

Feeding habits of European hake (*Merluccius merluccius*) in the central Mediterranean Sea

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European hake (*Merluccius merluccius*) is an important predator of deeper shelf-upper slope Mediterranean communities. It is a nectobenthic species distributed over a wide depth range (20–1000 m) throughout the Mediterranean Sea and the north east Atlantic region (Fisher et al., 1987). Notwithstanding the ecological and economic importance (Oliver and Massutí, 1995) of hake in the Mediterranean, many aspects of its biology (e.g., recruitment and reproduction), due to multiple spawning (Sarano, 1986) and the current state of exploitation, are poorly understood (Arneri and Morales-Nin, 2000).

Recent studies on hake feeding habits in the Mediterranean (Papaconstantinou and Caragitsou, 1987; Bouaziz et al., 1990; Oliver and Massutí, 1995) have focused on 0–3 age groups using data from trawl catches (Recasens et al., 1998; Colloca et al., 2000). For this reason, trophic habits of older individuals (Bozzano et al., 1997) and possible ontogeny-related diet changes are almost

unknown. Therefore, in this study we combined samples from trawl and gillnet fisheries collected in the same fishing ground (Colloca et al., 2000) to address these issues.

Materials and methods

The study area is located off the central western coasts of Italy, covering 13,404 km² between 20 and 700 meters depth (outer boundaries: latitude 40°52'64, longitude 13°23'13; latitude 42°20'30, longitude 11°16'32).

Monthly size-stratified samples were obtained from spring 1997 to winter 1998 both from bottom-trawls, gillnet commercial-vessels, and from commercial landings. Trawlers catch mainly 0–2 year-old juveniles; they rarely capture adults (Aldebert et al., 1993; Abella et al., 1997; Ardizzone and Corsi, 1997). The gillnet fishery exploits mainly adults of the species (>25 cm TL).

Caught fish were kept on ice, subsequently frozen to prevent di-

gestion of their stomach contents, taken to the laboratory, measured (total length: TL) to the nearest 1 mm, and weighed to the nearest 0.01 g. Sex and maturity stage were also recorded. Maturity state was determined by macroscopic analysis of the gonads by using the maturity scale for partial spawners (Holden and Raitt, 1974).

Stomachs were removed and their contents weighed to the nearest 0.001 g. Prey items were identified and sorted into taxonomic groups to the species level whenever possible. When the state of digestion was more advanced, prey were checked and grouped into unidentified fish, cephalopods, or crustaceans. The degree of digestion of the prey was not considered in the analysis. Empty stomachs and those with partially everted or unidentified contents were excluded from the total sample.

With the exception of the largest individuals (grouped into two heterogeneous length classes), all remaining hakes in the sample were grouped into 5-cm length classes. The study of size-related diet variations was based on these groups. The contribution of each food item to the diet of these fish length groups was evaluated by using the index of relative importance (IRI, Pinkas et al., 1971) as modified by Hacunda (1981): $IRI = F(N + W)$.

This index, expressed as

$$IRI\% = IRI - \sum IRI \times 100,$$

incorporates the percentage by number (N%), wet weight (W%), and frequency of occurrence (F%) (Hyslop, 1980). Hierarchical cluster analysis and nonmetric multidimensional scaling (NMDS), based on Bray-Curtis similarity and on the IRI%, were used for classification and ordination of hake size classes (Clarke and Warwick, 1994).

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Results

A total of 2761 hakes between 5 and 90 cm TL were collected (Table 1). The total number of prey was about 1700, divided into 46 different species. Cluster and NMDS analysis (stress=0.02) based on the IRI allowed the identification of four groups below 50% similarity that were separated along a size gradient (Fig. 1).

Euphausiids (*Nictiphanes couchi*, IRI=76%) and mysids (*Lophogaster typicus*, IRI=22%) dominated the diet of group A (hake between 5 and 10.9 cm TL), and decapods were the secondary prey.

Group B (hake from 11 to 15.9 cm TL) showed a more heterogeneous diet characterized by a high occurrence of euphausiids but also with a considerable number of decapods (IRI=18%). Decapods were represented by a wide variety of species, such as *Chlorotocus crassicornis*, *Alpheus glaber*, *Plesionika heterocarpus*, *Pasiphaea sivado*, and *Solenocera membranacea*. Pisces and mysids showed lower percentages (IRI=15% and 4%, respectively). Sepiolidae (IRI=0.9%), *Sepietta oweniana* and *Alloteuthis media*, dominated among cephalopods.

The data suggest a gradual change towards a fully piscivorous diet (Fig. 2) which begins around 16 cm TL and is completed when sexual maturity is attained (TL=32 cm for males and TL=38.5 cm for females; Colloca et al., 2002).

The importance of teleosts strongly increased in group C (hake from 16 to 35.9 cm TL), where they accounted for 91% of hake diet. The main prey were Clupeiformes (IRI=61%), *Sardina pilchardus* and *Engraulis encrasicolus*. Fish (IRI=96%) represented almost the entire diet of group D (>36 cm TL). In this group a shift towards Centranchthidae (*Spicara flexuosa*, *Centranchthus cirrus*) and a simultaneous decline in consumption of Clupeiformes was observed. Among decapods (IRI=4%), two species occurred most frequently: *Processa* spp. and *S. membranacea*. Euphausiids, mysids, and cephalopods were absent in the diet of hakes larger than 36 cm TL.

Cannibalism of hake juveniles also accounted for some of the diet and increased with predator size. In hake between 36 and 40 cm TL cannibalism represented 12% of IRI, reaching the highest values (IRI=17%) among larger individuals (TL >51 cm).

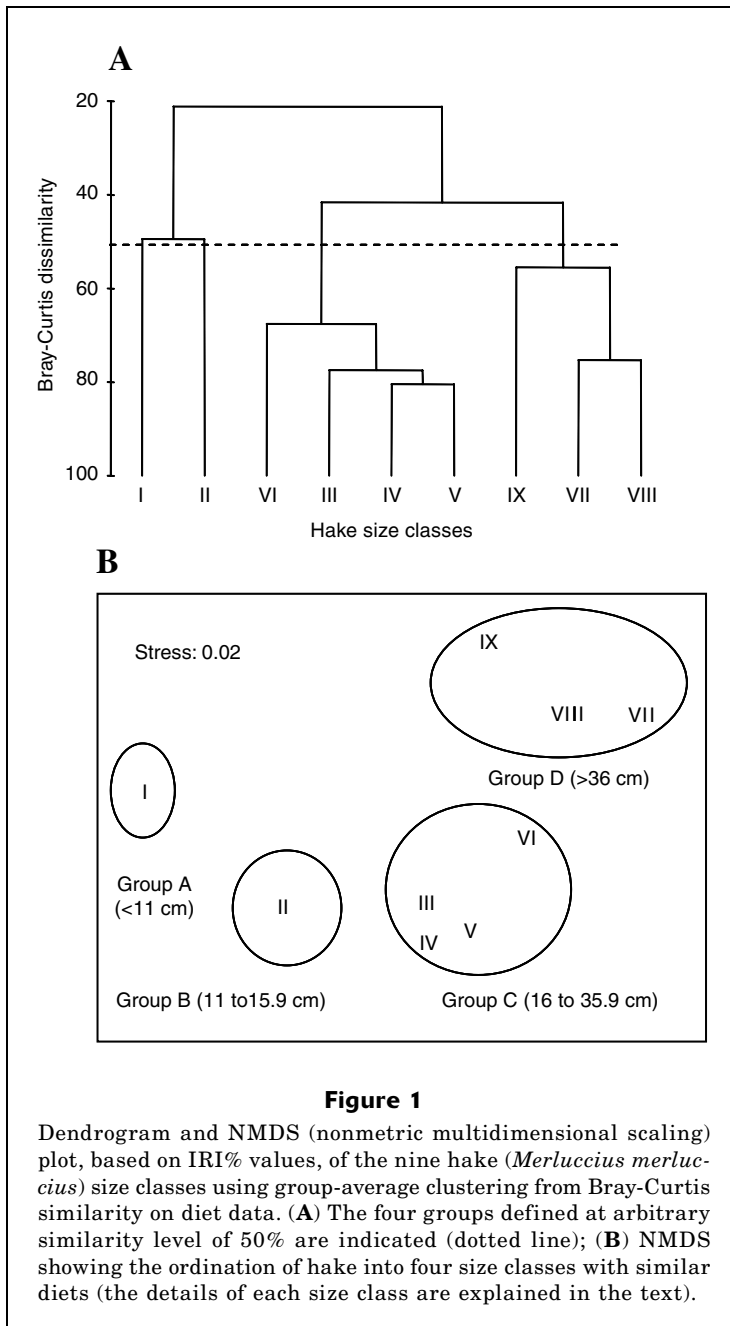


Figure 1

Dendrogram and NMDS (nonmetric multidimensional scaling) plot, based on IRI% values, of the nine hake (*Merluccius merluccius*) size classes using group-average clustering from Bray-Curtis similarity on diet data. (A) The four groups defined at arbitrary similarity level of 50% are indicated (dotted line); (B) NMDS showing the ordination of hake into four size classes with similar diets (the details of each size class are explained in the text).

Discussion

Hake is a top predator that occupies different trophic levels during its ontogenetic development. Hake size classes are differentiated along food niche dimensions according to different prey sizes or different prey taxa. Hake diet shifted from euphausiids, consumed by the smaller hakes (<16 cm TL), to fishes consumed by larger hakes. Before the transition to the complete ichthyophagous phase, hake showed more generalized feeding habits where decapods, benthic (Gobiidae, *Callionymus* spp., *Arnoglossus* spp.) and nektonic fish (*S. pilchardus*, *E. encrasicolus*) dominated the diet, and cephalopods had a lower incidence. Specific size-related differences in prey spectrum seem to be associated with different spatial distributions or genetic needs (or with both) (Flamigni, 1984; Jukic and Arneri, 1984; Velasco and Olaso, 1998).

The patterns observed in the present study indicated a strong partitioning among hake

Table 1

Number of hakes and values of IRI (index of relative importance) (%) for the nine size classes. The four groups identified from the cluster analysis are indicated.

Size group	A		B		C			D		
	I	II	III	IV	V	VI	VII	VIII	IX	
Length (cm)	5.0–10.9	11.0–15.9	16.0–20.9	21.0–25.9	26.0–30.9	31.0–35.9	36.0–40.9	41.0–50.9	51.0–90.0	
Number of hakes	202	430	564	454	555	224	139	107	75	
Stomach contents	93	215	239	173	170	78	45	35	26	
Prey										
Cephalopoda										
<i>Alloteuthis media</i>		0.22	0.02	0.01						
<i>Sepietta oweniana</i>		0.02	0.02	0.01						
Unid. Sepiolidae		0.35	0.30	0.03						
Unid. Cephalopoda		0.42	0.10	0.01	0.02					
Crustacea										
<i>Alpheus glaber</i>		0.02	0.33	0.05	0.22	0.05	0.81	1.54		
Aristeidae			0.01	0.02						
<i>Aristeus antennatus</i>		0.02								
<i>Chlorotocus crassicornis</i>		1.61	1.83	1.09	1.10	0.48				
Crangonidae			0.01	0.01						
Pandalidae		0.03		0.01						
<i>Parapenaeus longirostris</i>				0.01						
<i>Pasiphaea multidentata</i>		0.02		0.01						
<i>Pasiphaea sivado</i>		0.20	0.04	0.05	0.02	0.05			0.33	
<i>Plesionika heterocarpus</i>		0.11	0.01							
<i>Plesionika</i> sp.		0.62	0.07	0.01	0.04	0.05				
<i>Pontocaris lacazei</i>		0.01	0.02	0.01			0.20			
<i>Pontophilus spinosus</i>		0.01	0.01	0.03	0.05	0.20				
<i>Processa</i> sp.		0.25	0.06	0.06	0.15	1.77	0.83	1.54		
<i>Solenocera membranaca</i>		0.04	0.02	0.05	0.34	0.58	3.27	3.53		
<i>Squilla</i> sp.					0.05					
Unid. Decapoda	3.05	19.91	6.19	2.84	2.73	1.45		1.58	1.32	
<i>Lophogaster typicus</i>	28.77	4.34	0.16			0.01				
<i>Nectiphanes couchi</i>	54.10	31.83	0.37							
Unid. Euphasiacea	13.99	3.43	0.11							
Unid. Isopoda	0.07	0.02	0.01							
Pisces										
<i>Argentina sphyraena</i>				0.08	0.41	1.06	4.04	3.29	2.34	
<i>Arnoglossus laterna</i>			0.01	0.01						
<i>Arnoglossus</i> sp.			0.01	0.01	0.01					
<i>Callionymus</i> sp.			0.01	0.01	0.01	0.06				
Centracanthidae				0.03	0.11	2.60	2.43	11.23	53.97	
<i>Centracanthus cirrus</i>						1.93	26.54	4.62	3.80	
<i>Clorophthalmus agassizi</i>			0.01							
<i>Conger conger</i>							0.34	0.85		
<i>Echiodon dentatus</i>					0.05					
<i>Engraulis encrasicolus</i>		1.95	11.61	1.28	4.45	9.91	0.87	1.27	1.86	
<i>Gadiculus argenteus</i>					0.08	0.65	0.31	0.58		
Gobiidae		0.04	0.02	0.01	0.01	0.05				
<i>Gobius quadrimaculatus</i>			0.02	0.02	0.01					
<i>Lepidotrigla dieuzedei</i>				0.01	0.01				0.78	
<i>Lesuerigobius friesii</i>			0.01	0.02	0.03					
<i>Merluccius merluccius</i>					0.07	0.18	12.00	4.10	17.95	

continued

Table 1 (continued)

Size group	A		B			C			D	
	I	II	III	IV	V	VI	VII	VIII	IX	
Pisces (continued)										
<i>Mullus barbatus</i>						0.12	0.44		0.49	
Myctophidae		0.30	0.28	0.03	0.15					
<i>Nettastoma melanurum</i>		0.02		0.01	0.01					
<i>Sardina pilchardus</i>		0.05	45.23	72.55	46.19	62.0	5.20	12.77	10.31	
<i>Sphyræna sphyræna</i>							0.60	4.98		
<i>Spicara flexuosa</i>				0.02	0.10	1.33	12.63	21.83	0.01	
<i>Spicara</i> sp.						0.37	4.57	0.54	1.69	
<i>Trachurus trachurus</i>					0.09	0.13	1.60	1.93		
<i>Trisopterus m. capelanus</i>			0.02	0.01	0.01	0.05				
Unid. Osteichthyes	0.04	34.19	33.14	21.61	43.44	15.01	23.09	22.90	4.25	
<i>Raja</i> sp.								0.50		

size classes. Two main thresholds associated with ontogenesis-related diet changes have been identified. The first one was observed around 16 cm TL and corresponded to a significant change in depth distribution. The second, around 36 cm TL, corresponded to the attainment of sexual maturity (Colloca et al., 2002).

Although hakes are demersal fishes, they feed typically upon fast-moving pelagic prey that are ambushed in the water column (Alheit and Pitcher, 1995). There is evidence that hakes feed in mid-water or near the surface at night, undertaking daily vertical migrations (Hickling, 1927; Papacostantinou and Caragitsou, 1987; Orsi-Relini et al., 1989) which are more frequent for juveniles. Small hakes feed daily on small Euphausiacea (*Nectiphanes couchi*). This school-forming planktonic crustacean carries out vertical migrations at night (Casanova, 1970; Franqueville, 1971; Vallet and Dauvin, 2001). They rise to near the surface at night to feed on phytoplankton and sink during daylight between 50 and 800 m depth (Buchholz et al., 1995). Juveniles of *M. merluccius* may follow such migrations, moving from near the bottom, 100–200 m depth, to midwater at night (Frogliia 1973; Papaconstantinou and Caragitsou, 1987; Orsi-Relini et al., 1989). Nocturnal vertical migration behavior has been described for gadoids such as hake and cod and is considered responsible for the reduction of trawl catches of these fish at night (Beamish, 1966; Bowman and Bowman, 1980).

Considerable diet changes have been observed after the first year of life (>16 cm TL) when juveniles move from nursery areas on the shelf-break and upper slope to the middle shelf (Andaloro et al., 1985; Ardizzone and Corsi, 1997). The data indicate that such migration is induced by a change in trophic requirements. In this size class, diet changed to fish prey (Clupeiformes), and the importance of the small epipelagic crustaceans

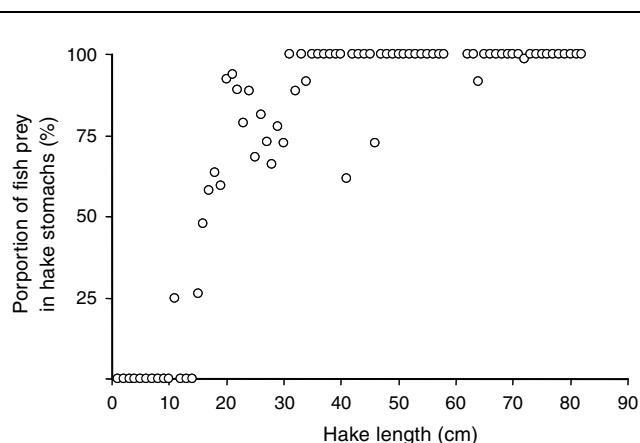


Figure 2

Proportion (%) of fish prey occurring in the diet of hake (*Merluccius merluccius*) during its growth.

(Euphausiacea) strongly decreased. Clupeiforms *S. pilchardus* and *E. encrasicolus* are distributed largely on the continental coastal shelf forming schools usually deeper than 25 m (Fisher et al., 1987).

The size-depth distribution pattern of hake was confirmed by experimental trawl surveys carried out in the Mediterranean (Relini and Piccinetti, 1996; Relini et al., 1999). Juveniles (modal length of 10 cm TL) are found mostly between 100 and 200 m depth. Intermediate hakes reach the highest abundance mainly on the shelf (<100 m). Large hakes (>36 cm) are found in a wide depth range but concentrate on the shelf break during the spawning period (Recasens et al., 1998; Colloca et al., 2000; Alvarez et al., 2001).

Growth induces a continuous qualitative and quantitative change in diet that is reflected in the increasing

mean weight of prey and decreasing mean number of prey items per stomach. The shift towards large fish prey (i.e., Centranchthidae) usually occurs slightly before maturity—the life history stage with much higher energetic demands due to gonad development (Ross, 1978). A similar pattern was observed for Atlantic cod (*Gadus morhua*) where sexual maturation and spawning are also associated with an ontogenetic change in diet (Paz et al., 1993). Thus, increased energy demands related to sexual requirements, gonad development, and breeding activity appear to be the critical factors driving the changes in feeding strategy of *M. merluccius*.

In large hakes (>36 cm), cannibalism played an important role and should be carefully considered in stock-recruitment analyses. Studies carried out in the Mediterranean (Macpherson, 1977; Bozzano et al., 1997) and in the Atlantic (Guichet, 1995; Link and Garrison, 2002) showed that cannibalism has some importance for hake. In silver hake (*M. bilinearis*), cannibalism notably increased with ontogeny (Link and Garrison, 2002). In the large cape hakes, *M. capensis*, hake is the dominant food item (50% of the diet) for individuals larger than 60 cm (Roel and Macpherson, 1988). Conversely, a low cannibalism rate was observed for *M. paradoxus* in the same area (Payne et al., 1987). This could be a response to the greater accessibility of conspecifics compared to other species. As Payne et al. (1987) pointed out, small hake are not found in the vicinity of adults of the species. This is supported by the observed size segregation by depth, which is more pronounced in *M. paradoxus* than in *M. capensis* (Gordoa and Duarte, 1991). Density-dependent cannibalism may be an important source of natural mortality that can stabilize fish populations (Smith and Reay, 1991), and for *M. capensis*, cannibalism has even been considered the main cause of natural mortality (Lleonart et al., 1985; Payne and Punt, 1985).

Our results on the trophic ecology of hake are of primary importance for future management of fish assemblages where this species plays an important predatory role. Multispecies management requires quantitative data on fish diet to elucidate the relationships between species and, consequently, to forecast temporal biomass fluctuations, under specific fishing regimes, in an integrated manner.

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