Dynamic of the Flemish Cap commercial stocks: use of a gadget multispecies model to determine the relevance and synergies between predation, recruitment and fishing

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0111.R2
Manuscript Type:	Article
Date Submitted by the Author:	11-Aug-2016
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Keyword:	Multispecies modelling, Species interactions, Ecosystem approach, Fishing, STOCK ASSESSMENT < General

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2 determine the relevance and synergies between predation, recruitment and fishing

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12

13 Abstract

14

15 Multispecies modelling is being increasingly accepted in stock assessment, especially in the
16 context of an ecosystem approach to fisheries management (EAF). To achieve a future
17 implementation of an EAF in Flemish Cap we present a multispecies model developed in
18 Gadget which covers the main commercial stocks over the period 1988-2012: cod *Gadus*
19 *morhua*, redfish *Sebastes* sp. and Northern shrimp *Pandalus borealis*. The model highlights
20 the interdependent dynamic of these stocks, and reveals strong interactions between
21 recruitment, fishing and predation (including cannibalism). These drivers have shown marked
22 changes in their relative importance by species, age, and length over time, producing a
23 transition from a traditional redfish-cod dominated system in the early 1990s, to an
24 intermediate shrimp-other fish species state by late 1990s, and in turn back to something close
25 to the initial state by late 2000s. The multispecies model developed in this paper shows that
26 disregarding the species interactions would lead to serious underestimates of natural

27 mortality, overestimations of the exploitable biomass, and highlights the need to move beyond
28 single-species management in this highly coupled ecosystem.

29 Keywords: multispecies modeling; species interactions; fishing; stock assessment; ecosystem
30 approach.

31 Introduction

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

44 Since the early 1980s, multispecies and ecosystem models have been developed more
45 intensively with diverse assumptions and scopes (Pinnegar et al. 2008). One of this models is
46 Gadget (Globally applicable Area Disaggregated General Ecosystem Toolbox), a powerful
47 and flexible framework that models marine ecosystems within a fisheries and eco-biological
48 context (Begley and Howell 2004). It has been classified as a dynamic multispecies or
49 minimum realistic model suitable for practical advice in fisheries management (Plagányi
50 2007). The model has potential applications both as an operating model in Management

51 Strategy Evaluations (MSE), and as a stock assessment modeling tool. As a multispecies
52 model, Gadget has been applied in the Barents Sea, Icelandic Sea and the Celtic Sea
53 (Lindstøm et al. 2009, Taylor and Stefansson 2004, Trenkel et al. 2004), and further models
54 are under development in the Baltic and the Bay of Biscay.

55 The Northwest Atlantic Fisheries Organization (NAFO) is in charge of the management and
56 conservation of most fishery resources in the Convention Area since 1949 (Figure 1).
57 Historically, the management of fishing resources has been based on a single-species
58 approach. However since the generalized collapse of cod stocks in the Northwest Atlantic,
59 NAFO has been promoting the development of a precautionary and more comprehensive
60 approach for fisheries management. After years of non-recovery of cod stocks, in 2008 the
61 Working group for the Ecosystem Approach to Fisheries Management (WGEAFM) was
62 created with the mission of advising the NAFO Scientific Council about the functioning of the
63 NAFO ecosystems, and more specifically on issues such as Vulnerable Marine Ecosystems
64 (VME), fisheries production potential, ecological production units and with special interest
65 the interactions between species (NAFO 2010a, b).

66 The Flemish Cap is a deep water sea-mount located in the international waters of NAFO
67 division 3M (Figure 1). Despite the influence of the North Atlantic Current, the Labrador
68 Current dominates the water mass properties (Colbourne and Foote 2000). The cap is
69 separated from the Newfoundland shelf by the Flemish Pass, a channel characterized by
70 depths greater than 1100 m. This channel hinders migratory movements for juvenile and adult
71 stages of shallow demersal species like Atlantic cod (*Gadus morhua*, Linnaeus, 1758)
72 (Templeman and Fleming 1963, Konstantinov 1970). In addition a quasi-permanent anti-
73 cyclonic gyre dominates the oceanography over the Cap (Colbourne and Foote 2000),
74 resulting in retention of eggs and larvae within the Flemish Cap. Accordingly, the Flemish
75 Cap is a largely separate ecosystem from the Grand Banks, as shown by the genetic

76 differences found in cod (Bentzen et al. 1996, Carr and Marshall 2008) and Northern shrimp
77 *Pandalus borealis* (Jordel et al. 2014), and reinforced by the different dynamics observed in
78 the 3NO and 3M cod stocks after the 1990s collapses (González-Troncoso 2015, González-
79 Troncoso et al. 2015).

80 As a typical boreal ecosystem, in the Flemish Cap most of the biomass and production is
81 concentrated in a few species connected by strong trophic interactions (Pérez-Rodríguez
82 2012). Zooplankton is mostly dominated by copepods, hiperiids and chaetognaths, which
83 constitute the basis of the diet for a pelagic fish community that in the Flemish Cap is
84 characterized by the lack of key traditional boreal fish species like sandlance (*Ammodytes sp.*)
85 or capelin (*Mallotus villosus*, Müller, 1776). Instead, the pelagic fish community is mostly
86 formed by deep water species like myctophiids, and especially by the demersal-pelagic redfish
87 species (*Sebastes norvegicus*, Ascanius, 1772; *Sebastes fasciatus*, Storer, 1854; *Sebastes*
88 *mentella*, Travin, 1951). The piscivorous guild preys on pelagic fishes and is mostly
89 represented by large cod, although wolffishes *Anarhichas sp* (Linnaeus, 1958) and Greenland
90 halibut *Reinhardtius hippoglossoides* (Walbaum, 1792) are also of high importance when the
91 cod stock is reduced (Pérez-Rodríguez et al. 2011). As a result of the absence of sandlance
92 and capelin, a particular feature in the Flemish Cap is the high relevance of zooplankton in the
93 diet of medium size individuals of piscivorous species (Gomes 1993, Pérez-Rodríguez 2012).
94 The Northern shrimp (hereafter named simply as shrimp) is a key component in the trophic
95 web in the Flemish Cap (Parsons 2005), being preyed on by most demersal fish species and
96 especially by cod and redfish (Pérez-Rodríguez et al. 2011, Román et al. 2004). Preliminary
97 studies in the Flemish Cap have suggested that the dynamics of redfish and shrimp stocks are
98 strongly influenced by cod predation (González-Iglesias and Casas 2012a, NAFO 2012,
99 Pérez-Rodríguez et al. 2011), while cannibalism might control the degree of recruitment
100 success in cod (NAFO 2013).

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

117 Based on the relative simplicity of the food web in the Flemish Cap with strong trophic
118 connections between the most important commercial species (i.e. cod, redfish and shrimp),
119 the relatively high isolation of the demersal community in relation to the nearby Grand Banks
120 and the high availability of data from the commercial fishery and the European Union bottom
121 trawl survey, the Flemish Cap constitutes an ideal case study for the development of the
122 multispecies and ecosystem approach to fisheries in NAFO. The purpose of this study was the
123 development of a Gadget multispecies model for the Flemish Cap ecosystem including cod,
124 redfish and shrimp. The first objective was therefore to parameterize a multi-species model
125 for a historical time-series of population and diet data. As a second goal, this 'base case'

model was used to investigate the relative importance of trophic interactions, fishing, and recruitment variability on the dynamics of the cod, shrimp and redfish populations. The influence of alternative food components was also evaluated.

Material & Methods

Data

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. Population length 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 (Vázquez et al. 2013). 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 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 species in general. 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 for zooplankton, demersal and pelagic fishes (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, time series of total biomass for these groups. Once estimated externally (as explained below), these biomass time series were fixed in the model during the optimization and served as alternative prey source to the predators cod and redfish.

With the exception of years 2007, 2009 and 2011, stomach content information for cod and redfish has been sampled annually since 1993 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. In addition, the lengths of sampled predator individuals and prey 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 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

Seasonal catch and size distribution 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 (average 80% of total catches), this seems a reasonable simplification. In the shrimp model, the information from the Icelandic fleet was taken as the basis for size distributions (average 30% of total catches).

Model:

Gadget is a process-based model that allows the user to include a number of biological and ecological features 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). The model is age and length structured, allowing length data to be used directly and for processes such as fishing selectivity and predation to be modeled on a length basis. The model is freely available and fully described at <http://www.hafro.is/gadget/index.html>. In this work the version 2.2.00 was employed.

Individual stock 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. 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

197 redfish stock. However, due to the important differences in age and length at maturation for
198 male and female redfish (Saborido-Rey 1994), both sexes were modeled separated. For
199 Northern shrimp, sex was also considered but in a sequential way. Since this species is a
200 protandrous hermaphrodite species, in the model individuals are recruited as male, and after a
201 reproductive period with this sex it changes to female primiparous, and later to female
202 multiparous (Bergström 2000). Sexes were combined in cod as growth has been reported as
203 being similar and data on size distribution by sex was not available. Sex change in shrimp and
204 maturation in all the three species were modeled internally (i.e. during the process of
205 optimization of model parameters) with a logistic model based on length (Begley 2005).
206 Based on information from previous studies showing high variability in the maturation
207 process in cod and shrimp (also for the sex change in shrimp) (Casas-Sánchez 2012, Pérez-
208 Rodríguez et al 2013), 12 and 9 periods were considered for cod and shrimp respectively.
209 However, for redfish maturity change only one period was considered for males and females.

210 For all the three stocks the initial population was modelled as abundance by age in 1988.
211 Recruitment was estimated annually as the number of individuals at age 1 on 1st January. In
212 the redfish stock, the estimated recruits were split assuming a 50% sex ratio, while for the
213 shrimp all recruits were assumed male.

214 The growth curves were set by fitting internally the parameters of the Von Bertalanffy growth
215 model. Preliminary analysis of length at age data justified fitting these parameters annually
216 for cod while three and two different periods were considered for redfish and shrimp
217 respectively (Tables 2 and 3). The annual mean length at recruitment, mean length at age for
218 the initial stock, and the standard deviations were estimated externally to the model (i.e.
219 through data analysis previous to the model optimization). A unique length-weight
220 relationship was also estimated externally for each modeled stock.

Cod was targeted in the model by trawl and gillnet fleets. The longline fishery was not explicitly modeled due to its low importance and the shortage of information. Since the size distribution was in between the trawl and gillnet ones, 50% of longliner's catches was assigned to each of these fleets. For redfish, the pelagic and bottom trawl fishery were simplified into a single trawl fishery due to a lack of information for the pelagic fleet. The shrimp fishery was also considered for the redfish stock due to the important by-catch of juvenile redfish before the introduction of a sorting grid in 1995. The only fishing gear targeting the shrimp stock was the bottom trawl.

For each stock, total catch by each fleet was modeled as a function of: 1) the model estimates of stock abundance by length; 2) the average individual weight at length; 3) a length based suitability (overall selectivity) function and 4) a scaling factor for the stock that is to be caught (linear fleet option; Begley (2005)). Suitability and scaling factor parameters were estimated internally in the model optimization. For commercial fleets, the scaling factor was estimated annually, which simulated variability in fishing effort over time, while for the survey fleets only one value was estimated, i.e. simulating a constant effort over time. While for most trawl fleets a logistic length suitability function was assumed (Exponential50 function, Begley 2005), for the cod gillnet fleet, redfish survey and redfish by-catch in the shrimp trawl fleet a dome shaped length suitability curve (Andersen function, Begley 2005) was employed instead. Due to the different patterns of exploitation expected before and after the collapse of cod, different sets of parameters were estimated for the suitability functions of cod and redfish trawl fleets in 1988-1998 and 1999-2012.

The residual natural mortality, defined here as the natural mortality due to other factors than predation mortality modeled internally, 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. For shrimp residual natural mortality was assumed to be 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. 2003). 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.

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 preys hyperiids, euphasiids, chaetognaths, wolffishes, demersal fish and *other food*. Meanwhile redfish preyed on immature redfish and shrimp; as well as the non-modeled preys: copepods, hyperiids, euphasiids, 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.

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 as kg per time step by individual predator as a function of length and water temperature (Begley 2005). Parameters related with feeding level, prey-predator length suitability function, prey preference and functional response were estimated externally and fixed in the model. All prey-predator length suitability functions were assumed to be dome shape relations with prey length, which implies that for a given predator size, there is a prey size when suitability is at a maximum and decreasing at higher or lower lengths. For the non-modeled preys, no length categories were considered and the suitability of the prey was considered constant with predator length. These parameters and functions (suitability functions, prey-preference, functional response and feeding value) determined the amount of each prey that each predator of a given length consumed on each time step (Begley 2005).

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 affects the survival of juvenile stages of the predator and future dynamic of mature stock; 2) the indirect effect that the abundance of alternative prey has on the intensity of cannibalism.

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), diet composition by time step. 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). A sensitivity test was conducted to confirm that an optimum was reached for all parameters.

Results

Model fit

The model output showed an overall close, although not exact, fit to the observed data. Diagnostic figures with the estimated versus the observed survey indices, total catches, maturation and sex ogives, size distributions and diet composition are presented in the supplementary material. For all three stocks, the estimated survey indices of biomass were similar to the observed ones, with the exception of a few years in each stock that usually were coincident with periods of high recruitment. The size distributions of survey catches was in general well fit (although with some deviations), and it is notable that the model performs well in simulating the peaks of the relative abundance of smaller individuals during years of good recruitment. The level of commercial catches were fitted with high precision due to the high weight given to these components, and the size distribution were in general fit with high precision, with the exception of some years and timesteps. The maturity ogives and the diet

composition, despite the slight deviations observed in some years, were also well represented.

Stock dynamics

Model estimates of annual recruitment at age 1 (Figure 4), total abundance (Figure 5) and total biomass by maturity and/or sex state (Figure 6) 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 sub-stocks. 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 yearclasses 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 4). This produced a marked increase in population abundance in 1991 (Figure 5), principally in immature individuals. However this did not translate into total biomass (Figure 6), 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 at the start of the model when caution is needed in interpreting the results, the model indicates that in 1988-1989 the shrimp stock experienced good recruitments (Figure 4) that produced the increase in the abundance of the male sub-stock in those years and was the start of a growing trend in the stock biomass. 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.

Diet composition

The estimated annual diet composition of both cod and redfish showed important changes over the study period (Figures 7 and 8), 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 their highest values in the late 1990s, and then remained 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 especially since 2000, when its proportion in the diet increased steadily until maximum values in 2009-2010 (25% in the small and 65% in large mature cod). Cannibalism provided an important percentage of the diet of mature redfish for those years when recruitment was high, in the early 1990s and 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. Hyperiid, euphasiid and chaetognath were very important prey for both predators; while copepods were a main prey only for redfish. The four groups of zooplankton 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 an average 35% and 20% of the diets 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 and especially in mature redfish (average 5% and 15% respectively).

Instantaneous and harvest rates by source of mortality

The mortality rates by age due to predation by cod (M_{cod}) and/or redfish (M_{redfish}) and fishing were estimated for each modeled stock (Figures 9, 11 and 13). In cod, cannibalism was the main source of mortality at age 1 all over the study period (Figure 9), with the highest values in the early and late years. In these years, cannibalism removed c.a. half of the age 1 population (Figure 10). 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 larger cod was higher (Figure 10). Fishing mortality (F_{trawl}) was very important at age 2 in years 1992-1997, and was above the effect of predation. During the period 1988-1998 F_{trawl} at age 3 reached extreme values ($F > 1.3$ in 1994), and removed on average around 50% of individuals at this age. However, since the reopening of the fishery in 2010, both M_{cod} and F_{trawl} had been similar at this age (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 ($F_{\text{trawl}} > 1.5$ at all ages in 1994). This level of mortality implied that in average half of the individuals at these ages were removed annually over the period 1988-1998. With this high fishing mortality, only 0.3% of individuals recruited before 1996 reached the age 5, whilst after the moratoria in 1998 50% of recruits survived until age 5. Survivorship also increased remarkably at ages 5-12 (Figure 10). Since the reopening of the fishery in 2010, F at ages 4 and older stayed relative low in comparison with the levels of mortality during the 1990s.

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 11). During this period cod predation removed an average of 12% of the redfish population at ages 1 to 4 annually when the abundance at these ages was in high values (Figure 12). These ages were also strongly affected by the shrimp trawl fishery ($F_{\text{trawl_shrimp}}$) in the period 1993-1995 which removed an important portion of the population (Figure 12; c.a. 20%, $F = 0.18$). Cannibalism was important in the early 1990s, but increased 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. During this period on average every year 28.5% and 12% of age 1 and 2 individuals respectively were cannibalized. For redfish older than age 9, the redfish trawl fleet was the main cause of mortality (F_{trawlred}) during the first part of 1990s, with values above 0.5 at most ages in years 1990-1992. During this period on average the 1/3 of individuals at these ages were removed by the redfish fleet each year. After 1996, the value of F_{trawlred} decreased and stayed at low levels (Figure 11), rising very slightly since 2007. With the recovery of the cod stock, M_{cod} became the most important source of mortality for all ages from 2007-2010, with values above 0.2 for ages 2 to 10 and between 0.1 and 0.2 for ages 11 to 18. The exception to this was the age 1 redfish, for which M_{red} remained as the main cause of 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 13), with M_{cod} above 0.2 for age 1, 0.2 for ages 3-4 and over 0.1 for ages 5 to 7. A very high proportion of individuals at these ages (close to 20%) were removed in these years by cod predation (Figure 14), although M_{cod} showed a steady decline in the period 1990 to 1995. Since 1993, when the shrimp fishery started, the fishing mortality (F_{trawl}) rapidly reached very high values (higher than 1 by 1996) for ages 3 to 7, removing a high proportion of the stock (Figure 14). Since 1997 to 2005 although the absolute catches in numbers at age increased, the estimated F_{trawl} 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 F_{trawl} showed a steady decline until 2011 when, with the moratoria, it became again zero. During the period 1988-1999 shrimp consumption in numbers by redfish stayed relatively at low values (Figure 14). However, since 2000, the estimated M_{red} showed an increasing trend for all ages, but especially at ages 1-3 (higher than 0.7 in 2008 for age 2 shrimp), and removed a very high proportion of population (Figure 14). M_{cod} increased steadily since 2005 for all ages and by 2012 was very similar to M_{red} .

440 Discussion

441 The model is tuned to both commercial and survey data, with the survey data giving long term
442 trends aiming at consistency in the sampling effort and selectivity. However, although this
443 was achieved much of the time, the selectivity can be affected by different factors which are
444 out of the control of scientists(e.g. variability in population demography, water temperature,
445 or predator-prey interactions). These changes may have been the reason for some of the
446 differences between observed and estimated survey indices and size distributions – i.e. the
447 model is fitting to overall trends while not fitting to short term variations (some of which is
448 likely to be survey noise). In the commercial fleet, selectivity is expected to change with
449 higher frequency than that of the survey.. In this model, two different sets of parameters were
450 fit before and after the collapse of cod in the mid 1990s. However it is likely that annual (or
451 even within year) changes in the size selectivity occurred, which are not captured by the
452 model, and are therefore probably the main reason for the observed differences between
453 observed and estimated size distributions. Much of the misfit between the model and the
454 survey indices occurs during periods of high recruitment. In these cases the model does
455 correctly identify the years of high recruitment, but does not exactly agree with the survey on
456 their magnitude. This is likely to arise partly from uncertainty in the data, combined with the
457 model failing to capture the variations in natural mortality occurring during these large
458 recruitment events. The model lacks the flexibility (and the data) to account for such changes
459 in mortality, and the size of the modeled recruitment events is thus based on their subsequent
460 impact on population development as well as the surveys at the time.

461 However, despite these drawbacks, in general the databases used in this study have shown a
462 consistent relation from year to year, and have been fitted by the model output with high
463 accuracy most years, describing the general patterns in total catches, survey indices,
464 maturation and sex change with size, diet composition, and very importantly capturing (both

in the survey index as in the size distribution) those years of high recruitment in all the three species. Hence, the multispecies model and the results of this study can be used to analyze the changes occurred during the study period in the three stocks studied, and evaluate the relevance of fishing, recruitment and predation in the dynamic of the cod-redfish-shrimp system.

Multispecies models have the potential to contribute to understanding the nature and magnitude of interactions among stocks in comparison to, and in combination with, other drivers such as fishing. In the present study the model suggests that, in addition to the strong variations in the magnitude of recruitment, both fishing and predation (and especially cannibalism) have combined in producing strong changes in the abundance and age structure of all the three modeled stocks over the modeled period (1988-2012). These drivers have shown marked changes in their relative importance by species-age-length over time, producing the transition from a cod-redfish to a shrimp dominated system by mid-late 1990s and the recovery to the initial structure by late 2000s.

In cod, cannibalism has been widely described 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 1982, Neuenfeldt and Köster 2000, Tsou and Collie 2001). In the present work, cod diet data started in 1993, however from previous studies it is known that cannibalism was important in the early 1990s in the Flemish Cap (Casas and Paz 1994). This cannibalism has been described by the model, which was coincident with the very good recruitments in 1991 and 1992. In addition, the model also showed that fishing pressure was extremely high in this period, including the young ages (ages 2 and 3). In light of these results it may thus be suggested that the joint effect of cannibalism and fishing produced the premature depletion of the successful 1990-1991 cohorts and the sharp decline in the immature sub-stock by 1995. Despite the trend to earlier maturation during the late 1980s and

early 1990s (Pérez-Rodríguez et al. 2013), this fast decline would have reduced considerably the contribution of these cohorts to the reproductive stock. Meanwhile, during this period the model described a very high fishing mortality in the older ages as well, which affected to the mid-late 1980s successful cohorts (Vázquez 1991). Accordingly, the model suggests that the coupled effect of cannibalism and fishing produced the drastic reduction of the cod stock and its reproductive potential. The lack of good recruitments during the mid and late 1990s aggravated the loss of individuals from the population by predation and fishing. This imbalance unavoidably produced the collapse of the cod stock in the second half of 1990s.

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 (e.g. Yagarina et al. 2011) as one of the most important sources of redfish mortality. In addition, catches of redfish in the early 1990s were the highest since 1960 (Ávila de Melo et al. 2013). In agreement with these studies, the model suggested that the joint effect of cannibalism, cod predation and fishing explained the decline of redfish in the 1990s as result of: 1) Cannibalism and predation by cod at ages 1 and 2 and by-catch from the shrimp fishery at ages 3 and 4 reducing the abundance of the successful 1990-1992 cohorts; 2) Predation by cod affecting to ages 3-10 and 3) fishing pressure removing individuals at ages 8-25+. In addition, as occurred in the cod stock in this period, the removal of individuals by predation and fishing was not compensated by new good recruitments, which reinforced the decline of the stock. However, unlike cod the redfish stock did not collapse, which is explained by the model as result of the reduction of cod predation

514 due to the collapse and the sharp decline of fishing pressure (redfish and shrimp fishery) by
515 mid 1990s, which allowed a relative high survivorship of the 1990-1992 cohorts.

516 In the Flemish Cap before 1993, there was no directed fishery for shrimp, and catches in the
517 Canadian survey during the period 1978-1985 were so low that this species was even not
518 included in the sampling protocol (Joanne Morgan, personal communication, August 2014).

519 However, stomach content analysis indicated that shrimp was part of the diet of the Flemish
520 Cap cod in the 1970s and 1980s (Lilly 1983, Turuk 1981) and the results of this study have
521 showed that cod predation induced high levels of mortality on the shrimp stock in the late
522 1980s and early 1990s. Hence it seems reasonable to suggest that in the past the shrimp stock
523 was never at a high enough level to sustain a commercial fishery in the Flemish Cap, and that
524 the predation mortality by cod was an important reason for this situation. This cod-shrimp
525 top-down control has been suggested before all over the North Atlantic (Beremboim et al.
526 2000, Frank et al. 2005, Link and Idoine 2009, Worm and Myers 2003). However, in this
527 work the results suggest that the dynamic of shrimp in the Flemish Cap in the early 1990s was
528 also influenced by redfish predation, which would be in agreement with previous studies in
529 the Northwest Atlantic (Pedersen and Riget 1993, Savenkoff et al. 2006b). Thus, it could be
530 concluded that the decline of cod and redfish in the early-mid 1990s reduced considerably the
531 mortality on shrimp. In parallel to the increase in survivorship, the model estimated very good
532 recruitments since mid 1990s. These two features, lower predation mortality and higher
533 recruitments, led to an increase of the stock despite the extremely high fishing mortality rates
534 at ages 3-7+ since the start of the shrimp fishery in 1993.

535 While the estimated fishing mortality continued at very high levels for shrimp (especially
536 affecting the older reproductive part of the stock), since late 1990s fishing pressure was very
537 low for redfish and negligible for cod due to the fishing moratoria established in 1998
538 (Vázquez and Cerviño 2002). Low fishing mortality coupled with good recruitments over the

period 2000-2007 allowed the abundance of redfish to increase sharply. This, added to the higher importance of shrimp in the diet, increased significantly the redfish predation mortality on shrimp, especially on the younger individuals. Hence, it could be suggested that the high redfish predation mortality on the young sub-stock since 2000 and the excessive fishing mortality on the older sub-stock, in conjunction with the failure of recruitment since 2005, produced the decline and eventual collapse of shrimp stock by 2010. The results also suggest that the effect of predation by cod on the dynamics of shrimp was only marginal in comparison with redfish, having a minor contribution to the collapse of the Flemish Cap shrimp. As argued in the previous paragraph, cod has been presented as the main top-down regulator of shrimp population. However it seems that this ecological role was lost in the Flemish Cap with reduced cod abundance, and redfish predation was the main factor controlling the shrimp population during the decline of shrimp stock.

The mandatory sorting grid introduced in the shrimp fishery in 1994 reduced drastically the redfish by-catch (Kulka 1999) which, coupled to the reduction of the redfish fishery and the collapse of cod, allowed the relative high survivorship of 1990-1992 redfish cohorts. The overlap of a high abundance of large individuals from these year classes with small individuals from the 2001-2007 successful cohorts increased the cannibalism levels since 2001, reducing the survivorship of these cohorts. However, since four different cohorts were successfully recruited in the course of a few years, cannibalism mortality was not enough to prevent the rebuilding of redfish stock. The model highlighted that the moratoria on cod fishery until 2010, and the relatively low fishing mortality since then, allowed a high number of cod from the relatively good 2005-2009 cohorts to survive to older ages. The higher growth rates in this period (Pérez-Rodríguez et al. 2013) also boosted the biomass of large cod. This produced not only a higher abundance of large cod consuming more redfish, but due to the predator-prey size relationship, a wider size range of consumption. This is reflected by the

model, which showed that since 2009 cod predation affected older redfish than in the early 1990s. In comparison, fishing mortality on redfish stayed at low levels since 2009, and was only comparable to predation by cod for ages 18 and older. Hence, it may be argued that predation by cod was the main driver producing the decline of redfish since 2008.

The co-occurrence of abundant large cod with the high recruitments from 2010-2012 favored the very high cannibalism shown by the model in recent years. The effect of cannibalism in the dynamic of cod from 2012 onwards will need to be evaluated in future studies. However based on the elevated estimates of consumption it seems evident that the success of these cohorts will be strongly diminished.

In a comprehensive way the modeling results presented in this work shows that overfishing, predation (including 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 for 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, increased 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 expected increase in 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 euphausiids for immature, small mature cod and redfish, wolfish species 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 result in 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. In agreement with this statement, since 2013 the estimates of the cod biomass at age in the stock assessment of one year have been systematically above the estimates of biomass in the next year's assessment (González-Troncoso et al, 2013, 2014, 2015). These downward revisions from one year to the next were especially important in the younger age categories (up to age 4; González-Troncoso, D. Spanish Oceanographic Institute, Vigo. Spain. Personal communication, 2015), which is in line with the expected effect of cannibalism found in this work. Another example is found in the assessment of the Flemish Cap beaked redfish, where it was shown that assuming higher than usual natural mortality levels produced assessment results more in line with the observed survey trends (Avila de Melo et al, 2013).

Meanwhile, it has been also shown in this work that in order to evaluate the magnitude of trophic interactions properly, the size relationship among prey and predators needs to be considered. It has been demonstrated that cod-redfish-shrimp trophic interactions have a high degree of plasticity depending on the dynamic and size distribution of prey and predator stocks. In this regard, higher recruitments for redfish and survivorship of older and larger cod individuals in the last years favored not just a more intense consumption of small and young redfish, but also of older and larger individuals than during the 1990s. This should be

seriously considered when evaluating the effect of a predator on a prey stock, otherwise the assessment of predation mortality could be misleading.

Understanding the key elements driving the ecosystem has been widely recognized as imperative in order for a science-based management of marine resource exploitation, optimizing benefits while minimizing the risk of jeopardizing the long-term sustainability (Garcia et al. 2003). In some areas, trophic interactions are already being taken into account for fisheries management. In the Barents Sea, information regarding the cod predation on mature capelin, the effect of capelin in cod cannibalism, and cod predation on haddock are currently included in the advised quota for cod, capelin and haddock (ICES 2014), and in the HCR for capelin. In Iceland, cod, capelin and shrimp are managed considering the trophic interactions among them as well as cannibalism in cod (Jakobsson and Stefánsson 1998). In the same way, the multispecies model developed in this work presents a tool suitable 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. 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.

Acknowledgments:

Special thanks to Fernando González and Diana González, from the Oceanographic Centre of Vigo (Spain) for their continued support in issues related with the cod and multispecies model. Thanks to Joanne Morgan and Pierre Pepin, from Fisheries and Oceans of Canada, for their contribution with the DFO and CPR databases. We are very grateful to Bjarki Þór

Elvarsson from the Marine Research Institute of Iceland for its assistance with the iterative reweighting of likelihood components. The research leading to these results has received funding from the People Programme (Marie-Słodowska Curie Actions) of the European Union's Seventh Framework Programme FP7/2007-2013/ under REA grant agreement n° [331004].”

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Table 1.- Model structure, main ecological and biological features for cod stock. 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, which is estimated with a maturity ogive defined by two parameters, L_{50} and α .

	Immature	Mature_small	Mature_large
Period	1988-2012		
Time step	3 months		
Age range	1-12		
Length range (cm)	1cm- L_{50}	L_{50} -85cm	85cm-140cm
Length resolution	1 cm		
Fishing fleets	CT_I; CT_II; CG; EUs		
Residual mortality	Age1: 0.2 Age2: 0.1 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		

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; L_{50} male and L_{50} fem: Length at 50% probability of maturing for male and female sub-stock respectively, which are estimated with the maturity ogive defined by two parameters, L_{50} and α , fitted separated for males and females.

	Male_immature	Male_mature	Female_immature	Female_mature
Period	1988-2012			
Time step	3 months			
Age range	1-25			
Length range (cm)	1cm- L_{50}^* male	L_{50}^* male-60cm	1cm- L_{50}^* fem	L_{50}^* fem-60cm
Length resolution (cm)	1 cm			
Fishing fleets	RT_I; RT_II; ST; EUs			
Residual mortality	Age1-10: 0.05*standardized EU survey biomass index of wolfish and Greenland halibut 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 3.- Model structure, main ecological and biological features for shrimp stock. ST: Shrimp trawl fleet; EUs: EU survey; $L_{50\text{sex}}$: length at 50% probability change from male to female primiparous. $L_{50\text{mat}}$: length at 50% probability change from female primiparous to multiparous, $L_{50\text{sex}}$ and $L_{50\text{mat}}$ have been estimated with the sex change (males to female primiparous) and maturity (female primiparous to multiparous change) ogives, defined by parameters L_{50} and α .

	Male	Female_primiparous	Female_multiparous
Period	1988-2012		
Time step	3 months		
Age range	1-7		
Length range (cm)	$0.05\text{cm}-L_{50\text{sex}}^*$	$L_{50\text{sex}}^*-L_{50\text{mat}}^*$	$L_{50\text{mat}}^*-3.8\text{cm}$
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 timestep		
Maturation		Bi-annual ogive	
Maturation date		4th timestep	
Recruitment	Annual estimate		
Age at recruitment	1		

865 Figure captions

866 Figure 1.- The Flemish Cap is located within the Division 3M of the Northwest Atlantic
867 Fisheries Organization (NAFO) area. The Flemish Pass, a channel deeper than 1100 meters,
868 separates the Flemish Cap from the Grand Banks of Newfoundland.

869 Figure 2.- Total catches and catches of the main targeted species in the Division 3M. These
870 species accounted for 94% of total catches since 1960. These data were obtained from the
871 NAFO website <http://www.nafo.int/about/frames/about.html>.

872 Figure 3.- Species interactions modeled in this study. Species in golden text boxes are fully
873 dynamically modeled, whereas species/prey groups in grey text boxes are incorporated as
874 time series or constant values.

875 Figure 4.- Annual recruitment at age 1 as estimated by the Gadget model for each of the three
876 stocks.

877 Figure 5.- Annual estimates of stock abundance, total and by maturity stage, for each of the
878 three modeled stock (top: cod, middle: redfish, bottom: shrimp).

879 Figure 6.- Annual estimates of stock biomass (in tones), total and by maturity stage, for each
880 of the three modeled stocks (top: cod, middle: redfish, bottom: shrimp).

881 Figure 7.- Model estimate of percentage of each prey in the diet of immature, mature small
882 and mature large cod over the study period.

883 Figure 8.- Model estimate of percentage of each prey in the diet of immature, mature small
884 and mature large cod over the study period.

885 Figure 9.- Predation mortality by cod (M_{cod}) and fishing mortality " F_{trawl} " by age in the
886 modeled cod stock. The "Age 12+" pannel shows the mortality rates for individuals of age 12
887 and older.

888 Figure 10.- Numbers of cod individuals by age removed by each modeled source of mortality
889 (" M_{resid} ": residual natural mortality; " M_{cod} ": predation mortality induced by cod; " F_{trawl} ":
890 Fishing mortality). Estimated survivors for the next year are also shown ("Survivors"). The
891 "Age 12+" pannel shows the number of individuals of age 12 and older.

Figure 11.- Predation mortality by age in the modeled redfish stock, by cod (M_{cod}), by redfish (M_{redfish}) and fishing mortality by the redfish trawl fleet ($F_{\text{trawl_red}}$) and the shrimp trawl fishery ($F_{\text{trawl_shrimp}}$). The “Age 25+” pannel shows the mortality rates for individuals of age 25 and older.

Figure 12.- Numbers of redfish individuals by age removed by each modeled source of mortality (“ M_{resid} ”: residual natural mortality; “ M_{cod} ”: predation mortality induced by cod; “ M_{red} ”: predation mortality induced by redfish; “ $F_{\text{trawl_red}}$ ”: Fishing mortality as result of the directed fishery; “ $F_{\text{trawl_shrimp}}$ ”: fishing mortality induced as result of by-catch from shrimp fishery). Estimated survivors for the next year are also shown (“Survivors”). The “Age 25+” pannel shows the number of individuals of age 25 and older.

Figure 13.- Predation mortality by cod (M_{cod}), by redfish (M_{redfish}) and fishing mortality by the shrimp trawl fleet (F_{trawl}) by age in the modeled shrimp stock.

Figure 14.- Numbers removed from the shrimp stock by age and by modeled source of mortality (“ M_{resid} ”: residual natural mortality; “ M_{cod} ”: predation mortality induced by cod; “ M_{red} ”: predation mortality induced by redfish; “ F_{trawl} ”: Fishing mortality as result of the directed trawl fishery). Estimated survivors for the next year are also shown (“Survivors”).

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

151x151mm (300 x 300 DPI)

Figure 2.- Total catches and catches of the main targeted species in the Division 3M. These species accounted for 94% of total catches since 1960. These data were obtained from the NAFO website <http://www.nafo.int/about/frames/about.html>.

317x190mm (200 x 200 DPI)

Figure 3.- Species interactions modeled in this study. Species in golden text boxes are fully dynamically modeled, whereas species/prey groups in grey text boxes are incorporated as time series or constant values.

120x96mm (300 x 300 DPI)

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Diagnostic figures of model fit

In this supplementary material a set of figures to assess the goodness of fit to the observed data are presented. These data include indices of biomass and abundance of the EU survey; total catch and size distributions for both the commercial fleet and the EU survey; maturation ogives and diet composition.

1.- Cod stock:

Figure S1.- Cod survey indexes of biomass, abundance and abundance of individuals smaller than 25 cm (from left to right in the first row). Total cod catches in tones by the international trawl and gillnet fleets, and catch in kg for the EU survey fleet (left to right in the second row). Red lines are the estimated values with Gadget versus black points which represent the observed data.

Figure S2.- 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.

Figure S3.- 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.

Figure S4.- 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.

Figure S5.- 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.

2.- Redfish stock:

Figure S6.- 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, and in kg for the EU survey fleet (left to right in the second row).

Figure S7.- 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.

Figure S8.- 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.

Figure S9.- 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.

Figure S10.- 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.

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3.- Shrimp stock:

Figure S11.- Shrimp survey indexes (swept area method) of biomass (upper-left panel) and abundance (upper-right), and catch in tones by the international trawl fleet (bottom-left), and in kg for the EU survey fleet (bottom right).

Figure S12.- 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.

Figure S13.- 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.

Figure S14.- 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.

4.- Diet composition

Figure S15.- 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.

Figure S16.- 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.