on Mediterranean demersal resources have allowed the collection of data not only on commercial species but also on many others that assume an important role in the deep-sea ecosystem. In the Ionian Sea (eastern Central Mediterranean) macrourid fish are generally found to be abundant during trawling carried out on the upper slope (Matarrese et al. 1996). The only data on their biology are reported in D'Onghia et al. (1996).

During 1996 to 1998, the study project 'Developing deep-water fisheries: data for their assessment and for understanding their interaction with and impact on a fragile environment' financed by the EC and coordinated by the Scottish Association of Marine Science gave us the opportunity to sample further data on the population biology of macrourids. The aim of this paper is to contribute further to the knowledge of their reproductive strategy in the Mediterranean Sea by considering whether or not their reproductive activity is seasonal.

MATERIALS AND METHODS

The family Macrouridae is known to be represented in the Ionian Sea by 4 species: *Hymenocephalus italicus* (Giglioli 1884), *Nezumia sclerorhynchus* (Valenciennes 1838), *Coelorhynchus coelorhynchus* (Risso 1810) and *Trachyrhynchus trachyrhynchus* (Risso 1810). Since the first 3 species are generally found to be abundant during trawling carried out in the upper slope of this eastern Central Mediterranean basin (Matarrese et al. 1996), this paper deals with data relating to them.

Specimens of *Hymenocephalus italicus*, *Nezumia sclerorhynchus* and *Coelorhynchus coelorhynchus* were collected during 8 seasonal trawl surveys carried out from April 1996 to March 1998 in the Ionian Sea (Fig. 1). The depth range examined was between 250 and 750 m; bottoms deeper than 750 m in the area are generally not suitable for trawling. The sampling design adopted was stratified. During each survey 12 hauls of 3 h in duration were carried out from dawn to dusk. The final data set comprises 96 hauls for a total of 288 h of sampling.

A 75 t gross tonnage motor powered vessel, with a 360 Hp engine and equipped with a nylon otter trawl net, with stretched mesh of 40 mm in the codend, was hired. A cover with stretched mesh of 20 mm was employed on the codend in order to collect very small specimens of the species.

The horizontal and vertical net opening, measured using the SCANMAR sonar system and depending on various factors (depth, warp length, towing speed, etc.), ranged respectively from 21.52 to 23.89 m and from 0.91 to 0.95 m (Fiorentini et al. 1994). The vessel speed, measured by using GPS (global positioning system), was maintained at 2.5 to 3.0 knots.

Pre-anal length (PAL) was measured to the nearest mm and weight to the nearest 0.1 g. Sex was recorded for each specimen captured. The maturity stage of gonads was recorded macroscopically according to Nikolsky (1963), considering the following maturity stages: (2) resting (immature); (3) maturing; (4) mature; (5) running ripe; (6) spent. The sex of the virgin gonad (stage 1) was indistinguishable in the very small specimens. Moreover, histological analysis was carried out on a subsample of mature and running ripe gonads. Ovaries and testes were removed and fixed in Bouin's solution. Then they were dehydrated in an ascending ethanol series and embedded in paraffin wax (melting point = 56°C). Serial sections 7 µm thick were cut and stained with Mayer's hematoxylin-eosin.

The percentage frequency of the maturity stages recorded in the sampled population was computed for both females and males of the 3 species. Temporal variations in gonad maturity was investigated. Further analysis on the reproduction was only carried out for the female populations. Particularly, considering that the proportion of juvenile or immature individuals in

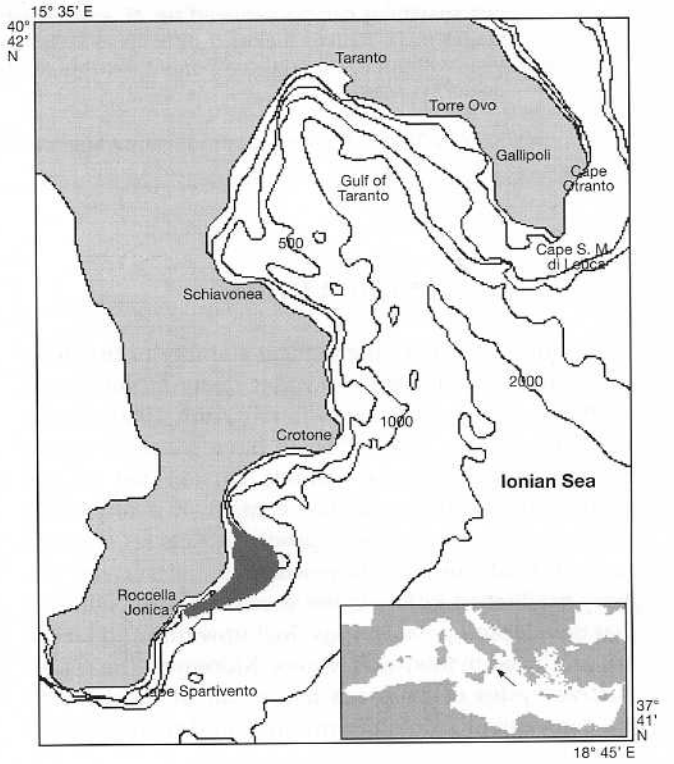

Fig. 1. Map of the north-western Ionian Sea with indication of the area (■) investigated from April 1996 to March 1998

the sampled populations varied monthly the percentage of mature females in each survey was also computed starting from the size at first maturity. The size at first maturity (size at which 50% of the fish in the population had ripe gonads) was determined, for the pooled data (8 surveys), from the logistic curve showing the percentage of mature specimens (stages 4 and 5) by size class. Since for many species the larger females in a cohort spawn earlier in a definite reproductive season (Ridgway et al. 1991, Van Winkle et al. 1997), mean, minimum and maximum sizes were recorded considering all ripe females during each season.

Total body weight and gonad weight were measured for a subsample of female specimens: 491 in *Hymenocephalus italicus*; 413 in *Nezumia sclerorhynchus* and 321 in *Coelorhynchus coelorhynchus*. The gonadosomatic index (GSI) was computed as follows:

$$GSI = (\text{gonad weight}/\text{total body weight}) \times 100$$

The relationship between GSI and length was performed as reported in Gordon et al. (1995) with the aim of highlighting the size at maturity within the population.

RESULTS

During the research a total of 6351 *Hymenocephalus italicus*, 9331 *Nezumia sclerorhynchus* and 10474 *Coelorhynchus coelorhynchus* specimens were collected in the study area. The number of indeterminate specimens (unsexed due to virgin gonad in small individuals or undefined in large ones), females and males caught during each survey is reported in Table 1. The percentage frequency of the maturity stage recorded in the sampled population of the 3 species is presented for females and males in Fig. 2.

In *Hymenocephalus italicus* and *Nezumia sclerorhynchus* mature specimens as well as maturing and immature ones were found throughout the year. Females with spent ovaries were caught during July and no males with spent gonads were observed. Particularly, in *H. italicus* the maturity stages 4 and 5 prevailed in the ovaries in each season with the highest percentage in summer and autumn of both years. A higher percentage of mature males than immature males was shown during the first 3 surveys.

A significantly lower percentage of mature individuals of both sexes was collected for *Coelorhynchus coelorhynchus*, even during October 1996 when a high number of specimens was caught. For this fish, juveniles dominated the sample in every survey. The few ripe females were almost exclusively found in autumn and spring.

Histological analysis carried out in the gonads considered macroscopically mature confirmed the maturity condition. The ovaries contained eggs of several sizes corresponding to previtellogenic, vitellogenic and postovulatory follicles. The largest mature oocytes had a diameter of 1.5 mm in *Hymenocephalus italicus* and *Nezumia sclerorhynchus* and 1.6 mm in *Coelorhynchus coelorhynchus*. Testicular cysts were shown in the testes with spermatogonia, spermatocytes, spermatids and spermatozoa.

The smallest sizes of mature specimens of both sexes and the size at attainment of 50% maturity in females shown in the sampled population of the 3 species are reported in Table 2. For sizes greater than the length at first maturity, high percentages of mature females were found in each survey for *Hymenocephalus italicus* and *Nezumia sclerorhynchus*, with the highest values during summer and autumn of both years in the former and without any seasonal trend in the latter. *Coelorhynchus coelorhynchus* only showed a high and significant percentage of mature females during October 1996 (Fig. 3).

Continuity in the maturation process throughout the year in females of *Hymenocephalus italicus* and *Nezumia sclerorhynchus* was highlighted by computing

Table 1. Number of indeterminate specimens (I), females (F) and males (M) of macrourids caught in the Ionian Sea from April 1996 to March 1998

	Hymenocephalus italicus				*Nezumia sclerorhynchus*				*Coelorhynchus coelorhynchus*			
	I	M	F	Total	I	M	F	Total	I	M	F	Total
Apr 1996	207	318	406	931	77	206	180	463	143	305	373	821
Jul 1996	48	439	476	963	549	227	205	981	108	51	72	231
Oct 1996	71	238	282	591	846	341	539	1726	1732	1465	1967	5164
Feb 1997	177	164	254	595	843	462	429	1734	772	225	154	1151
May 1997	266	80	178	524	318	322	330	970	185	89	90	364
Jul 1997	124	111	159	394	253	233	197	683	207	89	15	311
Dec 1997	170	238	353	761	600	273	354	1227	279	136	197	612
Mar 1998	514	567	511	1592	660	391	496	1547	1101	424	295	1820
Total	1577	2155	2619	6351	4146	2455	2730	9331	4527	2784	3163	10474

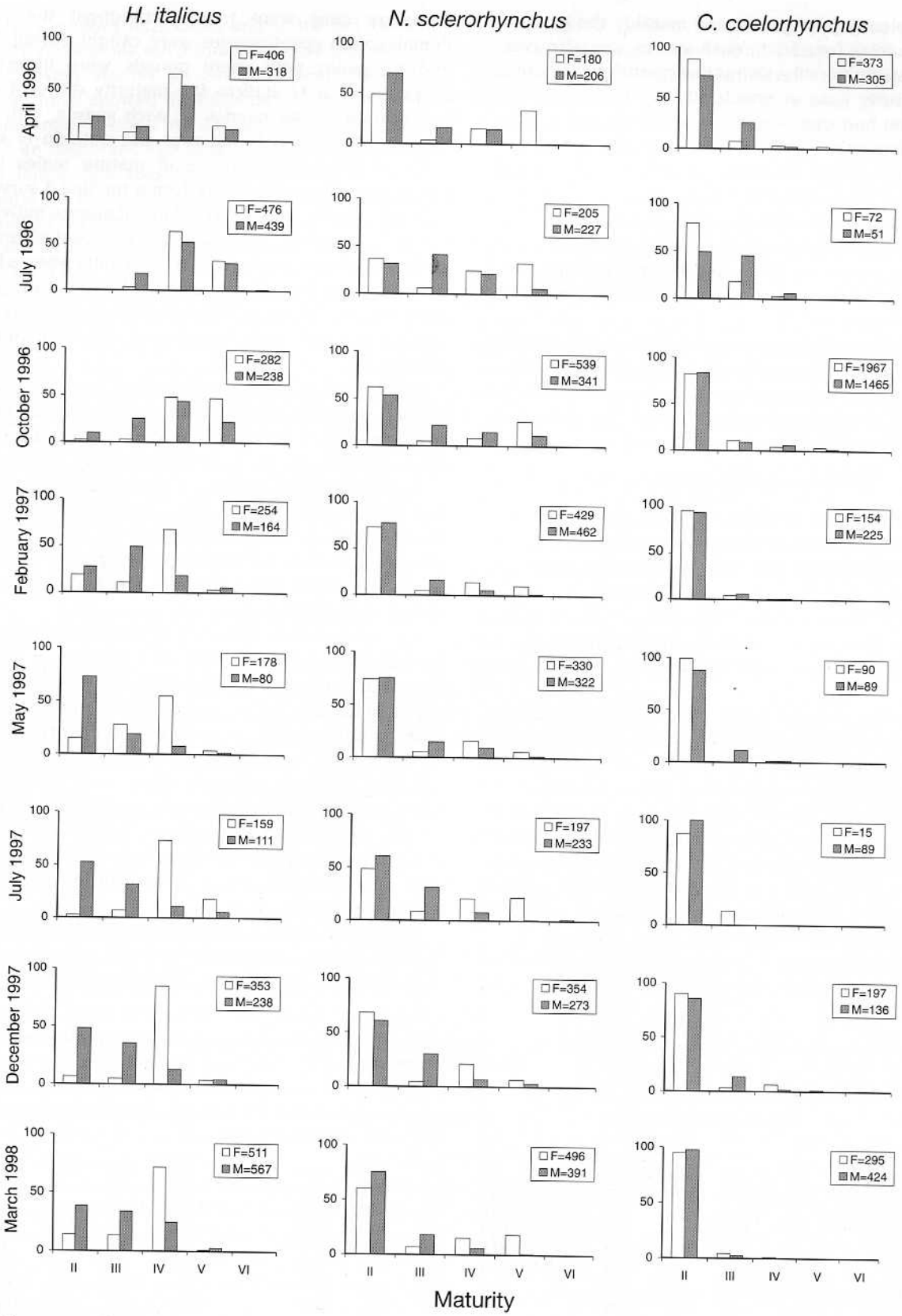

Fig. 2. Percentage frequency of maturity stages of macrourids, females (F) and males (M), found in the upper slope of the Ionian Sea from April 1996 to March 1998

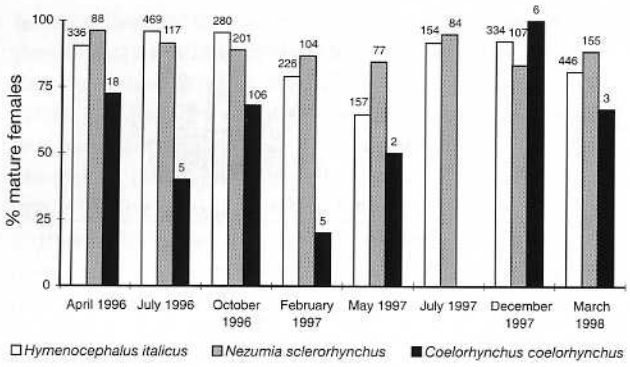

Fig. 3. Percentage of mature females with size > $PAL_{50\%}$ in macrourid populations caught in the Ionian Sea from April 1996 to March 1998 (the total number of females with size > $PAL_{50\%}$ is reported at the top of each column)

data pooled by season and considering mean, minimum and maximum sizes of ripe individuals (Fig. 4). The percentage of mature females was greater than 80% in each season (greater than 90% during summer and autumn in *H. italicus*) with overlapping sizes at maturity in both species. This kind of analysis was not carried out for *Coelorhynchus coelorhynchus* due to the small number of females, or even no mature females, sampled during some periods.

The average values of the GSI of females by survey are shown in Fig. 5. Such values, with their relative variability, appear to be fairly comparable throughout the year in *Nezumia sclerorhynchus*. In *Hymenocephalus italicus* the highest mean GSIs were observed during autumn of both years and in May 1997. However, during this month the highest standard deviation was computed. The changes shown in the GSI of *Coelorhynchus coelorhynchus* were in general agreement with the trend observed in the percentage of mature individuals. This grenadier had the lowest GSI values among the 3 species.

From the relationship between the GSI and length for the whole female sampled population it can be seen that GSI values increase with size in every species, but the rate of the increment is not continuous throughout (Fig. 6). Although the highest GSI values were for the larger size classes in the sampled populations, a high individual heterogeneity characterized the whole process. The length at maturity corresponded to the beginning of the second peak in the globally bimodal length distribution, in agreement with the size at first maturity computed by logistic function.

Table 2. The smallest mature specimens (PAL_{min}) and the size at attainment of 50% maturity in females ($PAL_{50\%}$) found in the sampled population of the 3 species of macrourids

	PAL_{min}		$PAL_{50\%}$
	Males	Females	Females
Hymenocephalus italicus	20	22	27
Nezumia sclerorhynchus	24	26	37
Coelorhynchus coelorhynchus	32	33	61

DISCUSSION

Although the results obtained in this research confirm that the macrourid fish *Hymenocephalus italicus*, *Nezumia sclerorhynchus* and *Coelorhynchus coelorhynchus* reproduce as serial spawners in the Ionian Sea (D'Onghia et al. 1996), they show different patterns for gonad maturity stages and the seasonal component in the reproductive cycle.

Of the 3 species, *Nezumia sclerorhynchus* appears to be the only one with a spawning pattern consistent with no seasonal component to its reproductive cycle. Throughout the seasons, females of this grenadier were found with a high frequency of eggs in all maturity stages, comparable high percentages of ripe females > $PAL_{50\%}$ and comparable GSI values. Moreover, considering that a decrease in the average size of spawners should occur as the season procedes until the reproductive peak (Ridgway et al. 1991, Van Winkle et al. 1997), the lack of such evidence constitutes further proof of aseasonal continuous spawning in *N. sclerorhynchus*.

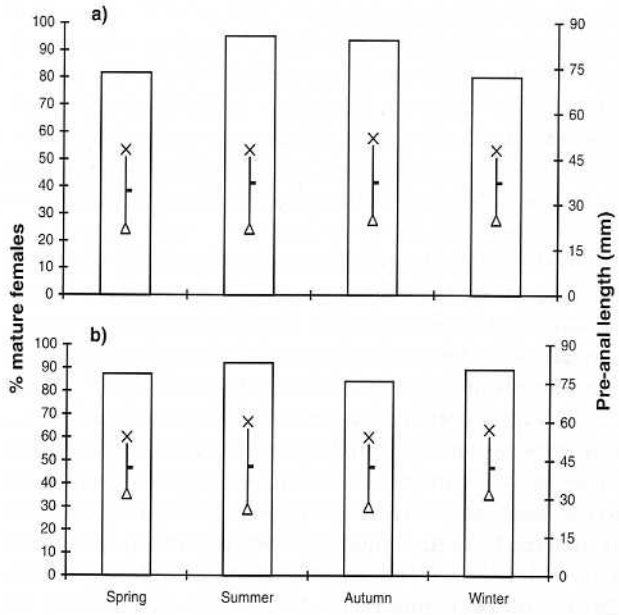

Fig. 4. (a) *Hymenocephalus italicus*; (b) *Nezumia sclerorhynchus*. Percentage of mature females with size > $PAL_{50\%}$ with indication of mean (–), minimum (Δ) and maximum (×) pre-anal length of all mature females in macrourid populations caught in the Ionian Sea from April 1996 to March 1998

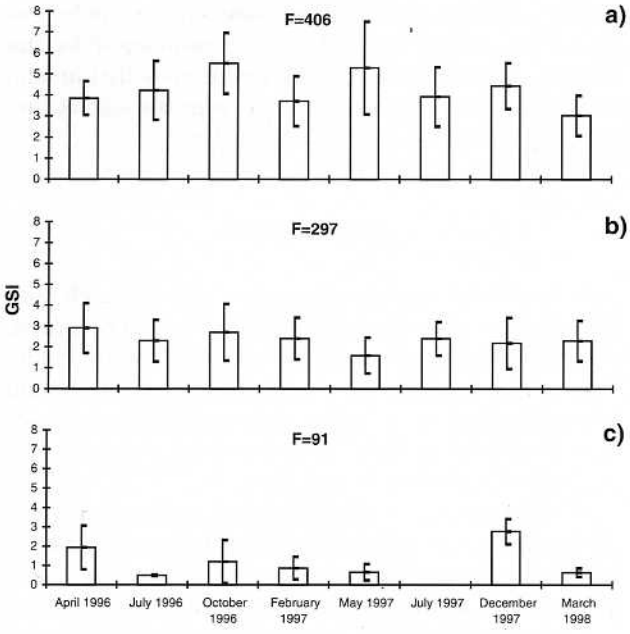

Fig. 5. (a) *Hymenocephalus italicus*; (b) *Nezumia sclerorhynchus*; (c) *Coelorhynchus coelorhynchus*. Changes in gonadosomatic index (GSI) with survey in macrourid females with size > $PAL_{50\%}$ caught in the Ionian Sea from April 1996 to March 1998 (mean values with standard deviation are shown)

A high percentage of *Hymenocephalus italicus* individuals in spawning condition were also collected all year round, despite a slight increase during summer and autumn. In addition, this grenadier showed a different temporal pattern to *Nezumia sclerorhynchus* in the proportions of different maturity stages. The early stages of maturity (or individuals with small-medium sizes) were less represented than the late stages (or individuals with medium-large sizes) in the sampled population. This was particularly evident in females.

Although the sampling was carried out each season in a depth range where the population of *Hymenocephalus italicus* is mostly distributed in the Mediterranean and juveniles have a shallower distribution than adults (Cohen et al. 1990, Massutì et al. 1995), the low proportion of immature specimens could be the consequence of their lower availability on the investigated bottoms and/or their lower vulnerability to the gear used. With a more pelagic feeding habit of *H. italicus* than the other 2 species (Marshall & Merrett 1977, McLellan 1977, Geistdoerfer 1978, Macpherson 1979), the juveniles could have more opportunity to escape throughout the larger mesh around the mouth and on the wings of the net before being caught in the codend or could be dispersed higher up the water column than adults, thus avoiding the mouth of the trawl.

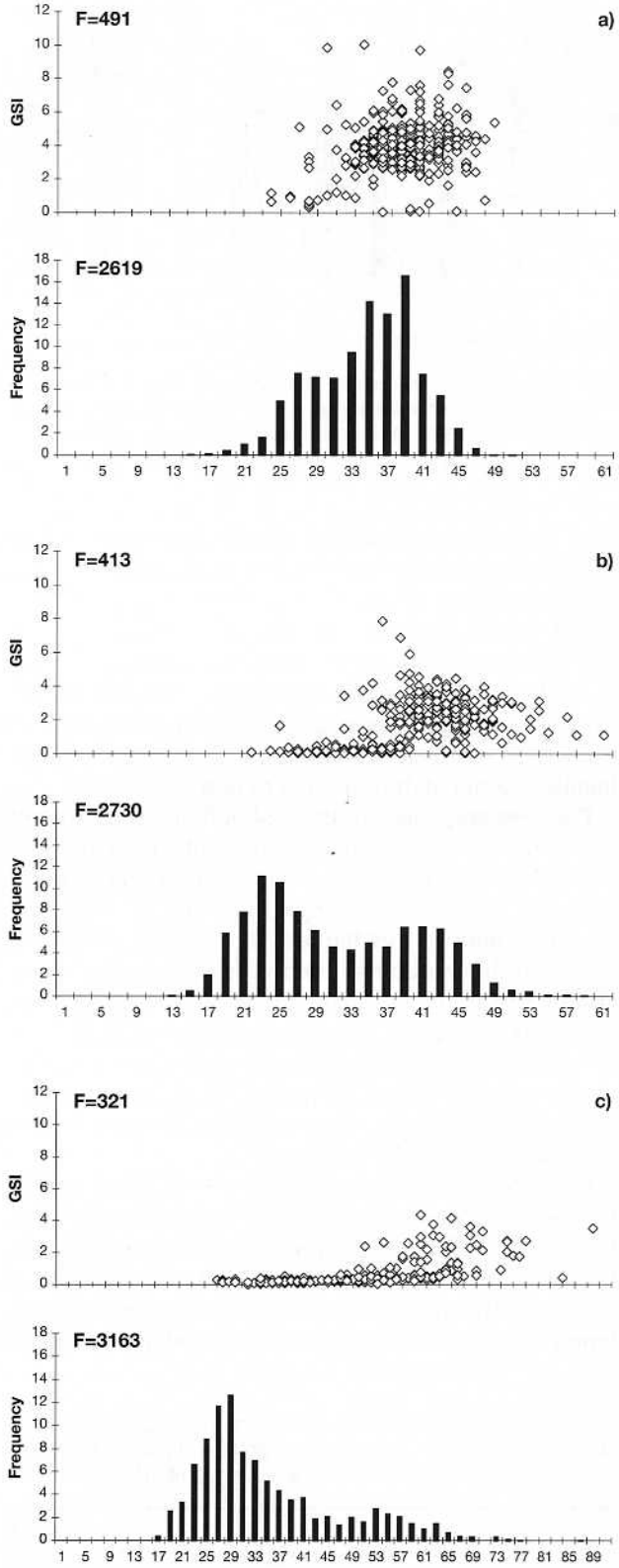

Fig. 6. (a) *Hymenocephalus italicus*; (b) *Nezumia sclerorhynchus*; (c) *Coelorhynchus coelorhynchus*. Relationship between GSI and size of females in macrourids caught in the Ionian Sea from April 1996 to March 1998

Since the low frequency of early maturity stages was particularly evident in females it is also probable that the trawl net used during the research could have a lower catchability of small-medium size females than the medium-large ones. As reported by Merrett & Haedrich (1997) for the macrourid *Coryphaenoides armatus*, the size-frequency distribution and sex ratio gathered by trawl may not necessarily be representative, being different from those revealed by AUDOS free vehicle sampling. Males that constitute a different size group may be the more active sex, avoiding trawls but attracted to bait. In the same way, the small-medium size (or stages 2 and 3) females of *Hymenocephalus italicus* in the Ionian Sea might be more active in avoiding the trawl net than medium-large (or stages 4 and 5) ones due to the significant smaller weight and volume of the ovaries in the body cavity. The fact that this did not occur in *Nezumia sclerorhynchus* and *Coelorhynchus coelorhynchus* might be due to the greater size of these 2 species and to a smaller proportion of the gonad weight to body weight even in mature females. On the other hand, in all 3 species mature males were found to be always less abundant than mature females, confirming observations by Merrett & Haedrich (1997). Lower percentages of early maturity stages in *H. italicus* were also shown in previous research, exploring the same depth range but a wider area of the Ionian Sea during more intense sampling at 2 mo intervals for 2 yr (D'Onghia et al. 1996).

Although the spawning can be assumed to be continuous throughout the year in *Hymenocephalus italicus*, the bias in the representativeness of the various size classes and maturity stages in the sampled population could mask the seasonal component. The little evidence of seasonality (a slight increase in the percentage of ripe females was recorded during summer and autumn of both years) could be enhanced or dampened in a more representative sample.

Autumn seems to be included in the breeding season of *Coelorhynchus coelorhynchus*. The small number of mature specimens found during the research does not allow reliable conclusions to be drawn on the extension of the reproductive period or on the occurrence of a seasonal component. Despite the depth range investigated for this grenadier covering the vertical gradient where the population is most abundant in the Mediterranean (Cohen et al. 1990, Massutì et al. 1995), the adult ripe individuals could be distributed at greater depths not explored during the research.

The GSI values estimated for the 3 species show that the greatest reproductive effort seems to be carried out by *Hymenocephalus italicus*. All 3 species seem to delay reproduction as shown by Gordon et al. (1995) for many Atlantic deep-water species. These authors report that in the slope-dwelling fishes, females become mature only after they reach full size and when somatic growth has slowed. The size at first maturity computed in this study for *H. italicus* is in agreement with that reported by Massutì et al. (1995). Considering the estimated size at first maturity and the age-length keys for *H. italicus* and *Coelorhynchus coelorhynchus* by Massutì et al. (1995), the age at first maturity for these 2 species would be around the 3rd and 6th yr respectively. Length-at-age for *Nezumia sclerorhynchus* in the Ionian Sea (unpubl. data) indicates an age at first maturity around the 5th yr.

Concerning the knowledge on the reproduction of macrourid fish in the Mediterranean, the finding of eggs and larvae of *Hymenocephalus italicus*, *Nezumia sclerorhynchus* and *Coelorhynchus coelorhynchus* from December to March was reported by Sanzo (1933). Massutì et al. (1995) found ripe females of *H. italicus* all year round with an increase during summer. Rannou (1975, 1976) considered spawning to be periodic for *N. sclerorhynchus* because of the presence of distinct size/age groups in the population. Year-round spawning of this species has previously been recorded in the Ionian Sea (D'Onghia et al. 1996) and spawning continuity of a species of the same genus, *N. aequalis*, is known in the Mediterranean (Relini Orsi & Wurtz 1979, Carrasson & Matallanas 1989, Massutì et al. 1995). In *C. coelorhynchus* reproduction was assumed to be between November and May by Sardou (1970) and during spring-summer by Massutì et al. (1995). D'Onghia et al. (1996), investigating a wider area in the Ionian Sea, found small numbers of ripe specimens of *C. coelorhynchus* throughout the year with little increase from autumn to spring.

In the North-East Atlantic both continual and seasonal spawning have been observed in different deep-sea species, with evidence that geographic location of the species affects the reproductive strategy (Gordon 1979a,b, Gage & Tyler 1991, Merrett & Haedrich 1997). Merrett (1987) reported that species living in eutrophic seasonal conditions in the waters north of 40° N exhibited high fecundity, with all eggs in the ovaries at the same stage of development and seasonal breeding, whereas species distributed south of this latitude in the oligotrophic, a less seasonal environment, showed low fecundity and asynchronous spawning. The present results, at least for *Hymenocephalus italicus* and *Nezumia sclerorhynchus*, are in agreement with this latter pattern of reproduction.

The fact that egg development might occur at adult living depths within the benthopelagic zone (Merrett & Barnes 1996) could reduce linkage with seasonal changes of thermocline and productivity in the surface layers. Even though the young stages may be able to feed on secondary production under the euphotic

zone, they exploit pelagic waters where planktonic abundance is less variable than in epipelagic waters (Marshall 1953). Concerning adults, macrourids utilize primarily epibenthic and infaunal invertebrates and appear to be generalist feeders (Pearcy & Ambler 1974, Macpherson 1979, Mauchline & Gordon 1984, Carrasson & Matallanas 1989). Their diversified diet can guarantee an extended period for them to become mature.

From all the above, there are unequivocal indications of aseasonal continuous spawning of *Nezumia sclerorhynchus*, while further studies are necessary to determine whether *Hymenocephalus italicus* spawns throughout the year without a seasonal component and to define the reproductive cycle of *Coelorhynchus coelorhynchus*. The uncertainty derived from the representativeness of the sample reaffirms, as stated by Merrett & Haedrich (1997), the advantages of using different methods to confirm evidence.

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