

Mediterranean Marine Science

Vol 15, No 3 (2014)

Vol 15, No 3 (2014)



A Bayesian population model to estimate changes in the stock size in data poor cases using Mediterranean bogue (Boops boops) and picarel (Spicara smaris) as an example

T. JUNTUNEN, A. C. TSIKLIRAS, S. MANTYNIEMI, K. I. STERGIOU

doi: [10.12681/mms.567](https://doi.org/10.12681/mms.567)

To cite this article:

JUNTUNEN, T., TSIKLIRAS, A. C., MANTYNIEMI, S., & STERGIOU, K. I. (2014). A Bayesian population model to estimate changes in the stock size in data poor cases using Mediterranean bogue (Boops boops) and picarel (Spicara smaris) as an example. *Mediterranean Marine Science*, 15(3), 587–601. <https://doi.org/10.12681/mms.567>

A Bayesian population model to estimate changes in the stock size in data-poor cases using Mediterranean bogue (*Boops boops*) and picarel (*Spicara smaris*) as an example

T. JUNTUNEN¹, A. C. TSIKLIRAS², SAMU MÄNTYNIEMI¹ and K.I. STERGIU²

¹Fisheries and Environmental Management Group (FEM), Viikinkaari 2, P.O. Box 65, FI-00014 University of Helsinki, Finland

²Department of Zoology, School of Biology, Aristotle University of Thessaloniki, UP Box 134, GR 54 124, Thessaloniki, Greece

Corresponding author: teppo.juntunen@helsinki.fi

Handling Editor: Konstantinos Tsagarakis

Received: 31 July 2013; Accepted: 8 May 2014; Published on line: 18 September 2014

Abstract

The paper presents an effort to build a biologically realistic, age-structured Bayesian model for the stock assessment of data-poor fisheries where only aggregated catch data is available. The model is built using prior information from other areas and ecologically or taxonomically similar species. The modelling approach is tested with data poor fisheries on the Cyclades islands in the Greek archipelago. The two most important species in the area are selected: bogue (*Boops boops*) and picarel (*Spicara smaris*). Both are hermaphroditic. The only data available is the total catch from 1950 to 2010. Information was gathered about natural mortality, recruitment, growth, body size, fecundity, and sex ratio. There were significant problems in finding reliable prior information and a uniform prior was used for fishing mortality. The models at their present stage are not used to give management advice. The biological characteristics of the species in that area should be further studied. However, the posteriors of biological parameters reflect the best available knowledge on these species and they could be used in future studies or in simpler biomass dynamics models as priors.

Keywords: Bayesian model, *Boops boops*, Cyclades, data poor, *Spicara smaris*, stock assessment.

Introduction

Many population models rely on large data sets collected over a long time and on species for which life history strategies are well known. However, many important stocks all around the world have not been studied thoroughly, their biological parameters are not known and there are no long or reliable data sets available. There is an apparent need to develop methodologies for modelling and managing data-poor species.

In data-poor situations, a normal approach has been to use a biomass dynamics model based on the principle of surplus production (Schaefer, 1957; Pella & Tomlinson, 1969). Depending on the implementation, minimally only aggregated catch, carrying capacity and intrinsic growth rate are needed for the analysis. The models are simple but still frequently used to guide management. However, simplicity comes with a cost and these models are known to produce incorrect and unreliable results (e.g. Tahvonen, 2008; Carruthers *et al.*, 2011). There are still other sources of information that can be used for stock assessment. Biological information, for example, growth, maturity and fecundity are known for most of the species and if not available, information from other species with similar life history can be used. Growth

and body size are strongly linked to stock productivity. Therefore, it is important that stock assessment includes these variables. Another typical problem is natural mortality, which is in many stock assessments is treated as constant (Cotter *et al.*, 2004). By linking it to length, we should obtain more realistic estimates (Gislason *et al.*, 2008). However, the most important variable linked to stock size is recruitment and there are methods for using existing knowledge to define stock-recruit parameters (Myers *et al.*, 1999; Myers, 2001). In conclusion, it seems that information and methods are available that can be used to incorporate biological knowledge into the data-poor stock assessment models.

Bayesian inference is particularly suitable in situations where we want to address the uncertainties and lack of data in stock assessment (Punt & Hilborn, 1997). The advantages of this approach are recognised and there are already several applications that improve those simple biomass dynamics models by accounting for uncertainty (e.g. Millar & Meyer, 2000; McAllister *et al.*, 2001; Yan *et al.*, 2011). However, there is a profound need for biologically realistic models in fisheries science (Kuparinen *et al.*, 2012) and here we aim to build a model that uses all available biological data in a case study where only aggregated catch statistics are known.

The Cyclades islands, located in the southern Aegean Sea (Greece), constitute an excellent case study to develop and test methods for truly data-poor fisheries. Fishing is an important activity on the islands and the demand for fish is high. The catches have declined significantly and more efficient management is needed. The total landings of all species from the Cyclades declined from 31 000 tonnes in 1994 to less than 4 000 tonnes in 2002. The total amount of boats registered in the Cyclades is 246 of which 225 are small coastal boats of lengths below 15 m (Kapadagakis *et al.*, 2001). The two most dominant species in the catch are selected for modelling, i.e. bogue (*Boops boops*) and picarel (*Spicara smaris*). The catch of these species is quite equally distributed between large commercial vessels and small-scale fishermen (Stergiou *et al.*, 2004). Not much is known about even their basic population parameters, such as growth and maturity in the area. To complicate matters, both species are hermaphroditic, i.e. they change sex at some point in their life.

In this study, the idea is to build a biologically realistic age-structured Bayesian population model based mainly on prior information gathered from several sources including literature, expert knowledge and data about other ecologically and taxonomically similar species. The approach is tested in the estimation of stock sizes and key population parameters for bogue and picarel in the Cyclades islands of the Greek archipelago.

Materials and Methods

Data

The only available data from the Cyclades area is total catches for both species between the years 1950-2010. The catch data is collected by the Hellenic statistical Authority (former National Statistical Service of Greece, NSSG). Statistics are collected from 18 fishing sub-areas. One of these is the Cyclades with an area of 42 083 km². Only the total quantity of the catches is available (in metric tons). The age or length composition of the catch is unknown. And there is no information about the maturity stage or weight of the fish in the catch. Scarce data means that a lot of prior information needs to be gathered from other sources.

It is known that the official NSSG data suffers from various biases and especially from the underreporting of the catches. That data have been reconstructed so as to have the same spatial resolution (fishing sub-areas) and species composition over the entire time period (1928-2007). Furthermore, the catches of small-scale coastal boats (i.e. those with engine horsepower lower than 19 HP), which are being reported by a different branch of the Statistical Service, were collected and allocated to species and fishing sub-area (in this case the Cyclades) based on survey data of the percentage contribution of each species to the total catch of each fishing sub-area (see Tsikliras *et al.*, 2007). Any missing information was inferred using bootstrap-

ping. From reconstructed data, we used catches from 1950 to 2007 (Moutopoulos & Stergiou, 2012), adding the years 2008-2010 (unpublished data), which are reconstructed in the same way. Altogether, we have reconstructed catch data for over 61 years. These catches include only commercial landings, so discards, illegal and unreported as well as recreational fisheries landings are not included.

Model

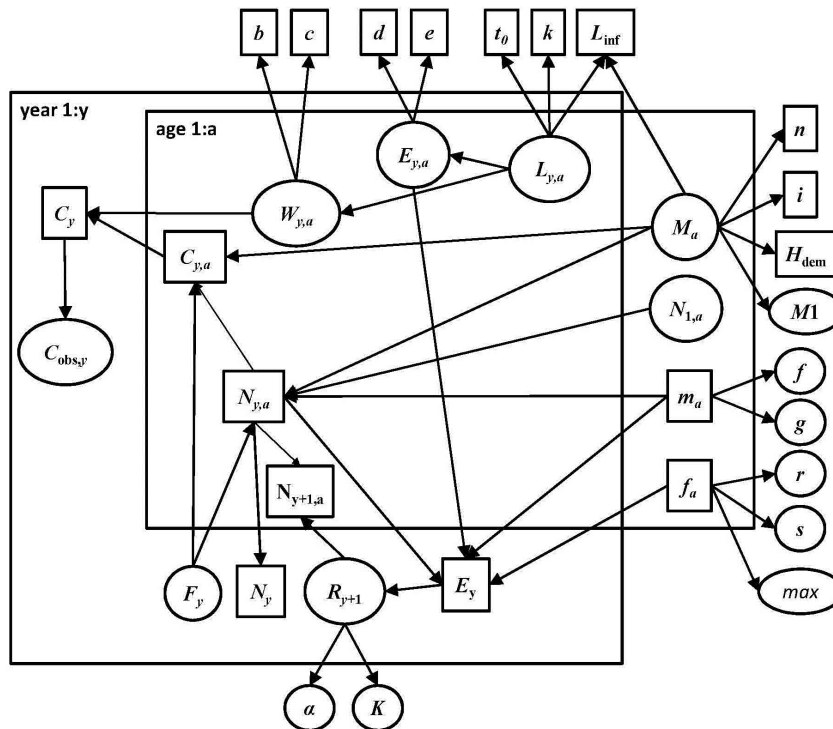
An age-structured Bayesian population model was constructed for both species (Fig. 1). The basic structures of the models are the same and only model parameters and priors were set according to the species. In the models, key population parameters and processes were modelled as stochastic variables. To simplify the model, the catch was assumed to be taken by a single fleet throughout the year. Spawning takes place at the start of the year after which fishing and natural mortalities occur at a constant rate throughout the year. Age of recruitment was set at age 1.

The model relies heavily on prior knowledge and appropriate distributions were used to depict our best knowledge about possible parameter values. The idea was to gather all our current knowledge with attained uncertainty to get estimates for stock sizes. Despite the limited amount of data from the particular area and stocks, the basic biology and population parameters define some boundaries and rules within which population dynamics must work; this information is formalized in our priors. If there was no information available for these species, then related species and species with similar life strategies were used as a source of information for setting the priors.

Markov chain Monte Carlo (MCMC) sampling was used in the estimation of posterior distributions of model parameters. The model was implemented using JAGS version 3.2.0 (Just Another Gibbs Sampler) (Plummer, 2003). We ran models for both species for 200 000 iterations in two chains using thinning of 3 and dropped first 140 000 iterations as burn-in, thus leaving 20 000 samples per chain in the analysis. The initial values of chains were drawn randomly from priors. The convergence was assessed by visual inspection of the chains.

Stock size and catch

The number of individuals N for next year $y+1$ in each age class $a+1$ is calculated according to the equation $N_{y+1,a+1} = N_{y,a} e^{-(F_y+M_a)}$, where $N_{y,a}$ is the number of fish in year y at age a . F_y is the annual fishing mortality and M_a is natural mortality at age a (all mortality units are 1/year). The variable of interest, stock size in a year N_y , is acquired by summing over age groups. The number of years y in the model is 61 according to the available catch data. The number of age classes a are 8 and 7 for bogue and picarel respectively, which are thought to be the maximum age of these species in the Cyclades area. We do not use a plus-group in the model.



- | | |
|---|---|
| <p>$C_{y,a}$ = yearly catch in number of fish in age group
 C_y = yearly catch in tonnes
 $C_{obs,y}$ = yearly observed catch
 $E_{y,a}$ = yearly mean number of eggs spawned per female in age groups
 d, e = fecundity function parameters
 E_y = total number of eggs spawned in a year
 f_a = ratio of females in age groups
 r, s, max = female ratio function parameters
 F_y = yearly fishing mortality
 $L_{y,a}$ = yearly mean length of fish in age groups
 t_0, k, L_{inf} = growth function parameters</p> | <p>m_a = maturity ratio in age
 f, g = maturity function parameters
 M_a = natural mortality in age
 $n, i, h_{dem}, M1$ = natural mortality function parameters
 $N_{y,a}$ = yearly stock size in number of fish in age group
 $N_{y+1,a}$ = stock size for next year for all ages
 N_y = total number of fish in a year
 $N_{1,a}$ = number of fish year in age groups in the first year
 R_{y+1} = total number of recruits for next year
 α, K = stock-recruit function parameters
 $W_{y,a}$ = yearly mean weight of fish in age group
 b, c = weight function parameters</p> |
|---|---|

Fig. 1: Directed Acyclic Graph (DAG) representing the structure of the population dynamics model. Circles represent stochastic variables and squares deterministic variables or deterministic calculations of variables (stochastic or deterministic). Arrows indicate a causal relationship between variables. Variables inside age-boxes are looped over every age group, variables inside year-boxes are looped over every year and finally variables inside both boxes are calculated annually for every age group. Variables outside boxes stay the same over years and ages. The figure does not include observation models for maturity and proportion of females.

A prior is needed for the number of fish in the first year $N_{1,a}$. For this purpose, we construct a log-normal prior, which gives the number of individuals in millions for each age group in the first year. For prior mean, we set 50 million individuals and for uncertainty, the width of the distribution, we use a coefficient of variation (CV). In this case, we want the prior to have a thick tail and use $CV = 1$. This prior is ad hoc but it is only essential to have some uninformative prior, which is updated to a correct level by data and other priors.

Catch in number of fish in year y in age class a is defined as $C_{y,a} = \frac{N_{y,a} (1 - e^{-(F_y + M_a)}) F_y}{F_y + M_a}$. Yearly catch C_y (in tonnes) is obtained by summing up the mean weights of fish with the number of catch in every age group $C_y = \sum_{\alpha} W_{y,a} C_{y,a}$. Data about the annual catch comes in the form of reconstructed total catch $C_{obs,y}$ (in tonnes). These catch figures are treated as uncertain and we use a log-normally distributed observation model $C1_{obs,y} \sim \text{LogN}(\mu = C_y, CV = 0.1)$ (see Table 1, which lists all priors).

Mortalities M and F

We found no information on natural mortality of these selected species in the Cyclades. To estimate mean natural mortality we use a length-based model (Gislason *et al.*, 2008) and information from other stocks. The expected mean mortality μM_a of age class in age a is calculated from $\mu M_a = M1 + h_{dem} L_{inf}^i L_a^n$, where $M1, h_{dem}, i$ and n are model parameters (mean values for demersal species: see Gislason *et al.*, 2008), L_a length at age and L_{inf} is asymptotic length (Table 2). To get L_a we take mean of predicted lengths (see 2.2.4) in every age over all years.

$L_a = \frac{1}{y} \sum_y L_{y,a}$ $M1$ is the parameter describing the non-length dependent natural mortality of species. Gislason *et al.* (2008) expect it to be constant and set it to 0.1. For bogue, we use that same value. This produces priors, which are close to the natural mortalities estimated in Cyprus, where combined natural mortality was estimated to be 0.25 (Hadjistephanou, 1992). However, for picarel,

Table 1. Collection of stochastic prior distributions used in the model and their parameters (μ and CV) for both species.

Variable	Explanation	Distribution*	Parameters	
			Bogue	Picarel
$N_{1,a}$	Initial stock size	LogN(M,S)	$\mu=50, CV=1.0$	
$C_{obs,y}$	Observed catch	LogN(M,S)	$\mu=C_y, CV=0.1$	
M_a	Natural mortality	Beta(α,β)	$\mu=\mu M_a, CV=0.1$	
F_y	Fishing mortality	Unif(a,b)	a=0, b=1.2	
K	Carrying capacity	LogN(M,S)	$\mu=400, CV=1.9$	
$L_{y,a}$	Mean length of fish	LogN(M,S)	$\mu=\mu L_{y,a}, CV=0.005$	
$W_{y,a}$	Mean weight of fish	LogN(M,S)	$\mu=\mu W_{y,a}, CV=0.005$	
$E_{y,a}$	Mean number of eggs	LogN(M,S)	$\mu=\mu E_{y,a}, CV=0.06$	
$M1$	Natural mortality parameter	Unif(a,b)	fixed 0.1	a=0.1, b=0.6
α	Egg survivability	Beta(α,β)	$\mu=0.000004, CV=0.24$	$\mu=0.0002, CV=0.25$
R_y	Number of recruits	LogN(M,S)	$\mu=\mu R_y, CV=0.7$	$\mu=\mu R_y, CV=1.0$
max	Maximum ratio of females	Beta(α,β)	$\mu=0.8, CV=0.125$	fixed 1.0
f	Maturity function parameters		These priors are posteriors from sub-models and calculated during the model run.	
g				
r	Female ratio parameters			
s				

$$*M = \log(\mu) - \frac{1}{2} \sqrt{(CV^2 + 1)}, S = \sqrt{(CV^2 + 1)}, \alpha = \mu\gamma, \beta = (1 - \mu)\gamma, \gamma = \frac{1 - \mu}{CV^2\mu} - 1$$

there are estimates for M in Turkish (M = 0.87; Ismen, 1995) and Croatian (M = 0.63; Dulčić *et al.*, 2003) waters, which are considerably higher than the ones produced by the length-based model we use. To allow higher values, we give the non-size-dependent part of natural mortality of picarel an uninformative prior with uniform distribution $M1 \sim Unif(0.1, 0.6)$. Finally, we assign non-parametric uncertainty to natural mortality (i.e. uncertainty not dependent on model parameters). We believe that M_a is between [0.1] and use Beta-distribution to present our prior knowledge $M_a \sim Beta(\alpha, \beta)$ where α and β are the shape parameters of beta distribution, which can be defined with mean μM_a and CV of the M. We use CV=0.1 for both species.

The modelling of fishing mortality F was considerably harder as there is no effort data available for these species in the Cyclades (Stergiou *et al.*, 2002, 2006; Erzini *et al.*, 2006). The number of boats (Kapadagakis *et al.*, 2001), gears used and their selectivity (Stergiou *et al.*, 2002, 2004, 2006; Erzini *et al.*, 2006) is known for some of the years but no data is available so that effort for one single year could be constructed, which would be needed for modelling purposes. Due to the multigear and multi-species nature of the fishery (Stergiou *et al.*, 2002, 2006; Erzini *et al.*, 2006), as well as the inconsistent and scattered data, it became too hard a task to get any reasonable effort estimates and catchabilities to set annual age specific prior distributions for fishing mortalities. Thus, at this stage, only a non-informative prior is used in the model. For both species, fishing mortality F_y is modelled as one annual value, which is the same for all age

classes. A uniform distribution is used as prior distribution $F_y \sim Unif(0, 1.2)$. This prior means that we believe that there is an equal chance for every value of F between 0 and 1.2.

Stock-recruitment

We found no information or even considerable efforts to estimate the stock-recruit dynamics of these species in the Cyclades or in the Mediterranean. Prior information from other stocks, species and similar species is gathered to form prior knowledge of the recruitment parameters. We use both hyperpriors and non-parametric uncertainty in the modelling of the recruitment.

The life history of bogue is studied in Cretan waters and it is known that bogue spawns in open waters and that its eggs are buoyant. After hatching, larvae drift to shallow waters (< 30 m), where they begin feeding before recruiting to demersal and pelagic stocks (Kallianiotis, 1992). It seems that the Beverton-Holt stock-recruitment function (Beverton & Holt, 1957) would be suitable for this case considering that before drifting to shallower coastal waters the chances of survival are evenly distributed and there is no over compensation as there is no evidence of cannibalism. We use the following parameterization

$$\mu R_{y+1} E_y = \frac{K}{\frac{K}{a} + E_y}, \text{ where } \mu R_{y+1} \text{ is the expected}$$

number of recruits for next year (age 1), E_y is the number of eggs produced in that year; parameter a can be interpreted as the survival of eggs, and parameter K as the car-

rying capacity of the area. It is biologically more realistic to use number of eggs instead of spawning stock biomass in stock-recruitment function and parameter α has a more understandable definition too.

To estimate α , which is not known for any stock of bogue, a similar species is studied. Red porgy (*Pagrus pagrus*) is taxonomically closely related to bogue and they belong to the same family (Sparidae). Also, their life histories are somewhat similar (Rochet *et al.*, 2000). The stock recruitment dynamics of red porgy is studied in the East Coast of the United States (Vaughan *et al.*, 1992). There is a 20-year data set on SSB (in this case thousand tonnes of females) and corresponding recruitment (individuals in millions). However, in order for these to be useful in our model, SSB must be converted into the same units (number of eggs). Mylonas *et al.* (2004) have studied the fecundity of red porgy in the Mediterranean and they came up with 425.4 eggs per gram of female. We fitted the recruitment curve in recruits per egg data of red porgy to get an estimate of parameter α , which was 0.000004. This is used as a prior mean value in beta distributed prior. The CV of distribution is set to 0.25.

Parameter K is no easier in this case. Two different approaches are used to estimate maximum possible value for recruits. Firstly, it can be argued that the biomass of the recruits could be as big as the biomass of the biggest catch. This is at least the amount of biomass that the area can support. If we assume that one recruit weighs around 10 g and that all fish in the biggest catch of around 4500 tonnes are this small, we have 450 million individuals.

Another approach is to use values calculated for other species. One good example is given by Myers *et al.* (2001) who estimated the carrying capacity of North Atlantic cod using 21 stocks. Their estimates varied between 6.8 and 12 900 tonnes, where the mean was 1 660 and the median 330 tonnes per square kilometre of juvenile habitat. The CV of these estimates was 1.9. The total area of the Cyclades is 42 083 km² and due to its situation on the Central Aegean Plateau, the waters are relatively shallow with a mean depth of around 200 m (Sakellariou & Alexandri, 2007). Remembering that juveniles feed in shallow coastal waters, this stage could be seen as the bottle-neck for the number of recruits. Assuming that one fifth of the Cyclades area is suitable juvenile habitat for bogue and that the average weight of one recruit is 10 g, we obtain an approximate median of 278 million and a mean 1 400 million recruits in that area. This estimate somewhat supports our first estimate of 450 million recruits. A lognormal prior is chosen to model our present belief about K with 400 million recruits as the mean and with CV 1.9, which is the same as that estimated by Myers *et al.* (2001).

Picarel spawns on shallow sandy bottoms and is a nest guarding batch spawner (Vidalis, 1994). In this case also, it seems reasonable to use the Beverton-Holt stock-recruitment function as no over compensation in this stock is likely either. There are no earlier studies of stock recruitment dynamics for picarel and we have not found any

data on taxonomically similar species either, or even with similar life history patterns (a small pelagic nest guarding batch spawner with a short life-span). However, sprat (*Sprattus sprattus*) has some similarities with picarel both being small, short-living pelagic species with similarities in larval stages, although their spawning habits are different. There is stock-recruit data of 43 years for Black Sea sprat (Prodanov *et al.*, 1997). SSB of sprat was converted to the number of eggs assuming equal proportions of females and males and using the estimated 413 eggs / (g females) from the Baltic Sea (Alheit, 1988). A stock-recruit curve was fitted to estimate parameters. This leads to an egg survivability of 0.002. The problem here is that the age of recruitment was 0 years. In our model, the age of recruitment is age 1. Thus, α is scaled assuming that 10 % of 0-year-old recruits would survive to age 1. This gives a mean value of $\alpha = 0.0002$ for the beta distributed prior. The coefficient of variation is set to 0.25 as was with bogue. For parameter K , we used the same prior as the one used for bogue. This is justified, because the weight of the recruits is more or less the same (~10 g) as is the area of the potential feeding grounds for juveniles of both species.

Finally, the yearly number of recruits R_y is assumed to have additional variation not dependent on stock size. We use a lognormal distribution with expected value μR_y to describe this uncertainty caused e.g. by environmental conditions, weather and other species. As the recruitment studies in Mediterranean are rare, it is hard to estimate what kind of variability there could be in recruitment. Myers' stock-recruitment database (Myers, 2008) has data series only for hake (*Merluccius merluccius*) in Mediterranean area. The CV of recruitment in that stock was 0.782. The stocks used to estimate α parameter had CV 0.615 (*Pagrus pagrus*) and CV 0.953 (*Sprattus sprattus*). Summarising the above scarce information we decided to use CV 0.7 for bogue and CV 1.0 for picarel.

Growth and length

As there was neither data nor other information on the growth or length of the modelled species in the Cyclades, prior knowledge is used from nearby Cretan waters. Growth is modelled using von Bertalanffy's equation, which gives the expected mean total length (TL) of the fish in centimetres for each age class per year $\mu L_\alpha = L_{\text{inf}}(1 - e^{-k(a-t_0)})$ where k , L_{inf} and t_0 are species-specific parameters. For bogue, we use parameter values estimated by Kallianiotis (1992) and for picarel by Vidalis & Tsimenidis (1996) (Table 2). For picarel parameters are for fork length (FL). According to Fishbase (Froese & Pauly, 2008), the following equation can be used for the conversion to the total length $TL = \frac{FL}{0.886}$.

For both modelled species, mean length $L_{y,a}$ of the annual age classes is expected to vary according to the lognormal distribution, where expected mean length is ob-

Table 2. Collection of non-stochastic parameter values used in the model.

Variable	Explanation	Bogue	Picarel
y	Year	1 ... 61	1 ... 61
a	Age	1 ... 8	1 ... 7
$M1$		0.1	Stochastic
h_{dem}	Parameters of natural mortality	1.71	1.71
i		0.8	0.8
n		-1.66	-1.66
L_{inf}	Length function parameters	23.7	13.78
k		0.418	0.393
t_0		-0.235	-0.678
b	Weight function parameters	0.01467	0.007416
c		2.877	3.212
d	Fecundity function parameters	6.354	6.973
e		0.019	0.015

tained from the above equations. The CV of distributions is set to 0.005, obtained from the standard error (SE) of mean lengths in the age groups observed by Vidalis & Tsimenidis (1996). We use this same CV for both species.

Weight

Annual expected mean weight (in g) of the fish in the age group is calculated from the mean length (in centimetres) as $\mu W_{y,a} = bL_{y,a}^c$, where parameters for bogue are set according to Moutopoulos & Stergiou (2002) and for picarel according to Vidalis & Tsimenidis (1996) (Table 2). The parameter estimates for bogue come from the Cyclades and for picarel from Crete. Mean weight at age $W_{y,a}$ is assumed to vary according to lognormal distribution with expected mean value $\mu W_{y,a}$ and CV=0.005, which is the same as we use for length. The mean weights of the fish in the age groups are used to calculate yearly total catch C_y .

Fecundity, maturity and sex ratio

The yearly fecundity of the population, the total number of eggs spawned, is calculated according to $E_y = \sum_a N_{y,a} m_a f_a E_{y,a}$, where N is the number of individuals in the age group, m is combined maturity in the age group, f is the proportion of females in that age group and $E_{y,a}$ is the annual age specific mean number of eggs spawned per female in that age group.

Mean annual length-specific fecundity in number of eggs of females in the age group is calculated according to the equation $\mu E_{y,a} = d + eL_{y,a}^g$, where $L_{y,a}$ is length in millimetres and parameters d and e are from Cretan waters (Kallianiotis, 1992; Vidalis, 1994) (Table 2). We add uncertainty to the mean number of eggs $E_{y,a}$ in a form of lognormal prior distribution with expected mean $\mu E_{y,a}$ and CV 0.06, which comes from SE of all age groups of bogue observed by Gordo (1996) along the Portuguese coast. We use the same CV for both species.

We use a simple logistic regression function to model maturity at age $a m_a = \frac{e^{f+ga}}{1+e^{f+ga}}$. We have prior informa-

tion on maturity for both species from Crete (Kallianiotis, 1992; Vidalis, 1994) (Table 3). We construct a sub-model for the estimation of maturity in Crete and use data to update the model and then use posteriors of parameters f and g as priors in our model. In the sub-model, we use a normally distributed observation model for $m_{obs,a}$ with m_a as a mean with CV 0.1 and priors of f and g are set to $N(0,1)$.

Both species are hermaphroditic and we need to model how the proportion of females changes according to age. Bogue is partly protandrous. Both genders are born in equal numbers but some fish change sex from male to female when getting older. Picarel is a protogynous hermaphrodite where all fish are born as females and change to males when getting older. The logistic regression, with coefficients r and s , gives the ratio of females in the age class $f_a = \frac{maxe^{r+sa}}{1+e^{r+sa}}$. For bogue, we

scale the logistic regression with variable max and give it a beta distributed prior $max \sim Beta(\mu = 0.8, CV = 0.125)$, which sets the maximum for the ratio of females, because not all of the fish change sex. For picarel, we set $max=1$. Priors for regression coefficients are obtained similarly to those of maturity using sub-models and observations elsewhere. We have the observations of sex ratios at age for bogue from Portugal (Monteiro *et al.*, 2006) and for picarel from Crete (Vidalis & Tsimenidis, 1996) (Table 3). We use the same observation model and priors in the sub-model as for maturity.

Prior sensitivity analysis

We do a simple prior sensitivity analysis for both species. Our main interest in the study was the stock size, so we test how sensitive it is to the change of priors. For sensitivity analysis, we choose two variables for which we are most uncertain and substitute them with other priors, run the model and observe the effect on stock size. We choose the initial stock size and fishing mortality and instantiate them with more vague priors $N_{1,a} \sim Unif(0,500)$ and $F_y \sim Unif(0,3)$.

Table 3. Observed proportion of mature fish (Kallianiotis, 1992; Vidalis, 1994) and females (Vidalis & Tsimenidis, 1996; Monteiro *et al.*, 2006) of bogue and picarel in age groups. Estimated combined maturity is based on observed maturities per sex at length.

Age	Maturity		Females	
	Bogue	Picarel	Bogue	Picarel
1	0.00	0.40	0.50	0.97
2	0.10	0.70	0.50	0.74
3	0.60	1.00	0.55	0.37
4	0.90	1.00	0.55	0.33
5	1.00	1.00	0.60	0.22
6	1.00	1.00	0.70	0.00
7	1.00	1.00	0.70	0.00
8	1.00		0.70	

Results

According to the model, the median posterior stock size of bogue started around 200 million fish, and then decreased in the period from 1950 to 1970 ending at around 100 million. Then again continuously increased over 30 years and peaked with around 400 million fish in 1992, which was followed by a rather sudden collapse with a median of only 20 million individuals and 95 % credible interval [13, 37] in 2010 (Fig. 2a). The median posterior stock size of picarel started at 190 [110, 330] million individuals, decreased for three years, and then steadily increased to around 380 million in 1966. From 1967 to 1990, the stock fluctuated between 250 and 500 million and after that rapidly increased and peaked at 880 [280, 1 740] in 1993. This stock, too, collapsed rapidly to under 200 million, ending at around 97 [44, 360] million in 2010 (Fig. 2b). The models seem to be quite certain, especially in the case of bogue, showing the collapse of the stocks. This is partly because we use CV as a measure of uncertainty in the observation model. This means that the standard deviation (SD) is a constant proportion of mean and that, in low stock sizes, the SDs are also low when compared with SDs in high stock sizes. In other words, the relative uncertainty in the observation process was assumed to be constant over time.

The biological prior information used in defining the model parameters did not change our belief about the past catches. The posterior median of catches remained very close to the reconstructed catch data (Fig. 3). This is explained by our uninformative prior on fishing mortalities. The model suggests that the median of posterior of the fishing mortality of bogue was rising but still below 0.1 for the first 14 years, which is explained by small catches during that same period (Fig. 2c and 3a), and then fluctuated around 0.1 until 1994. In the period between 1994 and 1998, the fishing mortalities were over 0.2. The last 12 years are characterized by a rapid increase from around 0.1 to 0.96 [0.46, 1.2] in 2010. The median posterior fishing mortality of picarel started around 0.1 but rapidly increased to stay above 0.5 with few exceptions (Fig. 2d). The first was the year 1975 when F was below 0.1 and is explained by low catch in that year. The second period was in the 1990's where the model shows F s between 0.2 [0.1, 0.8] and 1.1 [0.9, 1.2] and is caused by

fluctuating catches that the model explains by changing F s (Fig. 2d and 3b). Uncertainties in the fishing mortalities of picarel are clearly higher compared with those of bogue. The posterior median natural mortality of bogue is 0.35 [0.26, 0.46] at age 1, then decreases to 0.28 [0.22, 0.34] at age 2 and then stays around 0.2 between ages 3-8 (Fig. 4a). For picarel, M is 0.57 [0.42, 0.73] at age 1, 0.44 [0.34, 0.64] at age 2 and then steadily decreases to 0.31 [0.23, 0.50] at age 7 (Fig. 4b). For both species, the posteriors of natural mortalities are lower than the priors.

The model indicates that quite a large part of the bogue individuals in the area are hermaphrodites. The median posterior ratio of bogue females is 0.48 [0.41, 0.56] at age 1 and then continuously increases to 0.78 [0.70, 0.85] at age 8 (Fig. 4c). Every picarel is born as a female and changes sex to male. At age 1, the ratio of females is 0.83 [0.77, 0.89] and at age 7 the ratio is 0.055 [0.038, 0.081] (Fig. 4d). The posterior ratio of females is at a higher level compared with the prior in all age classes of bogue, whereas with picarel the data did not bring any new information about the sex ratio and the posterior is very close to the prior distribution.

Median posterior recruitments varied between 3-90 million for bogue and 53 – 699 million for picarel (Fig. 5). Modelled recruitments are below the median of K , which is 1 570, [260, 6 130] million for bogue and 1 670, [640, 6 850] million for picarel (Fig. 6). The uncertainty in parameter K is considerable. The posterior of the α parameter for bogue is 0.000020 [0.000017, 0.000024] and for picarel 0.00042 [0.00033, 0.00053], which indicates that picarel eggs have better survivability compared with that of bogue (Fig. 6). This is an expected result because of the nest guarding behaviour of picarel. The data provided new information on α parameters and posteriors changed considerably when compared with priors.

The prior sensitivity analysis with more vague priors shows that in the case of bogue the mean stock sizes were at a higher level for the first twenty years and credible intervals are wider for the whole period (Fig. 7). With picarel, there is no considerable change in the outcome independent of priors although F was estimated to be higher. Most importantly, in both cases, the results do not change in a way that could affect our management decisions.

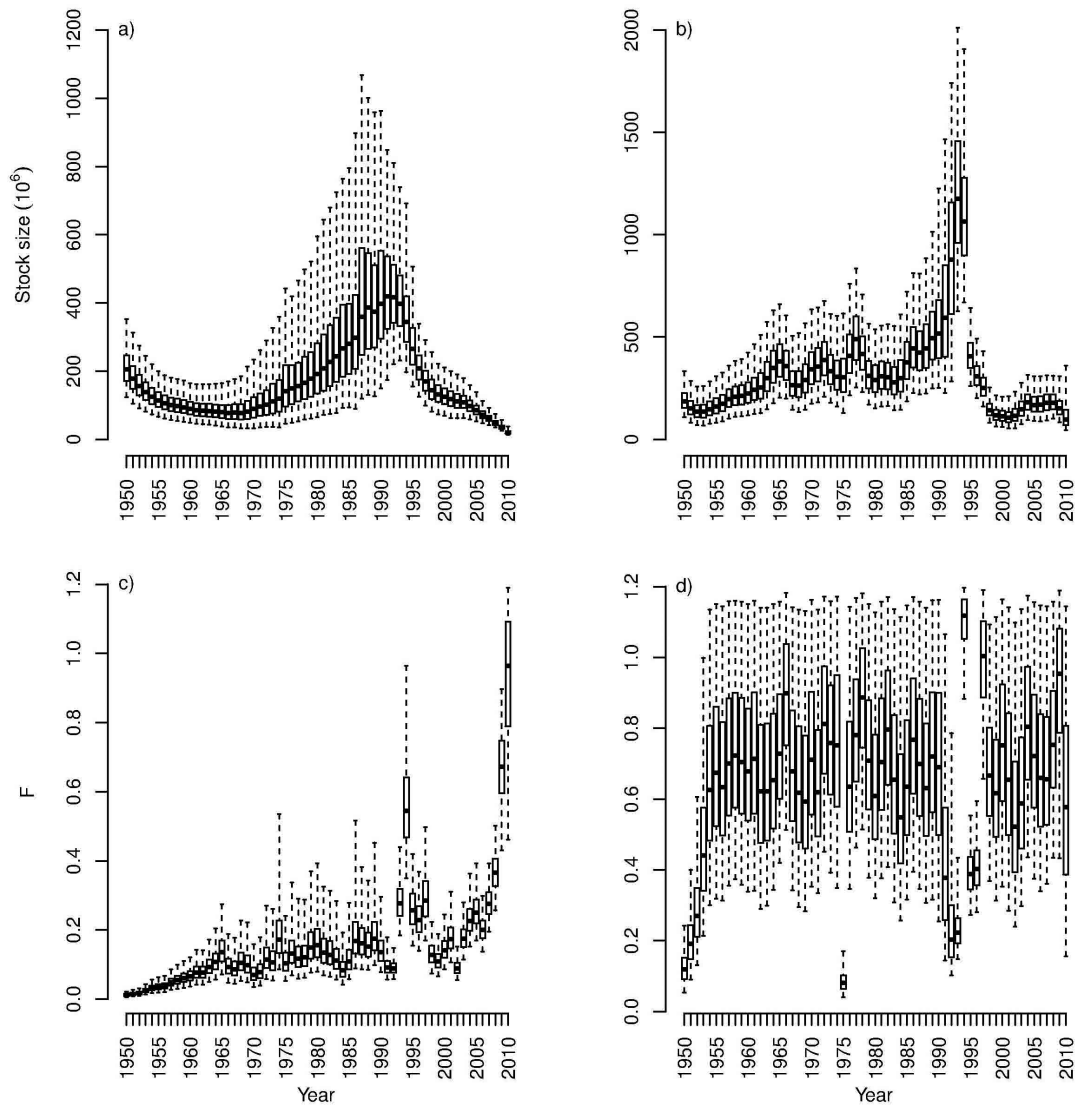


Fig. 2: Estimated yearly stock sizes (in million individuals) and fishing mortalities for bogue (a,c) and picarel (b,d). Box plots show probability interval 0.25-0.75 with horizontal thick line as median and whiskers 0.025-0.975 credible interval.

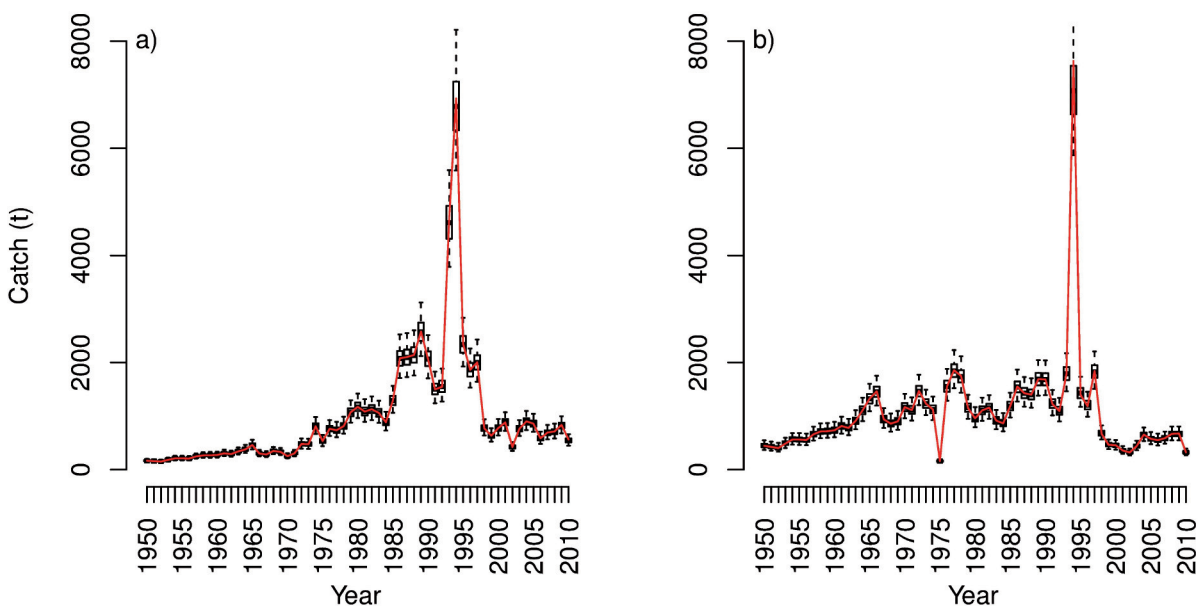


Fig. 3: The box plots show posterior catches of bogue (a) and picarel (b) in tonnes. The red line is reconstructed catch data.

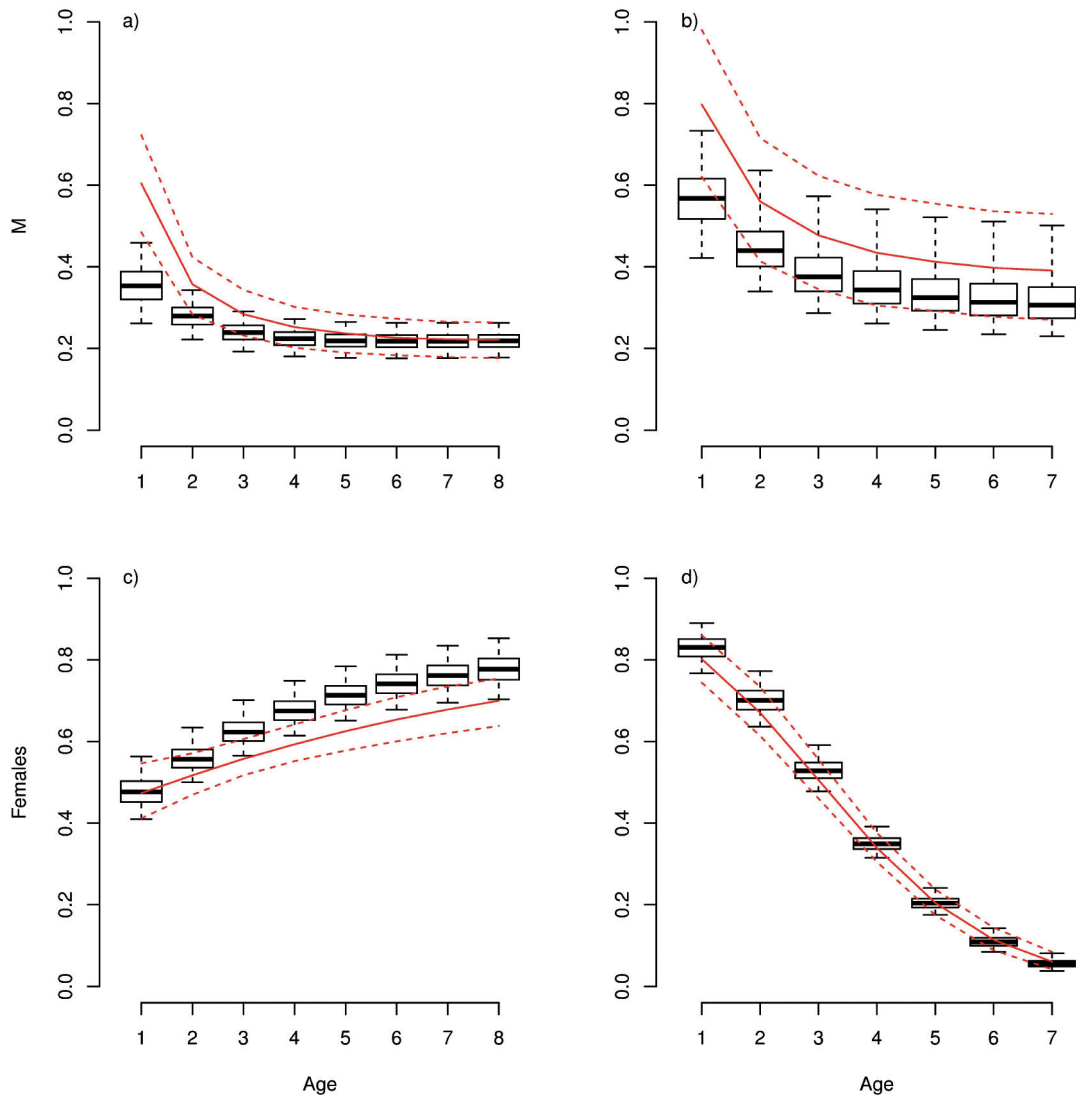


Fig. 4: Age-specific posteriors of natural mortality and proportion of females as box plots for bogue (a, c) and picarel (b, d). Solid red lines represent prior medians and dashed lines show prior 95 % credible intervals.

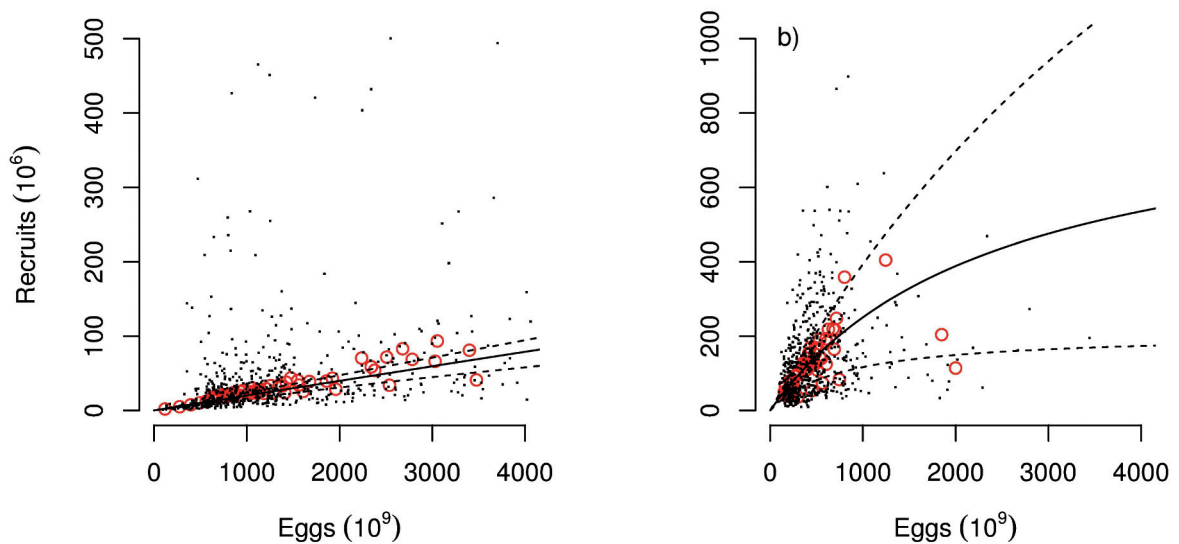


Fig. 5: Beverton-Holt stock-recruitment curve for bogue (a) and picarel (b). The dotted lines represent credible intervals where we have used 95 % credible intervals of α and K parameters of recruitment functions. Red circles are posterior median values of recruitment and small black dots are randomly sampled ($n=10$) from every posterior recruitment distribution ($n=61$).

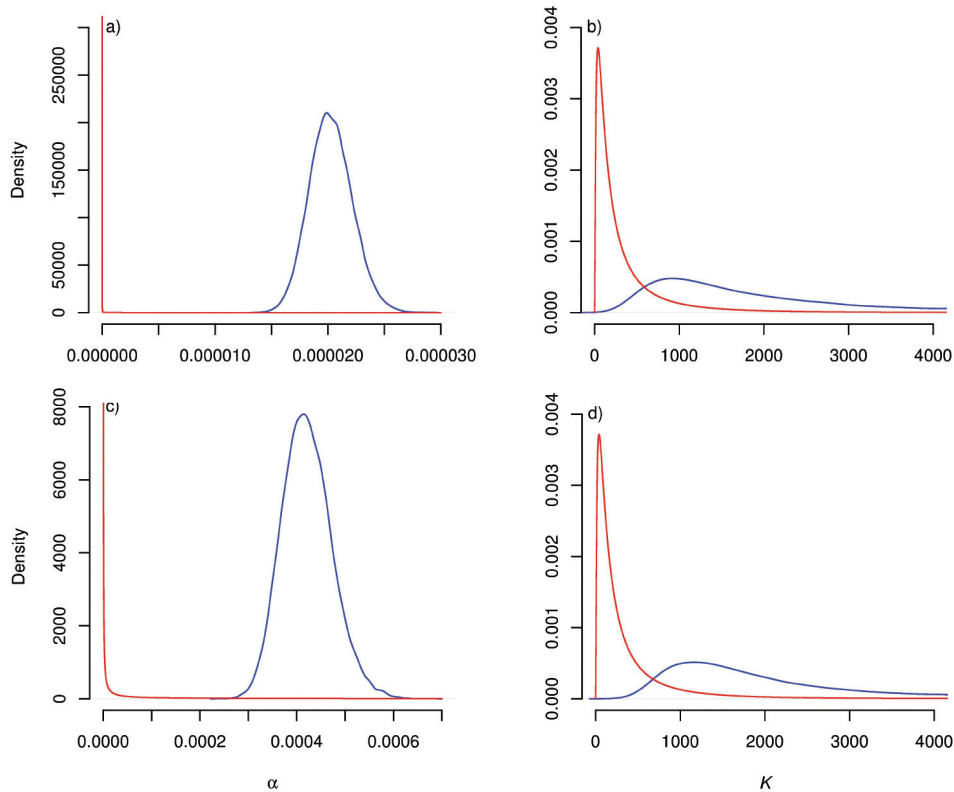


Fig. 6: Priors of α and K parameters of bogue (a, b) and picarel (c, d) in red and kernel density distributions of posteriors in blue.

In addition, we inspected posterior correlations in general. There do not seem to be any significant correlations between parameters; only F and N showed a clear correlation (Fig. 8). Finally, the plot of the data against posterior catch (Fig. 3) shows that our model is consistent with the data.

Discussion

With this modelling approach it was possible to construct a biologically realistic, age structured population model using prior information from other areas and species. In the model, we linked natural mortality with length, used realistic growth, body size, fecundity

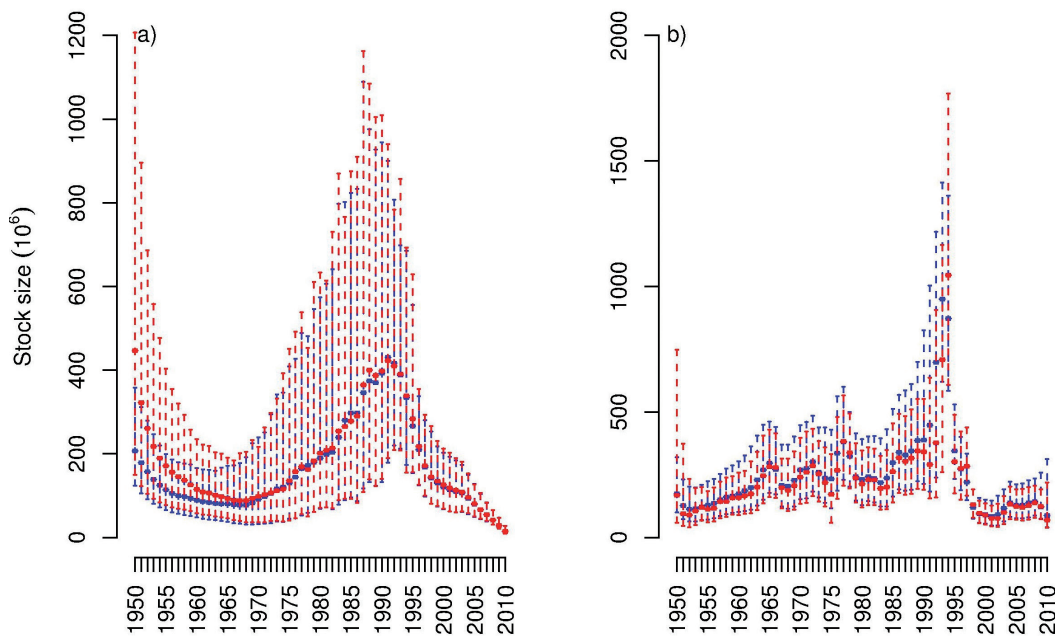


Fig. 7: A plot of prior sensitivity analysis for bogue (a) and picarel (b), where stock size with original priors for F and $N_{1,a}$ is plotted in blue and for alternate priors in red.

and sex ratio equations. The priors and the model structure imply a structure for the joint prior of all unknowns. When some of these (the catches) become known, all the marginal priors become updated, which is one of the main advantages of using an integrated assessment model with a state-space structure and the core idea of the Bayesian approach. The amount of updating for each parameter depends on how informative the priors have been relative to the priors of other parameters and the interpretation of data through the likelihood. In this case, F has the weakest prior, so most of the updating is seen there. Nevertheless, given the model structure and priors for the biological parameters, catch data provides information not only about annual F but also about the annual size of the stock, which then means that M , the slope of the S-R function and K must be updated to some extent as well. So if nothing else, the posteriors of these key parameters should be useful in future studies.

According to the model, the bogue stock seemed to be in strong decline in 2010. However, the decline of bogue stock in the last few years is most likely related to some artefact in the model. Regardless of the time period used, bogue always ended up in a fast decline in the final years. It seems that this is because there are no future

observations of the catches that would “keep the stock alive”, which implies that there is something seriously wrong either in the catch statistics or in the biological parameters of the model.

The stock of picarel seems to be in better shape and the model behaved more logically compared with the one of bogue. However, the stock is easily affected by overfishing. Even if the recruitment conditions are good, once the stock is down it takes time until the number of males reverts to “normal” because of the hermaphroditism. This is a problem that is not fully accounted for in the model. It considers only the number of eggs produced, and the majority of young fish being females combined with early maturity leads to the wrong assumption that recruitment is secured. It is quite evident that there might be sperm limitation in the overfished populations. Picarel being a nest builder and guarder, the role of the older males is very important in reproduction. As indicated by gear selectivity studies carried out in the area, it is clear that most of the fish are caught at too small a size before their optimal exploitation length and even before the length of 50 % maturity (Stergiou *et al.*, 2004). The modelling and management of hermaphroditic species need special care and size selectivity of the fisheries in particular could present a problem through re-

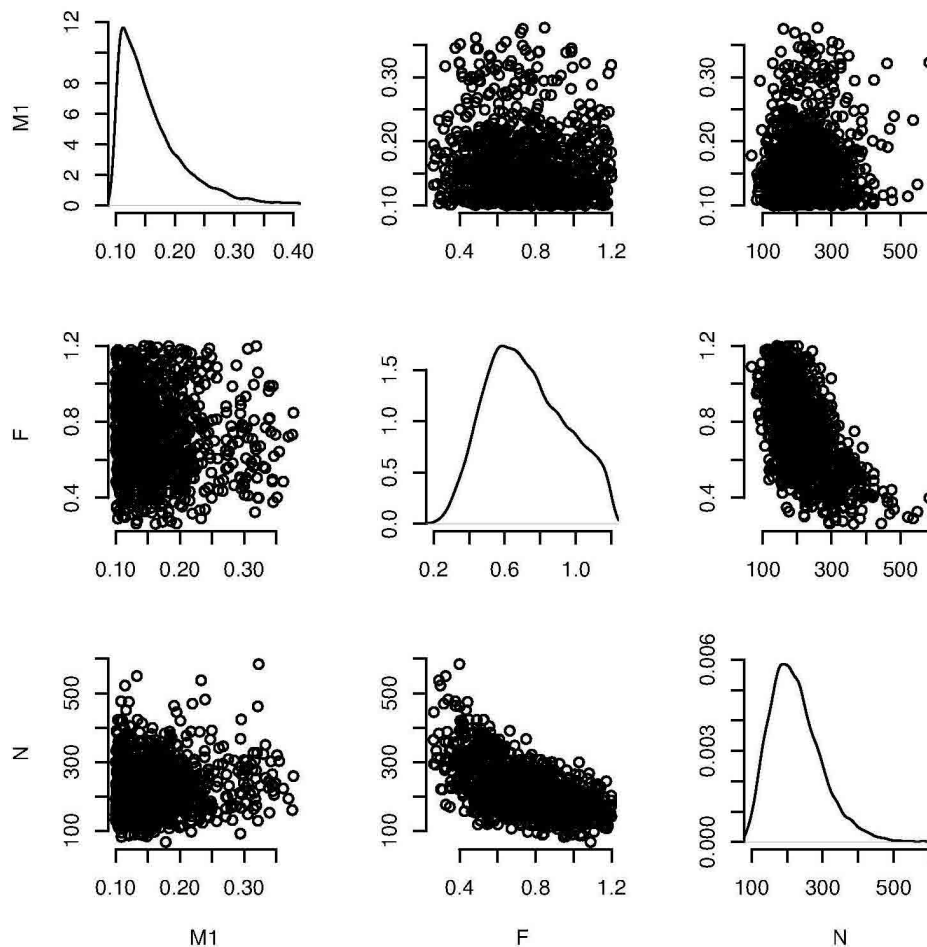


Fig. 8: An example of posterior correlations. These figures are from picarel model on year 1960 and show kernel densities and correlations between parameters $M1$, F , and N .

duced reproductive ability resulting from removal of sexes in unequal proportions (Alonzo & Mangel, 2004; Heppell *et al.*, 2006; Molloy *et al.*, 2007).

Initially, we used OpenBUGS (Thomas *et al.*, 2006) to implement the model but after several convergence issues ended up using JAGS, which handled the long deterministic calculations in the model much faster. Still, the model was simplified to speed up the sampling and to achieve convergence. However, all the key variables are stochastic. On some of the variables, we used only non-parametric stochasticity and hyper parameters were fixed (e.g. length, weight). We chose not to use a plus-group in the model to keep it as biologically realistic as possible. Having all age groups increases the complexity of the model as well as uncertainty but in this case we did not see it as a problem. On the other hand, it is important to have all age groups realistically modelled, especially with short lived and hermaphroditic species. However, we had to use too confident (i.e. narrow) priors especially with natural mortality and egg survivability; otherwise the model produced unrealistic results (e.g. where natural mortality increased with age). Due to these restrictions, the model ended up explaining catches mostly with changes in the weakest prior F , as discussed earlier. This is problematic because stock size is strongly correlated with F .

The most important thing required to improve the present model is fishing mortality. It requires another study to model the changes in F over years. That could be done by using expert knowledge combined with the little information currently available (e.g. number of boats) in order to show how F has changed over the years. Yet another improvement would be the inclusion of selectivity in the models, which would mean a modelling of F annually for every age group. Mediterranean fisheries are traditionally multigear and multispecies in nature (Stergiou *et al.*, 1997, 2007). The commercial fleet is divided between large vessels that use trawls and purse seines and small-scale coastal fisheries which operate with beach seines, long lines, traps, trammel and gill nets (Kapadagakis *et al.*, 2001). All these characteristics of the fishery, combined with inaccurate and often biased data, introduce challenges especially in catch and effort analyses and thus in management decisions (Papaconstantinou & Conides, 2007; Tsikliras *et al.*, 2007).

Incorporating biological knowledge into stock assessment models is important. However, if even the basic biology of species is unknown problems arise. For example, FishBase claims bogue to be a demersal species but Kallianiotis (1992) identified the existence of both pelagic and demersal stocks in Crete. Also, according to Bauchot & Hureau (1986), bogue is a protogynous hermaphrodite. The prior data used in the model (Monteiro *et al.*, 2006) suggest that it would instead be a partly protandry species, i.e. some of the males change to females. The same can be seen from another study in Egypt (El-Agamy *et al.*, 2004), where the ratio of the females also

increased in older age classes. It is also possible that sex change is connected with environmental conditions or is highly stock-specific. The type of hermaphroditism and its mechanism is very important when building models and giving advice to management (Molloy *et al.*, 2007). There are indications that species would adapt to size-selective fishing by altering the age of their sex change (Hamilton *et al.*, 2007; Molloy *et al.*, 2007). Thus, the population should be sampled rather than use data collected elsewhere.

Correct stock-recruitment estimates play a key role for successful management. In this case there were many sources of uncertainty and lack of information in stock-recruitment analysis. Especially, the posterior distributions of K parameters were wide. This makes it very unwise to use any management strategy, which is dependent on a good estimate of carrying capacity. In the parameterization of the stock-recruit model, we used number of eggs instead of SSB. This introduced yet another problem as most of the studies use the steepness parameter h instead of egg survivability that we used. Each re-parameterization and conversion introduces yet another source of error in the model. In the end, the posterior of the egg survivability for both species was significantly different from the prior.

Not only is the biological knowledge about the species insufficient but the reconstructed catch data itself is dubious. Reconstruction surely improves the quality of the data but there still remain many uncertainties. The observation error might be much larger than accounted for in our model. For example, the discards are not accounted for and they can be significant in the area (Tsagarakis *et al.*, 2012). The present model is also bound to the Cyclades but the stocks are likely not. It is likely that species should be modelled and managed on a larger spatial scale. There are no studies on fish migrations in the area and it is possible that a pelagic picarel migrates in a large area. On the other hand, there are indications of the existence of island-specific stocks in the area (Stergiou *et al.*, 1997).

Because of these problems and shortcomings, the model in its present form, is not suitable for management purposes. However, we still consider it important to experiment with new possibilities for data-poor fisheries management and believe that the proposed modelling approach, with an improved modelling of fishing mortality, could provide valuable results for management. At least, we have tried to take into account the uncertainties in the assessment, where traditional approaches would yield too confident results. We are of opinion that the biological complexity of the problem is independent of the amount of data available about that problem. Having more data does not increase biological complexity, while having less data does not mean that the dynamics is simpler. The model structure is a prior belief based on current knowledge of the species's biology and it should be formulated before seeing the data and before know-

ing how much data will be available. When more data becomes available, uncertainty about the structural form and the parameters of the model would then decrease. Ignoring sources of variation that we believe do actually exist, would naturally make us overconfident compared with our current uncertainty. Thus, we do not see any point in comparing our results with other models used for data-poor modelling although new types of solutions have emerged lately (e.g. Dick & MacCall, 2011; Punt *et al.*, 2011). If there is a need to use a simpler model for stock assessment and provide advice to management, the posteriors of our model should be useful. They incorporate the best current knowledge about several important stock parameters.

At the moment there is a wide variety of different management measures in the Cyclades (Stergiou *et al.*, 2004). Various technical measures and regulations apply for all gears and there is a minimum landing size of 11 cm for both picarel and bogue (Stergiou *et al.*, 2004). Commercial gears, trawls and purse seines, are subject to closed seasons and areal restrictions on use (Stergiou *et al.*, 2004). Closed areas (marine reserves) could be an effective management option for these and other species in the Cyclades and the Mediterranean in general (Stergiou *et al.*, 2004). Good results are obtained when using them for rebuilding stocks of hermaphroditic species (Beets & Friedlander, 1999; Bohnsack, 2000).

Conclusions

For a better understanding of stock dynamics and in order to be able to make better management decisions, further study of the basic biology of the species in the area is required. The present model could be improved by adding different gears and their selectivity information. In data-poor cases, in particular, Bayesian analysis is dependent on prior knowledge and meta-analytic approaches are needed. In this case, collection of prior information was a considerable effort. To ease the task, the units and representation of biological (especially stock-recruit) parameters should be unified and standardised for easy use of data. The information should be made readily available in standardized format and there should be a measure of its credibility. FishBase (Froese & Pauly, 2008) is a good effort to build such a database but more contributors are needed.

Acknowledgements

The research leading to these results has received support from the European Union's Sixth Framework Programme (FP6/2002-2006) under grant agreement 022745/POORFISH and Seventh Framework Programme (FP7/2007-2013) under grant agreement 244706/ECOKNOWS. However, the paper does not necessarily reflect EC views and in no way anticipates the Commission's future policy in the area.

References

- Alheit, J., 1988. Reproductive biology of sprat (*Sprattus sprattus*): Factors determining annual egg production. *ICES Journal of Marine Science*, 44 (2), 162-168.
- Alonzo, S.H., Mangel, M., 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fishery Bulletin*, 102, 1-13.
- Bauchot, M.-L., Hureau, J.-C., 1986. Sparidae. p. 883-907. In: *Fishes of the north-eastern Atlantic and the Mediterranean. Volume 2*. Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese E. (Eds). UNESCO, Paris.
- Beets, J., Friedlander, A., 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environmental Biology of Fishes*, 55, 91-98.
- Beverton, R.J.H., Holt, S.J., 1957. *On the dynamics of exploited fish populations*. Chapman and Hall, London, 544 pp.
- Bohnsack, J.A., 2000. A comparison of the short-term impacts of no-take marine reserves and minimum size limits. *Bulletin of Marine Science*, 66, 635-650.
- Carruthers, T.R., Walters, C.J., McAllister, M.K., 2011. Evaluating methods that classify fisheries stock status using only fisheries catch data. *Fisheries Research*, 119-120, 66-79.
- Cotter, A.J.R., Burt, L., Paxton, C.G.M., Fernandez, C., Buckland, S.T. *et al.*, 2004. Are stock assessment methods too complicated? *Fish and Fisheries*, 5, 235-254.
- Dick, E.J., MacCall, A.D., 2011. Depletion-Based Stock Reduction Analysis: A catch-based method for determining sustainable yields for data-poor fish stocks. *Fisheries Research*, 110, 331-341.
- Dulčić, J., Pallaoro, A., Cetinić, P., Kraljević, M., Soldo, A. *et al.*, 2003. Age, growth and mortality of picarel, *Spicara smaris* L. (Pisces: Centranchidae), from the eastern Adriatic (Croatian coast). *Journal of Applied Ichthyology*, 19 (1), 10-14.
- El-Agamy, A., Zaki, M.I., Awad, G.S., Negm, R.K., 2004. Reproductive biology of *Boops boops* (Family Sparidae) in the Mediterranean environment. *Egyptian Journal of Aquatic Research*, 30 (B), 241-254.
- Erzini, K., Gonçalves, J.M.S., Bentes, L., Moutopoulos, D.K., Hernando Casal, J.A. *et al.*, 2006. Size selectivity of trammel nets in southern European small-scale fisheries. *Fisheries Research*, 79, 183-201.
- Froese, R., Pauly, D., 2008. *FishBase*. <http://www.fishbase.org>, version (Accessed September 2008)
- Gislason, H., Pope, J. G., Rice, J. C., Daan, N., 2008. Coexistence in North Sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science*, 65, 514-530.
- Gordo, L.S., 1996. On the fecundity of the bogue, *Boops boops* (L., 1758), from the Portuguese coast. *Journal of Applied Ichthyology*, 12, 27-30.
- Hadjistephanou, N., 1992. *Assessment of five demersal marine fish stocks of Cyprus for the year 1989*. FAO Fisheries Report 477, 23-34 pp.
- Hamilton, S.L., Caselle, J.E., Standish, J.D., Schroeder, D.M., Love, M.S. *et al.*, 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecological Applications*, 17 (8), 2268-2280.
- Heppell, S.S., Heppell, S.A., Coleman, F.C., Koenig, C.C., 2006. Models to compare management options for a protogynous fish. *Ecological Applications*, 16 (1), 238-249.

- Ismen, A., 1995. Growth, mortality and yield per recruit model of picarel (*Spicara smaris* L.) on the eastern Turkish Black Sea coast. *Fisheries Research*, 22 (3-4), 299-308.
- Kallianiotis, A., 1992. *Biology and structure of Bogue populations [Boops boops (L.)], in the coastal area of island of Crete*. Doctorate Thesis, University of Crete, Greece, 233 pp. (In Hellenic with English abstract).
- Kapadagakis, A., Machias, A., Stergiou, K., Somarakis, S., Tsimenides, N. *et al.*, 2001. *Patterns and propensities in Greek fishing effort and catches*. Final Report to the Commission of the European Communities, DG XIV/C/1, Project Ref. No 00/018, 208 pp.
- Kuparinen, A., Mäntyniemi, S., Hutchings, J.A., Kuikka, S., 2012. Increasing biological realism of fisheries stock assessment: towards hierarchical Bayesian methods. *Environmental Reviews*, 20, 135-151.
- McAllister, M.K., Pikitch, E.K., Babcock, E.A., 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences*, 58 (9), 1871-1890.
- Millar, R.B., Meyer, R., 2000. Non-linear state space modelling of fisheries biomass dynamics by using Metropolis-Hastings within-Gibbs sampling. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 49, 27-342.
- Molloy, P., Goodwin, N., Côté, I., Gage, M., Reynolds, J., 2007. Predicting the effects of exploitation on male-first sex-changing fish. *Animal Conservation*, 10 (1), 30-38.
- Monteiro, P., Bentes, L., Coelho, R., Correia, C., Gonçalves, J. *et al.*, 2006. Age and growth, mortality, reproduction and relative yield per recruit of the bogue, *Boops boops* Linné, 1758 (Sparidae), from the Algarve (south of Portugal) longline fishery. *Journal of Applied Ichthyology*, 22 (5), 345-352.
- Moutopoulos, D., Stergiou, K., 2002. Length-weight and length-length relationships of fish species from the Aegean Sea (Greece). *Journal of Applied Ichthyology*, 18, 200-203.
- Moutopoulos, D.K., Stergiou, K.I., 2012. Spatial disentangling of Greek commercial fisheries landings by gear between 1928-2007. *Journal of Biological Research – Thessaloniki*, 18, 265-279.
- Myers, R.A., 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science*, 58, 937-951.
- Myers, R.A., 2008. *Stock recruitment database*. <http://www.mscs.dal.ca/~myers/welcome.html> (Accessed September 2008)
- Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 2404-2419.
- Myers, R.A., MacKenzie, B.R., Bowen, K.G., Barrowman, N.J., 2001. What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1464-1476.
- Mylonas, C., Papadaki, M., Pavlidis, M., Divanach, P., 2004. Evaluation of egg production and quality in the Mediterranean red porgy (*Pagrus pagrus*) during two consecutive spawning seasons. *Aquaculture*, 232 (1-4), 637-649.
- Papaconstantinou, C., Conides, A., 2007. The fisheries in the Mediterranean Sea. p. 97-103. In: *State of Hellenic fisheries*. Papaconstantinou, C., Zenetos, A., Vassilopoulou, V., Tserpes, G. (Eds). HCMR Publ, Athens, Greece.
- Pella, J.J., Tomlinson, P.K., 1969. A generalized stock production model. *Inter-American Tropical Tuna Commission. Bulletin*, 13, 419-496.
- Plummer, M., 2003. JAGS: A Program for analysis of Bayesian graphical models using Gibbs sampling. In: *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna, Austria, 20-22 March 2003.
- Prodanov, K., Mikhailov, K., Daskalov, G., Maxim, C., Cashchin, A. *et al.*, 1997. *Environmental management of fish resources in the Black Sea and their rational exploitation. Studies and Reviews*. General Fisheries Council for the Mediterranean, No 68, Rome, FAO, 53-72 pp.
- Punt, A.E., Hilborn, R., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries*, 7, 35-63.
- Punt, A.E., Smith, D.C., Smith, A.D.M., 2011. Among-stock comparisons for improving stock assessments of data-poor stocks: the “Robin Hood” approach. *ICES Journal of Marine Science*, 68, 972-981.
- Rochet, M-J., Cornillon, P-A., Sabatier, R., Pontier, D., 2000. Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *Oikos*, 91 (2), 255-270.
- Sakellariou, D., Alexandri, M., 2007. Geomorphology of the Hellenic sea-floor. p. 17-23. In: *State of Hellenic fisheries*. Papaconstantinou, C., Zenetos, A., Vassilopoulou, V., Tserpes, G. (Eds). HCMR Publ., Athens, Greece.
- Schaefer, M.B., 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. *Inter-American Tropical Tuna Commission. Bulletin*, 2, 247-268.
- Stergiou, K.I., Christou, E.D., Georgopoulos, D., Zenetos, A., Souvermezoglou, C., 1997. The Hellenic seas: physics, chemistry, biology and fisheries. *Oceanography and Marine Biology: an Annual Review*, 35, 415-538.
- Stergiou, K.I., Moutopoulos, D.K., Erzini, K., 2002. Gill net and longlines fisheries in Cyclades waters (Aegean Sea): species composition and gear competition. *Fisheries Research*, 57, 25-37.
- Stergiou, K.I., Moutopoulos, D.K., Krassas, G., 2004. Body size overlap in industrial and artisanal fisheries for five commercial fish species in the Mediterranean Sea. *Scientia Marina*, 68 (1), 179-188.
- Stergiou, K.I., Moutopoulos, D.K., Soriguer, M.C., Puente, E., Lino, P.G. *et al.*, 2006. Trammel net catch species composition, catch rates and métiers in southern European waters: A multivariate approach. *Fisheries Research*, 79, 170-182.
- Stergiou, K.I., Moutopoulos, D.K., Tsikliras, A.C., Papaconstantinou, C., 2007. Hellenic marine fisheries: a general perspective from the National Statistical Service data. p. 132-140. In: *State of Hellenic Fisheries*. Papaconstantinou, C., Zenetos, A., Vassilopoulou, V., Tserpes, G. (Eds). Hellenic Centre for Marine Research, Athens.
- Tahvonen, O., 2008. Harvesting an age-structured population as biomass: Does it work? *Natural Resource Modeling*, 21, 525-550.
- Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS Open. *R News*, 6 (1), 12-16.
- Tsagarakis, K., Vassilopoulou, V., Kallianiotis, A., Machias, A., 2012. Discards of the purse seine fishery targeting small pelagic fish in the eastern Mediterranean Sea. *Scientia Marina*, 76(3), 561-572.
- Tsikliras, A.C., Moutopoulos, D.K., Stergiou, K.I., 2007. Reconstruction of Greek marine fisheries landings: national

- versus FAO statistics. p. 121-137. In: *Reconstruction of marine fisheries catches for key countries and regions (1950-2005)*. Zeller, D., Pauly, D. (Eds). Fisheries Centre Research Reports. 15 (2), Fisheries Centre, University of British Columbia, Vancouver, Canada.
- Vaughan, D., Huntsman, G., Manooch III, C., Rohde, F., Ulrich, G., 1992. Population characteristics of the red porgy *Pagrus pagrus* stock of Carolinas. *Bulletin of Marine Science*, 50, 1-20.
- Vidalis, K., 1994 *Biology and population structure of Spicara smaris (L.) in the Cretan Sea*. Doctorate Thesis, University of Crete, Greece, 271 pp. (In Hellenic with English abstract).
- Vidalis, K., Tsimenidis, N., 1996. Age determination and growth of picarel (*Spicara smaris*) from the Cretan continental shelf (Greece). *Fisheries Research*, 28 (4), 395-421.
- Yan, J., Cortés, E., Andrews, K., Guo, F., 2011. Poor-data and data-poor species stock assessment using a Bayesian hierarchical approach. *Ecological Applications*, 21, 2691-2708.