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P. Merella, P. Oliver, F. Alemany and E. Massutí
IEO, Centre Oceanogràfic de Balears, Moll de Ponent s/n,
P.O. Box 291, 07080, Palma de Mallorca, Spain

SUMMARY - A methodology of Multispecies Virtual Population Analysis (MSVPA) for the Mediterranean fisheries has been developed. As an example, the impact of hake (*Merluccius merluccius*) predation on anchovy (*Engraulis encrasicolus*), two of the most important commercial species in north-western Mediterranean fisheries, has been analysed. The predator-prey relationships which exists between these species were described by two hypothetical predation matrices, derived from the current bibliography about biology, population dynamics and trophic ecology of both species. The results of the model showed that changes in the biomass of anchovy population, as well as in the economic values of landings of both species, could be obtained by varying the hake exploitation patterns. However, the variations predicted by the model must only be considered as a preliminary approach, as the figures which represent these changes do not take into account the interactions with other species, which could influence significantly the results of the analysis.

Key words: *Merluccius merluccius*, *Engraulis encrasicolus*, trophic interactions, population dynamics, multispecies model, north-western Mediterranean.

RESUME - *"Approximation à une Analyse Virtuelle de Populations multiespèces (VPA) en considérant les interactions trophiques merlu-anchois en Méditerranée nord-occidentale". Une méthodologie a été mise au point pour l'Analyse Virtuelle de Populations multiespèces (VPA) pour les pêcheries méditerranéennes. Comme exemple, on a analysé l'impact de la déprédation du merlu* (Merluccius merluccius) *sur l'anchois* (Engraulis encrasicolus)*, deux des espèces commerciales les plus importantes dans les pêcheries de la Méditerranée nord-occidentale. Les relations prédateur-proie qui existent entre ces espèces ont été décrites par deux matrices de prédation hypothétiques, dérivées de la bibliographie actuelle sur la biologie, la dynamique des populations et l'écologie trophique de ces deux espèces. Les résultats du modèle ont montré que l'on peut modifier la biomasse de la population d'anchois, ainsi que la valeur économique des débarquements des deux espèces, en faisant varier l'exploitation du merlu. Cependant, les variations pronostiquées par le modèle sont à considérer uniquement comme une approximation préliminaire, car les valeurs représentant ces changements ne tiennent pas compte des interactions avec d'autres espèces, qui pourraient influencer de façon significative les résultats de l'analyse.*

Mots-clés : Merluccius merluccius, Engraulis encrasicolus, *interactions trophiques, dynamique des populations, modèle multiespèces, Méditerranée nord-occidentale.*

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), Majkowski (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) developed an empirical Multispecies Virtual Population Analysis model (MSVPA), to study the effects of burbot (*Genypterus capensis*) predation on Cape hake (*Merluccius capensis*) off the Namibia coast, in which the victims of predation were treated as caught by another fishing fleet. Brander (1988), studying the interactions between cod (*Gadus morhua*) and Norway lobster (*Nephrops norvegicus*) in the Irish Sea, considered cod predation as the activity of a fishing fleet on the *N. norvegicus* stock. On the basis of these studies a MSVPA model was elaborated. This model was used to simulate the interactions and population dynamics of hake and anchovy stocks in the north-western Mediterranean and to evaluate the effects of fishing activity on hake on the anchovy stock and yields.

Hake *Merluccius merluccius* (L., 1758) and anchovy *Engraulis encrasicolus* (L., 1758) are two of the most important commercial species, both for value and weight of catches, in the western Mediterranean (Abad *et al.*, 1991).

The current bibliography pertaining to the biology and population dynamics of hake and anchovy in the Mediterranean is relatively numerous, as well as data about their trophic interactions. For these reasons both species were chosen to apply the experimental model.

The importance attributed to anchovy as part of hake's diet varies greatly from author to author; from not even being considered as prey (Macpherson, 1977) to constituting the primary element of its diet (Jukic, 1972). These differences can be attributed to the sampling methodology, because in the first case hake was sampled on the slope, between 200 and 400 m, were anchovy is scarce, and in the second one was mainly sampled hake between 20 and 30 cm of total length, when the predation on anchovy is maximum. However, in other studies where the samples where taken on wider depth intervals and the analysed hakes comprised a wide length distribution, the percentage of stomachs which contained anchovies, in comparison to the total of full stomachs oscillates widely, among 3.7% (Bozzano *et al.*, in press), 8.4% (Karlovac, 1959) and approximately 24% (Larrañeta, 1970). These differences could be attributed to the density of anchovy populations at each study area. Other authors mention that the most intense predation of hake onto anchovy occurs in autumn-winter (Olaso, 1990; Sartor, 1993). Hake belonging to the age groups 1, 2. and even 3, 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 anchovy over the continental shelf. This gives place to the greatest predatory activity of hake on anchovy. Once hake reaches 30 cm in length, the frequency and amplitude of its vertical movements decreases, a transition is observed in its diet away from small pelagic fishes, and to demersal fishes (Yannopoulos, 1977). By other hand, the bigger hakes usually inhabit regions further off the coast, where anchovy is scarce. Therefore the predation on anchovy of these hakes would be lower. At the same way, when the spawning anchovy come closer to shore towards the end of the winter, they are not subject to predatory activity by hake.

Material and methods

Description of the model

The substantial difference between VPA and MSVPA models is that in the first one natural mortality (M) is considered as an unique global factor, generally constant, while in the second natural mortality is split into two components (Pope, 1979; Lleonart *et al.*, 1985): predation (F''_t), which depends fundamentally on predator stock, and residual natural mortality (M'), which is the mortality caused by other predators, by diseases, by other natural causes, etc. This last one have been considered constant, then the total natural mortality for each age group is:

$$M_{(t)} = M' + F''_{(t)} \qquad (1)$$

In the MSVPA analysis hake predation on anchovy is considered as a supplementary fishing activity exercising a fishing effort on the prey stock (Lleonart *et al.*, 1985; Brander, 1988). Then the consumption of anchovy by hake is added to the human fishing catches to obtain the starting data for the MSVPA analysis.

The principal model procedures and equations are:

(i) VPA on hake to obtain the number of individuals for each age group ($N_{m(i)}$).

(ii) Assessing *M. merluccius* predation on *E. encrasicolus* (C''_t), calculated from hake VPA and predation matrix ($P_{t,i}$).

$$C''_{(t)} = \sum_i (P_{(t,i)} * N_{m(i)}) \qquad (2)$$

(iii) MSVPA for anchovy, obtained with a VPA which considers the sum of human catches (C'_t) and hake predation (C''_t).

$$C_{(t)} = C'_{(t)} + C''_{(t)} \quad (3)$$

(iv) Splitting anchovy fishing mortality in fishing mortality (F'_t) and hake predation mortality (F''_t).

$$F_{(t)} = F'_{(t)} + F''_{(t)} \quad (4)$$

$$\frac{F_{(t)}}{C_{(t)}} = \frac{F'_{(t)}}{C'_{(t)}} = \frac{F''_{(t)}}{C''_{(t)}} \quad (5)$$

(v) Long term predictions for *M. merluccius* of the number of individuals and catches, according to the new exploitation hypothesis.

(vi) Evaluation of the new hake predation on anchovy on the basis of the long term hake forecasts and the predation matrix (equation 2).

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

$$C''_{(t)} = N_{(t)} * \frac{F''_{(t)}}{F'_{(t)} + F''_{(t)} + M'} * (1 - e^{-(F'_{(t)} + F''_{(t)} + M')}) \quad (6)$$

$$C'_{(t)} = N_{(t)} * \frac{F''_{(t)}}{F'_{(t)} + F''_{(t)} + M'} * (1 - e^{-(F'_{(t)} + F''_{(t)} + M')}) \quad (7)$$

$$N_{(t+1)} = N_{(t)} * e^{-(F'_{(t)} + F''_{(t)} + M')} \quad (8)$$

To evaluate predation mortality the catch equation is employed in relation to predation and predation mortality rate (equation 6). Successively human catches are calculated (equation 7) and finally the number of individuals for the following age group are found (equation 8).

Due to the relative scarcity of historical data about fishing exploitation patterns and trophic interactions of these species and in order to simplify the model equations, some starting hypotheses were considered, which must be taken into account when interpreting the results. So it is assumed that:

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

(ii) Steady state condition of both stocks with fishing exploitation activities.

(iii) 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.).

(iv) Variations of trophic relations with other predator or prey species, like blue whiting (*Micromesistius poutassou*), mackerel (*Scomber spp.*), pilchard (*Sardina pilchardus*), etc., are not considered.

The two first conditions are necessary for the application of a VPA based on pseudocohort data. The third is a simplification of the predation equation proposed by Shepherd (1988); according to this hypothesis predation is proportional to predator biomass. In this simplification there is the implicit assumption that the level of prey available to the predator does not have to shift sufficiently to affect the predation mortality per unit biomass imposed (Pope and Macer, 1991). The last condition is another simplification necessary to limit the model to two species only. It is assumed that all the other predation mortalities and the other causes of mortalities can be resumed with a constant factor called residual natural mortality (M').

Data employed

Total catches per age group of hake and anchovy (Table 1) have been obtained from total landings (Abad *et al.*, 1991) and length distribution of catches (Sánchez and PDPEM, 1991; Pertierra, 1992), taking into account the parameters of the von Bertalanffy Growth Function and the length-weight relationships presented in recent studies on Mediterranean hake (Farrugio, 1994) and anchovy (Pertierra, 1987), reported in Table 2.

Table 1. Catches of hake and anchovy per age group in the north-western Mediterranean

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 2. Biological parameters of hake and anchovy for the north-western Mediterranean

	L• (cm)	k	t_0	a	b
Hake	94.70	0.1310	-0.1220	0.00590	3.06730
Anchovy	18.19	0.4487	-1.0896	0.00215	3.41216

Regarding to the mortality parameters, some authors have estimated values between 0.2 and 0.3 for natural mortality of hake. However, the low predation and low cannibalism impacting Mediterranean hake (Macpherson, 1981), and the importance of these factors within the natural mortality rate (Lleonart *et al.*, 1985; Vetter, 1988), suggest to consider lower values as more realistic. Pertierra (1992), considering the short life-span of anchovy in the area (maximum age of 5 years), concluded that predation was an important element of natural mortality. This author, comparing the values attained by other authors, 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 (Anon, 1991).

To quantify the trophic interaction between the considered species, two predation matrices were estimated from works carried out in the study area (Bozzano *et al.*, in press; Larrañeta, 1970) on hake stomach contents, as well as on data about feeding behaviour of hake included in the aforementioned bibliography (Table 3). These matrices could be considered as examples of low and high values of predation rate respectively. One important problem in putting together a matrix, was that there were no data on the sizes of the prey. Therefore it was considered that predation occurs proportionally to the number of individuals in each age group of anchovy. 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 hake. Even so, 85% of all the predation on anchovy will be on this age group.

Table 3. Predation matrices expressed in number of anchovies eaten by one hake per year

Anchovy (Age)	Minimal predation				Maximal predation			
	Hake (Age)				Hake (Age)			
	1	2	3	4	1	2	3	4
0	15.33	13.63	11.07	4.26	80.90	43.43	25.55	5.11
1	2.30	2.04	1.66	0.64	12.12	6.51	3.83	0.77
2	0.34	0.30	0.24	0.09	1.78	0.95	0.56	0.11
3	0.04	0.03	0.03	0.01	0.19	0.10	0.06	0.01
Total	18.00	16.00	13.00	5.00	95.00	51.00	30.00	6.00

Results

The purposes of this MSVPA model are to describe the phenomena regulating prey-predator interactions in a complex fishing system, and to evaluate the possible trends of the results with different hypotheses of predator stock exploitation. Referring to hake and anchovy and to a particular zone (north-western Mediterranean) does not imply the intention to give suggestions for a multispecies management of this stocks; simply this zone was chosen for the presence in the area of both resources 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, the fishing predation and residual natural mortality rates per age group of anchovy was obtained (Table 4). These results indicate that hake predation on anchovy cause a predation mortality that may vary between 0.06 and 0.48 for the age classes 0 to 3, depending on the predation matrix considered, while for the older age classes this is negligible. These show that a variation of the total natural mortality rate due to hake predation exists. With these evaluations could be explicated a 5 to 38% of natural mortality (Fig. 1).

Table 4. Anchovy mortality rates per age group

Age	Minimal predation					Maximal predation				
	M'	F"	F'	M	Z	M'	F"	F'	M	Z
0	0.80	0.16	0.19	0.96	1.16	0.80	0.48	0.13	1.28	1.41
1	0.80	0.09	0.54	0.89	1.42	0.80	0.31	0.43	1.11	1.54
2	0.80	0.07	1.17	0.87	2.04	0.80	0.27	1.02	1.07	2.09
3	0.80	0.06	1.32	0.86	2.18	0.80	0.26	1.23	1.06	2.29
4	0.80	0.00	1.00	0.80	1.80	0.80	0.00	1.00	0.80	1.80

M': Residual natural mortality; F": Hake predation mortality; F': Fishing mortality; M: Total natural mortality; Z: Total mortality

To evaluate the possible effects in changing hake exploitation on anchovy yields and on total yields, the long term forecast for both species were calculated. So were assessed: hake yields, anchovy yields, total yields (hake+anchovy), and economic yields, in relation to various possible exploitation patterns of hake (tc: age at first capture; ø: multiplication factor of fishing mortality-fishing effort), between the two predation hypothesis (Tables 5 and 8).

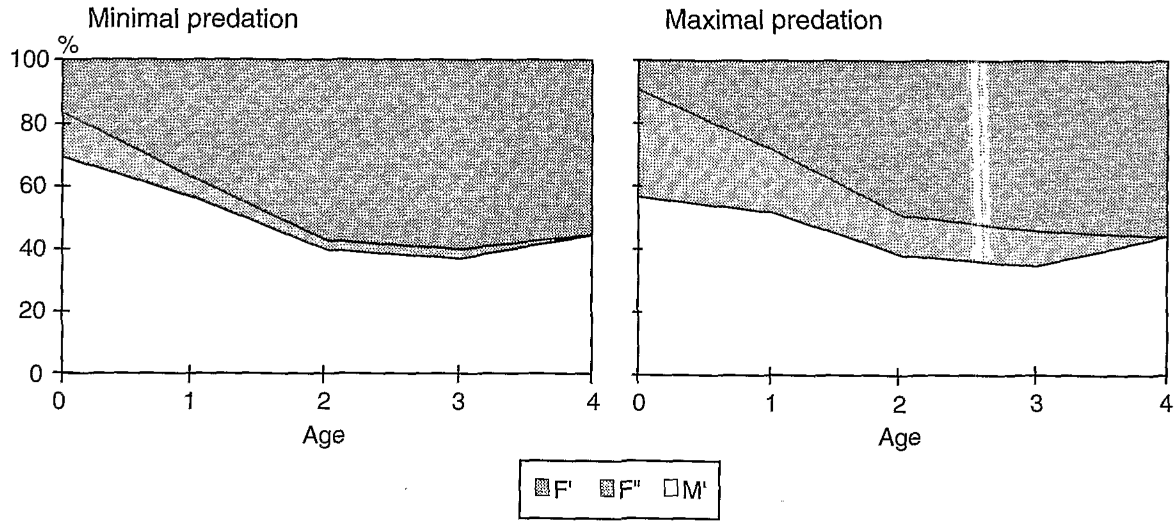

Fig. 1. Composition percentage of anchovy mortality.

Hake yields

Long term assessed hake catches in relation to exploitation patterns are reported in Table 5. The maximum of catches is set at a fishing effort similar to the actual, but with a much higher age at first capture.

Table 5. Hake yields (MT) in relation to exploitation patterns

tc/ø†	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
0	0	8833	4767	2764	1806	1304	1012	825	696
1	0	10309	6471	4339	3259	2686	2369	2188	2081
2	0	14402	12026	9978	8652	7780	7189	6776	6483
3	0	16751	15925	14542	13536	12827	12314	11932	11639
4	0	17915	18137	17296	16631	16169	15854	15639	15492

†tc: Age at first capture; ø: Multiplication factor of fishing mortality-fishing effort

Anchovy yields

Long term assessed anchovy catches in relation to hake exploitation patterns (tc, ø) for the two predation hypothesis are reported in Table 6. It can be observed the influence of *M. merluccius* exploitation on *E. encrasicolus* yields, in effect anchovy catches are maximized for a more intensive hake exploitation, and they can rise notably if the hypothesis of elevated predation is considered, while this influence is lower for the other predation hypothesis. Note that tc exercises a great influence, in effect by augmenting the age at first capture is left 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.

Table 6. Anchovy yields (MT) in relation to hake exploitation (tc, ø)

tc/ø[†]	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Minimal predation									
0	28648	32030	33957	35127	35887	36415	36802	37100	37336
1	28648	30930	32268	33067	33553	33853	34042	34162	34239
2	28648	29277	29751	30112	30387	30598	30761	30886	30983
3	28648	28743	28823	28892	28951	29001	29044	29080	29112
4	28648	28648	28648	28648	28648	28648	28648	28648	28648
Maximal predation									
0	27388	36888	42940	47019	49930	52113	53815	55182	56302
1	27388	32673	35915	37926	39188	39989	40503	40836	41053
2	27388	28504	29367	30034	30552	30956	31270	31516	31708
3	27388	27491	27580	27655	27720	27775	27822	27862	27896
4	27388	27388	27388	27388	27388	27388	27388	27388	27388

[†]tc: Age at first capture; ø: Multiplication factor of fishing mortality-fishing effort

Total catches

Total catches (the sum of hake and anchovy landings) are reported in Table 7 for the two predation hypothesis. Through these it can be observed the effects of hake exploitation on total yields. If the lower predation is considered, the results are analogous to the *M. merluccius* yields and the influence of *E. encrasicolus* catches is only relevant for important hake exploitation patterns, where the rise in anchovy catches masks the decrease in hake catches. This fact determines the reduction of total yields for ø>2, when tc varies from 0 to 1, despite the rise observed in the table of hake yields. For the higher predation hypothesis the results changes substantially, in actual fact the maximum of the catches is set for maximum *M. merluccius* exploitation, due to the very important rise of *E. encrasicolus* catches. In this case when tc varies from 0 to 2, for ø>1, is observed a reduction of total landings, because the rise in hake catches is relatively low and the augmentation of predation determines a relevant decrease in anchovy catches.

Table 7. Total (hake+anchovy) yields (MT) in relation to hake exploitation (tc, ø)

tc/ø[†]	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Minimal predation									
0	28648	40864	38724	37891	37694	37718	37814	37925	38032
1	28648	41239	38739	37406	36812	36540	36411	36349	36320
2	28648	43678	41778	40090	39039	38379	37949	37662	37466
3	28648	45494	44749	43434	42487	41828	41358	41012	40751
4	28648	46564	46786	45945	45279	44818	44503	44287	44140
Maximal predation									
0	27388	45721	47707	49783	51737	53417	54827	56007	56997
1	27388	42981	42386	42265	42447	42676	42873	43024	43134
2	27388	42906	41393	40012	39204	38736	38459	38292	38191
3	27388	44242	43505	42197	41256	40602	40136	39794	39536
4	27388	45303	45525	44684	44018	43557	43242	43026	42879

[†]tc: Age at first capture; ø: Multiplication factor of fishing mortality-fishing effort

Economical Yields

The total values of catches are indicated in Table 8. These values are the sum of anchovy and hake catches multiplied by their respective prices (to simplify the calculation prices are considered constant, independent to the individuals size and to the landings). In respect to the total catches the influence of *M. merluccius* is more important, because of the considerable commercial value of this species. Nevertheless for the high predation hypothesis there remains a zone of decreasing economic yields when tc varies from 0 to 1 (ø>1), while for the other hypothesis, when hake is intensively exploited, a reduction of losses is observed, due to the partial gains related to the rise of the anchovy catches.

Table 8. Total (hake+anchovy) value of landings (Millions of ptas) in relation to hake exploitation (tc, ø). Prices (ptas/kg): hake 800; anchovy 280

tc/ø†	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Minimal predation									
0	8022	16035	13322	12047	11494	11239	11114	11048	11011
1	8022	16907	14212	12730	12002	11628	11427	11315	11252
2	8022	19719	17951	16414	15430	14792	14364	14069	13861
3	8022	21449	20811	19723	18935	18382	17984	17688	17463
4	8022	22354	22531	21859	21326	20957	20705	20532	20415
Maximal predation									
0	7669	17395	15837	15376	15426	15635	15878	16111	16321
1	7669	17395	15233	14090	13580	13346	13236	13184	13160
2	7669	19503	17844	16392	15476	14892	14507	14246	14065
3	7669	21098	20463	19377	18591	18039	17642	17347	17123
4	7669	22001	22178	21506	20973	20604	20352	20179	20062

†tc: Age at first capture; ø: Multiplication factor of fishing mortality-fishing effort

Discussion and conclusions

Anchovy is one of the main prey of hake, even though hake does not prey upon 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. This is not only due to hake's preferences with respect to the size of its prey (Pillar and Barrange, 1993), but also to hake's behaviour: the maximum predatory activity of hake on anchovy occurs when the first tends to separate itself from the bottom in order to search for food (Angelescu and Prenska, 1987), while larger hake display more benthic habits and inhabit deeper waters which anchovy only occasionally frequents.

As a result of the MSVPA analysis anchovy natural mortality has been broken down into hake predation component and other natural causes. By retrocalculation, the importance of hake predation on anchovy natural mortality has been estimated to represent 5 to 38% for the 0-3 age groups, in function of the predation hypothesis considered. The long term forecasts varying the hake exploitation patterns indicated that *E. encrasicolus* yields are related to *M. merluccius* exploitation, and that to a more intensive fishing of hake corresponds a rise in anchovy yields. In effect these may be more or less doubled if the hake exploitation changes from a condition of unexploitation to another of intensive exploitation. This determines that the total (hake+anchovy) and the economical yields are conditioned too; but while the total catches results almost correlated with *M. merluccius* exploitation, the economical yields outcomes suggest a management with an optimal exploitation of the predator stock, due to the high market value of hake.

The results achieved by the model and the relative conclusions should be considered cautiously. If the existing trophic interactions with other species were considered the results of the analysis could vary significantly. 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 interaction of hake and anchovy on other species were not studied. Therefore the conclusions that can be drawn must be viewed with caution. However, without concrete data of predation figures it is possible to define what these relationships could be and their possible effects. In the first place, one must consider three groups of species: species of the same trophic level as anchovy which are also prey of hake, species that are prey of hake but predators of anchovy, and species that are predators of anchovy, but have no direct trophic relation with hake. The problems related to the evaluation of predation matrices and its possible variations have been described by Pope (1979) and Cohen *et al.* (1981), who show the importance of carrying out further and more complete studies on stomach contents, in order to widen the knowledge within this field. Even though this model could be considered a first approach for the study of multispecific population dynamics in the Mediterranean area, were the monospecific analysis is currently in use.

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Appendix

List of symbols

$C_{(t)}$	=	anchovy	*total catches*	for t age group
$C'_{(t)}$	=	"	fishing catches	"
$C''_{(t)}$	=	hake	predation on anchovy	"
$F_{(t)}$	=	anchovy	total fishing mortality	"
$F'_{(t)}$	=	"	fishing mortality	"
$F''_{(t)}$	=	"	predation mortality	"
$M_{(t)}$	=	"	natural mortality	"
M'	=	"	residual natural mortality	
$N_{(t)}$	=	"	number of individuals	"
$N_{m(i)}$	=	hake	number of individuals of i age group	
$P_{(t,i)}$	=	number of anchovy of t age group predated by hake of i age grou		