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Impact de la dégradation des habitats côtiers et estuariens sur la dynamique des stocks nourriceries dépendants de Manche Est.

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Soutenu à Rennes le 16/09/2022

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List of abbreviations

EEC : Eastern English Channel

ICES : International Council for the Exploration of the Sea

SSB : Spawning Stock Biomass

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1. Introduction

Estuaries and coastal areas are highly productive ecosystems (Costanza et al., 1997), and are essential habitats for many fish species (Seitz et al., 2014). Essential habitats are defined as habitats that support at least one phase of the life cycle of fish (Delage et Le Pape, 2016). They are described in the Magnuson-Stevens Fishery Act (2007) as "the waters and substrates necessary for fish to spawn, reproduce, feed, and grow to maturity". Estuaries and coastal areas are essential habitats as they act as nurseries for a large proportion of fisheries resources (Miller et al., 1984; Minello, 1999; Beck et al., 2001). A high density of juveniles, presence of prey that allows stronger growth, conditions that enhance survival of juveniles, and migration of subadults to adult habitats are the four criteria proposed by Beck et al., (2001) to characterize nurseries. These habitats have a major role in the renewal of nursery-dependent species (Rijnsdorp et al., 1992; Gibson, 1994; Le Pape et al., 2007). These nursery-dependent species are also of great importance to fisheries, for example two-thirds of commercial landings in the North-East Atlantic come from species using coastal and estuarine systems as nursery habitat (Brown et al., 2018).

However, the coastal location of these nurseries makes them particularly vulnerable to human activities, which are highly concentrated on the coast (Lotze et al., 2006; Airoldi and Beck, 2007). These anthropogenic pressures can lead to habitat losses but also to the degradation of the quality of the remaining habitats. Brown et al. (2018), showed that 92% of species that use coastal habitats are impacted by human pressures, which can be related to pollutants, eutrophication, anoxia, invasive species and physical development of the coastline. These pressures can have important consequences on both size and quality of these habitats that are key features for stock renewal as well as for fisheries management (Johnson et al., 1998; Peterson et al., 2000; Rochette et al., 2010; Le Pape and Bonhommeau, 2015; Champagnat et al., 2021). For example, studies have shown the toxic effects of exposure to pollutants (Davoodi and Claireaux, 2007; Foekema et al., 2008; Wessel et al., 2010). Other general lab studies have demonstrated that the future reproductive success of fish exposed to pollutants at the juvenile stage can be altered through decrease in fecundity, egg viability, and survival (Fonds et al., 1995; Daouk et al., 2011; Horri et al., 2018). Due to the complexity of the life cycle of fish and the multiple sources of natural variation in their abundance, the quantification of the effects of exposure to pollutants on their survival and future fecundity in the wild remains unknown (Hamilton et al., 2016). Consequences for demographic rates and population dynamics are generally unknown (Rose et al., 2003; Ono et al., 2019), but these estimates are necessary to predict the effects of coastal habitat degradation on the dynamics of

exploited marine populations (Vasconcelos et al., 2014; Boyd et al., 2018). The impacts of local anthropogenic disturbance on juveniles of nearshore nursery-dependent species are thus well documented (Brown et al., 2018), but the consequences of these mortalities for population renewal are still poorly quantified (Lotze et al., 2006; Sundblad and Bergström, 2014; Vasconcelos et al., 2014).

Some studies have quantified the impact of nursery habitat degradation for specific populations with models spatially structured by stages and ages (Rose et al., 2018; Archambault et al., 2018; Camp et al., 2020; Champagnat et al., 2021). These models are very case-specific due to the complex parameterisation and the large amount of data and knowledge required (Lipcius et al., 2019). Consequently, their application to other case studies is difficult, although necessary for management orientation (Brown et al., 2018). In this context a more generic model would be beneficial for application to more species.

In this work, we build on a generic age and stage structured model developed by Champagnat et al. (in prep) to quantify the importance of nursery degradation/restoration on stock dynamics and productivity. In this model, survival in nursery area is described by a Beverton-Holt relationship which underlies competition mechanism between juveniles in nursery (Beverton and Holt, 1957). This relationship is parametrized in terms of steepness and carrying capacity.

Steepness is the proportion of unfished equilibrium recruitment produced when the spawning stock biomass is reduced to 20% of its unfished level (Mace and Doonan, 1988). It characterizes the drop off in recruitment when the reproductive potential is reduced. This parameter is dimensionless and can therefore be compared between different species. The value of steepness can vary from 0.2, for a linear stock-recruitment relationship, to 1, for a constant recruitment above 20% of pristine biomass (Myers et al., 1999). When steepness is close to 1, the density-dependent mortality between eggs and recruits is very high, while conversely, it is low for a low steepness value (Mangel et al., 2013). Steepness is an indicator of the resilience of a stock to fishing: if steepness is high, the stock will be able to maintain high productivity even in a state of overexploitation (Mangel et al., 2013). The shape of eggs-recruit density dependent survival relationship is therefore very important as it determines the resilience to fishing and therefore the management reference points associated with the stock (Brodziak and Legault, 2005; Punt and Dorn, 2014; Rindorf et al., 2022). However, parameterizing a relationship between the spawning stock biomass and the number of recruits, a stock-recruitment relationship, is very complex due to the limited availability of data and the imprecision of parameter estimates (Haltuch et al., 2008; Conn et al., 2010). Hierarchical analysis

approaches have been used to estimate stock-recruitment relationship patterns, ad to relate estimates to the life history traits of species in a generic way (Myers and Mertz, 1998; Myers et al., 1999; Hilborn, 2003). In particular, this approach has been used to estimate steepness for all fish in Thorson's model (2019).

The Beverton-holt relationship is also parameterized by an asymptote, linked to the carrying capacity of the nursery. Carrying capacity is defined as the maximal population size of a given species that an area can support (Daily and Ehrlich, 1992). The carrying capacity tends to be higher for wider and more productive nurseries areas, but vary depending on the species; species that have lower resource requirements can be more easily supported in areas of lower productivity or resource availability (Seitz et al., 2008). One hypothesis, supported by several studies, is that the main mechanism controling carrying capacity is competition for food due to a limited number of prey (Le Pape and Bonhommeau, 2015; Saulnier, 2019; Day, 2020). But other mechanisms can also affect this carrying capacity of nursery areas such as predation, competition for space, parasitism, or environmental variability (Day, 2020).

The previous use of the model by Champagnat et al., (in prep) remained conceptual with application to theoretical populations and scenarios based on hypothetic values. It evidences the sensitivity of population response to species life history traits, and especially steepness. The objective of our study is to develop practical applications by applying this model to a group of species at the stock level and for a given management unit. The Eastern English Channel, ICES division 7.d, is fisheries area of main interest but also highly anthropized. It includes in particular the Seine estuary, which has very high levels of degradation (Le Pape et al., 2007; Archambault et al., 2018). Seine estuary has experienced important morphological changes from channel dredging and the building of dikes and harbors, with a resulting substantial reduction in suitable shallow muddy nursery areas (Rochette et al., 2010; Champagnat et al., 2021). In addition, this area has been facing high levels of chemical contamination for decades (Barjhoux et al., 2018), causing reductions in habitat quality for juveniles (Gilliers et al., 2006; Amara et al., 2007; Courrat et al., 2009). Other nurseries in the Eastern English Channel have also suffered from degradation of both surface area and quality. Four species of high fisheries interest were accounted for this analysis: sole (*Solea solea*), plaice (*Pleuronectes platessa*), whiting (*Merlangius merlangus*) and seabass (*Dicentrarchus labrax*). These species have similar life cycle with juveniles dependent to estuaries and coastal habitats. Adults of these species spawn on large spawning grounds, mostly outside the coast (Pawson et al., 2007, Rochette et al., 2013). The fertilized eggs released into the water column became larvae then

drift with the current (Rochette et al., 2012; Dambrine, 2020). Some of these larvae reach the coastal and/or estuarine areas and metamorphose into juveniles that settle in nurseries. For a species-specific period of time, juveniles grow in these habitats, which offer protection against predators and conditions that maximize their survival (Gibson, 1994; Beck et al., 2001; Parlier, 2006; Carpentier et al., 2009). Around sexual maturity, fish leave the coastal nursery areas to move to adult habitats and subsequently participate in reproduction. While sharing dependency to nursery areas, the juveniles of these species are not distributed over the same areas. Their distribution of juveniles stage depends on habitats features such as depth, salinity and prey, with optimum that differs between species (Morin et al., 1999; Amara et al., 2001; Day, 2021), which leads to a distinct distribution at juveniles stage (Ysebaert et al., 2003). This group of species is therefore particularly interesting for studying the degradation of nurseries in a highly anthropized area.

The present study aims to quantify the effects of human disturbance on nurseries in the Eastern Channel and establish their consequences on this four population of interest. A two step approach was used: (i) Parameterize the generic stage-based life cycle model of Champagnat et al. (in prep) for four populations of interest in the Eastern Channel based on available literature and on the most recent results of stock assessment. (ii) Combine the model with scenarios of habitat degradation to assess the effect of nursery habitat degradation on the four species. For this purpose, the area loss in Eastern English Channel nursery was quantified since 1870 and the effects of quality degradation were estimated. A quantification of the effects of the restoration of both surface and quality of these habitats on the population dynamics was carried out and compared between species.

2. Materials and Methods

A schematic diagram of the simulation framework is summarized in figure 1. To quantify the effects of the degradation of common nurseries the model has been parametrized with literature and stock assessment and the carrying capacity has been calibrated. Then, habitat scenarios has been built with historical data and literature. Finally, the model outputs were used to simulate the population dynamics and estimate the equilibrium reference points. The effects of nursery restoration could finally be compared between species.
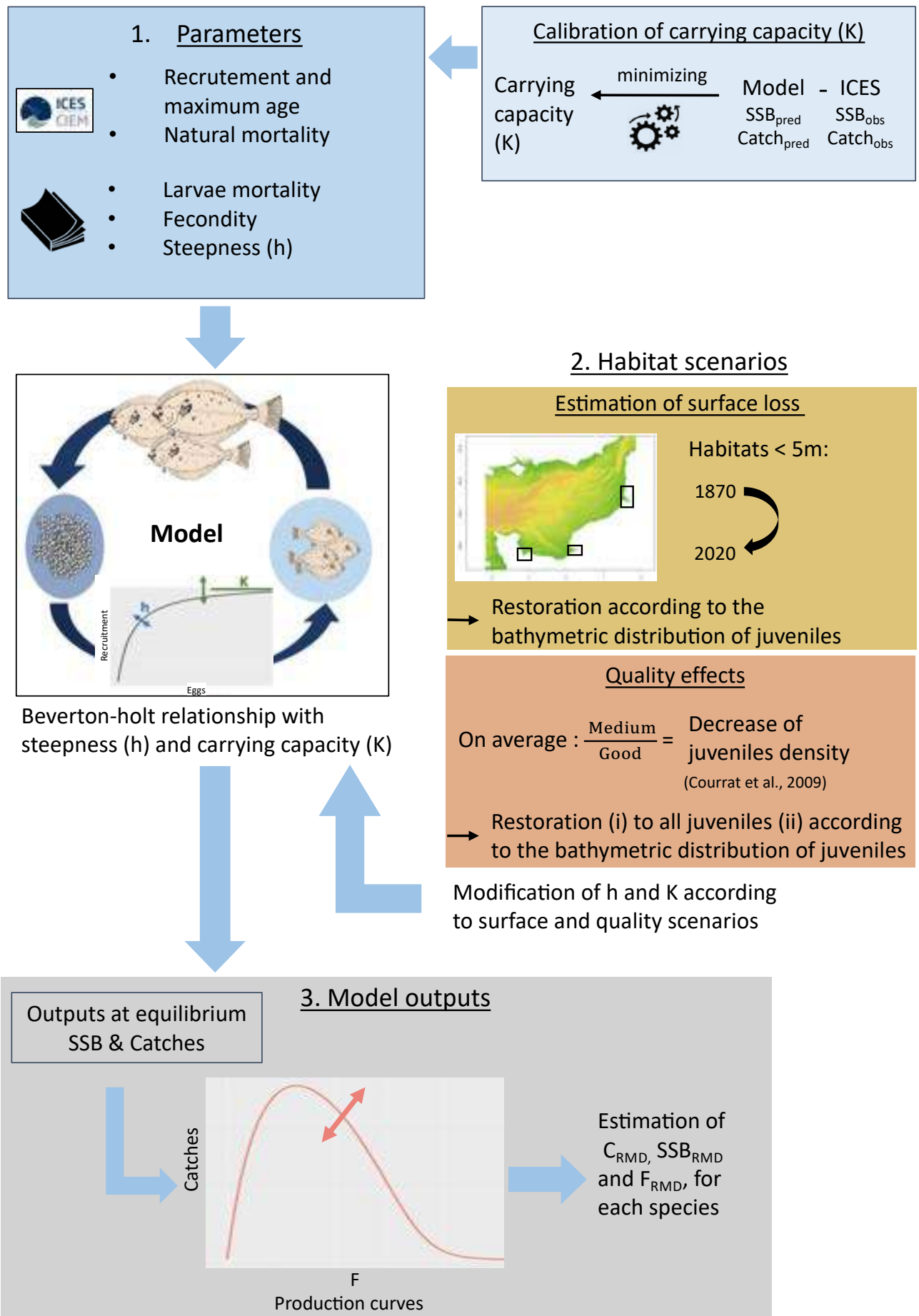
Figure 1. Schematic diagram of the simulation framework

2. 1. Model overview

The impact of the degradation of nursery areas on stock productivity was simulated with a deterministic life cycle model, structured by stage and age (Champagnat et al., in prep). This model considers a single closed population and a unique nursery area. After recruitment age (a_{rec}), fish undergo natural mortality and fishing mortality, and population abundance ($N_{a,y}$) at age a for year y is described by the classical population dynamics equation :

(1) $$N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})}$$

with M and F the natural and fishing mortality rates, respectively.

For the last age group a_{max}, the population abundance is described as :

(2) $$N_{a_{max},y+1} = N_{a_{max},y} \times e^{-(M_{a_{max},y}+F_{a_{max},y})} + N_{a_{max}-1,y} \times e^{-(M_{a_{max}-1,y}+F_{a_{max}-1,y})}$$

Recruitment, defined as the number of juveniles arriving in nurseries, is the critical component of this model. It must account for the habitat-mediated mortalities during juvenile stage while remaining generic for parametrization.

The recruitment $N_{a_{rec},y}$ is computed from eggs numbers produced in a year, ω_y, defined by equation (3):

(3) $$\omega_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times Mat_{a,y} \times pf_{a,y} \times Fec_{a,y}$$

with, Mat_a the probability of being mature at age a, pf_a the female proportion at age a, and Fec_a the fecundity at age a.

The mortality from eggs to recruited juveniles was assumed to follow a compensatory density dependent mortality process resulting from intra-cohort competition for trophic resources and/or space (Beverton and Holt, 1957). Recruitment ($N_{a_{rec},y}$) is modelled by a Beverton-holt relationship but reparametrized in terms of its asymptote, K, interpreted as the carrying capacity of the nursery, and steepness (h) according to the equation (4):

$$(4) \quad N_{a_{rec},y} = \frac{4h\omega_{(y-1)}}{\bar{W}(1-h) + \frac{4h\omega_{(y-1)}}{K}}$$

with $\bar{W}$ the average number of eggs produced by a recruit during its lifetime in the absence of fishing, equation (5):

$$(5) \quad \bar{W} = \sum_{a=a_{rec}}^{a_{max}} S_a \times Mat_a \times pf_a \times Fec_a$$

with S_a the cumulative survival at age a without fishing (equation in appendix 1).

This recruitment relationship underlies a density-dependent mortality process (M^{dd}), linked to competition between juveniles, and a density independent mortality (M^{di}) (equations are available in appendix 1). These mortalities are related to the steepness (h) and carrying capacity (K). The parameter h is described by an equation integrating a density independent mortality rate (6). While the parameter K integrates both density independent mortality and density dependent mortality rates, and S, the surface of the nursery (7).

$$(6) \quad h = \frac{e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}{4 + e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}$$

$$(7) \quad K = lim_{\omega \to +\infty} N_{a_{rec}} = \frac{M^{di} \times S}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1}$$

With M_{larvae} the larvae mortality occurring during larvae drift which is only density independent.

Once parameterized (see next section), the model is used to simulate equilibrium states by exploring a wide range of fishing mortality rate (F, from 0 to 1). Results obtained were used to empirically construct the equilibrium curve for Catch (C) and Spawning Stock Biomass (SSB), therefore enabling the estimation of management reference points such as SSB_{MSY}, C_{MSY} and F_{MSY} (MSY, Maximum Sustainable Yield) (equations for catch and SSB are available in appendix 1).

2. 2. Case study

The analysis explored the impact of disturbance of common nursery areas for a group of species of fisheries interest. Our case study focuses on the Eastern English Channel (EEC; ICES Division 7.d., figure 2) management unit. The study area include (i) coastal nursery dependent species with (ii)

analytical stock assessments data and outputs, (iii) quantitative knowledge on juvenile distribution. In Eastern English Channel, the four selected species fulfill these requirements: Sole (*Solea solea*), Plaice (*Pleuronectes platessa*), Whiting (*Merlangius merlangus*), and Seabass (*Dicentrarchus labrax*).

Figure 2. Map of ICES divisions 7.d.

2. 2.1. Parameterization of the case study

Parameterization use a combination of parameters extracted from stock assessments and literature and a calibration of carrying capacity (K).

Parameters from stock assessment and literature

To parametrize the model, the data used were taken from stock assessments and literature. Recruitment age, maximum age, weights at ages, maturity ogive, and fishing and natural mortality were taken from stock assessment reports (ICES. WGNSSK., 2021 and ICES. WGCSE., 2021).

In addition to stock assessment outputs, fecundity equations, larvae mortality, and length at ages were necessary; they were collated from literature. Steepness was extracted from the Fishlife package (Thorson, 2019) which analyzes stock-recruitment series from the RAM database (Myers et al., 1995) based on a multivariate hierarchical Bayesian model with taxonomic structure extracted

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from Fishbase (Froese and Pauly, 2022). The taxonomic structure embedded within the hierarchical structure of the model strengthens the estimate for taxa for which data are insufficient, we extracted the values at the taxonomic level of the Order to obtain a robust estimate. The different data needed for parametrization and their sources for each species are presented in Table 1, all the data used to calculate the parameters ω, $\bar{W}$ and the fecundity equations are available in appendix 2.

Table 1. Data for model parameterization.

	Recruitment age (a_{rec})	Maximum age (a_{max})	Steepness (h) (Thorson, 2019)	Natural mortality (M)	Larvae mortality (Le Pape and Bonhommeau, 2015)
Sole	**2** (ICES. WGNSSK, Stock Annex, 2021)	**11** (ICES. WGNSSK., 2021)	**0.771**	**0.1** (ICES. WGNSSK., 2021)	**3×log(10)**
Plaice	**2** (ICES. WGNSSK, Stock Annex, 2021)	**7** (ICES. WGNSSK., 2021)	**0.771**	**Vector** (see appendix 2) (ICES. WGNSSK., 2021)	**3×log(10)**
Whiting	**1** (Henderson and Holmes, 1989)	**8** (ICES. WGNSSK., 2021)	**0.626**	**Matrix** (ICES. WGNSSK., 2021)	**3×log(10)**
Seabass	**4** (ICES. WGCSE., 2021)	**16** (ICES. WGCSE., 2021)	**0.736**	**0.24** (ICES. WGCSE., 2021)	**3×log(10)**

Given the information available, only the parameter K, the carrying capacity of the nursery areas, which ultimately determines the population size, requires calibration.

Calibration of K

For each species, the carrying capacity K was calibrated from stock assessment outputs. The value of K was estimated by minimizing the difference between the SSB and catches simulated by our

model with thus of the stock assessment outputs. Estimates of K were obtained by minimizing the following objective function:

$$(8) \qquad \sum_{y=y_{min}}^{y_{max}} (log(SSB_{pred,y}) - log(SSB_{ICES,y}))^2 \ + \ (log(C_{pred,y}) - log(C_{ICES,y}))^2$$

with y_{min} and y_{max} the first and the last year of the stock assessments respectively, SSB_{pred} the model predictions of SSB, SSB_{ICES} the SSB provided by ICES, C_{pred} the model predictions of catches and C_{ICES} the catches provided by ICES.

Spawning stock biomass and catches are taken from the stock assessments for sole and plaice. While for whiting and seabass, SSB and catches were derived from stock assessments covering a wider area and were therefore scaled to the EEC proportionally to the relative landings in this area. Landings data by area are taken from the historical catch database. For seabass, the landings data covered the entire stock assessment period. For whiting, the first twelve years of the stock assessment period did not have landings data by area, for this period, the proportion of catches was calculated as the average proportion for the first 5 years with spatialized data. The proportion of catches in divisons 7.d for seabass and whiting are available in appendix 3.

Assessing the realism of the model

Once calibrated, the realism of baseline population dynamic was assessed by looking at the values of F_{MSY} , $\frac{C_{MSY}}{SSB_{MSY}}$ and $\frac{SSB_{MSY}}{SSB_0}$ (SSB$_0$ is the unfished spawning biomass at equilibrium). Realism of F_{MSY} and $\frac{C_{MSY}}{SSB_{MSY}}$ values will be assessed by comparing to stock assessment outputs and $\frac{SSB_{MSY}}{SSB_0}$ will be discussed regarding Froese et al. (2016).

2. 3. Parameterization of habitat scenarios

Scenarios of habitat degradation/restoration were parameterized by modifying both the surface of available habitats and the quality of nursery habitat.

The stock-recruitment relationship depends directly on the surface of the nursery habitats (Eq (4) and Eq (7)). This surface can be modified: a multiplier ($\lambda_{surface}$) is applied on the S factor of the parameter K.

It is assumed that the alteration of the quality of juvenile habitats induces change in mortality rates M^{dd} and M^{di}. To represent this change in mortality, in relation to the modification of the environmental quality, a multiplier ($\lambda_{quality}$) is applied to M^{dd} and M^{di} which modifies the h and K values (Eq (6) and Eq (7)). No information was available to define how a quality scenario would impact M^{dd} and M^{di}. Thus we assumed a common multiplier ($\lambda_{quality}$). To have quality and surface scenarios with similar meaning we used $\lambda_{quality}$ and $\lambda_{surface}$ with values < 1 represent habitat restoration. The expression of parameters h and K can therefore be rewritten from Eq (6) and (7) as:

$$(9) \qquad h = \frac{e^{-\lambda_{quality} \times M^{di} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}{4 + e^{-\lambda_{quality} \times M^{di} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}$$

$$(10) \qquad K = \frac{M^{di}}{M^{dd}} \times \frac{S}{\lambda_{surface}} \times \frac{1}{e^{\lambda_{quality} \times M^{di} \times a_{rec}} - 1}$$

These formulations of h and K as a function of quality and surface make it possible to easily simulate habitat restoration scenarios and thus study their impact on population dynamics.

2. 3.1. Parameterization of surface losses

Quantification from historical maps

The construction of the surface scenarios was based on estimation of surface losses since 1870. This estimation was derived from bathymetry data in three coastal sectors of the French EEC coastline in 1870 (Bay of Veys, Seine Estuary, Somme Bay and Canche) available on the EMODnet Bathymetrie website. The sectors selected were of major interest for our study as they cover areas identified as common nursery for the four studied species (Riou et al., 2001; Rochette et al., 2010; Carpentier et al., 2009; Bacq et al., 2013). To our best knowledge, no similar data were available for the English coast. The sampled points were transformed into maps using a universal kriging method. In a first step, a semi-variogram was constructed with a spherical model, without nugget

effect. Then, spatial interpolation by kriging was realized on the area covered by the sampling. The resulting maps were compared with the 2020 bathymetry map, with the same spatial coverage. The loss of habitats of less than 5 meters bathymetry (in relation to the 0 of the maps) was estimated in each sector. This depth was chosen because it concentrates anthropic pressures and surfaces loss in coastal nursery areas (Rochette et al., 2010). Finally, habitat loss at the EEC scale (S_{loss}) was estimated as the sum of the areas lost in each sector between 1870 and 2020 divided by the total EEC area above 5 meters in 2020. For the other areas for which we had no information, it was assumed that no change had occurred. A surface restoration multiplier is calculated according to the equation:

$$(11) \qquad S_{restoration} = \frac{1}{1 - S_{loss}}$$

2. 3.2. Bathymetric distribution of juveniles

The juveniles of the different species have different bathymetric distributions, and especially in shallow areas (i.e. less than 5m). Those differences in concentration is shallow areas will therefore induce differences in the way species are impacted by surface loss and quality degradation in shallow areas. The proportion of juveniles present in less than 5 meters depth was therefore estimated from the nursery and bathymetric maps. The nursery maps for each species were available on Sextant (appendix 4). A fine-scale bathymetric map of the EEC was downloaded from the Emodnet bathymetry site. The resolution of the bathymetry map was first degraded, with bilinear interpolation method, to match that of the nursery. The two maps were then coupled to obtain the proportion (*Prop*) of juveniles present in the band above 5 meters depth.

The proportion of juveniles (henceforward called *Prop,* see 2.3.1) was used to calculate a surface restoration factor ($\lambda_{surface}$) which we apply to S, to simulate a restoration of the nursery area as in 1870. The area lost was only applied to the proportion of juveniles present in this area according to the equation:

$$(12) \qquad \lambda_{surface} = \frac{\frac{1}{Total\ Density + (Prop \times S_{restoration}) - Prop}}{Total\ density}$$

With *Total density* the sum of density of all juveniles of a species.

2.3.3. Parameterization of quality effects

Quantification of quality effects from literature

Despite the numerous studies of the impact of toxic pollution carried out at the individual fish level (Davoodi and Claireaux, 2007; Foekema et al., 2008; Wessel et al., 2010), the quantitative effects on density dependent survival are not known (Lotze et al., 2006; Sundblad and Bergström, 2014; Vasconcelos et al., 2014). Here we rely on previous work by Courrat et al. (2009) who measure the density of marine juvenile fish in the different English Channel estuaries and correlated the spatial variations to anthropogenic pressures to estimate the ecological status of transitional waters based on fish for the EU (European Union) water framework directive (Delpech et al., 2010). Three categories of ecological status of the estuaries were identified according to the density of juveniles: good, average and poor quality status. The estuaries with a good ecological status had a density of juveniles 20% higher than estuaries of average quality and 40% higher than estuaries of poor quality.

Parameterization of quality multipliers

In our model the different estuaries cannot be treated separately. The quality scenarios have therefore been constructed by considering a homogeneous quality status of the nursery areas for all the nursery sectors (i.e., a single parameter $\lambda_{quality}$ for the whole EEC). An assumption of the ecological status of the different estuaries in the EEC has been made: on average, all estuaries are considered to be in average condition. Our scenarios will therefore seek to restore these estuaries to a good ecological status. We derive two different scenarios for habitat quality restoration. A first one where the restoration is applied to all juveniles (*quality all*). A second one where the restoration is applied to the most coastal juveniles only (*quality band*) (i.e. < 5m). This assumption was made to differentiate juveniles present in very coastal areas, a priori subject to high levels of contamination, and juveniles present in more offshore waters less affected by the degradation of shallow habitat quality.

The first restoration scenario (*quality all*) was based on a new K ($K_{scenario\ all}$) calculated to simulate a value of K increased by 20% according to the equation:

(13) $$K_{scenario\ all} = K \times 1.25$$

The second restoration scenario (*quality band*) is only applied to the proportion of juveniles present in less than 5 meters (*Prop*) (see 2.3.1). In this case, $K_{scenario\ band}$ is calculated according to the equation:

(14) $$K_{scenario\ band} = (K \times Prop \times 1.25) + (K \times (1 - Prop))$$

In a first step, we calculate M^{di} and M^{dd} according to the equations available in appendix 5. In a second step, we calculate the multiplier $\lambda_{quality}$ that will be applied to M^{di} and M^{dd} to simulate an increase in juveniles density linked to a quality restoration. The equation of $\lambda_{quality}$ can be deduced from equations (10) and (13) or (14), according to the scenario:

(15) $$\lambda_{quality} = \frac{log\left(\dfrac{\frac{M^{di}}{M^{dd}}}{K_{scenario}} + 1\right)}{M^{di}}$$

2. 3.4. Summary of scenarios

The estimates of surface losses and quality effects lead us to obtain four scenarios: (i) surface restoration, (ii) quality restoration applied to all juveniles (*quality all*), (iii) quality restoration applied to the most coastal juveniles (*quality band*) and finally (iv) a scenario that combines surface and quality band restoration.

3. Results

3. 1. Habitat loss since 1870 and restoration factors

The loss of the surface areas in the three coastal sectors under 5 m was estimated to 12.93% between 1870 and 2020 at the EEC scale (figure 3). The proportions of juveniles present in habitats above 5 m were calculated, and then the surface and quality restoration factors were estimated for each species (table 2). Seabass was the species with the most coastal distribution with 80% of his juveniles concentrated in less than 5 m, followed by sole with almost 50%. Due to highly concentrated, these two species are the most affected by surface loss since 1870 and quality degradation. Thus they will be associated with a higher restoration factor than the others (i.e., a lower $\lambda_{surface}$ and $\lambda_{quality}$). In contrast, plaice and whiting have a very low restoration factor due to the very less coastal distribution of their juveniles.
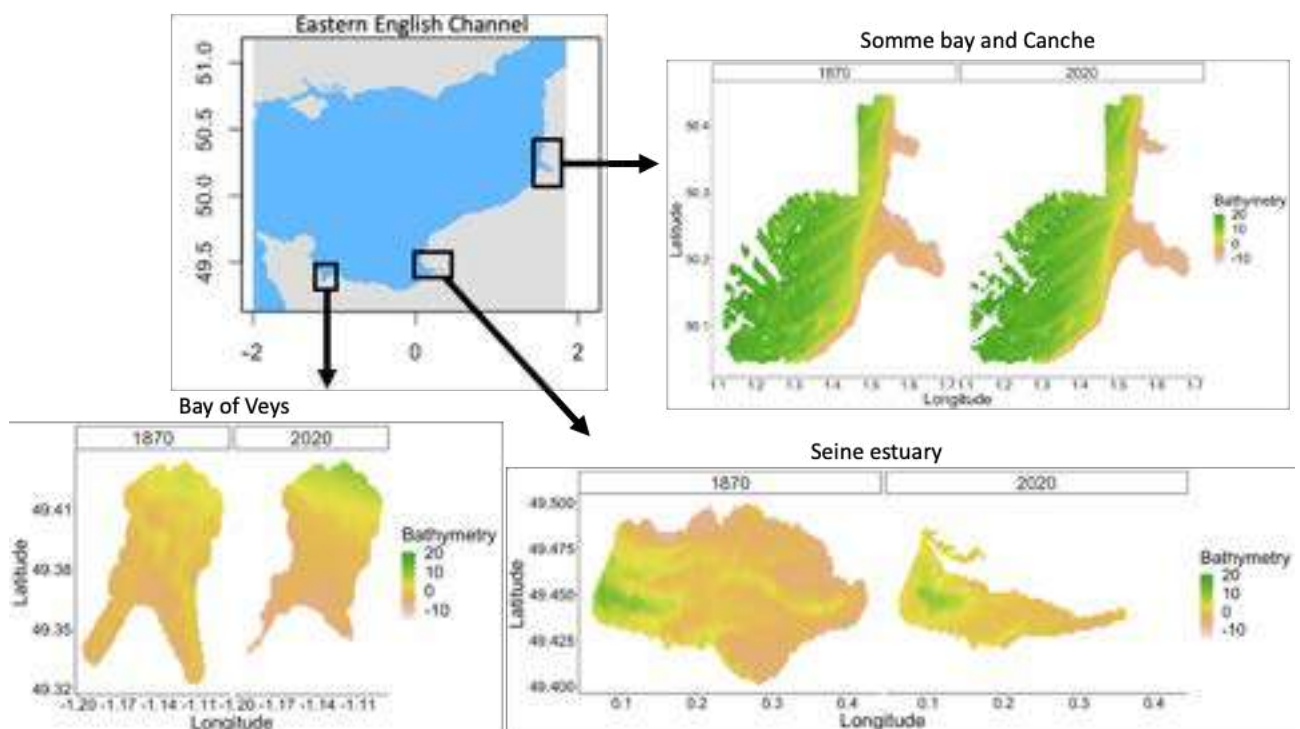

Figure 3. Habitat loss in the three areas of interest since 1870.

Table 2. Percentage of juveniles present in habitats under 5 m and associated restoration factor.

	Sole	Plaice	Whiting	Seabass
Percentage	49.71	16.72	4.10	80.23
Surface restoration factor ($\lambda_{surface}$)	0.9313	0.9758	0.9939	0.8935
Quality restoration factor *Quality all* ($\lambda_{quality}$)	0.9439	0.8277	0.8504	0.9327
Quality restoration factor *Quality band* ($\lambda_{quality}$)	0.9706	0.9663	0.9928	0.9448

In a first step, the results will be illustrated only with the second quality scenario applied to inshore juveniles (*quality band*). Finally, a sensitivity analysis of the assumptions on the quality scenario will be conducted in order to compare the results of the two quality scenarios.

3. 2. Seabass

A detailed interpretation of both calibration and results of the habitat scenarios is presented for seabass. For the other species, fit plots was available at appendix 6, value of K, reference points, MSY related indicators and average SSB and catch values at appendix 7, and production curves in appendix 8. Note the results for seabass are expressed as a percentage of SSB or catch reallocated to area 7.d and not in relation to the management unit used by ICES

3. 2.1. Calibration assessment

The calibration of the model estimates K at 1.1×10^7 juveniles. Model predictions of catches and SSB do not fit perfectly with annual ICES data (figure 4). But the average SSB values estimated by ICES and the average SSB values predicted by our model are similar with 5.8×10^6 and 5.6×10^6 Kg respectively for this period. The same conclusion can be made for catches with ICES values at 1.4×10^6 Kg and our model predictions at 1.2×10^6 Kg.
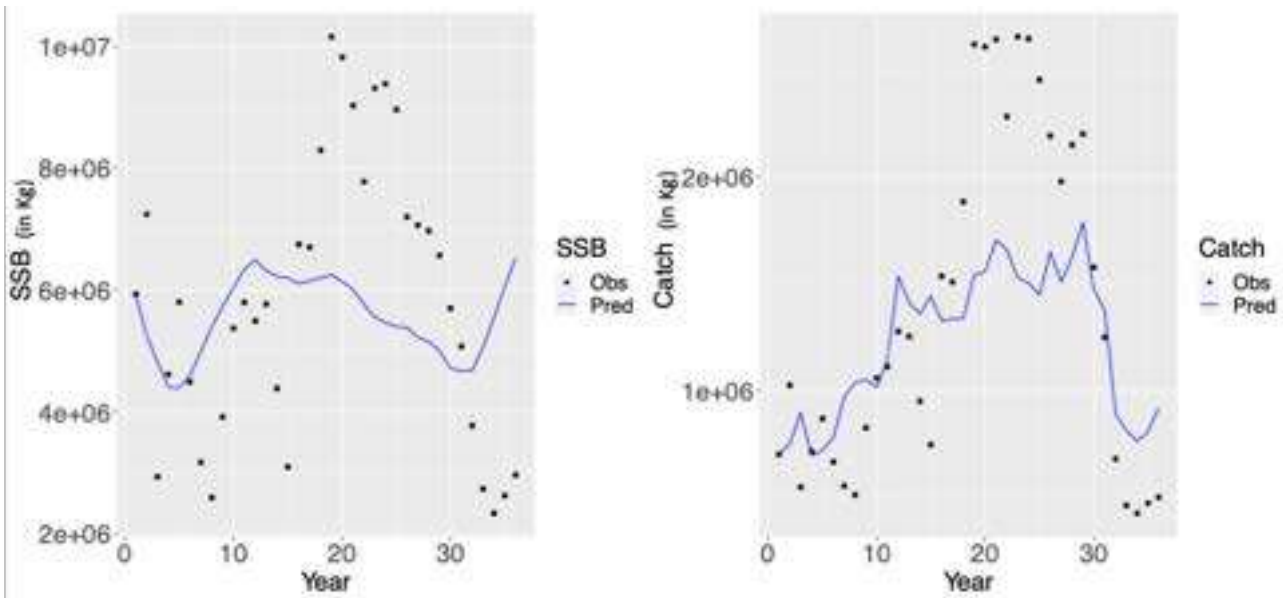
Figure 4. Fit between data (*Obs*) and model prediction (*Pred*) of seabass for SSB (left) and catch (right).

Overall, model behavior at equilibrium is considered as realistic as different indicators of the population dynamics range in the expected range. The F_{MSY} value is 0.16 without habitat restoration scenario (figure 5), while the F_{MSY} value estimated by ICES was 0.17 (ICES. WGCSE, 2021). The other indicators of stock dynamics are also in the expected range with ratio $\dfrac{C_{MSY}}{SSB_{MSY}}$ estimated at 0.25 (0.35 for ICES estimate) and ratio $\dfrac{SSB_{MSY}}{SSB_0}$ estimated at 0.27.

3. 2.2. Production curves under habitat scenarios

The population dynamics and productivity were represented by the construction of equilibrium curves for catch as a function of SSB and F under a wide range of fishing mortality for the reference and the 3 scenarios of habitat restoration (figure 5). Restoring the surface of juvenile habitat only impacts K (equation (10)), and hence only impacts the scale of the productivity curve, with increased catches, and increased level of biomass at MSY (figure 5 A), but F_{MSY} remains unchanged (figure 5 b). By contrast, restoring habitat quality affects both K and h parameters (equation (9) and (10)), and hence not only increases catches and SSB_{MSY} but also increases F_{MSY} (+ 0.01) which maximizes the catch.
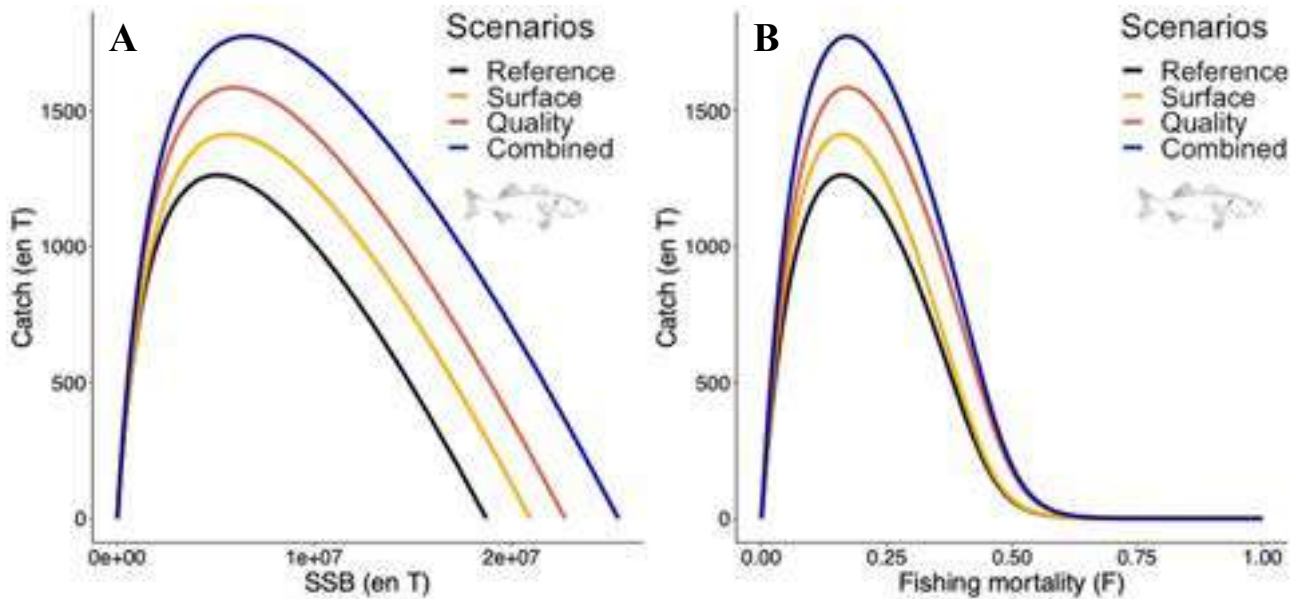
Figure 5. Production curves according to habitat scenarios as function of SSB (A) or fishing mortality (B) for seabass in divisions 7.d.

3. 3. Comparison between species

The effects of habitat restoration scenarios were compared across that species, by estimating relative gains in SSB and catches at MSY equilibrium state (figure 6). As for the seabass, whiting are expressed as a percentage of SSB or catch reallocated to area 7.d and not in relation to the management unit used by ICES. The surface scenario has the least impact on SSB with gains ranging from 0.6% for whiting to 11.9% for seabass (figure 6 A). This great heterogeneity between species is also found in the gains linked to the restoration of quality with an increase in SSB ranging from 1.3% for whiting to 16.5% for seabass. Finally, when the two restoration scenarios are combined the effects of separate restoration measures become synergistic, and two groups of species emerge. Whiting and plaice are the species for which the combined restoration has the least effect with gains of 1.9% and 7%, respectively, whereas sole and seabass have a strong increase in SSB with gains of 22.7% and 30.3%, respectively.

In a similar way, the gain of catch at MSY follows those of the SSB (figure 6 B). However, the catch gains for seabass are even greater than for SSB because the MSY state is attained for a higher fishing mortality ($F_{MSY} + 0.01$) which therefore increases the catch. For the combined scenario, the gains represent an increase of 1.9, 7, 22.7 and 40.4 % for whiting, plaice, sole and seabass respectively. In terms of tons, the restoration of habitat surface and quality under our scenarios

represents an increase of 250, 480, 1015 and 510 tons for whiting, plaice, sole and seabass respectively.
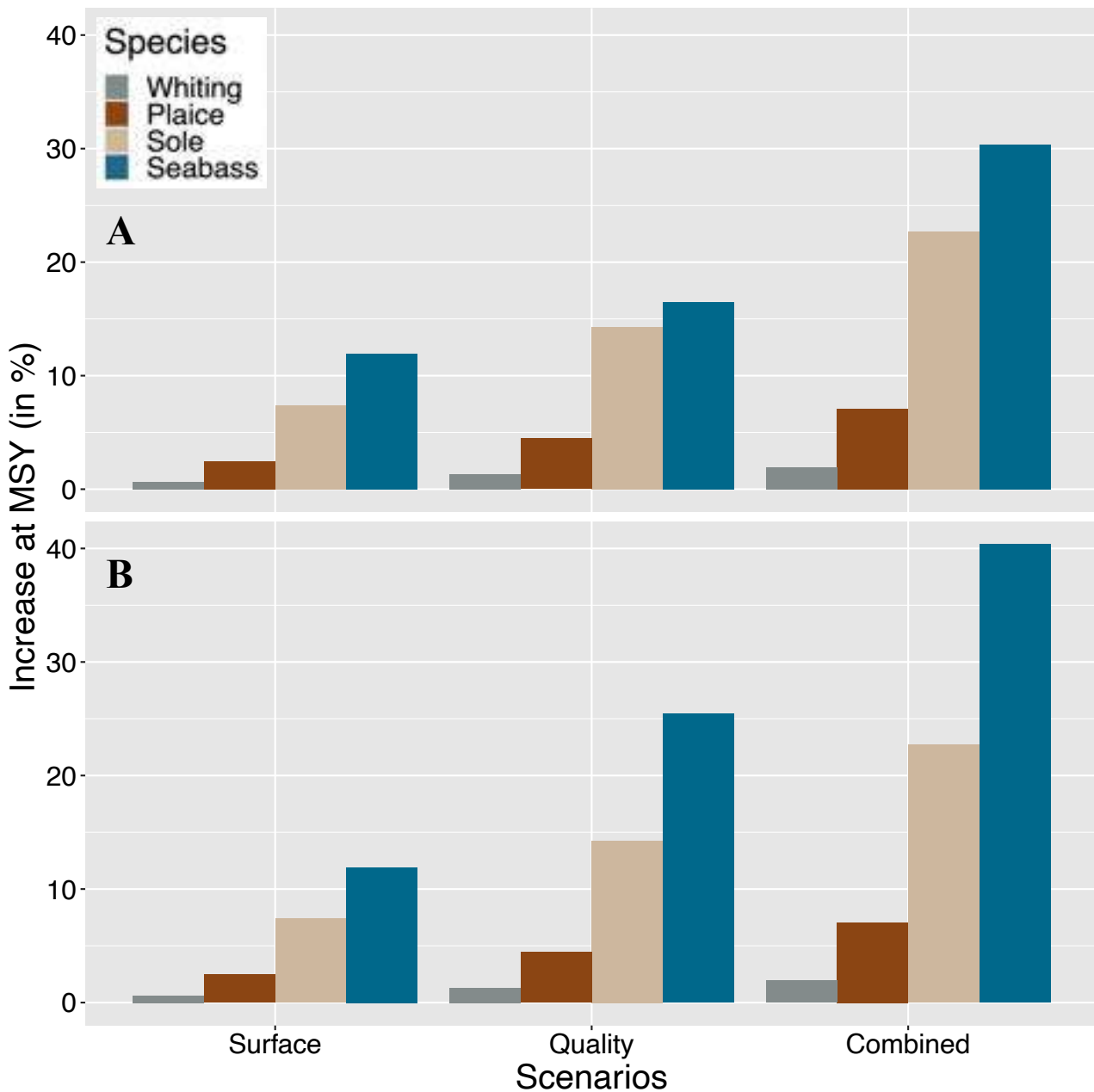
Figure 6. Effects of habitat scenarios on SSB (A) and Catch (B) gain at MSY by species.

3. 4. Sensitivity analysis on the hypotheses on quality scenario

When we conceptualize the quality scenario, we assumed that only the juveniles present in less than 5 m were impacted by the quality. This assumption has been formulated by experts knowledge, but no quantitative data can really support it. We tested another assumption in which nursery quality would impact all juveniles present in the EEC with no restriction to the shallow areas below 5m. To

illustrate the differences generated by these two hypotheses, the model was run with this second scenario and difference was compared in a histogram of catch gains at MSY by species (figure 7). Large differences emerge from these two quality scenarios. Firstly, as expected, the restoration of quality for all juveniles in the EEC leads to a greater homogeneity in the gains than when the restoration was carried out according to the bathymetric distribution of juveniles. The differences found between this species are therefore only related to demographic parameters, and especially h and fecundity, which strongly differ between species. This scenario shows a higher sensitivity to quality restoration for species with lower steepness (whiting, figure 7). Moreover, all species have greater catch gains in this "global" restoration scenario due to a larger quantity of juveniles impacted by the restoration. This scenario generates an increase of 31, 22, 14 and 6 percentage units compared to the partial scenario (figure 6 and 7), for whiting, plaice, sole and seabass respectively. The results of our model are thus very sensitive to the assumptions made regarding nursery habitat quality restoration scenarios.
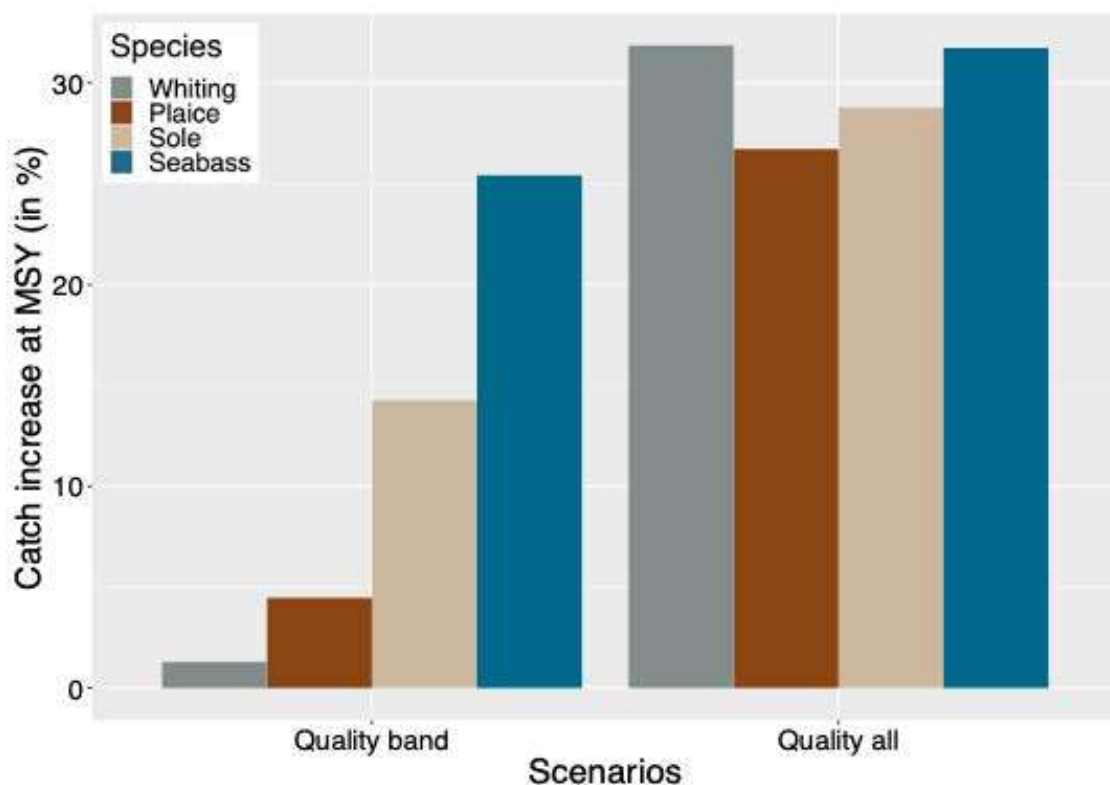

Figure 7. Difference in catch gain per species according to the assumption made for quality scenarios. *Quality band* for the scenario apply restoration only on the juveniles in shallow habitats and Q*uality all* for the restoration on all the juveniles.

4. Discussion

In that study, we assessed the consequences of nursery restoration through an age and stage structured model. We developed a generic model with a stock-recruitment relationship directly related to the quality and surface of the nursery habitat. The model was parameterized from the literature and stock assessments and the carrying capacity was calibrated on stock assessments output to simulate realistic population size and dynamics. The model was applied to four nursery-dependent EEC species characterized by various life history traits and various degrees of concentration on the same coastal nursery habitats. The model was used to simulate equilibrium catch curves obtained under different scenarios of nursery quality and surface restoration for the four species. Surface restoration increased the catches and biomass at MSY. The restoration of quality lead to a stronger increase in catches and biomass at MSY, but also an increase of fishing mortality at MSY. Overall, the species with the higher level of concentration on shallow nursery areas were the most sensitive to the habitat restoration scenarios. The response also depends to other life history traits. Species with lower steepness exhibit a stronger response to habitat scenarios. Thus, seabass was the species for which habitat restoration had the greatest impact, while whiting was the least affected.

4. 1. Model calibration

Our study was based on a model parameterized with data from stock assessments and literature.
Of course, a limit of the method is that it directly depends upon the estimates made by ICES and therefore cannot be applied to stocks that are not assessed, or for which the assessments do not estimate the necessary data.
Beyond those limits, an advantage of the method is that only one parameter, the carrying capacity (K), remained to be calibrated from stock assessment outputs. This makes it very easy to use and greatly limits the calibration time. The calibration of K implies two ecological assumptions, the first being that the carrying capacity of the nursery habitat is reached and limiting. This assumption is still debated, although recent studies tend to validate a seasonally limiting capacity (Le Pape and Bonhommeau, 2015; Saulnier, 2019; Day, 2020). Then, the output of our model were fitted to catch and SSB data from ICES working groups. For whiting and seabass, as the assessment unit of the stock is larger than area 7.d, a biomass reallocation was made according to the proportion of catches in this area. This reallocation adds uncertainty to the data, particularly in relation to fishermen's

behaviour, which may differ from one year to the next, or due to changes in fishing regulations. However, the objective of the study was not to reproduce annual fluctuations in SSB and catches but to simulate realistic population dynamics. This poor ability to reproduce the annual fluctuations is due to the second assumption made in the calibration of K. The carrying capacity does not vary over time, although studies have shown that this capacity can vary on an inter and intra-annual scale (Luo et al., 2001; Le Pape et al., 2003), for instance as a response to a trophic cascade from the supply of nutrients and organic matter that would then support primary and secondary production (Day, 2020). First, our calibration lead to an average estimate of SSB and catches close to the average estimate of the ICES over the same period, for all species (appendix 7). In addition to the calibration on SSB and catches, some indicators characteristics of the dynamics (MSY and related indicators like ratios $\frac{C_{MSY}}{SSB_{MSY}}$ and $\frac{SSB_{MSY}}{SSB_0}$, and F_{MSY}) were used to assess the realism of the population dynamics. For sole, whiting and seabass, the indicators $\frac{C_{MSY}}{SSB_{MSY}}$ and F_{MSY} were relatively close to those provided by the ICES (appendix 7). For whiting, the model predictions were higher than published values. The $\frac{SSB_{MSY}}{SSB_0}$ ratio was within the expected range for all four species. Nevertheless for plaice, estimate of the $\frac{C_{MSY}}{SSB_{MSY}}$ ratio was very high compared to ICES value (0.63 and 0.29 for ICES). In view of the $\frac{SSB_{MSY}}{SSB_0}$ ratio which seems to be a realistic value, this very high value can be explained by a parameterization of the model leading to a very high production of the stock. This high productivity would explain the very high catches supported by a low biomass. Discrepancies between the simulated and published values of those indicators for plaice are mainly explained by the values of steepness and fecundity which are two parameters that have a great influence on population productivity. The high productivity of the plaice in our model can be explained by a too high fecundity. Several equations from different studies (Dorel, 1986; Vérin et al., 2001; Jennings et al., 1998; ICES. WGNSSK. Stock Annex, 2021; for length at age and four equations from Horwood, 1993 for fecundity at length) have been tested in order to modify the fecundity and thus obtain a dynamic closer to that of ICES, but none of the tested combinations allowed for improving the ratio.

4. 2. Effects of nursery restoration and comparison between species

To our knowledge, our study is the first that assess the effect of restoration of common nursery areas for a group of species at the scale of a management unit. This study allowed us to accurately

estimate the effect of the loss of nursery areas on the French EEC coastline since 1870 on 4 species simultaneously (sole, plaice, whiting and seabass). In addition, we applied our model to a group of species for quantifying the impact of juvenile habitat degradation.

Results show that surface restoration, which leads to an increase in the carrying capacity of the nursery, increased the catches and biomass at MSY, but to a lesser extent than the restoration of habitat quality. Indeed, the restoration of quality increases both the carrying capacity and the steepness, leading to a stronger increase in catches and biomass at MSY, but also an increase of fishing mortality at MSY. In the case of a combined restoration, the effects are in synergy. Indeed, the restoration of the surface increases the carrying capacity, and the restoration of the quality increases the density of juveniles in this new surface, the effects of the combined restoration are higher than the addition of the effects of both surface and quality restoration.

The difference in gains between species due to surface restoration is mainly due to a different degree of concentration of juveniles in shallow nursery habitat. The differences in quality restoration are also due to this difference in distribution, but it is also related to steepness and demographic parameters. This difference linked to steepness and demographic parameters is reinforced by results obtained through the sensitivity analysis on the hypotheses on quality scenario. In a quality scenario that ignores the distribution of juveniles, the species that is the most affected by habitat restoration is the one with the lowest steepness. In this scenario, the contrast in responses is only related to the demographic parameters of the stock, especially to the steepness and fecundity, as demonstrated in Champagnat et al. (in prep).

Previous studies, focusing on sole, have already examined the effect of areas and/or habitat quality scenarios with more complex and specific models. Rochette et al. (2010) and Archambault et al. (2018) demonstrated the effects of quality degradation and area loss of sole nursery areas in EEC. But these study only looked at the restoration of the quality of the Seine estuary and its surface area as in 1850. Our model therefore provided consistent results with these two studies. But the main interest result is that the general approach allowed to extract the results of 3 other species.

4. 3. Limitations

4. 3. 1. Demographic hypotheses

Our study has some limitations related to the demographic hypotheses made in the model. First, the model considered juvenile habitat as a single block whereas coastal and estuarine areas are

composed of a multitude of habitats with high heterogeneity that can vary over time («shifting habitat mosaic», Peterson, 2003; Stanford et al., 2005; Wimberly, 2006; Nagelkerken et al., 2015) and their accessibility is characterised by transient phases of connectivity (Zeigler and Fagan, 2014). Our model considered nurseries as a single homogeneous habitat but ignored the connectivity which is of primary importance in the nursery function (Sheaves et al., 2015; Alp and Le Pichon, 2021). Considering the nursery areas as a single block is limiting, especially for the construction of realist quality restoration scenarios. However, considering such spatial heterogeneity would require parameterizing specific Beverton-Holt relationships for each nursery area with different ecological status and various strengths of density dependence, which is inaccessible for most of the case studies (but see Rochette et al. (2013) for an example). Moreover, considering different sector of the EEC nursery area would greatly complicate our model and the elaboration of restoration scenarios by raising questions about population connectivity (Archambault et al., 2016) and estimation of steepness (White, 2010). Indeed, diffusion of the outcomes of local nursery restoration at a metapopulation scale highly depends on the level of connectivity at different stage of the life cycle (Archambault et al., 2018). Our results should therefore be treated with caution. The interpretations are made at the metapopulation level without consideration of its spatial structure, which may lead to a poor estimate of exploitation rates, especially when based on an MSY approach (Ying et al., 2011). For example, our model does not consider the connectivity between possible EEC sole subpopulations yet it has been shown that this can lead to a different estimation of restoration effects (Champagnat et al., 2021; Archambault et al., 2016).

Another limitation of the model is that the different sources of uncertainty are not considered. The parameters are considered known without errors, the population dynamics is considered deterministic and no environmental variations is represented. Yet, environmental variability (Pfister and Stevens, 2003) is large, especially in the recruitment process. This structural limitation characteristic has notably led to poor predictions of annual variations in SSB and catches.

Finally, our model considers a density dependence that only takes into account the juveniles of the recruitment age, but the older age groups can also share some of the same areas. Moreover, mortality rates considered a single species, but the nursery areas are partly shared by several species, so an inter-species density-dependent could also occur (Gibson, 1994), as show during a short period of time, late summer (Amara et al., 2001; Van der Veer et al., 2010; Day, 2020). It would be interesting to take these characteristics into account, but there are no estimates that would allow us to integrate them into the model.

4.3.2. Quality scenario

The effects of quality degradation have been estimated based on loss of juvenile density in nursery areas based extracted from Courrat et al. (2009) estimations. Other studies have estimated these effects as a decrease in survival of juveniles, but also a decrease in their growth rate and future fecundity (Champagnat et al., 2021). This method was not applicable to our study due to the lack of knowledge on the impact of quality degradation on the demographic parameters of plaice, whiting and seabass stocks.

In the parametrization of the quality scenario, we assumed a common multiplier on density-dependent and density independent mortality rate. This is a strong assumption because both mortality terms are associated with different processes. The density-dependent mortality rate refers to interactions between juveniles of the same cohort, mostly competition for food or space (Gibson, 1994). Density-independent mortality may involve other mortality processes linked to a large panel of environmental stresses (e.g. pollutant, Rose et al., 2003; oxygen, Gibson, 1994) and/or predation (Gibson, 1994). However, no previous knowledge nor experimental studies were available to build sensible quantification of how density independent and density-dependent mortality rates should be impacted separately. The assumption of using a single multiplier may have led to high estimate of the impact of quality scenarios, and caution should be taken when comparing habitat surface and quality scenarios (Champagnat et al., in prep).

Also, as shown in the section 3.4, the results of the model are very sensitive to the assumptions made on which specific sectors of the nursery habitat are affected by habitat restoration/degradation (i.e. the whole nursery area or the area <5m only). Other methods of separating the juveniles most affected by the degradation of quality could have been tested. The salinity plume of the estuaries could have been used as an estimator of the distribution of contaminants, but this hypothesis was not retained due to the very large interannual variability that may exist. For future studies it would be interesting to develop a more robust method to apply the quality restoration to the proportion of juveniles really impacted by the degradation of estuarine quality. However, no such information is available yet to our best knowledge.

4.3.3. Surface scenario

The estimation of surface losses could be made on the basis of a sampling of French nursery areas in 1870, but no data were available for the English coasts which also have nurseries (Kelley, 1988;

Rochette et al., 2010; Carpentier et al., 2009). We chose to estimate surface losses since this date due to the large proportion of EEC nurseries that could be considered by the data. The inclusion of this large proportion in our study gives it an original character, as most other studies in the EEC have focused on the Seine Estuary (Rochette et al., 2010, Rochette et al., 2013, Grasso and Le Hir, 2019). The other data available did not allow us to consider such a large proportion of the nursery areas for other dates.

In our scenario, the nursery habitat is only defined by depth. Defining an ecological niche by a single variable is however a very simplifying assumption (Grinnell, 1917; Hutchinson, 1957), and as many studies have shown, the nursery areas of the species in this study can be defined by other parameters. Salinity and hydrodynamics can have an effect (Kennedy and Fitzmaurice, 1972; Kelley, 1988; Le Pape et al., 2003), as well as sediment structure (Riou et al., 2001; Rochette et al., 2010). The estimation of surface losses is therefore very simplified in this study and could be refined by using species distribution models integrating these many factors, provided that the necessary historical data are available. For example, Champagnat et al., (2021) used a distribution model of sole juveniles based on historical data available for the Seine estuary to quantify habitat loss based on bathymetry and sediment structure. However, we did not have the data to apply this method to other species and areas in our study.

Also, only the loss/restoration of habitats less than 5 metres depth were considered. This limit is not based on any prior study or knowledge. However, this depth is also the one that concentrates the most anthropic pressures and surface losses (Rochette et al., 2010). The importance of this assumption can be moderated, if a greater depth had been chosen to define scenarios, the proportion of juveniles affected would have been greater, but the proportion of surface area lost would have mathematically decreased, hence balancing the effect on population dynamics. The results of the scenarios would therefore have been approximately the same. However, analysis based on another depth threshold could not be carried out because we did not have enough data to make a reliable estimate of the loss of surface of habitats with a bathymetry higher than 5m.

Overall, the proportion of juveniles impacted by habitat loss that we used is likely to be underestimated and the effects of surface restoration may be greater. Indeed, this proportion was calculated on maps representing present habitats. It can be hypothesized that if habitats less than 5 metres depth were of larger surface (i.e. as in 1870), the proportion of juveniles present in this habitat would also be greater

4. 4. Management implications

This study quantified the effects of both surface and quality losses on the dynamics of nursery-dependent species in the Eastern Channel. The estimates of habitat loss provided by this study give us information on the historical evolution of the EEC nurseries, but these estimates are difficult to apply to a management context. Indeed, the loss of surface area is mainly due to human activities such as land reclamation or the construction of port infrastructures (Ducrotoy and Dauvin, 2008; Brown et al., 2018). Although we have demonstrated the real impact of these developments on stocks and fisheries, habitat restoration is unfortunately difficult to apply. The destruction of dykes and the restoration of intertidal areas would require large financial resources and would be done at the expense of other activities carried out on the coast (Levin and Stunz, 2005). However, this evidences the need to protect and even partially restore the remaining essential nursery habitat.

This study also demonstrated the considerable importance of shallow nurseries for species with a very coastal distribution of juveniles. Furthermore, it demonstrated that the gains from MSY management could be greatly increased if nursery areas were restored. Restoring both nursery habitat surface and quality would increase a gain of annual catches of 1015, 250, 480, and 510 tons for sole, plaice, whiting and seabass respectively. In addition to catch gains, the spawning stock biomass would also be increased, which could have beneficial consequences for the whole ecosystem (Froese et al., 2008; Smith et al., 2011; Cury et al., 2011; Froese et al., 2016; Gascuel, 2019).

More broadly, this study supports the need to consider essential fish habitat in the management of stocks and underlines the interest of an ecosystem-based management of fisheries. Restoring coastal nurseries may be even more beneficial than regulating fishing pressure (Levin and Stunz, 2005; van de Wolfshaar et al., 2011). Ongoing management measures to restore the surface area (Ducrotoy and Dauvin, 2008) and quality of estuarine habitats, with some results already observable, such as significant decreases in pollutant levels, should therefore be encouraged and continued (Meybeck et al., 2007; Tappin and Millward, 2015).

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Appendices

Appendix 1. Age structured model

The description of this model comes from Champagnat et al., (in prep).

Population dynamics is simulated by a deterministic life cycle model structured by age (a) with a year time step (y).
Fish are supposed to recruit at age a_{rec}. For all ages classes $a_{rec} < a < a_{max}$, population abundance (N) is described by:

(a)
$$N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})}$$

And for $a = a_{max}$, population abundance is described by:

(b)
$$N_{a_{max},y+1} = N_{a_{max},y} \times e^{-(M_{a_{max},y}+F_{a_{max},y})} + N_{a_{max}-1,y} \times e^{-(M_{a_{max}-1,y}+F_{a_{max}-1,y})}$$

with M and F the natural and fishing mortality rates, respectively.

Fishing mortality at age is defined, in a simulation mode, as the product of selectivity at age and a maximum fishing mortality value:

(c)
$$F_{a,y} = sel_a \times F_y$$

With sel_a, a logistical function of age specified for each stock.

Catches in weight are computed based on Baranov equation:

(d)
$$C_y = \sum_{a=a_{rec}}^{a_{max}} \frac{F_{a,y}}{F_{a,y} + M_{a,y}} \times N_{a,y} \times (1 - e^{-(F_{a,y}+M_{a,y})}) \times SW_{a,y}$$

With $SW_{a,y}$, the stock weights at age, available in appendix 2.

Spawning Stock Biomass (SSB) is computed according to the equation:

(e)
$$SSB = \sum_{a=a_{rec}}^{a_{max}} N_a \times SW_a \times pf \times Mat_a$$

With SW_a, the stock weights at age, pf the female proportion, and Mat_a the maturity ogive, all available in appendix 2.

The number of eggs spawned in year y is computed based on adult abundance:

(f)
$$\omega_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times Mat_{a,y} \times pf_{a,y} \times Fec_{a,y}$$

with Mat_a, the probability of being mature, pf_a the female proportion and Fec_a the fecundity (number of eggs per female). All values used are available in appendix 2.

Eggs are supposed to first survive to the larval drift with density-independent survival before settling in nursery areas. The larval mortality during larval drift, M_{larvae}, are available in appendix 2.

The number of recruits for year y is computed with a Berverton-Holt relationship based on eggs numbers of the previous year:

(g)
$$N_{a_{rec},y} = \frac{4h\omega_{(y-1)}}{\bar{W}(1-h) + \frac{4h\omega_{(y-1)}}{K}}$$

with h the steepness, $\bar{W}$ the number of eggs produced on average by a recruit during its lifetime in the absence of any fishing and K the carrying capacity of the nursery.

The number of eggs produced on average by a recruit during its lifetime in the absence of fishing, $\bar{W}$, is defined as:

(h)
$$\bar{W} = \sum_{a=a_{rec}}^{a_{max}} S_a \times Mat_a \times pf_a \times Fec_a$$

With S_a the cumulative survival to age a as defined according to the equation:

(i)
$$S_a = \prod_{i=a_{rec}}^{a-1} e^{-Mi}$$

The parameters h and K of the Beverton-Holt relation are related to the independent density and dependent density mortality (M^{di} and M^{dd} respectively) according to the equations:

(j)
$$h = \frac{e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}{4 + e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}$$

(k)
$$K = lim_{\omega->+\infty} N_{a_{rec}} = \frac{M^{di} \times S}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1}$$

The expression for M^{di} and M^{dd} can therefore be derived as:

(l)
$$M^{di} = -log(\frac{4 \times h}{e^{-M_{larvae}} \times \bar{W} \times (1-h)})$$

(m)
$$M^{dd} = \frac{M^{di}}{K \times (e^{M^{di}} - 1)}$$

Appendix 2. Data and equation to calculate fecundity and associated values for each species.

For the female proportion (*pf*) we assumed a value at 0.5 for each species.

Sole (Solea solea)

Parameters	Value	Source
Stock weights-at-age (SW$_a$)	Matrix	ICES. WGNSSK., 2021
Maturity ogive (Mat)	Age 1: 0; Age 2: 0.53; Age 3: 0.92; Age 4: 0.96; Age 5: 0.97; Age 6: 1; Age 7: 1; Age 8: 1; Age 9: 1; Age 10: 1; Age 11: 1	ICES. WGNSSK., 2021
Cumulative survival to age (S$_a$)	Age 1: 0.905; Age 2: 0.819; Age 3: 0.670; Age 4: 0.670; Age 5: 0.670; Age 6: 0.670; Age 7: 0.670; Age 8: 0.670; Age 9: 0.670; Age 10: 0.670, Age 11: 0.670	Computed from eq. (i) given in appendix 1.
Fecundity (Fec)	$e^{(5.619+1.17\times log(SW_a\times 1000))}$	Anon, 1992
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ($\bar{W}$)	662795.9	-

Plaice (Pleuronectes platessa)

Parameters	Value	Source
Natural mortality at age	Age 1: 0.3531; Age 2: 0.3132; Age 3: 0.292; Age 4: 0.2749; Age 5: 0.2594; Age 6: 0.2474; Age 7: 0.2329	ICES. WGNSSK., 2021
Stock weights-at-age (SW_a)	Matrix	ICES. WGNSSK., 2021
Maturity ogive (Mat)	Age 1: 0; Age 2: 0.15; Age 3: 0.53; Age 4: 0.96; Age 5: 1; Age 6: 1; Age 7: 1	ICES. WGNSSK., 2021
Cumulative survival to age (S_a)	Age 1: 0.703; Age 2: 0.514; Age 3: 0.280; Age 4: 0.280; Age 5: 0.280; Age 6: 0.280; Age 7: 0.280	Computed from eq. (i) given in appendix 1.
Length at age (L_a)	$54.4 \times (1 - e^{(-0.11 \times a)})$	Jennings et al., 1998
Fecundity	$2.33 \times L_a^{3.10}$	ICES. WGNSSK, stock Annex., 2021
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ($\bar{W}$)	19610.72	

Whiting (Merlangius merlangus)

Parameters	Value	Source
Stock weights-at-age (SW$_a$)	Matrix	ICES. WGNSSK., 2021
Maturity ogive (Mat)	Matrix	ICES. WGNSSK., 2021
Length at age (L$_a$)	$(\dfrac{SW_a \times 1000}{0.00621})^{\frac{1}{3.10286}}$	Dorel, 1986
Cumulative survival to age (S$_a$)	Age 0: 0.063; Age 1: 0.063; Age 2: 0.007; Age 3: 0.007; Age 4: 0.007; Age 5: 0.007; Age 6: 0.007; Age 7: 0.007; Age 8: 0.007	Computed from eq. (i) given in appendix 1.
Fecundity	$0.0065 \times L_a^{5.28}$	Mestorff, 1959
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ($\bar{W}$)	13931.71	-

Seabass (Dicentrarchus labrax)

Parameters	Value	Source
Stock weights-at-age (SW_a)	Age 0: 0.003; Age 1: 0.024; Age 2: 0.097; Age 3: 0.210; Age 4: 0.369; Age 5: 0.571; Age 6: 0.807; Age 7: 1.071; Age 8: 1.357; Age 9: 1.655; Age 10: 1.962; Age 11: 2.272; Age 12: 2.579; Age 13: 2.882; Age 14: 3.176; Age 15: 3.460; Age 16: 4.176	ICES. WGCSE., 2021
Maturity ogive (Mat)	Age 0: 0; Age 1: 0; Age 2: 0; Age 3: 0; Age 4: 0.186; Age 5: 0.419; Age 6: 0.638; Age 7: 0.792; Age 8: 0.885; Age 9: 0.937; Age 10: 0.965; Age 11: 0.980; Age 12: 0.989; Age 13: 0.993; Age 14: 0.996; Age 15: 0.998; Age 16: 0.998	ICES. WGCSE, Stock Annex. 2018
Cumulative survival to age (S_a)	Age 0: 0.619; Age 1: 0.619; Age 2: 0.619; Age 3: 0.619; Age 4: 0.301, Age 5: 0.186; Age 6: 0.186; Age 7: 0.186; Age 8: 0.186; Age 9: 0.186; Age 10: 0.186; Age 11: 0.186; Age 12: 0.186; Age 13: 0.186; Age 14: 0.186; Age 15: 0.186; Age 16: 0.186	Computed from eq. (i) given in appendix 1.
Fecundity	$557.12 \times SW_a \times 1000 - 226020$	Mayer et al., 1988
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ($\bar{W}$)	262908.3	-

Appendix 3. Proportion of catches in division 7.d for whiting (4 and 7.d) and seabass (4.b–c, 7.a, and 7.d–h).
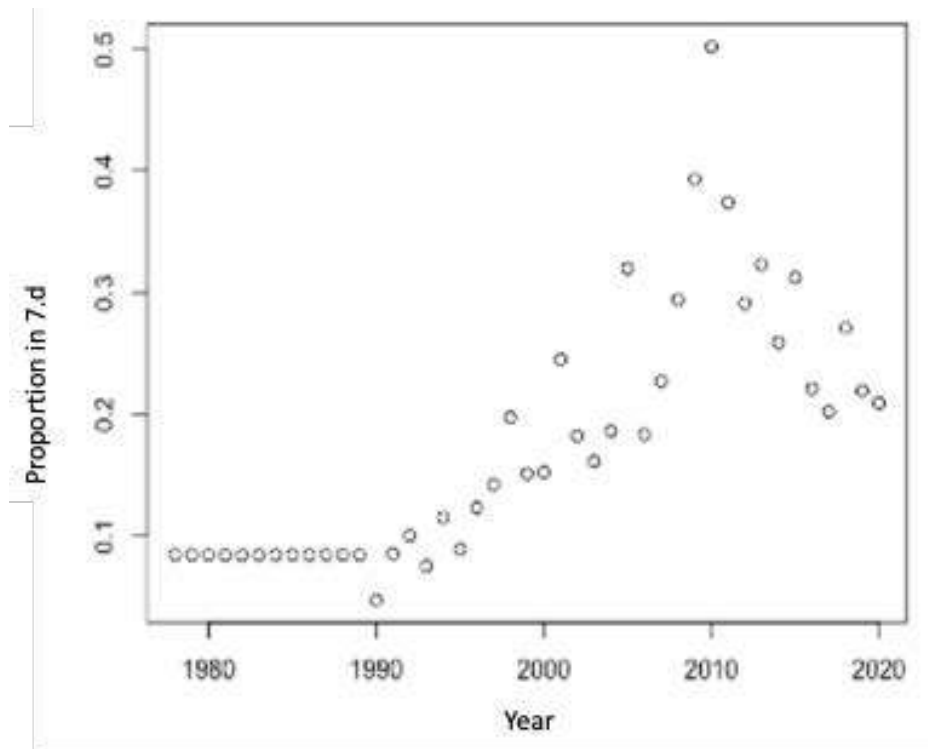
Proportion of catches in division 7.d for whiting
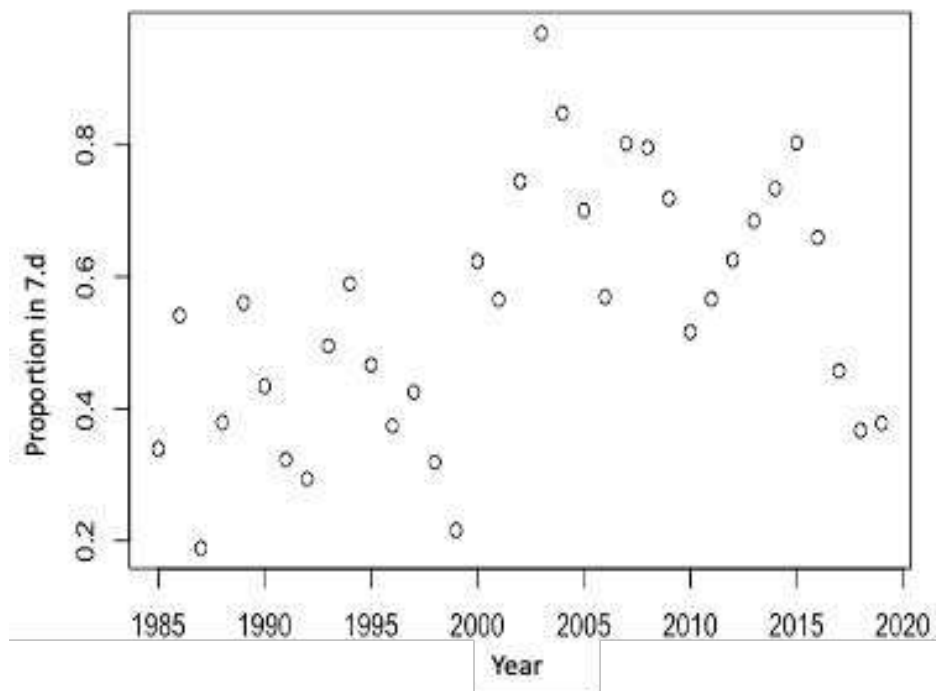
Proportion of catches in division 7.d for whiting

## Appendix 4. Nursery maps for each species
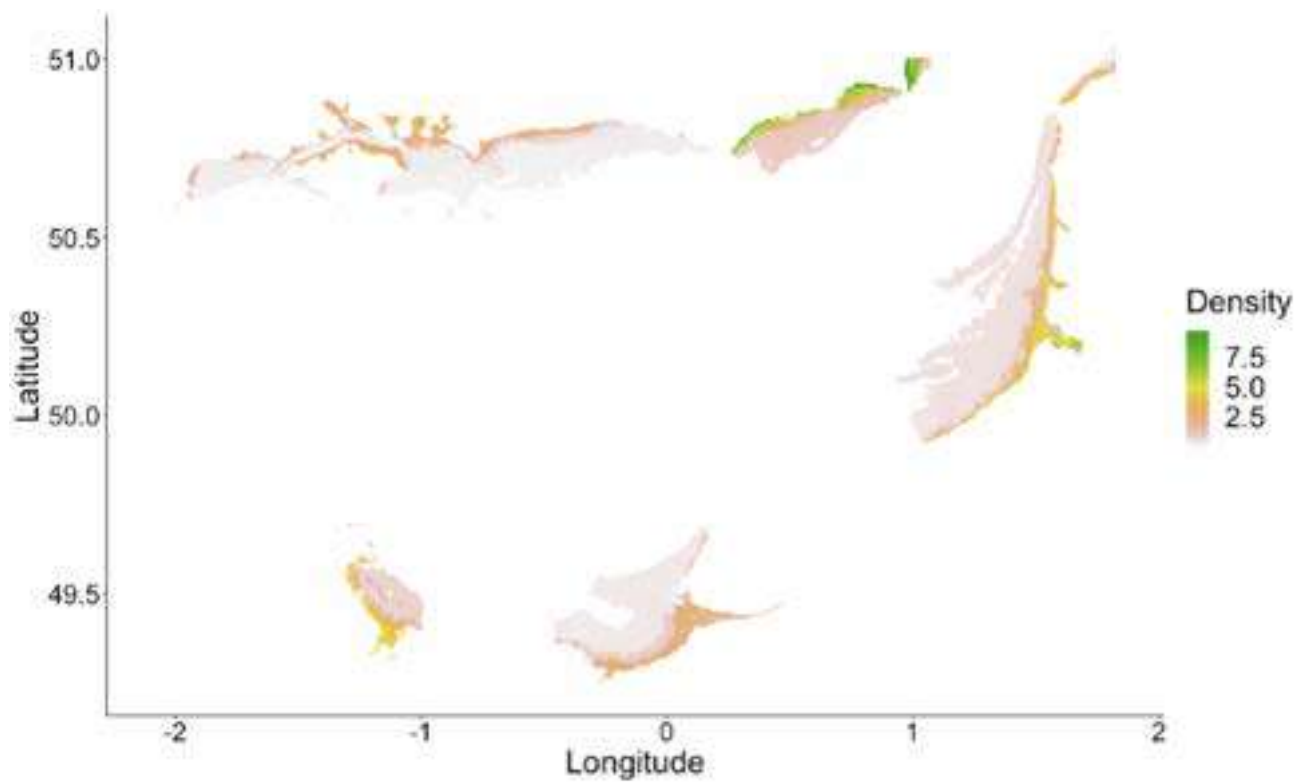
Map of Eastern English Channel nursery areas for sole (in juveniles/m^2). Source : Rochette et al., 2010. (Modified)
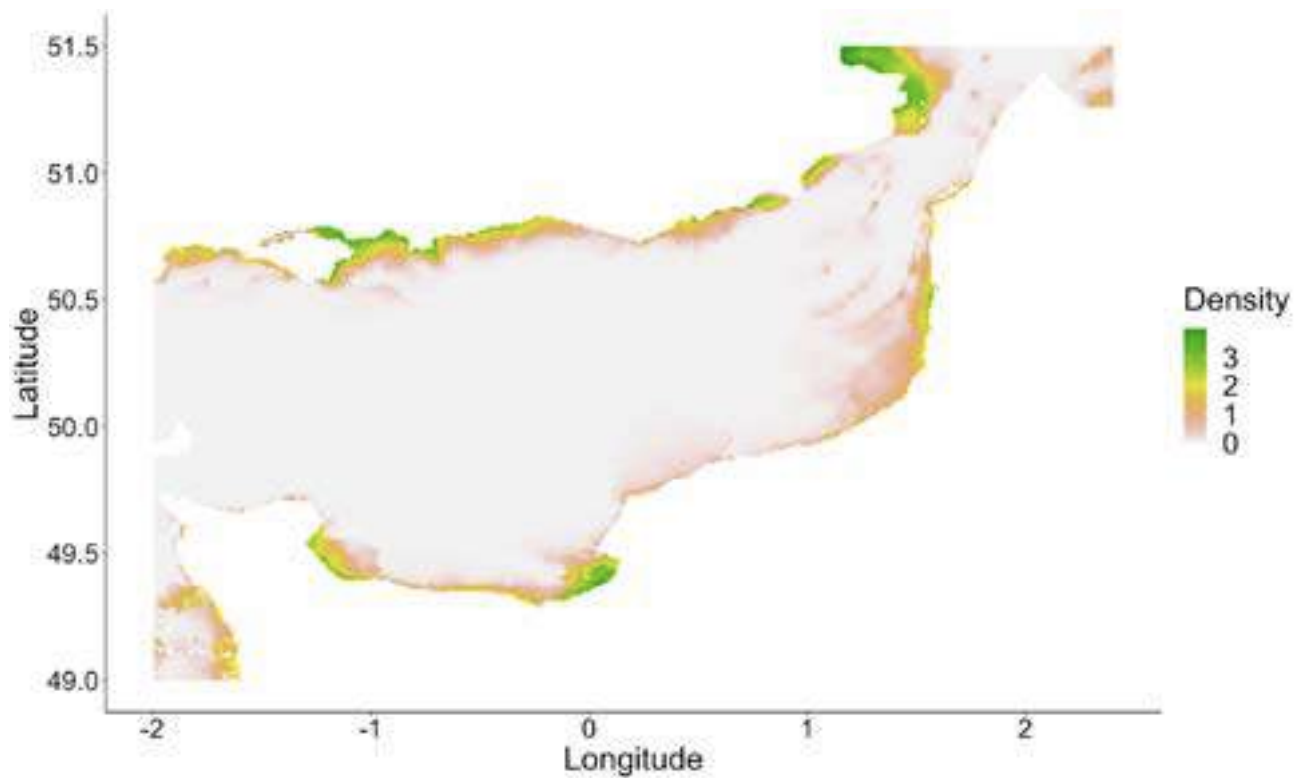
Map of Eastern English Channel nursery areas for plaice (in juveniles/m^2). Source : Carpentier et al., 2009. (Modified)
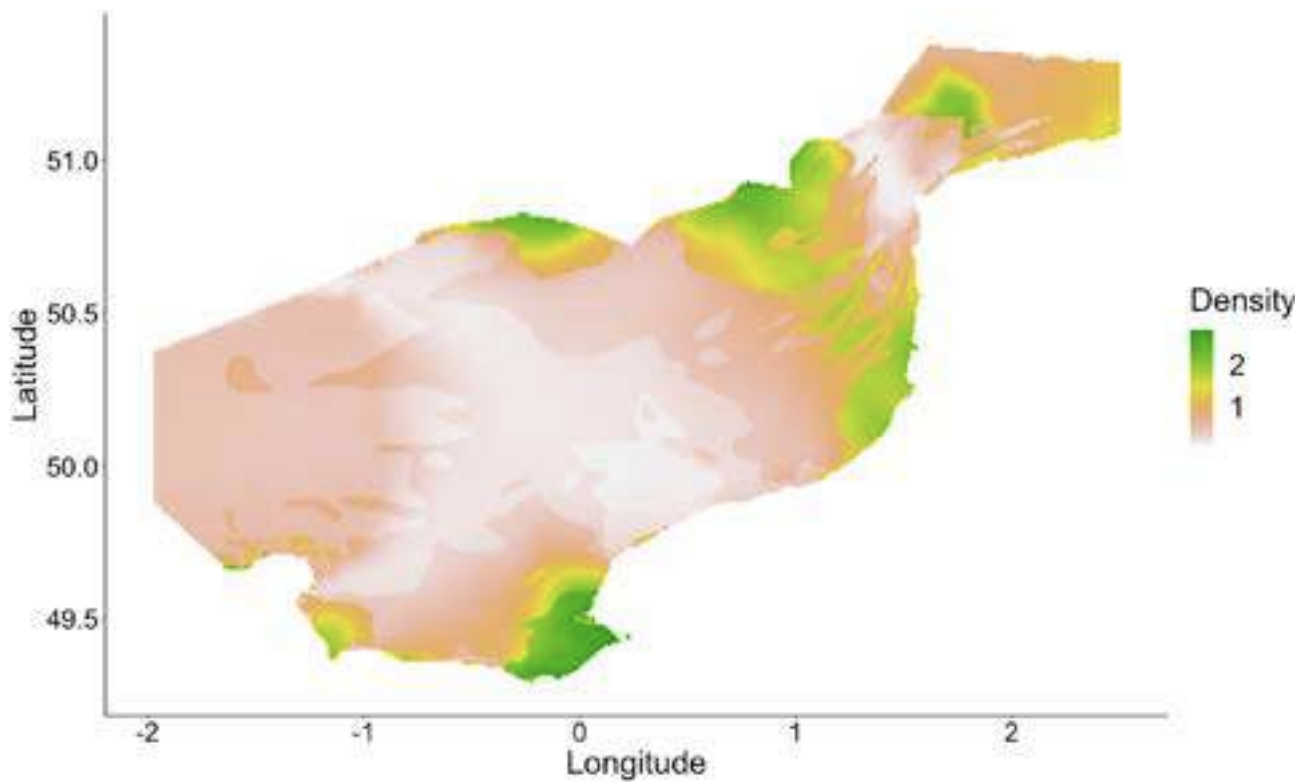
Map of Eastern English Channel nursery areas for whiting (in juveniles/m^2). Source : Carpentier et al. 2009. (Modified)
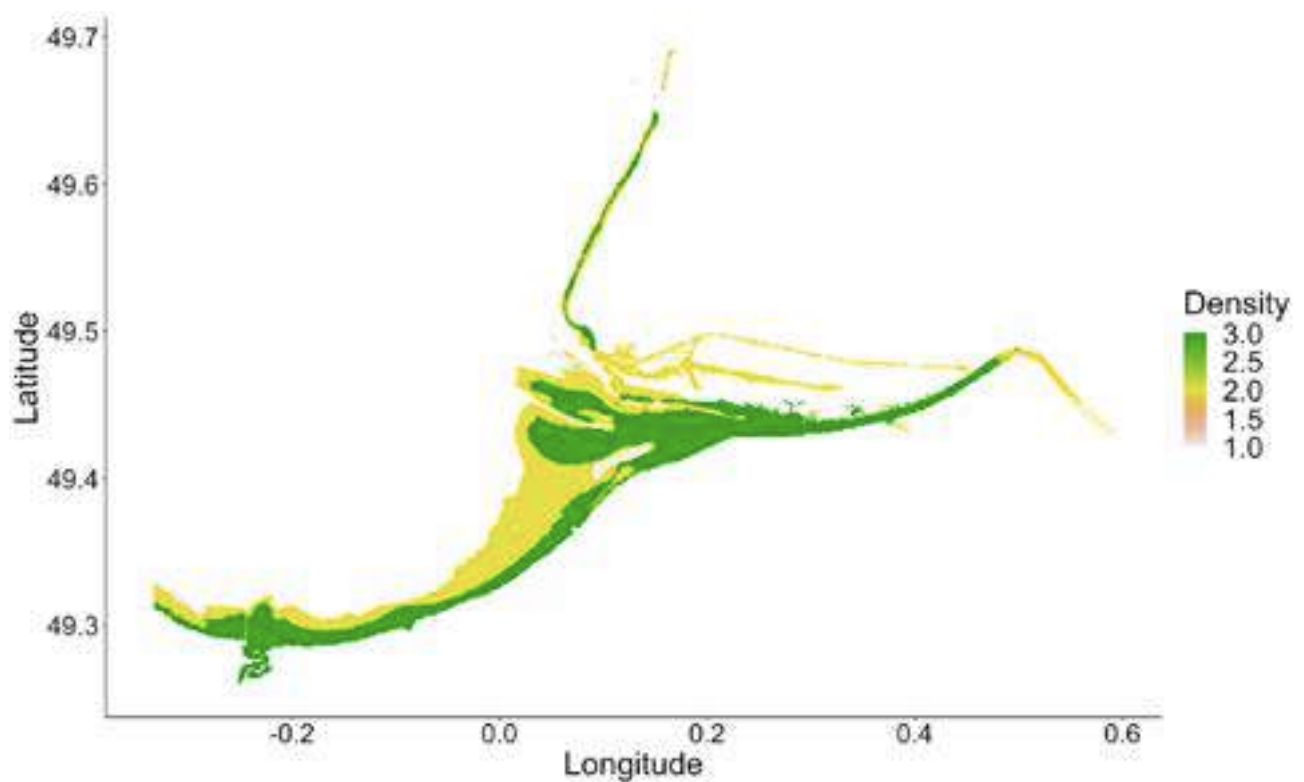
Map of Seine nursery areas for seabass (in juveniles/m^2). Used as an estimator of the distribution of juveniles across the EEC nurseries. Source : Bacq et al., 2013. (Modified)

Appendix 5. Complementary equations for parameterization of quality multipliers.

The density independent mortality (M^{di}) is described by the equation:

$$M^{di} = \frac{-log(\frac{4 \times h}{e^{-M_{larvae}} \times \bar{W} \times (1-h)})}{deltaT}$$

With deltaT = 1

The density dependent mortality (M^{dd}) is dependent to M^{di} according to the equation:

$$M^{dd} = \frac{M^{di}}{K \times e^{(M^{di} \times deltatT)} - 1}$$

With the values of M^{di} and M^{dd} calculated from the parameters h, K and the value of M_{larvae} and $\bar{W}$, we can calculate a multiplier to simulate a quality restoration.

Appendix 6. Fit plot for each species
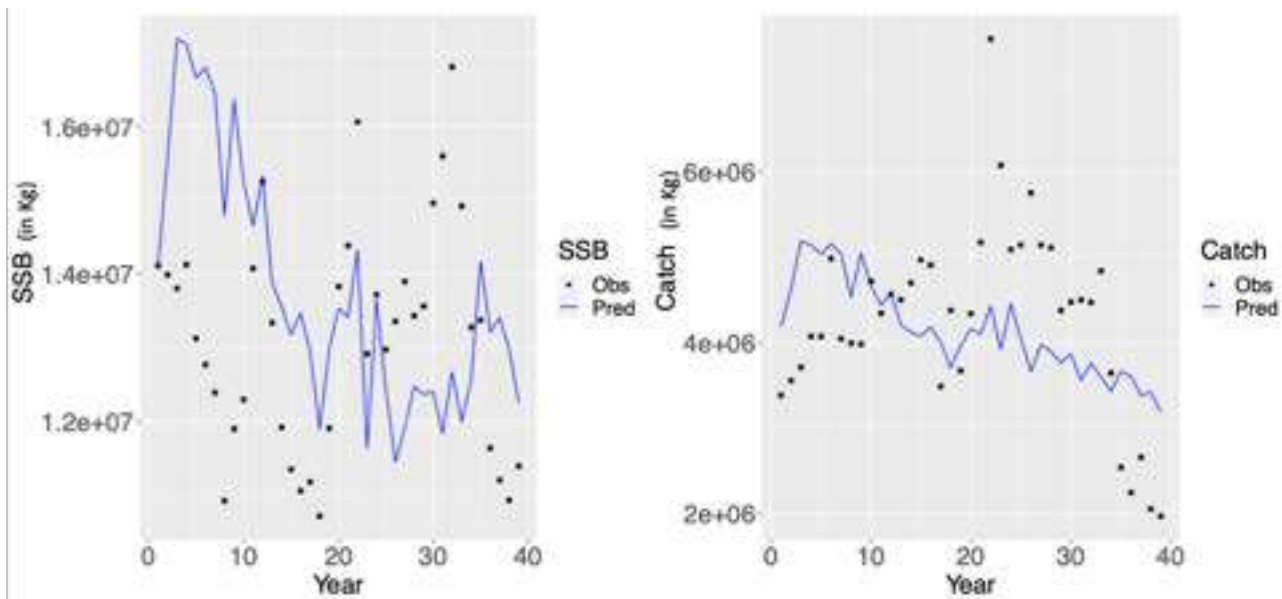
Fit between data (*Obs*) and model prediction (*Pred*) of sole for SSB (left) and catch (right).
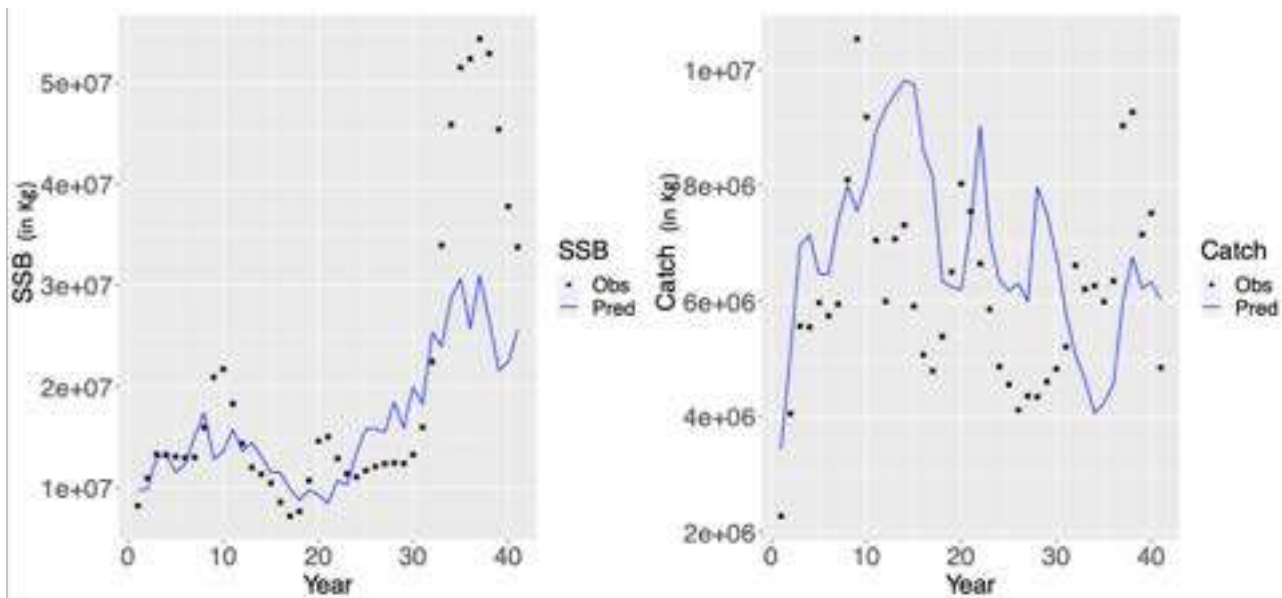
Fit between data (*Obs*) and model prediction (*Pred*) of plaice for SSB (left) and catch (right).
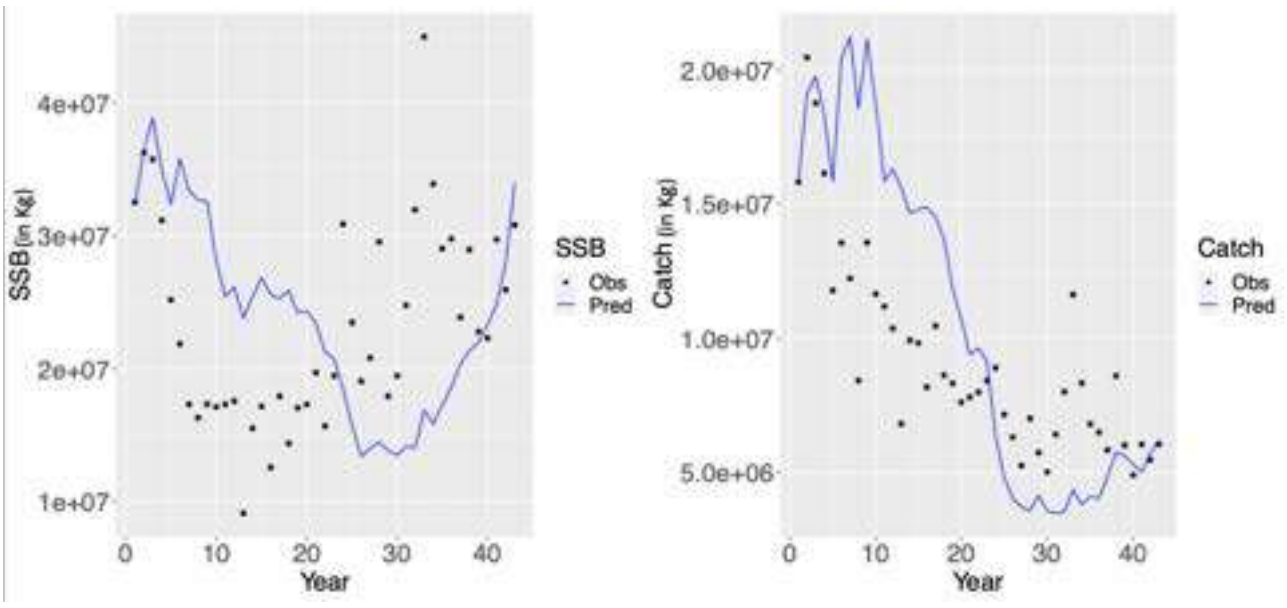
Fit between data (*Obs*) and model prediction (*Pred*) of whiting for SSB (left) and catch (right).
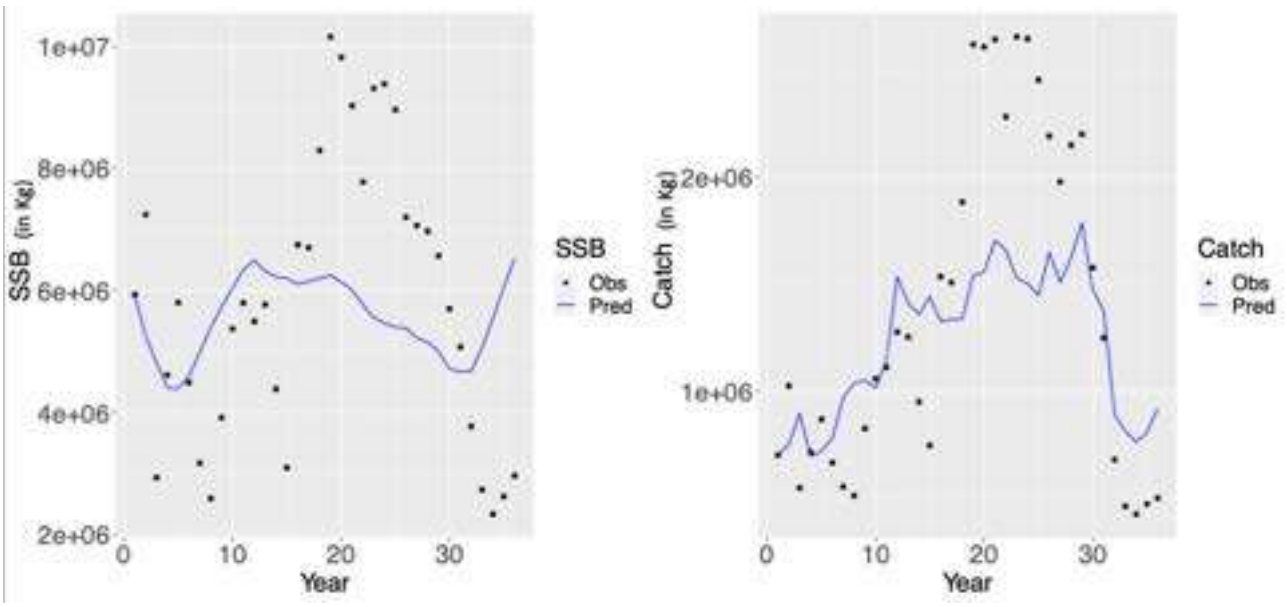
Fit between data (*Obs*) and model prediction (*Pred*) of seabass for SSB (left) and catch (right).

Appendix 7. Comparison between K value, reference points, MSY related indicators from the estimation of our model and ICES prediction.

Table of K values, reference points, MSY related indicators.

	K* (in number of juveniles)	$\dfrac{C_{MSY}}{SSB_{MSY}}$	$\dfrac{SSB_{MSY}}{SSB_0}$*	F_{MSY}	Average SSB (in Kg) (ICES values)	Average Catches (in Kg) (ICES values)
Sole	3.8×10^7	0.16 (ICES=0.30)	0.23	0.18 (ICES=0.19)	1.3×10^7 (1.3×10^7)	4.2×10^6 (4.3×10^6)
Plaice	6.8×10^7	0.63 (ICES=0.29)	0.19	0.33 (ICES= 0.25)	1.6×10^7 (2×10^7)	6.8×10^6 (6.1×10^6)
Whiting	4.7×10^9	0.46 (ICES=0.33)	0.29	0.49 (ICES=0.37)	2.4×10^7 (2.3×10^7)	1×10^7 (9.2×10^6)
Seabass	1.1×10^7	0.25 (ICES=0.35)	0.27	0.16 (ICES=0.17)	5.6×10^6 (5.8×10^6)	1.2×10^6 (1.4×10^6)

* not available in the ICES
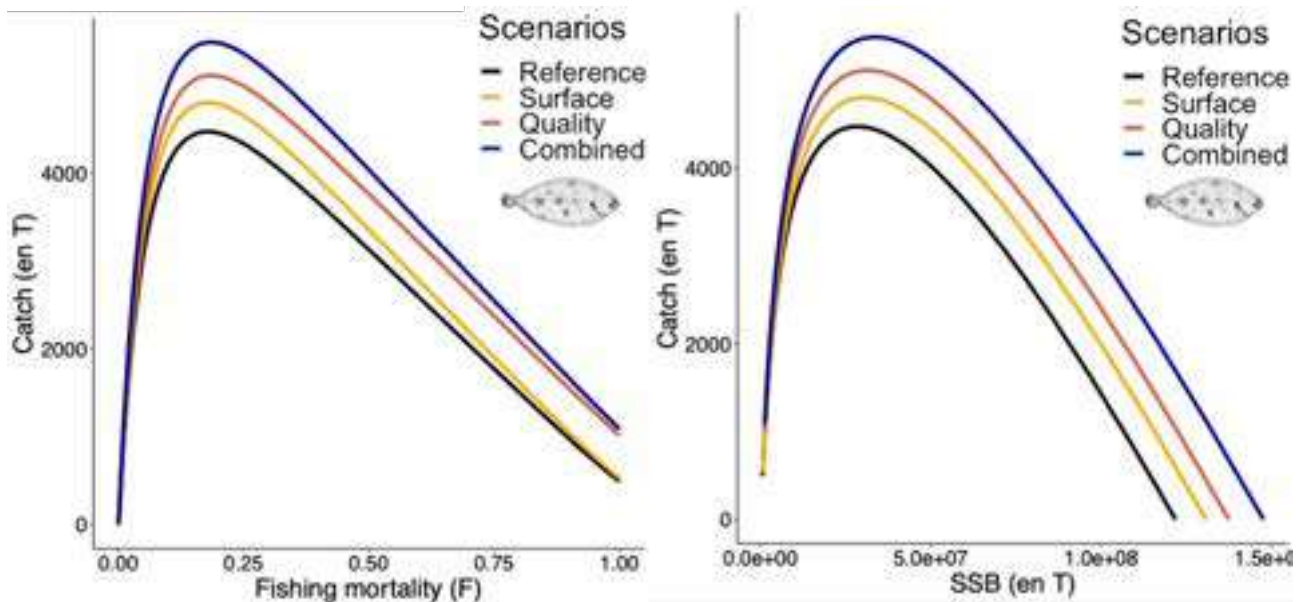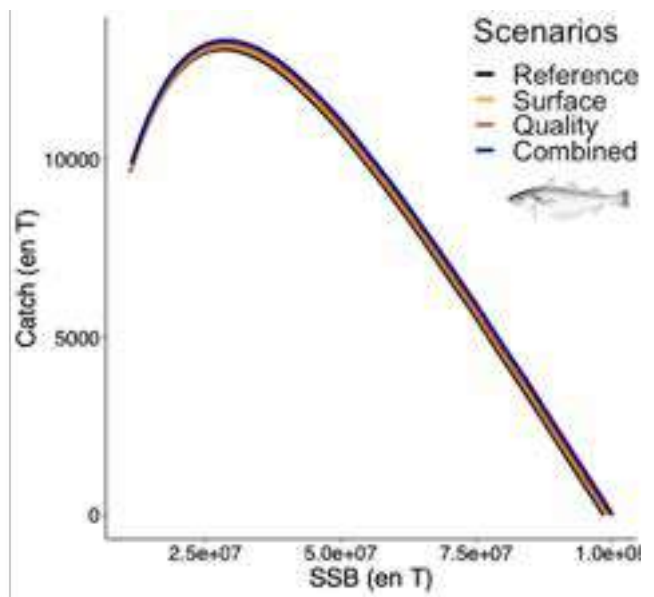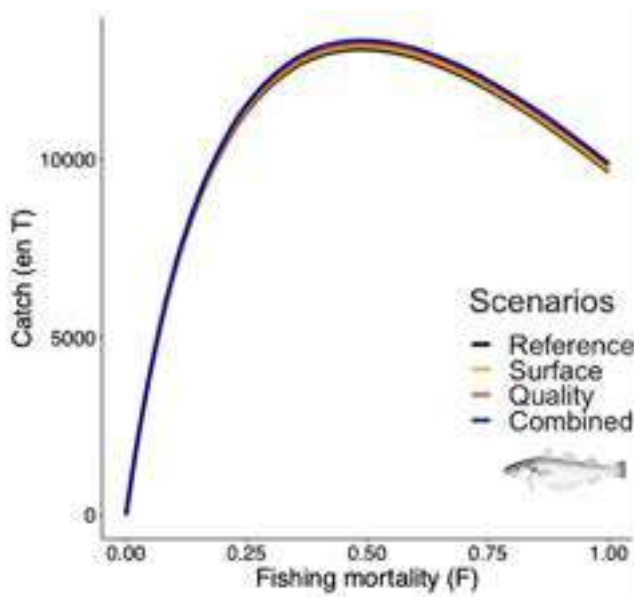
Production curves according to habitat scenarios as function of fishing mortality or SSB for sole.
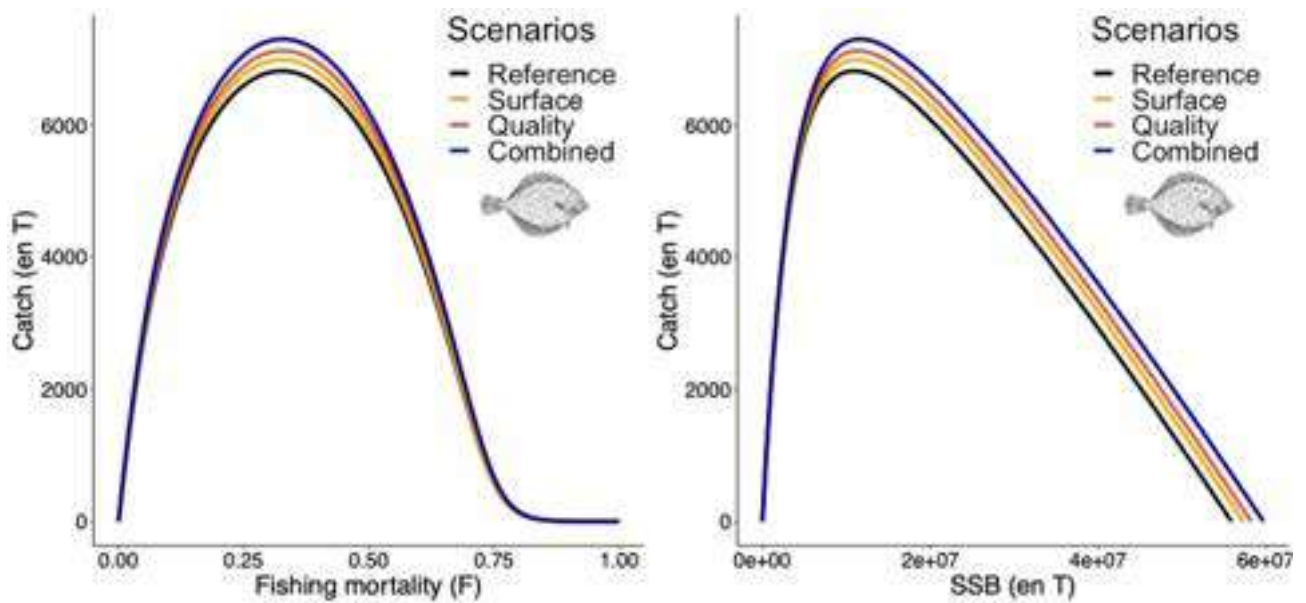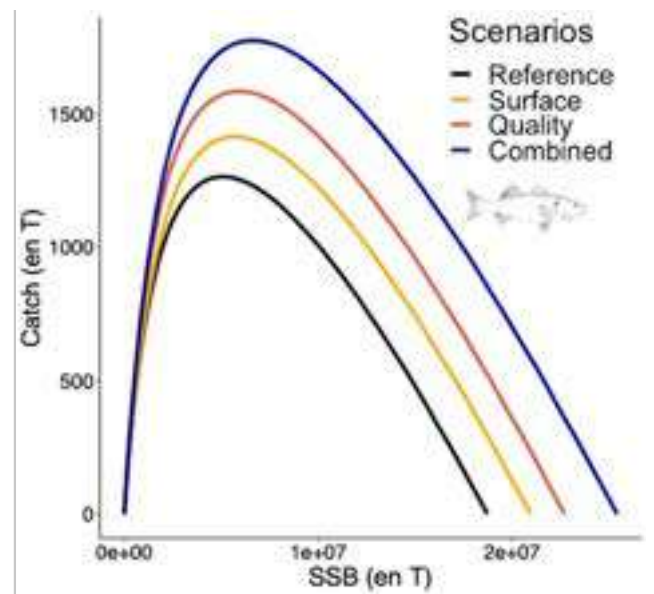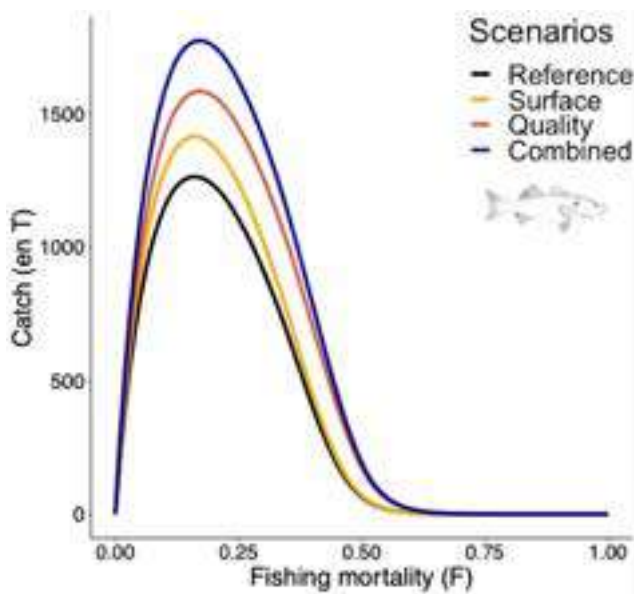

Production curves according to habitat scenarios as function of fishing mortality or SSB for plaice.

Production curves according to habitat scenarios as function of fishing mortality or SSB for whiting.

Production curves according to habitat scenarios as function of fishing mortality or SSB for seabass.

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	Diplôme : Master SML-Biologie
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Année de soutenance : 2022	

Titre français : Impact de la dégradation des habitats côtiers et estuariens sur la dynamique des stocks nourriceries dépendants de Manche Est.

Titre anglais : Impact of coastal and estuarine habitats degradation on the dynamics of nurseries dependent stocks in the Eastern Channel.

Résumé: Les estuaires et les zones côtières sont des habitats de nourricerie essentiels pour de nombreuses espèces d'intérêt halieutiques. Leur localisation côtière les rend particulièrement vulnérables aux pressions anthropiques. Une analyse de l'impact de la dégradation des habitats pour les populations d'intérêt halieutique manque a ce jour. Notre étude vise à évaluer l'impact halieutique de la dégradation des nourriceries communes à plusieurs espèces de Manche Est (sole, plie, merlan et bar). Un modèle de simulation générique est utilisé. Il permet d'évaluer l'effet combiné de la dégradation des nourriceries et de l'exploitation par la pêche sur la dynamique des stocks. Le modèle est calibré pour chaque espèce à partir des résultats des évaluations de stocks complétés par la littérature. Des scénarios de restauration de surface et de qualité des habitats de nourricerie ont été construits à l'aide d'une estimation des pertes de surfaces depuis 1870 et de la littérature. La restauration de la surface a un plus faible impact que la restauration de la qualité sur les gains de biomasses et de captures au RMD (Rendement Maximum Durable) pour les quatre espèces. Les espèces ayant le plus haut niveau de concentration sur les zones de nourricerie peu profondes étaient les plus sensibles aux scénarios de restauration de l'habitat. La réponse dépend également d'autres caractéristiques du cycle biologique notamment la dynamique du recrutement.

Abstract: Estuaries and coastal areas are essential habitats for many fish species. These habitats act as nurseries for a large proportion of species of fisheries interest. Their coastal distribution at juveniles stage makes them particularly vulnerable to anthropogenic pressures. However, a comprehensive analysis of the impacts of nursery habitat degradation for exploited fish species is still lacking. Our study aims at assessing the effects of degradation/restoration of nursery habitat common to four Eastern English Channel species of large fisheries interest: sole, plaice, whiting and seabass. A generic simulation model representing the dynamics of exploited populations and the dependence of recruitment on juvenile habitats is used. It evaluates the combined effect of nursery degradation and fisheries exploitation on stock dynamics. The model was calibrated for each species based on the results of stock assessments complemented by literature. Restoration of both surface and quality for nursery habitats were built using estimated area losses since 1870 and literature. Surface restoration had a smaller impact than quality restoration on biomass and catch gains at MSY (Maximum Sustainable Yield) for the four species. The species with the higher level of concentration on shallow nursery areas were the most sensitive to the habitat restoration scenarios. The response also depends to life history traits; species with lower steepness exhibit a stronger response to habitat scenarios.

Mots-clés : Dégradation côtière; Nourriceries; Dynamique de population; Manche Est.

KeyWords: Coastal degradation; Nurseries; Population dynamics; Eastern Channel.