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GadCap: A GADGET multispecies model for the Flemish Cap cod, redfish and shrimp.

by

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ABSTRACT

Since late 1980s, the demersal community of Flemish Cap (NAFO area 3M) has experienced large variations (including the collapse) in the abundance and population structure of its main fishing resources: cod *Gadus morhua*, redfish *Sebastes* sp. and shrimp *Pandalus borealis*, with alternation in their dominant role in the ecosystem. GadCap is an EU project dealing with the development of a GADGET multispecies model for the Flemish Cap cod, redfish and shrimp, as part of the NAFO roadmap for the EAF. The effect of fishing, trophic interactions (including cannibalism) and water temperature in the dynamic of these three major fishing resources has been modeled. The results highlight the interdependent dynamic of these stocks, and reveals strong interactions between recruitment, fishing and predation (including cannibalism), with marked changes in their relative importance by species-age-length over time. The multispecies model shows that disregarding the species interactions would lead to serious underestimates of natural mortality, overestimations of the exploitable biomass, and highlights the need to move beyond single-species management in this highly coupled ecosystem. Preliminary estimates of total SSB and MSY, under different combinations of fishing mortality for all the three stocks, are also presented.

INTRODUCTION

Traditional approaches to fisheries management frequently consider species exploited in the same ecosystem as if they were completely independent populations (i.e. a single species approach), setting the Total Allowable Catches (TACs) without any consideration of species interactions. However, it has been widely demonstrated that predation is in many cases more important than fishing mortality and that natural mortality could be much higher than it is assumed by single species models (Bax 1998, Jennings et al. 2001, Wooton 1998). Accordingly, disregarding trophic interactions could lead to overestimations of yield per recruit (Pinnegar et al. 2008), which would imply exploitations of resources beyond the real surplus production. It has been widely recognized that the development of a more holistic approach is required, taking into account the relationship of fishing resources with their environment, and with special attention to the trophic interactions and other sources of mortality (Garcia et al. 2003).

Since early 1980s, multispecies and ecosystem models have been developed more intensively with diverse assumptions and scopes (Pinnegar et al. 2008). One of this models is GADGET (Globally applicable Area Disaggregated General Ecosystem Toolbox), a powerful and flexible framework that models marine ecosystems within a fisheries and eco-biological context (Begley and Howell 2004). It has been classified as a

dynamic multispecies or minimum realistic model suitable for practical advice in fisheries management (Plagányi 2007). It has potential applications both in stock assessment and as an operative model in Management Strategy Evaluation (MSE). As a multispecies model, GADGET has been applied in the Barents Sea, Icelandic Sea and the Celtic Sea (Lindstøm et al. 2009, Taylor and Stefansson 2004, Trenkel et al. 2004), and it is being developed in the Baltic sea.

Flemish Cap is a deep water mountain located in the NAFO division 3M (Figure 1). The oceanographic conditions are the result of a transition between arctic and temperate waters, although the Labrador Current dominates the water mass properties (Colbourne and Foote 2000). Two features provide high degree of isolation to the Flemish Cap ecosystem. First, the cap is separated from the Newfoundland shelf by the Flemish Pass, a channel characterized by depths beyond 1100 m and 30 miles wide in the narrowest point at 400 m depth. This feature hinders the migration to and from surrounding areas for juvenile and adult stages of shallow demersal species, such as Atlantic cod Gadus morhua (Konstantinov 1970, Templeman and Fleming 1963) and American plaice Hippoglossoides platessoides (Morgan and Bowering 2004). Second, a quasi-permanent anti-cyclonic gyre dominates the oceanography over the Cap (Colbourne et al. 2016, Kudlo et al. 1984), producing a retention effect on eggs and larvae, that would eventually stay over the Flemish Cap and recruit to the population. This isolation provides to the Flemish Cap a high degree of independence in the dynamic of its populations in relation to the Grand Banks, as reflected by the genetic differences found in cod (Bentzen et al. 1996, Carr and Marshall 2008) and shrimp populations (Jordel et al. 2014).

As a typical boreal ecosystem, in the Flemish Cap (NAFO Div. 3M) most of the biomass and production is concentrated in a few species, which are connected by strong trophic interactions (Pérez-Rodríguez 2012). Zooplankton is mostly dominated by copepods, hyperiids, euphausiids and chaetognaths, which constitute the basis of the diet for a pelagic fish community that in the Flemish Cap is characterized by the lack of key traditional boreal fish species like sandlance Ammodytes sp. or capelin Mallotus villosus. Instead, the pelagic fish community is mostly formed by deep water species like myctophids, and with an outstanding relevance by the demersal-pelagic redfish species Sebastes norvegicus, S.fasciatus and S.mentella. The piscivorous guild prey on pelagic fishes and is mostly represented by large cod *Gadus morhua*, although wolffishes *Anarhichas* sp. and Greenland halibut *Reinhardtius hippoglossoides* are also of high importance when the cod stock is reduced (Pérez-Rodríguez et al. 2011, 2012). As a result of the absence of sandlance and capelin, a particular feature in the Flemish Cap food web is the high relevance of zooplankton (mainly hyperiids, chaetognaths and euphausiids in the diet of medium sized individuals of piscivorous species (Gomes 1993, Pérez-Rodríguez 2012). The Northern shrimp *Pandalus borealis* is a key component in the trophic web in the Flemish Cap, being preyed on by most demersal fish species and especially by cod and redfish (Parsons 2005, Pérez-Rodríguez et al. 2011). Preliminary studies in the Flemish Cap have suggested that the dynamic of redfish and shrimp stocks is strongly influenced by cod predation (González-Iglesias and Casas 2012a, Pérez-Rodríguez and Saborido-Rey 2012), while cannibalism might control the degree of recruitments success in cod (NAFO 2013).

The Flemish Cap has been a traditional fishing ground for cod and redfish especially since mid 20th century (Figure 2). After a period of extreme high fishing pressure, the Flemish Cap cod experienced a sharp decline that ended up with the collapse of the stock by mid 1990s (Vázquez and Cerviño 2002). In parallel, redfish catches also showed a steep decline, after a period of very high values. The declines of cod and redfish were followed by the increase of shrimp, Greenland halibut, wolffishes and other demersal stocks (Pérez-Rodríguez et al. 2012). New fisheries targeting shrimp and Greenland halibut started by mid 1990s and kept total landings from the area at similar levels than before the cod stock collapsed. The recovery of both redfish and cod stocks since 2000-2005 (Ávila de Melo et al. 2013, González-Troncoso 2015) were followed by the decline and collapse of shrimp by 2010 (Casas-Sánchez 2012) when the cod fishery was reopened. The fisheries for cod and redfish have been traditionally made by pelagic and bottom trawlers, although gillnetters and longliners were of importance before mid 1990s. Interaction between fisheries was especially important for redfish since discard of juveniles were high in the bottom trawl shrimp fishery, especially before the introduction of a sorting grid in 1995 (Ávila de Melo et al. 2013).

Hence, in addition to the above mentioned trophic interactions between cod, redfish and shrimp, the commercial catches and the survey indexes showed complementary patterns that resembled the classical

prey-predator dynamics. The cumulative number of evidences and the importance of all these three stocks in commercial fishing lead in 2011 to the NAFO Fisheries commission to request the Scientific Council to provide an explanation on the possible connection between population dynamic of these stocks and explore the feasibility and the manner by which these three species are maintained at levels capable of producing a combined maximum sustainable yield, in line with the objectives of the NAFO Convention (NAFO 2011).

Based on the relative simplicity of the food web in the Flemish Cap with strong trophic connections between the most important commercial species (i.e. cod, redfish and shrimp), the relative high isolation of the shallow demersal community in relation to the nearby Grand Banks (expected low rate of migrations) and the high availability of data from the commercial fishery and the European Union bottom trawl survey, the Flemish Cap is an ideal case study for the development of the multispecies and ecosystem approach to fisheries in NAFO. In 2012 the European Union, through the Marie-Slodowska Curie program financed the project GadCap, which has as main goal the development of a GADGET multispecies stock assessment model including cod, redfish and shrimp to provide answer to the Fisheries commission requests.

MATERIAL AND METHODS

<u> 1.- Data</u>

Most of the data employed in the present work have been obtained from the International European Union (EU) bottom trawl surveys, conducted annually in June-July since 1988. The surveys followed the NAFO recommendations with a random stratified design (Vázquez et al. 2013). This design allows estimating indexes of total abundance and biomass for the three stocks modeled in this work using the swept area method (Gunderson 1993). These indices of biomass were employed in the model fitting as Catch per Unit of Effort (CPUE) indices. The population size distributions were also obtained from the EU survey and used as input data in the model optimization. A detailed biological sampling (age, length, weight, sex, maturity state) was carried out during the survey to a subset of individuals. These data were used to estimate externally to the model optimization the length-weight relationships for all the three stocks, as well as to optimize internally the growth functions, the sex change (for shrimp) and maturity ogives.

In addition to the three modeled stocks (cod, shrimp and redfish), the survey database was used to estimate the index of biomass of the demersal fish community. Although the survey is not designed for pelagic fish species, it can be also used to estimate a proxy of the index of total biomass. Data from the Continuous Plankton Recorder (CPR) marine monitoring program of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS; website: http://www.sahfos.ac.uk) were used to estimate a five years moving geometric average reflecting long term patterns in biomass of copepods, hyperiids, chaetognaths and euphausiids over the study period. The estimated average values of annual ecosystem potential production (Koen-Alonso et al. 2013) were employed to estimate, together with the CPR indexes for zooplankton prey groups and the EU survey indexes of demersal and pelagic fish biomass, the time series of total biomass for these groups. Once estimated externally, these biomass time series were fixed in the model during the optimization and served as alternative prey source to the predators cod and redfish.

Since 1993 (with the exception of years 2007, 2009 and 2011) stomach content information for cod and redfish has been sampled annually during the Flemish Cap survey (Román et al. 2004). This information was used to calculate the contribution of each prey (in percentage) to the diet of cod and redfish. These databases have been used as likelihood components in the optimization process. In addition, the lengths of sampled predator and prey individuals found in stomachs were used to calculate externally the parameters defining the prey-predator length relationship. The stomach content database, in conjunction with the estimates of biomass for all the preys considered in this model, were used to estimate the suitability function and prey preference for each pair of prey-predator.

Water temperature was measured during the EU survey from surface to the bottom using conductivity-temperature-depth instruments (CTDs). The raw data was processed with Seabird Data Processing version 7.25.0.319. The average annual bottom temperature was estimated as the mean value of all CTDs at maximum depth, and was used to model the total consumption by fish length.

Total catches by season as well as the size distribution of these catches by the commercial fleet for cod, redfish and shrimp fisheries were obtained from research reports and research documents published in the NAFO website http://www.nafo.int/publications/frames/publications.html as well as the information collected from database STATLANT21B (http://www.nafo.int/data/frames/data.html). Due to the lack of detailed information for several countries fishing in NAFO, most of the information on size distribution and allocation of catches over the year were gathered from the Spanish and Portuguese annual research reports. Since Spain and Portugal are two of the four main nations fishing cod and redfish in Flemish Cap, this seems a reasonable simplification. In the shrimp model, the information from the Icelandic fleet was taken as the basis for size distributions. These databases were used as likelihood components in the model optimization.

<u> 2.- GADGET</u>

GADGET is a flexible tool that allows the user to include a number of features of the ecosystem into the model: one or more species, each of which may be split into multiple components; multiple areas with migration between areas; predation between and within species; growth; maturation; reproduction and recruitment; multiple commercial and survey fleets taking catches from the populations (Begley 2005, Begley and Howell 2004). GADGET is a first-order Markovian model, i.e. the state at time t+1 is calculated as a function only of the state at time t and the model parameters. The main state variables are the number and mean weight of individuals in each age/length group for a given population and area. It is a process-based model and for each modeled population GADGET allows modeling different biological and ecological processes, setting the parameters for sub-models of predation, growth, maturation, length-weight relationship or change of sex.

The GADGET framework consists of three different and interdependent steps:

- a) A parametric model to perform simulations of the modeled system.
- b) Statistical functions to compare the simulation model with original data.
- c) Search algorithms to optimize the model parameters.

An initial population (in the form of abundance at age) needs to be defined, as well as the annual recruitment (as an abundance value at the defined age of recruitment) as an estimated annual value or through a stock-recruitment model. The way that each fleet interacts with each fished population need to be also defined. Fleets are considered as predators without length or age structure, affecting the fished stocks based on a suitability function, which parameters need to be set. Once all these parameters are defined, GADGET runs a forward simulation and different datasets are produced. These simulated datasets (hereafter likelihood components) are compared with the original datasets obtained from surveys or commercial catches. A goodness of fit value, or likelihood score, is estimated using different statistical likelihood functions. Then, parameters defining the fishing, biological and ecological modeled processes are randomly changed, and the simulation and likelihood score estimation are repeated. Search algorithms are employed to find the set of parameters that produce the best fit to the original data.

In this work the GADGET version 2.2.00 was employed (<u>http://www.hafro.is/gadget/index.html</u>) to create an age-length structured multispecies model considering different fleets and sub-populations as well as their interactions. Cod and redfish were considered both as prey and predators; while shrimp was modeled as prey (Figure 3). In addition other zooplankton invertebrate groups, as well as demersal and pelagic fishes were included as exogenous input variables in the model. The approach followed was developing first three separate single-species models (cod, redfish and shrimp), and second a multispecies model that incorporates the interactions among these modeled and other external species.

3.- Single species models

All the three stocks were modeled over the period from 1988-2012, with a 3 month time step and the assumption of no migration and no differences all over the Flemish Cap in mortality (whether predation, fishing or residual mortality) or growth. For this reason a unique area was considered for all the three stocks.

Other characteristics for each single-species model are outlined in tables 1, 2 and 3 for cod, redfish and shrimp respectively.

Due to data limitations and based on the previous knowledge that points to similar mortality rates, diet composition and growth up to age 15 for *S.mentella*, *S.fasciatus* and *S.norvegicus* (Saborido-Rey et al. 2004), these three species were considered together in this model as the redfish stock. However, due to the important differences in age and length at maturation for male and female (Saborido-Rey 1994), redfish was split in male and female sub-stocks. For Northern shrimp, sex was also considered but in a sequential way. Since this species is a protandrous hermaphrodite species, in the model individuals are recruited as male, and after a reproductive period with this sex it changes to female primiparous, and later to female multiparous (Bergström 2000). Sexes were combined in cod since data on size distribution by sex was not available. Sex change in shrimp and maturation in all the three species were modeled internally (i.e. during the process of optimization of model parameters) with a logistic model based on length (Begley 2005). Based on information from previous studies showing high variability over the study period in the maturation process in cod and shrimp (also for the sex change in shrimp) (Casas-Sánchez 2012, Pérez-Rodríguez et al. 2013), 12 and 9 periods were considered respectively. However, for redfish maturity change only one period was considered both for males and females. Sex change and maturation were modeled with a logistic model based on length:

$$P(l) = \frac{1}{1 + e^{-4\alpha(l_l - l_{50})}} \tag{1}$$

where P(l) is the probability of maturing (or changing the sex) at a given length l, l_i is the middle length of the length group i, l_{50} is the length at which 50% of the individuals become mature (or changing the sex in shrimp) in a given year, and α is a parameter to be estimated. It was assumed that all the three stocks mature or change from male to female in the last time step (4th time step) of the year.

For all the three species the initial population was estimated as the number of individuals by age in year 1988. Recruitment was annually estimated for all the three stocks as the number of individuals at age 1 on 1st January. In the redfish stock, the estimated recruits were split into males and females assuming that 50% of individuals at age 1 belonged to each sex. The mean length and standard deviation at recruitment was fit every year for the cod stock, while for redfish three different periods 1988-1993, 1994-1997 and 1998-2012 were considered; and for shrimp two periods, 1988-2003 and 2004-2012. As part of the GADGET performing, the mean length and standard deviation at age 1 are used to produce the size distribution of recruits assuming a normal distribution.

The Von Bertalanffy growth model was used to define the growth curves for all the three species. For cod, the model was fit to the data annually, while for the redfish and shrimp stocks this model was fit separately for the same periods defined above for the mean length at recruitment. For each species the average standard deviation at age around the mean length was calculated externally for the whole time period. In gadget the mean growth in length during a time step is estimated for each length group using the fit Von Bertalanffy growth function. The length distribution around the mean was estimated according to the average standard deviation at age assuming a beta-binomial distribution. A unique length-weight relation was fit for all time steps and years. Although GADGET can model all the processes in a monthly basis, here a 3 month framework (4 time steps by year) was considered instead.

The commercial fleet targeting cod in the Flemish Cap was modeled as two different fleets: trawl and gillnet. The longline fishery was not considered due to its low importance and the shortage of information. For redfish the pelagic and bottom trawl fishery were simplified to a unique trawl fishery due to the lack of information about total catches and size distribution by season in the pelagic fleet. The shrimp fishery was also considered for the redfish stock due to the important by-catch of juvenile redfish during the early-mid 1990's, especially before the introduction of a sorting grid in 1995. The only fishing gear targeting the shrimp stock was the bottom trawl.

Instead of assuming that the declared catches were exact, some flexibility around the total catch was allowed for all the fleets considered in this study, including the survey fleet. Total catches were simulated in the model for each fleet and time step using the equation:

$$C_{sl} = E S_{sl} \Delta_t N_{sl} W_{sl} \tag{2}$$

where C_{sl} is the catch in kg for a given species and length cell, E is the scaling factor for the part stock that is caught, Δ_t is the length of the time step, N_{sl} is the number of individuals and W_{sl} the mean weight of that species in the length cell. The parameter E was estimated annually for each commercial fleet, resembling the changes in effort over time. However for the survey fleets only one parameter was estimated for each species, in order to keep the effort constant over time. S_{sl} is defined by the suitability function and determine the proportion of the length group that will be caught by the fleet.

The suitability function employed in the model was variable depending on the fleet. Most trawl fleets were assumed to fit to a logistic function of length, called in gadget the Exponential50 suitability function:

$$S(l) = \frac{1}{1 + e^{-4\alpha(l_i - l_{50})}}$$
(3)

where S(l) is the proportion of the species at a given length l that is potentially caught by the fleet, l_i is the middle length of the length group I, l_{50} is the length at which 50% of the individuals are potentially fished, and α is a parameter to be estimated.

For the cod gillnet fleet, the redfish survey fleet and catches of redfish by the shrimp trawl fleet, the suitability curve was assumed to have a dome shaped relation with length. In gadget this is called the Andersen suitability function and is implemented for any prey-predator interaction:

$$S(l,L) = \begin{cases} p_0 + p_2 e^{\frac{-\left(ln_l^L - p_1\right)^2}{p_4}} & \text{if } ln_l^L \le p_1 \\ p_0 + p_2 e^{\frac{-\left(ln_l^L - p_1\right)^2}{p_3}} & \text{if } ln_l^L \ge p_1 \end{cases}$$
(4)

where S(l, L) is the proportion of the species at a given length l that is potentially caught by the fleet. L denotes the length of the predator, which is a meaningless concept when the predator is a fleet and takes a constant value, the average length of the species. p_0 , p_1 , p_2 , p_3 and p_4 are parameters to be estimated and define respectively the lowest suitability (assumed to be 0), the dispersion of the curve, the maximum suitability (assumed to be 1) and the shape of the left and the right slope.

With equations 2, 3 and 4, total catches (numbers and biomass) by time step, fleet and species are estimated and distributed by length. Due to the expected different pattern of exploitation for cod and redfish before and after the collapse of cod stock, the commercial fleets for these species were split into two different periods, 1988-1998 and 1999-2012. Consistently, two different sets of parameters for the suitability functions were fit.

The residual natural mortality, defined here as the natural mortality due to other factors than predation mortality was defined externally (tables 1, 2 and 3) and fixed during the model optimization. In previous studies a natural mortality of 0.5 for all ages was estimated as the most plausible value for the Flemish Cap shrimp (Skúladóttir 2004). Considering that natural mortality due to predation by cod and redfish is explicitly modeled here and added to the final mortality, a lower residual natural mortality was assumed for each age: 0.2 at age 1 and 0.1 for the remaining ages. For cod the same approach was followed and reference natural mortality values were taken from González-Troncoso and González-Costas (2014). Lower values were set at ages 1, 2 and 3 (when cannibalism is more important), and residual natural mortality was fixed as 0.1, 0.07 and 0.05 respectively. At ages 4 to 12, when predation was expected to be non-significant, the natural mortality values were fully taken from González-Troncoso and González-Costas without modifications

(2014). In the Flemish Cap redfish, traditionally natural mortality has been assumed as 0.1 (Ávila de Melo et al. 2013). In this study, since predation by cod and cannibalism is explicitly modeled, a lower basic natural mortality of 0.05 was considered. With the intention of including the additional effect of predation by wolffishes and Greenland halibut, residual natural mortality values at ages 1-10 were set by multiplying 0.05 by the standardized EU survey biomass index of these predators over the study period. At ages 11-16, when the effect of predation by these predators is lower, a 0.05 residual natural mortality was assumed. For ages 17-25 residual values for natural mortality were taken from Efimov et al. (1986), representing the added mortality due to ageing in a long living species.

4.- Multispecies model

Cod and redfish act as both predators and prey (Figure 3). Immature and mature cod prey on immature cod, redfish, shrimp and the non-modeled prey hyperiids, euphausiids, chaetognaths, wolffishes, demersal fish and other food. Meanwhile redfish preyed on immature redfish and shrimp; as well as the non-modeled preys: copepods, hyperiids, euphausiids, chaetognaths, pelagic fish and other food. Non-modeled preys were considered in the model to estimate the importance that the state of populations of these alternative prey has in the dynamic and interactions between the modeled stocks. The "other food" category represents all the remaining prey species not specified in this model and has as main function avoiding excessive and unrealistic predation mortality in the modeled prey.

The present model has not been designed for the consumption of any prey having any effect on growth and survival of predators. The exceptions to this are 1) the direct effect of cannibalism, which by affecting the dynamic of the prey it affects the survival of juvenile stages of the predator; 2) the indirect effect that the abundance of alternative prey has on the intensity of cannibalism.

Total consumption by length, both for cod and redfish, was estimated annually for each time step using a bioenergetic model (Temming and Herrmann 2009). In GADGET, these estimates were used to model maximum total consumption rate M_L (as kg/time step) by an individual predator as a function of length and water temperature as follows:

$$M_L = m_0 \Delta t e^{(m_1 T - m_2 T^3)} L^{m_3} \tag{5}$$

Where M_L is the maximum consumption for a predator of length *L*; *T* is the water temperature; *L* is the predator length and $m_0 m_1 m_2$ and m_3 are parameters to be estimated.

Next, gadget estimated the consumption of a given prey stock at length l by the predator stock of length L (Begley 2005).

$$C_p(l,L) = \frac{N_L M_L \psi_L F_p(l,L)}{\sum_p F_p(l,L)}$$
(6)

$$F_p(l,L) = (S_p(l,L)E_pN_lW_l)^d$$
(7)

$$\psi_L = \frac{\sum_p F_p(l,L)}{H\Delta_t + \sum_p F_p(l,L)} \tag{8}$$

where $C_p(l,L)$ is the total consumption of prey p of length l by the whole predator population at length L, which is determined by N_L , the number of predator in length cell L; $F_p(l, L)$ the consumption of prey p of size lby an individual predator in the length cell L; and ψ_L the feeding level at predator length L. In addition to the sum of $F_p(l, L)$ for all prey species, ψ_L is dependent on the half feeding value H, the biomass of prey required for the predator consuming prey at a half the maximum consumption level. Due to the lack of information about this parameter it was assumed that the total prey consumption by both cod and redfish was independent of the amount of available food, and hence, the half feeding value H was set to zero. $F_p(l, L)$ depends on the suitability function S_p ; the prey energy content E_p ; N_l the number of prey at length and W_l the average weight of prey at length l. The parameter d determines the shape of the functional response of predator consumption to the abundance of the prey. In this model d was set as 1, a functional response type I.

For the modeled species, the suitability of a prey for a predator was set assuming a dome shape relation over prey length, the above mentioned Andersen function (equation 4). For a given predator size, there is a prey size for which suitability is maximum, and decreases at both sides. The maximum suitability, the relation between prey and predator size, as well as the asymmetry of this curve was set by the parameters: p_0 , p_1 , p_2 , p_3 and p_4 . For the non-modeled preys chaetognaths, hyperiids, copepods, euphausiids, wolffishes, demersal fish and pelagic fish a constant suitability function was assumed and hence, no variations with the predator-prey size ratio was considered.

Prey suitability is in gadget a relative index, set at 1 for the most preferred prey and decreasing in order to the lowest value for the less preferred one. Suitability values are representative of the importance of a prey in the diet related with its relative importance in the ecosystem. These parameters, as done for all the other parameters of the prey-predator size curve and the consumption model were estimated externally.

5.- Parameter estimation and model validation

Parameters in GADGET are optimized using a two-stage iterative process combining a wide area search (Simulated Annealing) and a local search (Hooke and Jeeves) algorithm (Begley and Howell 2004). The iterative nature of the procedure is designed to try and arrive to a global rather than local solution. The model minimizes a total quasi-likelihood value, i.e. the result of a weighted sum of the score of all the components in the model. In this model different likelihood components were specified for each modeled stock: total commercial catch, survey index of biomass, size distributions of catches, age-length keys, maturity state, sex state (only shrimp) and diet composition. The optimal weight given to each likelihood component was estimated with the function gadget.iterative, of the R package Rgadget (https://github.com/rforge/rgadget), which follows the process described in Taylor et al. (2007). An exception to this were the weights given to all the commercial catch likelihood components, which were fixed at very high values with the intention of allowing some differences between observed and estimated catches, but simulating as much as possible the declared catches. A sensitivity test was conducted to confirm that an optimum was reached for all the parameters.

RESULTS and DISCUSSION

<u>1.- Model fit</u>

<u> 1.1.- Cod</u>

The model estimated values of biomass and abundance survey indices (including the recruitment index proxy, or smaller than 25cm individuals), as well as catches in kg for the trawl and gillnet were very close to the observed values (Figure 4). The high similarity obtained for the estimated and observed commercial catches was due to (as pointed in the material and methods section) to the high weight assigned to these likelihood components. The estimated size distribution of catches showed also in general a high similarity with the observed distributions in gillnet and trawl commercial catches as well as in the survey fleet catches (Figure 5, 6 and 7 respectively). However, in the trawl fishery there was a marked deviation of the estimated size distribution relative to the observed since 2012. This deviation could be related with the observed change in the pattern of selectivity of this fleet in the last years (González-Costas et al. 2015). Similarly the model estimated survey fleet size distribution tends to have higher proportions of individuals at larger sizes. This is especially observed in those years of high recruitments, like 1991 or 2010-2012. This fact may be argued to be potentially a reflection of two factors: 1) a removal of individuals larger than 50 cm in those years of high recruitments either as result of increased natural mortality or migratory processes; 2) a change in the catchability (maybe dome shaped curve instead of logistic) of larger individuals in those years of high abundance of juveniles. This will need to be explored in the future. The maturity ogives by length were fit by the model in a two years group basis. The estimated proportion of mature individuals was in general very similar to that described by the observed maturity ogives (Figure 8), with the exception of year 1994.

1.2.- Redfish

In the redfish stock, the model estimates were very similar to the observed indices of biomass, total abundance and abundance of individuals smaller than 12 cm length, as well as total redfish trawl fleet catches and shrimp trawl fleet by-catches (Figure 9). However, in this stock there was a higher deviation from the observed biomass and abundance indices in some years between 2005 and 2011. The size distribution of the redfish by-catch from the shrimp trawl fishery was well fitted by the model (Figure 10). With the exception of a few seasons in some years, the size distribution of catches from the redfish trawl fishery was also well simulated (Figure 11), like the EU survey fleet size distribution (Figure 12). Although already mentioned in the material and methods section it is important to highlight again that in order to obtain a closer similarity between model estimates of size distribution to the observed in the survey catches an Andersen suitability function (dome shaped selectivity function) was utilized for the survey fleet. In figure 12 it can be observed that in the observed size distribution (black points) those years of high recruitments (as those of 1991 and 2001), the peak in the size distribution nearby to 30cm the year before (in 1990 and 2000) disappeared. If an Exponential50 (logistic selectivity function) was used instead for the survey fleet suitability function the estimated size distribution did not simulated properly this sudden disappearance at 30 cm size (Figure 13) and hence, the estimated size distribution in years after (especially after 2001) showed a higher proportion of large individuals than were really observed. This fact, as already mentioned above for cod, may be suggested to be a reflection of either a removal of individuals larger than 30 cm in those years of high recruitments (as result of increased natural mortality or migratory processes), and/or a change in the survey catchability of larger individuals in those years of high abundance of juveniles. These questions need to be explored in the future and will probably require of directed research work as the analysis of the acoustic signal during the EU survey or specific analysis in order to evaluate the vertical distribution and migratory patterns of redfish under different oceanographic and demographic conditions. The maturity ogives were fit assuming a constant maturity ogive over time. As shown in figure 14 the observed proportion of mature individuals was well fit by the model.

1.3.- Shrimp

All the observed data for survey indexes of biomass and abundance, as well as the catches from the commercial fleet showed a very similar pattern, which were well fitted by the model (Figure 15). In years 2002, 2003 and 2005 there were higher differences especially in the index of abundance. However despite these higher differences it could be considered that the model fit properly the observed data. The size distribution of the survey fleet (Figure 16) despite was globally well fitted, showed marked deviations from the observed values in years 1988-1989 and 2011-2012. The observed size distribution for the commercial trawl fleet was in general well fit by the model (Figure 18). Since the data from the shrimp trawl fishery was thoroughly sampled by the Icelandic fleet, and this size distribution was very well fitted by the model, the deviation in the survey fleet size distribution of males, females primiparous and multiparous was fit from year 1994 onwards by means of optimizing the parameters that defined the female maturity and sex change ogives. These estimated proportions showed some difference in relation to the observed values (Figure 17), especially in the last years. This could be improved in the future, but at this moment is expected to be of low impact in the results since recruitment is not connected to the mature stock at this stage.

1.4.- Diet composition

The model estimated diet fit very closely the observed one, both for cod (Figure 19) and redfish (Figure 20). In both species the model represented important changes over the study period, with variations in the relative importance of all modeled and non-modeled preys. The proportion of shrimp exhibited an increasing trend since 1988 both in cod and redfish diets, and reached the highest values in the late 1990s and stayed at similar proportions until 2004-2005. In these years shrimp was around 25-30% of the diet for immature and mature small cod, 15-20% for mature redfish and large cod and 10% for immature redfish sub-stock. Redfish was a relevant prey all over the study period for both small and large mature cod but it was especially since 2000 when its proportion in cod diet increased steadily until maximum values in 2009-2010 (25% in the small and 65% in large mature cod). Cannibalism provided an important percentage to the diet of mature

redfish those years when recruitment was high, like in the early 1990s and all over the period 2001-2007 (4.5%). In cod, cannibalism was also important and related to successful recruitments in late 1980s and early 1990s (average 12%) and 2010-2012 (average 7.8%).

The estimated percentage of the non-modeled prey in the diet of both cod and redfish was noteworthy. Hyperiids, euphausiids and chaetognaths were very important prey for both predators; while copepods were a main prey only for redfish. The four pelagic groups together accounted for c.a. 50% of diet in immature cod, 75% in immature redfish, and 50% in mature redfish. In small and large mature cod, although it was lower, these prey still contributed to an average 35% and 20% respectively. Wolffishes were a very important prey in the diet of large mature cod, until late 1990s, with an average 32% of the diet. Pelagic fishes (mostly myctophids) had a prominent role as fish prey in immature, but especially in mature redfish (average 5% and 15% respectively).

2.- Model population and mortality estimates

2.1.- Cod, redfish and shrimp stock dynamic

Model estimates of annual recruitment at age 1 (Figure 21), total abundance (Figure 22) and total biomass by maturity and/or sex state (Figure 23) over the study period were highly variable. Cod recruitment was high in years 1991 and 1992, which was reflected in a subsequent rise in the immature and total stock abundance. However, this increase was followed by a steep decline in years 1993-1995, due to the lack of good recruitments and the reduction in the abundance of both immature and mature sub-stocks. Cod biomass remained at relative high values up to 1995, followed by a sharp decline until 1998, when the lowest value in the study period was reached. Over the period 1995-2004 estimates of cod recruitment were very low and consequently modeled stock abundance and biomass continued at minimum values over this period. However, in 2005 recruitment was above the average of the previous years and stayed at similar values until 2009, which produced an increase in the abundance of the immature and subsequently the mature substocks. In the period 2010-2012 recruitment was very high, especially in year 2011 when the highest recruitment of the study period was estimated. The immature and total stock abundance reached the highest values since 1988 in these years, while the total biomass reached the highest value in 2012, with good year classes in both the mature stock stemming from cohorts 2005-2009 and the immature stock from recent recruitments (2010-2012).

Estimates of recruitment in the redfish stock were very high in the period 1990-1992 (Figure 21). This produced a marked increase in population abundance in 1991 (Figure 22), principally in immature individuals. However this did not translate into total biomass (Figure 23), which showed a marked reduction in total biomass produced by the drop of the mature biomass and since 1990 also the immature sub-stock. After the increase in 1991-1992, the stock abundance showed a sharp decline due to the decrease in the immature stock, reaching the lowest values in the late 1990s. However, over the period 2001-2007 the model estimated a series of high annual recruitments, which were especially high in 2001, 2004, 2006 and 2007. These recruitments produced an increase of the stock abundance until 2007, when the highest value was attained. The increase in total stock biomass as result of these successful recruitments became more pronounced since 2003 due to the contribution of the immature sub-stock, and reached the highest value in 2009. Despite the mature sub-stock continuing the increasing trend in abundance, since 2007 total abundance declined sharply due to the reduction in the immature stock. The decline in total abundance was followed by the reduction of total stock biomass since 2010.

Despite being during the "burn in" period when caution is advised in interpreting the results, the model indicates that in 1988-1989 the shrimp stock experienced good recruitments (Figure 21) that produced the increase in the abundance of the male sub-stock in those years (Figure 22) and was the start of a growing trend in the stock biomass (Figure 23). However it was after 1993 that the highest recruitment values were estimated, in a series of successful cohorts that lasted until 2006. These high recruitments were reflected in the abundance of male, female primiparous and multiparous sub-stocks with a delay of c.a. two years from one sex-maturation stage to the next. The stock biomass showed a steady improvement until a maximum value in 2001, followed by a steady and continued decline that was not compensated by the high recruitments

that kept the abundance at high values until 2004. This declining trend was mostly due to the reduction in the male sub-stock, however it was also observed in the primiparous and multiparous stocks. In 2012 the total biomass reached the lowest value since 1988.

2.2.- Instantaneous and harvest rates by source of mortality

The mortality rates by age due to fishing (F) and to predation by cod (M_{cod}) and/or redfish ($M_{redfish}$) were estimated for each modeled stock (Figures 24, 25 and 26). In cod cannibalism was the main source of mortality at age 1 all over the study period (Figure 24), with the highest values in the early and late years. At age 2, cannibalism showed a similar pattern but in this case the highest values occurred in the last years, when the abundance of older and cannibalistic cod was higher. Since the reopening of the fishery in 2010, both M_{cod} and F had been similar at age 3 (close to 0.2). At age 4 and older, cannibalism was negligible and fishing accounted for most of annual mortality, which was extremely high before the collapse (F>1.5 at all ages in 1994). Since the reopening of the fishery in 2010, F at ages 4 and older stayed at relative low values in comparison with the levels of mortality during the 1990s. These high levels of cannibalism are in agreement with the observed in other areas at both sides of the Atlantic, with a high variability that has been related with fluctuations in recruitment (Bogstad et al. 1994, Fromentin et al. 2000, Lilly and Gavaris 1982, Neuenfeldt and Köster 2000, Tsou and Collie 2001).

In the redfish stock before 1996 the main cause of mortality for individuals younger than age 7 was predation by cod, with M_{cod} ranging from 0.1 to 0.3 (Figure 24). This range of ages were also affected by the shrimp trawl fishery in the period 1993-1995, with F=0.2 in average, that removed an important portion of the small population. Cannibalism was important in the early 1990s, but it was since 2000 when M_{red} showed an increasing trend from 0.07 to 0.36 in 2009 at age 1 and values above of 0.1 at age 2. For redfish older than age 9, the redfish trawl fleet was the main cause of mortality during the first part of 1990s, with values above 0.5 at most ages in years 1990-1992. After 1996, fishing mortality by the redfish trawl fleet decreased and stayed at very low levels despite the slight increase observed since 2007. From 2007-2010, M_{cod} became the most important source of mortality for all ages, with values above 0.2 for ages 2 to 9 and between 0.1 and 0.2 for ages 10 to 18. The exception to this was the age 1 redfish, for which M_{red} remained as the main cause of mortality. In agreement with these results, cannibalism in redfish has been reported before not just in the Flemish Cap (Albikovskaya and Gerasimova 1993), but also in other areas in the Northwest Atlantic including West Greenland (Pedersen and Riget 1993) or the Gulf of St. Lawrence (Savenkoff et al. 2006a), where it was responsible for 10-15% of total mortality. Equally, redfish predation by cod has been described in the Flemish Cap (Casas and Paz 1994, Lilly 1980, Pérez-Rodríguez and Saborido-Rey 2012) and other North Atlantic areas (Yagarina et al. 2011) as one of the most important sources of redfish mortality.

Other than the residual natural mortality, before the start of the shrimp fishery in 1993 the main source of mortality for shrimp was cod predation (Figure 16), with M_{cod} above 0.2 for ages 1-2, 0.2 for ages 3-4 and over 0.1 for ages 5 to 7. Since 1990 to 1995 M_{cod} declined steadily. Since 1993 until 1996 F raised to very high values (higher than 1) for ages 3 to 7. Since 1997 to 2005 F was lower for all ages, but it was still above 0.1 for age 2, 0.3 for age 3 and 0.6-1 for ages 5-7. Since 2006 fishing mortality showed a steady decline until 2011 when, with the moratoria, it became again zero. Since 2000, the estimated M_{red} showed an increasing trend for all ages, but especially at ages 1-3 (higher than 0.5 in 2009 for age 2 shrimp). M_{cod} increased steadily since 2005 for all ages and by 2012 was very similar to Mred.

3.- Comparison with single species stock assessment results

<u> 3.1.- Cod</u>

Trends in the estimates of total population biomass were very similar to the estimated by the current Bayesian XSA single species stock assessment model (Figure 27) (González-Troncoso 2015). However the multispecies model produced higher values of biomass in the last years, which was due to differences in the estimated Spawning Stock Biomass (SSB). These differences in the total SSB could be partially explained by the higher estimates on recruitment in years 2005 and 2006, as well as by the difference in the age of the plus group. While in the multispecies model the plus group is set at age 12, in the single species model this group

is defined at age 8. This difference could lead to a higher biomass in the SSB of the multispecies model in the last years, especially after a long period without fishing activity that would allow in the model a high proportion of survivors for those cohorts after 1996. Estimates of recruitment at age 1 were much higher in the multispecies model since 2010 which could be due to the fact that cannibalism is not considered in the single species model. All these questions will need further research in the future.

<u> 3.2.- Redfish</u>

The estimated total stock biomass for individuals older than age 4 (Figure 28) showed very important differences in relation to the estimates from the single species stock assessment model (Ávila de Melo et al. 2013). These differences may be related with different factors: 1) they are in essence two different model approaches; 2) in the single species stock assessment only the beaked redfish species (*Sebastes mentella* and *S. fasciatus*) are included, while in the multispecies model, in addition to these species *S. norvegicus* was also considered; 3) despite the single species stock assessment tried to include in 2013 part of the mortality due to predation (Ávila de Melo et al. 2013), it is not comparable to the explicit modelling of natural mortality by predation considered by the multispecies model, which would lead to higher estimates of biomass. In addition to this structural features survivorship of cohorts 1990-1991 from the intense by-catch from the shrimp trawl fishery was higher in the multispecies model than in the single species XSA model (Ávila de Melo et al. 2013). These, in addition to other factors as migrations, changes in natural mortality and catchability, as well as the difference due to a different plus group in both models (19+ in the single species model in comparison to the 25+ group in the multispecies model) will be explored in the future.

4.- <u>Multispecies Maximum Sustainable Yield (MSY) estimates</u>

In order to show the potential of this gadget multispecies model for the estimation of joint MSY for cod, redfish and shrimp a preliminary exercise was conducted. The fit model was employed to perform long term simulations, where:

- Simulation was run for the period 2013-2200
- Length-weight relationship, growth, consumption, and several other life-history related parameters were averaged to the period 2007-2012
- Ricker stock recruitment relationship fit to the model estimates of recruitment at age 1 and SSB.
- 10 different levels of fishing mortality for each species: 1000 combinations (1000 different runs).
- For each of these 1000 runs the total stock biomass, SSB, total catches and recruitment for each species was estimated.
- Using these 1000 estimations exploring the stock biomass, SSB and MSY for different fishing mortality levels.

Figures 29 and 30 show preliminary estimations for total SSB and MSY respectively. In the lower and upper box limits the boxplots depict the 25 and 75 percentiles of all the different SSB and MSY values obtained by fishing mortality level, and the median in the black centered line. Despite the model is still in an early stage of development the overall values of biomass and MSY estimated for each species in relation to changes in fishing mortality in the other species were in sensible orders of magnitude. In addition it showed interesting patterns result of the negative effect of fishing mortality in prey or predator stocks. On this regard, it is interesting to note that the expected patterns of decrease in biomass as result of increasing fishing pressure were observed in all the three stocks. But other than this trivial fishing-stock reaction, more interesting secondary reactions were observed like the negative effect of higher fishing mortality on redfish or shrimp in total production and MSY for cod. The effect of prey abundance on predator growth has not been model at this stage, and this negative impact was the result of the increased cannibalism that the reduction in main prey as redfish and shrimp produced in cod stock. It is also interesting the positive effect in redfish biomass and MSY produced by increasing cod fishing mortality. The same is observed in shrimp biomass and MSY in relation to redfish and cod fishing pressure. In conclusion, estimated stock biomass and MSY values cannot be taken for any management decision at this stage, since the SSB-Recruitment relationships and the multispecies model that produce these estimations still need further work, improvements and checking. However, it is evident that the multispecies model for the Flemish Cap is already producing estimates and simulations of population dynamic that are in reliable orders of magnitude and that further work in this line would produce useful estimates.

CONCLUSIONS

The modeling results presented here are able to disentangle the interconnected drivers of the abundance of the cod, redfish and shrimp stocks in the Flemish Cap. Overfishing, predation and cannibalism, and variable recruitment success have combined to produce strong swings in the biomass of all three stocks. The model has shown that predation was the explanation to most of the changes observed lately in the three main commercial species in the Flemish Cap. In shrimp, both predation by redfish and fishing have worked together driving the collapse of the shrimp stock, with the final contribution of predation by cod. The portion of large cod in the stock, especially since 2010, raised the predation mortality on redfish and seems to be the main factor inducing the decline of abundance and biomass in the last years. The model has also described that during those years of high recruitment cannibalism has been the main source of mortality both in juvenile cod and redfish, and has reduced significantly the expectative of increasing the biomass of the stock. In this regard, predation (including cannibalism) and fishing have co-occurred at age 3 in cod and most ages in redfish and shrimp in recent years. Additionally, the model has revealed the relevance of external prey groups like hyperiids and eupaussids for immature, small mature cod and redfish, the genus Anarhichas sp for large mature cod, and copepods for redfish. These results suggest that the potential decline of some of these alternative prey groups may have important consequences in the dynamic of the commercial species by changing predatory (and cannibalism) interactions.

Therefore, the results of this work clearly indicate that disregarding the species interactions in the assessment of the Flemish Cap cod, redfish and shrimp would lead to serious underestimates of both the magnitude and the variability of natural mortality. This would involve an overestimation of the exploitable biomass in the short-term projections supporting management decisions, both by an excessive positivism in relation to the future survival of successful recruitments and the overestimation of survivorship for the fishable part of the stock. Meanwhile, it has been also shown that due to the prey-predator size relationship and the dynamic of prey-predator stock populations induced by variable recruitment, trophic interactions have a high degree of plasticity and are beyond of being only species interactions but size-modulated specific interactions. This should be seriously considered when evaluating the effect of a predator on a prev stock, otherwise the assessment of predation mortality could be misleading. The multispecies model developed in this work presents a very suitable tool not just to understand the importance of predation, fishing and recruitment as drivers in the dynamic of the Flemish Cap system but also to quantify the shape and magnitude of species interactions as well as synergies among drivers, which could be used to support the stock assessment in the Flemish Cap. Finally, due to the capacity of this multispecies model to simulate complex interactions and feedbacks between the modeled stocks, it appears as an ideal operative model to be used for risk analysis in a management strategy evaluation framework for the Flemish Cap.

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FIGURES



Fig. 1. The Flemish Cap is located within the regulatory area of the Northwest Atlantic Fisheries Organization (NAFO) corresponding to the Division 3M. The Flemish Pass, a channel deeper than 1100m, separates the Flemish Cap from the Grand Banks of Newfoundland.



Fig. 2. Total catches and catches of the main targeted species in the Division 3M. These species accounted for 94% of total catches since 1960. The vertical dotted line indicates the start of the study period (year 1988). These data were obtained from the NAFO website http://www.nafo.int/about/frames/about.html.



Fig. 3. Species interactions modeled in this study. Cod, redfish and shrimp are fully dynamically modeled, whereas species/prey groups in grey text boxes are incorporated as time series or constant values. The fleets fishing each species are also represented, as well as the effect of water temperature in total consumption.



Fig. 4. Cod survey indexes of biomass, abundance and abundance of individuals smaller than 25 cm (upper row). Total cod catches in tones by the international trawl and gillnet fleets (lower row). Red lines are the estimated values with GADGET versus black points which represent the observed data.



Fig. 5. Size distribution (in proportion relative to 1) of cod catches by the gillnet fleet. The label in each subpanel represents the year and the season (Years: 1988 to 2012; Seasons: 1 to 4. For example 1988-1 refers to winter of 1988). Red lines are the estimated values versus black points which represent the observed data.



Fig. 6. Size distribution (in proportion relative to 1) of cod catches by the commercial trawl fleet. The label in each subpanel represents the year and the season (Years: 1988 to 2012; Seasons: 1 to 4. For example 1988-1 refers to winter of 1988). Red lines are the estimated values versus black points which represent the observed data.



Fig. 7. Size distribution (in proportion relative to 1) of cod catches by the survey fleet. The label in each subpanel represents the year (Years: 1988 to 2012). For this fleet the season is always 3 (summer), when the survey takes place. Red lines are the estimated values versus black points which represent the observed data.



Fig.8. Cod maturity ogives as probability, relative to 1, of being mature with total fish length. Estimated probabilities by the fit model in red color lines; Observed proportions in black color points.

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Fig. 9. Redfish survey indexes of biomass, abundance and abundance of individuals smaller than 12 cm (from left to right in the first row). Total redfish catches in tones by the international redfish trawl, shrimp trawl (as by-catch) fleets.



Fig. 10. Size distribution (in proportion relative to 1) of redfish by-catches in the shrimp trawl fleet. The label in each subpanel represents the year and the season (Years: 1988 to 2012; Seasons: 1 to 4. For example 1988-1 is winter of 1988). Red lines are the estimated values versus black points which represent the observed data.



Fig.11. Size distribution (in proportion relative to 1) of redfish catches in the redfish trawl fleet. The label in each subpanel represents the year and the season (Years: 1988 to 2012; Seasons: 1 to 4. For example 1988-1 is winter of 1988). Red lines are the estimated values versus black points which represent the observed data.



Fig. 12. Size distribution (in proportion relative to 1) of redfish in the survey fleet. The label in each subpanel represents the year (Years: 1988 to 2012). For this fleet the season is always 3, when the survey takes place. Red lines are the estimated values versus black points which represent the observed data.



Fig.13. Size distribution (in proportion relative to 1) of redfish in the survey fleet. The label in each subpanel represents the year (Years: 1988 to 2012). For this fleet the season is always 3, when the survey takes place. Red lines are the estimated values assuming an Exponentical50 suitability function (logistic selectivity function) versus black points which represent the observed data.



Fig. 14. Redfish maturity ogives as probability, relative to 1, of being mature by total fish length. Estimated probabilities by the fit model in red color lines; Observed proportions during the survey as black color points.



Fig. 15. Shrimp survey indexes (swept area method) of biomass (upper-left panel) and abundance (upperright), and catch in tones by the international trawl fleet (bottom-left), and in kg for the EU survey fleet (bottom right).



Fig. 16. Distribution by carapace length (in proportion relative to 1) of shrimp in the survey fleet. The label in each subpanel represents the year (Years: 1988 to 2012). For this fleet the season is always 3, when the survey takes place. Red lines are the estimated values versus black points which represent the observed data.



Fig.17. Shrimp sex change and maturity ogives as probability, relative to 1, of being male (grey color), female primiparous (red color) and female multiparous (blue color) with carapace length (in cm). Estimated probabilities by the fit model are represented by continuous lines while the observed proportions are represented by points.

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Carapace length (cm)

Fig. 18. Distribution by carapace length (in proportion relative to 1) of shrimp catches by the trawl fleets. The label in each subpanel represents the year and the season (Years: 1988 to 2012; Seasons: 1 to 4. For example 1988-1 is winter of 1988). Red lines are the estimated values versus black points which represent the observed data.



Fig. 19. Model estimated diet (left column) and observed diet during the EU survey (right column) for immature cod (cod.imm), small mature cod (<85cm; cod.mat.small) and large mature cod (>85cm; cod.mat.large), represented as the average proportion (relative to 1) of each prey in the stomach content from 1993 to 2012.



Fig. 20. Model estimated diet (left column) and observed diet during the EU survey (right column) for immature redfish (red.imm) and mature redfish (red.matu), represented as the average proportion (relative to 1) of each prey in the stomach content from 1993 to 2012.



Fig.21. Annual recruitment at age 1 as estimated by the GADGET model for each of the three stocks.



Fig. 22. Annual estimates of stock abundance, total and by maturity stage, for each of the three modeled stock (top: cod, middle: redfish, bottom: shrimp).



Fig.23. Annual estimates of stock biomass, total and by maturity stage, for each of the three modeled stocks (top: cod, middle: redfish, bottom: shrimp).



Fig. 24. Predation mortality by cod (M_pred by cod) and fishing mortality by age in the modeled cod stock. The "Age 12+" pannel shows the mortality rates for individuals of age 12 and older.



Fig.25. Predation mortality by age in the modeled redfish stock, by cod (M_pred by cod), by redfish (M_pred by redfish) and fishing mortality by the redfish trawl fleet (F_red_trawl) and the shrimp trawl fishery (F_shrimp_trawl). The "Age 25+" pannel shows the mortality rates for individuals of age 25 and older.



Fig. 26. Predation mortality by cod (M_pred by cod), by redfish (M_pred by redfish) and fishing mortality by the shrimp trawl fleet by age in the modeled shrimp stock.



Fig. 27. Comparison of the estimated total cod stock biomass, SSB and recruitment at age 1 by the multispecies (black dotted lines) and the bayesian XSA single species model (red dotted lines).



Fig. 28. Estimated total stock biomass by the multispecies (black dotted line) and the XSA single species stock assessment model (red dotted line) (Ávila de Melo et al. 2013) of individuals older than age 4.



Fig. 29. Estimated spawning stock biomass by species (defined by column) under varying fishing mortality for another species (defined by row). The boxplots contain the variability of estimated stock biomass for all the possible combinations of fishing mortality for the other two species. Thus, the right column depicts the biomass of shrimp on the y-axis under different target fishing mortalities on cod (top), redfish (middle) and shrimp (bottom) on the x-axis.



Fig.30. Estimated MSY by species (defined by column) under varying fishing mortality for another species (defined by row). The boxplots contain the variability of estimated MSY for all the possible combinations of fishing mortality for the other two species. Thus, the right column depicts the MSY of shrimp on the y-axis under different target fishing mortalities on cod (top), redfish (middle) and shrimp (bottom) on the x-axis.

TABLES

Table 1.- Model structure, main ecological and biological features for cod stock.

	Immature	Mature_small	Mature_large		
Period	1988-2012				
Time step	3 months				
Age range	1-12				
Length range (cm)	$1 \text{ cm-} \text{L}_{50}^{*}$	L_{50}^{*} -85cm	85cm-140cm		
Length resolution	1 cm				
Fishing fleets	CT_I; CT_II;CG; EUs				
Residual mortality	Age1: 0.1				
	Age2: 0.07				
	Age3: 0.05				
	Age4-12: González-Troncoso & González-Costas (2014)				
Growth	Von Bertalanffy; annual estimate				
Maturation	Biannual maturation ogive				
Maturation date	4th timestep				
Recruitment	Annual estimate				
Age at recruitment	1				

 CT_I and CT_II : cod trawl fleet 1988-1998 and 1999-2012 respectively. CG: cod gillnet fleet. EUs: EU survey; L_{50} : Length at 50% probability of maturing.

* L_{50} refers to the maturity ogive defined by two parameters, L50 and α .

	Male_immature	Male_mature	Female_immature	Female_mature		
Period	1988-2012					
Time step	3 months					
Age range	1-25					
Length range (cm)	1 cm- L_{50}^* male	L_{50}^* male-60cm	1 cm- L_{50}^* fem	L_{50}^{*} fem-60cm		
Length resolution (cm)	1 cm					
Fishing fleets	RT_I; RT_II; ST; EUs					
	Age1-10: 0.05*standardized EU survey biomass index of wolfish and Greenland hal					
Residual mortality	Age 11-16=0.05; Age 17-25: Efimov et al (1986)					
Growth	Von Bertalanffy; 3 periods					
Maturation	One maturation ogive		One maturation ogive			
Maturation date	4th timestep		4th timestep			
Recruitment	Annual estimate		Annual estimate			
Age at recruitment	1		1			

Table 2.- Model structure, main ecological and biological features for redfish stock.

RT_I and RT_II: redfish trawl fleet 1988-1998 and 1999-2012 respectively; ST: Shrimp trawl fleet; EUs: EU survey; L₅₀ male and L₅₀

fem: Length at 50% probability of maturing for male and female sub-stock respectively.

* L_{50} refers here to the maturity ogive defined by two parameters, L50 and α , fitted separated for males and females.

Table 3.- Model structure, main ecological and biological features for shrimp stock.

	Male	Female_primiparous	Female_multiparous		
Period	1988-2012				
Time step	3 months				
Age range	1-7				
Length range (cm)	0.05 cm- L_{50sex}^*	L_{50sex}^* - L_{50mat}^*	L_{50mat}^{*} -3.8cm		
Length resolution (cm)	0.05				
Fishing fleets	ST; EUs				
Residual mortality	Age1=0.2; Age2-7=0.1				
Growth	Von Bertalanffy; two periods				
Sex change	Bi-annual ogive				
Sex change date	4th tir				
Maturation		Bi-annu	al ogive		
Maturation date		4th timestep			
Recruitment	Annual estimate				
Age at recruitment	1				

ST: Shrimp trawl fleet; EUs: EU survey; L50 sex: length at 50% probability change from male to female primiparous. L50 mat: length at 50% probability change from female primiparous to multiparous.

L50sex and L50mat refers to the sex change (males to female primiparous) and maturity (female primiparous to multiparous change) ogives ogives, defined by parameters L50 and α .