

**FEEDING HABITS OF EUROPEAN HAKE, *MERLUCCIUS MERLUCCIUS*
(ACTINOPTERYGII: GADIFORMES: MERLUCCIIDAE),
FROM THE NORTHEASTERN MEDITERRANEAN SEA**

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Background. European hake, *Merluccius merluccius*, is a major predator in demersal ecosystem, and of great importance for the fishery. Knowledge of the feeding ecology of fish species is essential for implementing a multispecies approach to fishery management. Therefore this work was intended to analyse stomach contents and dietary changes according to fish size, season, sex, and depth to better understanding the ecological role of this species in Adriatic demersal marine communities.

Materials and methods. A total of 1646 specimens of hake were collected in the Adriatic Sea by oceanographic bottom trawl surveys carried out from 2005 to 2006 during summer- and winter seasons. Principal feeding indices, species diversity Bray–Curtis similarity index, feeding strategy plot, barplot on numeric, and weight abundance data were obtained in order to increase knowledge on the diet of hake.

Results. The hake diet mainly consisted of crustaceans (particularly Decapoda) and teleosts (particularly European anchovy, *Engraulis encrasicolus*, and red bandfish, *Cepola macrophthalma*). Cluster analysis of %N (numeric prey abundance percent) showed different feeding habits of three mainly groups: small hakes (<150 mm), medium sized hakes (from 150 to 300 mm) and large hake (> 300 mm) from crustaceans (small specimens) to teleost fishes (medium and large specimens).

Conclusion. Feeding habits were size-dependant with fish diet being higher in stomachs of larger specimens. Feeding activity seemed to increase during growth, being smaller in immature individuals compared to adults, while no differences were found between females and males diet. Seasonal variation in diet showed an increase of teleost fishes in winter and crustaceans in summer.

Keywords: *Merluccius merluccius*, feeding habits, diet; northeastern Mediterranean Sea

INTRODUCTION

European hake, *Merluccius merluccius* (Linnaeus, 1758), is an important predator of deep Mediterranean upper shelf slope communities, being a nektobenthic species inhabiting a wide depth range (20–1000 m) throughout the Mediterranean Sea and the northeastern Atlantic region (Carpentieri et al. 2005). It is one of the chief commercial and most heavily exploited species of demersal fishery in all northern Mediterranean countries. Recent time-series studies referring to the western part of the Adriatic Sea have shown catches to be made up mainly of specimens shorter than 20 cm TL, with survey catch rates apparently increasing between 1985 and 1995 and decreasing in the following years both in the northern- (Piccinetti and Piccinetti Manfrin 1971, Manfrin et al. 1998) and southern Adriatic Sea (Marano et al. 1998). In 2006, annu-

al hake landings were estimated to be around 76 000 t in the Mediterranean (Anonymous 2008) and around 18 000 t in the Adriatic Sea (Anonymous 2007), with the species being the most abundant in the demersal group of the Adriatic Sea (Ungaro et al. 2001).

As a rule, hake feeds predominantly on fish and crustaceans, and the proportion of piscivory increases with hake length; crustaceans appearing mostly in the stomach of <16 cm hakes in the northern-central Adriatic Sea (Karlovac 1959, Županović 1968, Piccinetti and Piccinetti Manfrin 1971, Jukić 1972, Froglija 1973, Jardas 1976). The presently reported study analysed the diet of the hake in the northeast Mediterranean, which, given its abundance, plays an important role in comprehending the food chain dynamics. Despite hake's environmental and economic importance (Oliver and Massuti 1995) in the Mediterranean, much of its

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biology and current exploitation status are scarcely known (Arneri and Morales-Nin 2000) and no data as to its feeding habits in the Adriatic have been analyzed over the last thirty years (Stergiou and Karpouzi 2002).

The purpose of this study was to determine the feeding habits and the trophic ecology of hake in the Adriatic Sea, northeastern Mediterranean. Our specific objectives were to examine the dietary changes according to fish size, sex, season, and depth to better understanding the ecological role of this species in Adriatic demersal marine communities.

MATERIALS AND METHODS

Sampling. European hake, *Merluccius merluccius*, were collected between 15 to 350 m depth along the coast of the Adriatic Sea (northeast Mediterranean) from the Gulf of Trieste to the Tremiti Islands (Fig. 1), during two oceanographic surveys, from June 2005 (MEDITS* survey: 62 hauls; 1176 specimens) to January 2006 (GRUND** survey: 29 hauls; 470 specimens).

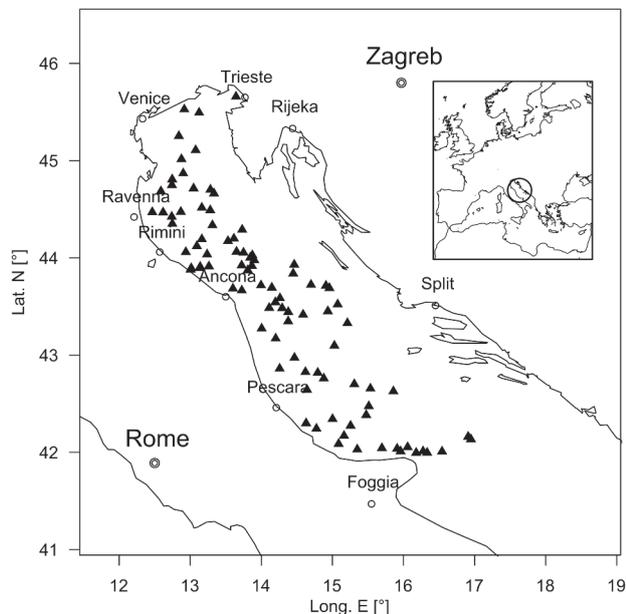


Fig. 1. Map of sampling sites of *Merluccius merluccius* in the Adriatic Sea

Catches were frozen to prevent digestion of their stomach contents (Carpentieri et al. 2005) and finally taken to the laboratory. A total of 1646 specimens was collected. Hake were measured (total length, TL, in mm) and weighed to the nearest 0.1 g. Sex was determined macroscopically and specimens were classified as females (F), males (M), undetermined (U, macroscopically unidentifiable sex) and not determinable (ND, individual not examined) (Relini et al. 2008). Stomachs were immediately removed and preserved in 70% ethanol solution, while preys were identified to the lowest possible taxonomic level, counted, and weighed to the nearest 0.1 mg after removal of surface water by blotting paper.

Data analyses. Feeding intensity and diet measurements were taken on the basis of the following indices:

feeding incidence percent (empty stomachs/total stomachs $\times 100$), frequency of occurrence (%F), numeric prey abundance percent (%N) and wet weight prey abundance percent (%W).

Prey specific abundance (PSA) was calculated according to the following formula:

$$P_i = (\sum S_i \cdot \sum S_{ii}^{-1}) \times 100,$$

where P_i is the prey-specific abundance of prey i , S_i the stomach content (number) comprising prey i , S_{ii} the total stomach content in only those predators with prey i in their stomach (Amundsen et al. 1996).

The main food items were identified using the index of relative importance (IRI) of Pinkas et al. (1971) as modified by Hacunda (1981):

$$\text{IRI} = \%F \times (\%N + \%W).$$

This index has been expressed as:

$$\text{IRI}\% = (\text{IRI} \cdot \sum \text{IRI}^{-1}) \times 100.$$

Prey species were sorted in decreasing order according to their percentage IRI contribution.

Statistical analyses. Feeding trends were determined by multivariate analyses performed with R software ver. 2.10 base and Vegan package (Anonymous 2010). Diet pattern according to fish size was evaluated by cluster analysis (complete methods) of square root transformed numeric prey abundance at species level, using the Bray–Curtis distance index. Feeding habits by category was performed by barplot on numeric and weight abundance data, displaying the main prey items. Depth strata were established for homogeneous specimens distribution. Seasons' sub-divisions were based on cruises seasonality (carried out in summer and winter of 2005 and 2006).

TROPH values were calculated from each dataset using TrophLab (Pauly et al. 2000), which is a stand-alone application for estimating TROPHs and their standard errors (SE). TROPHs were estimated from the list of prey items known to occur in the diet using the “qualitative approach” of TrophLab.

RESULTS

General diet description. The usual hake diet consisted mainly of Crustacea (especially Decapoda) and teleost fishes (Table 1). In terms of the number, crustaceans (*Processa* sp. 22.2%, *Philocheira* sp. 15.2%, *Solenocera membranacea* 6%) were the most abundant prey followed by teleost fishes (*Engraulis encrasicolus* 19.2%, *Cepola macrophthalma* 4.7%, *Gaidropsarus biscayensis* 2.9%). In terms of the weight, teleost fishes (*E. encrasicolus* 54.5%, *C. macrophthalma* 17.8%, *Gobius niger* 4.4%, *M. merluccius* 4.1%), were the most important prey followed by Crustacea (*S. membranacea* 2.2%, *Processa* sp. 0.9%, *Alpheus glaber* 0.9%) (Table 2). Other preys, such as molluscs, were occasionally recorded. In terms of specific prey abundance (PSA) plotted against six most occurring prey items, the most important fish prey items were found to be *E. encrasicolus* and *C. macrophthalma* while *S. membranacea*, *A. glaber*, *Processa* sp., and *Philocheira* sp. were the most important crustacean items (Fig. 2). Cannibalism was relatively rare

* International bottom trawl surveys in the Mediterranean.

** GRUPPO Nazionale risorse Demersali.

in hake diet, being recorded in only 0.53% of stomach contents and 1.04% of frequency of occurrence.

Diet variation with predator categories. Length range between 53 and 670 mm displayed two modal components at 135 mm and 215 mm, respectively. Cluster analysis based of %*N* (numeric prey abundance percent) according to length class showed clear diet variation as a function of length, pointing out three main groups: small hakes (<150 mm), medium sized hakes (from 150 to 300 mm) and large hakes (> 300 mm) (Fig. 3). Small hakes were feeding more on crustaceans, while medium and larger ones (>150 mm) preferred fish. Both types of prey gradually increased in importance with predator size. The main prey organisms occurring in all three length groups

and in progressively increasing amounts are the fish species *E. encrasicolus*, *C. macrophthalma*, and crustaceans such as *S. membranacea*, *Processa* sp. and *A. glaber*. During predator growth, prey numbers decreased but individual prey weight increased (Fig. 4).

Seasonal diet change was dependent on hake weight (Fig. 5). An increased fish content was observed in winter (*E. encrasicolus*, *C. macrophthalma*, *G. biscayensis*), while in summer the hake mainly fed on crustaceans (*Processa* sp., *S. membranacea*). It should be emphasized that some crustaceans, such as *A. glaber* and *P. bispinosus*, were found exclusively during the summer. In all seasons, the bulk of the prey weight constituted *E. encrasicolus*, being followed by *C. macrophthalma* and *G. biscayensis*.

Trophic spectrum of *Merluccius merluccius* from the Adriatic Sea

Table 1

Prey class item	% <i>F</i>	% <i>N</i>	% <i>W</i>	IRI%
Teleostei	51.34	28.02	93.31	72.73
Malacostraca	31.02	55.25	5.03	21.83
ND	27.24	15.79	1.25	5.42
Cephalopoda	1.10	0.63	0.40	0.01
Gastropoda	0.32	0.16	0.01	*
Bivalvia	0.16	0.16	0.01	*

ND = prey class not determined; %*F* = prey occurrence frequency, %*N* = numeric prey abundance percent, %*W* = wet weight prey abundance percent, IRI% = percentual index of relative importance (* index < 0.01).

Trophic spectrum of *Merluccius merluccius* from the Adriatic Sea

Table 2

	Prey item	% <i>F</i>	% <i>N</i>	% <i>W</i>	PSA	IRI%
CRUSTACEA	<i>Processa</i> sp.	16.06	22.24	0.92	10.47	13.59
	<i>Philocheras</i> sp.	5.70	15.19	0.06	9.67	3.18
	<i>Alpheus glaber</i>	8.29	7.05	0.87	23.50	2.40
	<i>Solenocera membranacea</i>	7.77	5.97	2.20	36.99	2.32
	<i>Philocheras bispinosus</i>	2.33	4.34	0.02	8.57	0.37
	<i>Lophogaster typicus</i>	1.30	1.27	0.04	90.47	0.06
	<i>Chlorotocus crassicornis</i>	1.04	0.72	0.25	55.15	0.04
	<i>Processa macrophthalma</i>	0.52	0.90	0.05	34.25	0.02
	<i>Rissoides desmaresti</i>	0.52	0.36	0.19	23.41	0.01
	<i>Liocarcinus</i> sp.	0.26	0.54	0.08	100.00	0.01
ACTINOPTERYGII	<i>Engraulis encrasicolus</i>	26.17	19.17	54.46	95.15	70.39
	<i>Cepola macrophthalma</i>	6.22	4.70	17.82	93.86	5.12
	<i>Gaidropsarus biscayensis</i>	4.15	2.89	1.85	89.74	0.72
	<i>Gobius niger</i>	1.81	1.63	4.37	97.06	0.40
	<i>Trisopterus minutus capelanus</i>	2.07	1.45	2.52	75.68	0.30
	<i>Merlangius merlangus</i>	1.55	1.08	2.63	86.46	0.21
	<i>Gadiculus argenteus</i>	2.33	1.99	0.41	100.00	0.20
	<i>Merluccius merluccius</i>	1.04	0.72	4.09	100.00	0.18
	<i>Lesuerigobius friesii</i>	2.07	1.45	0.82	96.60	0.17
	<i>Micromesistius poutassou</i>	1.30	0.90	1.70	100.00	0.12
	<i>Callionymus</i> sp.	1.30	0.90	0.28	61.22	0.06
	<i>Callionymus maculatus</i>	0.78	0.54	0.35	92.93	0.03
	<i>Gaidropsarus</i> sp.	0.52	0.36	0.82	100.00	0.02
	<i>Argentina sphyraena</i>	0.78	0.54	0.23	100.00	0.02
	<i>Maurolucus muelleri</i>	0.78	0.54	0.12	100.00	0.02
	<i>Sardina pilchardus</i>	0.26	0.18	1.45	98.43	0.02
	<i>Atherina boyeri</i>	0.52	0.36	0.32	73.34	0.01

%*F* = prey occurrence frequency, %*N* = numeric prey abundance percent, %*W* = wet weight prey abundance percent, PSA = prey specific abundance, IRI% = percentual index of relative importance.

Pronounced food composition variations were recorded as a function of depth (Fig. 6). Three depth strata (I: <50; II: 50–100; III: >100) were considered. Preys present in high quantities in hake specimens from all three strata include teleost fish (*E. encrasicolus*) and crustaceans (*A. glaber*, *Processa* sp., *Philocheras* sp.). Fish such as *C. macrophthalma*, *Trisopterus minutus capelanus*, *G. niger*, and *Lesuerigobius friesii* and crustaceans such as *P. bispinosus* and *Processa* sp. were found in substantial quantities only in first and second depth strata, while a limited number of fish such as *Atherina boyeri* were found in first depth layer. No significant differences in feeding habits were found in relation to sex ($\chi^2 = 0.42$, $df = 1$, $P = 0.51$).

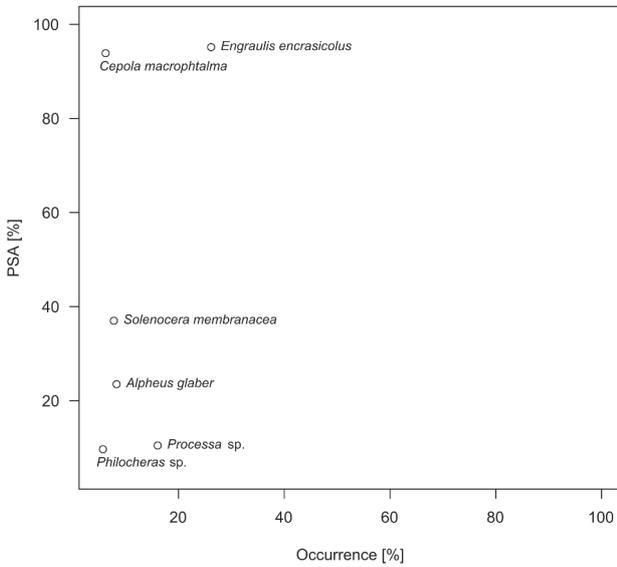


Fig. 2. Feeding strategy diagram for *Merluccius merluccius* from the Adriatic Sea: prey specific abundance (PSA) plotted against frequency of occurrence of prey (showed only first six most abundant prey item)

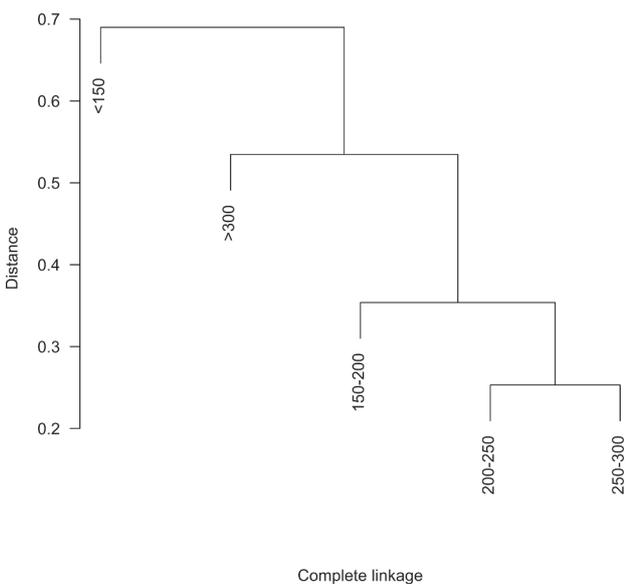


Fig. 3. *Merluccius merluccius* from the Adriatic Sea: cluster analysis of numeric preys abundance by predator size classes

Feeding activity. Feeding incidence index variation and trophic levels are shown in Table 3. Feeding activity was lower in immature specimens when compared to adults (I–F $\chi^2 = 80.75$, $df = 1$, $P < 0.001$; I–M $\chi^2 = 53.07$, $df = 1$, $P < 0.001$), with no difference being recorded between females and males ($\chi^2 = 1.06$, $df = 1$, $P = 0.3$). Depth-wise, feeding activity was inversely correlated with depth being greater at shallower depths and less at greater depths (I–II $\chi^2 = 3.89$, $df = 1$, $P < 0.05$; I–III $\chi^2 = 29.17$, $df = 1$, $P < 0.001$; II–III $\chi^2 = 13.94$, $df = 1$, $P < 0.001$).

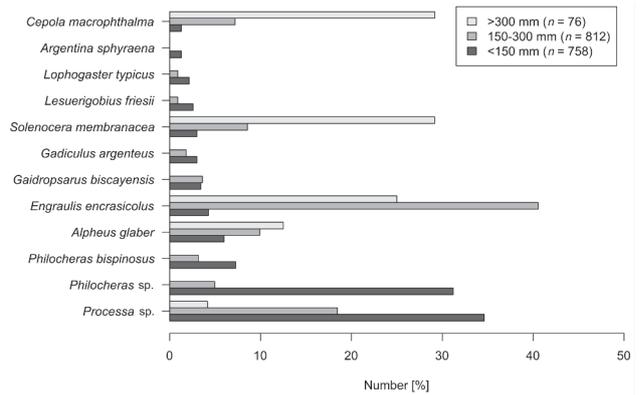


Fig. 4. *Merluccius merluccius* from the Adriatic Sea: length-wise numeric prey abundance percent of first 12 most abundant prey items

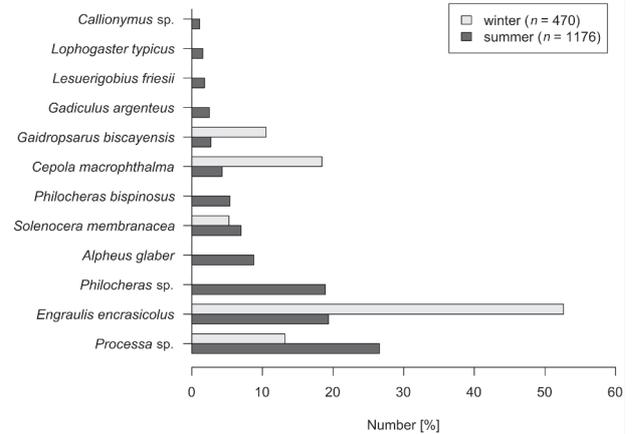


Fig. 5. *Merluccius merluccius* from the Adriatic Sea: season-wise numeric prey abundance percent of first 12 most abundant prey item

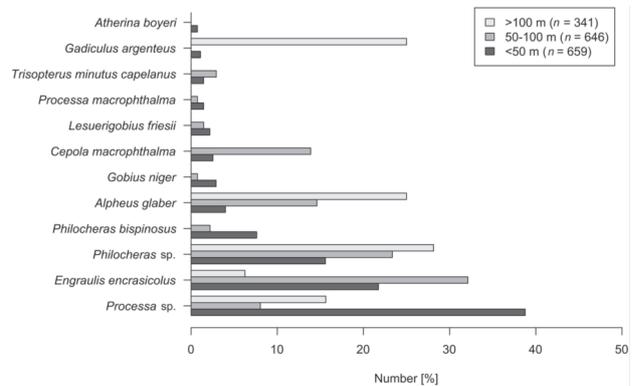


Fig. 6. *Merluccius merluccius* from the Adriatic Sea: depth-wise numeric prey abundance percent of first 12 most abundant prey item

Season-wide, feeding activity seemed to be greater in summer than in winter ($\chi^2 = 19.48$, $df = 1$, $P < 0.01$).

DISCUSSION

European hake is one of the most important bathypelagic trawl-fishery species in the northern-central Adriatic, making up 8%–18% of total landings (Paolini et al. 1995). According to available literature, the stock is mainly composed of 1-year-old individuals (<200 mm) (Ungaro et al. 2001) with two modal lengths at 135 and 215 mm, the latter being less than that recorded for specimens caught in the same area fifty years ago (125 and 325 mm: Karlovac 1959, 180 and 330 mm: Piccinetti and Piccinetti Manfrin 1971). Recent catches were therefore made up of specimens that had not yet attained first sexual maturity, namely the length of around 250 mm TL (Županović 1961, 1968, Jukić and Piccinetti 1981, Ungaro et al. 1993).

Hake has been recorded to have a high impact on fish population patterns including anchovy and other species as well as on crustaceans in the Adriatic Sea (Županović 1968, Piccinetti and Piccinetti Manfrin 1971, Froglija 1973) and in the Tyrrhenian Sea (Carpentieri et al. 2005). According to literature, the specific composition of the hake is more different in Mediterranean than in the Atlantic waters. In the Atlantic waters, the main role in the hake's diet is played by the blue whiting, *Micromesistius poutassou*; European anchovy, *Engraulis encrasicolus*; and, in largest individuals, by Atlantic horse mackerel, *Trachurus trachurus* (see: Olaso 1990, Guichet 1995, Bozzano et al. 1997, Velasco and Olaso 1998, Cabral and Murta 2002). The variations found in this study, are primarily due to the different communities considered. In fact, according to our findings, main hake prey items are closely correlated to most frequently encountered benthic and pelagic net catches, bearing out the fact that temporal variations in hake diet reflect differences in prey availability as reported in the literature (Pillar and Barange 1993, Huse et al. 1998, Velasco and Olaso 1998, Bozzano et al. 2005). The main fish species in the adult diet was found to be anchovy *E. encrasicolus* and it played a prominent role

(as a food item) in the shallowest depth level (<100m) (Karlovac 1959, Piccinetti and Piccinetti Manfrin 1971, Jukić 1972, Froglija 1973, Mužinić and Karlovac 1975), red bandfish, *Cepola macrophthalma*, that was found to prevail in predator specimens taken from muddy beds at between 50–150 m (Martin and Sabates 1991), and Gadidae (such as *Gaidropsarus biscayensis*). Compared to the Eastern Adriatic Sea where a sardine nursery ground exists (Županović 1968, Piccinetti and Piccinetti Manfrin 1971), the number of catches containing anchovy was greater than that containing sardine and sprat in the Western Adriatic Sea where our study was conducted. In fact, sardine and sprats were found to be more abundant in predator stomachs in the areas in which these preys prevailed in the catches (Karlovac 1959, Mužinić and Karlovac 1975, Bozzano et al. 1997).

In our specimens cannibalism is in line with the literature, according to which this phenomenon is relatively of slight importance in north-Atlantic and Mediterranean waters (Macpherson 1977, Guichet 1995, Bozzano et al. 1997). High cannibalism rates have instead been reported in areas with a broad continental shelf, presumably due to the coexistence of hakes of different lengths (Cabral and Murta 2002). Cannibalism may be accidental because hake has a huge mouth and some prey may reach the stomach accidentally, or it may be a population survival mechanism when resources are scarce in the environment and also serves as an important recruitment control factor (Sale 1982).

Hake feeding habits changed during growth. Decapoda (Natantia) of the families Processidae and Crangonidae were the preferential preys of hake with lengths <150 mm, where the most important change in diet was observed at around this size, in agreement with the literature (Froglija 1973, Papaconstantinou and Caragitsou 1987, Sartor et al. 2003, Carpentieri et al. 2005). Shrimps, such as *Solenocera membranacea*, *Processa* sp., and *Alpheus glaber*, were among the most common preys found in all specimens regardless of size in the muddy bottom communities of the Mediterranean Sea. Owing to their high density, crustaceans play an important ecological role (Despalatović et al. 2006, Rufino et al. 2006). Besides the Adriatic

Table 3

Feeding incidence (percentage) of *Merluccius merluccius* from the Adriatic Sea by length, depth, sex, and season

Parameter and value		Full	Empty	TROPH	SE
Length [mm]	<150	35.0	65.0	3.77	0.63
	150–300	55.0	45.0	4.12	0.72
	>300	51.3	48.7	4.17	0.73
Depth [m]	<50	51.6	48.4	3.91	0.67
	50–100	46.0	54.0	4.02	0.70
	>100	33.4	66.6	4.00	0.69
Sex	U	25.3	74.7	3.83	0.65
	F	53.4	46.6	4.04	0.70
	M	50.1	49.9	3.91	0.67
S	Summer	49.0	51.0	3.85	0.67
	Winter	37.2	62.8	4.34	0.77

TROPH: trophic level; SE: standard error of TROPH, S = season, U = undetermined, F = Female, M = male.

(Županović 1968, Piccinetti and Piccinetti Manfrin 1971, Frogliola 1973), such trophic habits have also been observed in the “Channel of Sicily” (Strait of Sicily) (Andaloro et al. 1985) and in the Ligurian Sea (Relini et al. 1999). Confirming the literature (Bozzano et al. 1997, Sartor et al. 2003), a growth was seen to be associated with a continual quality and quantity change in diet as reflected in the increasing mean weight of each prey and in the decreasing mean number of prey items per stomach. Our findings point to an energy maximizing switch in predator feeding strategy during growth, that is larger specimens feed in such a manner as to maximize their energy intake (Griffiths 1975).

Several seasonal differences were observed in the diet. In accordance with earlier studies (Olaso 1990, Bozzano et al. 1997, Sartor et al. 2003), fish such as *E. encrasicolus*, *C. macrophthalma*, *G. biscayensis* were found to make up main stomach contents all year round, especially in winter. Prey diversity in the diet appeared to be greater in summer in correspondence to specific prey occurrence. Despite these differences, however, the main prey species in the diet were found to be the same for all seasons, and namely *E. encrasicolus*, *C. macrophthalma*, *Processa* sp., *S. membranacea*.

In terms of depth, both Engraulidae and Cepolidae proved to play a dominant role in the shallowest depth level (<100m), not surprisingly given that they are very abundant at this depth in the western Adriatic Sea (Piccinetti and Piccinetti Manfrin 1971). Gadidae such as *Gadiculus argenteus* were seen to progressively increase in number as depth increased.

No significant differences were found between sexes for the same length, season and depth in accordance with most of the literature that reports no difference in diet prey composition between females and males (Karlovac 1959, Bozzano et al. 2005).

The percentage of empty stomachs was generally found to be higher in winter because the peak of abundance of most prey populations occurs in summer (Larraneta 1970, Piccinetti and Piccinetti Manfrin 1971, Velasco and Olaso 1998, Cabral and Murta 2002). Feeding activity was inversely proportional to depth (Cartes et al. 2004, Hidalgo et al. 2008). As far as depth is concerned, it should however be borne in mind that, as is known (Papaconstantinou and Caragitsou 1987), hakes brought to the surface sometimes regurgitate. Regurgitation rate, and hence observed stomach content, may thus be affected by differences in depth and consequently pressure changes as catch is hauled up.

Feeding activity was directly proportional to length, the percentage of empty stomachs being generally higher in sexually immature and hence smaller specimens (Papaconstantinou and Caragitsou 1987). These modifications in feeding behavior could be related to changes in the sensory organs that enhance capability of fish to detect and locate prey, according to Lombarte and Popper (1994). Juvenile hakes feed almost exclusively on relatively low mobile preys, whilst prey items of adult specimens

have a good capability of swim (Bozzano et al. 1997). Despite being demersal fishes, hakes typically feed on fast-moving pelagic prey ambushed in the water column (Alheit and Pitcher, 1995). Findings have in fact shown hakes to be benthopelagic feeders, their diet being made up of benthic (Gobiidae, *C. macrophthalma*) and nektonic fish (*E. encrasicolus*, *G. argenteus*) throughout all development stages from recruitment to adult and all seasons of the year (Papaconstantinou and Caragitsou 1987). This is in line with Du Buit (1996), who stated that hakes exhibit an opportunistic behavior, not making any specific choice in feeding activity but devoting more time and expending more energy in actively pursuing swimming prey than any other predator that tends to feed on less mobile preys. The lack of clear relationships between hake and the trophic resource is not new for this species (Maynou et al. 2003). Previous studies are already considered the relative independence of hake with respect to its prey, explained by its nocturnal vertical migrations (Bozzano et al. 2005) and opportunistic predator activity (Bozzano et al. 1997, Carpentieri et al. 2005). Additionally, as hakes' preys are common to other teleost predator species, such as whiting and poor cod, the nature and abundance of preys available to hakes are necessarily affected by the competition among these species.

In conclusion, useful information about benthic communities on continental shelves may indirectly be derived by routine and systematic sampling of fish stomachs (Link 2004). For the purpose of working out multi-species fishery assessment models, quantitative data as fish diet are required in order to determine the relationship among species.

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