ICES Journal of Marine Science: Journal du Conseil
June 2016, Volume 73 Issue 5 Pages 1370-1381
http://dx.doi.org/10.1093/icesjms/fsw050
http://archimer.ifremer.fr/doc/00327/43794/

Emergence of a new predator in the North Sea: evaluation of potential trophic impacts focused on hake, saithe, and Norway pout

Cormon Xochitl [1, *], Kempf Alexander [2], Vermard Youen [3], Vinther Morten [4], Marchal Paul [1]

[1] IFREMER, Channel and North Sea Fisheries Research Unit,150 quai Gambetta, B.P. 699, Boulogne-sur-Mer 62321, France
[2] Thünen Institute of Sea Fisheries, Palmaille 9, Hamburg 22767, Germany
[3] IFREMER, Unit of Fisheries Ecology and Modelling, Nantes B.P. 21105, Cedex 03 44311, France
[4] DTU Aqua Technical University of Denmark, Jægersborg Allé 1, Charlottenlund 2920, Denmark

* Corresponding author : Xochitl Cormon, tel: +33 321 995 684;
email address : xochitl.cormon@ifremer.fr

Abstract :

During the last 15 years, northern European hake (*Merluccius merluccius*) has increased in abundance, and its spatial distribution has expanded in the North Sea region in correlation with temperature. In a context of global warming, this spatial shift could impact local trophic interactions: direct impacts may affect forage fish through modified predator–prey interactions, and indirect impacts may materialize through competition with other resident predators. For instance, North Sea saithe (Pollachius virens) spatial overlap with hake has increased while saithe spawning-stock biomass has decreased recently notwithstanding a sustainable exploitation. In this context, we investigated the range of potential impacts resulting from most recent hake emergence in the North Sea, with a particular focus on saithe. We carried out a multispecies assessment of North Sea saithe, using the Stochastic MultiSpecies (SMS) model. In addition to top-down processes already implemented in SMS, we built in the model bottom-up processes, relating Norway pout (*Trisopterus esmarkii*) abundance and saithe weight-at-age. We simulated the effects, on all North Sea species being considered but focusing on Norway pout and saithe, of combining different hake abundance trends scenarios with the inclusion of bottom-up processes in SMS. North Sea saithe *FMSY* was then evaluated in a multispecies context and contrasted with single-species value. The different scenarios tested revealed a negative impact of hake emergence on saithe biomass, resulting from an increase of predation pressure on Norway pout. These results confirm the competition assumption between saithe and hake in the North Sea and might partially explain the most recent decrease of saithe biomass. This study also highlighted that taking into account bottom-up processes in the stock assessment had a limited effect on the estimation of saithe *FMSY* which was consistent with single-species value.

Keywords : hake, interspecific competition, maximum sustainable yield, multispecies stock assessment, Norway pout, predator–prey interactions, saithe, simple foodweb, SMS

1 Introduction

In 2002, the Johannesburg World Summit on Sustainable Development provided a legally binding framework to implement and develop science relevant to the Ecosystem Approach to Fisheries (EAF) and associated management tools (FAO, 2003). In that context, Plaganyi (2007) reviewed models available to take into account species interactions in fisheries research and management. Models are ranging from complex and holistic ecosystem models to minimum realistic models, which are restricted to marine organisms known to have strong interactions with the species of interest. Such minimum realistic models have been preferred by different advisory agencies worldwide to account for multispecies interactions in stock assessment-based fisheries advice, because of their flexibility and ability to fit to observations (Plaganyi, 2007). The International Council for the Exploration of the Sea (ICES), *i.e.* the main advisory body of fisheries management in the Northeast Atlantic, has promoted a multispecies assessments, building in biological interactions since the late 1980's. ICES has recently drawn particular attention to multispecies considerations for stock management in the North Sea, and clearly expressed the objective to provide regular multispecies advice on fisheries in this area (ICES, 2013b).

A major assumption of most single-species stock assessments is that natural mortality (M) is a static and exogenous scalar. In addition to the usual single-species stock assessment parameters, multispecies stock assessment models often separate M into a static natural mortality (*M1*) and a dynamic predation mortality (*M2*) exerted on prey stocks by predator's (top-down control). The age-structured Stochastic MultiSpecies (SMS) model developed by Lewy and Vinther (2004) is used by ICES Working Group on multiSpecies Assessment Methods (WGSAM) as a basis for advice on multispecies considerations for the North Sea area. In its standard version, the SMS model assumes that consumption rates of predators are constant over time because changes in the availability of certain prey species are assumed to be of minor importance. Multispecies models focusing on top-down processes only, such as SMS, provide an improvement for the stock assessment of forage fish populations and predator juveniles. However, such models are less informative when focusing on top-predator populations where older ages are more likely impacted by decreasing prey availability and resulting consumption rates than by predation. Indeed, bottom-up control, *e.g.* dependency of predators on forage fish (Frederiksen *et al.*, 2006; Engelhard *et al.*, 2014; Pikitch *et al.*, 2014), and competitive interactions, are often not taken into account in multispecies stock assessment models, even if their importance is acknowledged (Hollowed *et al.*, 2000).

Changes in environmental factors reported during the last 20 years in the North Sea (ICES, 2008) have led to changes in species distribution and abundances (Beaugrand, 2004; Perry *et al.*, 2005; Jones *et al.*, 2013) but also in ecosystem functioning. The recent increase of Northern hake (*Merluccius merluccius*) abundance in the North Sea

(Baudron and Fernandes, 2014; Cormon *et al.*, 2014) could impact other exploited species through changes in the food-web. These trophic impacts could be direct, *e.g.* on prey species, or indirect, *e.g.* on other predator species feeding on similar prey assemblages *i.e.* competitors. These concerns led in 2013 to an initiative to collect hake diet data from stomach contents within an EU-funded project (MARE/2012/02) in order to include hake in the North Sea multispecies assessment. North Sea hake is currently considered as a small component of the larger Northern hake stock (ranging from the Spanish to the Norwegian coast, (ICES, 2013a)). As a result, the biomass of North Sea hake is input in SMS as an exogenous factor and it is not explicitly assessed within the model. Using the newly sampled hake diet data, the most recent predation mortality outputs (ICES, 2014a) indicate a direct impact of hake on two forage fish species: Norway pout (*Trisopterus esmarkii*), and herring (*Clupeus harengus*). These two preys are also predated by other species such as saithe (*Pollachius virens*).

Saithe and hake are generally found at depth ranges that largely overlap (Scott and Scott, 1988; Cohen *et al.*, 1990). Although they are demersal species, they both exhibit pelagic behaviour (Scott and Scott, 1988; Cohen *et al.*, 1990; Bergstad, 1991a), particularly when feeding (Cohen *et al.*, 1990; Homrum *et al.*, 2013). Saithe and hake are top-predators and have similar diet with Norway pout being an important prey for both species (Bergstad, 1991b; Du Buit, 1991; DuBuit, 1996). In addition, Cormon *et al.* (2014) showed an increasing spatial overlap between hake and saithe in the North Sea, which was positively correlated with Norway pout presence. For these reasons, it is reasonable to assume that both species are subject to competitive interactions (Link and Auster, 2013) particularly when feeding on Norway pout. The emergence of hake in the North Sea might then affect food availability and, as a result, the growth of North Sea saithe (Cormon *et al.*, 2016) with knock-on effects on saithe biomass, spawning success, and recruitment (Jakobsen *et al.*, 2009). These might partly explain the recent decline in saithe biomass and weight-at-age, notwithstanding an exploitation at around Maximum Sustainable Yield (MSY) for several years (ICES, 2013d).

Fishing mortality corresponding to MSY or F_{MSY} is a commonly used limit or target reference point based on long-term yield predictions. Species interactions may adversely affect the estimation of F_{MSY}, and therefore the reliability of fisheries advice (ICES, 1997; Gislason, 1999; Collie and Gislason, 2001). Gislason (1999) compared several reference points (including F_{MSY}) estimated in single- and multispecies models for the main Baltic Sea species, *i.e.* cod (*Gadus morhua*), herring and sprat (*Sprattus sprattus*). Collie and Gislason (2001) investigated the sensitivity of reference points to changes in natural mortality (changes of predation pressure on prey population) and growth changes (changes of prey availability to predators). However, to our best knowledge, the sensitivity of predator's F_{MSY} estimates to prey availability and growth changes. have never been investigated, when bottom-up processes are built in multispecies stock assessments.

This study focuses on the hake, Norway pout and saithe trio. The SMS model was extended with a correlation between Norway pout abundance and saithe growth (Cormon *et al.*, 2016) and the estimation of consumption rates as a function of predator's estimated mean weight-at-age. Including these bottom-up processes allowed the investigation not only of direct impacts of hake on Norway pout, but also of the indirect impacts of hake on saithe. We investigated the effects of increased future levels of hake abundance, reflecting that in the context of global warming (Boyd *et al.*, 2014) hake might settle or even expand in the North Sea (Cormon *et al.*, 2014). In addition, North Sea saithe MSY, and its associated fishing mortality F_{MSY}, were investigated taking into account bottom-up processes between saithe and Norway pout, and potential competitive interactions with hake.

2 Materials and methods

2.1 Model presentation

2.1.1 Stochastic MultiSpecies (SMS) model

The SMS model (Lewy and Vinther, 2004) was used to study the biological interactions between Norway pout, saithe and hake. SMS is an age-length structured model extending the MultiSpecies Virtual Population Analysis (MSVPA) (Helgason and Gislason, 1979; Pope, 1979) used by the International Council for the Exploration of the Sea (ICES) to carry out multispecies fish stock assessments in the North Sea and the Baltic Sea. SMS allows the estimation of predation mortality based on prey suitability, prey availability, predator' stomach contents and predator' consumption rates (Andersen and Ursin, 1977; Gislason and Helgason, 1985). Estimated prey suitabilities are constant over time leading to a Holling type II feeding functional response in the model (Magnusson, 1995). SMS is operated with a quarterly time-step with spawning occurring in winter (1^{st} quarter) and recruitment occurring in summer (3^{rd} quarter), while yearly biomass is calculated at the beginning of the year. The model can be used in hindcast and forecast mode and it is subject to a so-called key-run every three years within the ICES Working Group on multiSpecies Assessment Methods (WGSAM), which aims to include and validate updates of input data and potential modifications of the model structures.

The present study is based upon the last key-run (ICES, 2014a), which includes 10 dynamically assessed fish species (predators and preys), four "other" fish predators as well as seabirds and marine mammal species (see Table 1 for details about species included in the model).

2.1.2 Implementation of bottom-up process

As a first step, we modified SMS 2014 key-run version to model the extent to which bottom-up processes (availability of Norway pout (*Trisopterus esmarkii*)) may limit the growth and consumption rates of saithe (*Pollachius virens*) and ultimately impact its Spawning Stock Biomass (SSB). We focused on the hake (*Merluccius merluccius*), saithe and Norway pout trio even if methods presented here could in principle be applied to other species. The implementation of bottom-up processes in the model had two components: (i) the implementation of saithe mean weight-at-age calculation depending on Norway pout biomass and (ii) the calculation of consumption rates as a function of saithe mean weights. All parameters described below and the values used in this study are presented in Table 2.

Saithe weight calculation As highlighted by Cormon *et al.* (2016), saithe growth was assumed to follow a sigmoidal relationship correlating length, l, and age, a, as described by Equation (1). The asymptotic length, l_∞, was expressed in centimetres, the relative growth constant, K_{LG}, in years^{-1}, and the sigmoidal curve inflection point, which represents the theoretical age at which individuals growth trajectory changes, a_i, in years.

$$l_a = l_\infty . \frac{1}{1 + e^{-K_{\mathrm{LG}} \cdot (a - a_i)}} \tag{1}$$

The two growth parameters, a_i and l_∞, were fixed as the median values of Cormon *et al.* (2016) estimations excluding years where these two parameters had no biological meaning ($l_\infty > 500$ cm and $a_i > 15$ y). Based on the empirical conclusions of Cormon *et al.* (2016), saithe growth constant K_{LG} was assumed to vary linearly, at a rate defined by coefficient β_1, in relation to previous year's Norway pout Total Stock Biomass (TSB) ($\mathrm{NP}_{\mathrm{TSB}_{t-1}}$ in tonnes), see Equation (2).

$$K_{\mathrm{LG}_t} = \mu + \beta_1 . \mathrm{NP}_{\mathrm{TSB}_{t-1}} \tag{2}$$

where t is the time in years and μ the intercept.

To estimate β_1, we first realised a multiple regression of K_{LG} as a function of Norway pout TSB, a_i and l_∞ using annual time-series of K_{LG} provided by Cormon *et al.* (2016). The strong correlation between a_i and l_∞ led to drop the variable with the highest variance inflation factor. This procedure allowed the estimation of the partial regression coefficient β_1 describing the effect of previous year Norway pout abundance on K_{LG}, taking into account the two other parameters effects. All these preliminary analyses were conducted using R 2.15.3.

Estimated saithe length-at-ages l_a were transformed in millimetres and weights-at-age

w_a in kg were derived from Equation (3):

$$w_{a_t} = a.l_{a_t}^b \tag{3}$$

where a and b are the allometric coefficients assumed constant over time and extracted from Froese and Pauly (2014).

Consumption rate calculation Saithe consumption rate r, at age a and time t, was calculated as a function of saithe weight-at-age w_a following Equation (4):

$$r_{a_t} = c_q.w_{a_t}^{d_q} \tag{4}$$

where c and d are the quarterly-dependent (q) allometric coefficients, estimated during model calibration or hindcast (see Section 2.2) using historical consumption rates and historical mean weight-at-ages.

2.2 Hindcast

In order to fit the model to historical data and to estimate the parameters needed for mutispecies stock assessment, a hindcast was conducted based on the last model key-run that was conducted over the period 1974-2013 (ICES, 2014a). Two changes were, however, brought about this model. First, the Ricker stock-recruitment relation used for saithe was replaced by a segmented regression (hockey stick) relation (ICES, 2013d) and was calibrated on a shortened time-series (1986-2013) to exclude the historically high recruitment values observed in the 1970's during the gadoid outburst (Cushing, 1984). Second, the described bottom-up effects on saithe mean weight-at-age and consumption rates were included.

2.3 Forecast

Forecasts were carried out over a period of 51 years (2014-2065) to simulate the effects of bottom-up processes in multispecies stock assessment, particularly for a top-predator such as saithe, and also to evaluate the effects of hake emergence on the Norway pout and saithe stocks.

2.3.1 Fishery context

Three F-based fishery contexts were considered to conduct the simulations in order to reduce fishery effects on saithe and Norway pout biomass before any further investigation.

- *Status-quo* fishery context (FSQ): fishing mortality (F) of all species assessed within the model were based on F estimated at the last year of the hindcast (F_{sq}).

- Sustainable fishery context (FST): all species were fished at sustainable levels preferentially based on presently used recovery/management plan targets, F_{plan}, or when not available, based on either single-species F_{MSY}, or the precautionary approach F level, F_{pa} (ICES, 2014b).

- Alternative sustainable fishery context (FSTx): all species were fished at sustainable levels (as defined above) except for Norway pout which was based on last year hindcast (F_{sq}).

All fishing mortality values are shown in Table 3.

2.3.2 Species interactions scenarios

Each of the three fishery contexts described in Section 2.3.1 were combined with four species interactions scenarios, focusing on the hake-Norway pout-saithe trio.

A baseline scenario involving saithe constant weight-at-ages and constant hake abundance over the whole period of forecast (BAS) was first investigated as basis of comparison with the three alternative scenarios integrating the newly implemented bottom-up processes between saithe and Norway pout. In the baseline scenarios (BAS, hake abundance was estimated as the average of the last three years of the hindcast (2011, 2012 and 2013). Saithe stock outputs resulting from BAS scenario were equivalent to outputs resulting from single-species assessment because of the absence of species interactions impacting saithe stock in the model: neither predation mortality (as saithe is an exclusive predator, Table 1), nor bottom-up processes were included in the model.

The three alternative scenarios, exploring hake predation pressure on Norway pout and its indirect effects on the saithe stock, were investigated through the implementation of bottom-up processes in the model as described in Equations (1) to (3). Including bottom-up preocesses results in saithe stock outputs, such as biomass and consumption rates, being dependent on the level of hake abundance used in forecast (see below and Figure 1).

- *CST*, hake abundance was constant over the whole period of forecast and was estimated as for BAS scenario.

- *MOD*, hake abundance increase was moderate: 5% per year during 11 years starting in 2014 (based on the 2011-2013 averaged abundance) and reaching a plateau from 2025 onwards.

- *HIG*, hake abundance increase was high: 10% per year during 11 years starting in 2014 (based on the 2011-2013 averaged abundance) and reaching a plateau from 2025 onwards.

A summary of the four species interactions scenarios is presented in Table 3.

2.3.3 Saithe yield optimization

Finally, we tested the sensitivity of saithe F_{MSY} (currently assessed within single-species model) to multispecies interations, including bottom-up control. To that purpose, we simulated North Sea saithe yield for each of the four scenarios (*BAS*, *CST*, *MOD*, *HIG*), considering the *status-quo* fishery context (*FSQ*). Only Norway pout and saithe fishing mortalities varied. Norway pout F took values of either F_{sq} or F_{pa} (Table 3). Saithe fishing mortality F ranged from 0 to 1, with an increment of 0.1. Saithe yield was optimized for the short-term by considering the average saithe yield over the first five years of forecast (2014-2018), and then for the long-term by considering the yield in the final forecast year (2065). These optimisations led to the estimation of F_{MSTY} (Maximum Short-Term Yield) and F_{MSY}, respectively.

3 Results

3.1 Baseline scenario and fishery context

Considering the baseline scenario (*BAS*), the comparison of different fishery context suggested to consider in subsequent analyses the alternative sustainable fishery context scenario, so to limit the effects of fishing on saithe (*Pollachius virens*) and Norway pout (*Trisopterus esmarkii*) biomass.

In the *status-quo* fishery context (*FSQ*), the baseline scenario (*BAS*) forecast, presented in the Supplementary material, showed that adult Norway pout (age 1 to age 3) were mainly predated by saithe, which contributed to about half of total predation mortality (*M2*); while hake (*Merluccius merluccius*), cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) contributed to the other half (Figure S1). In contrast, young Norway pout (age 0) were mainly predated by other predatory fishes (about half of total *M2*). Norway pout and saithe biomass trends (Figure S2) were opposite with a decrease of Norway pout Total Stock Biomass (TSB) concurrent with the increase of saithe Spawning Stock Biomass (SSB) and the associated *M2* increase (Figure S1).

The results obtained when combining the *BAS* scenario and the *FSQ* fishery context were used as a basis for further comparisons of the three fishery contexts. Saithe SSB (Figure 2a) increased following the reduction of saithe F in the sustainable fishery context (*FST*) and in the alternative sustainable fishery context (*FST*x). However, Norway pout biomass (Figure 2b) was severely impacted by the strong increase of fishing mortality in *FST* compared to *FSQ* (×10, see Table 3). The alternative sustainable fishery context (*FST*x), where Norway pout F is at *status-quo* level, was more sustainable with an increase of Norway pout biomass compared to the two other fishery contexts (*FSQ* and *FST*). For these reasons, the alternative sustainable fishery context was selected to simulate the effects of the various hake abundance scenarios under considerations.

3.2 Interactions scenarios

In order to understand the differences resulting from the inclusion of bottom-up processes between saithe and Norway pout, at a constant hake abundance, we first compared the status of Norway pout and saithe stocks as derived from the baseline (BAS) and the constant (CST) scenarios. Then, th effects of increased hake abundance on both Norway pout and saithe stocks were investigated by comparing the outputs of scenarios CST, *MOD*, and *HIG*. As explained in Section 3.1, all hake abundance scenarios were simulated within alternative sustainable fishery context (FSTx).

3.2.1 Inclusion of bottom-up processes between saithe and Norway pout

The inclusion of bottom-up processes between saithe and Norway pout had negative effects on both saithe and Norway pout biomass, even when hake abundance remained constant (CST). Norway pout and saithe biomass were reduced by around 10% (Figure 3a) and 17% (Figure 3b), respectively, compared to the baseline scenario where no bottom-up processes were included (BAS).

Age 1 Norway pout predation mortalities (*M2*) in the baseline scenario (Figure 4) were similarly distributed to the ones derived from *status-quo* fishery context (Figure S1): half of *M2* due to saithe predation, while hake, cod and whiting contributed to the remaining half. There was, however, a slight increase of total *M2* exerted on Norway pout when bottom-up processes were included (Figure 4), which is an indirect consequence of the reduction in saithe biomass (Figure 3b). Indeed, the lower predation exerted by saithe on young whiting and haddock (*Melanogrammus aeglefinus*) resulted in an increase of their biomass, and hence in the increase of the predation exerted by these two species on Norway pout (not shown). Accordingly, there was a slight decrease in the predation pressure induced by saithe.

3.2.2 Hake abundance increase

In scenarios where hake abundance increased and bottom-up processes were included, there were negative effects on both saithe and Norway pout forecast biomass (Figure 3). These effects were generally proportional to the magnitude of hake abundance changes (moderate or high).

When hake abundance increased moderately (*MOD*), the resulting Norway pout biomass was about 30% lower compared to the scenario where hake abundance was kept constant (CST). In the high hake abundance scenario (*HIG*), Norway pout biomass decreased swiftly to finally collapse in 2030 (Figure 3a). Concerning indirect effects, a moderate increase of hake abundance (*MOD*) had only a slight negative impact on saithe biomass compared to the CST scenario (around 1%, Figure 3b). However, in the *HIG* scenario, saithe biomass decreased relatively swiftly to finally reach a stable level, around

5% lower compared to the *CST* scenario.

Changes in hake abundance induced changes of Norway pout *M2* allocation (Figure 4). In the *MOD* scenario, hake became almost as important as saithe and as cod, whiting and haddock combined. In the *HIG* scenario, hake became the major predator of Norway pout, followed by saithe while the predation exerted by other species became insignificant ($< 5\%$). In addition, the high level of hake abundance in *HIG* had a severe impact on Norway pout predation mortality with estimated Norway pout *M2* reaching extreme values ($M2 > 7.5$) after 15 years. These extreme *M2* values explain the decrease and subsequent collapse of Norway pout biomass in 2030.

3.3 Saithe yield

Saithe F_{MSY} estiamted from single-species stock assessments (0.3) was not altered when derived from multispecies stock assessments, even with bottom-up processes being built in the model. However, the inclusion of bottom-up processes narrowed the plateau around the maximum long-term yield versus fishing mortality relationship, and highlighted the importance of Norway pout fishing mortality level.

The relationship between short-term saithe yield and saithe fishing mortality (F) was similar across the different species interactions scenarios investigated (Figure 5a). Saithe Maximum Short-Term Yield (MSTY) was reached at around $F_{\text{MSTY}} = 0.5$ for all scenarios. Only absolute yield estimates differed depending on whether or not bottom-up processes were included, while Norway pout fishing mortality and hake abundance had limited effects. The inclusion of the bottom-up processes between saithe and Norway pout led to lower saithe yield estimates, compared to the baseline scenario (*BAS*) for the same saithe F.

The inclusion of bottom-up processes between saithe and Norway pout affected long-term saithe yield, while hake abundance level had barely any effect (Figure 5b). When no bottom-up processes were included, a large plateau was found around the maximum long-term saithe yield versus F relationship, from $F = 0.2$ to $F = 0.6$, a range where F_{sq}, F_{MSY}, and F_{MSTY} were all included. Exploiting saithe within that F range, which includes the values of F_{sq}, F_{MSY}, and F_{MSTY}, woudl then lead to a long-term yield close to Maximum Sustainable Yield (MSY). However, when bottom-up processes were included, the plateau including F_{MSY} narrowed (from $F = 0.2$ to $F = 0.4$). Consequently, when saithe fishing mortality was set to F_{MSTY} and bottom-up processes were not taken into account, long-term saithe yields were barely changed compared to F_{sq}, while they became very low when bottom-up processes were included. Overall, long-term saithe yields were maximised in all scenarios when F was set to current single-species target: $F_{\text{MSY}_{\text{multispecies}}} \simeq F_{\text{MSY}_{\text{single-species}}} \simeq 0.3$. Finally, the inclusion of bottom-up processes highlighted differences depending on the levels of Norway pout fishing mortality. Indeed, the general decrease of absolute saithe yield resulting from the inclusion of bottom-up processes was even more dramatic when Norway pout fishing mortality was set to $F_{pa} = 0.6$ instead of $F_{sq} = 0.06$.

4 Discussion

4.1 Species interactions in top-predator assessment

In this study, we conducted a comprehensive multispecies assessment of North Sea saithe (*Pollachius virens*) stock, including bottom-up processes relating saithe weight-at-age to Norway pout (*Trisopterus esmarkii*) abundance. It revealed in particular the adverse effects, on the precision of top-predator assessments, of neglecting such bottom-up processes, particularly in a context of competition for a common prey with another top-predator. This study thus highlighted that an increase of hake (*Merluccius merluccius*) abundance in the North Sea would have a strong impact on Norway pout biomass through predation, resulting in indirect negative effects on saithe stock through competitive interactions.

4.1.1 Importance of prey availability for top-predator assessment

In the absence of bottom-up control linking saithe growth and Norway pout abundance, saithe Spawning Stock Biomass (SSB) increased in the first years of the forecast period, as a result of initial saithe recruitments being set above recent average in the baseline forecast. These relatively high values used in the forecast stem from the three peaks observed in the saithe recruitment hindcast period (1986, 1995 and 2001), from which they are calculated.

The negative effect of Norway pout biomass reduction on saithe SSB, when the correlation between saithe weight-at-age and Norway pout biomass was taken into account, bears out the results of Lynam *et al.* (2015), who found a direct correlation between the SSB of these two species using Generalized Additive Models (GAMs). There are numerous examples of such bottom-up relationships between preys and predators all along the marine food web, *e.g.* Atlantic mackerel (*Scomber scombrus*) dependency on copepods (Ringuette *et al.*, 2002), North Sea demersal fishes dependency on sandeel (*Ammodytes sp.*) (Engelhard *et al.*, 2013, 2014), and bottlenose dolphins sensitivity to resource depletion in the Bay of Biscay (Lassalle *et al.*, 2012).

The importance of taking into account prey availability for predator assessment was confirmed by the differences in saithe yield prediction depending on, whether or not, bottom-up processes were built in the assessment. Indeed, when saithe growth was related to Norway pout availability, saithe long-term yield predictions were reduced by around 25% when saithe was exploited at *status-quo* (F_{sq}), compared to the scenario with no bottom-up processes.

The lower estimations of saithe long-term yield, when taking into account bottom-up processes, are consistent with recent assessment results (ICES, 2013d). Therefore, taking into account Norway pout availability in saithe assessment may lead to more realistic yield predictions that could inform management (Rice, 2011). For instance, Buchheister *et al.* (2015) showed that an increase in prey availability may have a positive impact on the Northeast U.S. Atlantic coast flounder stock and suggest that taking into account these bottom-up processes may support the management of that depleted stock. Several studies suggested similar ideas concerning management of forage fish predators worldwide (Pikitch *et al.*, 2014; Essington *et al.*, 2015) including the North Sea (Engelhard *et al.*, 2014).

In addition, an increase of saithe F to F_{MSTY} (Maximum Short-Term Yield) would only increase slightly short-term yields, but at the expense of a dramatic decrease of long-term yields. This pattern was only revealed when bottom-up processes were built in the model, which confirms the importance of taking prey availability into account when studying long-term yields of fish predators like saithe (Rice, 2011; Plaganyi, 2013).

Finally, the inclusion of bottom-up processes in multispecies models, through prey availability, is necessary to study indirect competitive interactions effects, which may disturb the functioning of marine ecosystems, particularly when combined with fishing (Jennings and Kaiser, 1998; Hollowed *et al.*, 2000).

4.1.2 Increased competitive interactions revealed

Despite the dramatic increase of hake abundance in the last 12 years (Baudron and Fernandes, 2014; Cormon *et al.*, 2014; ICES, 2014a), its abundance was still around four times lower than saithe abundance in the North Sea at the beginning of the forecast period. This explains the higher Norway pout predation mortality *M2* induced by saithe when hake abundance was constant. However, an increase of hake abundance led to an increase of the predation mortality M2 exerted by this predator. In the high hake abundance scenario, hake became the major predator of Norway pout leading directly to its collapse and indirectly to a decrease of saithe biomass (when bottom-up processes were built in the assessment).

The collapse of the Norway pout stock could result from the Holling functional feeding response assumed in the model. Indeed, the Holling type II function did not allow Norway pout predators to switch prey at low Norway pout abundance which compromised Norway pout stock recovery. Another functional response, *e.g.* Holling type III feeding response, could have been considered (Kempf *et al.*, 2008), although that would likely only have delayed, and not prevented, the collapse of the Norway pout stock (Floeter *et al.*, 2005). In the Scotian Shelf, Carruthers *et al.* (2005) showed that saithe persistently preyed upon euphausiids even at low euphausiids abundance, instead of switching to other preys, which resulted in a loss of saithe body condition. These results provide some support to the Holling type II assumption. In that case, the absence of prey shift coudl be expmained by the the high energetic value of euphausiids (Mauchline and Fisher, 1969).

Being a highly piscivorous predator, hake may impact other forage fish preys contributing to its diet such as herring (*Clupeus harengus*) (ICES, 2014a). Herring, which is a prey with high energetic value (Pedersen and Hislop, 2001), is also consumed by saithe. The variation of saithe growth as a function of prey availability was here reduced to a dependency on Norway pout abundance, based on Cormon *et al.* (2016). The potential bottom-up processes between saithe and other preys, such as herring, need to be further investigated to be integrated, when evidenced, in future multispecies assessments. In addition, saithe is not the only predator sharing prey with hake in the North Sea. For instance, Norway pout and herring are also consumed by cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) (Engelhard *et al.*, 2014; ICES, 2014a). Therefore, hake might have an impact on these other demersal species, particularly if their spatial overlap is important. These questions need to be investigated in order to broaden the understanding of the potential impact of hake on the North Sea ecosystem.

Finally, the uncertainty around the logistic growth parameters *i.e.* l_∞ and a_i, may also bias our results (Payne *et al.*, 2015). For instance, current estimates of ai are probably too high to realistically reflect actual changes in life-stage and/or maturation. Lower a_i values would have resulted in a slower growth, thereby impacting saithe weight-at-age and biomass more substantially. In addition, the absence of bottom-up processes between hake and Norway pout and the fact that hake biomass is not assessed but forced into the model suggest that our results should be interpreted with caution. The lack of information available about hake stock identity and dynamics in the North Sea is an important issue, which needs to be addressed to explicitly assess hake within the model. For instance, the question of the existence of one or two hake stocks needs to be investigated. Baudron and Fernandes (2014) assumed that the recent increase of hake abundance in the North Sea is exclusively due to density dependent effects in West Scotland, consistently with the current definition of the Northern hake stock (ICES, 2013a). However, hake is a batch spawner (Murua, 2010) and, when present around Shetland Islands during spawning, its larvae might drift, along with saithe larvae, towards Norwegian coast and Skagerrak (Munk *et al.*, 1999). These processes would lead to different dynamics than those currently assumed and would need to be further investigated to better inform the management of hake in the North Sea.

4.2 Multispecies advice

When bottom-up processes of Norway pout on saithe were not included, the overestimation of saithe biomass (around 17%) had no marked effect on the estimation of F_{MSY}. Saithe *status-quo* fishing mortality ($F_{\mathrm{sq}} = 0.31$) was very close to single-species and multispecies Maximum Sustainable Yield (MSY) and recovery plan fishing mortalities ($F_{\mathrm{MSY}} = F_{\mathrm{plan}} = 0.3$), which confirms that the exploitation of saithe in the North Sea is probably not subject to overfishing and also the robustness of F_{MSY} estimates to changes in growth, even if these changes lead to different absolute yields (Collie and Gislason, 2001).

The suitability of Norway pout single-species management measures in a multispecies context is more questionable. Indeed, single-species precautionary approach fishing mortality ($F_{pa} = 0.6$) was 10 times higher than *status-quo* fishing mortality ($F_{sq} = 0.06$). When applied in a multispecies context, F_{pa} would lead to stock collapse (even with no increase of natural mortality). Even if F_{pa} should be an upper limit reference point in an escapement strategy and not a permanent target, the sensitivity of Norway pout stock to an increase of mortality (F and/or $M2$) should be taken into account in the next management decisions concerning this key forage fish species. In addition, Norway pout recruitment, which is to a large extent determined by environmental factors during egg and larval phase, is an important driver of its stock dynamics (ICES, 2013c). The forecast are consequently largely dependent upon assumptions made concerning Norway pout recruitment. These uncertainties reinforce the fact that single- and multispecies advices are not comparable because of the different assumptions used in the different methods, *e.g.* shape of the stock-recruitment relationships and natural mortality settings.

Potential environmental disturbances were not taken into account in this study. In a context of global warming (GIEC, 2014), an increase of temperature in the North Sea might have different consequences on the ecosystem, *e.g.* changes in predator-prey spatial overlap (Perry *et al.*, 2005; Jones *et al.*, 2013), or change in size- or age-at-maturation (Thorsen *et al.*, 2010; Baudron *et al.*, 2011), which may influence our results. Such environmental changes could be more explicitly built in our model. As an example, a more accurate estimation of hake abundance in the future years, *e.g.* by downscaling climate scenarios, could allow inferring hake distribution in the area as a function of temperature and reduce our scenarios uncertainties (Payne *et al.*, 2015). In addition, a reduction of prey availability might have consequences for predator spawning success and recruitment (Jakobsen *et al.*, 2009). Köster *et al.* (2009) showed that environmentally sensitive stock recruitment of Eastern Baltic cod might lead to unsuitable biological reference point estimations where not taken into account. As the latter processes were not included in the model this study might have underestimated the negative impacts of reduced Norway pout availability on saithe biomass. Thus, the resulting effects of saithe and hake competitive interactions may have been underestimated, which may have adversely affected the estimation of multispecies saithe F_{MSY}.

5 Conclusion

This study revealed the importance of taking into account bottom-up processes, in addition to more usual top-down processes, to assess the status of predators in a multispecies context. To our best knowledge, it is the first time that both processes are combined in a multispecies stock assessment model parameterised for the North Sea. We focused here on North Sea saithe, for which predator dependency on prey as well as interspecific competition were accounted for and we showed some potential negative effects of hake emergence in the area on both Norway pout and saithe biomass.

North Sea saithe was a good case to study competitive interactions with hake due to the absence of spatial overlap between adult and juvenile individuals ICES (2013b) which allowed to disentangle top-down and bottom-up effects. However, interspecific competitive processes need to be investigated for other North Sea species. For instance, cod might become another "victim" of hake emergence in the area, should it also compete for preys with hake. In the Northwest Atlantic and in the Barents Sea, cod was found to depend on capelin (*Mallotus villosus*) abundance (Krohn *et al.*, 1997; Gjøsaeter *et al.*, 2009). In the North Sea, Norway pout and/or herring may affect cod stock as these preys contribute importantly to its diet (Engelhard *et al.*, 2014).

In this study, the competition between hake and saithe was investigated through their preying on Norway pout. Actually, competition may also occur for other preys (particularly if the Norway pout stock collapses), such as herring, blue whiting (*Micromesistius poutassou*) or euphausiids. Herring and euphausiids may be key forage species in the North Sea due to their high energetic content (Mauchline and Fisher, 1969; Pedersen and Hislop, 2001). Combined with fishing and potential environmental disturbances (Beaugrand, 2004), an increased predation mortality exerted by hake on these key species might inflate some of the adverse effects of hake emergence on the North Sea ecosystem. For instance, herring density-dependency was assumed to have implications for the management of harbour porpoises and mackerel in the eastern North Sea, Skagerrak and Kattegat (Sveegaard *et al.*, 2012). In the Baltic Sea, herring was found sensitive to competition with sprat (*Sprattus sprattus*) on zooplankton (Casini *et al.*, 2006) while in the North Sea it was assumed to compete with sprat and anchovy (*Engraulis encrasicolis*) (Raab *et al.*, 2012). Concerning euphausiids, the dependency of predators, such as saithe, was shown in the Scotian Sea (Carruthers *et al.*, 2005; Plaganyi, 2013). Ultimately, this work could be extended to other species if sufficient data were available. Indeed, understanding distribution and dynamics of hake, as well as of key forage species such as herring and euphausiids, would help the precision of multispecies stock assessment and thereby of the science basis supporting the management of the heavily exploited North Sea marine ecosystem.

Finally, the negative impact of hake on saithe biomass through a reduction of Norway pout availability bears out the competition hypothesis (Link and Auster, 2013), suggested between the two species by Cormon *et al.* (2014) and might explain partially the most recent reduction observed in saithe biomass and weights-at-age.

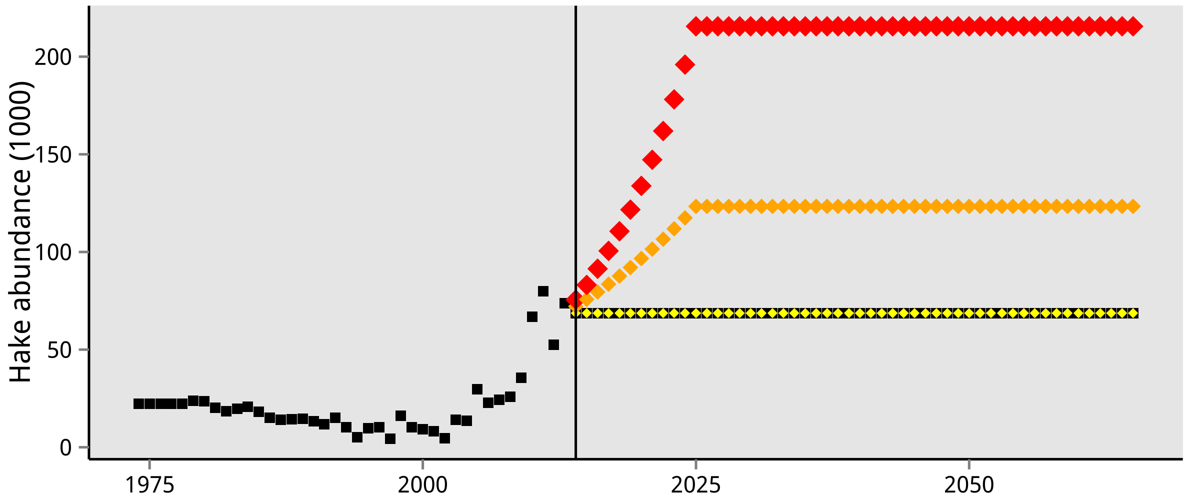
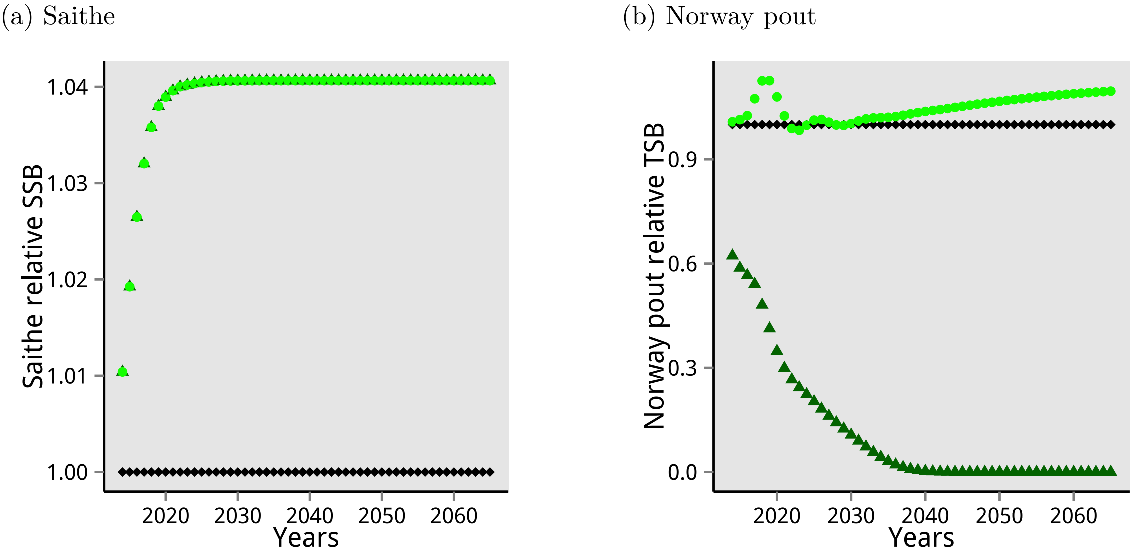


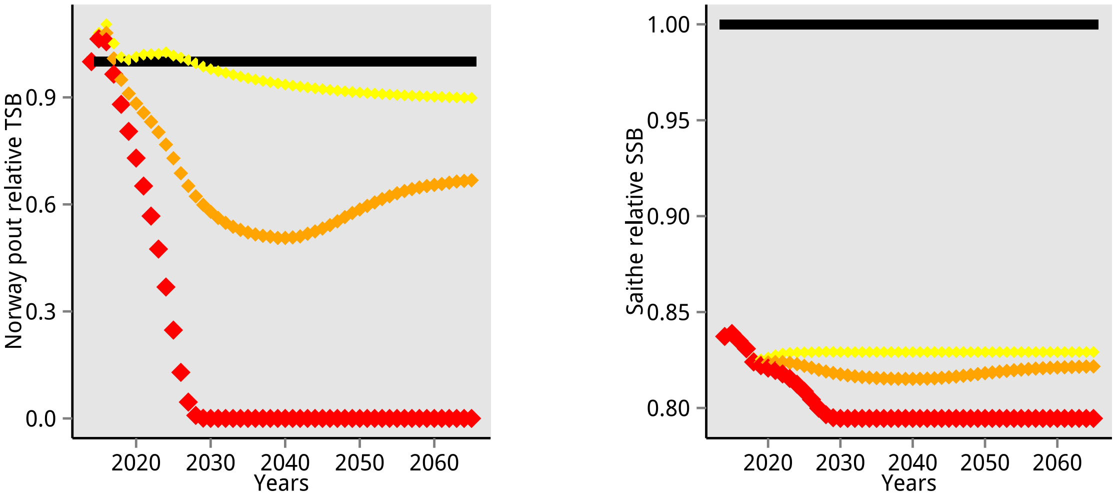
Figure 1: Hake abundance in number of individuals over time depending on the four different scenarios investigated. Black square: baseline scenario where hake abundance is constant and no bottom-up processes are included (*BAS*). Small yellow diamond: constant hake abundance (*CST*). Orange diamond: moderate hake abundance (*MOD*). Large red diamond: high hake abundance (*HIG*).



(a) Saithe

(b) Norway pout

Figure 2: Difference between saithe and Norway pout relative biomass depending on three fishery contexts while hake is assumed constant and no bottom-up processes between saithe and Norway pout are included (*BAS*). (a)Saithe Spawning Stock Biomass (SSB) estimates comparison. (b)Norway pout Total Stock Biomass (TSB) estimates comparison. Black diamond: *status-quo* fishery context (*FSQ*). Olive triangle: sustainable fishery context (*FST*). Green circle: alternative sustainable fishery context (*FST*x).



(a) Norway pout

(b) Saithe

Figure 3: Differences between Norway pout and saithe relative biomass estimated for each of the species interaction scenarios. (a)Norway pout Total Stock Biomass (TSB) and (b)saithe Spawning Stock Biomass (SSB). Black square: baseline scenario used for comparisons where hake abundance is constant and no bottom-up processes are included (BAS). Small yellow diamond: constant hake abundance and bottom-up processes (CST). Orange diamond: moderate hake abundance and bottom-up processes (MOD). Large red diamond: high hake abundance and bottom-up processes (HIG).

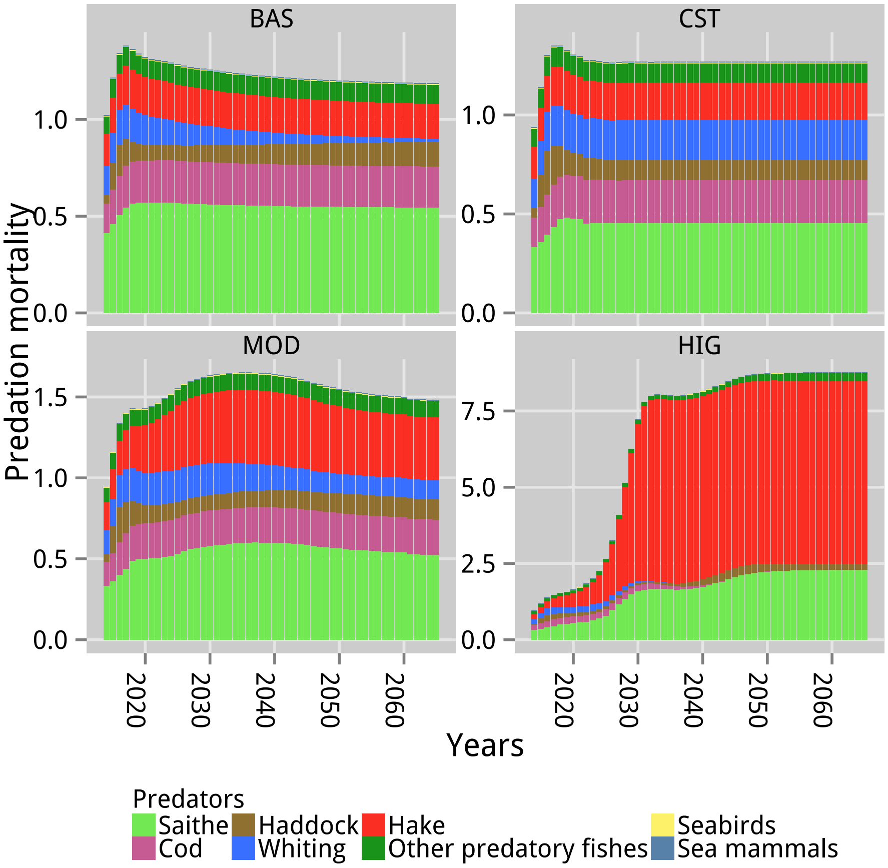
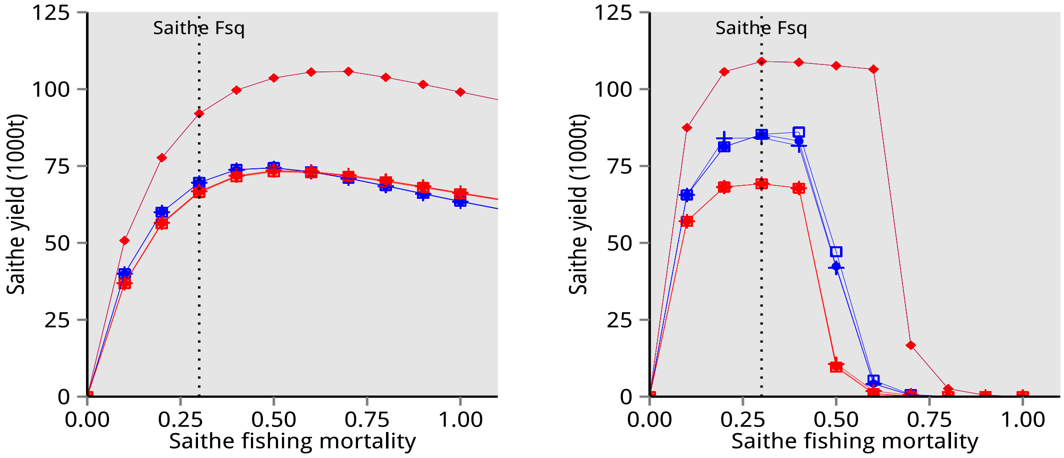


Figure 4: Age 1 Norway pout predation mortalities for each of the species interaction scenarios. BAS: baseline scenario used for comparisons with constant hake abundance and no bottom-up processes included. CST: constant hake abundance and bottom-up processes. MOD: moderate hake abundance and bottom-up processes. HIG: high hake abundance and bottom-up processes.



(a) Short-term yield

(b) Long-term yield

Figure 5: Saithe yield as a function of saithe fishing mortality depending on the species interaction scenarios and Norway pout fishing mortality. (a)Short-term yield estimated by averaging yield from 2014 to 2018 included. (b)Long-term yield estimated at final year of the forecast period value (2065). Blue: Norway pout status-quo fishing mortality (F_{sq}). Red: Norway pout precautionary approach fishing mortality (F_{pa}). Diamond: baseline scenario where hake abundance is constant and no bottom-up processes are included (BAS). Plus: constant hake abundance and bottom-up processes (CST). Dot: moderate hake abundance and bottom-up processes (MOD). Square: high hake abundance and bottom-up processes (HIG).

Table 1: Species included in the Stochastic MultiSpecies model.

Assessed species		
	Predator only	
		Saithe (*Pollachius virens*)
	Predator and prey	
		Cod (*Gadus morhua*)
		Haddock (*Melanogrammus aeglefinus*)
		Whiting (*Merlangius merlangus*)
	Prey only	
		Norway pout (*Trisopterus esmarkii*)
		Herring (*Clupeus harengus*)
		Sprat (*Sprattus sprattus*)
		Sandeel (*Ammodytes sp.*)
	No predator-prey interaction	
		Common sole (*Solea solea*)
		Plaice (*Pleuronectes platessa*)
"Other" predators (biomass assumed known)		
	Fish	
		Hake (*Merluccius merluccius*)
		Grey gurnard (*Eutrigla gurnardus*)
		Horse mackerel (*Trachurus trachurus*)
		Mackerel (*Scomber scombrus*)
		Starry ray (*Raja radiata*)
	Seabird	
		Fulmar (*Fulmarus sp.*)
		Guillemot (*Uria aalge.*)
		Herring gull (*Larus argentatus*)
		Kittiwake (*Rissa sp.*)
		Great-black-backed gull (*Larus marinus*)
		Gannet (*Morus sp.*)
		Puffin (*Fratercula sp.*)
		Razorbill (*Alca torda*)
	Sea mammal	
		Grey seals (*Halichoerus grypus*)
		Harbour porpoise (*Phocoena phocoena*)

Table 2: Parameters used for the implementation of bottom-up process between saithe and Norway pout. q: quarter.

	Value	Equation
Growth		
K_{LG}		1,2
μ	0.17	2
β_1	1.01×10^{-7}	
a_i	5.9	1
l_∞	131	1
Length-weight relationship		
a	2.8322×10^{-8}	3
b	2.7374	
Consumption rates		
c_q		
$q = 1$	0.4528	
$q = 2$	1.3127	
$q = 3$	0.6991	
$q = 4$	0.8230	4
d_q		
$q = 1$	1.0334	
$q = 2$	1.0160	
$q = 3$	1.0153	
$q = 4$	1.0123	

Table 3: Synthesis of the different scenarios explored (Section 2.3). Average fishing mortalities (y^{-1}) are computed for ages indicated in square brackets. BAS: baseline scenario. CST: constant hake abundance scenario. MOD: moderate hake abundance scenario. HIG: high hake abundance scenario. Dash: constant parameter. Tilde: varying parameter. Non-constant hake abundance indicates an increase rate ($\%.y^{-1}$) over the time period (y) indicated between brackets.

Fishery context scenario

		Status-quo fishery (*FSQ*)	Sustainable fishery (*FST*, *FST*x)			
Fishing mortality		F	F_{plan}	F_{MSY}	F_{pa}	F
Cod	[2-4]	0.26		0.33		
Whiting	[2-6]	0.17	0.15			
Haddock	[2-6]	0.16		0.37		
Saithe	[3-6]	0.31	0.30			
Herring	[2-6]	0.26	0.25			
Sandeel	[1-2]	0.30				0.30
Norway pout	[1-2]	0.06			0.60	
Sprat	[1-2]	0.30		0.70		

Species interactions scenario

	BAS	CST	MOD	HIG
Saithe weight-at-age	–	∼	∼	∼
Hake abundance	–	–	+5% (11)	+10% (11)

Supplementary material

Supplementary materials presenting hindcast and status-quo fishery context forecast results are available at the *ICES Journal of Marine Science* online version of the paper.

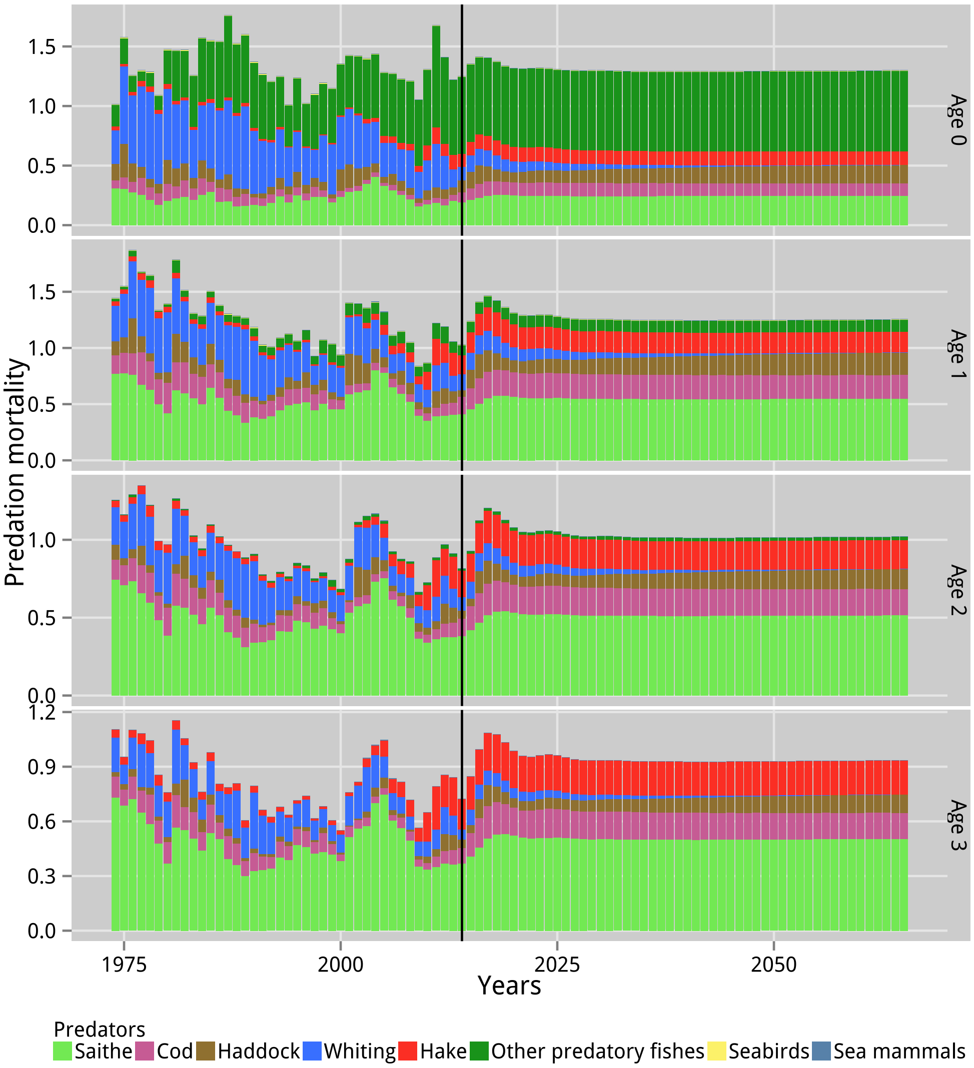
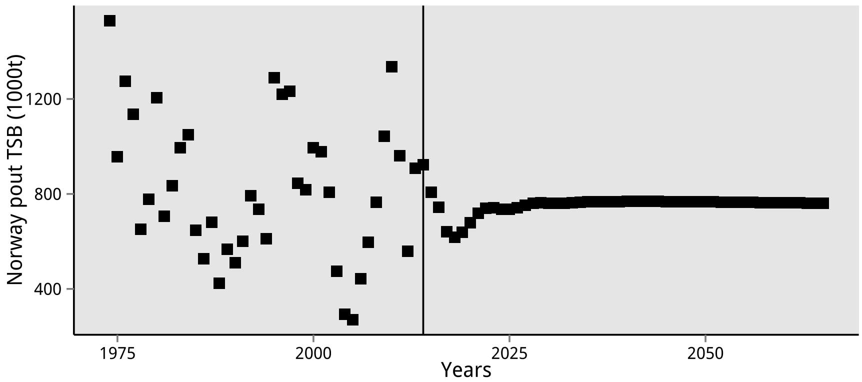
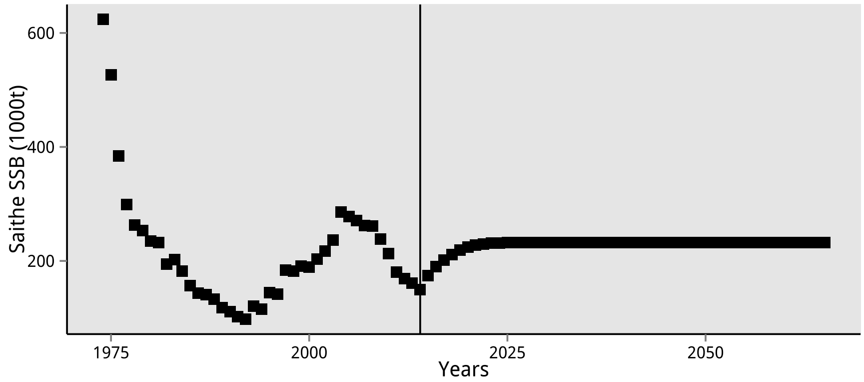


Figure S1: Norway pout predation mortalities from age 0 to age 3 over time for the hindcast and the baseline scenario forecast within *status-quo* fishery context (*FSQ*) context (1974-2065). Vertical black line indicates first year of forecast (2014).

(a) Norway pout biomass



(b) Saithe biomass



(c) Saithe recruitment

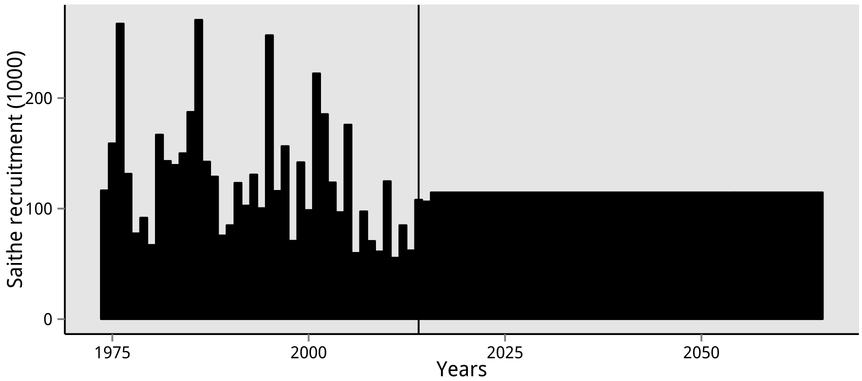


Figure S2: Biological stock parameters of saithe and Norway pout over time for the hindcast and the baseline scenario forecast within *status-quo* fishery context (*FSQ*) context (1974-2065). (a)Norway pout Total Stock Biomass (TSB). (b)Saithe Spawning Stock Biomass (SSB). (c)Saithe recruitment (age = 3). Vertical black line indicates first year of forecast (2014).

Acknowledgements

The authors acknowledge gratefully financial support from France Filière Pêche without which this study would not have been carried out. The authors would also like to thank International Council for the Exploration of the Sea (ICES) and PICES for the travel support which was granted to X.C. to present this study at the "Third International Symposium on Effects of Climate Change on the World's Oceans" in Santos, Brazil, 21-27 March 2015. Finally, the authors acknowledge G. Engelhard and two anonymous referees whom thoughtful suggestions help to improve the initial manuscript.

References

Andersen, K. P. and Ursin, E. A. 1977. A multispecies extension to the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. Meddelelser fra Danmarks Fiskeri- og Havundersøgelser, p. 319–345.

Baudron, A. R. and Fernandes, P. G. 2014. Adverse consequences of stock recovery: European hake, a new "choke" species under a discard ban? Fish and Fisheries. doi: 10.1111/faf.12079.

Baudron, A. R., Needle, C. L., and Marshall, C. T. 2011. Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. Journal of Fish Biology, 78: 1874–1889.

Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Progress in Oceanography, 60: 245–262.

Bergstad, O. A. 1991a. Distribution and trophic ecology of some gadoid fish of the Norwegian deep. 1. Accounts of individual-species. Sarsia, 75: 269–313.

Bergstad, O. A. 1991b. Distribution and trophic ecology of some gadoid fish of the Norwegian deep. 2. Food-web linkages and comparisons of diets and distributions. Sarsia, 75: 315–325.

Boyd, P. W., Cheung, W., Lluch-Cota, S. E., Nojiri, Y., Schmidt, D., and Zavialov, P. 2014. Ocean systems. Intergovernemental Panel on Climate Change (IPCC).

Buchheister, A., Wilberg, M. J., Miller, T. J., and Latour, R. J. 2015. Simulating bottom-up effects on predator productivity and consequences for the rebuilding timeline of a depleted population. Ecological Modelling, 311: 48–62.

Carruthers, E. H., Neilson, J. D., Waters, C., and Perley, P. 2005. Long-term changes in the feeding of *Pollachius virens* on the Scotian Shelf: responses to a dynamic ecosystem. Journal of Fish Biology, 66: 327–347.

Casini, M., Cardinale, M., and Hjelm, J. 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos, 112: 638–650.

Cohen, D. M., T., I., Iwamoto, T., and Scialabba, N. 1990. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date., vol. 125(10) of *FAO Fisheries Synopsis*. FAO species catalogue., 442 pp.

Collie, J. S. and Gislason, H. 2001. Biological reference points for fish stocks in a multispecies context. Canadian Journal of Fisheries and Aquatic Sciences, 58: 2167–2176.

Cormon, X., Ernande, B., Kempf, A., Vermard, Y., and Marchal, P. 2016. North Sea saithe (*Pollachius virens*) growth in relation to food availability, density dependence and temperature. Marine Ecological Progress Series, 542: 141–151.

Cormon, X., Loots, C., Vaz, S., Vermard, Y., and Marchal, P. 2014. Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. ICES Journal of Marine Science, 71: 1342–1355.

Cushing, D. H. 1984. The gadoid outburst in the North Sea. Journal du Conseil international de Exploration de la Mer, 41: 159–166.

Du Buit, M.-H. 1991. Food and feeding of saithe (*Pollachius virens*) off Scotland. Fisheries Research, 12: 307–323.

DuBuit, M. H. 1996. Diet of hake (*Merluccius merluccius*) in the Celtic Sea. Fisheries Research, 28: 381–394.

Engelhard, G. H., Blanchard, J. L., Pinnegar, J. K., van der Kooij, J., Bell, E. D., Mackinson, S., and Righton, D. A. 2013. Body condition of predatory fishes linked to the availability of sandeels. Marine Biology, 160: 299–308.

Engelhard, G. H., Peck, M. A., Rindorf, A., C. Smout, S., van Deurs, M., Raab, K., Andersen, K. H., *et al.* 2014. Forage fish, their fisheries, and their predators: who drives whom? ICES Journal of Marine Science, 71: 90–104.

Essington, T. E., Baskett, M. L., Sanchirico, J. N., and Walters, C. 2015. A novel model of predator–prey interactions reveals the sensitivity of forage fish: piscivore fishery trade-offs to ecological conditions. ICES Journal of Marine Science, 72: 1349–1358.

FAO 2003. 2. The Ecosystem Approach to Fisheries. Fisheries Management Technical Guidelines for Responsible Fisheries 4. Suppl. 2, FAO.

Floeter, J., Kempf, A., Vinther, M., Schrum, C., and Temming, A. 2005. Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator? Canadian Journal of Fisheries and Aquatic Sciences, 62: 1853–1864.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., and Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology, 75: 1259–1268.

Froese, R. and Pauly, D. 2014. FishBase. URL `http://www.fishbase.org`. Accessed: March 8, 2016.

GIEC 2014. Fifth assesment reports. Tech. rep., Intergovernemental Panel on Climate Change (IPCC).

Gislason, H. 1999. Single and multispecies reference points for Baltic fish stocks. ICES Journal of Marine Science, 56: 571–583.

Gislason, H. and Helgason, T. 1985. Species interaction in assessment of fish stocks with special application to the North Sea. Dana, 5: 1–44.

Gjøsaeter, H., Bogstad, B., and Tjelmeland, S. 2009. Ecosystem effects of the three capelin stock collapses in the Barents Sea. Marine Biology Research, 5: 40–53.

Helgason, T. and Gislason, H. 1979. VPA-analysis with species interaction due to predation. ICES CM 1979 G:52.

Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., *et al.* 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Science: Journal du Conseil, 57: 707–719.

Homrum, E. I., Hansen, B., Jonsson, S. P., Michalsen, K., Burgos, J., Righton, D., Steingrund, P., *et al.* 2013. Migration of saithe (*Pollachius virens*) in the Northeast Atlantic. ICES Journal of Marine Science, 70: 782–792.

ICES 1997. Report of the study group on the precautionary approach to fisheries management. CM 1997/ASSESS:7, ICES.

ICES 2008. Advice. Report of the ICES Advisory Committee Book 6, ICES.

ICES 2013a. Hake in division IIIa, subareas IV, VI and VII and divisions VIIIa,b,d (Northern stock). Report of the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk and Megrim (WGHMM). CM/ACOM:11 Sec11:34:73, ICES.

ICES 2013b. Multispecies consideration for the North Sea. Report of the ICES Advisory Committee. Advice Book 6, ICES.

ICES 2013c. Norway pout in subareas iv and division iiia. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). CM/ACOM:13 Sec05:291:338, ICES.

ICES 2013d. Saithe in subareas iv, vi and division iiia. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). CM/ACOM:13 Sec11:565:609, ICES.

ICES 2014a. Annex 5: North Sea SMS model key run. Report of the Working Group on Multispecies Assessment Methods (WGSAM). CM 2014/SSGSUE:11, ICES.

ICES 2014b. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). CM/ACOM:13, ICES.

Jakobsen, T., Fogarty, M., Megrey, B. A., and Moksness, E. 2009. Fish Reproductive Biology: Implications for Assessment and Management. Wiley-Blackwell, Hoboken, 440 pp.

Jennings, S. and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems, vol. 34 of *Advances in Marine Biology*, pp. 201–352. Elsevier, Amsterdam.

Jones, M. C., Dye, S. R., Fernandes, J. A., Frolicher, T. L., Pinnegar, J. K., Warren, R., and Cheung, W. W. L. 2013. Predicting the impact of climate change on threatened species in UK waters. Plos One, 8.

Kempf, A., Floeter, J., and Temming, A. 2008. Predator-prey overlap induced holling type iii functional response in the north sea fish assemblage. Marine Ecology Progress Series, 367: 295–308.

Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 113–121.

Köster, F. W., Vinther, M., MacKenzie, B. R., Eero, M., and Plikshs, M. 2009. Environmental effects on recruitment and implications for biological reference points of Eastern Baltic cod (*Gadus morhua*). Journal of Northwest Atlantic fishery science, 41: 205–220.

Lassalle, G., Gascuel, D., Le Loc'h, F., Lobry, J., Pierce, G. J., Ridoux, V., Santos, M. B., *et al.* 2012. An ecosystem approach for the assessment of fisheries impacts on marine top predators: the bay of biscay case study. Ices Journal of Marine Science, 69: 925–938.

Lewy, P. and Vinther, M. 2004. Modelling stochastic age-length-structured multi-species stock dynamics. ICES CM FF:20 1-33.

Link, J. S. and Auster, P. J. 2013. The challenges of evaluating competition among marine fishes: who cares, when does it matter, and what can we do about it? Bulletin of Marine Science, 89: 213–247.

Lynam, C., Helaouet, P., Mollmann, C., Llope, M., Mavor, R., Bayliss-Brown, G., and Stenseth, N.-C. 2015. Long-term trends in the biomass of commercial fish in the north sea: The role of fishing impacts, predator-prey interactions and temperature change. PICES 2015 S:10.

Magnusson, K. G. 1995. An overview of the multispecies VPA - theory and applications. Reviews in Fish Biology and Fisheries, 5: 195–212.

Mauchline, J. and Fisher, L. R. 1969. The biology of euphausiids, vol. 7 of *Advances in Marine Biology*. Academic Press, London, 454 pp.

Munk, P., Larsson, P. O., Danielssen, D. S., and Moksness, E. 1999. Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the Northeastern North Sea. Marine Ecology Progress Series, 177: 221–233.

Murua, H. 2010. The biology and fisheries of European hake, *Merluccius merluccius*, in the Northeast Atlantic, vol. 58 of *Advances in Marine Biology*, pp. 97–154. Elsevier, Amsterdam.

Payne, M. R., Barange, M., Cheung, W. W. L., MacKenzie, B. R., Batchelder, H. P., Cormon, X., Eddy, T. D., *et al.* 2015. Adverse consequences of stock recovery: European hake, a new “choke” species under a discard ban? ICES Journal of Marine Science. doi: 10.1093/icesjms/fsv231.

Pedersen, J. and Hislop, J. R. G. 2001. Seasonal variations in the energy density of fishes in the north sea. Journal of Fish Biology, 59: 380–389.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., *et al.* 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries, 15: 43–64.

Plaganyi, E. E. 2007. Models for an ecosystem approach to fisheries, vol. 477 of *FAO fisheries technical paper*. Food and Agriculture Organization of the United Nations, Rome, 129 pp.

Plaganyi, E. E. 2013. Fitting the puzzle-modelling species interactions in marine ecosystems. Bulletin of Marine Science, 89: 397–417.

Pope, J. G. 1979. A modified cohort analysis in which constant natural mortality is replaced by estimates of predation levels. ICES CM 1979 H:16.

Raab, K., Nagelkerke, L. A. J., Boeree, C., Rijnsdorp, A. D., Temming, A., and Dickey-Collas, M. 2012. Dietary overlap between the potential competitors herring, sprat and anchovy in the north sea. Marine Ecology Progress Series, 470: 101–111.

Rice, J. 2011. Managing fisheries well: delivering the promises of an ecosystem approach. Fish and Fisheries, 12: 209–231.

Ringuette, M., Castonguay, M., Runge, J. A., and Gregoire, F. 2002. Atlantic mackerel (scomber scombrus) recruitment fluctuations in relation to copepod production and juvenile growth. Canadian Journal of Fisheries and Aquatic Sciences, 59: 646–656.

Scott, W. and Scott, M. 1988. Atlantic fishes of Canada., vol. 219 of *Canadian Bulletin of Fisheries and Aquatic Sciences.* University of Toronto Press, 731 pp.

Sveegaard, S., Nabe-Nielsen, J., Staehr, K. J., Jensen, T. F., Mouritsen, K. N., and Teilmann, J. 2012. Spatial interactions between marine predators and their prey: herring abundance as a driver for the distributions of mackerel and harbour porpoise. Marine Ecology Progress Series, 468: 245–253.

Thorsen, A., Witthames, P. R., Marteinsdottir, G., Nash, R. D. M., and Kjesbu, O. S. 2010. Fecundity and growth of Atlantic cod (*Gadus morhua* L.) along a latitudinal gradient. Fisheries Research, 104: 45–55.