

## MULTISPECIES FISHERIES. A PREDATOR-PREY MODEL FOR THE EUROPEAN HAKE AND BLUE WHITING SPANISH FISHERIES

Pérez-Pérez, Marcos<sup>1</sup>; Garza-Gil, M. Dolores<sup>2</sup>; Varela-Lafuente, Manuel<sup>3</sup>; Surís-Regueiro, Juan C<sup>4</sup>.

<sup>1</sup> Department of Applied Economics, University of Vigo, [marcos.perez@uvigo.es](mailto:marcos.perez@uvigo.es)

<sup>2</sup> Department of Applied Economics, University of Vigo, [dgarza@uvigo.es](mailto:dgarza@uvigo.es)

<sup>3</sup> Department of Applied Economics, University of Vigo, [mmvarela@uvigo.es](mailto:mmvarela@uvigo.es)

<sup>4</sup> Department of Applied Economics, University of Vigo, [jsuris@uvigo.es](mailto:jsuris@uvigo.es)

### Abstract:

The aim of this work is to develop a predator-prey model for two species of commercial importance captured by the European fishing fleet in the European fishing grounds. In this model, the hake (*Merluccius merluccius*) represents the predator, and the blue whiting (*Micromesistius poutassou*) is the prey. Both the predator and prey population dynamics follow the Lotka-Volterra formulation. It is assumed a logistic population dynamics and a linear interaction between predator and prey populations, with two interaction coefficients:  $\alpha$  (effect of a unit change in the prey on the percent growth rate of the predator) and  $\beta$  (attack rate or searching efficiency of the predator). The populations interact randomly in proportion to population density. Logistic predator-prey equations were applied to the hake and blue whiting stocks, including biomass, intrinsic rates of growth, carrying capacity and capture for both species. The goal is to maximize the present value of profit, forming the current value Hamiltonian for the maximization problem. Capture costs depending on stock and prices of hake and blue whiting and discount rate were introduced at this point. Once the theoretical model was made, landings and biomass data from both stocks over the period 1988-2014 were used for an econometric Ordinary Least Squares estimation, to determine the form taken by the predator-prey net growth functions. Optimal biomass, catches and profits were determined by solving the applied model with quadratic net growth functions. The sensitivity analysis results show that the landings profits are larger at low discount rates.

### 1. INTRODUCTION

The multi-species bioeconomic models try to evaluate and predict the population dynamics and economic performance of the mixed fisheries, which show ecological interdependence between two or more target species. In particular, the predator-prey models take into account the trophic relationships between two or more ecologically interdependent species in the same ecosystem. The European Union fishing fleets

usually capture species in mixed fisheries. The possibilities of fishing these species must be determined jointly by using multi-species models, because catches of one species will impact the natural growth of the others. The multi-species approaches in fisheries management are increasingly recommended by scientists because single-species models cannot properly represent the complex feedbacks resulting from predatory interactions. Multi-species models can explicitly consider the interactions resulting from predation to predict the dynamics of commercial populations. This is especially important in the evaluation of management strategies.

This work develops the application of a bioeconomic multi-species predator-prey model with capture to a mixed fishery composed of two commercial species caught by the European fishing fleet operating in the EU fishing grounds. The selection criteria for the species of this model were economic (two species of commercial importance), geographic (species caught in the EU Atlantic waters by the European fishing fleet) and biological (species with a significant trophic interaction). According to these criteria, the selected predatory species was the European hake (*Merluccius merluccius*) and the selected prey was the blue whiting (*Micromesistius poutassou*). The study period is 1988-2014. Biomass and catch data from that period will be used. From Brown *et al.* (2005), costs dependent on the level of biomass are introduced into the net benefits function and the optimum levels for biomass and catches of both species are estimated. In Section 2 hake and blue whiting fisheries are described. After the construction of the theoretical model using the Maximum Principle of the Optimal Control Theory (Section 3), the applied model is resolved in Section 4, the sensitivity analysis is shown in Section 5, and finally the main conclusions are highlighted in Section 6.

## 2. HAKE AND BLUE WHITING FISHERIES

European hake (*Merluccius merluccius*) and blue whiting (*Micromesistius poutassou*) are marine species of commercial value in North-eastern Atlantic grounds. European hake is a demersal benthopelagic species widely distributed throughout the European waters at depths from 30 to 1,000 meters. The hake is caught in mixed fisheries by a multi-rigged fleet. The stock status was critical in the 1990s, but it has recovered after the management plans implemented by the European Union (EC 2004, 2005), and the landings have increased. Blue whiting is a demersal species of the gadus family widely distributed throughout the North Atlantic at depths from 150 to 1,000 meters. Its diet is composed mainly of crustaceans, namely copepods, krill, the larvae of decapods and a decapod known as white glass shrimp (*Pasiphaea sivado*). The primary method used to catch the blue whiting as a target species is the bottom pair trawling, and individual bottom trawling picks it up as a by-catch. This species plays a major role in fishing quota exchanges between European countries to obtain higher-value species. The blue whiting's biomass has been significantly reduced over the past several years, but now the stock status is good.

Table 1. Hake and blue whiting biomass and landings (tons). 1988-2014

	<b>Hake biomass (<math>X_t</math>)</b>	<b>Blue Whiting biomass (<math>Y_t</math>)</b>	<b>Hake landings (<math>h_{t,m}</math>)</b>	<b>Blue Whiting landings (<math>h_{t,L}</math>)</b>
<b>1988</b>	118588	1615000	81476	558000
<b>1989</b>	109002	1550000	80259	627000
<b>1990</b>	96661	1334000	73144	562000
<b>1991</b>	92221	1732000	70956	370000
<b>1992</b>	89329	2546000	70415	475000
<b>1993</b>	76533	2637000	63628	481000
<b>1994</b>	66594	2523000	61124	459000
<b>1995</b>	71535	2.294000	69860	579000
<b>1996</b>	66257	2180000	56925	646000
<b>1997</b>	56283	2471000	50963	672000
<b>1998</b>	53453	3757000	42743	1125000
<b>1999</b>	60443	4611000	46984	1256000
<b>2000</b>	68171	4291000	49928	1412000
<b>2001</b>	66339	4648000	44255	1780000
<b>2002</b>	70492	5184000	46797	1556000
<b>2003</b>	76179	6934000	49906	2321000
<b>2004</b>	77313	6689000	53359	2378000
<b>2005</b>	73287	5850000	54883	2027000
<b>2006</b>	74754	5885000	52283	1966000
<b>2007</b>	83886	4672000	59960	1612000
<b>2008</b>	101518	3489000	64534	1246000
<b>2009</b>	147964	2610000	78058	636000
<b>2010</b>	209575	2538000	88167	540000
<b>2011</b>	244663	2572000	104602	105000
<b>2012</b>	230370	3396000	100250	384000
<b>2013</b>	221233	3918000	89106	626000
<b>2014</b>	222132	3965000	103400	1146000

Source: ICES

Blue whiting is in general the hake's main prey in these grounds according to several studies. In particular, the blue whiting is the hake's primary prey in Portuguese waters according to Cabral and Murta (2002). In the Cantabrian Sea, the blue whiting is also noted as the hake's primary prey by Sánchez (1993) and Velasco and Olaso (1998). However, its importance as prey is moderate in the Celtic Sea according to Mahe et al. (2007).

### 3. THEORETICAL MODEL

The theoretical model is based on Lotka-Volterra's predator-prey model (Volterra 1926; Lotka 1932), and the logic equations used by Brown et al. (2005):

$$\frac{dX}{dt} = r_m X \left[ 1 - \frac{X}{\bar{X}} \right] - h_m + \alpha XY \quad (1)$$

$$\frac{dY}{dt} = r_L Y \left[ 1 - \frac{Y}{\bar{Y}} \right] - h_L - \beta YX \quad (2)$$

where  $X$  denotes the predator's stock,  $Y$  is the prey's stock;  $r_m$  and  $r_L$  denote the intrinsic population growth rates for both species, respectively;  $h_m$  and  $h_L$  are the predator and prey catches, and  $\alpha$  and  $\beta$  denote the interaction coefficients. The net benefits from fishery at moment  $t$  are defined as follows:

$$\pi(X, Y, h_m, h_L) = (P_m - C_m(X))h_m(t) + (P_L - C_L(Y))h_L(t) \quad (3)$$

Where subscripts  $m$  and  $L$  denote predator and prey,  $P$  is the unit price, and  $C$  the catch unit cost. For  $\rho$  as social discount rate, the objective function is as follows:

$$J = \int_0^{\infty} e^{-\rho t} \pi[X(t), Y(t), h_m(t), h_L(t)] dt \quad (4)$$

Under these premises, the central manager must solve the following problem:

$$\max \int_0^{\infty} e^{-\rho t} [(P_m - C_m(X))h_m(t) + (P_L - C_L(Y))h_L(t)] dt \quad (5)$$

$$\begin{aligned} \text{s.t.} \quad & \frac{dX}{dt} = f(X) - h_m \\ & \frac{dY}{dt} = g(Y) - h_L \\ & 0 \leq h_m(t) \leq h_m \max \\ & 0 \leq h_L(t) \leq h_L \max \\ & 0 < X(t) \\ & 0 < Y(t) \end{aligned}$$

Given the Hamiltonian function is lineal in control variables, applying optimum control theory (Clark, 1976; Clark and Munro, 1985; Rozonoer, 1959; Spence and

Starrett, 1975), and adapting it to the multispecies case, we obtain the equilibrium equations for (5):

$$[F'(X_u) + \alpha Y_u] - \frac{[P_L - C_L(Y_u)]\beta Y_u + C_m'(X_u)[F(X_u) + \alpha X_u Y_u]}{(P_m - C_m(X_u))} = \rho \quad (6)$$

$$[G'(Y_u) - \beta X_u] + \frac{[P_m - C_m(X_u)]\alpha X_u - C_L'(Y_u)[G(Y_u) - \beta Y_u X_u]}{(P_L - C_L(Y_u))} = \rho \quad (7)$$

These two equations and constitute a system whose solution would give us the steady state optimal biomass levels for predator and prey.

#### 4. APPLIED MODEL

The hake and blue whiting biomass and catch data for the 1988-2014 period, published by ICES (2015a, 2015b), were used for a econometric regression by the ordinary least squares method, in order to determine the functional form of the dynamics of each fish stock. In addition to the standard quadratic form, the following exponential and potential expressions, respectively, were considered for both species:

$$X_{t+1} = \alpha X_t - \beta X_t^2 + \gamma X_t Y_t - h_m \quad (8)$$

$$Y_{t+1} = \varphi Y_t - \mu Y_t^2 + \omega X_t Y_t - h_L \quad (9)$$

$$X_{t+1} = \alpha e^{\beta X_t} + \gamma X_t Y_t - h_m \quad (10)$$

$$Y_{t+1} = \varphi e^{\mu Y_t} + \omega X_t Y_t - h_L \quad (11)$$

$$X_{t+1} = \alpha e^{\beta X_t + \gamma X_t Y_t} - h_m \quad (12)$$

$$Y_{t+1} = \varphi e^{\mu Y_t + \omega X_t Y_t} - h_L \quad (13)$$

The results of the econometric estimations for hake and blue whiting stock dynamics are shown in Tables 2 to 7.

Table 2. Results of the econometric estimations for hake quadratic stock dynamic.

Model 1: OLS, observations 1988-2014 (T = 27)					
Dependent variable: endomerlu					
	<i>Coefficient</i>	<i>St. deviation</i>	<i>t-statistic</i>	<i>p-value</i>	
xmer	1.98802	0.114474	17.3666	<0.0001	***
sq_xmer	-2.94291e-06	4.05357e-07	-5.4962	<0.0001	***

Model 1: OLS, observations 1988-2014 (T = 27)				
Dependent variable: endomerlu				
xy	1.83165e-09	2.39363e-08	0.0161	0.9873
Dep.vble. mean	180815.7	S.D. of dep. vble.		84253.74
Sum of squared res.	7.23e+09	S.D. of the regression		17357.50
R-square	0.993225	Corrected R-square		0.992661
F(3, 24)	1172.854	p-value (F)		3.76e-26
Log-likelihood	-300.2893	Akaike criterion		606.5787
Schwarz criterion	610.4662	Hannan-Quinn crit.		607.7346
rho	0.488674	Durbin-Watson		0.990641

Table 3. Results of the econometric estimations for blue whiting quadratic stock dynamic.

Model 2: OLS, observations 1988-2014 (T = 27)					
Dependent variable: endlirio					
	<i>Coefficient</i>	<i>St. deviation</i>	<i>t-statistic</i>	<i>p-value</i>	
ylirio	1.49868	0.151384	9.8999	<0.0001	***
sq_ylirio	-8.21632e-08	2.2982e-08	-1.0099	0.3226	
xy	-3.12827e-06	6.59481e-07	-1.3164	0.2005	
Dep.vble. mean	4658741	S.D. of dep. vble.		2097691	
Sum of squared res.	1.02e+13	S.D. of the regression		651719.3	
R-square	0.985446	Corrected R-square		0.984233	
F(3, 24)	541.6818	p-value (F)		3.61e-22	
Log-likelihood	-398.1802	Akaike criterion		802.3605	
Schwarz criterion	806.2480	Hannan-Quinn crit.		803.5164	
rho	0.439072	Durbin-Watson		1.120075	

Table 4. Results of the econometric estimations for hake exponential stock dynamic.

Model 3: OLS, observations 1988-2014 (T = 27)					
Dependent variable: l_endomerlu					
	<i>Coefficient</i>	<i>St. deviation</i>	<i>t-statistic</i>	<i>p-value</i>	
xmer	6.2841e-05	2.66062e-05	2.3619	0.0263	**
xy	7.13e-012	7.7206e-012	0.9235	0.3646	
Dep.vble. mean	11.97023	S.D. of dep. vble.		0.384159	
Sum of squared res.	792.7804	S.D. of the regression		5.631271	
R-square	0.795283	Corrected R-square		0.787094	
F(3, 24)	48.55990	p-value (F)		2.45e-09	
Log-likelihood	-83.93742	Akaike criterion		171.8748	
Schwarz criterion	174.4665	Hannan-Quinn crit.		172.6455	
rho	0.967083	Durbin-Watson		0.062242	

Table 5. Results of the econometric estimations for blue whiting exponential stock dynamic.

Model 4: OLS, observations 1988-2014 (T = 27)					
Dependent variable: l_endolirio					
	<i>Coefficient</i>	<i>St. deviation</i>	<i>t-statistic</i>	<i>p-value</i>	
ylirio	2.85098e-06	5.85171e-07	4.8721	<0.0001	***
xy	8.2693e-012	5.32886e-012	1.5518	0.1333	
Dep.vble. mean	15.25821	S.D. of dep. vble.		0.447234	
Sum of squared res.	815.3606	S.D. of the regression		5.710904	
R-square	0.870396	Corrected R-square		0.865211	
F(2, 24)	83.94738	p-value (F)		8.09e-12	
Log-likelihood	-84.31655	Akaike criterion		172.6331	
Schwarz criterion	175.2248	Hannan-Quinn crit.		173.4037	
rho	0.876967	Durbin-Watson		0.169199	

Table 6. Results of the econometric estimations for hake potential stock dynamic.

Model 5: OLS, observations 1988-2014 (T = 27)					
Dependent variable: l_endomerlu					
	<i>Coefficient</i>	<i>St. deviation</i>	<i>t-statistic</i>	<i>p-value</i>	
xyL_xmer	2.01014e-012	2.43724e-013	8.2476	<0.0001	***
Dep.vble. mean		11.97023	S.D. of dep. vble.		0.384159
Sum of squared res.		1070.873	S.D. of the regression		6.417743
R-square		0.723472	Corrected R-square		0.723472
F(2, 24)		68.02305	p-value (F)		9.94e-09
Log-likelihood		-87.99664	Akaike criterion		177.9933
Schwarz criterion		179.2891	Hannan-Quinn crit.		178.3786
rho		0.985883	Durbin-Watson		0.068781

Table 7. Results of the econometric estimations for blue whiting potential stock dynamic.

Model 6: OLS, observations 1988-2014 (T = 27)					
Dependent variable: l_endolirio					
	<i>Coefficient</i>	<i>St. deviation</i>	<i>t-statistic</i>	<i>p-value</i>	
xyL_ylirio	2.03629e-012	2.34986e-013	8.6656	<0.0001	***
Dep.vble. mean		15.25821	S.D. of dep. vble.		0.447234
Sum of squared res.		1618.020	S.D. of the regression		7.888698
R-square		0.742810	Corrected R-square		0.742810
F(2, 24)		75.09263	p-value (F)		3.83e-09
Log-likelihood		-93.56849	Akaike criterion		189.1370
Schwarz criterion		190.4328	Hannan-Quinn crit.		189.5223
rho		0.978454	Durbin-Watson		0.075548

Based on the results shown in tables 2-7 and taking into consideration also the value of  $R^2$  adjusted, the quadratic expression is most appropriate for the natural dynamic of predator and prey in these grounds (value for  $R^2$  is higher than 0.98 for both species). On other hand, only that expression shows a positive predator-prey interaction coefficient for predator while at the same time negative for prey, which would be typical of a trophic relationship. As a consequence, the quadratic forms as follows for predator and prey, respectively:

$$\dot{X} = \alpha X - \beta X^2 + \gamma XY - h_m = 1.98802 X - 0.0000029429 X^2 + 0.00000000183165 XY - h_m \quad (14)$$

$$\dot{Y} = \varphi Y - \mu Y^2 - \omega XY - h_L = 1.49868 Y - 0.0000000821632 Y^2 - 0.00000312827 XY - h_L \quad (15)$$

Starting from the theoretical model, and once we know that the stock dynamics are quadratic, we can set the applied model including the growth functions and the cost functions (16) and (17) in the expressions (6) and (7). We obtain the expressions (18) and (19):

$$C_m(X_t) = a - bX_t; \quad C_m'(X_t) = -b \quad (16)$$

$$C_L(Y_t) = c - dY_t; \quad C_L'(Y_t) = -d \quad (17)$$

$$[(\alpha - 2\beta X_u) + \gamma Y_u] - \frac{[P_L - (c - dY_u)]\omega Y_u + (-b)[(\alpha X_u - \beta X_u^2) + \gamma X_u Y_u]}{P_m - (a - bX_u)} = \rho \quad (18)$$

$$[(\varphi - 2\mu Y_u) - \omega X_u] + \frac{[P_m - (a - bX_u)]\gamma X_u - (-d)[(\varphi Y_u - \mu Y_u^2) - \omega Y_u X_u]}{P_L - (c - dY_u)} = \rho \quad (19)$$

And the hake and blue whiting biomass levels corresponding to the maximum sustainable yield (MSY) are given as follows:

$$X_{mrs} = \frac{\frac{\alpha}{\gamma} - \frac{\varphi}{2\mu}}{\frac{-\omega}{2\mu} + \frac{2\beta}{\gamma}} \quad (20)$$

$$Y_{mrs} = \frac{\alpha - 2\beta X_{mrs}}{\gamma} \quad (21)$$

The equations (18) and (19) system was solved by iterations in order to determine the optimum values of the hake and blue whiting biomasses, substituting in the equations the 2001-2014 average prices in constant 2014 monetary units ( $P_m=4619.23$  €/tonne;  $P_L=399.13$  €/tonne), the cost functions and the discount rate  $\rho = 0.05$ . The MSY biomasses were calculated from the expressions (20) and (21). The shadow prices were calculated from the commutation functions, introducing the discount rate  $\rho = 0.05$ , the 2001-2014 average prices in constant 2014 monetary units and the capture cost functions. The benefits produced by the capture of both species were calculated from the expression (3), introducing the 2001-2014 average prices, the cost functions and the optimal capture values. The results are shown in Table 8.

Table 8. Optimum levels of biomass, catches, MSY biomass, shadow prices and benefits

	Hake	Blue Whiting
<b>Optimal biomass</b>	281,000 t.	4,871,500 t.
<b>Optimal catch</b>	47,800 t.	1,068,700 t.
<b>MSY biomass</b>	336,922 t.	2,706,178 t.
<b>Shadow prices</b>	3044.54 €/t.	171.40 €/t.
<b>Benefits</b>	1052 mill. €	193 mill. €
<b>Total benefits</b>	1245 mill. €	



## 5. SENSITIVITY ANALYSIS

The sensitivity of the model was analyzed performing different simulations of variation of the discount rate and the prices of both species, recalculating the benefits generated by the capture of both species. The results of the sensitivity analysis are shown in Table 9.

Table 9. Optimum benefits under different discount rates and prices.

Simulations		$\pi_m$	$\pi_L$	$\pi_{total}$	var. $\pi_m$	var. $\pi_L$	var. $\pi_{total}$
rho	-0.05	1,098.15	146.92	1,245.07	104.4%	76.3%	100.0%
	0	1,079.19	166.47	1,245.66	102.6%	86.4%	100.1%
	<b>0.05</b>	<b>1,052.26</b>	<b>192.57</b>	<b>1,244.83</b>	<b>100.0%</b>	<b>100.0%</b>	<b>100.0%</b>
	0.1	1,034.46	207.96	1,242.42	98.3%	108.0%	99.8%
	0.15	1,016.14	222.36	1,238.51	96.6%	115.5%	99.5%
<b>P<sub>m</sub></b>	<b>P<sub>L</sub></b>						
4400	399.13	1,000.78	171.26	1,172.04	95.1%	88.9%	94.2%
4500	399.13	1,031.18	174.13	1,205.31	98.0%	90.4%	96.8%
<b>4619.23</b>	<b>399.13</b>	<b>1,052.26</b>	<b>192.57</b>	<b>1,244.83</b>	<b>100.0%</b>	<b>100.0%</b>	<b>100.0%</b>
4700	399.13	1,070.04	201.55	1,271.60	101.7%	104.7%	102.2%
4800	399.13	1,099.85	204.79	1,304.65	104.5%	106.4%	104.8%
<b>P<sub>L</sub></b>	<b>P<sub>m</sub></b>						
300	4619.23	1,014.79	126.48	1,141.27	96.4%	65.7%	91.7%
350	4619.23	1,020.35	173.57	1,193.92	97.0%	90.1%	95.9%
<b>399.13</b>	<b>4619.23</b>	<b>1,052.26</b>	<b>192.57</b>	<b>1,244.83</b>	<b>100.0%</b>	<b>100.0%</b>	<b>100.0%</b>
450	4619.23	1,064.03	223.09	1,287.12	101.1%	115.9%	103.4%
500	4619.23	1,078.32	241.87	1,320.19	102.5%	125.5%	106.1%
<b>P<sub>m</sub></b>	<b>P<sub>L</sub></b>						
4700	450	1,026.52	302.37	1,328.89	97.6%	157.0%	106.8%
4500	350	1,090.15	78.35	1,168.51	103.6%	40.7%	93.9%
<b>4619.23</b>	<b>399.13</b>	<b>1,052.26</b>	<b>192.57</b>	<b>1,244.83</b>	<b>100.0%</b>	<b>100.0%</b>	<b>100.0%</b>
4700	350	1,070.90	152.30	1,223.21	101.8%	79.1%	98.3%
4500	450	1,036.97	208.99	1,245.96	98.5%	108.5%	100.1%

As we can see in the table, as the rate of discount diminishes, the total net benefits increase, being greater the sensitivity for the hake's profits. Regarding prices, the increase in the price each species always generates an increase in the net benefits overall, with a higher sensitivity shown by blue whiting's benefits. The higher net benefits are obtained by a simultaneous increment in the price of both species.

## 6. CONCLUSIONS

This research work has developed the application of a multispecies bio-economic model of the predator-prey type to the mixed fishery of hake and blue whiting of the EU Atlantic waters. These species display a significant ecological predatory interdependence, along with a commercial importance for the European fishing fleet which makes them suitable for applying this type of model. Optimal biomasses, optimal catches, MSY biomasses, shadow prices and benefits were determined for both species of this mixed fishery.

The sensitivity analysis results reveals that the selection of discount rates close to zero leads to more efficient managing results for this fishery than the use of high discount rates. It is also remarkable the high sensitivity of the optimal solutions to changes in the price of hake. The sensitivity analysis of the benefits results shows that the maximum benefit of the hake fishery and the maximum benefit of the mixed fishery are reached under the minimum discount rate.

According to the results of this study, the management of the mixed fishery of hake and blue whiting on the EU Atlantic waters should base the objectives and technical measures in the use of discount rates close to zero, since both the larger effective capture and the maximum economic benefit are reached with a low pressure over the resources.

## References

- Anderson LG., 1975. Analysis of open-access commercial exploitation and maximum economic yield in biological and technologically interdependent fisheries. *Journal of the Fisheries Research Board of Canada* 32: 1825–1842.
- Begon M, Harper JL, Townsend CR., 1990. *Ecology. Individuals. Populations and Communities*. Boston: Blackwell Scientific Publications.
- Botsford LW, Castilla JC, Peterson CH., 1997. The management of fisheries and marine ecosystems. *Science* 277: 509–515.
- Brown G, Berger B, Ikiara M., 2005. A Predator-Prey Model with an Application to Lake Victoria Fisheries. *Marine Resource Economics* 20: 221–247.
- Cabral HN, Murta AG., 2002. The diet of blue whiting, hake, horse mackerel and mackerel off Portugal. *Journal of Applied Ichthyology* 18(1): 14-23.
- Clark C. W., 1976, *Mathematical Bioeconomics - the Optimal Management of Renewable Resources*, J. Wiley and Sons, Sussex.
- Clark CW., 1985. *Bioeconomic Modelling of Fisheries Management*. New York: J. Wiley & Sons.

- Clark C.W., Munro G. R., 1975. The economics of fishing and modern capital theory: a simplified approach. *Journal of Environmental Economics and Management* 5(2): 96–106.
- Eide A., Skjold F., Olsen F., Flaaten O., 2003. Harvest functions: the Norwegian bottom trawl cod fisheries. *Marine Resource Economics* 18(1): 81-93.
- Ekerhovd N-A., Steinshamn S.I., 2016. Economic benefits of multi-species management: The pelagic fisheries in the Northeast Atlantic. *Marine Resource Economics* 31(2): 193-210.
- European Commission, 2004. Council Regulation (EC) No. 811/2004 of 21 April 2004, establishing measures for the recovery of the Northern hake stock. *Official Journal of the European Union*, L 150, 30 April 2004, pp. 1-11.
- European Commission, 2005. Council Regulation (EC) No 2166/2005 of 20 December 2005, establishing measures for the recovery of the Southern hake and Norway lobster stocks in the Cantabrian Sea and Western Iberian peninsula and amending Regulation (EC) No 850/98 for the conservation of fishery resources through technical measures for the protection of juveniles of marine organisms. *Official Journal of the European Union* L 345, 28 December 2005, pp. 5-10.
- FAO, 1978. Fishery commodity situation and outlook. FAO: Committee on Fisheries, 12th Session, COFI/78/inf. 5: 1–15.
- Flaaten O., 1991. Bioeconomics of sustainable harvest of competing species. *Journal of Environmental Economics and Management* 20: 163–180.
- Fletcher JJ, Howitt RE, Johnston WE., 1988. Management of multipurpose heterogeneous fishing fleets under uncertainty. *Marine Resource Economics* 4: 249–270.
- Garza-Gil M-D., Varela-Lafuente M.M., 2007. Bioeconomic Management and Fishing Selectivity: An Application to the European Hake Fishery. *Journal of Agricultural and Biological Sciences* 2: 69–74.
- Giller PS., 1984. *Community Structure and the Niche*. London: Chapman & Hall.
- Gonzalez R, Olaso I, Pereda P., 1985. Contribución al conocimiento de la alimentación de la merluza (*Merluccius merluccius* L.) en la plataforma continental de Galicia y del Cantábrico. *Boletín del Instituto Español de Oceanografía* 2: 49–60.
- Guichet R., 1995. The diet of European hake (*Merluccius merluccius*) in the northern part of the Bay of Biscay. *ICES Journal of Marine Science* 52: 21-31.
- Guichet, R., Meriel-Bussy, M., 1970. Association du merlu *Merluccius merluccius* (L.) et du merlan bleu *Micromesistius poutassou* (Risso) dans le Golfe de Gascogne. *Revue des Travaux de l'Institut des Pêches Maritimes* 34(1): 69-72.

- Huppert D., 1979. Implications of multipurpose fleets and mixed stocks for control policies. *Journal of the Fisheries Research Board of Canada* 36 (7): 845–854.
- ICES. 2015a. Report of ICES Advice on fishing opportunities, catch, and effort. ICES Advisory Committee, ICES Advice, 2015. Book 7. [www.ices.dk](http://www.ices.dk).
- ICES. 2015b. Report of ICES Advice on fishing opportunities, catch, and effort. ICES Advisory Committee, ICES Advice, 2015. Book 9. [www.ices.dk](http://www.ices.dk).
- Keddy PA., 1989. *Competition*. London: Chapman & Hall.
- Larkin PA., 1982. Aquaculture in North America: an assessment of future prospects. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 151–154.
- Link JS. 2009. *Ecosystem-Based Fisheries Management: Confronting Tradeoffs*. New York: Cambridge University Press.
- Lotka, A.J., 1932. The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* 22: 461–469.
- Mahe K, Amara R, Bryckaert T, Kacher M, Brylinski JM., 2007. Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES Journal of Marine Science* 64: 1210–1219.
- Majkowski J., 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. In: Pauly D. and Murphy GI (Ed), *Theory and Management of Tropical Fisheries*. ICLARM Conference Proceedings, 9: 149–165.
- May RM., 1984. *Exploitation of Marine Communities*. Report of the Dahlem Workshop on Exploitation of Marine Communities. Dahlem Konferenzen 1984. Berlin: Springer-Verlag.
- May RM, Beddington JR, Clark CW, Holt SJ, Laws RM., 1979. Management of multispecies fisheries. *Science* 205: 267–277.
- Mitchell CL., 1982. Bioeconomics of multispecies exploitation in fisheries: management implications. *Can. Spec. Publ. Fish. Aquat. Sci.* 59: 157–162.
- Neuenfeldt S, Koster FW., 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. *ICES Journal of Marine Science* 57: 300–309.
- Rothschild BJ., 1991. Multispecies interactions on Georges Bank. *ICES Marine Science Symposia* 193: 86–92.
- Rozonoer, L. I., 1959. L.S. Pontryagin's Maximum Principle in Optimal Control Theory. *Automat, i Telemekh*, 20, 1320–34, 1441–48, 1561–78.

- Sánchez F., 1993. Las comunidades de peces de la plataforma del Cantábrico. Publicación Especial del Instituto Español de Oceanografía 13.
- Seijo JC, Defeo O, Salas S., 1997. Bioeconomía pesquera. Teoría, modelación y manejo. FAO Documento Técnico de Pesca. No. 368. Roma: FAO.
- Spence M., Starrett, D. 1975. Most Rapid Approach Paths in Accumulation Problems. International Economic Review 16(2): 388-403.
- Ströbele WJ, Wacker H., 1991. The concept of sustainable yield in multi-species fisheries. Ecological Modelling 53: 61–74.
- Sugihara G, García S, Gulland JA, Lawton JH, Maske H, Paine RT, Platt T, Rachor E, Rothschild BJ, Ursin EA, Zeitzschel BFK., 1984. Ecosystem dynamics. In: May RM (Ed), Exploitation of marine communities, report of the Dahlem Workshop on Exploitation of Marine Communities.
- Tsou TS, Collie JS., 2001. Predation-mediated recruitment in the Georges Bank fish community. ICES Journal of Marine Science 58: 994–1001.
- Velasco F, Olaso I., 1988. European Hake *Merluccius merluccius* (L., 1758) feeding in the Cantabrian Sea: seasonal, bathymetric and length variations. Fisheries Research 38: 33-44.
- Velasco F, Olaso I, Sánchez F., 2003. Annual variations in the prey of demersal fish in the Cantabrian Sea and their implications for food web dynamics. ICES Marine Science Symposia 219: 408–410.
- Volterra V., 1926. Fluctuations in the abundance of species, considered mathematically. Nature 118: 558–560.
- Wespestad V, Fritz L, Ingraham W, Megrey B., 2000. On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye Pollock (*Theragra chalcogramma*). ICES Journal of Marine Science 57: 268–274.