

Abstract—The patterns of distribution and feeding habits of juvenile red porgy, *Pagrus pagrus*, were studied for fish collected in experimental trawl surveys carried out along the Cretan continental shelf over a period of four years. Abundance increased significantly in shallow waters, with a maximum between 20 and 50 m for all seasons, negatively correlated to depth and positively correlated to temperature. Patterns of bathymetric distribution were similar for all sizes of juvenile red porgy, varying little among seasons. The fact that no specimens larger than 219 mm FL were caught in the trawlable fishing grounds indicates that larger individuals aggregated over hardbottom areas that could not be sampled by trawling. Feeding intensity varied among the size classes of fish examined. Stomach-content analysis revealed that juvenile red porgy are carnivorous, feeding mainly on decapods. Diet composition did not vary seasonally; decapods were the most important prey throughout the year. However, the composition of the prey consumed varied considerably with predator size, coupled with differences in mean prey sizes found in each size class. Feeding rates of juveniles in terms of both feeding intensity and amount of food consumed were high and increased with fish size. The Cretan continental shelf habitat offers increased growth rate, reduced predation risk, and increased food abundance to juveniles and therefore they direct energy entirely into somatic growth. Juvenile red porgy appeared to be a separate unit, from a management as well as from an ecological point of view. Habitat segregation is of importance; juvenile specimens were differentiated from mature fish on the basis of their selection of bottom type and prey and to a lesser extent by depth.

Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758)

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Spatial and temporal variation in population attributes, size and age structure, abundance and distribution, generally reflect life history properties of a species. Changes in diet or habitat (or both) during ontogeny are extremely common in fishes (Werner and Gilliam, 1984). Fish partition food resources between species as well as between size classes within a species. Similar mechanisms such as differences in morphological features, foraging behavior, period of activity and habitat use, affect segregation of resource use in both cases (Werner, 1979; Mittelbach, 1981; Ross, 1986; Norton, 1991). However, different ecological processes have been emphasized in interpreting the adaptive value of resource partitioning in these two situations. Partitioning among species has been argued to reduce interspecific competition (Sale, 1979; Osenberg et al., 1992; Schluter, 1994). By contrast, differential vulnerability to predators or the ability to exploit prey (or both) may lead to *de facto* partitioning of prey among age classes within a species, with the consequence that intraspecific competition is reduced (Werner et al., 1983). Many fish un-

dergo ontogenetic changes in prey use between young-of-year and older stages. Both the ability to utilize the full spectrum of prey and to escape predators may be highly size related. Apart from changes in foraging demands, the vulnerability to predators decreases with increasing body size. Smaller fish frequently use sheltered habitats to reduce predation risk, whereas larger fish are often found in unprotected areas (Miller, 1979; Werner and Hall, 1988; McCormick, 1989). As a result of these changes in life style, fish may occupy different niches during ontogeny (Liem, 1984; Werner and Gilliam, 1984).

The red porgy, *Pagrus pagrus* (Linnaeus 1758), is a protogynous, sublittoral, demersal marine fish associated with a variety of temperate to subtropical habitats in the Atlantic and the Mediterranean Sea. It is commonly found on sandy, gravel, and hard bottoms, or around rocks, at depths ranging from 18 to 185 m (Manooch and Hassler, 1978; Vaughan et al., 1992). The correlation of age with maturity suggests that the majority of the females reach sexual maturity at three years (Manooch, 1976; Pajuelo and

Lorenzo, 1996; Harris and McGovern, 1997). The red porgy is of great commercial importance and consequently a highly exploited species in the areas of its distribution (Manooch and Hassler, 1978; Stergiou and Pollard, 1994). It is one of the most promising new species for fish farming in the Mediterranean Sea, having remarkably high growth rates under intensive rearing conditions. Therefore, the ambient demands of young individuals are of special interest for aquaculture (Divanach et al., 1993). The young individuals are distributed inshore of the adult population in trawlable areas. Even though they occur inshore as juveniles, adverse conditions of low water temperatures, competitive exclusion and unsuitable substrate reduce the longevity of this inshore distribution.

Adult red porgy do not occur in the same shallow waters as those inhabited by juveniles. The larger fish predominate in deeper waters, preferring hard substrate (Manooch and Hassler, 1978). A general trend for larger fish to occur in deeper water has long been known with respect to deep sea fishes (Haedrich and Rowe, 1977); however it has also been mentioned by Macpherson and Duarte (1991) for many demersal fishes of the continental shelf. Caddy (1993) has stated that offshore movements of older fish to locations on untrawlable bottoms possibly contribute to the continuing good recruitment, as well as to the stock recovery.

The aim of the present study was to define the habitat use of juvenile red porgy along the Cretan continental shelf and to examine whether red porgy undergo considerable changes in resource utilization during ontogeny. In addition to determining bathymetric trends in mean size of red porgy, the relationship between density, depth, and temperature within size groups are defined. Furthermore, we investigated the effects of the feeding habits, prey choice, and trophic interactions among the different size groups on the distribution patterns of red porgy.

Material and methods

Study area and sampling procedure

A three-year survey on the distribution of red porgy was carried out along the Cretan continental shelf,

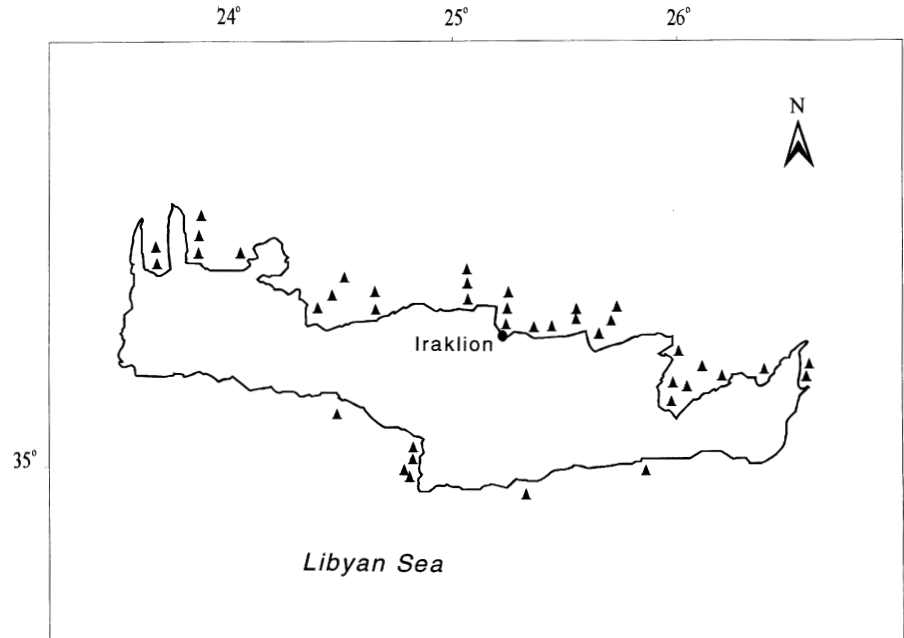


Figure 1

Location of the sampling stations on the Cretan continental shelf.

from August 1988 to April 1991. Nine seasonal experimental bottom trawl survey cruises were conducted by the Institute of Marine Biology of Crete at 40 fixed sampling stations selected to cover all the trawlable fishing grounds of the region (Fig. 1). The collected data included abundance of fishes caught and supporting data on depth, temperature, and salinity. The cruise periods were as follows: late August to early September (summer), December (winter), and late March to early April (spring). The sampling stations were distributed over three distinct depth zones: 26–70 m (zone I), 71–150 m (zone II), and 151–350 m (zone III). Zone I covered 25%, zone II 24%, and zone III 51% of the total study area. Algae and marine angiosperms, mainly *Caulerpa prolifera*, *Posidonia oceanica*, and *Halophila stipulacea*, dominated the sand-silt substrate in zone I. The substrate of zone II was muddy and the substrate of zone III was covered by the crinoid *Leptometra phalangium*. Monthly samples (excepting January) from August 1990 to August 1992 were also taken from experimental trawl surveys in Iraklion Bay for stomach-content analysis. These samples were collected from a fixed station on the trawlable fishing ground of the region between 25 and 35 m during the morning, between 0830 and 0930 hours.

The trawl used was equipped with a codend bag liner of 22-mm stretched mesh size. The duration of each haul (bottom time) was 50–90 min and the trawling speed fluctuated from 1.8 to 3 knots, depending on the depth and nature of the bottom. Be-

cause all trawls were carried out with the RV *Philia*, it was assumed that gear selectivity was constant. Bottom temperature and salinity were measured with a SEA-BIRD CTD unit. The measurements recorded for the 5 m above the bottom of each station were averaged and the resulting values were considered as the temperature and salinity at the specific station.

Laboratory methods

Fork lengths (FL, mm) were measured for at least 100 individuals collected at each station and cruise. Of a total of 3280 fish, all specimens were found to be immature. To evaluate size-related variations in food habits and habitat use, red porgy were separated into five size classes: 0 (40–104 mm FL), 1 (105–147 mm FL), 2 (148–186 mm FL), 3 (187–219 mm FL), and 4 (>219 mm FL) which were chosen as they approximate the age of the fish within each size class as determined from the von Bertalanffy growth equation derived by Machias et al. (1998).

Each month 20–30 specimens were preserved in 10% buffered formalin immediately after capture for stomach-content analysis. Samples were taken to the laboratory, measured to the nearest mm (FL), and weighed to the nearest 0.1 g. Thereafter, the stomachs were removed and the contents wet weighed. Prey items were identified to the lowest possible taxonomic level, counted under a binocular microscope and weighed to the nearest 0.01 g. Prey species were measured to the nearest 0.1 mm by using an ocular micrometer or a vernier caliper, where possible. Fork length of the fish examined ranged from 41 to 185 mm, mean (\pm SD) FL was 87.2 (\pm 26.9) mm.

Data analysis

In accordance with the procedure described by Carrothers (1980), the door spread of the trawl net was calculated for each haul and then multiplied by the speed of the boat and fishing time to estimate the total area sampled. The abundance of fish caught was expressed as number of individuals per square nautical mile (nmi^2), making the comparison of fish abundance between sampling stations possible. After logarithmic transformations (Middleton and Musick, 1986; Stefanescu et al., 1992), mean abundances ($\text{number}/\text{nmi}^2$) were calculated for each cruise: 1) for 20-m depth intervals, 2) for 50-m depth intervals, and 3) per zone (I, II, III), as well as for each 1°C temperature interval. Salinity showed little variation (Table 1), having no effect on the distribution of fishes on the Cretan shelf (Tsimenides et al., 1991).

Analysis of variance showed no significant differences in the mean abundance among the three surveys in each season, nor among each zone during the same season ($0.377 < P < 0.610$, Bartlett test $0.201 < P < 0.462$). Results and conclusions for each season were similar and independent of whether survey-specific or pool data were used. Hence, only the latter are presented. Correlation analyses (Pearson correlation coefficient) were performed to determine if there were any significant changes in abundance with depth and water temperature, as well as to test the hypothesis that fish size was depth or temperature dependent. Geometric mean was preferred for calculating the mean fish size of each sample, because the arithmetic mean is susceptible to the influence of few large specimens and does not accurately represent the central tendency in fish size at a given station (Stefanescu et al., 1992). The bathymetric distribution of different size fish was simplified by converting lengths into the above-mentioned five size classes.

The contribution of prey items to diet was estimated by using both the numerical abundance and the biomass of prey items in stomachs (Berg, 1979; Hyslop, 1980; Bowen, 1983). Breadth of diet was calculated by using Levin's standardized index (Hurlbert, 1978; Krebs, 1989):

$$B_i = \frac{1}{n-1} \left(\frac{1}{\sum_j p_{ij}^2} - 1 \right),$$

where B_i = Levin's standardized index for predator i ;
 p_{ij} = proportion of diet of predator i that is made up of prey j ; and
 n = number of prey categories.

This index ranges from 0 to 1; low values indicated diets dominated by few prey items (specialist predators), higher values indicated generalist diets (Gibson and Ezzi, 1987; Krebs, 1989). Diet overlap between the size classes was calculated by using the simplified Morisita's index (Krebs, 1989; Hall et al., 1990):

$$C_{ik} = \frac{2 \sum_j p_{ij} p_{kj}}{\sum_j p_{ij}^2 + \sum_j p_{kj}^2},$$

where C_{ik} = simplified Morisita's index for predators i and k ; and
 p_{ij} and p_{kj} = proportions of predator i and k with prey j in their stomachs.

Diet overlap increases as the Morisita's index increases from 0 to 1. Overlap is generally considered

to be biologically significant when the value exceeds 0.60 (Keast, 1978; MacPherson, 1981; Wallace, 1981; Langton, 1982). Bias-corrected bootstrap 95% confidence intervals, based on 1000 simulations, were used to estimate the reliability of these indices (Efron and Tibshirani, 1986; Hall et al., 1990). Differences in diet composition and stomach fullness by fish size and month were tested by χ^2 on combined data for both years because diet did not vary significantly between the two years. The logit model used to investigate monthly variations in the proportion of full and empty stomachs, as a function of fish size was

$$\log(p_d/p_d - 1) = a_d + b_d L + e$$

where p_d = the probability that a stomach is nonempty in month d ;
 L = the fish length; and
 e = the error term.

One-way ANOVAs were used to compare the mean number, the mean weight, and the mean size of prey items among the size classes and the *a posteriori* Tukey's test was employed to locate the source of any differences. Numbers and weights of prey items were log-transformed to remove the dependency of the variance on the mean (Zar, 1984). Mean number and mean weight of prey per fish in each size class was based only on specimens with food items in their stomach. All statistical inferences were based on the 0.05 significance level.

Results

Distribution patterns

Red porgy were found to occur to 250 m depth, between temperatures of 14.5 and 24.2°C and salinities of 38.1 and 40.0‰ (Table 1). Abundance in the trawlable fishing grounds was negatively related to depth during all seasons and positively related to temperature during summer and winter (Table 2). No significant correlations between abundance and temperature were observed during spring.

The distribution of red porgy by depth intervals indicated that although fish generally occur in all zones, their abundance significantly increased in shallow waters (zone I), with highest values during summer (Fig. 2). Relative abundance was significantly higher in the shallow zone, with a maximum between 20 and 50 m depth for all seasons. Furthermore, the relative abundance increased progressively from winter to a maximum of 2985.6 individuals per m^2 in summer. These differences of the relative

Table 1

Seasonal ranges of depth and temperature over the Cretan shelf where *Pagrus pagrus* occurred.

	Minimum	Maximum	Range
Depth (m)			
Spring	30	110	80
Summer	28	210	182
Winter	29	250	221
Temperature (°C)			
Spring	14.5	17.3	2.8
Summer	14.5	24.2	9.7
Winter	15.0	17.8	2.8
Salinity (‰)			
Spring	38.66	39.05	0.39
Summer	38.12	39.72	1.60
Winter	38.65	39.99	1.34

abundance in the shallow zone were mainly due to recruitment during summer.

The relationships between mean FL and depth were significantly positive in summer and winter (Table 2). Maximum FL increases with depth only in summer, whereas the minimum and the mean FL increase during summer and winter. However, no significant correlation between FL and temperature was found (Table 2). Depth distribution by size revealed that fish larger than 186 mm do not occur in shallow waters, which were dominated by young fish (Fig. 3). Moreover, individuals larger than 147 mm were poorly represented at depths below 80 m. The abundance of the size classes 0–2 was greatest in warm waters during all seasons (Fig. 4).

Feeding intensity

Of the 634 stomachs of red porgy examined, 226 were found to be empty (35.7%). The proportion of empty stomachs varied significantly among the size classes of fish examined ($\chi^2=11.78$, $P<0.001$), with a maximum of 39.6% for the 0 size class (Table 3). The logit model revealed that the interaction between month and fish size on the probability that a stomach is nonempty was significant ($F=2.07$, $P<0.01$). The slope was always >0 , indicating a positive allometry on full stomachs, whereas no differences on the estimated probabilities were detected between the two years ($t\text{-test}=-0.50$, $P>0.05$).

Composition of the diet

There were at least 58 different prey species belonging to four major groups (decapods, small crusta-

Table 2

Correlation analysis between *Pagrus pagrus* abundance and fork length with depth and temperature. *r*: Pearson correlation coefficient, *P*: significant level of probability.

	Abundance		Mean fork length (mm)		Minimum fork length (mm)		Maximum fork length (mm)	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Depth (m)								
Spring	-0.524	0.03	0.084	0.79	0.207	0.52	0.217	0.50
Summer	-0.621	0.00	0.693	0.00	0.670	0.00	0.689	0.00
Winter	-0.598	0.00	0.701	0.00	0.685	0.01	0.167	0.58
Temperature (°C)								
Spring	0.224	0.10	0.633	0.07	0.070	0.85	0.585	0.10
Summer	0.787	0.00	0.401	0.25	0.510	0.13	0.621	0.06
Winter	0.349	0.01	0.138	0.74	0.097	0.82	0.299	0.47

Table 3

Feeding indices of *Pagrus pagrus* from the Cretan shelf, in relation to size.

Size class	Fork length (mm)	No. of stomachs analysed	No. of full stomachs	Mean no. of prey items per stomach ¹	Mean weight prey items (g) per stomach ¹	No. of prey species	Diet breadth (Levin's index) ²	
							Number	Biomass
0	42–104	450	271	2.96 ^a (± 0.23)	0.17 ^a (± 0.01)	45	0.39 (0.22–0.50)	0.45 (0.31–0.56)
1	105–145	161	117	1.98 ^b (± 0.20)	0.46 ^b (± 0.01)	36	0.38 (0.22–0.50)	0.29 (0.15–0.38)
2	146–185	23	20	2.23 ^b (± 0.30)	0.77 ^c (± 0.01)	27	0.373 (0.21–0.49)	0.20 (0.12–0.33)

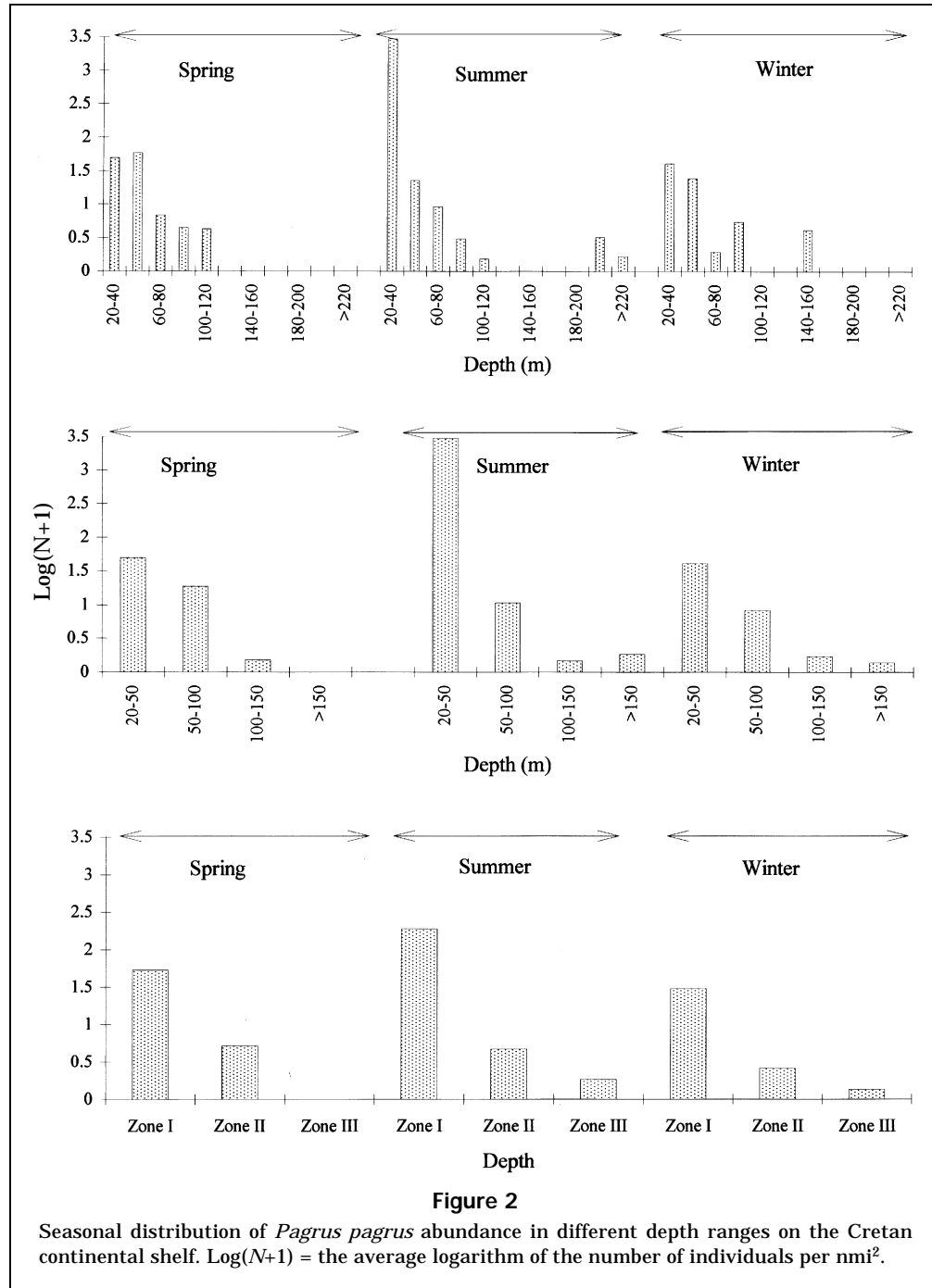
¹ Standard error given in parentheses, different letters indicate significant differences among means (Tukey's test).

² Ranges in parentheses: 95% bootstrap confidence intervals.

ceans, polychaetes, and fish) (Table 4). Polychaetes predominated in terms of percentage by number (35.1%), whereas decapods made up 54.2% of the total weight of stomach contents. Small crustaceans were also consumed in fairly large proportions by number (25.2%), but their contribution by weight was minor. Fish were a considerable dietary staple by weight (23.5%), although their contribution by number (6.7%) was comparatively low. At the species level, the thalassinid *Upogebia tipica*, the caprellid *Phthisica marina*, and the sedentary polychaete *Terebellides stroemi* were the most exploited prey. Among fish prey, *Gobius niger* was the species having greatest contribution in the diet of red porgy. Diet breadth was found to be 0.39 (±0.01) for the numerical abundance and 0.31 (±0.07) for the biomass of the prey species.

Food in relation to fish size

Although the contribution of prey groups, in terms of both number and weight, varied with fish size (Table 4), there were significant differences only between ingestion of small crustaceans ($\chi^2=28.46$, $P<0.001$), *U. tipica* ($\chi^2=15.38$, $P<0.001$), and *Liocarcinus maculatus* ($\chi^2=8.24$, $P<0.01$). Small crustaceans occurred in the younger specimens (0 size class), whereas *U. tipica* and *L. maculatus* occurred in greater percentages in the diet of fish corresponding to size classes 1 and 2. The total amount of food ingested varied significantly among size classes ($F=51.95$, $P<0.001$). Pair-wise group comparisons showed three homogeneous groups: the mean consumption rate per individual (i.e. g food/size class)

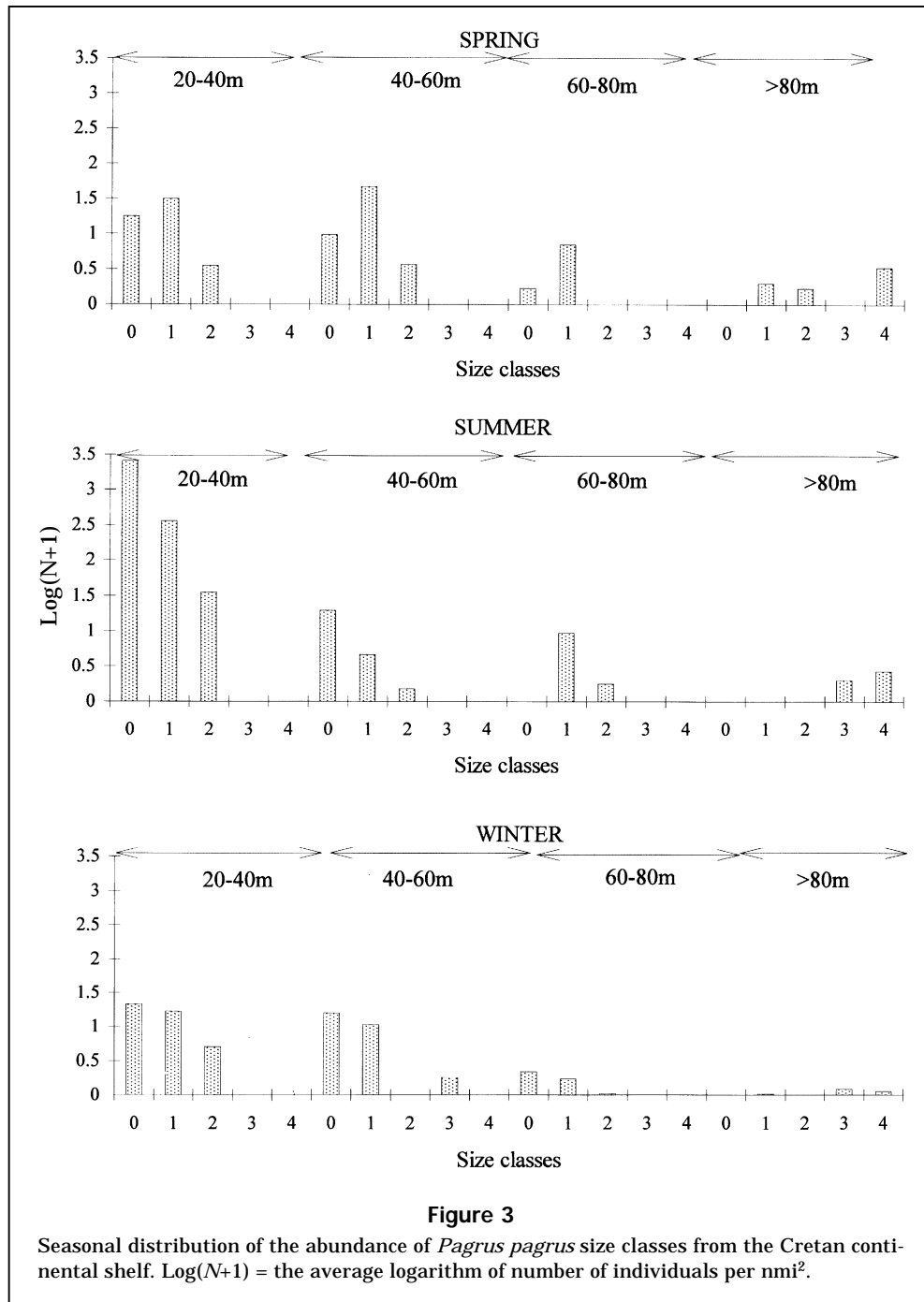


increased with increasing size, with 0-size-class fish to exhibit the lowest consumption rate (Table 3). The mean number of prey items consumed decreased significantly with size ($F=3.33$, $P<0.05$) (Table 3).

Breadth of diet decreased with fish size, both numerically (abundance) and with biomass of prey species (Table 3). In general, values for dietary overlap between size classes were similar irrespective of the resource matrix used. A significantly high overlap was observed only between specimens of 1 and 2 size classes (Table 5).

Seasonal variation in diet

Diet composition was fairly consistent over the months (Fig. 5, A and B). Decapods were the most important prey throughout the year, especially during winter months and March, owing to the increase of the importance of the thalassinid *U. tipica*. Polychaetes were also an important component in the diet of red porgy throughout the year. Dietary breadth varied little, except for low values in winter months



and March, when *U. tipica* dominated (Fig. 6, A and B).

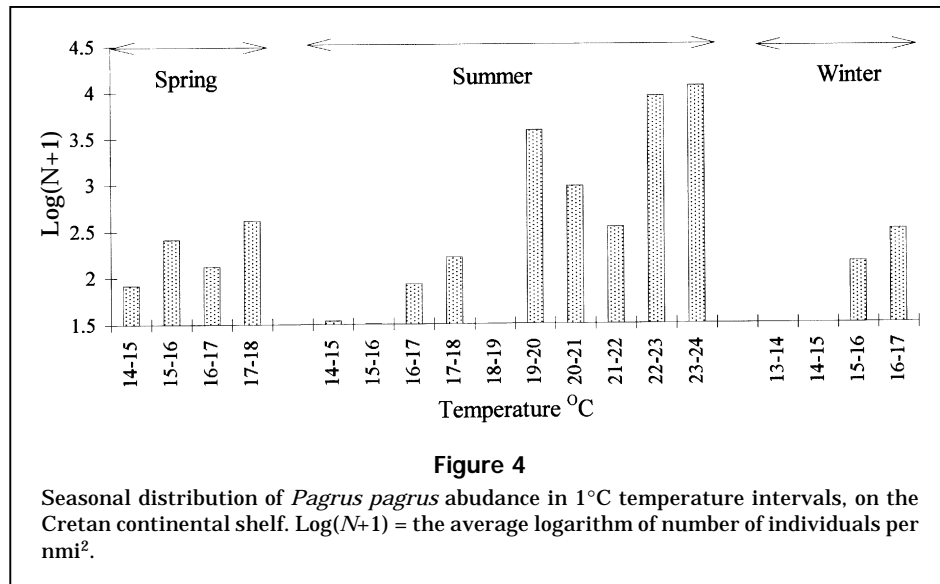
Relationship of length of predator to length of prey

Significant positive correlations were found between the size of red porgy and the mean size of prey consumed ($P < 0.001$, $r^2 = 0.85$, $n = 169$). Furthermore, analysis of variance on the mean prey sizes consumed by the three size classes revealed significant differ-

ences ($F = 93.7$, $P < 0.001$). The 0-year fish exploited prey with smallest mean size (18 ± 6.6 mm), 1-year fish consumed prey 26.2 ± 5.4 mm, and 2-year fish fed on the largest prey (41.6 ± 5.8 mm).

Discussion

Juvenile red porgy on the Cretan continental shelf tend to occur in shallows (20–50 m), where the sub-



strate is sandy and interspersed with patches of algae and seagrass. At this depth range, bottom water temperature is the highest during all seasons. Thus, this depth preference is consistent with the tendency for red porgy to select warm temperatures in relation to those available in other areas of its distribution (Manooch and Huntsman, 1977; Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996). Although red porgy were found to occur down to 250 m depth, their densities were significantly greater at shallow stations. Furthermore, specimens smaller than 186 mm predominated in the trawl catches, whereas relative abundances of larger specimens was low. High densities of red porgy in shallow waters were due to the large number of juveniles, i.e. specimens that have not reached sexual maturity (Manooch and Hassler, 1978). The lack of larger fish from the trawl catches in shallower depths could not be due to gear selectivity because larger specimens were occasionally found in deeper waters, indicating that they could have also been caught in shallower depths, if present. A similar distribution pattern has also been reported for the Indo-Pacific species *Pagrus auratus* which has been studied in many different areas (Azeta et al., 1980; Kingett and Choat, 1981; Tanaka, 1985).

Size (or age) tends to be positively correlated with depth in many demersal fishes. Tremblay and Sinclair (1985) reported that the mean depth of occurrence tended to increase with age of cod in the southern Gulf of St. Lawrence. Similarly, Sinclair (1992) noted a positive correlation between age and median depth of cod on the eastern Scotian Shelf. Macpherson and Duarte (1991) found that mean fish length increased with depth in most south-east At-

lantic and north-west Mediterranean demersal fishes. Bathymetric trends in demersal fish distribution may be linked to other physical factors correlated with depth (e.g. temperature, salinity, bottom type). Temperature is a key factor in the metabolism of fishes and many studies have reported relationships between temperature and fish distribution (Fry, 1971; Nakken and Raknes, 1987; Rose and Leggett, 1989; Macpherson and Duarte, 1991). However it is unlikely that fish distributions are determined by physical factors alone. Biotic factors, in particular prey abundance, have also been shown to be important determinants of distribution. Productivity generally decreases with increasing depth and distance from land; therefore prey resources are greater in shallow waters. Haedrich and Rowe (1977) concluded that selection for mobility and metabolic efficiency should favor larger size in the relative barren deep sea, whereas Macpherson and Duarte (1991) suggested that the positive size-depth relationship in demersal fish may result from age-specific differences in temperature preferences. They argued that younger fish occupy warmer waters, where food supply and growth rates may be greater, whereas older fish occupy colder waters, where they may benefit from lower metabolic costs and greater longevity.

The most striking aspect of our results, was the lack of variation in the bathymetric pattern of red porgy and the fact that depth distribution varied little among size classes, during all seasons. The scarcity of specimens larger than 187 mm in the bathymetric range >50 m is noteworthy, especially for a species with a life span more than 12 years (Vassilopoulou and Papaconstantinou, 1992). Thus the absence of mature specimens in trawl nets during the present

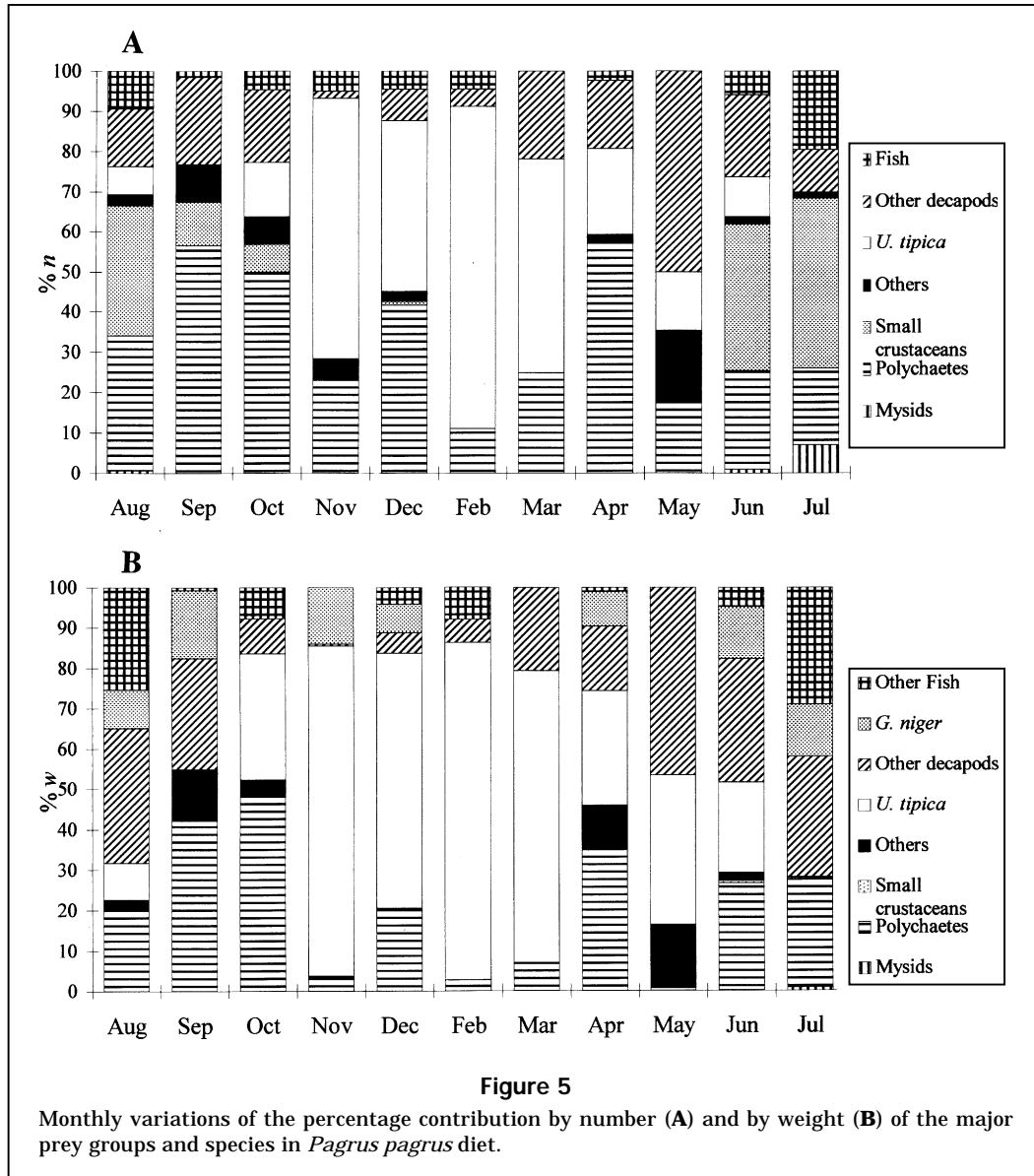
Table 4

Percentage contribution by number (*n*) and by weight (*w*) of the major prey taxa and species in the diet of each size class of *Pagrus pagrus* from the Cretan shelf. Prey occurring in >1% of the total are given. (+ = <1%; - indicates absence).

Prey category	<i>n</i>			<i>w</i>		
	Size classes			Size classes		
	0	1	2	0	1	2
Mysids	1.76	+	-	+	+	-
Polychaetes						
<i>Terebellides stroemi</i>	12.13	14.62	2.63	9.11	6.43	+
<i>Aponuphis bilineata</i>	7.35	9.67	-	5.22	2.57	-
Onuphidae	9.82	+	-	7.31	+	-
<i>Glycera rouxii</i>	+	11.12	4.13	+	4.22	1.03
<i>Laetmonice hystrix</i>	+	+	4.78	+	+	1.11
Other species	5.33	3.74	5.71	2.90	3.29	+
(Total polychaetes)	34.64	39.15	17.24	24.54	16.52	2.91
Small crustaceans						
<i>Phthisica marina</i>	20.95	+	-	+	+	-
<i>Leptochelia savignyi</i>	7.95	+	-	+	+	-
<i>Apherusa chiereghinii</i>	2.78	+	-	+	+	-
Other species	1.07	-	-	+	-	-
(Total small crustaceans)	32.75	+	-	+	+	-
Decapods						
<i>Processa nouveli</i>	2.14	+	-	2.47	+	-
<i>Upogebia tipica</i>	11.71	23.58	37.93	38.12	27.63	38.69
Paguridae	4.16	9.91	3.45	6.66	10.60	4.82
<i>Ethusa mascarone</i>	+	3.30	6.90	+	3.83	+
<i>Liocarcinus</i> sp.	+	2.83	-	+	4.00	-
<i>Liocarcinus maculatus</i>	1.76	6.13	24.14	2.49	5.74	26.13
Other species	2.14	+	-	3.11	+	-
(Total decapods)	21.91	46.69	72.42	52.85	52.20	70.15
Fish						
<i>Gobius</i> sp.	+	1.89	-	1.88	11.00	-
<i>Gobius niger</i>	+	4.25	6.90	5.34	9.22	23.52
<i>Mullus barbatus</i>	-	-	3.45	-	-	3.42
Other species	5.04	1.88	-	12.95	6.28	-
(Total fish)	5.79	8.02	10.35	19.47	26.50	26.94
Others	3.15	5.19	-	2.58	4.78	-

study almost certainly reflects aggregations of larger individuals on hard bottoms that were not trawlable. The maximum abundance of juveniles at 20–50 m could be related to the major availability of food resources at this depth range. Because nearshore areas typically contain a greater abundance of food (e.g. Hawkins et al. 1985; Swain, 1993) and a lower incidence of teleost predators (Werner and Gilliam, 1984; L'Abée-Lund et al., 1993; Ruiz et al., 1993), aggregations of young red porgy into shallow zone will result in an increase rate of growth and a lower mortality of these juveniles.

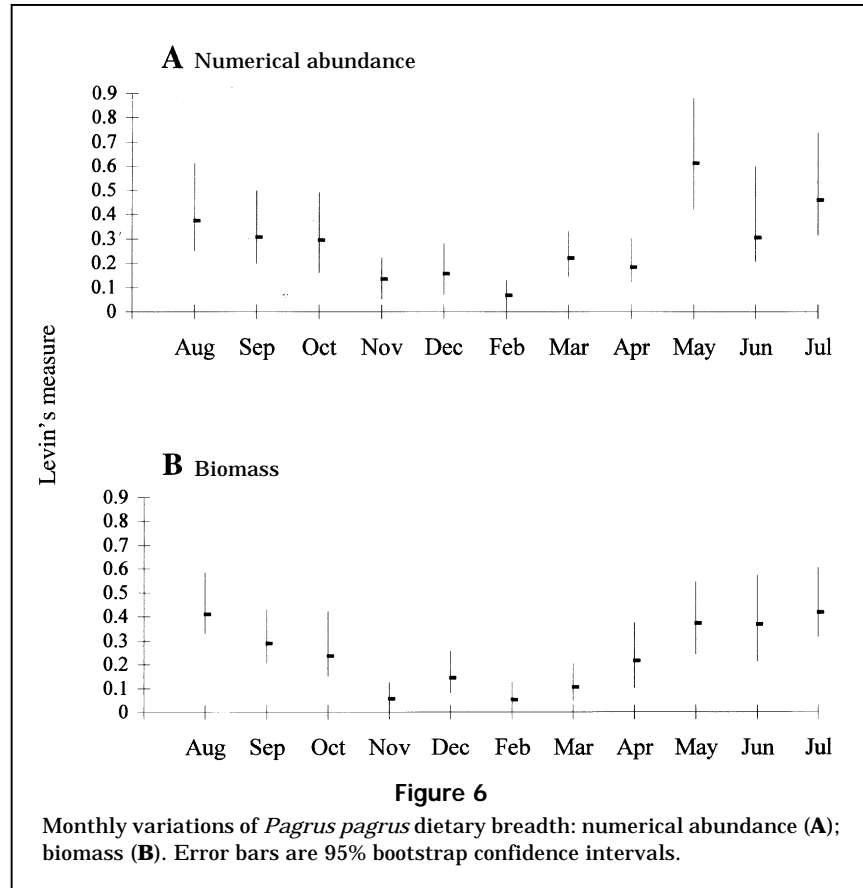
The composition of food suggests that the red porgy is a carnivorous species that relies on epibenthic invertebrates, mainly decapods. Despite the large number of taxa found in stomach contents, few species accounted for most of the prey consumed. The fact that the mean number of prey items per stomach was small (there was also a tendency for number of prey to decrease with fish size), indicates an active selection for prey taxa of large size. Moreover, specimens of each size class showed a further trend towards segregation of their feeding niches by consuming dif-



ferent prey sizes. There is evidence that prey size differences reflect changing food preference with fish size, as well as the ability of larger individuals to capture larger animals. Mean prey-size increases with increasing predator size so that the energy return per unit of effort is optimal. The relatively high percentage of empty stomachs found in the 0 size class and the positive allometry on full stomachs suggest that feeding intensity increased with fish size. These results are not consistent with the general tendency of a decreased rate of metabolism typical of larger fish found in many studies (e.g. Smith and Page, 1969; Martin, 1970; Kislialioglu and Gibson, 1976; Fange and Grove, 1979; Werner, 1979; Grove and Crawford, 1980; Robb and Hislop, 1980), presumably because the specimens examined were

immature. Hence it may be concluded that feeding rates exhibited by juveniles were high in terms of both feeding intensity and the amount of food consumed. Because red porgy on the Cretan shelf does not become mature until the third year of life, it remains for a long period in highly productive shallow waters and thus directs its effort entirely into somatic growth. The resultant increase in body size would thereby lead to an increase in the fecundity of individuals when they do, finally, become mature (Stearns, 1992).

Papaconstantinou and Caragitsou (1989) reported that in specimens >200 mm FL the importance of decapods, fish, and polychaetes declined rapidly with size, being replaced by anthozoans, brachyurans, and echinoderms. Unlike the results of the present study,



their results showed pronounced seasonal changes in the diet of red porgy. It is possible that these differences in feeding habits between juvenile and mature individuals are associated with habitat change from soft bottom to hard substrates. Manooch (1977) stated that red porgy is an opportunistic browser feeding on a variety of invertebrates as well as small fish. He also noted that its diet appeared to be dependent on species availability, rather than preference or selection. These differences between our results and those of the previous studies may be due in part to the fact that in both studies dietary analysis was based on mature specimens, probably reflecting the distinct spatial zones occupied by juvenile and mature specimens.

According to our results, habitat of juvenile red porgy appears to be well separated from that of adult specimens. The absence of mature individuals in the trawlable fishing grounds indicates that recruitment in shallow waters is followed by an ontogenetic movement to a new habitat, at the time they reach sexual maturity. Further examination of this phenomenon is important from a biological, as well as from a management, point of view. Red porgy have previously been described as a food generalist obtaining most of its food from the benthos and epibenthos as well

Table 5
 Diet overlap for the three size classes (0, 1, and 2) of *Pagrus pagrus* based on the numerical abundance and biomass of prey species. Ranges in parentheses: 95% bootstrap confidence intervals. Significantly high overlap values are in bold.

Size class	Biomass	
	0	1
1	0.44 (0.32–0.56)	
2	0.31 (0.18–0.48)	0.73 (0.67–0.82)
Size class	Numerical abundance	
	0	1
1	0.51 (0.31–0.66)	
2	0.36 (0.19–0.47)	0.72 (0.57–0.84)

as a habitat generalist occupying a variety of habitats (Manooch, 1977; Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996). Patterns observed in the

present study suggest that habitat segregation is of importance; juvenile specimens are differentiated from mature ones on the basis of the bottom type and prey selection and to a lesser extent on the basis of depth.

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