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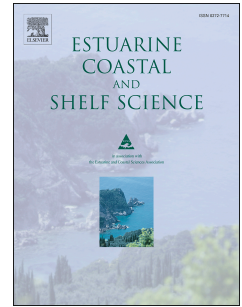


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Potential impacts of the restoration of coastal and estuarine nurseries on the stock dynamics of fisheries species

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Highlights

- The effects of nursery habitat restoration were assessed for four species of main fisheries of interest in the Eastern English Channel.
- Potential restoration gains in terms of biomass and catches were substantial, up to more than 50% of spawning biomass at maximal sustainable yield for the most shallow nursery-dependent species.
- Species with higher concentrations in shallow nurseries were the most sensitive to habitat restoration.
- Contrasts in life history traits lead to species-specific responses: a lower resilience to fishing pressure induces a stronger response to habitat restoration.

Abstract

Coastal and estuarine (CE) areas are essential fish habitats; they act as nurseries for a large proportion of species of fisheries interest but face high levels of cumulative anthropogenic pressures. A comprehensive analysis of the impacts of CE nursery habitat degradation at the population scale for exploited fish species is still lacking. Our study aims to assess the effects of CE nursery habitat

restoration for four species of main fisheries of interest in the Eastern English Channel (EEC): sole (*Solea solea*), plaice (*Pleuronectes platessa*), whiting (*Merlangius merlangus*) and seabass (*Dicentrarchus labrax*). A generic age- and stage-based population model representing the dynamics of exploited populations and integrating the dependence of recruitment on juvenile habitats was used. This model allowed us to evaluate the combined effect of nursery degradation and fishing pressure on stock dynamics. The model was parameterized for each of the four species based on stock assessment outputs in the EEC and literature and then used to simulate equilibrium states under different habitat restoration scenarios. These scenarios were built using previous estimates of both surface area loss and decrease in marine juvenile fish density in CE habitats facing anthropogenic pressures in the EEC. Surface area and quality restoration enhanced both biomass and sustainable catch levels for the four species in the EEC. The species with higher concentrations in shallow nursery areas were the most sensitive to habitat restoration. The response also depended on life history traits, i.e., species with lower resilience to fishing pressure (i.e., steepness) exhibited a stronger response to habitat quality scenarios.

Keywords: Coastal degradation; Nursery; Population dynamics; Maximum Sustainable Yield; Eastern English Channel.

1 **1. Introduction**

2 Coastal and estuarine (CE) areas are essential habitats for many fish species (Seitz et al., 2014). CE
3 ecosystems act as nurseries for a large proportion of fish resources (Miller et al., 1984; Minello, 1999;
4 Beck et al., 2001) and play a major role in the renewal of nursery-dependent species (Rijnsdorp et al.,
5 1992; Gibson, 1994); thus, they are of great importance to fisheries. For instance, two-thirds of
6 commercial landings in the North–East Atlantic come from species using CE systems as nursery
7 habitats (Brown et al., 2018).

8 However, the concentration of juveniles in CE areas renders them particularly vulnerable to human
9 activities (Lotze et al., 2006; Airoidi and Beck, 2007). These pressures can impact both the surface
10 extent and suitability of these nursery habitats (Johnson et al., 1998; Peterson et al., 2000). Surface
11 area losses in the CE zone led to a dramatic decrease in nursery habitat capacity (Rochette et al.,
12 2010). The toxic effects of exposure to pollutants at the juvenile stage impact growth and survival
13 (Davoodi and Claireaux, 2007; Foekema et al., 2008; Wessel et al., 2010) as well as future
14 reproductive success (Fonds et al., 1995; Daouk et al., 2011; Horri et al., 2018). Ninety-two percent
15 of species that use coastal habitats are impacted by human pressures, which can be related to
16 pollutants, eutrophication, anoxia, invasive species and physical development of the coastline (Brown
17 et al., 2018).

18 Although the impacts of local anthropogenic disturbance on juveniles of nearshore nursery-dependent
19 species are well documented (Brown et al., 2018), their consequences for population renewal remain
20 poorly quantified (Lotze et al., 2006; Sundblad and Bergström, 2014; Vasconcelos et al., 2014) and
21 even largely unknown (Rose et al., 2003; Hamilton et al., 2016; Boyd et al., 2018). Few studies have
22 quantified the impact of nursery habitat degradation at the population scale with age- and stage-based
23 models (Rose et al., 2018; Ono et al., 2019; Camp et al., 2020; Champagnat et al., 2021). These
24 models are very case-specific, especially regarding the large amount of data and knowledge needed
25 for parameterization (Lipcius et al., 2019). Consequently, their application to numerous other case

26 studies is difficult or not realistic, although such approaches are needed for management purposes
27 (Hayes et al., 2009; Kraufvelin et al., 2018).

28 In this work, we used a generic age- and stage-structured population model for nursery-dependent
29 exploited species (Champagnat et al., in rev.) to quantify the importance of nursery restoration to
30 population dynamics and productivity. This model describes density-dependent survival in nursery
31 areas (hereafter called the stock-recruitment relationship) with a Beverton and Holt (1957)
32 relationship parameterized in terms of steepness (Mace and Doonan, 1988; Punt and Dorn, 2014) and
33 carrying capacity. Parameterization of a specific stock-recruitment relationship between the spawning
34 biomass and the number of recruits is spurious (Myers et al., 1999; Rose et al., 2001; Zhou, 2007).
35 Steepness is a dimensionless proxy of the resilience of a stock to fishing pressure (Myers et al., 1999;
36 Mangel et al., 2013; Munyandorero, 2020). Hierarchical meta-analyses have been conducted to
37 identify relationships between steepness and life history traits that can be used to provide reliable
38 estimates of steepness for a wide range of species (Myers and Mertz, 1998; Myers et al., 1999;
39 Hilborn, 2003; Thorson, 2019). Formulating our model in terms of steepness thus provides a sensible
40 way to parametrize stock-recruitment relationships for different species of fisheries interest. In
41 addition, following Champagnat et al. (in rev.), the steepness-based parameterization of the stock-
42 recruitment relationship is extended, directly depends upon the habitat quality and surface area of
43 nursery habitats, and allows for simulating juvenile habitat restoration scenarios.

44 The model was applied to nursery-dependent species of fisheries of interest on a fishery management
45 unit in the Eastern English Channel (EEC). The EEC (ICES division 7.d; Figure 1) is a fishery unit
46 of main interest (Ulrich et al., 2002). CE areas of the EEC face high levels of anthropogenic pressures
47 (Le Pape et al., 2007). They have experienced important morphological changes from land
48 reclamation, channel dredging, and the building of dikes and harbours (Ducrotoy and Dauvin, 2008,
49 Stamp et al., 2022), resulting in a substantial reduction in the extent of suitable nursery areas
50 (Rochette et al., 2010, Champagnat et al., 2021). In addition, land-sea interfaces have faced high
51 levels of chemical contamination for decades in the EEC (Meybeck et al., 2007; Tappin and Millward,

52 2015; Barjhoux et al., 2018), causing reductions in habitat quality for marine juvenile fish (Gilliers et
53 al., 2006; Amara et al., 2007; Courrat et al., 2009).

54 Four species of high fisheries interest were considered in this analysis: sole (*Solea solea*), plaice
55 (*Pleuronectes platessa*), whiting (*Merlangius merlangus*) and seabass (*Dicentrarchus labrax*). These
56 species have similar life cycles, with juveniles concentrated in CE habitats while adults show a wider
57 distribution (Riou et al., 2001; Leakey et al., 2008; Day et al., 2021).

58 The study aims to quantify the effects of human disturbance on nurseries in the EEC and assess their
59 consequences on the four populations of interest. We first parameterized the generic stage-based
60 population model of Champagnat et al. (in rev.) for the four populations of interest. Then, the model
61 was used to simulate the response of populations to nursery habitat restoration scenarios. For this
62 purpose, the loss of nursery habitat area extent in the EEC since 1870 was quantified, and the effects
63 of quality degradation on marine juvenile density were also estimated. Then, the potential effects of
64 the restoration of both the surface area and quality of these habitats on population dynamics and
65 fishery productivity were assessed and compared between the species.

66



67

Figure 1. Location of the Eastern English Channel (Fishery management unit, ICES division 7.d), highlighted in grey. The Bay of Veys, Seine and Somme-Canche estuaries are three major CE nursery areas. Inset in the lower right corner: general location in Western Europe.

68 **2. Materials and Methods**

69 A diagram of the framework summarizing the articulation of modelling steps, parameterization, and
70 construction of habitat scenarios is shown in Figure 2.

71

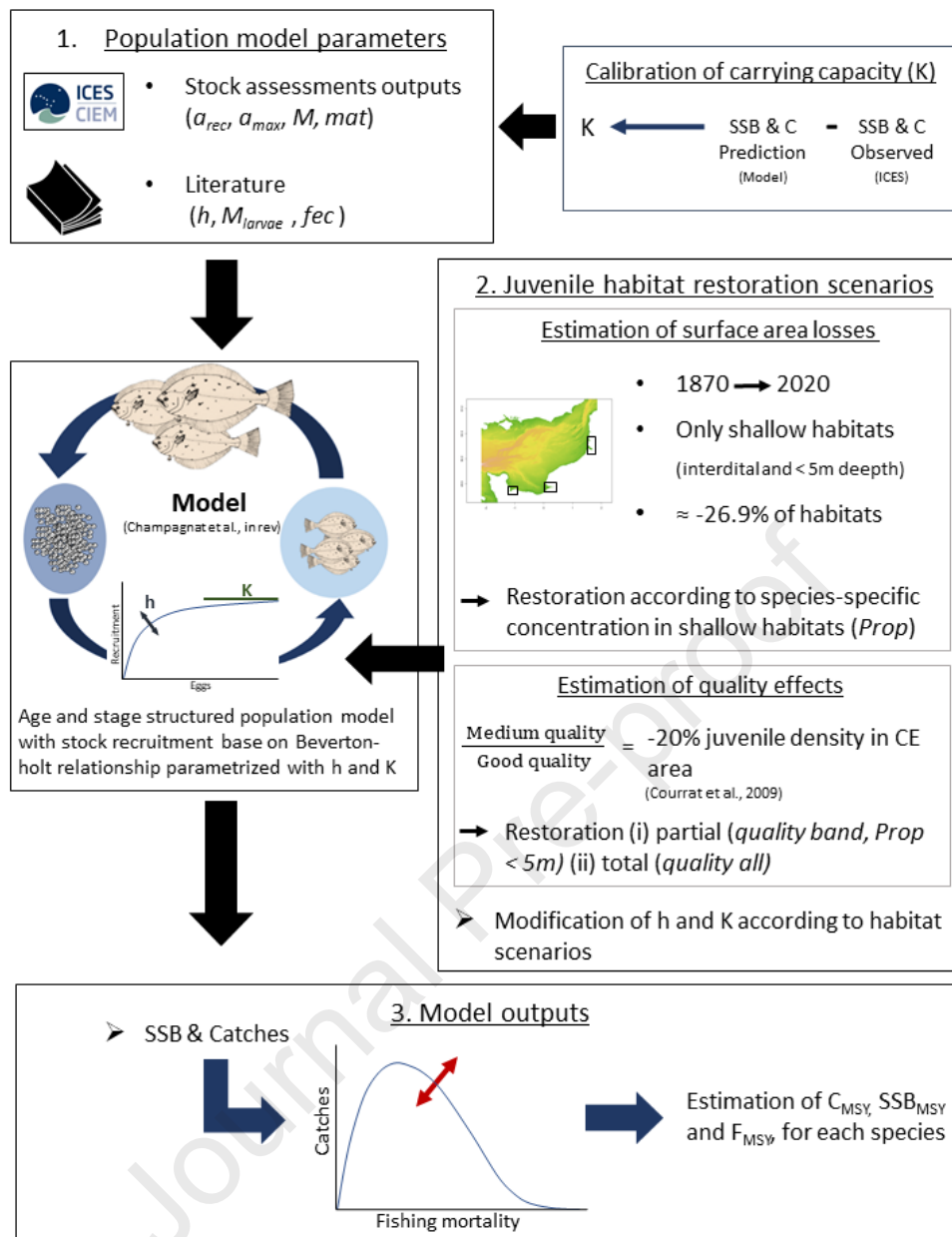


Figure 2. Diagram of the framework summarizing the articulation of the modelling steps: parameterization of the population model, construction of habitat scenarios, and simulation. 1. Recruitment age (a_{rec}), maximum age (a_{max}), natural mortality (M) and maturity (mat) were extracted from stock assessments, whereas steepness (h , e.g., resilience to fishing pressure), larval mortality (M_{larvae}) and fecundity (fec ; except for plaice, extracted from stock assessment) were collected from the literature. Carrying capacity (K) was calibrated by minimizing the difference between the spawning stock biomass (SSB) and catch (C) simulated by our model with those of the stock assessment outputs. 2. The surface area scenario was based on an estimation of area loss since 1870 in three coastal sectors of the French EEC coastline. Surface scenario was only applied to the proportion of juveniles present in habitats above 5 m ($Prop$). Quality scenarios relied on Courrat et al. (2009), with restoration applied to all juveniles ($Quality\ all$) or only to juveniles located above 5 m bathymetry ($Quality\ band$). 3. Finally, the gains in SSB and C at maximum sustainable yield (MSY) are estimated for each habitat restoration scenarios.

73 2.1. Population dynamics model

74 The impact of the degradation of nursery areas on stock productivity was simulated with a
 75 deterministic life cycle model structured by stage and age (Champagnat et al., in rev.). This model
 76 considers a single closed population and a unique nursery and homogeneous area. After recruitment
 77 age (a_{rec}), fish undergo both natural and fishing mortality. Population abundance ($N_{a,y}$) at age a for
 78 year y is described by classical population dynamics (Equation 1):

$$79 \quad (1) \quad N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})}$$

80
 81 where M and F are the natural and fishing mortality rates, respectively.

82 For the last age group a_{max} , the population abundance is described as (Equation 2):

$$83 \quad (2) \quad N_{a_{max},y+1} = N_{a_{max},y} \times e^{-(M_{a_{max},y}+F_{a_{max},y})} + N_{a_{max}-1,y} \times e^{-(M_{a_{max}-1,y}+F_{a_{max}-1,y})}$$

84

85 Recruitment, defined as the number of juveniles produced in nurseries, accounts for habitat-mediated
 86 mortalities during the juvenile stage and is the critical component of this model.

87 The recruitment $N_{a_{rec},y}$ is computed from egg numbers produced in a year, ω_y (Equation 3):

$$88 \quad (3) \quad \omega_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times Mat_a \times pf_a \times Fec_a$$

89 where Mat_a is the probability of being mature at age a , pf_a is the proportion of females at age a , and
 90 Fec_a is the fecundity at age a , all considered constant in time.

91 The mortality from eggs to recruited juveniles follows a compensatory density-dependent mortality
 92 process resulting from intra-cohort competition for trophic resources and/or space (Beverton and
 93 Holt, 1957). Recruitment ($N_{a_{rec},y}$) is modelled by a Beverton-Holt relationship parameterized in
 94 terms of its asymptote, K , interpreted as the carrying capacity of the nursery, and steepness (h)
 95 (Equation 4):

$$96 \quad (4) \quad N_{a_{rec},y} = \frac{4 \times h \times \omega_{y-1}}{\bar{W} \times (1-h) + \frac{4 \times h \times \omega_{y-1}}{K}}$$

97

98 where h is the steepness, defined as the proportion of unfished equilibrium recruitment produced
99 when the spawning stock biomass is reduced to 20% of its unfished level (Mace and Doonan, 1988).
100 It characterizes the drop-off in recruitment when the reproductive potential is reduced. It varies in
101 theory from 0.2 for a linear stock-recruitment relationship to 1 for a constant recruitment above 20%
102 of pristine biomass (Myers et al., 1999; Mangel et al., 2013; Rindorf et al., 2022). K is the carrying
103 capacity (Daily and Ehrlich, 1992), defined as the maximal number of juveniles that a nursery area
104 (here considered unique for the population) can produce. \bar{W} is the average number of eggs produced
105 by a recruit during its lifetime in the absence of fishing (equation in Appendix A).
106 Once parameterized for each species (see next section), this simulation model is used to simulate
107 equilibrium states under a range of fishing mortality rates (F , from 0 to 1) to empirically construct
108 equilibrium curves for catch (C) and spawning stock biomass (SSB), enabling the estimation of
109 management reference points such as SSB_{MSY} , C_{MSY} and F_{MSY} (MSY , Maximum Sustainable Yield).
110 Equations for computation C and SSB are available in Appendix A. F_{MSY} and the $\frac{SSB_{MSY}}{SSB_0}$ ratio will be
111 used as indicators to be compared with stock assessment outputs and with the empirical results of
112 Froese et al. (2016), respectively.

113 **2.2. Parameterization of the case studies**

114 For each of the four case studies, all stock-specific parameters were extracted from both stock
115 assessment outputs and the literature (Table 1), except for the carrying capacity (K), which was
116 calibrated.

117 *Parameters from stock assessments and literature*

118 Recruitment age, maximum age, weights at ages, maturity ogive and natural mortality were taken
119 from the assessment reports for the four studied stocks (ICES, 2021ab). Fecundity equations, larval
120 mortality, and lengths at ages were collated from the literature (Appendix B).

121 The FishLife package (Thorson, 2019) was used to parameterize steepness for the baseline scenarios.
 122 This package analysed stock-recruitment series from the RAM database (Myers et al., 1995) in
 123 relation to life-history data extracted from FishBase (Froese and Pauly, 2022) using a multivariate
 124 hierarchical Bayesian model with taxonomic structure. Steepness values were extracted at the
 125 taxonomic level of order to obtain a robust estimate (Thorson, 2019).

126 *Calibration of carrying capacity for the baseline habitat scenario*

127 Only the parameter K , the carrying capacity of the nursery area (considered a unique entity), which
 128 ultimately determines the population size, requires calibration. For each of the four case studies, the
 129 carrying capacity K representative of the current state (baseline habitat scenario) was estimated by
 130 minimizing the difference between the SSB and catches simulated by our model with those of the
 131 stock assessment outputs (i.e., by minimizing the objective function in Equation 5):

$$132 \quad (5) \quad \sum_{y=y_{min}}^{y_{max}} (\log(SSB_{pred,y}) - \log(SSB_{ICES,y}))^2 + (\log(C_{pred,y}) - \log(C_{ICES,y}))^2$$

133 where y_{min} and y_{max} are the first and last year of the stock assessments, respectively, SSB_{pred} is the
 134 model predictions of SSB, SSB_{ICES} is the SSB provided by the stock-specific assessment (ICES
 135 2021ab), C_{pred} is the model predictions of catches and C_{ICES} is the catches (ICES, 2021ab).

137 For sole and plaice, SSB and catches were taken directly from stock assessments (ICES, 2021a). For
 138 whiting (ICES, 2021a) and seabass (ICES, 2021b), SSB and catches were derived from stock
 139 assessments covering a wider area. They were scaled to the EEC proportionally to the average
 140 proportion of landings in division 7.d with respect to total landings (Appendix C).

141

142 Table 1. Species-specific model parameterization for the baseline habitat scenario.

	Recruitment age (a_{rec})	Maximum age (a_{max})	Steepness (h) (Thorson, 2019)	Natural mortality rate (M)	Larval survival rate ($e^{-M_{larvae} \times \Delta t}$) (Le Pape and Bonhommeau, 2015)	Carrying capacity (K) (calibrated)
Sole	1 (ICES, 2021a)	11 (ICES, 2021a)	0.771	0.1 (ICES, 2021a)	10^{-3}	4.0×10^7
Plaice	1 (ICES, 2021a)	7 (ICES, 2021a)	0.771	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, 2021a)	10^{-3}	7.1×10^7
Whiting	0 (ICES, 2021a)	8 (ICES, 2021a)	0.626	Age 0: 2.0057 ; Age 1: 1.1510 ; Age 2: 0.6560 ; Age 3: 0.5107 ; Age 4: 0.4690 ; Age 5: 0.4477 ; Age 6: 0.3387 ; Age 7: 0.2797 ; Age 8: 0.2610 (ICES, 2021a)	10^{-3}	5.3×10^9
Seabass	0 (ICES, 2021b)	16 (ICES, 2021b)	0.736	0.24 (ICES, 2021b)	10^{-3}	1.1×10^7

143

144 **2.3. Parameterization of scenarios for CE nursery habitat**

145 Habitat restoration scenarios were parameterized by modifying both the surface area and the quality
146 of nursery habitat (Champagnat et al., in rev.), which will impact the two key parameters h and K in
147 the stock-recruitment relationship in Equation (4).

148 Modelling scenarios of surface area modification are straightforward. The carrying capacity K
149 depends directly on the surface area S of the nursery habitats (Equation 6). Writing the carrying

150 capacity K as the product of a carrying capacity per unit of surface area K^* and the surface area
 151 $S_{baseline}$, we parameterized surface area scenarios using a multiplier ($\lambda_{surface_area}$) as:

$$152 \quad (6) \quad K = K_{baseline}^* \times \frac{S_{baseline}}{\lambda_{surface_area}}$$

153
 154 so that $\lambda_{surface_area} = 1$ corresponds to the baseline situation and a value of $\lambda_{surface_area} < 1$
 155 denotes an increase in surface area.

156 To model scenarios of habitat quality alteration/restoration, we relied on Champagnat et al. (in rev.),
 157 with a parameterization of the stock-recruitment relationship (Equation 4) in terms of instantaneous
 158 density-independent (M^{di}) and density-dependent (M^{dd}) mortality rates between larvae and juveniles
 159 (Quinn and Deriso, 1999). Relationships between classical (h, K) and new (M^{di}, M^{dd}) parameters
 160 can be written as (Equations 7 & 8; see Champagnat et al. in rev. and Appendix A for more details):

$$161 \quad (7) \quad h = \frac{e^{-M^{di} \times a_{rec}} \times e^{-M^{larvae} \times \Delta_l \times \bar{W}}}{4 + e^{-M^{di} \times a_{rec}} \times e^{-M^{larvae} \times \Delta_l \times \bar{W}}}$$

$$162 \quad (8) \quad K = \frac{M^{di}}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1} \times S$$

163 where $e^{-M^{larvae} \times \Delta_l}$ is the resulting survival from density-independent mortality occurring during
 164 larval drift of duration Δ_l and S is the surface area of the nursery. Hence, looking at Equation (6), the
 165 carrying capacity per unit of surface area is written as a function of M^{di} and M^{dd} ($K^* =$
 166 $\frac{M^{di}}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1}$).

167 This alternative formulation allows us to parameterize the restoration (resp. alteration) of the quality
 168 of juvenile habitats in terms of a decrease (resp. increase) in both density-independent and density-
 169 dependent mortality rates, M^{di} and M^{dd} (Champagnat et al., in rev.). A common multiplier ($\lambda_{quality}$)
 170 is applied to M^{dd} and M^{di} , which in turn modifies the values of h and K^* .

171 Finally, the combination of scenarios of surface area alteration/restoration (varying $\lambda_{surface_area}$)
 172 and quality alteration/restoration (varying $\lambda_{quality}$) modifies stock-recruitment parameters (h, K) as
 173 (Equations 9 & 10):

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

175

$$(10) \quad K(\lambda_{quality}, \lambda_{surface_area}) = \frac{M^{di}}{M^{dd}} \times \frac{1}{e^{\lambda_{quality} \times M^{di} \times a_{rec} - 1}} \times \frac{S_{baseline}}{\lambda_{surface_area}}$$

177

178 2.3.1. Parameterization of surface area losses

179 The habitat surface area scenarios were based on estimation of surface area losses since 1870, derived
 180 from bathymetry data in three coastal sectors of the French EEC coastline in 1870 (Bay of Veys,
 181 Seine Estuary, Somme and Canche) available on the EMODnet website. The maps from 1870 were
 182 compared with the 2020 bathymetry map (Appendix D). The loss of habitats above a bathymetry of
 183 5 m, including the intertidal area, was estimated in each sector. This limit was chosen because it
 184 integrates almost all surface area loss in CE nursery areas (Rochette et al., 2010; Stamp et al., 2022).
 185 The proportion of habitat loss (S_{loss}) was estimated as the surface areas lost in each French sector
 186 between 1870 and 2020 for the total habitats above 5 m of the EEC French coast: $S_{loss} = 26.9\%$
 187 (Appendix D).

188 In the scenarios, S_{loss} was considered a proxy of the surface area loss at the EEC scale. Indeed, (i)
 189 these sectors represent major nursery areas for the four studied species (Riou et al., 2001; Carpentier
 190 et al., 2009); (ii) to the best of our knowledge, no similar data were available for the English coast.
 191 However, English intertidal habitats have lost surface area during the same period with similar levels
 192 of loss (Stamp et al., 2022). Thus, a global surface area restoration multiplier ($\lambda_{surface_area|global}$)
 193 was calculated as (Equation 11):

$$(11) \quad \lambda_{surface_area|global} = \frac{1}{1 - S_{loss}}$$

195 2.3.2. Species-specific bathymetric distribution of juveniles

196 The juveniles of the four studied species have different bathymetric distributions (Riou et al., 2001;
 197 Carpentier et al., 2009; Ellis et al., 2012) and hence different concentrations in shallow areas (<5 m).

198 These different concentrations determine the proportion of juveniles impacted by surface area loss in
 199 these shallow areas. The species-specific proportion of juveniles present in habitats above 5 m
 200 ($Prop_{species}$) was estimated from both bathymetric and nursery maps (Appendix E; $Prop_{species} =$
 201 49.7, 16.7, 4.1 and 80.2 for sole, plaice, whiting and seabass, respectively).

202 The nursery surface area loss factor was only applied to the proportion of juveniles present in this
 203 shallow area. Consequently, a species-specific surface area restoration factor ($\lambda_{surface_area|species}$)
 204 was calculated to simulate the restoration of the nursery area extent to the 1870 level (Equation 12;
 205 Table 2):

$$(12) \quad \lambda_{surface_area|species} = \frac{1}{1+(Prop_{species} \times \lambda_{surface_area|global}) - Prop_{species}}$$

208 2.3.3. Parameterization of quality effects

209 We relied on Courrat et al. (2009), who quantified the impact of the chemical quality of French
 210 estuaries on the density of marine juvenile fish, to estimate the ecological status of estuarine waters
 211 for the European water framework directive (Delpech et al., 2010). Courrat et al. (2009) found that
 212 estuaries with a medium ecological status had densities of juveniles 20% lower than estuaries of good
 213 quality. We assumed that this loss of density directly reflected a loss in carrying capacity per unit of
 214 surface area (K^*) due to degradation of habitat quality only (without loss of surface area). We denote
 215 $K_{scenario}^*$ as the new carrying capacity under the habitat restoration scenario.

216 Based on Equation (10) (but see also details in Appendix F), we back-calculated the habitat quality
 217 multiplier $\lambda_{quality}$ to be applied to M^{di} and M^{dd} that corresponds to the change from the baseline
 218 carrying capacity K^* to $K_{scenario}^*$ (Equation 13):

$$(13) \quad \lambda_{quality} = \frac{\log\left(\frac{M^{di}}{M^{dd}} \frac{K_{scenario}^*}{K^*} + 1\right)}{M^{di}}$$

221 The quality scenarios have been constructed by considering a homogeneous quality status of the
 222 nursery areas for all the nursery sectors (i.e., a single parameter $\lambda_{quality}$ for the whole EEC). Then,
 223 an additional assumption of the ecological status of CE areas in the EEC was made: on average, all
 224 estuaries were considered of average quality, and our scenarios simulated the restoration of these
 225 estuaries to a good ecological status (Courrat et al., 2009; Delpech et al., 2010).

226 The sensitivity of juveniles to changes in habitat quality likely depends upon their concentration in
 227 shallow habitats (<5 m), which varies greatly among species (Table 2; parameter *Prop*). Logically,
 228 the higher the concentration of juveniles in shallow areas, the higher their sensitivity to changes in
 229 habitat quality. To assess the sensitivity of the response to habitat quality to the concentration in
 230 shallow areas, we tested two different scenarios for habitat quality restoration.

231 - The first scenario (*quality all*) considers the restoration applied to all juveniles. This restoration
 232 scenario was based on a new carrying capacity ($K_{scenario\ all}^*$) calculated to simulate a restoration of
 233 the 20% loss (Equation 14):

$$234 \quad (14) \quad K_{scenario\ all}^* = K^* \times 1.25$$

235
 236 - The second scenario (*quality band*) considers the restoration applied only to the proportion of
 237 juveniles located above the 5 m bathymetry (*Prop*). This assumption was made to differentiate
 238 juveniles present in very shallow coastal areas, sensitive to high levels of contamination, from those
 239 located in deeper waters, considered not impacted ($K_{scenario\ band}^*$; Equation 15)

$$240 \quad (15) \quad K_{scenario\ band}^* = (K^* \times Prop \times 1.25) + (K^* \times (1 - Prop))$$

241

242 **2.3.4. Summary of scenarios**

243 The estimates of surface area losses and quality effects (Table 2) were used to simulate four species-
 244 specific scenarios: (i) surface area restoration, (ii) quality restoration applied to all juveniles (*quality*
 245 *all*), (iii) quality restoration applied to the most coastal juveniles (*quality band*) and finally (iv) a
 246 scenario that combines surface area and “*quality band*” restoration.

247

248 Table 2. Percentage of juveniles present in habitats above 5 m and associated restoration factors.

	Sole	Plaice	Whiting	Seabass
Percentage of juveniles in shallow nurseries ($Prop_{species}$)	49.71	16.72	4.10	80.23
Surface area restoration factor ($\lambda_{surface_area species}$)	0.8446	0.9417	0.9850	0.7711
Quality restoration factor <i>Quality all</i> ($\lambda_{quality}$)	0.9453	0.9330	0.8574	0.9367
Quality restoration factor <i>Quality band</i> ($\lambda_{quality}$)	0.9712	0.9877	0.9932	0.9481

249

250 In the first step, the results will be illustrated only with the second quality scenario (impact on inshore
251 juveniles, *quality band*). Then, a sensitivity analysis will compare the two quality scenarios.

252 3. Results

253 A detailed interpretation of both the calibration and results of the habitat scenarios is presented for
254 seabass before interspecific comparisons.

255 3.1. Seabass case study

256 The results are expressed as a percentage of seabass SSB or catch reallocated to fishery unit 7.d
257 (Figure 1; Appendix C) and not in relation to the actual management unit (ICES, 2021b).

258 Calibration of the carrying capacity to stock assessment outputs

259 K is estimated at 1.1×10^7 juveniles. The results highlight discrepancies between model predictions
260 and catches and SSB reported by ICES (Appendix G). However, the average SSB values estimated
261 by ICES and the average SSB values predicted by our model are quite similar (5.8×10^6 and
262 5.6×10^6 kg, respectively). The same conclusion holds for catches (average ICES values at

263 1.4×10^6 kg and model predictions at 1.2×10^6 , Appendix H). Model behaviour at equilibrium is
 264 realistic: an F_{MSY} of 0.15 without habitat restoration scenario (Figure 3), while the F_{MSY} from ICES
 265 (2021b) was 0.17, and a $\frac{SSB_{MSY}}{SSB_0}$ of 0.28.

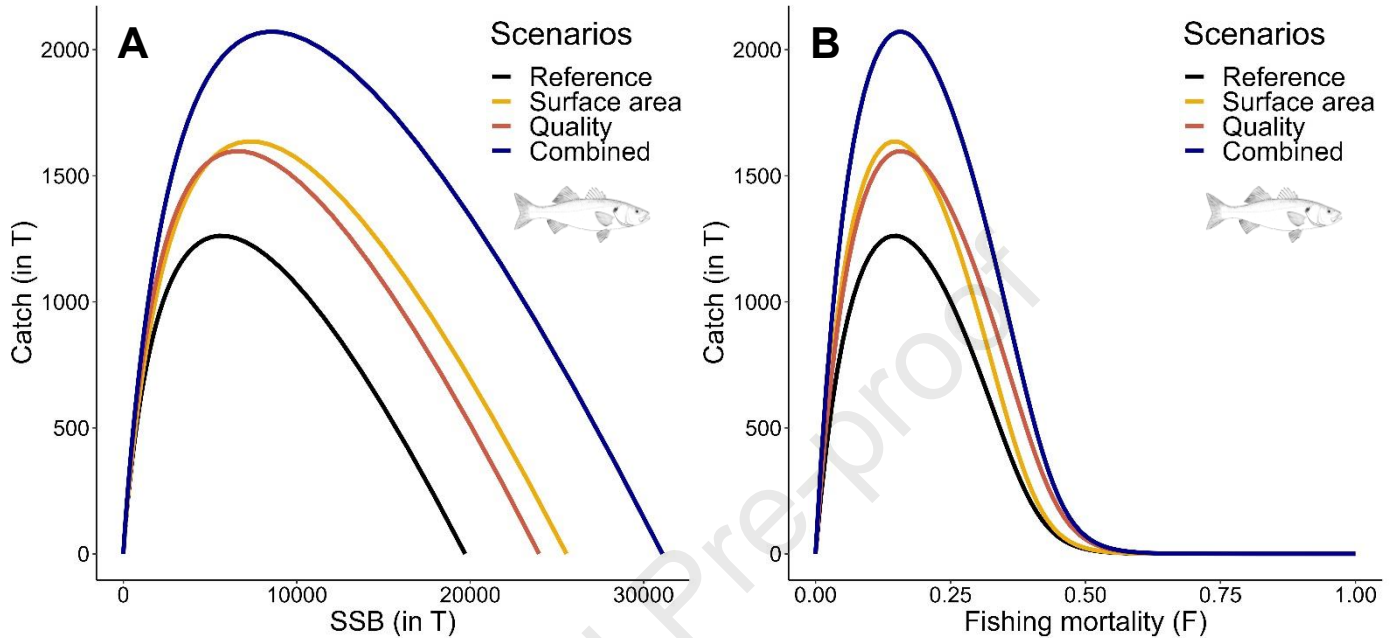


Figure 3. Production curves according to habitat scenarios as function of SSB (A) or fishing mortality (B) for seabass in ICES division 7.d. Quality and combined effect based on the *quality band* hypothesis.

266 **Equilibrium production curves under habitat restoration scenarios**

267 Restoring the surface area of juvenile habitat only impacts K (Equation 10) and hence the scale of the
 268 productivity curve, with increased catches and increased levels of biomass at MSY (Figure 3A), while
 269 F_{MSY} remains unchanged (Figure 3B). In contrast, restoring habitat quality (*quality band* scenario)
 270 affects both the K and h parameters (Equations 9 and 10), hence increasing catches, SSB_{MSY} and
 271 F_{MSY} (Figure 3B).

272 **3.2. Comparison between species**

273 **Population model fit**

274 For all four species, as shown for seabass, the calibration of the model led to predictions of catches
275 and SSB that did not match perfectly with annual ICES data (Appendix G). However, the average
276 SSB and catches estimated by ICES and predicted by our model were similar. Overall, the model
277 outputs at equilibrium, F_{MSY} and $\frac{SSB_{MSY}}{SSB_0}$ ratio fit within the expected range (0.2 to 0.34; Horbowy and
278 Hommik, 2022) (Appendix H).

279 **Maximum sustainable yield indicators under habitat restoration scenarios**

280 The impacts of habitat restoration scenarios were compared across species by estimating relative
281 gains in SSB and catches at MSY equilibrium states (Figure 4). The surface area scenario has the
282 largest impact on SSB, with gains ranging from 1.5% for whiting to 29.6% for seabass (Figure 4A).
283 This interspecific pattern also concerned the gains linked to the restoration of quality, with an increase
284 in SSB ranging from 0.4% for plaice to 17.1% for seabass. When combining the surface area and
285 quality restoration scenarios, the effects are multiplicative (i.e., greater than the sum of both effects),
286 and two groups of species emerge: whiting and plaice, for which the combined restoration has the
287 lowest effect, with gains of 2.9% and 6.6%, respectively, whereas sole and seabass had gains of 27.4%
288 and 51.8% in SSB, respectively. The catch increase at MSY almost followed that of SSB (Figure 4B).
289 In volume, the restoration of both habitat surface area and quality represents an increase in catches of
290 327, 957, 1990 and 810 tons for whiting, plaice, sole and seabass, respectively.

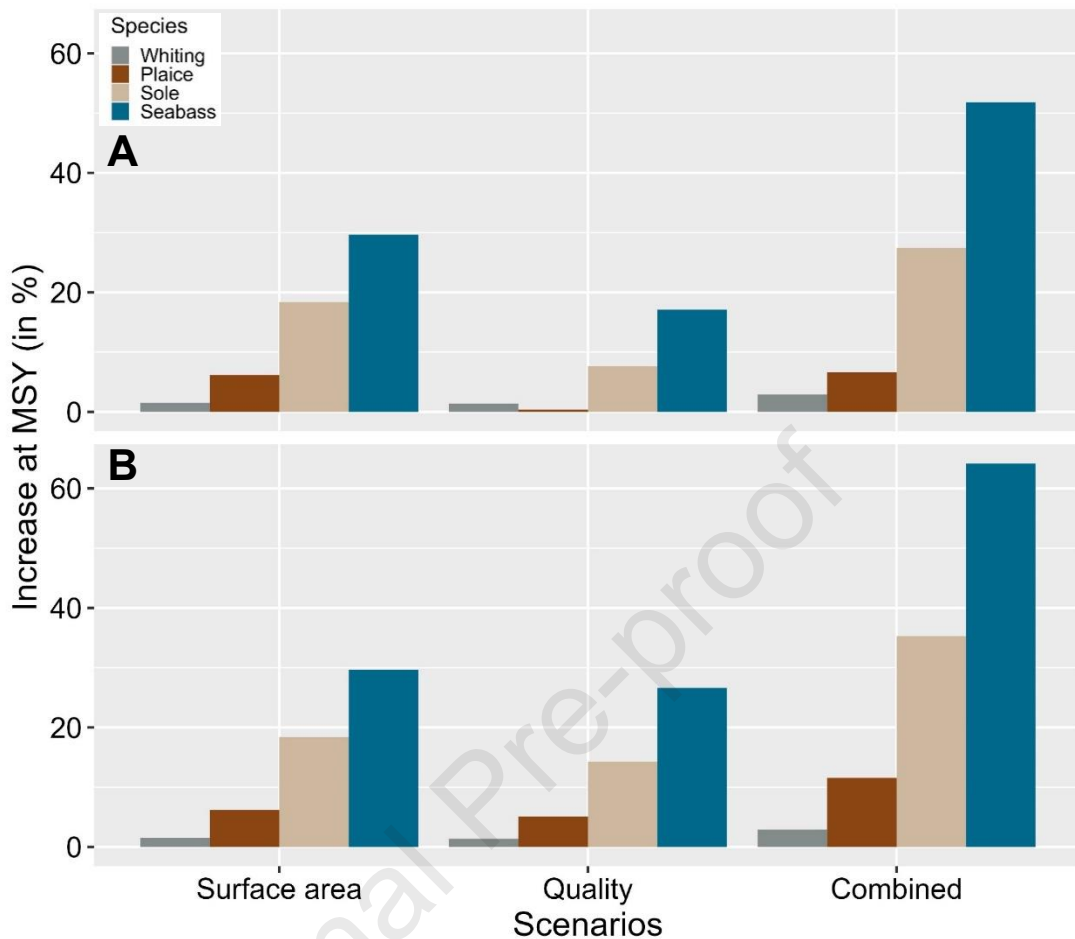


Figure 4. Effects of habitat scenarios on SSB (A) and Catch (B) gain at MSY by species. The quality and combined scenarios are based on the *quality band* hypothesis.

292 Sensitivity to the quality scenario hypothesis

293 Large differences emerged between the two scenarios for quality restoration (*quality band* = impacts
 294 only the juveniles located in shallow (<5 m) habitat; *quality all* = impacts all juveniles). The
 295 restoration of quality for all juveniles in the EEC leads to a greater homogeneity in the gains than
 296 when the restoration is carried out according to the bathymetric distribution of juveniles (Figure 5).
 297 Under the *quality all* scenario, interspecific patterns depended on demographic parameters only,
 298 especially steepness and fecundity, which differed between species. The results show that the
 299 sensitivity to quality restoration is higher for species with lower steepness (whiting; Figure 5).
 300 Moreover, all species have greater catch gains in this “global” restoration scenario due to a larger

301 quantity of juveniles impacted by the restoration (an increase of 32%, 26%, 15% and 7%, compared
 302 to the “partial” scenario, for whiting, plaice, sole and seabass, respectively; Figure 5).

303

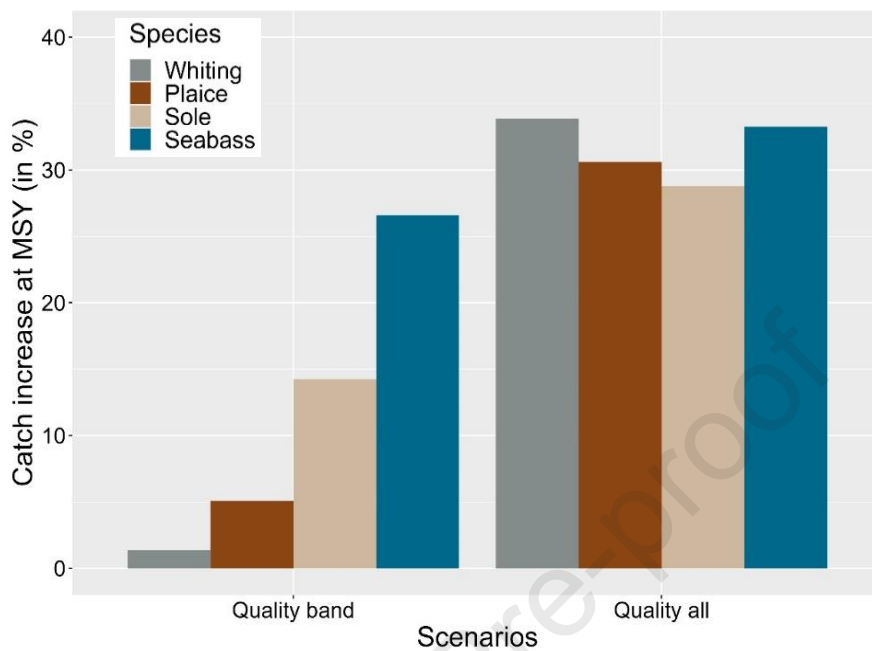


Figure 5. Difference in catch gains per species according to the assumption made for quality scenarios. *Quality band* is the restoration scenario applied only to the juveniles in shallow habitats (<5 m) and *quality all* is the restoration scenario applied to all the juveniles.

304

305 4. Discussion

306 4.1 Main findings

307 We assessed the consequences of CE nursery restoration through a generic age- and stage-structured
 308 model with a stock-recruitment relationship that directly depends upon the quality and surface area
 309 of the nursery habitat (Champagnat et al., in rev). The model was applied to four nursery-dependent
 310 species, i.e., sole, plaice, whiting and seabass, characterized by different life history traits and various
 311 degrees of concentration in EC nursery habitats in the EEC. For the four species, models were
 312 parameterized from the literature and stock assessment outputs (ICES, 2021a,b), except for the

313 carrying capacity, which was calibrated to stock assessment outputs to achieve realistic population
314 sizes.

315 The model was used to simulate equilibrium catch curves obtained under different scenarios of
316 nursery quality and surface area restoration for the four species. Surface area restoration increased
317 the catches and biomass at MSY. The restoration of quality led to an increase in catches and biomass
318 at MSY but also in fishing mortality at MSY. Overall, the species with higher levels of concentration
319 in shallow nursery areas were the most sensitive to the habitat restoration scenarios. Thus, seabass
320 was the species for which habitat restoration had the greatest positive impact, while whiting was the
321 least affected species. However, the response also depended upon species-specific life history traits:
322 lower steepness led to a stronger response to habitat quality scenarios.

323 **4.2 Limitations in model assumptions and scenarios**

324 *Generic model to simulate population dynamics without stochastic recruitment variability*

325 In this generic model, only one parameter, the carrying capacity (K), needed to be calibrated to stock
326 assessment outputs. This makes it easy to apply for several case studies, i.e., four stocks herein, as
327 needed parameters and data were available from the literature and stock assessments. Indeed, the
328 model used requires age-based stock assessment outputs to be implemented, and this is the main
329 limitation to its use. However, the calibration of K implies two ecological assumptions, the first being
330 that the carrying capacity of the nursery habitat limits recruitment (Beverton and Iles, 1992; Le Pape
331 and Bonhommeau, 2015). The second is that this carrying capacity does not vary over time, which is
332 a strong assumption. Indeed, fluctuations were previously evidenced (Luo et al., 2001; Le Pape et al.,
333 2003), for instance, as a response to the supply of nutrients and organic matter that support food
334 provisioning (Kostecki et al., 2010; Day et al., 2021).

335 Considering a deterministic population dynamic is another limitation of the model. Indeed,
336 environmental variability dramatically impacts population dynamics, especially regarding the
337 recruitment process (Pfister and Stevens, 2003). This has led to poor predictions of annual variations

338 in SSB and catches. However, the objective was not to reproduce these annual fluctuations but to
339 simulate realistic average population dynamics. The calibration led to an average estimate of SSB
340 and catches close to the average estimate of the ICES over the same period for the four studied
341 species. In addition, population indicators (F_{MSY} and $\frac{SSB_{MSY}}{SSB_0}$ ratio) confirmed the realism of the
342 dynamics.

343 Finally, the model structure does not take into account the ecosystem relationships between different
344 life stages within a species or among species (Day et al., 2021). Such interactions may also impact
345 the carrying capacity, thus SSB and catches.

346 *Model without spatial population structure*

347 The model considered juvenile habitat as a single homogeneous block, whereas CE areas are
348 composed of a multitude of habitats with high heterogeneity that can vary over time (“shifting habitat
349 mosaic”, Peterson, 2003; Wimberly, 2006; Nagelkerken et al., 2015). Considering the nursery areas
350 as a single block is limiting, especially for the construction of quality restoration scenarios. However,
351 considering spatial heterogeneity would require parameterizing specific Beverton-Holt relationships
352 for each nursery area (Rochette et al., 2013), which is inaccessible. Moreover, considering different
353 nursery sectors in the EEC would greatly complicate our model and the elaboration of restoration
354 scenarios by raising questions about steepness estimation for the different nursery sectors (White,
355 2010) and population connectivity (Archambault et al., 2016).

356 Diffusion of the outcomes of local nursery restoration at a metapopulation scale highly depends on
357 the level of connectivity at different stages of the life cycle (Archambault et al., 2018; Randon et al.,
358 2021; Ma et al., 2022). The results therefore provide global estimates at the stock scale, with caution
359 regarding the interpretations of both internal and external spatial structures, especially when based on
360 estimates at MSY (Ying et al., 2011).

361 ***Realistic but simplified scenarios***

362 The estimation of surface area losses was based on historical data available on three CE nursery areas
363 on the French side of the EEC in 1870. Accounting for surface area losses in these three CE areas
364 was an innovative step forward, as previous studies in the EEC have focused on the single Seine
365 Estuary (Rochette et al., 2010, Archambault et al., 2018; Champagnat et al., 2021). However, no
366 similar data were available for the English coasts, where nurseries have experienced surface area
367 losses over the same period (Stamp et al., 2022). This proxy of French surface area loss was
368 considered the best available knowledge for the EEC.

369 To fit with available information on CE surface area loss, the concentration of juveniles in the shallow
370 nursery habitat was considered dependent on depth only. Depth is a main driver of juvenile fish
371 distribution for the studied species in the EEC (Riou et al., 2001; Carpentier et al., 2009; Ellis et al.,
372 2012), but defining an ecological niche by a single variable is a very simplifying assumption
373 (Grinnell, 1917; Hutchinson, 1957). CE nursery areas can be defined by other parameters, e.g.,
374 salinity and hydrodynamics (Kennedy and Fitzmaurice, 1972; Kelley, 1988; Le Pape et al., 2003),
375 sediment structure (Riou et al., 2001; Rochette et al., 2010), and coastal shelter (Trimoreau et al.,
376 2013). The estimation of species-specific surface area losses was therefore oversimplified. Moreover,
377 the proportion of juveniles above 5 m was calculated on maps representing present habitats. When
378 shallow habitats were of larger surface extent, as in 1870, the proportion of juveniles present in this
379 shallow fringe was likely greater, which could have led to underestimation of species-specific
380 consequences of surface area loss.

381 The scenarios of quality degradation were based on a global estimate of juvenile density drop in
382 nursery areas (Courrat et al., 2009). This proxy was used due to the lack of knowledge on the species-
383 specific impact of nursery habitat quality degradation on the demographic parameters of juvenile fish.
384 Indeed, despite the well-documented impacts of local anthropogenic disturbances on juveniles of CE
385 nursery-dependent species (Brown et al., 2018), the consequences of these impacts on demographic

386 rates are still poorly understood and need to be quantified to infer impacts at the population scale
387 (Vasconcelos et al., 2014; Lipcius et al., 2019; Schneeweiss et al., 2022).

388 Given this lack of knowledge, two strong hypotheses were put forward. First, the parameterization of
389 the quality scenario assumed a common multiplier on density-dependent and density-independent
390 mortality rates. This is a strong assumption, as different processes are associated with these mortality
391 rates (Jonhson, 2007; Juanes, 2007). Density-dependent mortality refers to interactions among
392 juveniles of the same cohort, mostly competition for food or space (Gibson, 1994; Craig et al., 2007;
393 Le Pape and Bonhommeau, 2015). Density-independent mortality involves other mortality processes
394 linked to a large panel of stressors (e.g., pollutants, Rose et al., 2003; oxygen, Gibson, 1994) and/or
395 predation (Gibson, 1994; Hilborn and Walters, 2021). Second, the simulation results were very
396 sensitive to the two assumptions made on which fraction of the nursery habitat is affected by quality
397 restoration/degradation (i.e., the whole nursery area or the <5 m band only). The lack of knowledge
398 on the gradient of land–sea impacts on marine juvenile fish in CE nurseries prevents selecting
399 between scenarios or developing more accurate scenarios.

400 Because survival rates are very low at young stages, the sensitivity of population dynamics to minor
401 changes in the mortality rate is high (Levin and Stunz, 2005; Hilborn and Walters, 2021) and would
402 require attention in future studies to design more accurate scenarios.

403 **4.3 Effects of nursery restoration and comparison between species**

404 To the best of our knowledge, our study is the first to assess the effect of restoration of CE nursery
405 areas for a group of species at the scale of a management unit.

406 Surface area restoration, which leads to an increase in the carrying capacity of the nursery, enhances
407 the catches and biomass at MSY. The restoration of quality increases both the carrying capacity and
408 the steepness, thus increasing catches, biomass and fishing mortality at MSY (Champagnat et al., in
409 rev.). For a combined restoration, the effects are multiplicative, i.e., higher than the simple sum of
410 the marginal restoration effects.

411 The difference in gains between species due to surface area restoration is mainly due to a different
412 degree of concentration of juveniles in the shallow nursery habitat. The differences in quality
413 restoration are also highly sensitive to assumptions regarding the proportion of juveniles impacted by
414 restoration. However, the impacts of quality restoration are also related to species-specific
415 demographic parameters (Champagnat et al., in rev.). Thus, an interesting result of this study is that
416 life history traits, especially steepness, not only drive the sensitivity of marine fish to fishing pressure
417 (Froese et al., 2016; Miller and Brooks, 2021; Horbowy and Hommik, 2022) but also their response
418 to essential fish habitat degradation.

419 Previous studies focusing on sole examined the effect of surface area and/or habitat quality scenarios
420 in the EEC with more complex and species-specific life cycle models. Archambault et al. (2018) and
421 Champagnat et al. (2021) demonstrated the effects of quality degradation and surface area loss in CE
422 nursery areas in the EEC, considering the restoration of the surface area and the quality of the Seine
423 estuary only. The present model provided outputs consistent with these species-specific approaches,
424 but the main focus was its generic formulation, allowing us to consider four species. This generic
425 steepness-based approach requires limited tuning (i.e., only of the carrying capacity parameter) to
426 parametrize the stock-specific population dynamics as long as an age-structured stock assessment is
427 available. Such a tool to infer the consequences of habitat degradation at the population and fisheries
428 scale is highly needed (Rabalais, 2015; Lipcius et al., 2019; Schneeweiss et al., 2022), and this model
429 could easily be applied for other study areas and fish species in the future.

430 However, the accuracy of the scenarios relies on the existing knowledge on both the fraction of
431 juveniles concentrated in impacted CE nurseries and the level of impact (surface area loss and drop
432 in demographic rates or density in response to lower quality). The sensitivity to these uncertain levels
433 of change (Levin and Stunz, 2005; Hilborn and Walters, 2021; Zimmerman et al., 2021) could be
434 high. However, both the use of simulation at equilibrium states and the lack of data allowing model
435 predictions to be directly compared to habitat scenarios related to field records on a long-term (i.e.,
436 since 1870 for surface area loss) temporal basis prevent further validation.

437 **4.4 Management implications**

438 The present approach shows that the gains from fisheries management could be greatly increased if
439 nursery areas were restored in the EEC. This restoration could lead to annual catch gains of 2.9%,
440 11.6%, 35.3% and 65.2% for whiting, plaice, sole and seabass, respectively, representing gains of
441 327, 957, 1990 and 810 tons, respectively. In addition to catch gains, the spawning stock biomass
442 would also be enhanced, which could have beneficial consequences for the whole ecosystem (Froese
443 et al., 2008; Froese et al., 2016). However, the lack of time series to compare model predictions and
444 habitat status prevents us from validating the simulation outputs. Nevertheless, ongoing management
445 measures to restore the surface area (in the Seine estuary, Ducrottoy and Dauvin, 2008) and quality of
446 CE habitats (decreases in pollutant levels; Meybeck et al., 2007; Tappin and Millward, 2015) in the
447 EEC should therefore be continued to enhance fish and fisheries production (Katara et al., 2021).

448 This study supports the need to consider essential fish habitat in the management of fishing resources
449 (Brown et al., 2018; Kraufvelin et al., 2018; Brown et al., 2019). The high level of surface area loss
450 and anthropogenic disturbances to the remaining CE ecosystems (Halpern et al., 2008) impact their
451 nursery function (Jokinen et al., 2015) worldwide (Barbier et al., 2011). Substantial recovery of the
452 function of habitats essential to marine life could be achieved (Duarte et al., 2020). Restoring coastal
453 nurseries (Buelow et al., 2022; Troast et al., 2022) may be even more beneficial than regulating
454 fishing pressure (Levin and Stunz, 2005; van de Wolfshaar et al., 2011).

455

456

457 **Authors contributions**

458 **Gernez Maël:** Conceptualization, Methodology, Software, Investigation, Writing - Original Draft,
459 Editing.

460 **Champagnat Juliette:** Conceptualization, Methodology, Software, Investigation, Writing - Original
461 Draft.

462 **Rivot Etienne:** Conceptualization, Methodology, Writing - Original Draft.

463 **Le Pape Olivier :** Conceptualization, Methodology, Writing - Original Draft, Funding acquisition.

464

465 **Declaration of Competing Interest**

466 None.

467

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Highlights “Potential impacts of the restoration of coastal and estuarine nurseries on the stock dynamics of fisheries species”

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- The effects of nursery habitat restoration were assessed for four species of main fisheries of interest in the Eastern English Channel.
- Potential restoration gains in terms of biomass and catches were substantial, up to more than 50% of spawning biomass at maximal sustainable yield for the most shallow nursery-dependent species.
- Species with higher concentrations in shallow nurseries were the most sensitive to habitat restoration.
- Contrasts in life history traits lead to species-specific responses: a lower resilience to fishing pressure induces a stronger response to habitat restoration.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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