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REFERENCE TO THE AUTHOR(S)

Northwest Atlantic



Fisheries Organization

Serial No. N 6136

NAFO SCS Doc. 12/ 068

## SC WG ON ECOSYSTEM APPROACHES TO FISHERIES MANAGEMENT–NOVEMBER 2012

### Food consumption of Flemish Cap cod *Gadus morhua* and redfish *Sebastes* sp. using generic bioenergetic models

by

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#### 1.- Abstract

The observed changes in the Flemish Cap demersal community since early 1990's, with cod (*Gadus morhua*), redfish (*Sebastes* sp.) and shrimp (*Pandalus borealis*) stocks fluctuating in opposite directions, in addition to the existing trophic interactions between them, led to the issue of the magnitude of trophic interactions between these commercial species and its implication for population dynamic and fisheries management. In this work, total consumption by cod and redfish, as well as consumption on preys like redfish, shrimp and other species was estimated using a generic bioenergetic model. Changes in feeding habits, growth rates and variations in total predator biomass (cod and redfish) produced changes in consumption at a population level. Variations in the diet were related with changes in prey availability. In turn, redfish consumption by cod and shrimp consumption by cod and redfish seems to have been one of the reasons for variations in population dynamic of these two commercial prey species. Consumption on alternative prey like hyperiids, copepods and other fishes was important and in some cases it was related with the abundance of other main prey like shrimp and redfish. The importance of the abundance of alternative prey for management of commercially exploited prey species is evaluated, as well as the importance of qualitative and quantitative features of interactions between fishing and fish predation for population dynamic and management strategies.

#### 2.- Introduction

In most unexploited fish and crustaceans marine populations, survivorship curves are usually of type III (Valiela 1995), and although survivorship increases remarkably after the early egg and larval stages, all size crustaceans and early and late juveniles fishes still support intense predation rates (Bailey 1994, Bax 1998). In marine ecosystems, prey-predator interactions are widely determined by proper size relationships (Gerking 1994). Under optimum size frequency distributions of prey and predator, annual predation mortality can be higher than 70% for juvenile fishes

(Wooton, 1998). Consequently, predation can be determinant for prey population dynamic by affecting mostly to the juvenile portion, although in the case of small crustaceans and small fish species like capelin, predation can be highly influential for adults as well (Bogstad and Gjosaeter 2001). As juvenile fishes grow, predation mortality rate decreases remarkably and chance of mortality becomes low (Wooton 1998). However, fishing mortality rates still can be very high for late juveniles and adult individuals of commercial species, introducing more variability and complexity to the dynamic of populations and fish communities. Fishing of prey populations of commercial interest affects the dynamic of predators of commercial interest by affecting the food availability, and vice versa.

Food consumption by a predator stock means the amount of prey eaten in a determined period of time. Due to the impossibility of direct observation in natural habitats, estimations of rates of food intake in aquatic organisms have been estimated indirectly using different methodologies like the gastric evacuation approach (Gerking 1994). This methodology is quite data demanding from laboratory experiments, which has spurred on the development of alternative methodologies, like generic bioenergetic models (Temming and Herrmann 2009). With these models, calculations of food consumption rates of wild populations are based in parameters of the von Bertalanffy growth equation and an estimate of the net food conversion efficiency of Beverton and Holt (Temming and Herrmann 2009).

In the Flemish Cap demersal community deep changes have been observed since early 1990's (Pérez-Rodríguez et al. 2011b). The decline of the cod stock *Gadus morhua* from 150000 tons (t) in 1989 to the collapse in 1995 was followed by important changes in the index of biomass of other demersal species. The most notable case was the increase in biomass in the Northern shrimp stock *Pandalus borealis* since 1993, which stayed at high levels until 2007. Since 2004 a sudden increase in stock biomass was observed in the golden redfish *Sebastes marinus* and Acadian redfish *S.fasciatus*, from less than 25000 t to more than 300000 t in both cases. Since 2006, the cod stock started a recovery trend, while redfish and shrimp stocks showed a declining pattern. Pérez-Rodríguez et al. (2011a) showed the increasing importance of shrimp in the diet of cod and redfish species across the period 1993-2008, coincident with the increment in biomass of this prey stock. In addition, redfish was found to constitute an important component in the diet of cod, especially in those years when successful recruitment events were observed in their population. The analysis of common trends in biomass time series showed that, in addition to fishing and environmental conditions, predation was one of the main drivers in the dynamic of the Flemish Cap demersal community (Pérez-Rodríguez et al. 2011b).

Across the period 1960-2012, cod, redfish and shrimp have been the three main commercial species in the Flemish Cap. Due to the apparent interconnections between the dynamic of these three commercial stocks, from a management perspective, it is necessary the estimation of the magnitude of these prey-predator interactions in the form of consumption estimates. Species interactions and especially trophic interactions have been one of the lines of work in the roadmap of the Working Group for the Ecosystem Approach to Fisheries Management (WGEAFM). Since 2011 the WGEAFM has been required to provide an explanation on the possible connection between the recent decline of the shrimp stock, the recovery of the cod stock, and the reduction of the redfish stock in the Flemish Cap ecosystem, as well as advice on the feasibility and the manner by which these three species could be maintained at levels capable of producing a combined maximum sustainable yield. The estimation of consumption of main Flemish Cap prey by their predators using generic bioenergetic models is one way of approaching this task.

In the present paper total annual consumption of shrimp by cod and redfish, as well as annual redfish consumption by cod are estimated using a generic bioenergetic model. In addition, due to the outstanding changes occurred in the stock biomass of this two predator stocks across the studied period, changes in annual consumption of other important prey species for cod and redfish are also studied in the period 1988-2012.

### 3.- Material & methods

Fish growth (considered as variation in weight) is dependent on two antagonistic processes, anabolism and catabolism.

$$\frac{dW}{dt} = \text{Anabolism} - \text{Catabolism} = EW_t^m - kW_t^n \quad (1)$$

Where  $W$  is weight,  $t$  is time, and  $E$  and  $k$  are the constants representing the numerical strengths of the anabolic and catabolic processes.  $n$  is the catabolic exponent ( $n=1$ ), and  $m$  is the allometric coefficient of consumption with fish weight. In previous experimental studies with cod and whiting it was determined that  $m=0.8$  (Temming and Herrmann 2003).

When food intake is higher than the maintenance ration necessary for catabolic processes, fish starts to grow in a proportional way to consumption. This proportionality is defined by the  $K_3$  parameter, which is the slope of the Growth-Food intake lineal relationship. From growth-feeding studies,  $K_3$  spans between 0.55 (when high quality food) and 0.35 (low quality food), with 0.45 as an intermediate value. With these concepts, growth as a function of time can be defined as:

$$\frac{dW}{dt} = (K_3 \times F) - WL \quad (2)$$

Where  $F$  is the food intake (biomass) and  $WL$  the weight lost due to catabolic processes. From equations 1 and 2:

$$E \times W_t^m = K_3 \times F \quad (3)$$

$$F = \frac{1}{K_3} \times E \times W_t^m \quad (4)$$

The constant that determine the strength of metabolism  $E$  may be defined by means of the parameters from the generalized von Bertalanffy growth function (*GBGF*),  $W_\infty$  and  $K$ :

$$E = 3 \times K \times W_\infty^{1-m} \quad (5)$$

From equation 4 and 5, fish annual consumption at age  $F$  may be determined as:

$$F = \frac{1}{K_3} \times 3 \times K \times W_\infty^{1-m} \times W_t^m \quad (6)$$

In the present preliminary study, in the absence of an alternative value for the allometric coefficient of consumption  $m$  for the Flemish Cap cod, the value 0.8, estimated by Temming and Herrmann (2003), was utilized. For redfish species of genus *Sebastes* no previous estimates of  $m$  have been conducted elsewhere. As a compromise solution to this problem, the  $m$  value from the standard von Bertalanffy growth function has been employed for this predator,  $m=2/3$ . It was consider that the prey of both redfish and cod are “good quality” preys, hence  $K_3=0.55$  was utilized.  $K$  and  $W_\infty$  where obtained by fitting the *GBGF* to each cohort age-weight relationship:

$$W_t = W_\infty \left[ \left( 1 - e^{\left( \frac{3D}{-b} \right) \times K \times (t-t_0)} \right)^{\frac{b}{D}} \right] \quad (7)$$

where  $b=3$  and  $D = b \times (1 - m) = 3 \times 0.2 = 0.6$ .

Due to the reduced and variable range of ages available for the different cohorts in cod and redfish, when the *GBGF* was fitted  $t_0$  and  $W_\infty$  were extremely variable between cohorts and were out of the ranges acceptable based in the biological knowledge. As a compromise solution, fixed values were assigned to this parameters;  $t_0=0$ ; and from the July EU survey database it can be assumed that  $W_\infty=14000g$  for cod and  $W_\infty=2200g$  for redfish are reasonable values. Consequently the only parameter to be estimated in both the equations 6 and 7 was  $K$ , as a proxy of the growth rate.

The data required for food consumption estimates with these bioenergetic models were obtained from various sources. Biological information for cod and redfish about age, size and weight were obtained from the annual EU surveys conducted on July in the Flemish Cap since 1988 (Vázquez 2012). Cod and redfish diet composition was recorded also in the EU surveys; however this information is only available since 1993 and was not recorded in years 2007, 2009 and 2011. The diet composition for these years was assumed as the average from the previous and the next years. Population abundance at age, and total population abundance and biomass for redfish, shrimp and cod were compiled from the annual stock assessment (Ávila de Melo et al. 2011, Casas-Sánchez 2012, González-Troncoso et al. 2012).

The average consumption by age and year was estimated in the period 1988-2012. Total consumption by cod and redfish stocks was estimated annually by multiplying average consumption and total abundance by age and year. Total population consumption for all ages was then split into consumption of each prey species across the period 1993-2012 using the information on diet composition for cod and redfish.

Since interannual changes in total biomass of a stock is expected to increase both due to new recruited individuals and growth of existing ones, the effect of predation on prey population could not be properly evaluated using total prey stock biomass, especially in the case of species that experience important changes in weight across lifetime, as it occurs with redfish. To overcome this difficulty, in addition to total redfish biomass consumed by cod, total number of individuals consumed in year  $t$  was also estimated and compared with changes in total redfish abundance between the year  $t$  and  $t-1$  ( $X_t - X_{t-1}$ ). Due to prey-predator size relationships, previous analyses suggested that juvenile portion of the redfish stock constitute most of the redfish consumed by cod (Lilly 1983, Casas and Paz 1994). In the present study it was assumed that on average, redfish individuals consumed by cod were 25 cm size. A 25cm redfish individual weighs 240g (estimated using the average size-weight relationship for redfish species;  $\text{Weight} = 0.018 \text{Length}^{2.95}$ ,  $p\text{-value} < 0.001$ ). Using this average redfish weight, the total number of juvenile redfish individuals consumed by cod was estimated from the total redfish biomass consumed.

Total consumption (biomass and abundance) on beaked redfish (*Sebastes mentella* and *S. fasciatus*) was estimated by multiplying total redfish consumption (*Sebastes marinus* and beaked redfish) by a factor that represent the proportion of beaked redfish over all three redfish species in the shallower 400 m of the Flemish Cap, since this is, on average, the maximum depth for cod distribution across the period 1988-2012. These values were obtained from the data collected during the EU July surveys.

#### 4.- Results

##### Total cod annual consumption

Total food consumption by the whole cod population was in average 3.3 times the total stock biomass; both time series showed a marked similarity with nearly parallel curves (Figure 1; Pearson=0.98,  $p\text{-value} < 0.001$ ). As occurred with the total cod biomass, consumption decreased from the highest value in 1989 (290000 t) to minimum values after 1995 (6200 t in 2001), and started to recover again since 2006 (Figure 1; Table 1).

##### Cod consumption on redfish

The annual total beaked redfish consumption by the cod population across the period 1993-2010 showed important similarities with the total beaked redfish stock biomass (Figure 2; Pearson=0.74,  $p\text{-value} < 0.001$ ). The decline of beaked redfish stock biomass since 1993 to 1996 was accompanied by a marked decrease in the total redfish consumption, and the increase in redfish biomass since early 2000's was followed by an increased consumption by cod. However since 2008 the redfish stock biomass started a declining pattern, but total consumption by cod population still continued a growing trend (Figure 2; Table 1).

Despite the increment in consumption by cod stock since 2003 to 2008, redfish biomass grew during this period. In addition, the estimated total redfish consumption by cod since 2008 was markedly higher than the loose of total

biomass by the beaked redfish stocks. As indicated in the material and methods section, interannual increments in total biomass could be observed due to both new recruited individuals and annual growth of survivors. A way of taking out the effect of interannual growth was the estimation and use of the number of redfish consumed by cod instead of biomass. Total redfish stock abundance (estimated assuming a constant natural mortality rate of 0.4 options, a natural mortality of 0.4 for ages 4-6 through 2006-2010, and ages 7+ on 2009 and 2011 (Ávila de Melo et al. 2011)) and total number of beaked redfish consumed by cod showed substantial opposite patterns since 2006 (Figure 3). Globally, changes in beaked redfish stock abundance between consecutive years showed a negative correlation with the number of redfish consumed by cod (Figure 4; Pearson=-0.5,  $p$ -value<0.01). If only those years of high cod abundance are considered (i.e. before the 1995 collapse, and after 2006), the Pearson correlation coefficient between cod consumption and interannual change in redfish abundance becomes -0.59 ( $p$ -value<0.01). On the contrary, between 2000 and 2005, when redfish recruitment was high and cod biomass was at their lowest values, relationship between cod consumption and change in redfish abundance was positive (Pearson=0.72,  $p$ -value<0.001).

#### Cod consumption on Northern shrimp

The average shrimp consumption by an individual cod aged between 4 and 5 showed high similarities with the index of shrimp biomass from the EU July survey (Figure 5). The decline in total shrimp biomass since 2005 was followed by the decrease in consumption by cod. However, the maximum values of shrimp biomass were not coincident with the maximum consumption by cod.

Total consumption of shrimp and cod population biomass time series showed a similar pattern (Figure 6). In 1993, simultaneously with the decline of cod stock a marked drop in shrimp consumption was observed. Values stayed at very low level until 2006, when a growing trend was observed. However, since 2009, despite the total cod stock biomass still continued growing, shrimp consumption started to decrease. This reduction was contemporaneous with the decline of the index of shrimp stock biomass to the minimum level observed since 1988.

#### Cod consumption on other prey species

The patterns of consumption of alternative prey species, as Myctophidae, barracudine (*Notolepis rissoi* and *Paralepis atlantica*) and other fishes (Figure 7) and Hyperiididae (Figure 8) showed also important similarities with cod stock indexes of biomass across the period 1993-2011. The reduction in the consumption of redfish in the period 1993-1995 was followed by an increment in consumption of myctophiids and other fish species (Table 1). Since 1996, coincident with the collapse of cod population, consumption over all fish prey species declined to the lowest level. Since 2006, with the recovery of the cod stock, the consumption on alternative fish prey species also showed a growing trend. But this increment was especially important since 2008 not just in other fishes, but also in barracudine and myctophiids, coincident with the decline of beaked redfish stocks. Total consumption of hyperiids showed a marked similarity with total cod stock biomass and did not present a complementary pattern with any other of the most important prey, neither redfish nor Northern shrimp (Figure 8). Total consumption on hyperiids was close to 100000 tons in the period 1993-1994. Since 2006 consumption on hyperiids increased, and in 2011 it was again at high levels, although it was lower than in 1993 despite cod stock biomass was at higher values.

#### Total redfish annual consumption

The total food consumption by redfish stock across the period 1988-2010 showed a similar pattern than the total beaked redfish biomass (Pearson=0.85;  $p$ -value<0.001; Figure 9). Consumption/biomass ratio was 0.85 in average, although this value was higher than 1 in the period 2003-2008. When an allometric coefficient of anabolism  $m=0.8$  was introduced in the model, as used for cod, total consumption values were higher and the ratio consumption/biomass increased to values over 1.3, with a maximum value of 1.95 in 2008 (Figure 9).

#### Redfish consumption on shrimp

Consumption of shrimp by an average redfish individual showed important similarities with the EU index of total shrimp biomass (Figure 10), with the highest values in the period of maximum biomass for the Flemish Cap shrimp

stock. However, as observed for cod, there were remarkable mismatches, especially during the late 1990's. Since 2005, both consumption and shrimp biomass decreased to the lowest level of the time series in 2010.

Total shrimp consumption by the beaked redfish populations exhibited a pattern with some similarities to the total redfish population biomass (Pearson=0.69; p-value<0.01). There was an initial period of relative stability with shrimp consumption usually below 5000 t (Figure 11; Table 1). In 2002 started a growing pattern leading to a maximum consumption of shrimp in 2008, more than 14000 t. Since this year shrimp consumption decreased again.

#### Redfish consumption on other prey species

Between the alternative prey species consumed by redfish, copepods are the main invertebrate, especially in the diet of juvenile stage. Consumption on these crustaceans increased from an average 6000 tons in the period 1993-2003 to 40000 tons from 2004 to 2009, with the maximum value in 2007, 61000 t (Figure 12). Since this year a declining pattern was observed, with the minimum value in 2010.

#### Joint shrimp consumption by cod and beaked redfish stocks:

The total consumption of shrimp by redfish and cod stocks experienced a marked increase since 2003, coincident with the raise of redfish biomass, and a further augmentation since 2006, when the cod biomass increased and the redfish still stayed at high levels (Figure 13). The rise in consumption by both redfish and cod was accompanied of a decline in the index of total shrimp biomass obtained from the July EU survey. Since 2006, total shrimp consumption by redfish and cod exceeded the EU index of shrimp biomass, with a maximum consumption in 2008, 31000 t, when the index of shrimp biomass was 11000 t.

## **5.- Discussion**

For both cod and redfish, there was a nearly parallel pattern between predator biomass and total prey consumption time series. The differences observed in redfish total consumption when the values 0.67 and 0.8 were used for the allometric coefficient of consumption highlight the importance of increasing the knowledge about metabolism for the most important species in the Flemish Cap. This would permit developing more precise estimates of food consumption. In any case, food consumption by cod (average ratio=3.3) was always higher than in redfish (average ratio=0.85) due probably to the higher relative annual growth rate at age in cod. Departures from the average consumption/biomass ratios across the period 1993-2010 (3.3 for cod and 0.85 for redfish) are probably due to the observed changes in growth rates (Ávila de Melo et al. 2011, González-Troncoso et al. 2012) that would imply variations in energy requirement and hence food consumption. Changes in growth rate in the Flemish Cap cod have been found in the studied period, especially since late 1990's, which were related to variability in water temperature (Pérez-Rodríguez et al. 2013). Variations in consumption rates are not just affected by variations in growth rate. There exist other factors not considered in this work, like the effect of temperature on catabolic processes, or changes in maturation and reproductive energy allocation that would affect our estimation of the total consumption based solely on growth. The analysis of these alternative sources of change in consumption will be necessary in future approach to consumption estimates. However, despite this limitation, the results showed in this work points to the importance of considering variations in growth rate when approaching a multispecies management strategy.

Although there have been described some influences from and to the Grand Banks fish populations (Konstantinov et al. 1985, De Cardenas-Gonzalez 1996), Flemish Cap is considered a relatively isolated system (Templeman and Fleming 1963, Konstantinov 1970, Morgan and Bowering 2004). Hence population dynamic and total biomass of prey is mainly driven by changes in recruitment, fishing and growth rates, but also in predation mortality at age.

Considering the whole period 1993-2010, total redfish stock abundance and total number consumed by cod showed a negative correlation as it would be expected from the effect of predation on a prey population. In addition, it is interesting to note that the negative changes in redfish abundance (i.e. losses) were observed in years when the cod stock was at high abundance level consuming a higher number of redfish individuals and redfish recruitment was not

especially good (i.e. before the 1995 collapse, and after 2006). If only those years of high cod abundance and relatively low recruitment in redfish are considered, the relation between cod consumption and redfish abundance loses becomes more negative, i.e. -0.59. On the contrary, between 2000 and 2005, when recruitment was high and cod biomass was at its lowest values, there was an intense and positive relationship.

From these findings it may be suggested that the dynamic of cod and redfish stocks, as predator and prey, is partially driven by top-down and/or bottom-up forces depending on the state of some population features like proper size frequency distributions of cod and redfish (Lilly 1980, Casas and Paz 1994), abundance of cod and redfish, and redfish recruitment success. When both cod and redfish size distributions overlap in the optimum range of sizes for prey-predator interactions, redfish recruitment is not excessively high and there is an abundant cod stock, dynamic of redfish stock is driven by top-down forces, as suggested by the negative correlation between cod consumption and interannual changes in redfish stock in the periods 1993-1996 and 2006-2010. When cod stock is at low level and recruitment is exceptionally good for redfish, there seems to be reduced capacity for cod to control the redfish populations through predation. The dominant force under these conditions, like in the period 2000-2005, could be the bottom-up influence of redfish on cod. This is supported by the positive correlation during this period between redfish biomass and cod consumption. The increase in redfish population induced a higher consumption of this prey and could have contributed to the recovery of cod stock. However the positive effect (i.e. predation release) of cod on redfish is not as clear. The absence of predation means the absence of a negative effect, but not necessarily a clearly positive effect. Other forces as those related with oceanographic conditions and secondary production can be highly influential on recruitment and population dynamic (Cushing 1982). This has been suggested as a plausible explanation for the delayed recovery of redfish in relation to the collapse of cod stock and release from a high predation pressure (Pérez-Rodríguez 2012).

The results observed in relation to the shrimp consumption by an average individual both in cod and redfish points that the consumption of shrimp seems to have been importantly driven by the biomass of this prey. However the mismatch between prey abundance and consumption observed especially in the late 1990's suggest that other factors have likely affected to this prey-predator relationship, like the spatial overlap between them, the abundance of an alternative preys and prey-predator size distributions.

Results on total shrimp consumption by cod stock suggest that changes in consumption across the period 1993-2012 was strongly influenced by total cod stock biomass especially in the periods 1993-1995 and 2005 onwards. However, in addition to this factor, the higher importance of shrimp in feeding habits of cod since this year also contributed to this increased consumption (Pérez-Rodríguez et al. 2011a). The decline in shrimp consumption observed since 2009, despite the still increasing trend in total cod stock biomass, is related with the reduction of this prey in the diet of cod, which in turn could have been related with the drop of shrimp population biomass since that year (Casas-Sánchez 2012). Similarly, shrimp consumption by the redfish stock was related with changes in total beaked redfish biomass. However, changes in feeding habits especially in the late 1990's and early 2000's were also determinant for predation pressure on shrimp stock by redfish (Pérez-Rodríguez et al. 2011a). The decline of shrimp population since 2008 led to a lower relevance of this prey in the diet of redfish, which in conjunction with the reduction of the redfish stock since this year could be suggested as the explanation in the drop of shrimp consumption by this predator in 2010.

Total shrimp consumption by cod and redfish stocks showed values that were over the total shrimp biomass since 2006. This could be due to an overestimation of shrimp consumption by these predators. The introduction of variability in the diet across the seasons, the degree of spatial overlap between both predator and prey stocks as well as variability between years in the value of parameters of bioenergetics models could contribute to the improvement of the estimations. Actually there is little information about diet of Flemish Cap fish demersal community across the seasons, and all data comes from summer EU surveys. Using information on seasonal variations for consumption estimates could decrease this apparent excess of shrimp consumption by cod and redfish.

As described for redfish, total shrimp consumption by cod and redfish are also driven by predator-prey size stock relationships. However, in this case this seems to be especially important for redfish since shrimp is an important prey in the diet of these species mostly from size 25 cm (Pérez-Rodríguez et al. 2011a), when redfish are approximately 7-9 years old onwards. However for cod it seems that consumption is not so dependent on cod size distribution since shrimp has a very similar importance in the diet for all ages.

The consumption by the cod stock of alternative fish prey species than redfish seems to have been mostly driven by total cod stock biomass. However, there are some differences between the dynamic of cod stock and the consumption on these alternative fish preys that could be related with the abundance of redfish. It was observed an increase of consumption on other fishes and myctophiids in the period 1994-1996 that was contemporaneous with the decline in redfish consumption. Since 2008, the decline of redfish was followed by an increase in consumption on these alternative prey species as well as on barracudine since 2008. This could be supported by the increase of cod stock and the decline of redfish since 2008.

Consumption on other invertebrates like Hyperidea did not present a complementary pattern with other prey species and was mostly driven by total cod biomass. Hyperiids have been found in this work the main prey group contributing to total food consumed by cod stock, with near 100000 tons in 1993-1994. The amount of hyperiids in relation to total cod biomass was higher before 1996 than after 2006. This was due to the greater importance in the diet in the first period (Pérez-Rodríguez et al. 2011a), and was not related with changes in the age structure of cod stock (González-Troncoso et al. 2012).

The sudden increase of redfish biomass in conjunction with the decline of shrimp could have triggered the consumption on copepods during the period 2004-2009. But the sudden reduction occurred in 2010 was probably influenced not just by the decline in redfish biomass, but also by the decline in the contribution of copepods to the diet of beaked redfish occurred in this year, which lead to the drop of consumption on this prey despite the total beaked redfish biomass was still at high levels.

From a management perspective the relevance of invertebrate species like hyperiids, and the importance of alternative fish prey species for cod should be consider. The state of these populations could be consider of importance for cod feeding opportunities, and hence for condition and reproductive potential when the redfish stock is at low levels or when there is an inappropriate size distribution between cod and redfish stocks from a trophic perspective. Copepods in redfish and hyperiids and redfish in cod were the main prey items until late 1990's and their relevance in the diet was driven by the abundance of these preys in the ecosystem (Pérez-Rodríguez et al. 2011a). Hence there seems advisable to consider the abundance of alternative prey in management strategies when both predators and main preys are of commercial interest. In addition, the information about alternative and non-commercial prey species, like copepods and hyperiids could be used to refine the management strategies for shrimp, varying the recommended strategy as a function of variations in the abundance of alternative preys. In turn, recommended management measures for redfish could be adapted as a function of these and other alternative fish preys, like barracudine, myctophiids, wolffishes and other.

Fish predation and fishing activity compete for the resources and affect deeply the dynamic of marine fish stocks. Fishing can reduce or even deplete prey populations that are the basis for diet of other commercially exploited fish species, reducing food availability and compromising body condition, reproductive potential and survival of predator stock (Greenstreet 2006). Management plans hence should consider multispecies interactions in marine ecosystems, and should take into account the portion of prey stock that needs to be maintained in the ecosystem to cover the energetic necessities of higher trophic levels commercial and non-commercial species. The Flemish Cap cod has a diet strongly based in other commercial species like redfish and shrimp, but also in other alternative fish and invertebrate species. All this information should be integrated to assess the most suitable fishing strategy to get the equilibrium between maximum productivity and sustainability.

The analysis and methodology employed in the present work is the first approach to the problem. A deeper development of this analysis as well as the refinement of some parameters and processes will be necessary in the



future in order of producing more accurate and reliable estimations of consumption by cod, redfish and other main predators in the Flemish Cap and the Northwest Atlantic ecosystems. Between these questions:

- Consideration of prey quality by means of different  $K_3$  values depending on the prey.
- Including information about changes in diet across seasons and space.
- Fractioning the growth across the year in four seasons.
- Further considerations of variability in  $W_\infty$  between cohorts.
- Inclusion of information in variability of age at maturation along time due to its effect in energy allocation.
- Improving the knowledge about alternative allometric coefficient of consumption,  $m$ .
- Introducing extra information in relation to the effect of temperature on metabolic rates related with catabolic processes.

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## 7.- Figures:

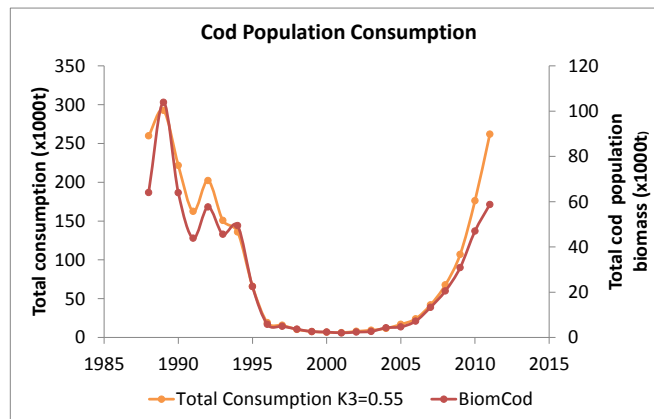


Figure 1.- Total annual food consumption and total population biomass estimates. The intermediate food quality value ( $K_3=0.55$  was employed).

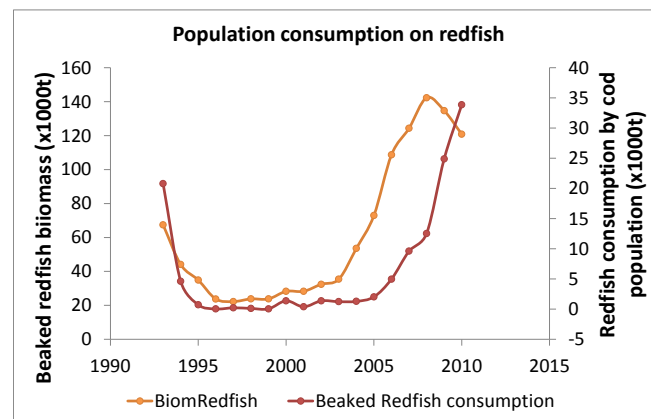


Figure 2.- Estimated total beaked redfish biomass, and estimated annual beaked redfish biomass consumed by the cod stock in the Flemish Cap.

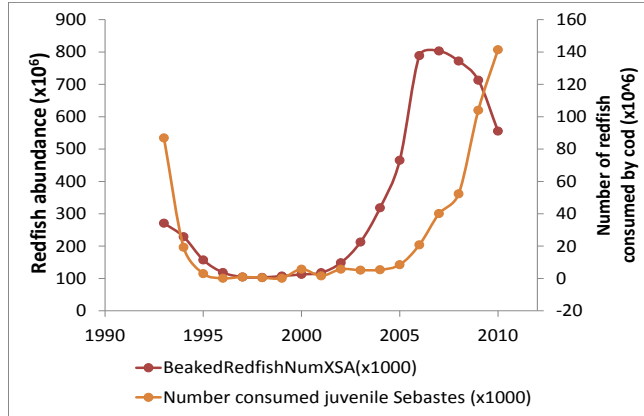


Figure 3.- XSA estimated abundance of beaked redfish (Ávila de Melo et al, 2011), and estimated number of redfish consumed by cod.

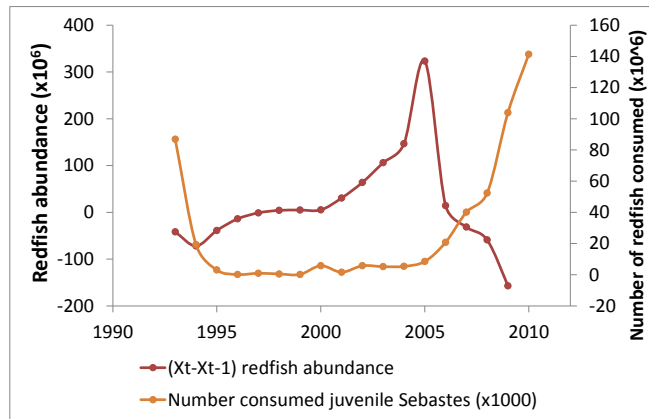


Figure 4.- Total number of redfish consumed by cod, and the difference between consecutive years in redfish XSA abundance ( $X_t - X_{t-1}$ ) in the Flemish Cap.

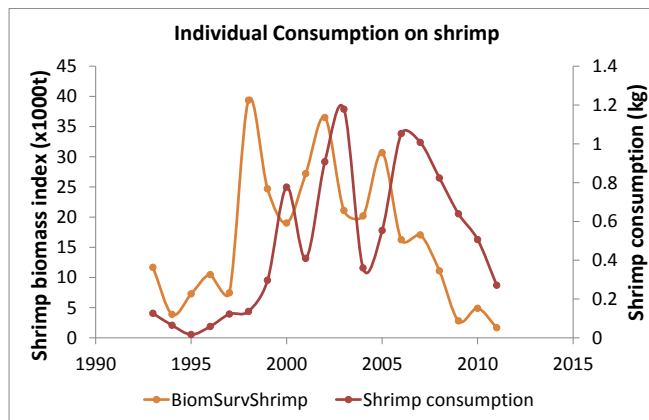


Figure 5.- Total shrimp biomass Index (Casas-Sánchez 2012) is shown in conjunction with the average consumption for an individual cod between 4-5 years old.

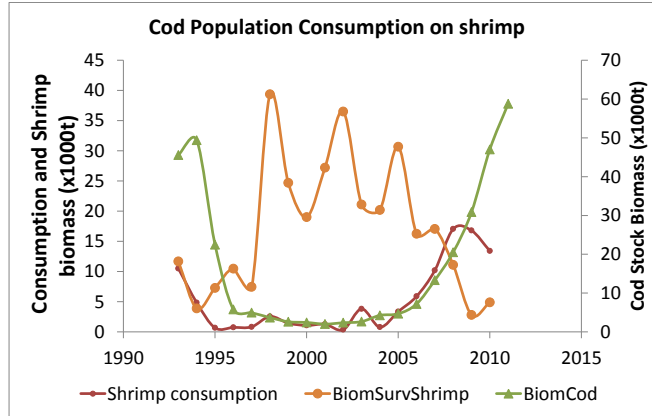


Figure 6.- Estimated total shrimp biomass index and total shrimp biomass consumed annually by the cod stock in the Flemish Cap. The total cod stock biomass is also shown.

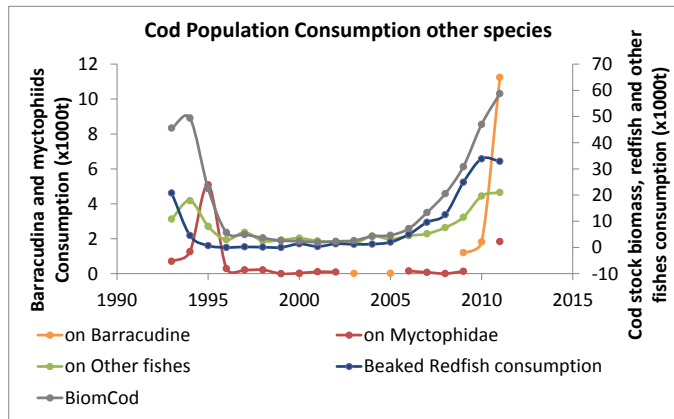


Figure 7.- Estimated total biomass of Barracudine, Myctophiids and other fishes consumed annually by the cod stock in the Flemish Cap.

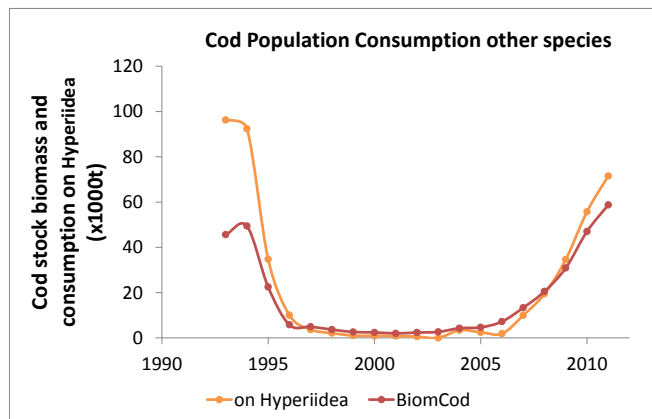


Figure 8.- Total cod biomass (González-Troncoso et al, 2012) and estimated biomass of hyperiids consumed annually by the cod stock in the Flemish Cap.

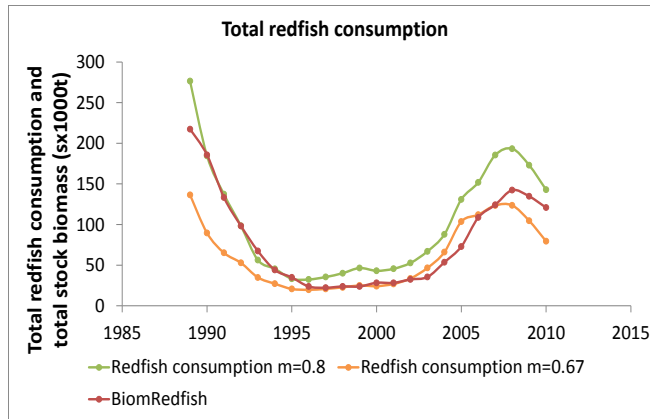


Figure 9.- Total beaked redfish (*S. mentella* and *S.fasciatus*) biomass in the Flemish Cap (Ávila de Melo et al, 2011) and total redfish consumption in the period 1998-2010.

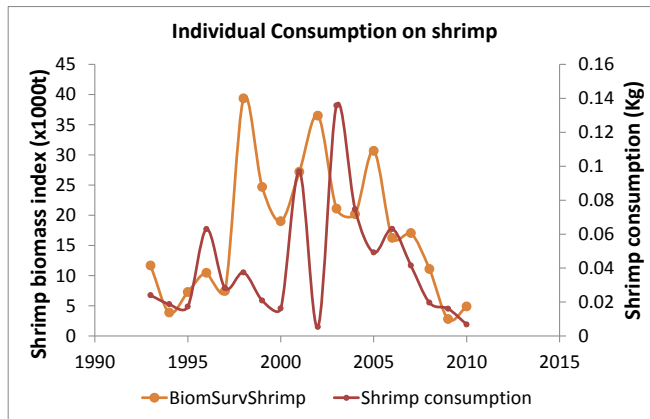


Figure 10.- Total shrimp biomass Index (Casas, 2012) is shown in conjunction with the average consumption for an individual beaked redfish in the range 7-47 cm.

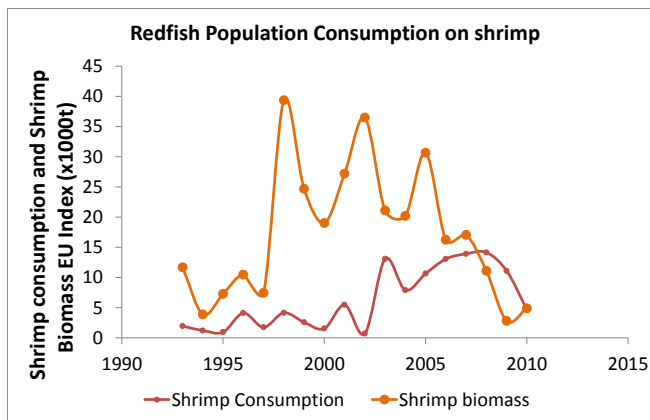


Figure 11.- Estimated total shrimp biomass index and total shrimp biomass consumed annually by the cod stock in the Flemish Cap.

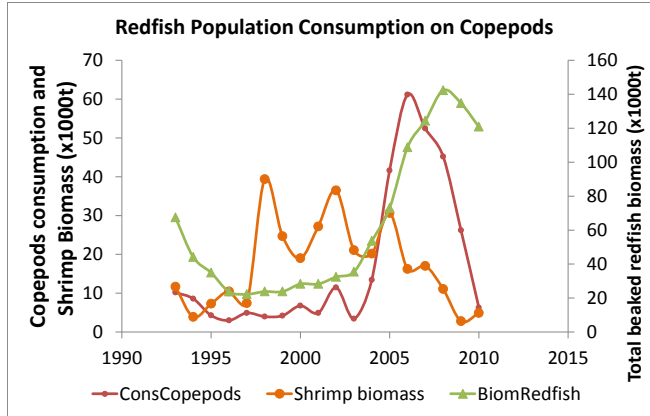


Figure 12.- Total redfish biomass (Ávila de Melo et al, 2011), EU biomass index for shrimp and estimated biomass of copepods consumed annually by the beaked redfish in the Flemish Cap.

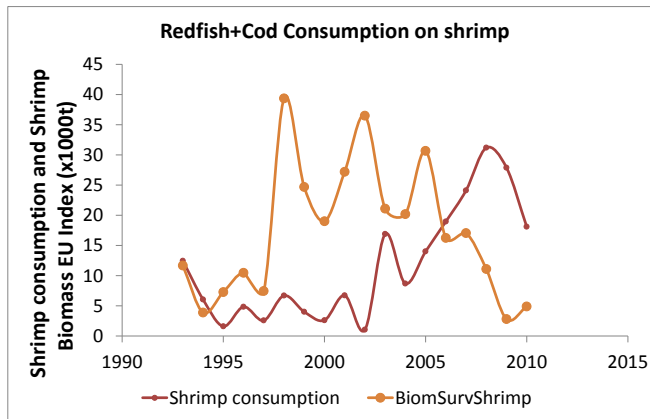


Figure 13.- Estimated total shrimp biomass index from the July EU surveys (Casas and González Troncoso 2011) and total shrimp biomass consumed annually by the cod and beaked redfish stocks in the Flemish Cap.

**8.- Tables:**Table 1.- Total consumption and consumption (x10<sup>3</sup> tons) for the most relevant prey species are shown for predators cod and redfish.

Year/Prey	Cod						Redfish		
	Total Consumption	Beaked Redfish	Shrimp	Cod	Barracudine	Myctophiids	Total Consumption	Shrimp	Copepods
1988	259.87						163.99		
1989	292.66						136.51		
1990	221.71						89.62		
1991	162.49						65.17		
1992	202.2						52.86		
1993	150.74	20.8	10.5	0	0	0.71	34.88	1.96	10.2
1994	135.93	4.62	4.84	6.49	0	1.26	27.13	1.21	8.58
1995	65.91	0.72	0.67	0	0	5.09	20.75	0.94	4.27
1996	19.1	0.03	0.74	0	0	0.3	19.69	4.1	2.98
1997	15.72	0.22	0.83	0	0	0.21	20.84	1.74	4.92
1998	10.38	0.11	2.55	0	0	0.22	22.68	4.15	3.97
1999	7.59	0.04	1.44	0	0	0	25	2.57	4.2
2000	6.75	1.38	1.07	0	0	0.03	24.18	1.54	6.77
2001	6.24	0.38	1.26	0	0	0.11	26.89	5.47	4.9
2002	7.85	1.38	0.36	0	0	0.1	33.65	0.69	11.47
2003	9.37	1.24	3.81	0	0.01	0	46.63	13.08	3.43
2004	11.67	1.29	0.78	0	0	0	66.02	7.9	13.43
2005	16.84	2.03	3.36	0.03	0.03	0	103.64	10.64	41.61
2006	24.02	4.97	5.89	0	0	0.15	112.03	13.07	61.15
2007	41.91	9.61	10.2	0.01	0	0.08	123.49	13.92	52.43
2008	67.69	12.53	17.04	0.17	0	0.01	123.56	14.15	45.22
2009	107.03	24.89	16.79	0.83	1.21	0.14	104.68	11.11	26.22
2010	176.2	33.86	13.41	4.87	1.82	0	79.46	4.7	6.29
2011	262.01	32.91	16.21	25.95	11.24	1.84			