



REVIEW

Lessons from the calibration and sensitivity analysis of a fish larval transport model

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ABSTRACT: Numerous fish populations show strong year-to-year variations in recruitment. The early life stages play a crucial role in determining recruitment and dispersal patterns. A helpful tool to understand recruitment and dispersal involves simulations with a Lagrangian transport model, which results from the coupling between a hydrodynamic model and an individual-based model. Larval transport models require sound knowledge of the biological processes governing larval dispersal, and they may be highly sensitive to the parameters selected. Various assumptions about larval traits, behaviour and other model parameters can be tested by comparing simulation results with field data to identify the most sensitive parameters and to improve model calibration. This study shows that biological parameterization is more important than inter-annual variability in explaining the year-to-year differences in larval recruitment of common sole in the North Sea and the eastern English Channel. In contrast, year-to-year variability of connectivity leads to higher variability than changes in the biological parameters. The most influential parameters are pelagic larval duration, spawning period and mortality. Calibration over a 12 yr recruitment survey shows that a scenario with low mortality associated with a long larval duration and behaviour involving nycthemeral and tidal migration best reproduces the observations. This research provides insights into factors influencing fish dispersal and recruitment, suggesting a strategy for enhancing the accuracy of models in upcoming studies. The study supports the improvement of larval dispersal modelling by incorporating an easily applicable sensitivity analysis for both calibration and validation. Incorporating sensitivity analyses enhances larval dispersal models, providing performing tools that can contribute to informed fisheries management and understanding of recruitment variability.

KEY WORDS: Biophysical model · Calibration · Common sole · Connectivity · Flatfish · Larval dispersal · North Sea · Parametrization · Recruitment · *Solea solea* · Sensitivity

1. INTRODUCTION

Marine connectivity, the realised movement between populations in a seascape, plays an essential role in the persistence and productivity of (meta)populations and in population structure, genetic diversity and population resilience (i.e. Cowen et al. 2007, Selkoe et al. 2016). The early life history of marine organisms plays a major role in this process and connectivity is

susceptible to large variations in the already low survival rate (McGurk 1986, Houde 2008, Le Pape & Bonhommeau 2015). Among the many potential indicators, spawning stock biomass (SSB) is a poor predictor of recruitment variability (Szuwalski et al. 2015). This is especially the case for demersal fishes, including flatfishes, for which SSB explains a mere 5% of the variation in recruitment (Cury et al. 2014). Recruitment success of demersal fish depends foremost on

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access to suitable nursery grounds after metamorphosis. In addition, demographic connectivity of fish is highly influenced by larval dispersal from the spawning grounds to the nursery grounds (Pineda et al. 2007). Hence, understanding both connectivity and recruitment dynamics is crucial for fisheries management (Fogarty et al. 2007, Kerr et al. 2010, 2016).

Models are widely used in fisheries science (Royce 2013, Aeberhard et al. 2018) and conservation (Ruth & Lindholm 2002, Marshall et al. 2014) to support management. They have multiple applications, ranging from the dynamics of one species to the functioning of a full ecosystem (Travers et al. 2007, Rose et al. 2015, Grüss et al. 2017). One interesting application is the prediction of individual exchanges and movement in supporting the design of marine protected areas (Baskett et al. 2005, Kaplan et al. 2009, Andrello et al. 2013). Over the past decades, coupled bio-physical models merging individual-based models (IBMs) and hydrodynamic models have become well established, especially in modelling dispersal of early life stages (Miller 2007, Pineda et al. 2007, Cowen & Sponaugle 2009). The models contribute to the understanding of the dynamics and critical drivers of ecosystems and facilitate management at specific spatio-temporal scales (Allain et al. 2007, Hinrichsen et al. 2011). However, IBMs require a sound knowledge of the biological processes governing larval dispersal. Even marine species with similar life cycles show large differences in potential and realised dispersal. Differences are related to larval traits (López-Duarte et al. 2012) such as behaviour (Fox et al. 2006, North et al. 2008, Robins et al. 2013), duration of the larval stage (Shanks 2009), seasonality (Lett et al. 2010), spawning period (Ayata et al. 2010) or structure of the water column and currents (Munk et al. 2009). Due to the challenges involved with direct observation in the marine environment, especially for the poorly documented early life stages (Levin 2006), life history traits are difficult to assess and parameterization remains uncertain. Furthermore, documentation regarding the confidence in the coupled bio-physical models remains incomplete. Numerous studies have investigated the sensitivity and robustness of Lagrangian transport models as well as the physical parameters, spatio-temporal resolution or density and number of particles released (Huret et al. 2007, Simons et al. 2013, Savina et al. 2016, Monroy et al. 2017, Kvile et al. 2018). Such insights provide useful practical recommendations for modellers (North et al. 2009). However, systematic sensitivity analyses of biological parameters are even more limited. Various parameters such as pelagic larval duration (PLD), swimming ability, vertical migration be-

haviour or mortality (Fox et al. 2006, Peck & Hufnagl 2012, Monroy et al. 2017) have been highlighted to influence drift patterns and retention. More formal analyses to identify the most influential parameters are rarely carried out because of the numerous parameters and long simulation times (with the notable exception of Silve et al. 2023). We suggest to rely on a sequential methodology combining sensitivity analysis and model selection as proposed by Lehuta et al. (2013) to improve a coupled bio-physical model in a case study on common sole *Solea solea* (Linnaeus, 1758). Here we propose to classify several alternative hypotheses on life traits according to their impact on larval drift.

Coupled bio-physical models, including LARVAE&CO, have captured some of the interannual and interregional variations in recruitment of common sole in the North Sea (Bolle et al. 2009, Savina et al. 2010, Lacroix et al. 2013). Common sole has been studied extensively and is one of the most economically valuable flatfish species in the area (Gibson et al. 2015). The demersal adults spawn in the coastal region in spring; eggs and larvae drift with the current. Following metamorphosis (e.g. Amara et al. 1998), juveniles settle in shallow coastal waters, whose spatial extent impacts year-class strength. From the abundant documentation of early life stages in the literature (Barbut et al. 2019 and references therein) covering a broad range of life history traits (such as PLD, spawning period and behaviour), which might be related to habitat or population-specific traits (Diopere et al. 2018). For example, vertical nycthemeral migration of larval sole is well documented in the Bay of Biscay (Koutsikopoulos et al. 1991), but remains uncertain in the more turbid North Sea waters. Improving the estimation of model parameters related to life history traits can be complex and expensive because it involves empirical field and experimental data. An alternative is to simulate and test various assumptions about larval traits, behaviour and other model parameters and to compare simulation results with field data to identify the most influential parameters.

Our overall aim was to carry out a sensitivity analysis of the larval transport model LARVAE&CO, parameterised for common sole inhabiting the North Sea and the eastern English Channel, to quantify the influence of biological parameters and inter-annual variability on recruitment and connectivity and to improve model calibration. Specific questions are (1) Is variability due to parameter uncertainty larger than the effect of interannual variability? (2) Which parameters have the most impact? (3) Is there a difference between equally likely parameterizations? (4) Which parameterization fits the recruitment data best?

2. MATERIALS AND METHODS

2.1. Research strategy

The Lagrangian transport model LARVAE&CO (Lacroix et al. 2013), which combines a hydrodynamics model and an IBM, was used to study early life survival of common sole in the North Sea and the Eastern English Channel. The parameter range for sensitivity analysis was estimated from observed data and experiments in the scientific literature were summarized. The number of discrete modalities used in the analysis is a compromise between the exploration of the parameter space (i.e. the number of parameter combinations) and the computational time required to perform the analyses. To improve model performance, the first step was to perform an exploratory analysis on 4 contrasting years in terms of hydrodynamics to determine which of the biological parameters or inter-annual variability has the strongest influence on connectivity and recruitment. A second step, an in-depth analysis, aimed to further determine which biological parameters have a strong impact on model output considering only one specific year. Both steps were realised through sensitivity analysis and the computation of sensitivity indices. Finally, in a third step, a calibration of the most influential parameters was performed by comparing predicted and observed recruitment over a 12 yr period.

2.2. Study area

The eastern English Channel and the southern and central North Sea are shallow coastal seas in which currents are mainly generated by tides and wind. The residual current is oriented from south to north (Turrell 1992), with some interannual variability in the flow field related to the North Atlantic Oscillation (NAO), in addition to strong seasonal variability.

2.3. Modelling of the early life stage

2.3.1. The hydrodynamic model

The 3D hydrodynamic NOS (North Sea) model, based on the COHERENS model (Luyten et al. 1999), has been implemented in the North Sea and English Channel between 48.5–57° N and 4–9° E. The model domain contains 157 × 205 horizontal grid cells with a resolution of 5' in longitude and 2.5' in latitude (approximately 5 × 5 km) and 20 σ -coordinate vertical

layers. Two open boundaries are located at the northern and western limits (at 4° W and 57° N) and the model includes daily river discharges of 14 rivers. The model is forced by weekly sea surface temperature data on a 20 × 20 km grid (Loewe 1996) downloaded from the BSH website (https://www.bsh.de/EN/DATA/Climate-and-Sea/Sea_temperatures/Sea_surface_temperatures/sea_surface_temperatures_node.html) and then interpolated in space and time according to the model resolution. For the meteorological forcing, the model is forced by 6-hourly surface wind and atmospheric pressure fields provided by the Royal Meteorological Institute of Belgium based on the forecast data of the UK Met Office 'Global Atmospheric Model, Hi_Res' as described in Walters et al. (2017). Details about the model implementation can be found in Savina et al. (2010) and Lacroix et al. (2013). The COHERENS hydrodynamic model is a key component of the Royal Belgian Institute of Natural Sciences' marine forecasting suite, with validation reports available bi-annually (see Baetens & Legrand 2022 for the latest report) demonstrating its accuracy in reproducing tide and temperature. Validation of current data is difficult due to the limited *in situ* data in this area. Nevertheless, the model performs well compared to other North Sea hydrodynamic models and contributes to the Copernicus Marine Environment Monitoring Service's Multi-Model Ensemble of forecast products (details can be found at <https://noos.eurogoos.eu/increasing-noos-awareness/community-tasks/multi-model-ensemble-of-forecast-products/>).

2.3.2. IBM

Larval trajectories of common sole were calculated in the Lagrangian larval transport model LARVAE&CO (Lacroix et al. 2013) using a particle tracking model coupled online to the COHERENS model. The vertical diffusion was modelled by the random walk technique, following Visser (1997). Since vertical turbulent diffusion is considered the dominant horizontal diffusion mechanism in the North Sea (Christensen et al. 2007), explicit representation of horizontal diffusion was neglected. The IBM was structured in 4 stages representing life stages from eggs to metamorphosis (eggs, yolk-sac larvae, first-feeding larvae and metamorphosis larvae). Each stage has a species-specific parameterization in terms of larval duration, behaviour and mortality.

Eggs are released in 6 main spawning grounds (off the French coast [EC], off the Belgian coast [BC], off Texel [Tx], the inner German Bight [GB], off the mouth

of the Thames River [Th] and on the Norfolk Banks [N]; ICES-FishMap 2005). Nursery grounds, located in the coastal area (<20 m depth) with soft sediment (a substrate of either mud to sand or sand to mud with <5% gravel, following the modified Folk classification of Kaskela et al. 2010), are divided into 6 zones based on national boundaries (France [Fr], Belgium [Be], the Netherlands [Nl], Germany [Ge], a combination of German and Danish national boundaries; and 2 in the UK: Norfolk [No] in the north and Thames estuary [Tha] in the south) (see details in Fig. 1).

2.3.3. Spawning period

The spawning period was estimated for each spawning ground in the domain of the present study. For the baseline situation, the spawning peak corresponds to the first day in which the local sea surface temperature reaches 10°C on average. A spawning period of 3 mo is considered, centred around the peak (details are available in Lacroix et al. 2013). For the sensitivity analysis, early spawning and late spawning are based on the baseline peak with a range of ± 15 d. This choice is informed by a comparison between temperature-based estimations and estimations based on gonad development, as described in Fincham et al. (2013) (see details in Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m731p067_supp1.pdf, for all supplemental figures).

2.3.4. PLD

Egg and larval duration were defined as a function of temperature according to the equation $D = \alpha T^{-\beta}$, where D is the stage duration (d) and T the temperature (°C). In the present study, β was fixed and a range was considered for α to allow covering the interval of values found in literature and described in Bolle et al. (2005). Parameter values representative for the reference and short and long PLDs for each stage are given in Table S1 (in Supplement 2 at www.int-res.com/articles/suppl/m731p067_supp2.xls, for all supplemental tables). We provide the values as the range and data used to estimate parameter space (Fig. S2).

2.3.5. Behaviour

Five active behaviours related to vertical migration and in addition to passive drift have been attributed to the particles. As the combination of these behaviours for

each stage would represent many cases, the first step before conducting a sensitivity analysis is to reduce the parameter space within a range of uncertainties based on the literature and considering scientific questions.

The position of eggs and larvae of common sole in the water column is well described in the Bay of Biscay (Lacroix et al. 2013 and references therein): an upward movement due to a positive buoyancy of eggs and yolk-sac larvae is followed by a nycthemeral migration during the first-feeding larval stage in which larvae swim towards the surface at night and downwards during the day. The tidal migration of metamorphosing larvae is synchronous with the tides.

We envisaged multiple objectives for the parametrization of behaviour. First, we assessed the impact of specific migration behaviours compared to the control situation without migration behaviour (i.e. passive behaviour at all stages: Mig0). We implemented the vertical movement of eggs and yolk-sac larvae due to density effects in all cases with a migration behaviour. Second, nycthemeral migration is biologically intriguing, as it has been observed in the Bay of Biscay (Koutsikopoulos et al. 1991) and has, to date, not been documented in the North Sea. Finally, the tidally influenced migration patterns during metamorphosis are of particular interest given their importance in, for example, the Celtic Sea (Nash & Geffen 2000, Fox et al. 2006).

Vertical migration rates have been defined within the range of the values observed in the literature (Berntsen et al. 1994, van der Molen et al. 2007) to obtain diel vertical migration and tidally associated vertical migration as described in Lacroix et al. (2013). Upward movement is due to a positive buoyancy for eggs and yolk-sac larvae (0.003 m s^{-1}) and downward movement due to negative buoyancy has been implemented for metamorphosing larvae (-0.003 m s^{-1}). Nycthemeral migration is implemented for larvae swimming towards the surface at night (0.003 m s^{-1}) and towards the bottom during the day (-0.001 m s^{-1}). Tidal migration is synchronous with the tides (-0.003 m s^{-1} at low tide; 0.001 m s^{-1} at high tide).

Two cases have been considered for tidal migration: (1) a 'pressure-based' vertical migration in which vertical migration rates switch from positive values (when the sea level is higher than the mean sea level) to negative values (when the sea level is lower than the mean sea level, as described in Lacroix et al. 2013) and (2) a 'current-based' vertical migration in which vertical migration rates switch from positive values during rising tide (when the sea surface level increases) to negative values during falling tide (when the sea surface level decreases) as in Barbut et al.

(2019). Additionally, apart from tidal or passive migration, a downward movement was tested for metamorphosing larvae (Mig1) to simulate settlement behaviour without tidal influence. Table 1 shows the 8 combinations of the 5 potential behaviours tested. Only the type of behaviour was tested and not the vertical velocity itself. The 'Mig3' and 'Mig7' test cases correspond to the parameterization used in Lacroix et al. (2013) and Barbut et al. (2019) respectively.

2.3.6. Settlement delay

Settlement occurred at the end of the larval stage (Gibson 1994, Haynes et al. 2011, van der Hammen et al. 2013). To represent competency windows of larval settlement, we tested 3 parameterizations. In the first parameterization, survival rates for larvae that ended up outside the nursery grounds at the end of their PLD were set to 0%, indicating their inability to survive in unsuitable habitats. However, in cases where larvae did not reach a nursery within this period, for the second and third parameterizations, we introduced an additional delay of 5 and 10 d to allow them to reach a suitable nursery habitat. During this additional period of drift, larval mortality was still applicable until settlement.

2.3.7. Larval mortality

A survival rate was computed during the full larval stage until metamorphosis to penalise long larval durations and to increase the realism of the simulations. The mortality rate used in Lacroix et al. (2013) was set to $0.0004 \cdot T^{3.0293} \text{ d}^{-1}$ (where T is temperature) for eggs and yolk-sac-larvae and a constant mortality rate of 0.035 d^{-1} for first-feeding and metamorphosis stage; all were applied separately for each stage. Mortality

rate is also associated with uncertainty, which is difficult to determine; an arbitrary increase of 10% is considered 'high mortality' and a decrease of 10% is considered 'low mortality'.

2.3.8. Model outputs

Local larval recruitment is the estimated number of larvae arriving in each nursery ground; total larval recruitment is the total number of larvae arriving in all nursery grounds at the end of the pelagic drift. The connectivity matrices represent the proportion of larvae originating from a given spawning ground arriving in a nursery ground.

2.3.9. Run specificities

The use of super-individuals (Scheffer et al. 1995) allows us to accommodate large numbers of eggs while keeping the number of particles released limited. The number of particles released is proportional to the egg density, as depicted in Fig. 1; the number per grid cell varies from 405 to 4320 each year and the total number of particles released annually is 1.9×10^6 , as described in Lacroix et al. (2013). Spawning covered the entire spawning ground and period. Particles were released on the bottom of the spawning ground (between 10 and 49 m depth) at midnight every day during the entire spawning period.

2.4. Sensitivity analyses

The sensitivity study focused on assessing the impact of biological parameters on recruitment and connectivity as well as estimating uncertainties associated with these outputs. It also aimed to point out

Table 1. Combination of vertical migration behaviour of the different life history stages of common sole. EGG: eggs; YSL: yolk-sac-larvae; FFL: first-feeding larvae; MTL: metamorphosing larvae

Migration of the different stages	EGG	YSL	FFL	MTL
Mig0	Passive drift	Passive drift	Passive drift	Passive drift
Mig1	Move upward	Move upward	Passive drift	Move downward
Mig2	Move upward	Move upward	Nycthemeral migration	Passive drift
Mig3	Move upward	Move upward	Nycthemeral migration	'Pressure-based' tidal migration
Mig4	Move upward	Move upward	Passive drift	Passive drift
Mig5	Move upward	Move upward	Passive drift	'Pressure-based' tidal migration
Mig6	Move upward	Move upward	Passive drift	'Current-based' tidal migration
Mig7	Move upward	Move upward	Nycthemeral migration	'Current-based' tidal migration

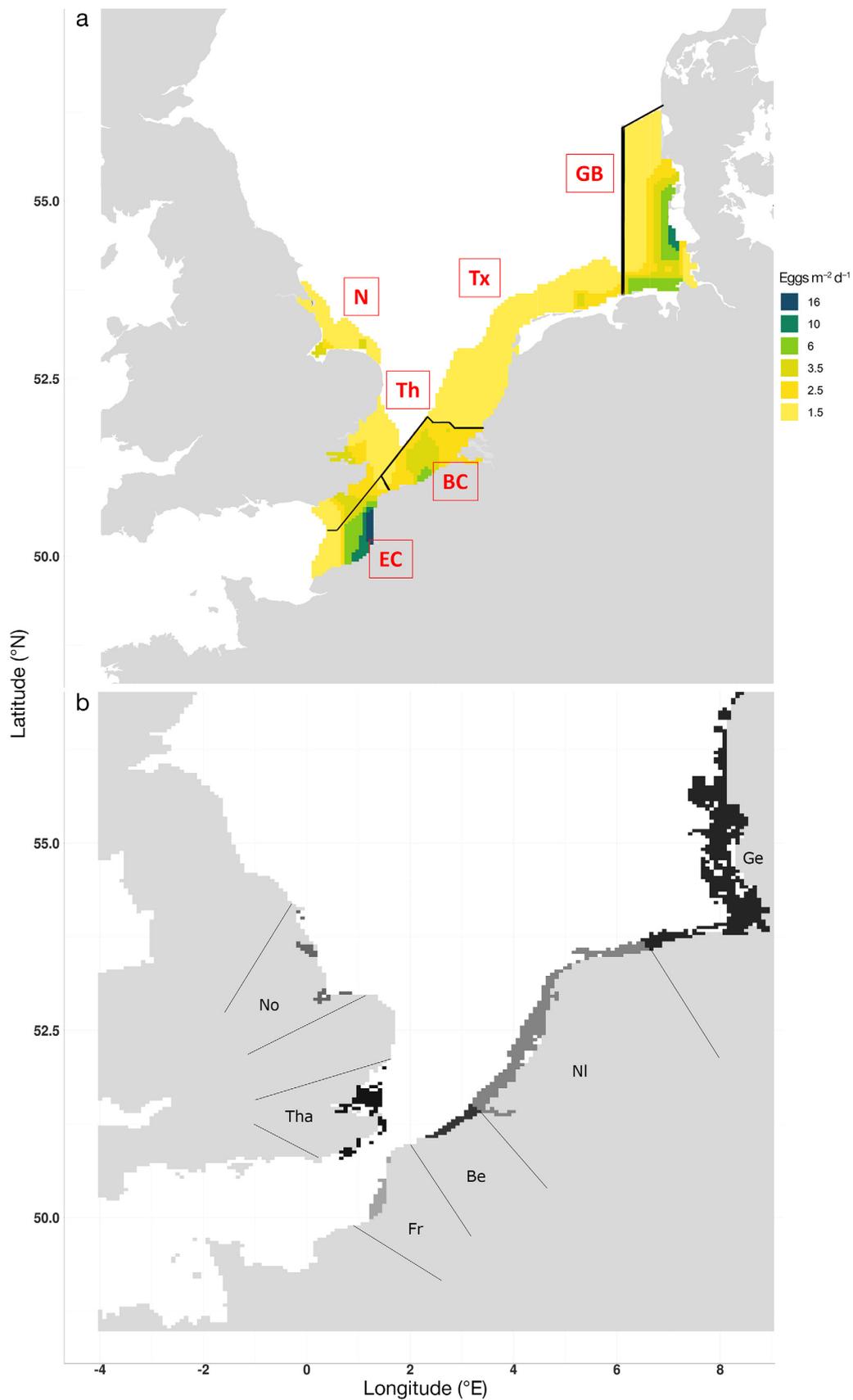


Fig. 1. Geographic implementation of the model. (a) Distribution of the main spawning grounds of common sole in the North Sea and the eastern English Channel (delineated by black lines), with contour plots of the mean daily egg production (redrawn from ICES-FishMap 2005). GB: Germain Bight; Tx: Texel; BC: Belgian coast; EC: French coast; Th: Thames River; N: Norfolk Banks. (b) The 6 nursery grounds of sole, defined as the coastal area with a depth of less than 20 m and soft sediment; levels of grey shading are used to distinguish them. Ge: Germany; NI: Netherlands; Be: Belgium; Fr: France; Tha: Thames estuary; No: Norfolk

priorities for calibration by identifying parameters that have the most impact on the output. The impact of the hydrodynamic model was assessed, while maintaining a reasonable computation time, by testing the impact of inter-annual variability in physical conditions on recruitment and connectivity. To assess the impact of biological parameters on model predictions (recruitment and connectivity), simulation designs are built, varying the parameter values, and then analysed using ANOVA to attribute the responsibility for the variance of the output variables to the parameters. Two sensitivity indices, based on variance decomposition (Saltelli et al. 2008), were computed. The first-order sensitivity index (SI) represents the contribution of a parameter to the variance of an output regardless of the interactions between parameters (main effect), whereas the total-effect sensitivity index (TSI) sums up the main effect of a parameter and all its contribution to the interaction effects. The sum of the sensitivity indices is equal to 1, with higher values indicating greater model sensitivity. SI and TSI were computed for local larval recruitment and the mean of SI and TSI were computed for each nursery to assess the impact of parameters on connectivity variability. The rank of the indices was used to determine the importance of the parameters. Details are available in Text S1 (in Supplement 1).

2.4.1. Step 1: Exploratory analyses

To explore the relative influence of biological parameters and inter-annual variability on model results, it was necessary to combine different years with alternative values for the biological parameters in the experiment. For feasibility reasons, it was impossible

to include all years, and only 4 years (representative of various environmental conditions) were combined with all alternative values of the biological parameters for the exploratory analyses (see details in Table 2). To explore model outputs and assess influential parameters within an acceptable computation time, a first approach using group screening (Dean & Lewis 2006) on a subset of biological parameters and years was chosen. In group screening, parameters are grouped and sensitivity is assessed. If a group is not influential, it is assumed that none of the parameters of the group is; if the group is influential, parameters in this group are usually studied separately in a second step. The 8 migratory behaviours, 3 PLDs and 3 mortality levels were selected and simulations were realised on 4 different years. Determining the years for a sensitivity analysis is a complex decision that requires a balance between feasibility and capturing variability from the exploration of the parameter space. We opted for the years 1995, 1997, 2003 and 2005, which show some differences in terms of spawning periods (Fig. S1) and present variations in recruitment and connectivity (Lacroix et al. 2013, Barbut et al. 2019). The full factorial design, representing 288 simulations ($8 \times 3 \times 3 \times 4$), was evaluated to assess the sensitivity indices (SI and TSI) and the range of variation of larval recruitment and connectivity.

2.4.2. Step 2: In-depth analyses

To determine which parameters have the strongest influence on model prediction, the sensitivity of all parameters was evaluated individually for the year 2003, which was chosen as a 'typical' mean year in

Table 2. Simulations carried out (parameters, years and experimental design chosen) for the different steps of the study. For each simulation, a total of 12 h of computation time is needed

Step	Parameter used (number of modalities)	Years	Experimental plan	Number of simulations
Step 1: exploratory analyses	Duration (3), mortality (3), migration (8), year (4)	1995, 1997, 2003, 2005	Group screening, full factorial design	72×4 yr = 288 runs
Step 2: in-depth analyses	Duration of each stage ($3 \times 3 \times 3 \times 3$), mortality of each stage ($3 \times 3 \times 3 \times 3$), spawning peak (3), migration (8), settlement delay (3)	2003	Optimised fractional design	353×1 yr = 353 runs
Step 3: calibration	Duration of egg and yolk-sac-larvae (3×3), mortality (3), spawning period (3), migration (3)	1995, 1996, 2000, 2001, 2002, 2003, 2004, 2005, 2006	Full factorial design	243×9 yr = 2187 runs

terms of winter temperature. For the parameters tested, duration ($3 \times 3 \times 3 \times 3$ modalities), mortality ($3 \times 3 \times 3 \times 3$ modalities), spawning peak (3 modalities), migration behaviour (8 modalities) and settlement delay (3 modalities), a full factorial design represents 472 392 combinations. An optimised factorial design of the second order was built with the Fedorov algorithm (Fedorov 1972) using the 'AlgDesign' library in R (v. 4.3.1) (Wheeler 2022) to maintain a reasonable computation time. This approach allows the computation of sensitivity indices on connectivity and recruitment for each parameter and first-order interaction based on only 353 simulations.

2.4.3. Step 3: Calibration

To determine the best parameterization, a calibration was conducted for each year on the most influential parameters identified in Step 2, namely duration of eggs (3 modalities) and yolk-sac larvae (3 modalities), mortality level (3 modalities), spawning period (3 modalities) and the 2 vertical migration behaviours for common sole in the North Sea (with nycthemeral then 'current-based' tidal migration [Mig5] and with solely 'current-based' tidal migration [Mig6]) as well as a passive behaviour (Mig0) to assess if including complex vertical migration process increases the model fit. A full factorial design (243 simulations for each year) was built and the recruitment predicted by the model in each nursery, as well as in the whole area, was compared with field observations.

The model-predicted recruitment was adjusted using SSB data on a yearly basis using stock evaluation data (ICES 2013) to account for the specific number of eggs produced each year. Recruitment was calculated by multiplying the total number of arrivals by the SSB values. For recruitment at the regional scale, we considered an estimation of sole recruitment at age 1 provided by scientific surveys in the whole North Sea from 1995 to 2006 (ICES 2013). For local recruitment in the nursery grounds, an estimation of juvenile density at age 0 for the east coast nurseries (Belgian, Dutch and German nurseries) is available for the period 1995–1996 and 2000–2006, and a relative recruitment rate based on fishing effort for the UK nurseries (ICES 2011) was considered from 1995 to 2006.

Given the diversity of local observations, to enable meaningful comparisons and to focus on trends rather than absolute values, both model predictions and observed data were normalized to obtain interannual variations (anomalies). This normalization process in-

involved dividing the recruitment values by the mean value calculated over the entire study period for each region (including Belgium, the Netherlands, Germany, the UK and the entire North Sea). Root mean square errors (RMSEs) were computed for each combination of parameters to evaluate model prediction accuracy locally ('RMSEloc' in French, Belgian, Dutch, German and UK nurseries) as well as at the scale of the whole North Sea ('RMSEtot') using the following equation:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}} \quad (1)$$

where P_i is the normalised recruitment predicted by the model for a specific year and nursery i , O_i is the normalised observed recruitment for the same year and nursery, and n is the total sample size. The best parameterization was estimated by minimising RMSEloc and RMSEtot. Calibration was conducted on the years 1995, 1996 and from 2000 to 2006, for which all data were available. A summary of the parameters tested, and the years considered for each step of the analysis is presented in Table 2.

3. RESULTS

3.1. Step 1: Exploratory analyses

Group screening of the Lagrangian transport model showed a high recruitment variance of common sole at the scale of the whole North Sea as well as at each nursery (Table 3). The standard variation was of the same order of magnitude as the mean. In the North Sea and on the local scale, sensitivity indices showed that the largest variance is due to PLD (rank 1 in all cases) and to a lesser extent to mortality (rank 2, except for the Be nursery, where year was the second most important parameter due to the limited size of the nursery, making the indicator particularly sensi-

Table 3. Mean settlement (number of larvae of common sole in million arriving in the nursery ground) and standard deviation (SD) predicted by the model for the different parameterizations over the years 1995, 1997, 2003 and 2005. Abbreviations as in Fig. 1

Area	Mean	SD
Total	36800	34600
Fr	1960	2610
Be	893	1290
Nl	3100	4700
Ge	25900	27000
No	747	947
Tha	1910	2410

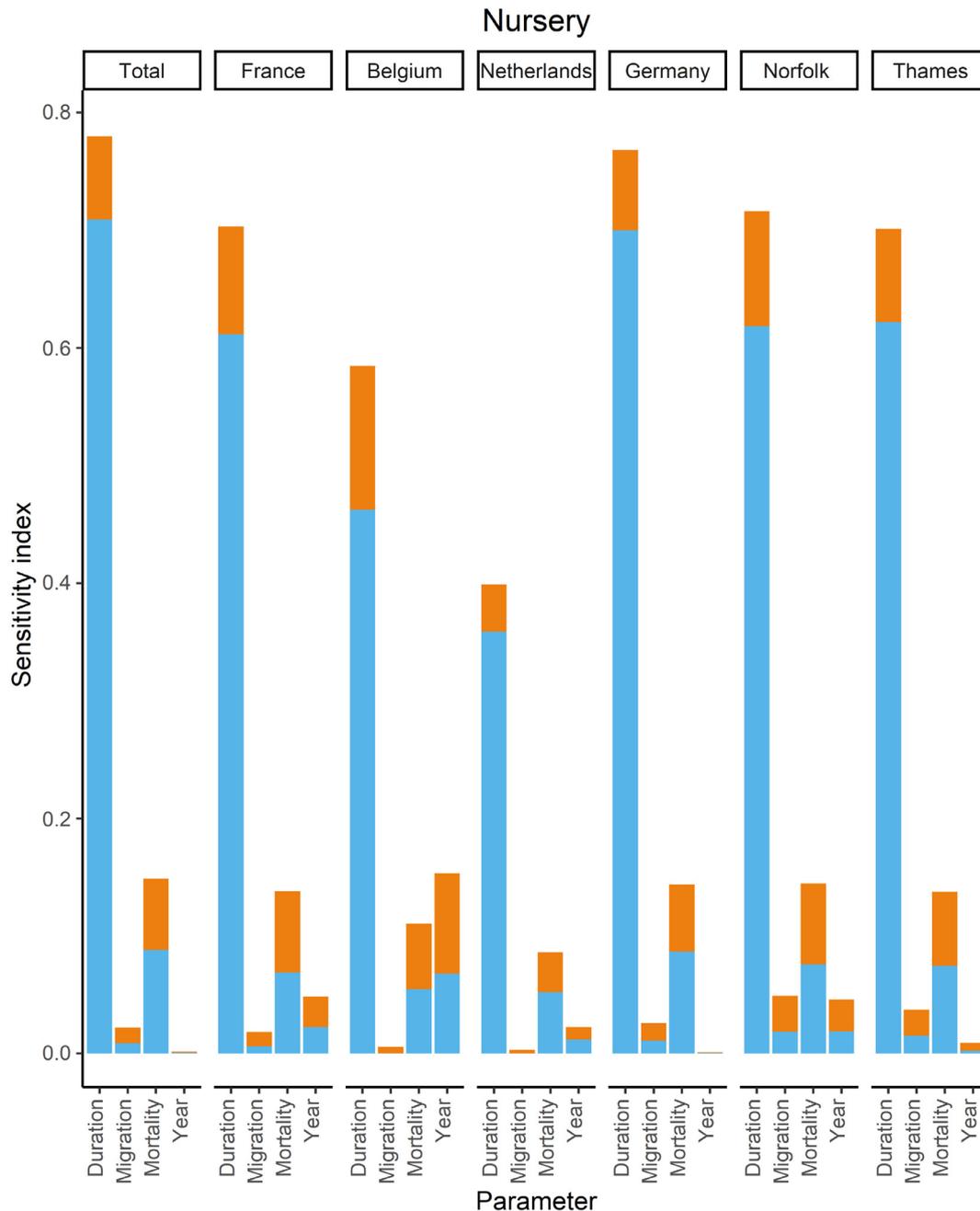


Fig. 2. Sensitivity indices for the recruitment of larval common sole in the North Sea and each nursery ground for the years 1995, 1997, 2003 and 2005 considering the different parameterizations presented in Step 1. Blue: first-order sensitivity index; orange: total-effect sensitivity index

tive to minor arrival variations and thereby resulting in recruits arriving at the Fr or Nl nursery) (Fig. 2 and details in Table S2). Whatever the scale (local or regional), vertical migration type and year were less important in recruitment variability than the other factors (except for the Be nursery, where year was ranked second). Local differences with a larger importance of the year effect appeared in the Be nursery ground, more so than elsewhere. Migration type had

a larger effect in the nursery grounds of No and Tha estuary than elsewhere. Overall, the parameterization is more influential than the year-to-year variability in the case of recruitment. The full design allows an assessment of all interactions among parameters; we interpret the first-order ones. Duration is an important parameter; hence, interactions with this parameter are the most important, especially the interaction between duration and mortality because

mortality is applied during the whole PLD. Secondly, the interaction between duration and migration behaviour (see details in Table S2). Interactions represent about half of the parameter effects after duration of the pelagic phase. Thus, the intensity of the effect

of one parameter is conditioned by the values of the other parameters.

Unlike larval recruitment, connectivity showed a relatively stable pattern at the North Sea scale regardless of parameterization (Fig. 3). In general, the more con-

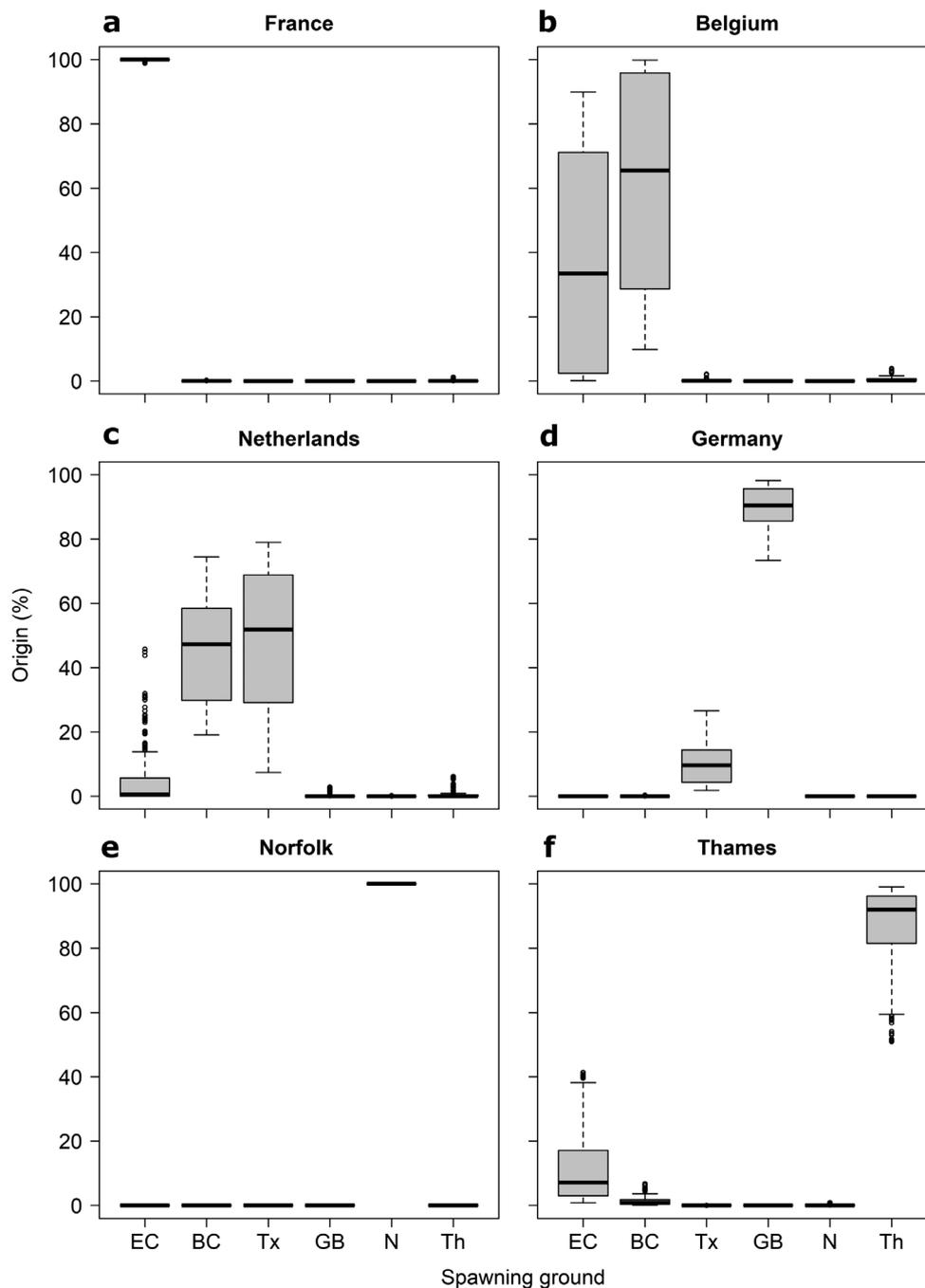


Fig. 3. Range of variation in the origin of common sole larvae in the nurseries of (a) France, (b) Belgium, (c) Netherlands, (d) Germany, (e) Norfolk and (f) Thames from the 6 spawning grounds off the French coast (EC), Belgian coast (BC), Texel (Tx), the inner German Bight (GB), mouth of the Thames River (Th) and the Norfolk Banks (N), for the years 1995, 1997, 2003 and 2005 considering the different parameterizations presented in Step 1. Upper and lower limits of box plots represent the 75th and 25th percentiles (IQR: interquartile range). Horizontal line within the box represents the median. Vertical bars at the ends of the lines outside the boxes indicate the range of data until $\pm 1.5 \times \text{IQR}$; black circles: values outside the $\pm 1.5 \times \text{IQR}$ boundaries

nected the nursery ground, the less robust the parameterization. There was no recruitment variation in the No and Fr nurseries, where respectively 100 and 97% of the recruitment was local, independent of the year or biological parameterization. Larvae mainly originated from local spawning grounds in the Ge and Tha nursery grounds (90 and 87% respectively on average) and to a lesser extent from a remote spawning ground (10% from Tx and 13% from EC respectively). For both nursery grounds, the variability due to biological parameterization and year-to-year variability was low (± 10 –20%). Only the Be and NI nursery grounds presented a strong variability in the origin of settlers depending on parameter values. In both cases, larvae originated both from local and the closest upstream spawning grounds and, to a lesser extent, from elsewhere. Larvae arriving in the Be nursery ground come from EC and BC; those arriving in the NI nursery ground originate from BC, Tx and, to a much lesser extent, from EC.

Group screening analyses (mean in Fig. 4 and details for each nursery and spawning ground in Fig. S3 and Table S3) related to connectivity showed that the most important factor in all nurseries was year, with exception of the Ge nursery for which it was the second most influential parameter. The duration of the pelagic phase is the second most influential parameter in the Fr, Be and NI nursery grounds, whereas vertical migration is the second most influential parameter for the Tha nursery and the first for the Ge nursery. Mortality had a negligible impact on connectivity. The absence of an indicator for the No nursery ground is attributed to the one link with the Norfolk spawning ground, regardless of the biological parameterization or year. Overall, biological parameters related to connectivity are less influential than interannual variability.

3.2. Step 2: In-depth analyses

Comprehensive sensitivity analyses on the recruitment of common sole (Fig. 5 and detailed in Table S4) allow us to identify influential parameters in much greater depth than in group screening, especially for the impact of parameters related to PLD or mortality during the various larval stages. In-depth analyses showed that the model was particularly sensitive to PLD, especially during the first developmental stages. Egg phase duration was the most influential parameter (rank 1 in each nursery), whereas duration of yolk-sac-larvae was the second (in Fr, Be and NI nursery grounds) or third most important parameter (total recruitment and in Ge, No and Tha nursery

grounds). Regardless of which nursery, the influence of the duration of the first feeding larvae was less than that of the 2 first stages; the duration of the metamorphosing larvae had an even lower influence. The date of peak spawning was also one of the most influential parameters, the second most for total recruitment in the Tha, No and Ge nursery grounds, the third in the NI nursery and the fourth in the Fe and Be nursery grounds. Settlement delay and vertical migration had a limited impact and, to a lesser extent, mortality of the various stages.

Sensitivity indices of connectivity showed lower values than recruitment; most TSI values were less than 0.1 (Fig. 6; details for each nursery and spawning ground are available in Fig. S4 and Table S5). The outcome shows that the responsibility of variation is more shared across parameters. Spawning period and vertical migration were the most important parameters for the Fe and Tha nursery grounds. In the case of connectivity, the settlement delay had a considerable importance in the Tha and Ge nursery grounds (TSI have rank 2 and 1 respectively). Duration of larval stages had a more limited impact than recruitment. Even when main effects of parameters are low, they appear to be heavily involved in interactions and often contribute more than half of the effect.

3.3. Step 3: Calibration

The calibration step of the Lagrangian transport model of common sole focussed on the most sensitive parameters. Fig. 7 shows the performance of 243 parameterizations as synthesised by the local (RMSEloc) and total (RMSEtot) indicators (details are available in Table S6). Low values indicate the best fit between model predictions and data. The baseline for spawning period performed better than an early or late spawning. The simulations in which nycthemeral and tidal migrations were associated performed better than simulations including the other migration types, both locally and in total. The model considering passive migration presented the worst performance. Overall and in addition to these 2 parameters, the most performant scenarios were the ones which associated a low mortality with long larval duration of eggs and yolk-sac-larvae. However, the choice of the best model is less clear for those last 3 parameters, and the performance of this model is represented in Fig. S5. Surprisingly, the quality of model fit was mainly influenced by parameters (spawning peak and migration) that had lower impact on recruitment and connectivity.

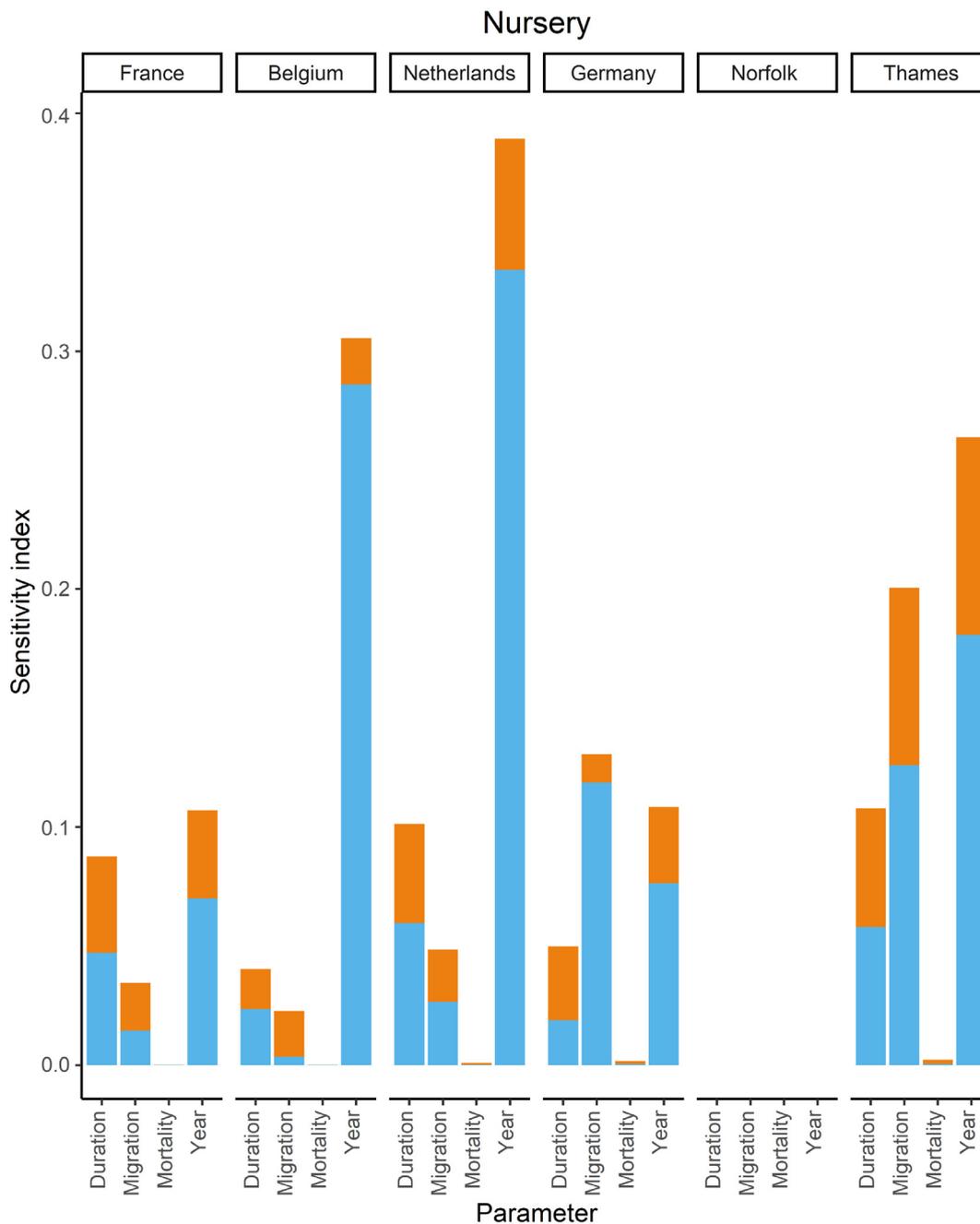


Fig. 4. Mean of sensitivity indices computed by nursery for connectivity in each nursery based on parameters tested in Step 1. Blue: first-order sensitivity index; orange: total-effect sensitivity index. A zero value in Norfolk is attributed to the absence of variation

4. DISCUSSION

Although biophysical models have been regularly used to identify the major factors impacting recruitment variability, sensitivity analyses considering several parameters are rare (Peck & Hufnagl 2012, Silve et al. 2023). Our study evaluated the impact of biological parameterization on model predictions of larval recruitment and connectivity of common

sole and compared it with the impact of interannual variation.

4.1. Impact of biological parameterization and year-to-year variability

A thorough sensitivity analysis is crucial to evaluate how parameter variation affects model predictions

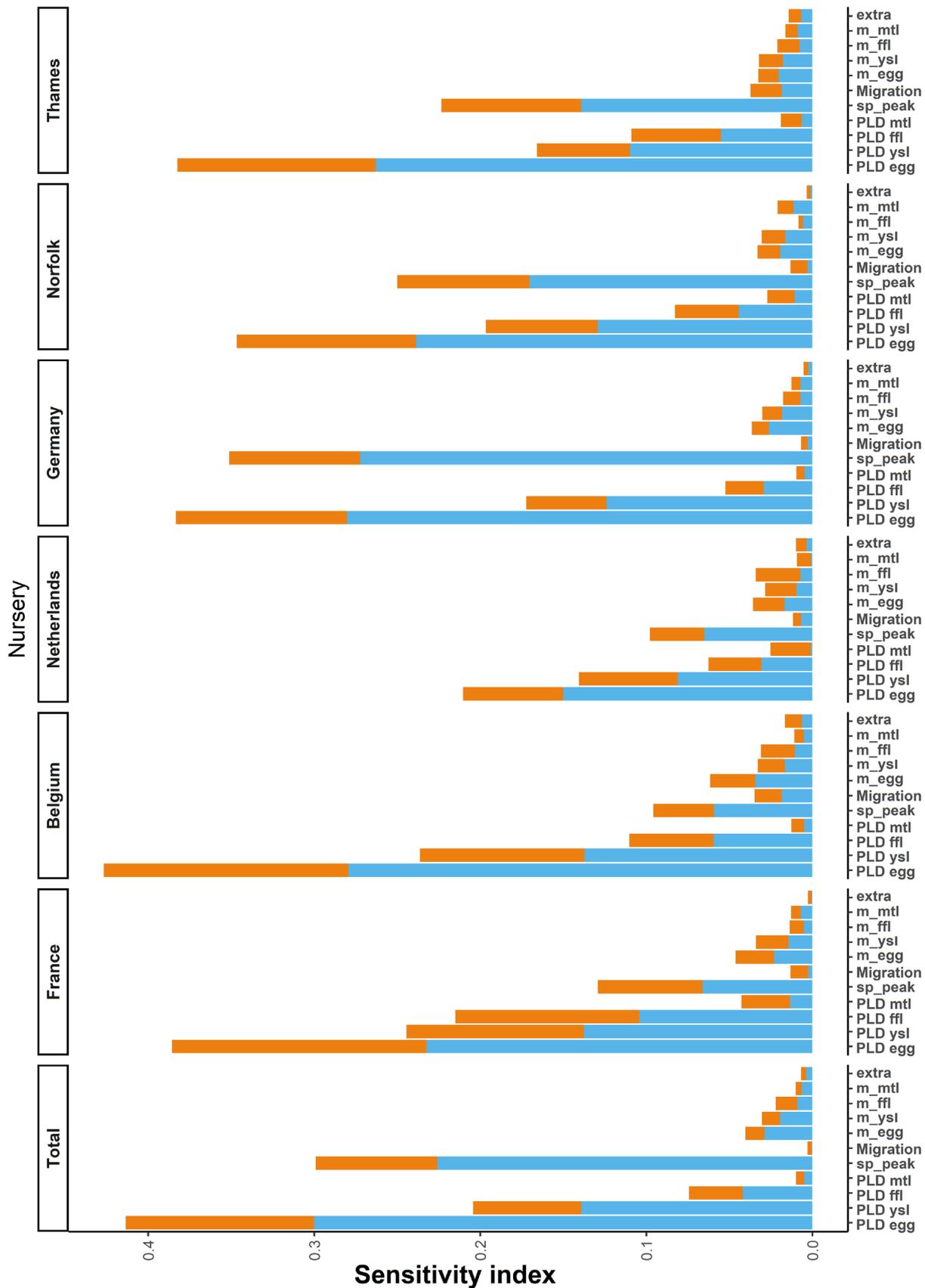


Fig. 5. Sensitivity indices of the recruitment of larval common sole for the biological parameters for the whole North Sea ('Total') and the 6 nursery grounds. PLD egg: duration of egg phase; PLD ysl: duration of yolk-sac larvae; PLD ffl: duration of first-feeding larvae; PLD mtl: duration of metamorphosis larvae; sp_peak: spawning peak date. Migration: vertical migration type. 'm_egg': mortality of the different stages ('m_egg', 'm_ysi', 'm_ffl' and 'm_mtl'). Extra: settlement delay. Blue: first-order sensitivity index; orange: total-effect sensitivity index

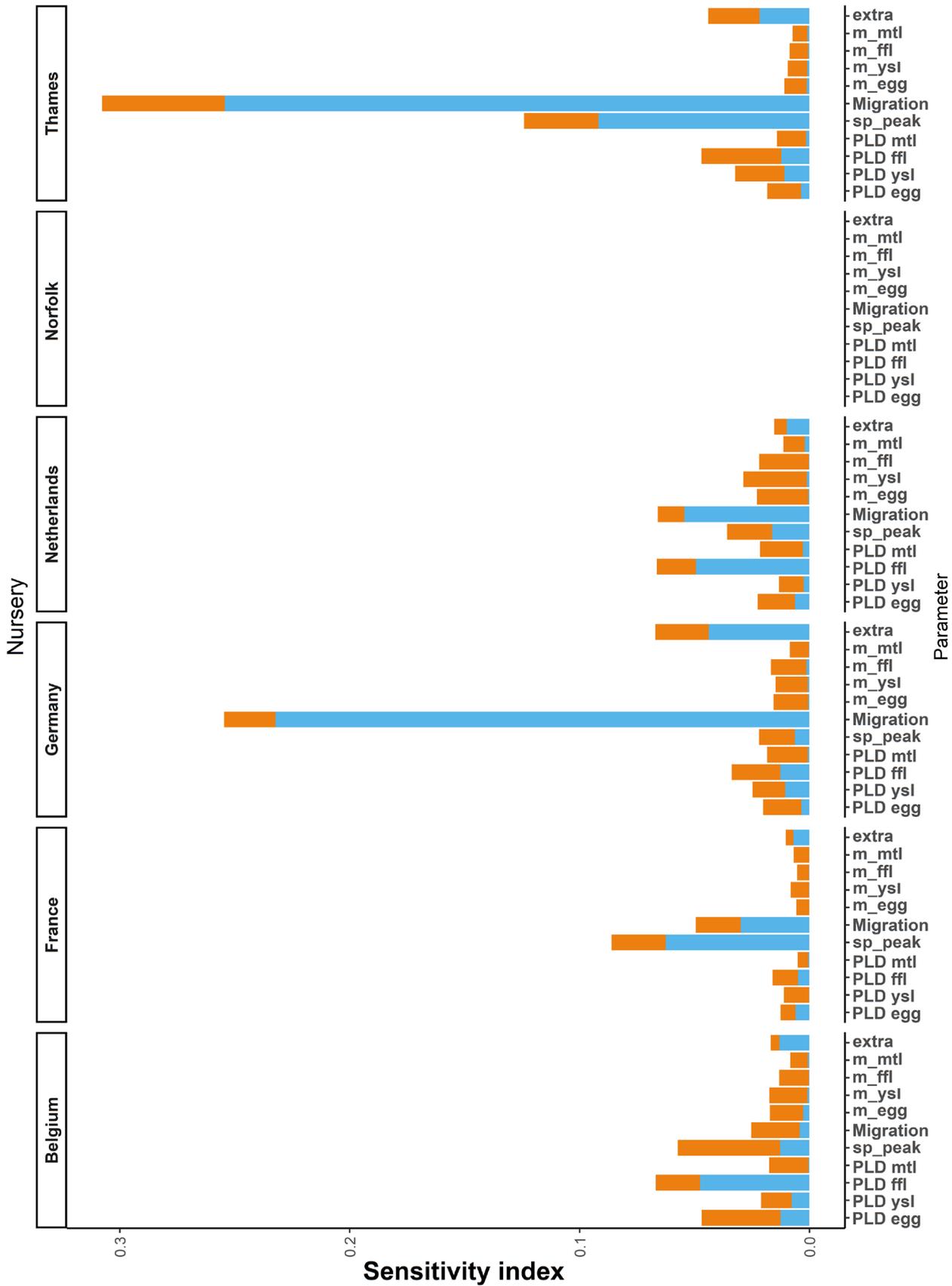


Fig. 6. Mean of sensitivity indices computed by nursery on connectivity for the biological parameters for the 6 nursery grounds. See Fig. 5 for definitions. A zero value in Norfolk is attributed to the absence of variation

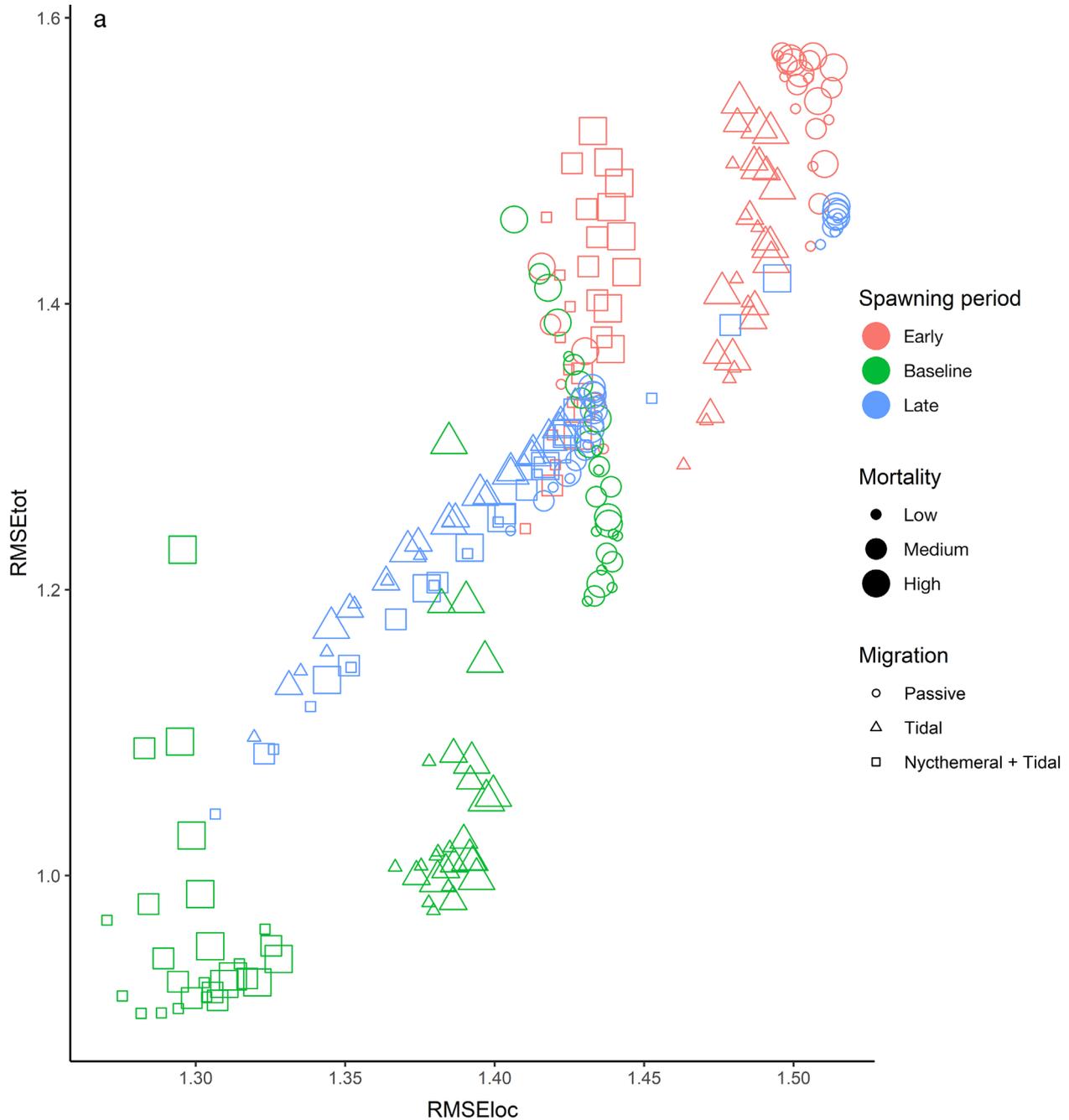


Fig. 7 continued on next page

Fig. 7. Fitting performances of the 243 parameterizations tested (Step 3) on the local recruitment of larval common sole (local root mean square error [RMSEloc]) (for the UK, Be, NI and Ge nurseries; see Fig. 1) and for the whole North Sea (RMSEtot). Lower values indicate higher model performance. (a) Performance for mortality, spawning peak and vertical migration type; (b) performance for larval duration (PLD) of egg stage (egg and yolk-sac larvae [ysl] stage)

compared to interannual variability in dispersal. Annual changes in North Sea hydrodynamics, influenced by factors like NAO, wind and temperature fluctuations (Bolle et al. 2009, Berglund et al. 2012, Kvile et al. 2018), lead to high recruitment variability in flatfish species, including common sole (Beverton

& Iles 1992, Gibson 1997, van der Veer et al. 2000, Gibson et al. 2015), possibly linked to climate variation (Le Pape et al. 2003, Henderson & Seaby 2005). The variability attributed to the biological parameterization is higher than the annual variation in hydrodynamics and highlights the need for a careful model

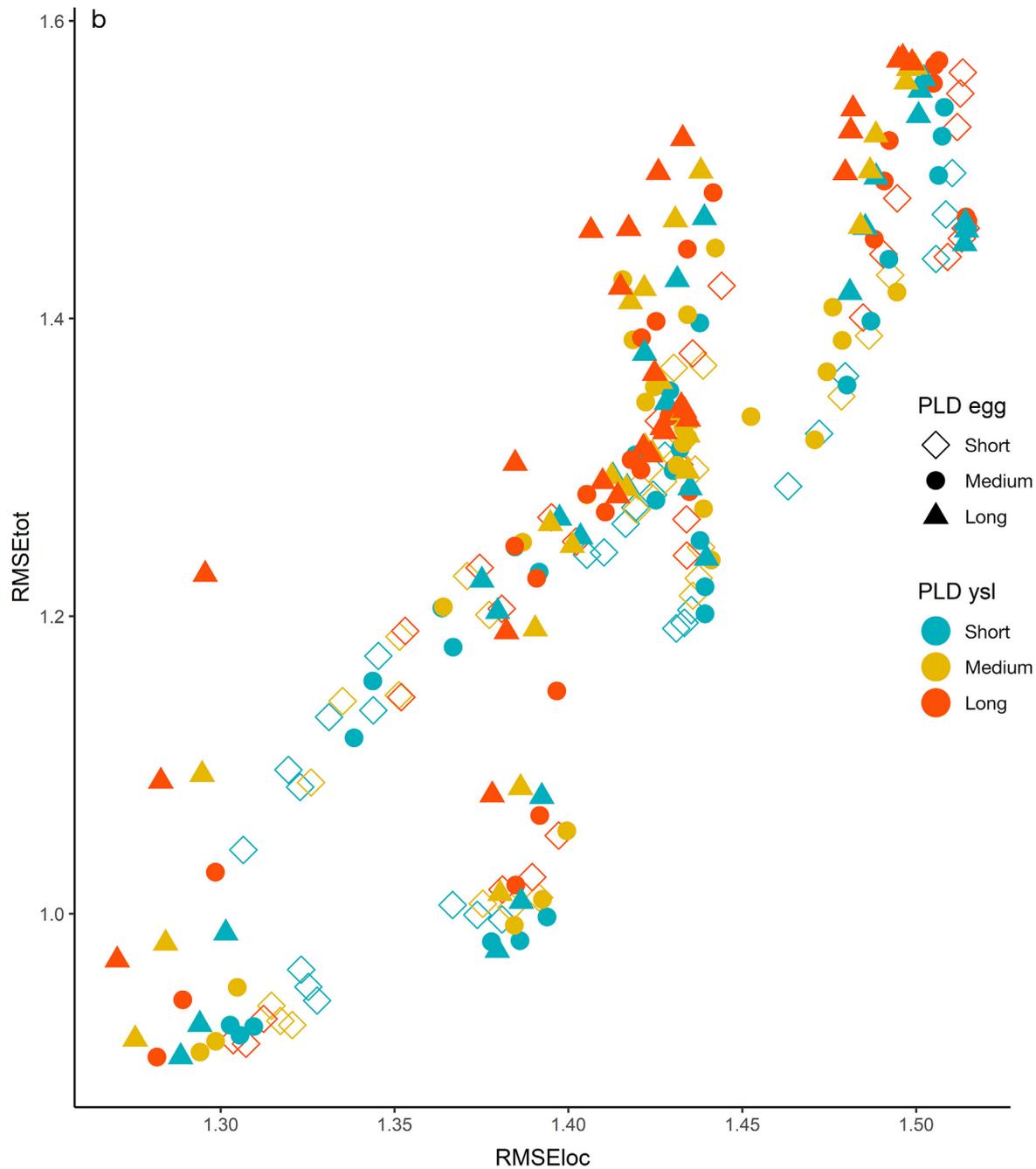


Fig. 7. (continued)

calibration to properly assess larval recruitment. As shown by the group screening approach, sensitivity analyses of connectivity highlight that year is the most influential parameter in model prediction. This observation might be influenced by the selection of years in our exploratory analyses. Further investigation, especially over an extended period and more contrasted years as well as by considering rapidly changing hydrodynamic conditions such as tempera-

ture shifts in the North Sea (Hughes et al. 2017) is warranted, as these factors are likely to impact larval transport. The connectivity pattern at the North Sea scale is quite stable regarding biological parameterization used in the model; the main sources of variation are limited to the local spawning ground and adjacent regions. This is, for example, the case in Germany, where the proportion of arrivals from Tx and GB varies as a function of the parameterization.

Larger ranges of variation are predicted in the case of Be and Nl. Variation might be attributed to the relatively small size of the nursery grounds and variation in settlement success. Overall, results show limited variation, mainly confined to adjacent nurseries and spawning grounds.

Uncertainties in the biological parameters mainly affect recruitment, while connectivity is more robust to parameter variation. This means that using the model to estimate connectivity, a common output of larval transport models (e.g. Miller 2007), requires less of a focus on the parameterization of biological traits and access to proper environmental conditions such as hydrodynamics and temperature. Using the model to predict recruitment would require thorough calibration. This is an encouraging result for common sole because relatively few data are available on connectivity (Burt & Millner 2008, Diopere et al. 2018), although recruitment surveys are organised on a regular basis (ICES 2023). This is of course not the case for all commercially exploited species and for all fish stocks.

While drift models might exhibit reduced accuracy in forecasting larval recruitment, they demonstrate enhanced efficacy in predicting population structure, thereby serving as a surrogate for connectivity (e.g. Legrand et al. 2022). Our assessment focuses on the percentage of exchange between spawning grounds and nurseries while considering national boundaries. While results tend to be more stable and consistent at larger scales, they may vary and become less stable when applied to smaller-scale scenarios such as offshore wind farms.

4.2. Influence of parameters on model output

Once the relative impact of interannual variability in comparison to biological parameters is analysed, classifying the importance of model parameters in the prediction process is an important goal. The duration of the larval stage is the most important parameter for recruitment, followed by the date of spawning peak and mortality. The period during which the eggs are suspended in the ocean is particularly crucial, and its importance diminishes for later development stages. Similarly, egg mortality has a greater influence than the mortality of metamorphosing larvae due to a higher and temperature-dependent mortality rate. This ranking corresponds to the empirical knowledge of the larval stage, with high importance attributed to the early life stages and a decreasing correlation between size and mortality (Houde 2008). The par-

ameters of PLD and mortality are related to temperature and hence to the date of the spawning peak (Greve et al. 2001, Rijnsdorp & Witthames 2007). The high level of interactions in the model illustrates the high correlation among parameters and the necessity of a joined exploration of the parameter space rather than an analysis of one parameter at a time.

Other parameters such as settlement delay or migration behaviour have less influence on output. A previous study showed the importance of settling delay to increase recruitment, decrease interannual variability and improve the correlation with recruitment (Lacroix et al. 2013). Here, this parameter was not considered in the calibration process because of its relatively lower importance in comparison to other parameters. Settling delay may influence drift duration. As various PLDs were tested here, it might explain the lower importance of this parameter. Similarly, in other modelling studies (Rochette et al. 2012, Savina et al. 2016), larvae are allowed to settle before metamorphosis as soon as they reach a suitable nursery area. Cues to set off larval settlement, which include sediment composition, trophodynamics, underwater sound and benthic chemical ecology (Gibson & Robb 2000, Dixson & Hay 2012, Dixson et al. 2014) hold the potential to improve model quality.

Differences in connectivity results are noticeable when considering the importance of the spawning peak as a parameter, with migration behaviour being highly influential and mortality and PLD holding less significance. Early or late spawning peaks alter larval hydrodynamic conditions and consequently affect dispersal patterns, consistent with findings in marine invertebrates (Ayata et al. 2010).

Vertical migration has been reported to influence dispersal (e.g. Fox et al. 2006, North et al. 2008). The inclusion of vertical behaviour in a biophysical model considerably affected both the mean distance and direction of larval dispersal, especially there where tides are important (Sundelöf & Jonsson 2012). In our study, this is especially the case in the Th estuary and GB.

The lower influence of PLD on the dispersal pattern is typical for species with a long pelagic phase such as common sole (Monroy et al. 2017).

Given the predominance of biological parameter effects compared to year effects (based on the 4 years tested) and the consistency between the results of the first and second step, the sensitivity results regarding recruitment would be similar if another year was investigated regardless of the importance of interactions between yearly effects and parameterization (details can be found in Fig. S4). On the contrary, con-

nectivity is highly influenced by yearly variations and sensitivity results are likely to be different if another year were selected.

4.3. Identification of the most optimal parameterization

Larval transport models are complex; they rely on many assumptions and might serve several purposes such as connectivity of early life stage, estimation of recruitment and its spatialisation, and timing of arrival in nurseries. The models imply interactions with strongly connected parameters, making calibration difficult because of confounding effects. The possibility that unique combinations do not achieve the same fit for different model outputs highlights the importance of having sufficient observation data and several criteria to sort out equally good parameterizations. The purpose of the sensitivity analysis was to help select the most influential parameters in order to properly calibrate the model. However, calibration was conducted on elements not directly addressed by the sensitivity analysis. Sensitivity analysis focussed on recruitment values. Calibration aimed to address the disparity between simulated recruitment and normalized observations over the considered period. This approach was due to computational constraints involving the construction of sensitivity indices over a reduced number of years. This might explain why the quality of model fit was mainly influenced by parameters (spawning peak and migration) that had a lower impact on recruitment and connectivity.

It is an important lesson that the sensitivity of the RMSE can be quite different than the sensitivity of the corresponding output. Therefore, sensitivity analysis should also be computed when it supports the selection of calibration parameters. The smaller variation in RMSE for each parameterization compared to the mean RMSE suggests the potential for adding significant parameters to enhance predictions. Notably, the distribution of sole in the North Sea has shifted in the past decade, a factor not yet considered (Engelhard et al. 2011), which makes exploring egg distribution a promising focus for future studies.

The parameterization that reproduces the best recruitment dynamics at the regional scale of the southern North Sea, as well as the local dynamics and particle distributions in the nursery grounds, does not necessarily reflect the true biological mechanisms involved. It is conditional on the rest of the model assumptions, the choice and quality of observation data and the way the parameter space was explored.

However, one might provide leads for model selection and offer the opportunity to direct biological research and improve parameter knowledge.

Calibration allows determination of the most efficient parameterization to reproduce recruitment dynamics. The performance of the model considering the 'baseline' parameterization for the spawning peak is clearly better than alternative hypotheses that consider late or early spawning, with the latter being the worst case. In the baseline scenario, the spawning period is based on a 10°C hypothesis for peak spawning in each spawning ground; early and late scenarios consider a shift in the timing from the baseline. In the future, it might be interesting to also test alternative hypotheses such as changing temperatures or to test a specific parameterization for each spawning ground. Therefore, the calibration results most likely indicate that the most frequent conditions are like the baseline.

Migration type presents an interesting pattern. In an environment forced by tides, where selective tidal transport may be important for flatfish such as sole (Duffy-Anderson et al. 2015), it is not surprising that the model showed a higher performance with tidal than with passive migration. The model showed improved performance due to nycthemeral migration compared to passive larval behaviour. This raises intriguing possibilities for further exploration, especially during *in situ* studies. While nycthemeral migration has been observed in common sole within the Bay of Biscay (Koutsikopoulos et al. 1991), such behaviour remains undocumented in the North Sea. The high turbidity of the North Sea (Fettweis & Van den Eynde 2003) results in limited differences in illumination during day and night, potentially affecting migration cues. In a well-mixed region like the North Sea, it is hypothesized that this behaviour might not significantly influence dispersal patterns. If larvae do exhibit this behaviour, it could also be due to reasons not accounted for in the model. The central part of the North Sea is stratified in summer (Otto et al. 1990), which may affect flatfish connectivity (Vandamme 2014, Barbut et al. 2019). The combination of a stratified water column and nycthemeral vertical migration might explain the better performance of the parameterization. In this study, migration speed was not considered, which likewise should impact model prediction (Weinstock et al. 2018).

Calibration showed fewer clear results regarding the mortality and duration of the larval stage. Best estimates of mortality suggested that low mortality improves model accuracy, but the result is less clear than for migration and spawning peak. Mortality is a

complex process which varies in space and time. In the present study, only abiotic conditions (current and temperature) were considered, neglecting other sources such as starvation, infection or predation (Peck & Hufnagl 2012).

The same conclusion of the lack of a clear impact on the results can be drawn for PLD. In the best model estimation, in the case of a long duration for eggs and yolk-sac-larvae, there is no clear pattern that performs better locally and at the scale of the southern North Sea. In the model, temperature is the only parameter directly influencing PLD, but variation in space and time linked to food availability should also be investigated (Raventos et al. 2021).

PLD and mortality might also be related to environmental conditions such as hydrodynamics, turbulence, infection and the match–mismatch between larvae and their food (Houde 2008, Peck & Hufnagl 2012). Several modelling studies have implemented more complex processes in larval dispersal models such as the prey field and spatial mortality (Fiksen & MacKenzie 2002, Huret et al. 2012, Pitois & Armstrong 2014). Testing such types of complex models with the same methodology can determine if an increasing level of complexity increases model performance.

An alternative approach might consist of using other data sources to improve model parameterization. Information such as otoliths, biological field data and arrival dates in the nurseries have been used successfully to evaluate a Lagrangian dispersal model (Paoletti et al. 2021). This type of approach was also used, for example, to assess body growth, movement and mortality of European eels based on larval information (Melià et al. 2013). Other sources of uncertainties such as model resolution or the choice of the hydrodynamic model (Hufnagl et al. 2017, Kvile et al. 2018) were not evaluated here and merit further investigation.

4.4. Lessons learned

Sensitivity analysis helps to determine the impact of parameters relative to the phenomenon studied, which, in this case, is interannual variability. Unlike connectivity, the impact of biological parameters is higher than the impact of year-to-year variability on the larval recruitment of common sole. This is encouraging because data on connectivity are limited in contrast to recruitment, for which survey data are available on exploited species. In addition, sensitivity analysis helps to focus calibration on a few influential parameters, which, in this study, reduces the simula-

tion design to 243 simulations instead of the hundreds of thousands needed to test all possible combinations. This approach allows us to optimise calibration on the most influential parameter identified, especially when data are scarce and calibration complex such as is the case for ichthyoplankton. The weight of interaction on the sensitivity index highlighted the importance of using global sensitivity analysis and not only elasticity by testing factors individually.

Our study shows that sensitivity analysis of a recruitment model is possible if efficient statistical methods (group screening, optimal designs) are combined with inventive investigation strategies. This leads to a better biological understanding of processes and in-depth comprehension of model behaviour under alternative parameterizations. We encourage modellers to carry out such analyses.

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