

THE ROLE OF TOP-PREDATORS IN RESOURCE REMOVAL AND THEIR INTERACTIONS  
WITH HUMAN EXPLOITATION

EFFECTS OF TOP-PREDATORS ON PREY SPECIES OF FISHERIES INTEREST: THE CASE OF HAKE (*Merluccius merluccius*) AND ANCHOVY (*Engraulis encrasicolus*) IN THE  
NORTHWESTERN MEDITERRANEAN

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ABSTRACT

As the hake and the anchovy are the most important species in Northwestern Mediterranean fisheries, one should take into account the predator-prey relationship which exists between them, in order to manage correctly the fisheries of both species. The importance of Mediterranean hake predation on Northwestern Mediterranean anchovy stock was evaluated using current bibliography about biology, population dynamics and trophic ecology of both species, all of which have been extensively analysed. From several papers which include numeric data about hake-anchovy interaction two hypothetical predation matrices have been elaborated. Based on them, a multispecies VPA has been developed, in order to evaluate the effects of hake's predation on the natural mortality of the anchovy and to assess the possible consequences of changes in the exploitation patterns of hake on anchovy population dynamics.

In conclusion, although the anchovy is one of the main prey items in hake's diet, mainly during the hake's second year of life, changes in the exploitation patterns of hake did not result in very remarkable oscillations of anchovy stock biomass, except when extreme and unrealistic situations are considered, e.g. halting all fishing of hake or multiplying by four the fishing effort upon it. On the other hand the variations predicted by the model probably do not reflect what actually would occur in a real situation, as the figures which represent these changes are probably overestimations bearing in mind the interactions with other species, such as sardines, blue whiting or horse mackerel, which are competitors or predators of anchovy and, in their turn, preys of hake.

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## 1. INTRODUCTION

The relation between primary production, mainly conditioned by the nutrient input into the euphotic zone, and the total production of fish in an area, which is labelled "bottom-up control", is a well studied phenomena. On the other hand the consequences derived from the fluctuations in predator populations, due to fishing or natural causes, have been generally ignored in marine fisheries. This has occurred despite the fact that "top-down control" is a recognised property of all ecosystems. This scarce interest from marine biologists is unjustified, as the removal of predators may have various important effects, including a replacement of exploited species by others in the same trophic position, an increase in production at lower trophic levels and long term effects involving ecosystem change (Caddy and Sharp, 1988; Parsons, 1992).

The aim of this study is to make a preliminary analysis of trophic interactions between the stocks of hake (*Merluccius merluccius* L., 1758, PISCES: Merluccidae) and anchovy (*Engraulis encrasicolus* L., 1758, PISCES: Engraulidae) in the Northwestern Mediterranean, where both species being subject to intense exploitation, and to infer the possible effects of management measures applied to hake fishery on the biomass of anchovy populations.

In order to do this, an area for study located between Cape of La Nao (Valencia, Spain) and Marseille (France) was delimited. This area was chosen because it presents some particular oceanographic features which make it rather different from other regions in the Western Mediterranean and it also is the area of distribution of an important anchovy stock distinguishable from other Mediterranean populations of this species. Up to now there have been no studies carried out which have been directed specifically to quantify predator-prey relationships and much less to model them. The exploited population's dynamics never have overcome the monospecific point of view of classic models. Hake and anchovy, besides red mullet (*Mullus* spp.) and sardines (*Sardina pilchardus*), are the most important commercial species, both for value and the weight of catches in the area. They can be considered as the target species of trawl and purse-seine fisheries respectively.

The current bibliography pertaining to the feeding habits of hake, and about biology and population dynamics of hake and anchovy in general, is relatively numerous, and furnishes data enough to fulfill the proposed objectives. By integrating the data about predation indexes, biological parameters, and biomass and population structures, it is possible to elaborate a model that can give us an approximate idea about the real importance of this interaction. However, other hardly quantifiable factors exist, which one must take into account as they finally determine the real biomass of both stocks. Among these factors the most important to consider are the primary production, the environmental factors that influence the success of annual recruitment, and relations with other components of the food web. The extent of the continental shelf is another important factor to bear in mind. Due to these factors the conclusions derived from applying the model mentioned above cannot be considered "sensu strictu", but merely as qualitative approximations.

## 2. RELEVANT ASPECTS OF THE ENVIRONMENT

In addition to the hydrographic and bioclimatic conditions of an area, which determine whether or not a biocenose can exist in a concrete region, there are two important factors which limit the biomass of the biocenose; the primary production and the space of the region. Eventhough the models of population dynamics in use do not take these two factors into account when making their projections, it is imperative to keep them in mind when interpreting results in order not to come to unreasonable conclusions. Because of this the most important environmental characteristics of the area of study related to the aforementioned aspects are described below.

In Figure 1 the area of study is defined. The area is located between the 38°N and 44°N parallels, which places it in the belt of mild climate, on the southern limit of the paths of the Northern Atlantic winter storms. It has been said that the Mediterranean Sea is a oligotrophic body of water, and therefore its fishing resources are limited. However the the study area contains a series of characteristics which make it one of the highest producing areas in the entire Mediterranean, in exception of the Black Sea and the Northern Adriatic. At first glance three large areas in the continental shelf, two with a relatively wide shelf, the Gulfs of Lions and Valencia, and one with a skinny shelf off the coast of Northern Catalonia. The zones with a wide continental shelf favor fishing exploitation. The size of the continental shelf (until 200 m depth) and the slope (200-1000 m depth) in the diverse regions of the study area are respectively, 17639 and 8301 Km<sup>2</sup> for the Gulf of Lions, 9102 and 8537 Km<sup>2</sup> for Catalonia, and 15785 and 5383 Km<sup>2</sup> for the Gulf of Valencia. The bottom is equally varied, from rocky substrates to fine bathyal muds, in between passing through sandy or detrital bottoms. The type of ocean floor determines the benthonic biocenose, also influencing the distribution of demersal species such as the hake, and their

potencial prey.

In the area of study several situations occur which notably increase productivity. Among these the most important are the existence of a permanent front of divergency which extends from the Ligurian Sea to the Gulf of Valencia, the influence of the rivers Rhône and Ebro, the processes of formation of deep water in front of the Gulf of Lions, intermittent basin fronts, small occasional upwellings associated with winds from the northwest, entrance of surface currents or of scattered cyclonical eddies from the principal current from the entrance of waters from the Atlantic, and other more localized occurrences that determine the carrying capacity of the system limiting directly the biomass of planktivorous populations like the anchovy. These mechanisms of fertilization are described by Margalef (1985) and Terradas *et al.* (1989).

Summing up it can be concluded that the considered area presents a relatively high primary productivity in respect to other Mediterranean areas. For this reason it can sustain important populations of planktivorous pelagic fishes like anchovy.

### 3. LIFE HISTORY STRATEGIES OF HAKE AND ANCHOVY

Hake can be considered a benthonic, typical k-strategist species, when one considers its biological and dynamic characteristics. In contrast the anchovy displays those features typical of a pelagic, or r-strategist species like anchovy. However some important characteristics of the hake's morphology, biology, and behaviour lead us to the conclusion that at least during several periods of its life, the hake's resembles pelagic fishes more than it does benthonic ones. It is also important to remember that the fish populations of the Mediterranean, due the low productivity of this sea, have to adapt its strategies of life to this fact and so hake, anchovy and other species present a dynamic characteristics and a behaviour quite different to those that is typical of these populations inhabiting other, more productive, areas of the planet.

#### 3.1. Reproduction and recruitment

The hake's length of first maturity (50%), in the Western Mediterranean is estimated by Oliver and Massutí (1994) and different authors, to be between 22-32 cm for males and 30-39 for females. These figures correspond to 3 and 4 years of

age respectively, as noted in the last published age-length relationship study (Farrugio, 1994).

Taking into account studies on the gonad cycle, the hake goes through a long spawning period. In the Catalanian Sea it is from May to February, peaking between October and January (Recasens, 1992). Campillo (1993) observed a protracted year-round spawning period, with peaks in autumn and spring. Complementary information from surveys on eggs and larvae is scarce. Sabatés (1988) studied the time-space distribution of ichthyoplankton in Catalonia and found hake larvae in all months from samples taken between April and October above the continental shelf edge.

Different observations exist about recruitment of hake. Small individuals (5-8 cm) caught by trawlers, suggest two periods of recruitment each year one in spring and another in autumn. These two periods of recruitment probably correspond to two peak spawning periods, much like what occurs in Balearic Islands (Alemany and Oliver, 1995; Reñones *et al.*, 1995) and in the Ligurian Sea (Orsi Relini *et al.*, 1989a, 1989b). In the Catalan Sea only one period of recruitment in spring-summer have been found (Recasens, 1992).

The anchovy in the Northwestern Mediterranean spawns over an extended period, from April to September-October, peaking between May and July. In 1992 and 1993 two fish, egg, and larval surveys were carried out with the main objective of delimitating the spatial distribution of the spawning areas and of estimating the daily egg production of the spawning biomass of anchovy and the peak spawning period of June-July was confirmed (Palomera *et al.*, 1995).

Females are mature when they reach 11 cm and a length of first maturity (50%) is estimated to be 12.5 cm. Males are considered mature at 10 cm, and their estimated length of first maturity (50%) is 12.7 cm (Perterra, 1992). When the individuals attain this length, they correspond to a first age class (Perterra, 1987).

The peak of recruitment of anchovy (individual of less than 11 cm corresponding to 0 age class) has been isolated between the period of October to November by means acoustic surveys carried out yearly since 1991 (Abad *et al.*, 1991a; Abad *et al.*, 1992).

### 3.2. Growth

The recent studies of growth of Mediterranean hake, which include examining annual and daily growth rings in otoliths, as well as length frequency modal progression analysis, indicate that the growth, lifespan, and biology of Mediterranean and North Atlantic hake do not differ notably. However a difference in growth between males and females has been clearly observed. Females present progressively larger annual increments of growth and, in consequence, higher values of length at the same age.

The growth of recruits has been studied following the modal length progression and daily growth rings showing an average monthly growth of 1.5 cm (Orsi Relini *et al.*, 1986; Morales-Nin and Aldebert, 1994; Oliver and Massutí, 1994). The most recent studies of hake's growth (Farrugio, 1994) give the following estimations of the von Bertalanffy Growth Function parameters:

		Linf	k	t <sub>0</sub>
Catalan Sea	Males+ Females	94.7 cm	0.131	-0.122
Gulf of Lions	Males	72.8 cm	0.149	-0.383
	Females	100.7 cm	0.124	-0.35

More recent analysis (Alemany and Oliver, 1995) found growth rates of hake to be much higher in the Balearic

Islands ( $k= 0.184$ ), which means that if this hypothesis is demonstrated as correct, our understanding of population dynamics of mediterranean hake would change.

Pertierra (1987) has estimated the growth parameters of anchovy of the Northwestern Mediterranean by means of otolith reading and length frequency analysis, obtaining the following results:

Catalan Sea	Linf	k	$t_0$
Males+Females	18.19-20.6 cm	0.38-0.45	0.94-1.1

### 3.3. Natural mortality

Some authors have estimated values between 0.2 and 0.3 for natural mortality ( $M$ ) of hake. However, considering the low predation and low cannibalism impacting mediterranean hake (Macpherson, 1981), and the importance of these factors within the natural mortality rate (Vetter, 1988; Leonart *et al.*, 1985a, 1985b), inclined the authors to consider lower values as more realistic. Whatever the situation, these estimates should be reviewed if the estimation of higher growth rates are confirmed.

Pertierra (1992) considering the short life-span of the anchovy in the area (maximum age of 5 years), concluded that the predation mortality was an important factor. Comparing the values attained by other authors by other means, he considered 0.81 a valid figure, which is supported by the ICES analysis of direct estimations and acoustic surveys, which show that  $M$  may vary between 0.7 and 1.77.

Palomera and Leonart (1989) confirm a density-dependent factor of the mortality of a species. High mortality values are associated with high levels of egg production in an area.

### 3.4. Feeding habits of hake

The trophic behaviour of the European hake and other species of its genus have been studied by numerous authors. The hake is an active predator. It must select the largest prey that it can possibly ingest whole, at the longest half of its own total length.

The composition of the hake's diet varies greatly throughout its ontogenic development. Its diet also changes with the season, the batimetry, and according to some authors with the hake's sexual maturity. During the first few months of life the hake consumes small crustaceans such as euphausiacea and mysidacea. Progressively, decapoda natantia of greater size, and small fish such as gobies become part of its diet. Once a hake reaches 10 cm in length it begins to catch small pelagic fish, mostly clupeidae. As it becomes larger, the hake relies less and less upon crustaceans for sustenance, and consumes more and more fish. By the time it reaches 30 cm in length, the hake is exclusively piscivorous. With its increase in size, the type of fish the hake preys upon change. It now eats fish with more demersal habits, such as other gadidae as well as other hake, since very few clupeidae have been found in hake larger than 30 cm. The number of fish the hake now holds in its stomachs at one is almost always one. A small part of the hake's diet, around 2% are made up of cephalopods, and occasionally Ophiuroidea. The composition of the hake's diet also varies according to the abundance of possible preys. For example, young hake eat mainly euphausiacea in the spring, while during the fall and winter they eat mainly clupeidae.

The variation of types of fish consumed depends mostly on the hake's size, as the bigger it is the larger its potential prey may be. However it also depends on the batimetry and behaviour. One year old hake eat mostly cludidae if they find themselves over the continental shelf, and if they find themselves on the slope, then they resort mainly to myctophidae. On the other hand young hake seem to make nictimeral migrations towards the surface which allows them to capture pelagic organisms. Older hake however do not stray far from the bottom, and therefore their prey are mostly organisms which inhabit benthic and demersal regions. Cannibalisms does not seem to be an important factor, except during periods of spawning when the adult hake move closer to the coast. There, they encroach upon the area inhabited by hake of age class 0 where the older hake can prey significantly upon the younger ones. The period of maximum predatory activity has not been completely isolated, although some author suggest that it is at night, the digestion cycle (detection, capture, digestion, and expulsion) being of 24 hours.

In conclusion the hake is a voracious carnivore, which maintains a certain level of selectivity as to the size of its prey. However, the hake does not have a preference for certain species, adapting its diet according to the availability of different potential prey species. ANNEX 1 deals in a short but detailed form, with the results and conclusions of studies that have been done on the trophic ecology of the hake, especially those relating to its interactions with the anchovy, in which these statements are based.

### 3.5. Geographic and bathymetric distribution

#### Hake

The hake is usually found off the Atlantic coast of Europe and the coasts of Western North Africa (from Norway and Iceland to Mauritania). The hake also inhabits the entire Mediterranean Sea as well as the southern coast of the Black Sea. Recent genetic studies seem to indicate that there are a clear genetic differences between the Atlantic and Mediterranean hake, whereby the Straits of Gibraltar, or the Alboran Sea constitute the geographic barrier between them. However no clear stock delimitations have been found in the Western Mediterranean (Pla *et al.*, 1989; Vila *et al.*, 1990; Pla *et al.*, 1991). These findings confirm the hypothesis which is based on morphometric studies (Maurin, 1965; Inada, 1981), that the Mediterranean hake is a distinct subspecies, separate from the Atlantic hake. Furthermore, according to Orsi Relini *et al.* (1992) the Mediterranean subspecies could be divided, based on vertebral counts, into western and eastern races. In any case the Northwestern Mediterranean hake can be considered an independent stock from the southern ones, while the doubt about the delimitation between the Gulf of Lions and Ligurian Sea hakes persists.

Different length groups of Mediterranean hake have different bathymetric distributions, presenting a wide range of depth from the coast line (6-30 m depth) to the lowest part of the slope (700-1000 m depth). In the Catalan Sea the hake is found between 50 and 400 m depths, with main concentrations between 50 and 200 m. The lower age groups are scarce at more than 300 m in depth and do not appear at more than 400 m depth. The spawning stock is distributed in all depth ranges but they are mainly located between 50 and 300 m depths. The largest individuals (more than 50 cm) are more frequent at and above depths of 300 m (Recasens, 1992).

Some studies in the Ligurian Sea demonstrated that the spawning stock is concentrated from 50-100 to 200-300 m depth, and that the nursery areas range from 50 to 250 m (with the main concentrations around 100 m) and that the eggs and larvae appear in pelagic waters above depths ranging from 50 m to 150-200 m (Orsi Relini *et al.*, 1986, 1989a, 1989b). In the Gulf of Lions, distribution and abundance of age classes 0, I and II have been studied using data from trawl surveys (Campillo *et al.*, 1991; Campillo, 1993). Main concentrations of group 0 were found from 100 to 150 m depth. Groups I and II however, appeared to be distributed along the continental shelf from 30 to 150 m depth. From these surveys, mean densities of 0.01-0.5 Kg/Ha have been obtained in the whole prospected area. The 0 group is the most abundant and shows an aggregating behaviour, with maximum abundance of 200-600 individuals/Ha, mainly at the edge of the underwater canyons.

#### Anchovy

Generally anchovy form large schools where relatively strong upwellings exist. The anchovy are present in the Eastern, Northern and Central Atlantic, from Bergen in Norway to Angola including the Mediterranean, Black and Azov Seas. However, they do not exist in the Baltic Sea. The level of knowledge and the updated conclusions about the stock delimitation of anchovy is similar to that of hake, but the mobility of anchovy stocks is more uncertain due to the possibility of separate northwestern Mediterranean stocks, mainly the ones of Gulf of Lions and Ligurian Sea.

Only the concentration of catches in the Catalonia-Gulf of Lions area, as well as the most recent results of the FAR-Anchovy Project on location of spawning areas (García, 1994) supported by morphometric and genetic analysis can endorse the hypothesis of locating an independent stock or at least a large portion of one in that area (Perterra, 1992).

The anchovy's bathymetric distribution in the Western Mediterranean can reach 100m to 180m in depth in the open sea. In winter the anchovy positions itself in areas far from the coast, and in waters deeper than those inhabited by the sardine. The anchovy's behavior has been observed to be directly linked to temperature, with periods of maximum activity occurring when water temperatures are between 18 and 22°C Suau (1979). The anchovy has established a horizontal migration related to the reproduction cycle, according to studies done south of the Ebro River runoff. According to this author the anchovy ready to spawn approach the coastline (35-50 m depth) beginning in April. During May, they fall back to

depths of 90 m, where they then spawn. The stock of recruits stay in coastal areas until they reach 6 cm in length, then in autumn-winter moving out into areas of the continental shelf with deeper waters.

In Catalonia, Pertierra (1992) describes the same cycle with a retreat from the coast during autumn once spawning is complete. Campillo (1993) associates this cycle with water temperatures, which would place times of maximum activity between April and September when water temperatures are between 18 and 22°C.

According to Palomera *et al.* (1995), several common features, characteristic of high productivity areas, can be pointed out in relation with anchovy spawning grounds distribution: (1) they are associated to river runoffs (e.g. Rhône, Ebro); (2) are influenced by the strong Liguro-Provenzal-Catalan current, producing associated cyclonic or anticyclonic eddies that can either disperse or retain larvae in nursery grounds favourable to growth or inversely; (3) hydrological phenomena associated to bottom topography (e.g. submarine canyons).

#### 4. EXPLOITATION PATTERNS

##### 4.1. Hake

In the Western Mediterranean, the hake is mostly exploited by a trawl fleet. However, in some specific areas as the Gulf of Lions, other gear such as longlines or gillnets are in use (Aldebert *et al.*, 1993). The trawl nets are towed on the bottom from 30 to 700 m depth. These nets should officially have a legal minimum mesh size of around 40 mm as recommended by the GFCM, although, in some areas, smaller mesh sizes than 32 mm or less are frequently used. This fishery is multispecific, in some cases demersal as well as pelagic species being exploited (Alvarez, 1990), but hake is one of the main target species. The trawling fleet is composed of about 900 boats, the 75% in the Spanish coast, with an average power and tonnage of 220 HP and 45 TRB, respectively, and the 25% in the French area, with 300 HP mean power (STCF, 1991).

The gillnet fleet of about 60 French boats operate in the eastern part of the Gulf of Lions. This fleet works the outer part of the shelf and slope between 90 and 300 m (Aldebert *et al.*, 1993). Also, there are about 20 Spanish longliners, which operate principally in the western part of the Gulf of Lions, on the slope along the canyons between 160 and 600 m depth.

The total catches of hake in the NW Mediterranean (Fig. 2a), have oscillated since 1945 between 1000 and 5500 annual tonnes (GFCM, 1976, 1980a, 1993; Abad *et al.*, 1991b). From 1975 an increase in the landings have been observed, which in general have come in a little above 3000 annual tonnes. However, the official data of hake annual landings in the Spanish NW Mediterranean harbours show considerable fluctuations. In the Balearic Islands, a well marked 12-year cycle has been found (Astudillo and Caddy, 1988; Oliver, 1993). In relation to hake catches, the gillnet and longline fisheries are less important than trawl fishery. In 1988, the landings of hake in the Gulf of Lions by these types of fishing methods were 2394 (81%), 384 (13%) and 162 tonnes (6%) for the trawl, gillnet and longline, respectively (Oliver and Massutí, 1994). However, these three different types of gear exploit distinct portions of the fish population, and both the population-strata exploited and the number of specimens in the catches for the three fisheries are very different.

Figure 3 shows the distribution length of the catches in relation to the type of fishing gear used. For trawl fishery, the values for 1991 correspond to catches for the whole Catalan coast (Sánchez and PDPEM, 1991), and in the case of longline and gillnet, length frequency distributions in the Gulf of Lions during 1988 have been used in areas where these two types of fishing methods are in use (Recasens, 1992). In all cases, the length frequency distributions were weighted towards the monthly catches. Although in the trawl fishery specimens between 3 and 73 cm are exploited, the catches are almost entirely immature specimens, with the larger portion of individuals caught measuring 9 to 16 cm in length, and a mean size of 16.19 cm. In 1991 the number of specimens captured by means of this fishery was 27 million. The longline exploits specimens from 29 to 85 cm, with a high percentage of catches measuring between 40 and 50 cm in length, and have a mean length value of 51.7 cm. The length range exploited with gillnets is similar (27-78 cm), catching fish of slightly smaller size, with most individuals caught between 35 and 45 cm in length, with an average length of 42.6 cm. In 1988, the number of specimens captured by means of these fisheries were 140000 and 600000 for longline and gillnet, respectively. According to Recasens (1992), the range of



sizes exploited by each method of fishing, has remained constant throughout the years.

#### 4.2. Anchovy

In the Mediterranean, the small pelagics fishery, and particularly the anchovy fishery has developed along the continental shelf and the beginning of the continental slope. In general, this species is distributed in zones more distant from the coast, and in a depth-range deeper than the sardine, the other target species of this fishery.

The anchovy fishery is characterized by its seasonal nature. Highest catches are obtained in spring and summer, and decrease during autumn and winter. According to Suau (1979), this fact is in line with the anchovy's spawning season. During this period, high concentrations of adults specimens are detected over the beginning of the continental slope, which then move to areas near the coast. In autumn, these specimens disappear progressively of the catches, probably due to their migration to oceanic waters, far from the fishing grounds.

Nowadays, anchovy is exploited by two different methods of fishing: purse-seine and trawling. According to the 19th Report of the Scientific and Technical Committee for Fisheries (STCF, 1991), in the NW Mediterranean Spanish coast, the purse-seine fishery has developed into a fleet of 205 boats, with an average power and tonnage of 220 HP and 40 TRB, respectively. Although the distribution of this fleet shows homogeneity throughout the whole area, it can change seasonally. In summer, a northwards movement has developed by these unities and by others proceeding from the Southmediterranean Spanish coast in order to fish in the Gulf of Lions and around the Ebro runoff. With the introduction of the pelagic trawl modality, the last 10 years the numbers of purse-seine boats has been reduced by half in the French coast (Griffiths, 1991). At this moment, the French fleet is composed by 41 unities of 200 HP mean power (STCF, 1991).

The anchovy trawl fishery is practiced in the whole area with traditional bottom trawl nets, modified with technical variations in order to obtain a higher vertical gear opening, and using an illegal mesh-size of about 32 mm, which make it suitable for the batymetric distribution of the target species, especially the anchovy (Alvarez, 1990). The fishing grounds are situated in a depth-range from 60 to 120 m, and the percentage of the catches of this fishery respect to the purse-seine fishery can arise to 15% of the total landings of this species (Pertierra, 1992).

The pelagic trawl, being forbidden in Spain, is only used in the Gulf of Lions by the French fleet. This fishery is practiced during the day-time and, in some cases, has replaced the purse-seine fishery. At this moment, a total of 24 unities with an average power of 600 HP are dedicated to this fishery (STCF, 1991). Its landings are increasing annually in relation to the purse-seine fishery, and in some cases, it represents 15% of the small pelagic total catches.

Since 1940, the annual catches of anchovy in the NW Mediterranean have oscillated from 1000 to 25000 tonnes (GFCM, 1976, 1980a, 1993; Abad *et al.*, 1991b), although it an increase has been observed since the 1960's (Fig. 2b). Before this period, sardine and mackerel (*Scomber scombrus*) were the main target species of the small pelagics fishery. Nevertheless, the decrease in the economic value of these two species due to its lower demand, and the high increase of the anchovy price, led to a change in the exploitation pattern of these species (Suau, 1979). A similar situation occurred in other Mediterranean areas such as the Alboran Sea, where in 1962 the market prices of anchovy and sardine rose to the same level, after which the later species attained higher market value (Abad *et al.*, 1988).

Along the Catalanian coast, although the landings from the purse-seine fishery have a mean annual size of 10.83 cm, very similar to that obtained in the trawl fishery (11.5 cm), its distribution lengths is bimodal (Fig. 4). This is due to the capture of bigger specimens during the summer, season in which the exploitation of this species is carried out exclusively with purse-seine. During the winter, season during which the anchovy is captured by trawling and purse-seineing, its exploitation falls in the recruits of the species (Pertierra, 1992).

### 5. POPULATION DYNAMICS

#### 5.1. Hake

Until 1980 production models were applied to hake NW Mediterranean stocks, of which historical series of catch and effort data existed, and a high level of overexploitation was detected both in the Spanish coast (Oliver and Bruno, 1980) and in the Gulf of Lions (GFCM, 1980b). After 1980, Yield per Recruit Analysis, and more recently Cohort Analysis have been applied in different areas off the Spanish coast (Recasens *et al.*, 1994) and in the Gulf of Lions

(Aldebert *et al.*, 1993; Aldebert and Recasens, 1994).

The results show a fishery that is overexploited. The exploitation pattern, with higher mortality levels in the age-classes 0 and I in the trawl fishery, is considered inadequate for global resource conservation. The length ranges exploited by longline and gillnets are the theoretically ideal sizes for the upkeep of the resource, without the danger of overexploitation (Recasens, 1992). According to this author in the case of taking conservationist measures, it would be best to diminish the fishing pressure by the implementation of closed areas or to reduce the number of fishing days per week, not considering converting the trawl fleet into another fleet with different methods of fishing: longline and gillnets. However this conversion would also give positive results. In any case, fishing with gillnets and longlines also needs regulation, as their effect, combined with the actual exploitation pattern of the trawlers, will be disastrous for the overfished Mediterranean hake stocks. This is due to the fishings effect on the hake's reproductive stock not exploited until now as it was inaccessible to the trawl (Oliver and Massutí, 1994).

The hake biomass estimates developed with VPA-based methods, give distinct results using set of different population parameters (Aldebert *et al.*, 1993). In addition, as general values we can consider those given by Recasens (1992), that obtained a mean biomass of 2800-3000 tonnes for the Catalanian coast, and 6400-8800 for the Gulf of Lions. Further, we can add 2300 annual tonnes to these results obtained by García-Rodríguez and Recasens (1994) in the rest of the NW Mediterranean Spanish coast.

## 5.2. Anchovy

Anchovy stock assessments have been carried out off the coast of Catalonia using analytical and direct methods to estimate the biomass and the level of exploitation. López-Cazorla and Sánchez (1985) applied a Cohort Analysis during the years 1978-1982 and found an apparently stable population. This was reflected in the number of individuals by length groups and by age. Pertierra (1992) indicates the great importance of the recruitment for the population, with the recruitment biomass making up 45% of the total biomass. From the study of competition between the various different fishing methods by the same author, we can deduce that the largest catches would be achieved by maintaining the actual fishing pressure of purse-seining, and halting all trawling. A reduction of 25% of the fishing effort of trawling and a 10% reduction of the effort of purse-seine, would be beneficial, augmenting the biomass by approximately 10%.

However, the estimates of anchovy biomass using different methods have obtained very different results. In one case López-Cazorla and Sánchez (1985) give a mean figure of 136127 tonnes for the Catalanian coast, while the VPA-based estimate of mean biomass for the same area, using landings data for the purse-seine fleet in 1988 and 1989, was around 18500 tonnes (Pertierra, 1992). More recently, based on length cohort analysis, Pertierra and Lleonart (1995) have obtained for the period 1992-93 a mean annual anchovy biomass of 28697 and 10648 tonnes for the Catalanian coast and the Gulf of Lions, respectively. In relation to direct methods, the differences are also evident. Pertierra and Castellón (1987) used on acoustic surveys in 1985, and concluded a biomass of 4200 tonnes for Southern Catalonia. For the same area, Palomera and Pertierra (1993) calculated a biomass of the spawning anchovy population of 4200 tonnes. In the NW Mediterranean Spanish coast, based on acoustic values, Abad *et al.* (1991a, 1992) gives figures of 25575 and 19558 tonnes for 1990 and 1991, respectively. The estimates of anchovy biomass in the Gulf of Lions have been developed by acoustic methods in French and Spanish surveys. In 1984, '88, and '90 the results obtained were 13000, 32800, and 8192 tonnes respectively (Campillo, 1993).

## 6. ANALYSIS OF HAKE-ANCHOVY TROPHIC INTERACTIONS

### 6.1. Index of interaction

To cautiously define the amount of predation of the hake on the anchovy in the area of study, the studies which refer to the trophic relations of both species has been exhaustively analyzed (see bibliography in ANNEX 1). The importance attributed to the anchovy as part of the hake's diet varies greatly from author to author; from not even being considered as prey (Macpherson, 1977), to only an occasional prey (Jardas, 1976), to constituting the primary element of its diet (Jukic, 1972).

At first, these results suggest it is practically impossible to elaborate a reasonably realistic predation matrix which can be applied to the study area. However these huge discrepancies are mainly attributed to the methods of sampling used. The absence of trophic interaction is attributed to the fact that the samplings were taken in an area where the anchovy is rare,

such as the Central Adriatic (Jardas, 1976) or off south Catalan coast (Macpherson, 1977), or that the samplings only included very young hake that still feed on small crustaceans (Zupanovic, 1968). However, when the spectrum of lengths of hake sampled is wide, and the samples are taken over the continental shelf (Bozzano *et al.*, 1994; Larrañeta, 1970; Karlovac, 1959; Jukic, 1972), the anchovy, along with the sardine, is found to be the most important prey of hake in between 15 and 40 cm in length.

The percentage of stomachs which contain anchovies in comparison to the total of full stomachs oscillates greatly, between 3.7% (Bozzano *et al.*, 1994), 8.4% (Karlovac, 1959), approximately 24% (Larrañeta, 1970), and 44% (Jukic, 1972). This last piece of data is not comparable to the others, as it refers only to hake between the lengths of 20 and 30 cm, which are the sizes when predation upon the anchovy is the greatest, and in the study area a large amount of small pelagic fishes were detected. These differences can be attributed to the abundance of the anchovy in each area, since the method of sampling is quite similar in all the studies. On the other hand, several authors mention that the most intense predation of the hake onto the anchovy occurs in autumn-winter. Concluding, the anchovy is one of the hake's principle prey in areas where both species coexist, concrete figures on amount of predation varying according to the size of the predator, the time of year, and the abundance of prey.

One of the predation matrices which have finally been used in applying the mathematical models which describe the relationship between both species, is based on original data (Bozzano *et al.*, 1994). We consider that the results presented by these authors is representative of reality, as the number of individuals sampled is great, the range of sizes of the samples is wide, and the fish sampled, were caught in equal amounts throughout the entire year.

One important problem in putting together a matrix, was that there is no data on the sizes of the prey. Therefore, we consider that the predation occurs proportionally to the number of individuals in each age group. However, for the 0 age group only individuals longer than 4.5 cm were considered, as the smaller individuals inhabit areas very close to the coast, which are not frequented by the hake. Even so, 85% of all the predation on the anchovy will be on this age group. This supposition is coherent with the observed phenomenon, that the maximum predation on the anchovy occurs in autumn and winter, precisely the time when the recruitment of the 0 age group occurs. An important inconvenience that makes it difficult to extrapolate data to the entire study area, is that the sampled area only covered a small part of it. The sampling area, an area on the edge of the continental shelf in the Gulf of Lions, is an area where the abundance of anchovy is low in comparison to other regions in the study area.

Therefore we believe that the predation figures could be substantially higher in other regions of the study area. For that and in order to compare the results, a second predation matrix based on the work of Larrañeta (1970), carried out on the continental shelf off the coast of Castellón, was applied. In this case the predation figures is significantly greater, probably because the area which was studied is an area that contains a high concentration of anchovy. In conclusion, these predation matrices can be considered to represent regions in which there is high and low density of anchovy population. As a result the mean predation figures of the entire area probably give values in between those of areas of high and low anchovy population density.

One very important aspect to keep in mind in interpreting correctly the base data, and in building predation matrices, is the amount of time that the prey spends in the digestive tract of the predator, and the time elapsed between the catch of the prey by the predator, and the catch of the predator by the trawl of the sampler. Several authors believe that the time of maximum predatory activity of the hake occurs at night. The average time which the prey spends in the digestive tract of the hake could be 15 hours (Olaso, 1993), with the complete predation cycle being 24 hours. Taking into account that the samples were taken in the morning, we believe that the values based on these samples underestimate by 50% what the hake has in reality ingested in a 24 hour period. The number of hake caught with empty stomachs is approximately 50%. As a result, the proportion of anchovy in the hake's diet is calculated in respect to the number of full stomachs, as we consider that the empty stomachs correspond to individuals that have previously evacuated.

In conclusion, although the bibliography used does not supply sufficient data to build a model which realistically describes the trophic interaction between both species in the entire study area, it does allow us to come to some conclusions about the nature of this relationship, and to present an approximate model.

## 6.2. Space-temporal overlap between populations

Those hake belonging to the age groups I, II, and even III, which undertake nictemeral vertical migrations with a

wide range of depth from the bottom to the surface, coincide in autumn and winter with the recruitment of the anchovy over the continental shelf. This gives place to the greatest predatory activity of hake on anchovy.

Once the hake reaches 30 cm in length, the intensity and amplitude of its vertical movements decreases, a transition is observed in its diet away from small pelagic fishes, and to demersal fishes. Therefore the predation of these hake on anchovy which does inhabit regions farther off the coast must be less. At the same time, when the spawning anchovy come closer to shore towards the end of the winter, they are not subject to predatory activity by the hake. This is because of spawning anchovy's bathymetric position, and because of their relatively low numbers in comparison to the abundance of recruits during the fall and winter.

## 7. EFFECT OF CHANGES IN EXPLOITATION PATTERNS OF HAKE ON THE ANCHOVY POPULATIONS

### 7.1. Possibilities of mathematical modelling of the hake-anchovy system

The elaboration of a mathematical model capable of simulating the hake-anchovy population dynamics and interactions is a difficult exercise, in part because of the complexity of the phenomena which must be described and also because of the lack of biological and ecological data of both species.

Various authors (Andersen and Ursin, 1977; Helgason and Gislason, 1979; Pope, 1979; Majkowsky, 1981; Dekker, 1982; Leonart *et al.*, 1985a; Brander, 1988) have analysed the possibilities to build mathematical models of the dynamics of a system of two or more populations which are interacting in trophic relations and are exploited by fishing activities; this is actually one of the goals in fisheries research. These models are built in order to make more realistic predictions about the size of future stock and to obtain a guide with which to develop strategies for managing multispecies fisheries.

The estimation of predation mortality by species and size/age category is the essence of multispecies fisheries modelling and research needs (Cohen *et al.*, 1981). The predation depends mainly on the total consumption by predators, predators preference for certain prey, abundance of the prey, abundance of the predators. Several functions have been elaborated to describe the variation of predation according to these parameters. These phenomena have been described by studying the energy requirements of predators, elaborating predation matrices, by looking at stomach contents analysis, and by the formulation of mathematical functions describing the dependence of predation on prey and predator abundance.

Due to the complexity of the predator-prey-fisherman system, and to the problems related to the evaluation of predation, all the models imply some simplifications, such as limiting the simulation to two species, not considering a change of trophic niche, eliminating the possibility of variations in ration size with variations in prey abundance, and ignoring the occurrence of density-dependent phenomena, etc. These problems can be solved with further biological and ecological data, which is relatively scarce, and by formulating new mathematical functions describing the effects of predation.

Some of these problems have been tackled by different authors. Pope (1979) elaborates a model considering several species, Leonart *et al.* (1985a, 1985b) examines the effects of cannibalism, Andersen and Ursin (1977) evaluate the variation of consumption rate in the function of prey abundance and consider the model in terms of the general ecosystem, and Brander (1988) takes into account the possible density dependent growth of the prey.

Accordingly models have been developed named MSVPA (Multispecies Virtual Population Analysis) (Helgason and Gislason, 1979; Pope, 1979; Majkowsky, 1981; Dekker, 1982; Leonart *et al.*, 1985a), in which general knowledge about the predator-prey interactions are mathematically modelled to estimate the mortality due to predation and its effects on the stocks population dynamics.

Although some differences exist between them, the general lines of the mathematical models of MSVPA are:

- Splitting natural mortality in two components; predation and other natural causes.
- Evaluating predation by the construction of matrices elaborated from results of stomach contents studies.
- Considering the predator to act like a fishing fleet on the prey stock.

Despite that the VPA serves mainly to show the historic changes in the parameters describing a population, it is also possible to make predictions with MSVPA models, in order to evaluate the possible effects of different management strategies, while still taking into account the limited use of VPA for these purposes (Dekker, 1982).

On the basis of the scientific works reporting MSVPA models, especially the indications of Lleonart *et al.* (1985), we have built a MSVPA model for the study of hake-anchovy interactions in the Northwestern Mediterranean Sea, and to evaluate the possible influence of different hake exploitation patterns (predator) on anchovy (prey) stock and yields. In the ANNEX 2 a detailed description of the multispecies model is given.

The objectives of the model are simply descriptive, and the results have been considered only in their qualitative aspects. With the MSVPA analysis we have evaluated that hake predation may influence anchovy total natural mortality from a minimum of 7% to a maximum of 38%, in function of the age group considered and of the predation matrix adopted (Fig. 5a, 5b); these facts indicate that in all likelihood hake predation is an important factor in the control of anchovy stock population dynamics.

Taking into account the model limits, the assessed forecasts indicate clearly the influence of managing the hake stock on the anchovy stock and on the relative yields, which are directly proportional with hake exploitation (with anchovy exploitation patterns remaining constant). In consequence of this fact the total yields and gains are also partially conditioned (see ANNEX 2).

Although the simulations have been conducted adopting different hypothesis on the subject of hake predation, the outcomes have been relatively similar, proving the importance of the general trends indicated in the model.

#### 7.2. Effects on other related species: Preliminary approach to the study of the food web in the area

As a result of the scarcity of base data, as well as the theoretical complexities associated with it, which would exceed the objectives of this study, the effects of fluctuations within the populations of hake and anchovy on other species were not studied. Therefore the conclusions that can be drawn from the application of the model must be viewed with caution. However, without concrete data of predation figures it is possible to define what these relationships would be and their possible effects.

In the first place, one must consider three large groups of species: species of the same trophic level as the anchovy which are also prey of the hake, species that are prey of the hake but predators of the anchovy, and species that are predators of the anchovy, but have no direct trophic relation with the hake.

The first group would include sardines and other Clupeidae and Centranchidae. A decrease in the population of the hake would favor the augmentation of these species, as well as that of the anchovy. A limiting factor in this case would be the abundance of food, and the competition for it would be intense. As a result, the values indicated by the model for the increase of anchovy biomass are, in this case, overestimations.

The second group would include small Carangidae such as the horse mackerel (*Trachurus* spp.) and the blue whiting (*Micromesistius poutassou*). An increase of the fishing pressure on the hake favors the augmentation of the biomass of these two species which also prey on anchovy, so that the increase which one theoretically would expect in the biomass of the anchovy would not occur in reality. The third group would be made up of Scombridae, large Carangidae, and thons, amongst others. In each case, the potential impact of anchovy population fluctuations on these species should be studied. As all of these species are of significant commercial value, it would be very imprudent to advise that fisheries management strategies be based on a bispecific model, even though the model gives a better approximation of reality than a monospecific model.

## 8. CONCLUSIONS

As a result of the particular characteristics of the study area, whose productivity is higher than average for the Mediterranean, and the intense fishing activity which occurs there, the biomass of the stocks is not actually limited by the carrying capacity of the system. Therefore, it is realistic, and not just a mere theoretical speculation, to initiate fisheries management strategies with the purpose of augmenting significantly the biomass of the stocks, and the value of catches. Given the proven trophic interaction between hake and anchovy, it is necessary to keep in mind these facts in order to predict the evolution of these stocks under certain conditions of exploitation.

In the area of study, hake and anchovy are one of the main target species of the demersal and pelagic fisheries, respectively, both in landings as well as in economic values of the catches. Hake is usually exploited by a trawl fleet. However, in some specific areas, longline and gillnet are used. These fleets are composed of about 900, 60 and 20 boats, respectively, which operate along the continental shelf and slope between 30 and 700 m depth. Since 1975 the total hake catches have in general been in the upper 3000 annual tonnes range. The trawl fishery catches are almost entirely immature specimens, with a mean size of 16.19 cm, while longlines and gillnets exploit specimens from 27 to 85 cm, with a mean value of 51.7 cm and 42.6 cm, respectively.

Anchovy is exploited along the continental shelf and the beginning of the continental slope by purse-seiners and trawlers (both pelagic as modified bottom trawl nets). Its fishery is characterized by its seasonal nature, with highest catches in spring and summer, which decrease in autumn and winter. Nowadays, the purse-seine fishery is practiced by a total of 246 unities, and the pelagic trawl is only used in France by 24 unities. Although it observes important fluctuations, the annual catches of anchovy in the NW Mediterranean in the last three decades have in general been in the upper 10000 annual tonnes range. This form of exploitation cuts into the recruits of the species, with a mean annual size of 10.3 and 11.5 cm for the purse-seine and trawl fisheries, respectively.

In the study area, a high level of overexploitation has been detected in the hake stock, with higher mortality levels in the age-classes 0 and I as a result of the trawl fishery. Although longlines and gillnets also need regulation due to its effect on the reproductive stock, not exploited until now. In general, estimations with VPA-based methods calculate a mean biomass of hake between 11000 and 14000 tonnes for the whole studied area. Anchovy stock assessment shows a great importance of the recruitment in relation to the whole population, which, in terms of biomass, can be estimated to be 45% of the total. Due to this fact, the estimations of anchovy biomass, made in different years and during different seasons using different methods have obtained very different results. However, the more recent estimations, calculated using VPA-based methods, show a mean anchovy biomass of around 40000 tonnes.

The anchovy is one of the principle prey of the hake, even though the hake does not prey upon the anchovy uninterrupted during its entire life-span. The highest level of hake predation upon anchovy comes from hake between 15 and 30 cm in length (age groups 0 and 1) This is not only due to the hake's choosiness in respect to the size of its prey, preferring prey approximately 1/3 of its own length, but also to the hake's behaviour. During the period of maximum predatory activity on the hake, the latter tends to separate itself from the bottom in order to search for food, while larger hake display more benthonic habits and inhabit deeper waters which the anchovy only occasionally frequents.

The population dynamics and the trophic interactions between Northwestern Mediterranean hake and anchovy stocks have been described by a MSVPA model. With this model the anchovy natural mortality rate have been split up into a hake

predation component and other natural causes. The values expressed by the percentage of anchovy natural mortality due to hake predation obtained from MSVPA vary depending on the predation matrix considered, from a minimum of 7% to a maximum of 38% of the total natural mortality (M), or a minimum of 3% and a maximum of 34% if the total mortality (Z) is referred to.

The long term predictions related to the hake exploitation patterns demonstrated that anchovy yields are conditioned from hake exploitation, and that a more intensive exploitation of hake corresponds a rising of anchovy yields. Despite the simulation limits, the simplicity of the model and the various basis hypothesis, as well as the relatively low accuracy of VPA predictions, the importance of the influence of managing the hake stock on the anchovy yields have been illustrated to be relatively significant. In effect, the anchovy yields may be doubled if the hake stock exploitation varies from a condition of unexploitation to another of intensive overexploitation. But if these extreme situations are not considered, then changes in the exploitation pattern of hake would not result in very remarkable oscillations of anchovy stock.

The results achieved by this model, and the conclusions arrived at based on the results, should be considered cautiously. Eventhough this model makes a better aproximation as to the population dynamics of the stocks than do the monospecific analysis currently in use, if the existing trophic interactions with other species were quantified and were included in the model, then the results could vary significantly.

However, a definite conclusion can be arrived at. As a result of the greater commercial value of the hake, the global value of the catches increase as fisheries management strategies are put into place which increase the biomass of the hake, eventhough catches of prey of the hake, such as the anchovy diminish. If on the other hand the final objective was to increase the total weight of the catch, then it would be best to increase the fishing effort upon the hake.

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## ANNEX 1

### RESUMEN DE LA BIBLIOGRAFIA MAS RELEVANTE REFERIDA A LOS HABITOS TROFICOS DE LA MERLUZA (*Merluccius merluccius* L.) EN EL MEDITERRANEO

La bibliografía consultada, cuyos resultados y conclusiones se exponen a continuación, incluye estudios realizados en la propia área de estudio y en otras regiones del mediterráneo (principalmente en el mar Adriático). Para elaborar este informe también se han tenido en cuenta trabajos sobre el comportamiento trófico de esta especie en otras áreas geográficas donde coexiste con la anchoa (*Engraulis encrasicolus*), así como estudios referidos a otras especies del género *Merluccius*, como *M. hubbsi*, *M. capensis* y *M. paradoxus* del Atlántico sur, que aportan datos interesantes sobre el comportamiento trófico del género.

A) Bozzano, A., L. Recasens and P. Sartor, 1994. Feeding habits of the european hake *Merluccius merluccius* (Pisces: Merlucciidae) in the gulf of Lions, Western Mediterranean, (*in press*).

- Zona de estudio: Mediterráneo Noroccidental (Golfo de León).

- Características del muestreo: Las características del muestreo se resumen en la Table 1A.

- Resultados generales: El porcentaje de estómagos llenos se mantiene alrededor del 50% en todos los grupos de tallas, mientras que el de estómagos evaginados aumenta con la talla, como se puede observar en la Table 2A. El TFI ( $TFI = (1/n) * (Weight * 10000) / Total Length^3$ ), que relaciona el peso del contenido estomacal con el del ejemplar, varía con la talla, la época del año y el estado de maduración según indica la Table 3A. Se identificaron 59 tipos de presas, principalmente peces, seguidos de decápodos, misidáceos y eufausiáceos y, por último, otros grupos como anfipodos, cefalópodos, isópodos, crinoideos y taliáceos (Table 4A). Entre los peces los más importantes son, por este orden, sardina, anchoa, cinta, góbidos y faneca. La composición de la dieta es bastante constante a lo largo del año, excepto en primavera, época en la que se encuentra un elevado número de eufausiáceos, aunque su importancia en peso sea escasa. La proporción relativa de los diferentes tipos de presa varía apreciablemente con el desarrollo ontogenético, según se aprecia en la Table 5A.

- Datos concretos referidos a depredación sobre anchoa: En la Table 6A se recogen los datos base respecto a la predación de merluza sobre sardina y anchoa. Siempre se encontró un solo ejemplar por estómago. Se menciona que los clupeidos se encuentran principalmente en los estómagos de las merluzas pescadas sobre la plataforma, mientras que en las pescadas en el talud son más abundantes los gádidos y mictófididos.

B) Larrañeta, M.G., 1970. Sobre la alimentación, la madurez sexual y la talla de primera captura de *Merluccius merluccius* (L.). *Inv. Pesq.*, 34(2): 267-280.

- Zona de estudio: Mediterráneo Noroccidental (Castellón).

- Características del muestreo: Los ejemplares analizados fueron pescados al arrastre sobre la plataforma continental frente a Castellón, a lo largo de seis años y en cada uno de los meses del año. Para el estudio de su contenido estomacal se analizaron 815 ejemplares, teniendo en cuenta sólo la frecuencia de cada clase de alimento.

(\*) Por su interés y su posible extrapolación al presente estudio, se comentan además los resultados de algunos trabajos sobre hábitos tróficos del género Merluccius en otras áreas geográficas.

- Resultados generales: La evolución de la dieta a lo largo del desarrollo es significativa. Al principio se alimenta casi exclusivamente de crustáceos, adquiriendo paulatinamente los peces mayor importancia, hasta constituir la base de la dieta. El resto de la misma la constituyen equinodermos y moluscos. Dicha evolución se especifica en la Tables 1B y 2B. Los crustáceos eran en su mayor parte pequeños macruros nadadores y larvas de decápodos y eufausiáceos. Entre los teleósteos destacan los peces pelágicos como sardina y anchoa, seguidos por especies bentónicas como faneca, góbidos y cinta, y otra pelágica como jurel. Ocasionalmente se encontró congrio, salmonete, peluda, merillo, boga, caballa, centracántidos, la propia merluza y alacha. Los moluscos eran principalmente cefalópodos (sepia, *Sepiolo* y calamar) y el resto pequeños bivalvos. Los equinodermos consistían en pequeñas holoturias del género *Cucumaria*. El tipo de peces ingeridos varía

según la talla, siendo en los ejemplares de menor talla principalmente clupeidos, adquiriendo los otros teleósteos una mayor importancia paralelamente al incremento de la longitud total, como se detalla en la Table 4B. La proporción entre peces y crustáceos varía según la época del año, como indican las Tables 3B y 5B.

- Datos concretos referidos a depredación sobre anchoa: No se aportan datos base directos, sino sólo porcentajes. No se especifica claramente si los 815 ejemplares analizados incluyen los estómagos vacíos y/o evaginados o son todos los estómagos llenos encontrados de un total de 2344 ejemplares. Teniendo en cuenta los porcentajes de estómagos vacíos y evaginados, el segundo caso parece ser el más probable ya que así las proporciones entre estómagos llenos y estómagos vacíos más evaginados son similares a las citadas en el resto de la bibliografía. Sin embargo, integrando los datos sobre porcentajes de las diferentes presas según la talla, los referidos al número de datos por talla de la Table IIB y el total de estómagos llenos, ha sido posible elaborar una matriz de interacción trófica entre ambas especies.

C) Macpherson, E., 1977. Estudio sobre relaciones tróficas en peces bentónicos de la costa catalana. PhD Thesis, Univ. Autònoma Barcelona, 220 pp.

- Zona de estudio: Mediterráneo Noroccidental (Cataluña).

- Características del muestreo: Fueron analizados 377 ejemplares, entre 5 y 70 cm, aunque más del 99% medían entre 5 y 48 cm, capturados al arrastre preferentemente entre 200 y 400 m de profundidad. El 46,4 % de los individuos presentaban el estómago evaginado y no se especifica el número de estómagos vacíos.

- Resultados generales: El coeficiente de repleción varía según las estaciones, siendo máximo en invierno. Los tipos de presa son peces (*Micromesistius poutassou*, *Antonogadus*, *Notoscopelus*, etc.), decápodos natantia (*Pasiphaea sivado*, *Processa mediterranea*, *Solenocera membranacea*, etc.), eufausiáceos y cefalópodos, cuya proporción en peso varía según la talla del depredador. Los eufausiáceos sólo aparecen en los estómagos de las merluzas de 5 a 14 cm y los cefalópodos en las de 25 a 34 cm. Los peces y los crustáceos decápodos aparecen en todos los rangos de tallas, oscilando los primeros entre el 75 y el 95% y los segundos entre el 5 y el 20%.

- Datos concretos referidos a depredación sobre anchoa: No se detectó ninguna anchoa en los contenidos estomacales de las merluzas aunque sí en los de algunas especies de escualos, en una de las cuales (*Etmopterus spinax*) llegaba a constituir el 20% en peso de su dieta. No es un dato muy significativo dado el escaso número de merluzas estudiadas y por otra parte posiblemente se debe a que las pescas se realizaron en zona de talud, donde los clupeidos son menos abundantes.

D) Macpherson, E., 1981. Resource partitioning in a Mediterranean demersal fish community. *Mar. Ecol. Prog. Ser.*, 4: 183-193.

- Zona de estudio: Mediterráneo Noroccidental, entre Alicante y Cabo de Creus.

- Características del muestreo: Las pescas se realizaron entre 200 y 800 m de profundidad con redes de arrastre de fondo, entre Septiembre de 1976 y Septiembre de 1978. Se analizaron un total de 664 ejemplares de merluza (24.8% entre 5 y 9 cm, 51.5% entre 10 y 19 cm, 12.4% entre 20 y 29 cm y 11.3% entre 30 y 39 cm).

- Resultados generales: Las principales presas encontradas fueron, por orden de importancia en cuanto al peso: *Micromesistius poutassou* (23.3%), *Lessuerigobius friessi* (19.9%), *Notolepis rissoi* (14.7%), *Pasiphaea sivado* (8%), *Nyctiphanes couchii* (6.1%), *Gadiculus argenteus* (5.5%) y *Notoscopelus elongatus elongatus* (4.8%).

- Resultados referidos a la predación sobre anchoa: No se menciona en concreto la presencia de anchoas como presas de merluza, pero sí aparece como presa relativamente importante, en términos de proporción en peso del contenido estomacal, de *Etmopterus spinax* (n=353, 20%), *Galeus melastomus* (n=1559, 13.2%), *Scyliorhynchus canicula* (n=1009, 6.6%) y *Conger conger* (n=242, 7.2%).

E) Bozzano, A. and L. Recasens, 1994. Dati preliminari sull'alimentazione del nasello, *Merluccius merluccius*, nel Mar Ligure e nel Golfo de Leone. *Biol. Mar., suppl. Notiz. SIBM, Atti XXIV Congresso SIBM*, 4 pp.

- Zona de estudio: Mar Ligur y Golfo de León.

- Características del muestreo: Se realizaron tres campañas experimentales en el Mar Lígur, una en primavera (Mayo 1989) y dos en invierno (Enero y Marzo de 1990), capturando un total de unos 3000 ejemplares de merluza, en pescas realizadas a unos 100 m de profundidad. Para los estudios de contenido estomacal se analizaron unos 45 estómagos llenos en cada campaña. En el Golfo de León se analizaron 927 individuos procedentes de muestreos mensuales realizados sobre desembarcos comerciales desde Enero a Mayo de 1993, de los cuales 706 estaban llenos (76.2%). Los datos sobre frecuencias de aparición de tipos de presas se agruparon por trimestres, refiriéndolos a tres grupos de tallas: 9-14 cm, 15-29 cm y 30-40 cm.

- Resultados generales: Las presas principales fueron crustáceos y teleósteos. Los primeros resultaron más abundantes en ambas áreas en invierno, mientras que en primavera lo fueron los teleósteos. Con el incremento de la talla disminuye la proporción de pequeños crustáceos en la dieta (Eufausiáceos, Misidáceos y Anfípodos), a la vez que aumenta la de decápodos y osteíctios, que a partir de los 30 cm constituyen, al 50% aproximadamente en cuanto a número de presas, el total de la dieta.

- Resultados referidos a predación sobre anchoa: No se presentan resultados concretos a nivel específico.

F) Karlovac, O., 1959. La nourriture du merlu (*Merluccius merluccius* L.) de la Mer Adriatique. *Document Technique CGPM*, 45: 333-339.

- Zona de estudio: Alto Adriático y algunas estaciones en el Adriático Central y Meridional.

- Características del muestreo: Pescas de arrastre de una hora de duración, a profundidades comprendidas entre menos de 50 y 400 m (la mayoría a unos 200 m), realizadas entre Febrero de 1948 y Marzo de 1949. Se capturaron 7064 ejemplares de merluza, entre 4 y 86 cm de longitud. Los datos sobre proporciones de estómagos llenos, vacíos y evaginados según estratos de profundidad se recogen en la Table 1F. El porcentaje de estómagos evaginados se incrementa notablemente con la profundidad de captura, desde apenas el 1.1% a menos de 50 m hasta un 66% a más de 300 m. Por el contrario, el porcentaje de estómagos vacíos disminuye, desde un 66.7% a un 19.4% a esas mismas profundidades.

- Resultados generales: En los estómagos de las merluzas se han encontrado principalmente peces y crustáceos y, en menor medida cefalópodos (Table 3F), variando la importancia relativa de los diversos grupos con la talla, tal como indica la Table 2F. En los ejemplares más pequeños predominan los eufausiáceos y misidáceos, mientras que en los mayores se encuentran crustáceos decápodos de mayor talla, como *Solenocera membranacea* y *Alpheus glaber*, y peces, principalmente sardina, anchoa, caballa, boga y la propia merluza.

- Datos referidos a predación sobre anchoa: En un total de 1087 estómagos llenos, correspondientes a ejemplares muestreados entre marzo y diciembre, se han encontrado 91 anchoas en 88 estómagos.

G) Piccinetti, C. and G. Piccinetti Manfrin, 1971. Osservazione sull'alimentazione del meluzzo (*Merluccius merluccius* L.) in Alto e Medio Adriático. *Note Lab. Biol. Mar. e Pesca Fano*. 4(3): 43-62.

- Zona de estudio: Alto y Medio Adriático.

- Características del muestreo: Se analizaron 199 ejemplares de tallas comprendidas entre 14 y 42.5 cm, capturados con redes de arrastre en tres áreas diferentes durante marzo y noviembre, a profundidades entre algo menos de 50 y 100 m. El número de ejemplares muestreados de cada zona, así como las proporciones de estómagos llenos, vacíos y evaginados, y las proporciones entre los distintos tipos de presas, se presentan en la Table 1G. La bajísima proporción de estómagos vacíos con respecto a los valores encontrados por otros autores en la misma zona, podría explicarse por el criterio adoptado para definir "estómago vacío", en este caso los estómagos cuyo contenido pesa menos de 0.3 g.

- Resultados generales: Los principales tipos de presas son peces y crustáceos, seguidos por los moluscos. Los datos concretos se resumen en la Table 2G. Los crustáceos aparecen en menor número de estómagos que los peces, aunque son más abundantes que éstos ya que se encuentran en cada estómago unos 4 por término medio, mientras que sólo hay una media de poco más de un pez por estómago. Entre los crustáceos los más abundantes son decápodos natantia y entre los peces los clupeiformes. La composición relativa en peso de los tipos de presa se indica en la Table 3G. La relación entre peso del contenido estomacal y peso del ejemplar disminuye con la talla, de un 8.6% a los 15 cm se estabiliza en torno al 2.5% entre 30 y 36 cm. Estos valores son menores que los presentados por otros autores, debido a que en este estudio se

han considerado como llenos, estómagos con muy poco contenido estomacal, que quizás hubieran sido incluidos en el apartado de "vacíos" por otros autores.

- Datos referidos a alimentación sobre anchoa: Se han encontrado ocho anchoas en los estómagos de 7 ejemplares, lo cual representa un 4.02% de los individuos muestreados. Este porcentaje es posiblemente más elevado porque hay un buen número de clupeiformes indeterminados (28 en 22 estómagos).

H) Jardas, I., 1976. Contribution to the knowledge of the biology of hake in the Adriatic Sea. *Rev. Trav. Inst. Pêches marit.*, 40(3-4): 615-618.

- Zona de estudio: Adriático Central.

- Características del muestreo: Se analizaron 295 ejemplares de entre 15 y 51 cm de longitud.

- Resultados generales: En número, los peces representan el 62.8% de la dieta, los crustáceos el 35.7% y los cefalópodos el 1.6%. En peso, las proporciones son 97.5%, 2.3% y 0.4%, respectivamente. Los datos concretos a nivel específico se presentan en la Table 1H. Cabe destacar que no aparecen apenas clupeiformes en la dieta. El autor lo atribuye a que éstos son poco abundantes en las ictioecocenosis de la zona estudiada.

- Datos referidos a predación sobre anchoa: Se encontraron 2 anchoas en los 295 estómagos analizados.

I) Zupanovic, S. 1968. Study of hake (*Merluccius merluccius* L.) biology and population dynamics in Central Adriatic. *Stud. Rev. CGPM*, 32: 14-15.

- Zona de estudio: Adriático Central y áreas del Canal de Otranto.

- Características del muestreo: Se analizó el contenido estomacal de un número indeterminado de pequeñas merluzas (<16 cm) capturadas en una estación del Adriático Central y el de 1308 ejemplares muestreados en estaciones de la zona del Canal de Otranto. De éstos últimos, el 67.23% de estómagos se encontraban vacíos.

- Resultados generales: El contenido estomacal de las pequeñas merluzas muestreadas en el Adriático Central se componía de un 95% de eufausiáceos, principalmente *Nyctiphanes couchi*, y el resto eran decápodos natantia, *Chlorotocus crassicornis* y algunos misidáceos (*Lophogaster typicus*). Los resultados referidos al contenido estomacal de los ejemplares muestreados en la zona del canal se recogen en la Table 1I. Los peces más abundantes fueron sardina y espadín.

J) Papaconstantinou, C. and E. Caratgisou, 1987. The food of hake (*Merluccius meluuccius*) in Greek seas. *Vie Milieu*, 37(2): 77-83.

- Zona de estudio: Mar Jónico y Golfos de Patraikos y Corinto.

- Características del muestreo: Se examinaron 1290 estómagos de merluzas pescadas en una serie de estaciones frente a las costas del oeste de Grecia, en lances de 30 a 45 minutos de duración efectuados con red de arrastre, llevados a cabo en cuatro campañas realizadas con una frecuencia trimestral a partir de junio.

- Resultados generales: El 32.5% de los ejemplares procedentes del Golfo de Patraikos, el 49.5% de los de Corinto y el 52% de los del Mar Jónico tenían el estómago vacío. En las Tables 1J, 2J y 3J se presentan los datos sobre porcentaje en peso ( $C_w$ ) y número ( $C_n$ ) de las especies presa, así como su porcentaje de ocurrencia (F), para cada una de las áreas estudiadas, para tres intervalos de tallas y para cada una de las estaciones del año. Los tipos de presa son en general los mismos en los distintos intervalos de tallas, aunque varían sus proporciones, aumentando la importancia de los peces en la dieta, a la vez que disminuye la de los crustáceos. La relación entre el peso del contenido estomacal y el peso del ejemplar aumenta con la talla, lo que contradice lo mencionado al respecto por otros autores. No se aportan datos detallados sobre cuales son las especies de peces depredadas.

K) Yannopoulos, C., 1977. The feeding niche of *Merluccius merluccius* L. and its influence on the length-weight relationship. *Rapp. Comm. int. Mer. Médit.*, 24(5): 69-71.

- Zona de estudio: Mediterráneo Oriental (Grecia).

- Características del muestreo: Se analizaron 504 ejemplares pescados con redes de arrastre en los meses de Noviembre, Enero, Abril y Junio de 1973 y 1974. El número de ejemplares con los estómagos vacíos fue de 151. Para análisis de contenido estomacal se utilizaron 206 individuos, ya que en el resto el contenido estomacal se encontraba total o parcialmente digerido.

- Resultados generales: Las merluzas de menor talla se alimentan principalmente de crustáceos, adquiriendo progresivamente mayor importancia los peces, que en las mayores de 30 cm constituyen la totalidad de la dieta. Los resultados del estudio sobre el peso seco de los contenidos estomacales en diversos intervalos de tallas, que se presentan en la tabla 1K, indican que se produce un brusco incremento del mismo a partir de los 30 cm, al tiempo que disminuye la proporción de estómagos vacíos.

L) Jukic, S., 1972. Nutrition of the hake (*Merluccius merluccius* L.), bogue (*Boops boops* L.), striped mullet (*Mullus barbatus* L.) and pandora (*Pagellus erythrinus*) in the bay of Kastela. *Acta Adriatica* 14(4): 3-39.

- Zona de estudio: Adriático (Bahía de Kastela).

- Características del muestreo: Se analizaron 363 ejemplares de merluza, de tallas comprendidas entre 21 y 29 cm, capturados entre Septiembre de 1963 y Agosto de 1964, a profundidades menores de 50 metros.

- Resultados generales: El número de ejemplares analizado en cada muestreo y los porcentajes de estómagos vacíos, evaginados y llenos, así como la descomposición de este último porcentaje según los tipos de presa, se indica en la Table 1L. El número real de individuos de cada especie presa hallados en los estómagos analizados se indica en la Table 2L. De estas tablas se deduce que el número de estómagos evaginado es muy escaso, lo cual es normal dada la escasa profundidad de las pescas. El valor medio del porcentaje de estómagos llenos es un 62.6%, lo que al relacionarlo con el número de presas, indica que sólo se encontró una presa por estómago. Los peces representan en número el 87.5% de la dieta y pequeños crustaceos como *Processa canaliculata* el 10.7%, mientras que el resto lo constituyen cefalópodos y ocasionalmente ofiuroideos. Entre los peces el grupo más importantes es, con diferencia, el de los clupeidos, que representa un 93.4% de los mismos.

- Datos referidos a predación sobre anchoa: La anchoa es en este caso la especie más importante en la dieta de la merluza, habiéndose hallado 99 ejemplares en los 363 estómagos analizados, es decir, un 27.6%. Las mayores tasa de predación sobre anchoa se produjeron en otoño e invierno, épocas en las que las ecosondas registraban una gran abundancia de peces pelágicos. Esta tasa de predación sobre anchoa es mayor que la sugerida en otros estudios. Este hecho puede ser debido a que en este caso el intervalo de tallas de las merluzas muestreadas corresponde precisamente con el de mayor predación sobre pequeños pelágicos y a que en el área de estudios los clupeidos eran especialmente abundantes.

M) Olaso, I., 1993. Posición trófica de la merluza en la Plataforma Cantábrica. *Jornadas sobre el estado actual de los conocimientos de las poblaciones de merluza que habitan la plataforma continental atlántica y mediterránea de la Unión Europea, con especial atención a la Península Ibérica*, Vigo, 13-17 Diciembre 1993, 16 pp.

En esta comunicación se exponen una serie de conclusiones resultantes de los trabajos realizados por el mismo autor y otros autores, sobre las redes tróficas de la merluza en la plataforma cantábrica. Los puntos destacables en relación con la interacción trófica merluza-anchoa son los siguientes:

- La anchoa es la principal presa de los reclutas de merluza (menores de 15 cm) en otoño, representando un 53% de los peces, que son un 72% del total de presas.

- Las merluzas entre 15 y 19 cm consumen en primavera un 9% de anchoas sobre un 40% de peces, mientras que en otoño éstas representan el 81% de su dieta, respecto al 89% de peces.

- Entre las de 20 a 24 cm la proporción se invierte, consumiendo en primavera un 57% de anchoas de un total del 97% de peces, mientras que en otoño son el 19% sobre el 99% de peces.

- En las de 25 a 29 cm las proporciones disminuyen, siendo del 24% en primavera y el 5% en otoño, respecto a un



porcentaje de peces del 99% y 100%, respectivamente.

- En las merluzas mayores de 30 cm, la anchoa deja de ser un alimento importante, representando sólo 4% de la dieta en primavera.

- También cita que las merluzas se alimentan principalmente de noche, siendo el ciclo completo de alimentación de 24 h y el tiempo medio de permanencia en el estómago de 15h.

A continuación se presenta un resumen de los resultados y conclusiones más relevantes de algunos autores, respecto al comportamiento trófico de algunas especies del género *Merluccius* en zonas del Atlántico sur.

N) Angelescu, V. and L.B. Prenska., 1987. La ecología trófica de la merluza común (*Merluccius hubbsi*) en el Mar Argentino. *Contribución INIDEP*, 561, 203 pp.

En este extenso trabajo, el más completo de los consultados, se exponen muchos resultados que, sin ser evidentemente extrapolables directamente a nuestro objeto de estudio, son de gran interés. De entre los que se refieren directamente a la interacción trófica de la merluza con la anchoa, en este caso anchoíta, cabe destacar las siguientes:

- La tasa de predación entre ambas especies se encuentra ligada a la superposición espacial de las poblaciones.

- El número de anchoas ingeridas en un período de entre 24 y 48h es de 1 a 3 en el 95% de los casos, pudiendo llegar en ocasiones a un valor máximo de 10.

- Las migraciones nictimerales de la merluza le permiten alimentarse en varias capas batimétricas o "pisos tróficos".

- La anchoíta es la principal presa de las merluzas comprendidas en un intervalo de tallas de 20 a 55 cm.

- Las merluzas mayores de 65 cm no depredan sobre anchoa, puesto que se encuentran en zonas profundas del talud continental.

O) Gordon, A. and E. Macpherson, 1991. Diurnal variation in the feeding activity and catch rate of the Cape Hake (*M. capensis* and *M. paradoxus*) off Namibia. *Fisheries research*, 12: 299-305.

La conclusión más importante de este trabajo es que el máximo de predación de ambas especies se produce entre las 01 y 07 horas, aunque *M. capensis* capture un número de presas total mayor durante las horas de luz.

P) Pillar, S.C. and M. Barrange, 1993. Feeding selectivity of juvenile Cape Hake (*Merluccius capensis*) in the southern Benguela. *S. Afr. J. mar. Sci.*, 13: 255-267.

Los juveniles de merluza son predadores bastante selectivos, con preferencia hacia las presas de mayor tamaño posible, que sean fácilmente detectables visualmente. En áreas donde el macrozooplancton (eufausiáceos y anfípodos) es relativamente más escaso, las merluzas jóvenes se alimentan en un 90% de anchoas. Ingeren presas de un tamaño máximo igual a la mitad de su propia talla, aunque las preferencias se dirigen a presas de 1/3 de la misma. Así, las merluzas de 20 cm comen principalmente anchoas de 5 a 6 cm. Las merluzas jóvenes realizan migraciones nictimerales hacia la superficie, pudiendo así alimentarse de zooplancton y pequeños peces pelágicos, mientras que las merluzas mayores se separan menos del fondo y en sus presas predominan peces bentónicos o demersales.

## ANNEX 2

### APPROACH TO A MULTISPECIES VPA FOR THE STUDY OF PREY-PREDATOR INTERACTIONS BETWEEN MEDITERRANEAN ANCHOVY AND HAKE IN THE NORTHWESTERN MEDITERRANEAN SEA

#### INTRODUCTION

The mathematical modelling of the population dynamics of a system of two or more stocks, interacting with each other by trophic relations and exploited by fishing activities, is one of the goals in fisheries research, in order to make more realistic forecasts of stocks and to obtain a guide to management strategies for multispecies fisheries. Andersen and Ursin (1977), Helgason and Gislason (1979), Pope (1979), Majkowsky (1981), Dekker (1982), Lleonart *et al.* (1985), Brander (1988), and many other authors have developed models to study multispecies population dynamics.

Among them, Lleonart *et al.* (1985) develops an empirical MSVPA model (Multispecies Virtual Population Analysis) to study the effects of Burbot predation on Cape Hake off the Namibia coast. They treated the victims of predation as if they had been caught by another fishing fleet; analogously Brander (1988), studying the interactions between Cod and Norway Lobster in the Irish Sea, consider Cod predation like the activity of a fishing fleet on the *Nephrops* stock.

On the basis of these studies we built a MSVPA model for the simulation of hake *Merluccius merluccius* (L., 1758) and anchovy *Engraulis encrancholus* (L., 1758) stocks' population dynamics and interactions in the Gulf of Lions (France) and off the Northwestern Mediterranean Spanish coast, to evaluate the importance of predation and to estimate the effects of fishing activity on hake (predator) on anchovy (prey) stocks and yields.

#### DESCRIPTION OF THE MODEL

##### The basis

The fundamental equations of the VPA model are the survival and catch equations, which are:

$$N_{(t)} = N_{(t-1)} * e^{-Z_{(t-1)}} \quad (1)$$

$$C_{(t)} = \frac{F_{(t)}}{Z_{(t)}} * N_{(t)} * (1 - e^{-Z_{(t)}}) \quad (2)$$

By inserting the number of catches of a cohort over the years into the VPA model, natural mortality (M) and fishing mortality of the last age group ( $F_t$ ), it is possible to evaluate the past history of the cohort: number of individuals ( $N_t$ ) and fishing mortality rate ( $F_t$ ) per age group, according to the equations:

$$N_T = C_T * \frac{(F_T + M)}{(F_T * (1 - e^{-(F_T + M)}))} \quad (3)$$

$$\frac{C_{(t-1)}}{N_{(t)}} = \frac{F_{(t-1)} * (1 - e^{-(F_{(t-1)} + M)})}{(F_{(t-1)} + M) * e^{-(F_{(t-1)} + M)}} \quad (4)$$

$$N_{(t-1)} = N_{(t)} * e^{(F_{(t-1)}+M)} \quad (5)$$

Equation 3 is used to calculate the number of individuals of the last age group, with 4 and 5 being used to interactively calculate fishing mortality and number of individuals per age group respectively.

When the last age group is a + group, that is, it comprises the fish of the age of the last group, in addition to the fish of all older age groups, the equation to calculate the number of individuals of this group is:

$$N_{T+} = C_{T+} * \frac{F_{T+}+M}{F_{T+}} \quad (6)$$

According to the pseudocoherents hypothesis, which requires the stock to be in steady state with fishing exploitation and exacts a certain constancy of recruitment, the catches of one year may represent the historic series of catches on a single cohort; this data matrix is named pseudocohort, and on it it is possible to apply the VPA.

By Describing the cohort (or pseudocohort) in past history, it is possible to carry out the long term/short term forecasts for assessing the number of individuals and of catches, according to the changing of the exploitation patterns. These forecasts have to be considered with care, as VPA equations are better and more reliably used to describe the past events rather than to make predictions for the future.

#### The multispecies model

In the MSVPA analysis hake predation on anchovy is considered like another fishing fleet exercise fishing pressure on the prey stock (Lleonart *et al.*, 1985; Brander, 1988). Then the consumption of anchovy by hake are added to the human fishing catches to obtain the starting data of a pseudocohort for the MSVPA analysis.

The substantial difference between VPA and MSVPA is that in the first, natural mortality (M) is considered constant, while in the second natural mortality is separated into two components (Pope, 1979; Lleonart *et al.*, 1985): Predation (F''), which depends fundamentally to predator stock, and residual natural mortality (M'), which is supposed constant; which for each age group is:

$$M_{(t)} = M' + F''_{(t)} \quad (7)$$

The sources and methodologies to obtain the starting data are described in the following chapter.

The principal model procedures and equations are described:

- 1) Classic VPA on hake.
- 2) Assessing hake predation on anchovy, calculated from hake VPA and predation matrix (P<sub>t,i</sub>).

$$C'_{(t)} = \sum_i (P_{(t,i)} * N_{m(i)}) \quad (8)$$

- 3) MSVPA for anchovy, obtained with a VPA which considers the sum of human catches (C'<sub>t</sub>) and hake predation (C''<sub>t</sub>).

$$C_{(t)} = C'_{(t)} + C''_{(t)} \quad (9)$$

4) Assessing human fishing mortality (F<sup>t</sup>) and hake predation mortality (F''<sup>t</sup>) of anchovy, by the equations:

$$F_{(t)} = F'_{(t)} + F''_{(t)} \quad (10)$$

$$\frac{F_{(t)}}{C_{(t)}} = F' \frac{C'_{(t)}}{C_{(t)}} = F' \frac{C'_{(t)}}{C'_{(t)}} \quad (11)$$

5) Long term predictions for hake of the number of individuals and catches, according to the new exploitation hypothesis, recruitment (R) is considered constant.

6) Evaluation of the new hake predation on anchovy on the basis of the long term hake forecasts and the predation matrix (equation 8).

7) Long term predictions for anchovy of the number of individuals and catches, according the new exploitation hypothesis and hake predation (leaving anchovy exploitation unchanged).

$$C'_{(t)} = N_{(t)} * F' \frac{C'_{(t)}}{F'_{(t)} + F''_{(t)} + M'} * (1 - e^{-(F'_{(t)} + F''_{(t)} + M')}) \quad (12)$$

$$C_{(t)} = N_{(t)} * F \frac{C'_{(t)}}{F'_{(t)} + F''_{(t)} + M'} * (1 - e^{-(F'_{(t)} + F''_{(t)} + M')}) \quad (13)$$

$$N_{(t+1)} = N_{(t)} * e^{-(F'_{(t)} + F''_{(t)} + M')} \quad (14)$$

To evaluate predation mortality the catch equation is employed in relation to predation and predation mortality rate (equation 12). Successively human catches are calculated (equation 13) and finally the number of individuals for the following age group are found (equation 14); recruitment (R) is considered constant.

Due to the scarcity of data about interactions between these species and in order to simplify the model equations, we considered some starting hypothesis (Pope, 1979; Cohen *et al.*, 1981, Brander, 1988) which must be taken into account when interpreting the results, because this hypothesis limits the predictive power of the simulation; it is assumed:

- Constancy of recruitment (R), of natural mortality (M), and of residual natural mortality (M') respectively for hake and anchovy stocks.

- Steady state condition of stocks with fishing exploitation activities.
- Absence of density dependent phenomena in hake predation, in growth and natural mortality of both species and in their general behaviour (possibility of cannibalism, changing of trophic niche, etc.).
- Trophic relations with other predator or prey species (blue whiting, mackerel, pilchard, etc.) and their possible changes are not considered.

All these hypothesis render the results of the model not completely reliable and that, for some cases, the simulation might indicate contradictory results. These situations have to be identified to prevent that the model admits impossible situations. This does not limit the usefulness of the model, as it has been built to describe the general phenomena of predation interactions and not to answer specific question about the stocks or to guide in the formation of future multispecies fisheries management strategies.

#### DATA EMPLOYED

Total catches for an age group of hake and anchovy (Tables Ia, Ib) are obtained from the total weight catches (see Chapter 5), and from the exploitation patterns of both species (see Chapter 4).

Von Bertalanffy equation parameters, size/weight conversion parameters and natural mortality of hake and anchovy (Table II), are those reported in bibliography (Farrugio, 1994; Pertierra, 1987; Recasens *et al.*, 1994) (see Chapter 3).

Table I. - Catches (thousand of individuals) of hake (a) and anchovy (b) per age group in the Northwestern Mediterranean Sea.

Ia		Ib	
Hake		Anchovy	
Age	Catches	Age	Catches
0	15086	0	922072
1	18697	1	713333
2	4752	2	289767
3	1799	3	39995
4	1544	4	7063
5	756	5+	753
6	364		
7	191		
8	148		
9	48		
10	32		
11+	28		

Table II.- Biological parametres of hake and anchovy for the North-Western Mediterranean Sea.

	K	Linf	$t_0$	a	b
Hake	0.1310	94.70	-0.1220	0.00590	3.06730
Anchovy	0.4487	18.19	-1.0896	0.00215	3.41216

To test the sensitivity of the model to changes we have considered two predation matrices, deduced from works carried out in the study area (Bozzano *et al.*, 1994; Larrañeta, 1970) on the hake stomach contents (see ANNEX 1). These matrices could be considered as examples of high and low values of predation index respectively (Tables IIIa, IIIb).

The anchovy's time of permanency in the hake's stomach is considered of about 15 h, and it is hypothesized that one hake catches one anchovy per day when its diet is based on fishes. If we suppose a greater or smaller number of prey per day, hake predation on anchovy will naturally be greater or smaller respectively.

The problems related with the evaluation of predation matrices have been described by Pope (1979) and Cohen *et al.* (1981), who evidence the importance to effectuate further and more complete studies about the stomach contents, to deepen the knowledge in this field. A further factor which may influence the predation matrix characteristics is the value of growth equation parameters of both species.

## RESULTS AND DISCUSSION

The purposes of this MSVPA model are the describing the phenomena of regulating prey-predator interactions in a complex fishing system, and the evaluation of the possible trends of results with different hypothesis of predator stock managing. Referring to a particular zone (Spanish coast and Gulf of Lions) does not imply aspirations to assess the resources of this zone, nor to give suggestions for a multispecies managing of stocks; simply we choose this zone for the presence in the area of both stocks and of fishing activities for both species, and moreover for the availability of bibliographical references about biology, ecology and fishing of both species.

With the MSVPA retrocalculation, we obtained the number of individuals per age group, and the fishing, predation and residual natural mortality rates, per age group of anchovy, which are indicated in Tables IV and V. These results indicate that predation mortality may vary in a range comprised of a minimum of 0.06 to that of a maximum of 0.48 respectively for the 3rd, group adopting the hypothesis of minimal predation, and for the 0th group, following the hypothesis of maximal predation. These facts determine that a variation of the total natural mortality rate exists. With these evaluations we can explicate a minimum of 7% to a maximum of 38% of total natural mortality (Fig. 1-6).

To evaluate the possible effects of hake exploitation on the anchovy yields and on total yields, we decided to calculate the long term forecast for both species. So we assessed: hake yields, anchovy yields, total yields, and economic yields, in relation to various possible exploitation patterns of hake ( $\phi$ : multiplication factor of fishing mortality/fishing effort;  $t_c$ : first catch age), among the two predation hypothesis (Tables VI-XII, Figures 7-13. The values indicated in Tables and Figures are simply theoretical and they have to be considered only to estimate the possible trends of the phenomena.

A brief discussion on the model results is reported:

### Hake Yields

Long term assessed hake catches in relation to exploitation patterns are reported in Table VI and in Figure 7. The maximum of catches is set at a fishing effort similar to the actual, but with a first catch age much more superior. In the diagram it results that a managing of hake stock is particularly efficient with the control of mesh size despite this of fishing effort.

### Anchovy yields

Long term assessed anchovy catches in relation to hake exploitation patterns for the two predation hypothesis are reported in Tables VII and X, and in Figures 8 and 11. We can observe the influence of hake exploitation on anchovy yields (anchovy exploitation remaining constant), in effect anchovy catches are maximised for a more intensive hake exploitation, and they can rise notably if we consider the hypothesis of elevated predation, while this influence is lower for the other predation hypothesis. Note that  $t_c$  exercises a great influence, in effect augmenting the age of first catch we leave in the sea the total number of potential predators of this age, especially for 1-2 age groups, which may negatively influence the anchovy stock and yields.

### Total Catches

Total catches (the sum of hake and anchovy catches) are reported in Tables VIII and XI, and in Figures 9 and 12 for the two predation hypothesis. Through these we can observe the effects of hake exploitation on total yields. If we consider the lower predation, the general diagram shape is analogous to the hake yields diagram and anchovy catches are only relevant for high hake exploitation patterns, where the rising of anchovy catches masks the decrease of hake catches. This fact determines the reduction of total yields for  $\phi > 2$ , when  $t_c$  varies from 0 to 1, despite the rising observed in the diagram of hake yields. For the higher predation hypothesis the diagram changes substantially, in actuality the maximum of catches is set for maximum hake exploitation, due to the very important rising of anchovy catches. In this case when  $t_c$  varies from 0 to 2, for  $\phi > 1$ , we observe a reduction of total catches, because the rising of hake catches is relatively scarce and the augmentation of predation determine a relevant decrease in anchovy catches.

### Economical Yields

The total value of catches are indicated in Tables IX and XII, and in Figures 10 and 13. These values are the sum of the anchovy and hake catches multiplied by their respective prices (to simplify the calculation the prices are considered constant, independent from the effects of individuals size and quantity of catches). In respect to the total catches diagram the influence of hake catches is more important, because of the considerable commercial value of this species. Nevertheless for the high predation hypothesis there remains a zone of a decreasing of economic yields when  $t_c$  varies from 0 to 1 ( $\theta > 1$ ). However for the other predation hypothesis when hake is superexploited we observe an attenuation of losses, due to the partial gains related to the rising of anchovy catches.

### CONCLUSIONS

The population dynamic and the trophic interactions between Northwestern Mediterranean hake and anchovy stocks have been described by a MSVPA model. In this area the two species are submitted to intensive exploitation and they interact with each other in a prey-predator relationship.

The natural mortality rate of the anchovy has been broken down into a hake predation component and into other natural causes. By the retrocalculation the value percentage of hake predation mortality have been estimated to vary from a minimum of 7% to a maximum of 38% of the total natural mortality. Further modification of the model and more detailed biological-ecological studies will consent to elaborate a more trustworthy model, and it will be possible to split up natural mortality into many different variable components in place to consider simply natural mortality rate constant.

The long term forecast of hake exploitation patterns demonstrate that anchovy yields are related to hake exploitation, and that for a more intensive exploitation of hake corresponds a rising of anchovy yields. Due to the simplicity of the model and to the various base hypothesis, and to the relative inaccuracy of VPA predictions, the results obtained have to be considered only in relative terms for the trend indications. Despite these limitations, the influence of managing hake stock on the anchovy yields have been illustrated to be relatively significant. In effect the anchovy yields may be more or less doubled if the hake stock exploitation varies from a condition of unexploitation to another of intensive overexploitation. This fact also determines that the total yields and the economical yields are conditioned by the variation of hake predation.

Taking into account this phenomena, and the possibly of other biological an ecological interactions, it will be possible to build models relatively closer to reality in respect of those actually employed in scientific research and for the halieutics resources managing, which do not consider interactions of a trophic nature between organism.

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#### **APPENDIX: List of symbols**

$C_t$  = total catches for t age group

$C'_t$  = human fishing catches for t age group

$C''_t$  = hake predation for t age group

$F_t$  = total fishing mortality for t age group

$F'_t$  = fishing mortality for t age group

$F''_t$  = predation mortality for t age group

$M_t$  = natural mortality for t age group

$M'$  = residual natural mortality

$N_t$  = number of individuals of t age group

$N_{mt}$  = number of hake individual of t age group

$P_{t,i}$  = number of anchovy of t age group predated by an hake of i age group

$Z_t$  = total mortality for t age group