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State-space modeling of multi-decadal mark-recapture data reveals low adult dispersal in a nursery-dependent fish metapopulation

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Abstract :

Quantifying connectivity within fish metapopulations is an important component in understanding population dynamics and providing an evidence base for assessment and management. We investigate meta-population connectivity of the common sole (Solea solea L.) in the Eastern English Channel (EEC). The EEC common sole stock is currently assessed as a single and spatially homogeneous population but connectivity induced through adult movements within this stock and with nearby stocks remains unknown. To fill this knowledge gap, we developed a state-space mark-recovery model, designed to estimate adult connectivity, using mark-recapture data from multiple release experiments from 1970 to 2018 across the EEC and adjacent management areas. The model estimates seasonal fish movements between five pre-defined areas, Western English Channel, Eastern English Channel (split into three discrete sub-areas) and North Sea. Over 32000 fish were tagged, 4036 of which were recovered via fisheries. Our results suggest minimal large-scale adult movements between these areas: movements among spatial units within the EEC were very low with even lower levels of immigration from areas adjoining the EEC. Our results support the hypothesis of segregated populations within the EEC. The importance of accommodating population substructure in the fisheries management is considered.

Keywords : Population structure, capture-mark-recovery, adult connectivity, multi-event modeling, Solea solea L., Eastern English Channel

1 INTRODUCTION

Movements of individuals determine connectivity between habitats, control meta-population dynamics (Hanski 1998; Benhamou 2014) and resilience of populations to natural and anthropic stressors. Understanding the movement and dispersal patterns of wild animals at every stage in their life cycle is therefore critical for a full understanding of population dynamics and the subsequent provision of an evidence base for population assessment and management.

In fisheries, an accurate definition of the spatial structure of fish populations is necessary for fish stock assessment and for setting appropriate fisheries management strategies (Kutkuhn 1981; Smith *et al.* 1990; Begg & Waldman 1999; Fogarty & Botsford 2007). A misspecification of the spatial limits of a stock can lead to biased estimates of population vital rates (Cadrin *et al.* 2014; Kerr *et al.* 2017). Dispersal process must be addressed at all life-history stages to accurately assess the spatial and temporal delineation of populations and to accurately specify spatial management measures that could potentially target specific areas and life stages (e.g. protecting nursery areas and spawning aggregations, Fogarty and Botsford 2007).

Recent studies have employed a wide variety of tools and methods to assess connectivity within populations (Le Bris *et al.* 2017; Rogers *et al.* 2017; Moreira *et al.* 2018). Genetic studies using genetic markers such as microsatellites (Cuveliers *et al.* 2012; Jasonowicz *et al.* 2016; Martinez *et al.* 2017) or single nucleotide polymorphism (Milano *et al.* 2014; Laconcha *et al.* 2015; Bekkevold *et al.* 2015) are often used to assess the spatial structure of a population and reproductive isolation within populations

(Östman *et al.* 2017; Marandel *et al.* 2017). Otoliths are also extensively used in connectivity studies, either through otolith morphology (Bacha *et al.* 2016; Hüssy *et al.* 2016; Mahe *et al.* 2016) or otolith chemistry (Tanner *et al.* 2016; Callicó Fortunato *et al.* 2017; Régnier *et al.* 2017; Moreira *et al.* 2018). Morphometry and meristics (Allaya *et al.* 2016; Sley *et al.* 2016), parasites (Catalano *et al.* 2014; MacKenzie & Abaunza 2014) and life history traits (Begg *et al.* 1999; Erlandsson *et al.* 2017; Du Pontavice *et al.* 2018; Randon *et al.* 2018) have also been used to assess stock structure. In the past decade, stock delineation studies have resulted in revised stock boundaries for numerous stocks (e.g. blue whiting Mahe *et al.* 2007, Atlantic cod Zemeckis *et al.* 2014, and horse mackerel Abaunza *et al.* 2008).

Although the information derived from mark-recapture experiments is limited (e.g. they cannot be used to quantify gene flow, Cadrin *et al.* 2014), they have nevertheless proven useful for the investigation of fish movements and the spatial structure of populations (Howe & Coates 1975; Hilborn 1990; Gillanders *et al.* 2001; Patterson III *et al.* 2001; McGarvey & Feenstra 2002; Adlerstein *et al.* 2008; Cadrin *et al.* 2014; Hanselman *et al.* 2014; Le Bris *et al.* 2017; Liljestrand *et al.* 2019). When considering commercial fish stocks, tagging data generally consist of mark-release experiments conducted on scientific surveys, with tag-recovery facilitated via the fisheries, the latter largely dependent on volunteer reporting by the harvesters. A weakness of such data is that the detection probability is usually unknown, and non-reporting can be substantial (Henny & Burnham 1976; Frusher *et al.* 2001; Pollock *et al.* 2002; Cadigan & Brattey 2003, 2006). However, ancillary information is often available (McGarvey & Feenstra 2002). Catch and fishing-effort data are collected for most exploited stocks. Classical stock assessment models (e.g. Virtual Population Analysis or Statistical Catch-at-Age

Analysis) typically provide estimates of total and fishing mortality, and thereby total abundance. Such information can be used as input in the analysis of tagging data of harvested fish populations (McGarvey & Feenstra 2002).

The common sole (*Solea solea*, L.) is a flatfish substantively harvested in the Western English Channel to the North Sea (ICES 2017). Today, stock assessment is conducted separately for three ICES stock divisions (VIIe, VIId, IV; ICES 2017). The Eastern English Channel (EEC, ICES division VIId) stock, managed as one homogeneous population, has been overexploited over the last ten years (ICES 2017). Dispersal of the subadult components has been described: the larvae drift passively over short distances to local coastal nurseries (Rochette 2011), where the juveniles remain prior to migration offshore at maturity (Riou *et al.* 2001), where the fish reproduce and enter the fishery. Observed contrast in key life history traits (density-at-age and length-at-age data) have suggested potential spatial structuring within the adult component of the EEC common sole stock within three discrete spatial areas (Du Pontavice *et al.* 2018; Randon *et al.* 2018). However, the movements of adult sole between these areas remain largely unknown. Here we have drawn on an extensive mark-recapture database collected over 49 years to analyze fish movements and assess connectivity of the adult common sole population within the EEC and adjacent management areas. We tested the hypothesis of metapopulation structure within the EEC and estimated the level of mixing between sub-populations. For that purpose, we developped a capture-recapture model (Royle *et al.* 2013; McCrea & Morgan 2014) built in a state-space model framework (recently reviewed in Aeberhard *et al.* 2018 in the context of fisheries) to estimate adult and subadult movement probabilities. Finally, based on our observations, we consider the implications for management of the common sole stock in the EEC (and more widely) of

105 acknowledging and incorporating population substructure in management and
106 assessment.

107 2 MATERIALS AND METHODS

108 2.1 Spatial structure

109 The spatial structure of the common sole population along the English Channel is
110 analyzed using five areas (Figure 1): the Western Channel (WC), the North Sea (NS)
111 and three areas for the EEC: English coast of the Eastern English Channel (UK),
112 Southern French coast (FrW) and Northern French coast of the Eastern English Channel
113 (FrE). The WC area is based on an existing spatial management unit (VIIe ICES 2017).
114 The spatial management unit IV currently used for stock assessment in the North Sea
115 (ICES 2017) is divided into three spatial subunits. Our study is restricted to the spatial
116 subunit IVc (ICES 2017) which contains the major part of the common sole commercial
117 catches in the North Sea. The division of the EEC into three areas (UK, FrW, FrE) is
118 based on the occurrence of natural barriers of habitat unsuitable for common sole
119 (Rochette *et al.* 2012). These natural barriers consist of deep gravel grounds, which
120 occur centrally in the EEC (separating UK from FrW & FrE), and wide rocky reefs from
121 the coasts out into deeper waters (separating FrW from FrE). These natural delineations
122 could potentially define the spatial structure of the common sole population within the
123 EEC and have recently been used to study its connectivity in the EEC (Du Pontavice *et*
124 *al.* 2018; Randon *et al.* 2018).

125 2.2 Data Collection

126 The dataset collates four mark-recapture experiments carried out by (i) the Center for
127 Environment Fisheries and Aquaculture Science (CEFAS, UK) from 1955 to 1985 and
128 2002 to 2007 (Burt & Millner 2008) and (ii) the French Research Institute for Exploitation

of the Sea (IFREMER, France) from 1976 to 1980 and 2016 to 2018 (Table 1, Figure 2). For each release experiment, Petersen discs were used (Burt & Millner 2008). Discs are uniquely numbered and are securely attached to the dorsal flank of the fish. Adults and subadults were released close to the capture position as soon as was possible after capture. Recaptured marked fish were recovered by fishermen, who provided dates and spatial coordinates of the recaptures. To assess temporal variations in key model parameters (see below), the entire dataset was divided into four release experiments denoted (1) CEFAS_{1970} from 1970 to 1985, (2) CEFAS_{2002} from 2002 to 2007, (3) $\mathrm{IFREMER}_{1976}$ from 1976 to 1980 and (4) $\mathrm{IFREMER}_{2016}$ from 2016 to 2018 (Tables 1 and 2). Data collected before 1970 were discarded, as information was not sufficient to estimate fish movements from mark-recovery data (i.e. no reliable estimate of fishing mortality, see section 2.4.2). Recaptured fish with no release or recovery position or date of recovery data were discarded. The mark-recapture dataset consists of 32739 released and 7010 recovered fish with known dates and areas of release and recovery respectively.

2.3 Time at liberty and time step

A discrete 4 months time step was used in our modeling approach, based on the life cycle of the adult common sole (Rochette 2011): spawning (February to May), foraging (June to September) and overwintering (October to January). For each individual, the time at liberty (time elapsed between the date of release and the date of recapture) was recorded. The time at liberty was computed in a number of time steps (Table 1 and Figure 3). Individuals recovered within the time step of release were removed from the analysis (2974 fish, 7% of released fish).

2.4 Modeling approach

2.4.1 Core modeling structure

The final dataset used in the modeling approach consists of 32739 released and 4036 recovered fish with the following associated information (individual based): dates and areas of release and recovery and release experiment. The dataset was analyzed through a multi-event mark-recapture modeling approach (Pradel *et al.* 2005) built in a state-space modeling framework that accounts for both processes and observation errors. The process model tracks the history of each individual released fish on a 'seasonal' (4-month discrete time step) basis. The trajectory of each individual starts with the release event, for which the date and areas are assumed to be recorded without errors. In our multi-event model, we consider 15 potential states for the true fate of individuals at each time step (Figure 4):

$$\{A_{WC}, A_{UK}, A_{FrW}, A_{FrE}, A_{NS}, F_{WC}, F_{UK}, F_{FrW}, F_{FrE}, F_{NS}, M_{WC}, M_{UK}, M_{FrW}, M_{FrE}, M_{NS}\}$$

State A relates to live fish, state F relates to fish dying by fishing and state M relates to fish dying of natural causes, all located respectively in areas WC, UK, FrW, FrE, NS, Figure 1). At any time step t, a fish can be in one (and only one) of those 15 states. The transition between time step t and $t+1$ consists of a three-step series of transitions representing ecological and observation processes (Figure 4):

1. Movement process. Any alive fish at time t can remain in its current area i ($i = 1,...,5$) or move to another area j ($j = 1,...,5$) between t and $t+1$. The dispersion of all fish present in the area i at time t is modeled through a Multinomial distribution with movement probabilities $\phi_{(i,j)}$ and $\sum_{j=1}^{5} \phi_{(i,j)} = 1$ (see details hereafter).

2. Survival. The model assumes that mortality occurs after movements. After movements, a fish can survive or die from either natural mortality or fishing mortality between t and $t+1$. For each individual, this transition is modeled as a Multinomial distribution with survival rate, mortality rate by fishing or mortality rate by natural causes as parameters (denoted r^s, r^f and r^m, respectively; see details hereafter).

3. Observation process. The observation process (that ultimately defines the likelihood) links observation to the true biological state of each individual at time t. Only fish caught by the fishery can potentially be observed. Alive fish or fish dead from natural causes are unobservable. Once a marked fish is caught by the fishery, it can eventually be declared. The declaration of a marked fish caught is modeled through a Bernoulli distribution with declaration rate T (see details hereafter).

2.4.2 Parameterization

We tested several versions of the model accounting for different levels of spatial and temporal variations in the parameters. Below, we detail the parameterization used in the full model that accounts for seasonal movements, spatial heterogeneity and inter-annual variation of survival, and survey-specific declaration rate (model 1, Table 3). Other challenging models are detailed in section 2.4.3.

Movement process

Probabilities of movement $\phi_{(i,j,s)}$ are estimated separately for each pair of departure ($i = 1,...,5$) and arrival areas ($j = 1,...,5$) and for each season s ($s = 1,...,4$). No variability between years is considered. Movement parameters from the WC to the NS, and from the NS to the WC are set to 0 and are not estimated (Figure 1). No fish were observed making these two migrations patterns in a single time step (i.e. 4 months). Therefore, it was assumed that the large distance separating the two areas does not allow for such movement in one time step.

Survival process

Survival probabilities for each time step are fixed and assumed known without errors, defined as:

$$r^f = \frac{f}{f+m}(1 - exp(-(f+m))$$

$$r^m = \frac{m}{f+m}(1 - exp(-(f+m))$$

$$r^s = 1 - (r^f + r^m)$$

where r^f is the probability of death by fishing, r^m is the probability of natural fish death and r^s is the probability of survival. m and f respectively are natural and fishing mortality (per time step of 4 months) as directly derived from published stock assessment evaluations (ICES 2017). For the three ICES areas (IVc, VIId and VIIe) the spatially and temporally constant natural mortality was fixed to $m = 0.1 \times timestep^{-1}$ (ICES 2017). Fishing mortality rate f was also considered known but with years and spatial variability. Available information from stock assessment differ among areas (ICES 2017): estimates of fishing mortality are available since 1955 for the NS area (ICES division IVc), from 1969 for the WC area (ICES division VIIe) and from 1982 for the UK, FrW, FrE areas jointly (ICES division VIId) (Figure 5).The data collected before 1970 were discarded because no reliable estimate of f in the EEC could be found before 1970. In order to use the longest time series of release data, we assumed that fishing mortality was equal in areas VIIe and VIId between 1970 to 1981. Temporal variations were smoothed to limit the influence of uncertainty that surrounds short term (year-to-year) variations in estimates of fishing mortality (Figure 5). Preliminary analysis demonstrated that smoothed time series of f improve numerical stability of dispersal estimates. The mortality rates were allocated to each time step within the same year by considering that m and f were homogeneous among seasons within a year.

Declaration

The probabilities that marked fish caught by the fishery are declared (and then observed) are estimated, and considered to be variable between release experiments (but spatially homogeneous and constant among seasons).

2.4.3 Hypotheses testing and sensitivity analysis

The full model (model 1, Table 3) accounts for (i) a movement process with parameters (estimated) that vary between seasons, (ii) yearly and spatially varying survival (fixed parameters), and (iii) declaration rates (estimated parameters) considered to be variable between release experiments. In all models, to avoid confusion between parameters and ensure stable numerical results in the maximum likelihood procedure, estimated parameters are the movement probabilities and the declaration rates, and all mortality rates (fishing and natural) are considered known.

The existence of dispersal patterns that differ among seasons is tested by fitting models with no variability of movement probabilities between seasons (models 2, 5 and 7, Table 3) and comparing the results obtained with the full model (model 1, Table 3). The variation of the declaration rates between release experiments is tested by fitting a model parameterized with a unique (but still estimated) declaration rate over the full time series (model 3, Table 3). The existence of inter-annual differences in movements during the time series is assessed by fitting separate models to the full time series of data (1970-2018; model 1, Table 3) and to the most recent (2002-2018; model 8, Table 3) and historical time series only (1970-1998; model 9, Table 3). Hypotheses made on the fishing mortality (considered known in our model) are critical. We therefore also assessed the robustness of our results to the quantity of expertize on the spatio-temporal variability of fishing mortality brought into the model. Models with less refined hypotheses were fitted using: (i) fishing mortality constant over time but different between areas, computed as the mean of fishing mortality over time series per area (models 4 and 5, Table 3), and (ii) fishing mortality constant over time and

248 homogeneous in space, calculated as the mean over areas and times series (models 6
249 and 7, Table 3).

250 2.4.4 Model fit and selection

251 All models were built and fitted using the E-SURGE program (version 1.9.0, Choquet
252 and Nogue 2010). Details about the implementation of the model in E-SURGE are given
253 in Appendix A. Parameters (movement and declaration rates) were estimated in the
254 maximum likelihood framework (MLE). The data consist in the sequence of observation
255 events for all individuals, starting with i (the area of release, $i = 1,...,5$) at the tagging
256 event, and ending with j (the area of recovery, $j = 1,...,5$) when the fish is recaptured and
257 declared (with a series of 0 between the tagging and the recapture event as the fish can
258 only be recaptured once) or ending with a series of 0 for fish that are never recaptured.
259 The likelihood writes down as the product of Bernoulli distributions (declaration process)
260 over all time steps and all fish (considered independent), marginalized over the
261 probability distribution of all possible hidden states defined from the product of
262 Multinomial distributions for the movement and mortality processes. The maximum
263 likelihood is estimated using the Maximization-Expectation algorithm (Choquet and
264 Nogue 2010).

265 A goodness-of-fit (GOF) test was conducted prior to model selection to check if our
266 release and recapture data met the assumption of a general model (the Arnason-
267 Schwarz Model, Pradel *et al.* 2003). We performed a GOF test using the U-CARE
268 software (version 2.2, Choquet *et al.* 2009). GOF tests a 'trap-dependence' effect by
269 comparing future recapture histories between individuals released on the current
270 occasion versus individuals released on a previous occasion, for all individuals that are
271 seen again (for more details on GOF test, see Appendix A).

Model selection was used to assess which model formulation in Table 3 was the best supported by the data. Model selection was based on the Akaike's information criterion corrected for overdispersion (QAIC). The model with the lowest score of QAIC is considered as the best model. Only models with the same dataset (same length of time series of data) were compared together.

2.4.5 Sensitivity to area boundaries

A sensitivity analysis to the delineation of the areas was performed through a buffering method consisting in removing fish released and recovered at or near a border. Such individuals were potentially crossing the border using migration paths shorter than those for centrally-based fish, creating a potential edge effect and introducing bias (i.e. overestimation of movements among spatial areas) in estimates of movement probabilities. We computed a 30 km buffer around each boundary to remove a substantial amount (i.e. 10%) of released and recovered fish inside the buffer (3364 fish were removed).

3 RESULTS

The GOF test performed on the full dataset (from 1970 to 2018) revealed a lack of fit ($\chi^2 = 57.476$, $\mathrm{P} = 0.000$ and $\mathrm{df} = 24$) when over-dispersion is not accounted for. An overdispersion coefficient (c) of 2.39 was applied to all models to account for overdispersion ($\hat{c}$ superior to one, Burnham and Anderson 2003, Choquet *et al.* 2009).

Overall, the full model (model 1, Table 3) best explains the tagging-recovery data including seasonal movements, specific declaration rate for each release experiment, and fishing mortality varying across space and time.

The data also support the hypotheses of different detection rates per release experiments (QAIC model 1 < QAIC model 3, Table 3) with the lowest declaration rates estimated for the CEFAS_{2002}, comparable detection rate between $\mathrm{IFREMER}_{1976}$ and $\mathrm{IFREMER}_{2016}$ experiments and a relatively high detection rate for the CEFAS_{1970} release experiment. Declaration rate estimates presented in Figure 6 for model 1 were similar among models 1, 2 and 4-7 (Supplementary Files; Table S1).

Even if the estimated movement's probabilities between areas remain overall very low, the results support the existence of seasonal movements (Figure 7 and Figure S2 in Supplementary Files for a focus on movement between areas). Furthermore, the conclusion that the data support the existence of seasonal movements patterns is robust to changes in the time series of fishing mortality used as input to the model. Indeed, models with seasonal movements in general presented better QAIC scores when considering pairs of models with the same survival input (QAIC model 1 < QAIC model 2; QAIC model 4 < QAIC model 5; Table 3).

Overall, the results support the hypothesis of very low connectivity between the different areas (model 1, Figure 7). For most areas and seasons, estimates of movement probability are very low, if not null (i.e. probabilities of staying in the areas of origin are close to one). Virtually no emigration is estimated from the NS and WC to the three areas of the EEC. This result highlights the primarily residential nature of the adult component of the common sole population, with only a very small proportion of adult fish migrating among areas. Low probabilities of movement are estimated ($\Phi_{i,j} < 0.25$) for fish in the UK and FrE areas which move to WC and NS. Thus low to moderate exports outside of the EEC occur between the overwintering and spawning season. Low probabilities of emigration from the FrW to the WC is also estimated between spawning

and foraging seasons. Movement probabilities estimated with model 2 (no seasonal variability of movements) also support the hypothesis of very low dispersion of common sole between areas (Supplementary Files; Figure S2). Results are also robust to the delineation of the five areas. The analysis performed on a dataset without fish released and recovered near a border provided results (Supplementary Files; Figure S3) comparable to those obtained with no buffering (Supplementary Files; Tables S2, S3 and S4).

Finally, the conclusion that very low connectivity exists between areas is robust to the time series of data considered. No strong differences exist between movement probability estimates obtained with the whole dataset (1970-2018), and with the shorter time series 1970-1998, corresponding to historical release experiments (CEFAS_{1970} and $\mathrm{IFREMER}_{1976}$; Tables S2, S3 and S4 in Supplementary Files). Movement probability between the FrE and NS areas is an exception. Between these areas, higher movements are estimated when considering historical release experiments only. Between foraging and overwintering seasons, all fish from NS move to FrE (Table S3), whereas from spawning to foraging and overwintering to spawning seasons all fish from the FrE move to NS (Supplementary Files; Table S2). However, these estimated probabilities of movements can be explained by the small amount of fish released and recovered in the FrE area: 82 over the 1970-1998 period in comparison with the 1307 fish released and recovered in the NS in the most recent period. Movement probabilities inferred from recent tagging data collected from 2002 to 2018 are similar to the ones estimated with the entire dataset (Supplementary Files; Tables S2, S3 and S4), with only small movements among areas. There are however small differences in estimates of movement probabilities between the recent tagging data and the full-time series, which

342 mostly concern the three areas of the EEC. Between the foraging and overwintering
343 seasons, higher than average movement probability are estimated from the UK to the
344 FrE areas, as well as from the FrW to the FrE areas (Supplementary Files; Table S2).
345 Limited movements are also estimated from the FrE to the WC and FrW areas from
346 spawning to foraging seasons (Supplementary Files; Table S2). Confidence intervals are
347 greater for the more recent period than for 1970-2018 and 1970-1998 time series,
348 because of the smaller amount of fish released during CEFAS_{2002} and $\mathrm{IFREMER}_{2016}$ in
349 comparison with the CEFAS_{1970} and $\mathrm{IFREMER}_{1976}$ experiments (Table 3a).

350 4 Discussion

351 In the present study, we have analyzed for the first time a substantive database of mark-
352 recapture data, with 32739 subadult and adult common sole being released over a
353 period of 49 years. Our results suggest minimal movements of sole among areas in the
354 EEC, and even lower immigration from adjacent areas, but low to moderate emigration
355 to the NS and to the WC, mainly between the overwinter and spawning seasons. Our
356 results provide evidence of low connectivity among common sole subpopulations within
357 the EEC, and no inputs from the adjacent spatial management areas. This evidence of
358 local segregation is consistent with recent studies using patterns in key life history traits
359 (Du Pontavice *et al.* 2018; Randon *et al.* 2018) for the common sole in the EEC.

360 Reliability of the estimates of movement

361 Commercially exploited fish populations are often widely monitored, which offers the
362 opportunity to use survey-generated estimates of population vital rates, expert
363 knowledge and/or stock assessment (McGarvey & Feenstra 2002). In our study, we
364 used estimates of fishing and natural mortality from published stock assessments (ICES

2017) as input fixed a priori in our state-space capture-mark-recapture modeling approach. Models incorporating all data available on the survival process (e.g. yearly and spatially varying fishing mortality) best explain the data.

Seasonal movement probabilities estimated in our study revealed low movements, with small variations when considering different periods within the time series. However, the historical release experiments (CEFAS_{1970} and $\mathrm{IFREMER}_{1976}$) were not designed specifically to study movement patterns at the scale of the English Channel, and relatively little tagging effort was expended in the two areas along the French coast (FrW and FrE). This deficit of data in the oldest release experiments can explain the difference in movement parameters estimated for the 1970 to 1998 time series with regards to the full time series or to the recent release experiment. Only the recent release experiments (CEFAS_{2002} and $\mathrm{IFREMER}_{2016}$) sampled all three EEC areas more evenly. Jointly analyzing all four tagging experiments allowed for a more balanced dataset, and reduced singularities and potential bias incorporated by the spatial locations of fish releases between release experiments.

We recognize, however, some weaknesses in our approach, some of which open up exciting opportunities for future research. Our model is structured on a seasonal time step of 4-months that reflect biological seasons of the life cycle of the sole in the Eastern Channel. Although this is justified from a biological point of view, this choice excludes data from fish that were released and recovered within the same seasonal time step. The percentage of fish removed because of the chosen time step remains low (7% of released fish). For those removed fish, 94% were recovered in their zone of release, in accordance with the results obtained on a 4-monthly basis. In all models, mortality rates (fishing and natural) were considered known and estimated parameters are the

movement and declaration probabilities. Estimating movement, mortality and detectability is possible in certain configuration of mark-recapture models (Royle *et al.* 2013) but separating temporal and spatial variations in those parameters is still difficult overall. In our model, attempts to estimate both natural mortality and declaration rates from our data have shown unstable numerical results and estimates that were non-robust to small changes in hypotheses, revealing some statistical confusion between mortality and declaration rates. In other terms, different combinations of mortality and declaration rates provide the same likelihood for the data. Because the total mortality estimated from statistical catch-at-age stock assessment models is robust (Quinn & Deriso 1999; ICES 2017), and because no expertize exists on the declaration rate, our choice here was to consider mortality as known, and to estimate declaration rates from the data. Although stock assessment results provide some measure of uncertainty about f (confidence intervals), only point estimates were considered in our approach. This simplification answers practical considerations as no methods exist to account for uncertainty in f using the E-SURGE software. However, we carefully assessed the sensitivity of our results to the hypothesis made on the temporal and spatial variation of the fishing mortality. Because temporal and spatial variation in f are much higher than estimation uncertainty (ICES 2017), the robustness of our results to those changes in f demonstrates the robustness of our inferences on movements to uncertainty about f.

However, estimates from stock assessment models (and especially fishing mortality) can be sensitive to hypotheses made on the spatial structure of the population (see for instance results by Archambault *et al.* 2016 on the same case study), and make inferences on dispersion by using fixed f from previous assessments that do not consider dispersion to be an issue. This paper is an important step toward the

construction of an integrated model to simultaneously estimate fishing mortality and dispersion by integrating tagging data within the stock assessment model. Tagging data, however, can have a complex structure, which when coupled with a poorly balanced sampling design, can provide further challenge to obtaining robust statistical inferences from tagging-integrated models (Maunder & Punt 2013). Consequently, we attempted here to develop a first analysis of the tagging data before integrating them in a more complex structure.

Our approach also considers natural mortality to be constant in space and in time. In stock assessment evaluations, natural mortality is usually fixed and the fishing mortality is estimated relative to the fixed value of natural mortality (ICES 2017). Preliminary exploration of the data (not shown) suggested that consideration of a higher value of m (but still considering m to be constant in time and space) has a simple and intuitive impact on estimates of declaration rates. Considering a higher value of m leads to lower estimates of declaration rates, as the same number of recorded marked fish must be explained by a lower actual number of marked fish in the sea due to higher m. On the opposite, considering a smaller value of m leads to higher estimates of declaration rates. The effect of introducing spatial heterogeneity in m which is operationally challenging was not tested here. However, there is no evidence of a spatially varying natural mortality for the common sole in the English Channel. Consequently, our assumption of constant natural mortality among areas was considered to be a realistic and parsimonious modeling approach for the estimation of fish movement.

Although Du Pontavice et al. (2018) and Archambault et al. (2016) suggested heterogeneity of fishing mortality within the EEC, with the fishing pressure in FrE being higher than in the UK and FrW areas, no spatial variability of fishing mortality within the

three EEC areas was considered in our approach. However, because the EEC common sole stock is considered homogeneous, no stock assessment results were available for the individual 'sub-stock' areas (UK, FrW, FrE), and no spatialized catch data were available in the time series. Furthermore, although the fishery is strongly seasonal (Vermard and Savina, com. pers.), available times series of within-year fishing effort distribution were too short to be considered in our analysis (2000-2016 for French and 2004-2016 for foreign fleets), precluding the application of varying fishing mortality between the 4-month 'seasons'. However, given (i) the very low level of dispersal estimated among the different areas in the EEC and (ii) the high robustness of these results to hypotheses on spatial and temporal variations in the fishing mortality that were tested, it is unlikely that using more refined data would have dramatically altered the conclusions. Furthermore, recapture probability in our approach depends only on m and f. However because the fleet and associated gear is not routinely recorded for mark recovery, heterogeneity due to the use of different fishing gears, which could have introduced further realism to our model, was unable to be considered. Finally, we found strong statistical evidence in favor of different declaration rates between the tagging periods. Unfortunately, we were not able to find definitive explanations for those differences. One potential explanation might be haphazard levels of communication with the fishermen to publicize the tagging programs and associated rewards at different periods in time. We considered the declaration rate to be homogeneous in time and space within a period, which might have been a source of bias, in that different fleets operating in different zones may not have had equivalent information, interest or motivation to participate in scientific tagging programs. As a result, our estimated movement probabilities may have been biased by reducing the number of declarations

of marked fish caught in a particular area. We have assumed that the aggregation of several tagging surveys from both UK and French research institutes in the present modeling approach should limit the overall related biases.

Combining different approaches to improve estimates of connectivity

Several authors have recently highlighted the importance of combining multiple approaches to study stock delineation (Pita *et al.* 2016). Indeed, individual methods each have their own strengths and weaknesses, and combining results of different methods generally improves the overall reliability of the results (Cadrin *et al.* 2014; Izzo *et al.* 2017). For marine fish in particular, high mortality in early life stages (eggs, larvae and juveniles, Le Pape and Bonhommeau 2015) and the lack of barriers in the ocean often rend the genetic signal of segregation relatively weak (Selkoe *et al.* 2008). Only a very small proportion of fish dispersing at each generation will erase genetics differences between populations (Palmer *et al.* 2014), which can result in a mismatch between ecological and genetic connectivity (Hawkins *et al.* 2016).

The common sole stocks in the English Channel and North Sea are recognized as genetically distinct populations (Diopere *et al.* 2017) and have been managed separately for decades. While common sole in the EEC has been managed as a single homogeneous stock unit thus far, evidence from different approaches is now accumulating in support of considering spatial structure at a finer scale. Here we demonstrate very low exchanges between the three delineated EEC areas, and virtually no immigration from adjacent stocks. This demographic isolation is consistent with the marked discrepancies in growth between the areas (Du Pontavice *et al.* 2018; Randon *et al.* 2018) and the lasting synchrony among density-at-age time series inside each area (Randon et al. 2018).

From low adult-mediated connectivity to segregation in EEC areas

In the EEC, larval connectivity of the common sole is low, since spawning areas directly feed adjacent coastal nursery grounds (Rochette *et al.* 2012). After metamorphosis, juveniles grow on shallow nursery grounds (Riou *et al.* 2001; Rochette *et al.* 2010). Limited movements of juvenile flatfish (Le Pape & Cognez 2016), and the dependence of the juvenile common sole upon shallow nursery habitats (Riou *et al.* 2001) result in low juvenile connectivity (Coggan & Dando 1988). After about two years on nursery grounds, the common sole move to deeper offshore adult foraging grounds. In addition to premature segregation, the lack of connectivity during the adult phase is a potentially important driver of segregation (Frisk *et al.* 2014). However, estimated levels of dispersal demonstrate that at subadult and adult stages, EEC export a low fraction of individuals to the NS and a very low fraction to the WC. The EEC may act as a limited source of fish for these adjacent stocks. These movements occur mainly during the overwintering period of movements of subadults (Dorel *et al.* 1991) and adults (Horwood 1993; Burt & Millner 2008) when common sole move out towards deeper sea areas.

Management implications

Ignoring the spatial structure of exploited fish population dynamics may induce mismatches between the stock units considered for stock assessment and management and the biological population structure (Carson *et al.* 2011; Frisk *et al.* 2014; Kerr *et al.* 2017). A better consideration of the spatial structure of populations and of metapopulation dynamics is critical for sound evidence-based decision-making (Heino *et al.* 1997; Porch *et al.* 1998; Ulrich *et al.* 2017). Inconsistencies between the spatial structure of populations and delineation of stock units could impede effectiveness and appropriateness of management measures (Kerr *et al.* 2017), resulting in the

overexploitation of the less productive subunits (Cadrin & Secor 2009; Ying *et al.* 2011; Goethel & Berger 2017). Adults' movements play a critical role in population connectivity (Frisk *et al.* 2014), especially for species with a low level of connectivity at previous life stages. Failure to appropriately consider the role of adults' movements (or local segregation) can lead to bias in assessment of stock status and the proposal of management non-adapted to the true dynamics and productivity of stocks (Punt & Restrepo 1995; Porch *et al.* 1998).

Rochette *et al.* (2013) and Archambault *et al.* (2016) have developed an integrated life cycle Bayesian model of the EEC common sole stock. The life cycle sequentially considers the production of eggs by adults, larval survival and drift, survival and settlements in coastal nurseries, habitat–dependent survival of juveniles on nurseries and finally natural and fishing mortality of the adult population. Archambault *et al.* (2016) consider two contrasted hypotheses: (i) one single homogeneous adult population supplemented by all coastal nurseries; (ii) three isolated subpopulation supplemented by separated pools of coastal nurseries. Results show that accounting for spatial segregation markedly influences stock assessment results (Archambault *et al.* 2016). Results, from both this and the previous study, show that estimates of fishing mortality and management reference points such as MSY of the common sole in the EEC strongly depend upon the underpinning hypothesis of adult connectivity. Further extension of the integrated life cycle modeling framework of Archambault *et al.* (2016) to integrate the analysis of tagging data within the integrated life cycle model would allow the simultaneous estimation of fishing mortality in the different areas of the EEC and connectivity between those areas. We suggest that such an exercise would contribute to

improving scientific advice for the spatial management of the fishery (Methot 2009; Goethel *et al.* 2011; Griffiths *et al.* 2018).

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547 Table 1: Number of marked and recovered fish, used in the analysis, per release
548 experiment and associated average time at liberty in number of 4-month periods and
549 recapture rates.

Experiment	Marked	Recovered	Average time at liberty	Recapture rate
$CEFAS_{1970}$	3627	3627	6.26	1
$IFREMER_{1976}$	305	305	4.07	1
$CEFAS_{2002}$	29	29	5.59	1
$IFREMER_{2016}$	85	85	3.07	1
Total	4046	4046	6.02	1

550550

Table 2: Number of fish released per area and time series and in parentheses the number of recovered fish per area and time series.

	Areas	1970-1998	2002-2018	1970-2018
1	WC	5025 (949)	250 (10)	5275 (959)
2	UK	6897 (1298)	1861 (13)	8758 (1311)
3	FrW	1448 (90)	1048 (7)	2496 (97)
4	FrE	1143 (93)	2148 (55)	3291 (148)
5	NS	12509 (1505)	410 (16)	12919 (1521)
6	Total	27022 (3935)	5717 (101)	32739 (4036)

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Table 3: Model definition. Models 1 to model 7 are fitted to the full time series. Model 1 is the most complex model. Model selection is performed on the full dataset (1970 to 2018) from model 1 to less complex alternatives in the dispersal, fishing mortality inputs and detection rates. ΔQAIC represents the difference in QAIC in comparison to model 1. Models 8 and 9 have the same structure as model 1, but are fitted to truncated time series and hence are not considered in the model selection process.

Model	Dispersal	Fishing mortality	Detection	Time Series	QAIC	ΔQAIC
1	Seasonal	Area x Years	Release experiments	1970-2018	144966	-
2	Constant	Area x Years	Release experiments	1970-2018	144976	10
3	Seasonal	Area x Years	Unique	1970-2018	145882	916
4	Seasonal	Area	Release experiments	1970-2018	145156	190
5	Constant	Area	Release experiments	1970-2018	145187	221
6	Seasonal	Homogeneous	Release experiments	1970-2018	145148	182
7	Constant	Homogeneous	Release experiments	1970-2018	145132	166
8	Seasonal	Area x Years	Release experiments	1970-1998	-	-
9	Seasonal	Area x Years	Release experiments	2002-2018	-	-

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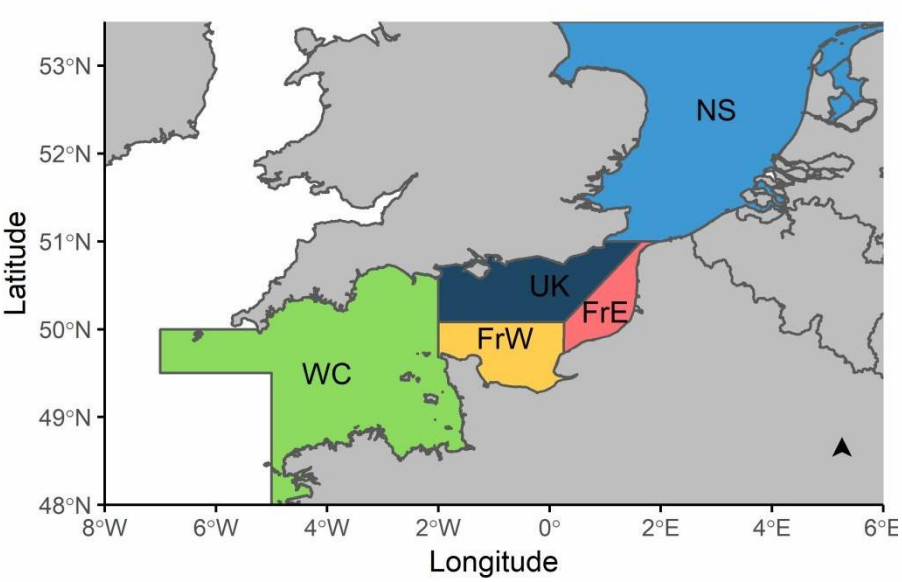

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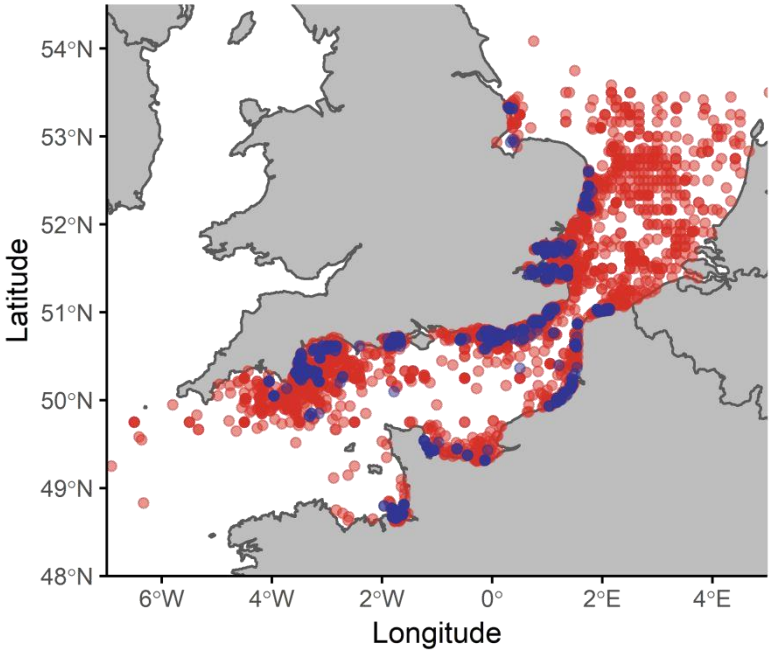
563 *Figure 1: Map of the model geographical definition with the five areas potentially*
564 *structuring common sole stocks (ICES. 2017; IFREMER 2019): Western Channel (WC,*
565 *ICES division VIIe), English coast of the Eastern English Channel (UK, ICES division*
566 *VIId), Southern French coast (FrW, ICES division VIId), Northern French coast of the*
567 *Eastern English Channel (FrE, ICES division VIId) and the southern part of the North*
568 *Sea (NS, ICES division IVc).*



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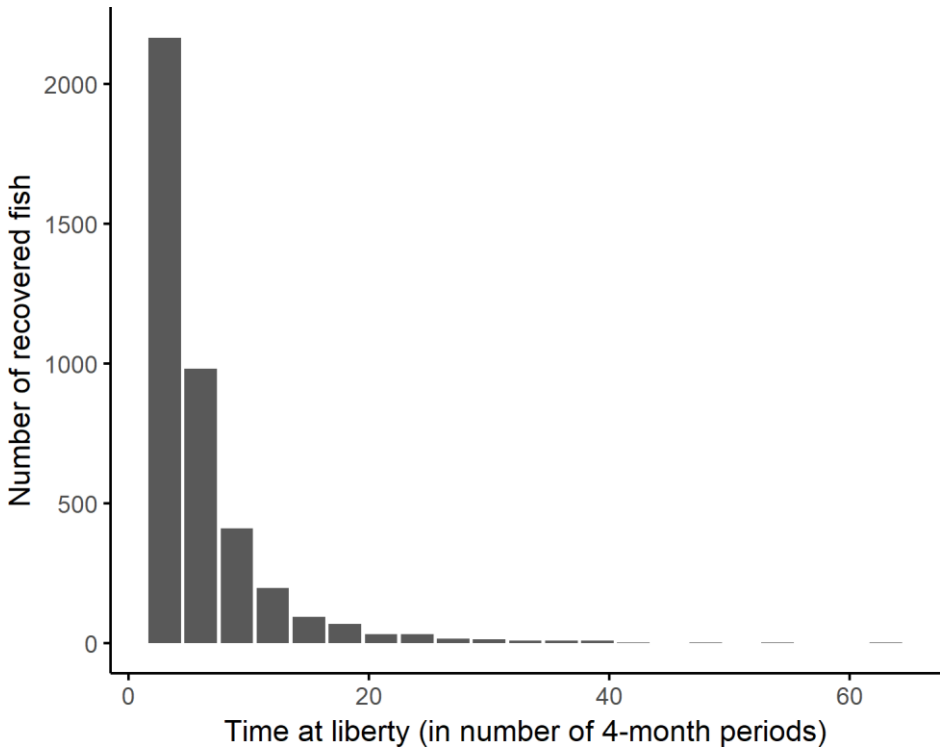
570 *Figure 2: Release locations (in blue) and recapture locations (in red) of tagged common*
571 *sole in the English Channel, east of the Western Channel and west of North Sea (Burt &*
572 *Millner 2008; IFREMER 2019).*



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574 *Figure 3: Time at liberty in number of seasons (4-month periods) for the 4036 marked*
575 *fish recovered between 1970 and 2018.*

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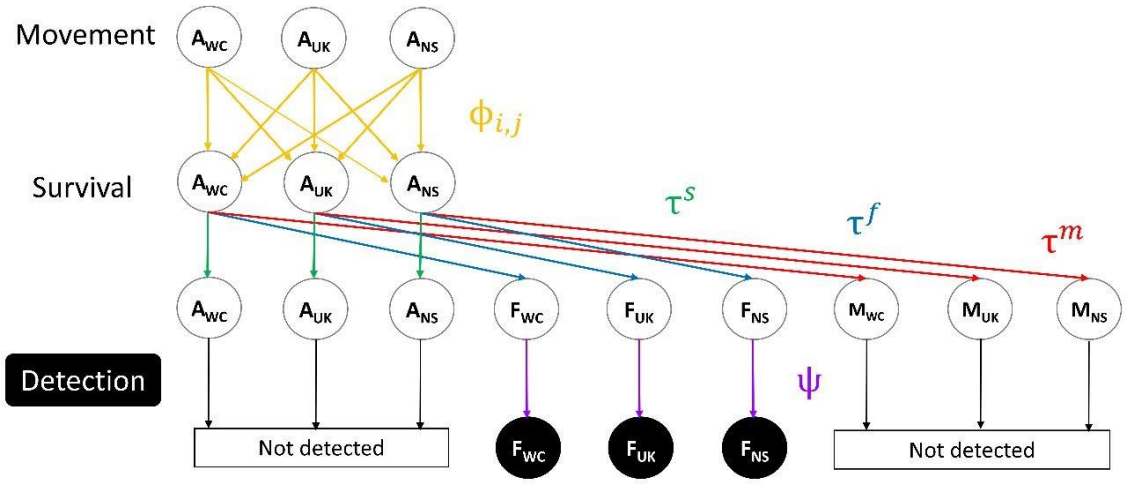

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581 *Figure 4: Diagram representing the model structure used in the analysis. Each step*
582 *represents a different model parameter or transition probability. Only three (WC, UK,*
583 *NS) of the five areas are represented for ease of reading. Live fish (A_{WC},A_{UK},A_{NS}) and*
584 *fish dying due to natural causes (M_{WC},M_{UK},M_{NS}) cannot be seen and hence cannot be*
585 *detected.*

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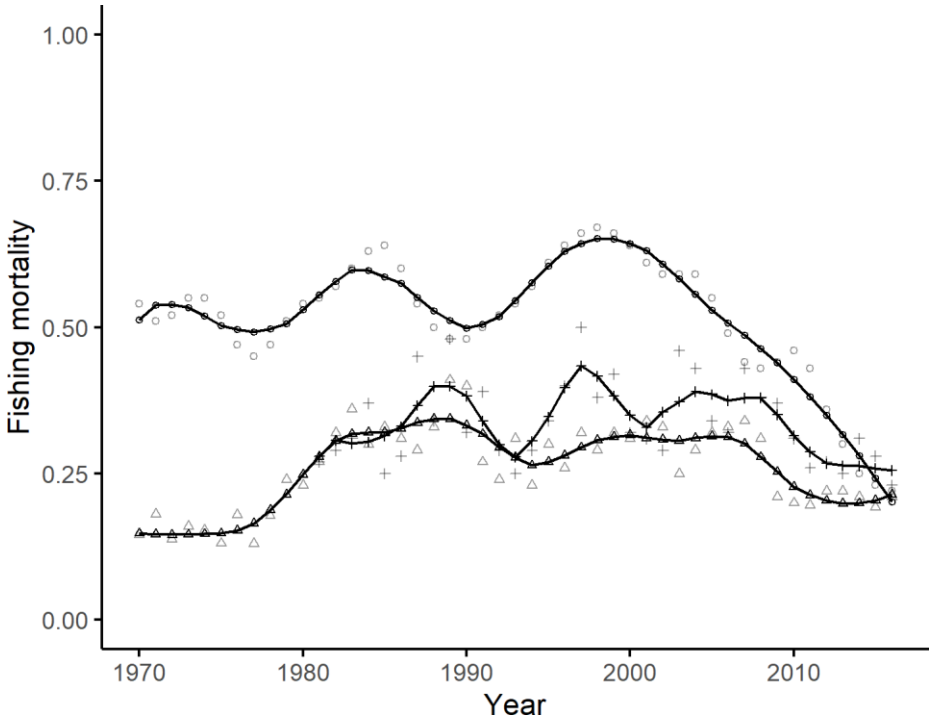

588588

589 *Figure 5: Annual fishing mortality rate estimated from stock assessments (ICES 2017).*
590 *Dotted line represents f for area IV, triangle line represents f for area VIId, and cross-*
591 *line is for area VIIe. Shaded triangle, dot and cross represent estimates from stock*
592 *assessment without smoothing. Locally weighted least squares regression was used to*
593 *perform smoothing with 30% of smoothing span.*

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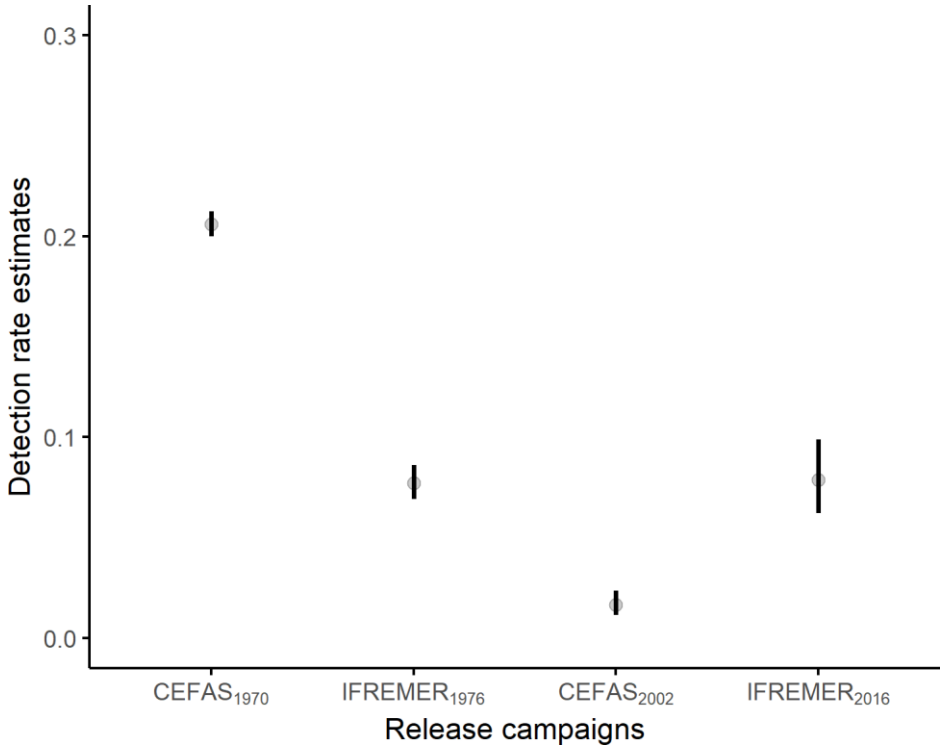

595

596 *Figure 6: Detection rate (ψ) estimates and their 95% confidence intervals per release*
597 *experiments from model 1 with the full time series (1970 to 2018).*

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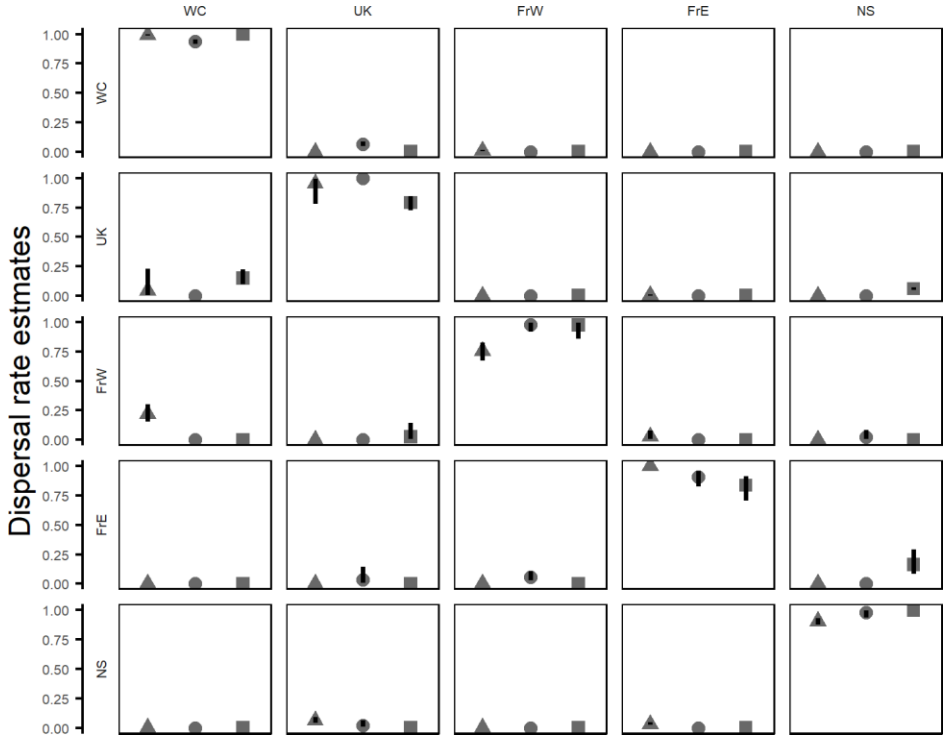

Figure 7: Movement probability estimates and their 95% confidence intervals from model 1. Rows represent areas of departure and columns areas of arrival. Triangles are MLE estimates of movement probabilities from spawning to foraging seasons. Circles from foraging to overwintering seasons. Squares from overwintering to spawning season.

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APPENDIX A

MODEL STRUCTURE AND E-SURGE SPECIFICATION

E-SURGE (Choquet & Nogue 2010) is used to implement multi-event models which are defined by steps representing biological and observation process. Each process is associated to a row-stochastic matrix for which each row corresponds to a multinomial distribution. All cells probability in the same row must sum to one and so one parameter is defined as the complement of the others (i.e. $1 - \sum \text{others}$) and is denoted by the symbol $\star$ in the following matrices. Cells with probabilities fixed at 0 are denoted with a dash (-). Matrices rows correspond to the starting state and columns correspond to the arrival state. In our multi-event model, we consider 16 biological states to inform on the true fate of individuals at each occasion:

$$\{A_{WC}, A_{UK}, A_{FrW}, A_{FrE}, A_{NS}, F_{WC}, F_{UK}, F_{FrW}, F_{FrE}, F_{NS}, M_{WC}, M_{UK}, M_{FrW}, M_{FrE}, M_{NS}, \dagger\}$$

State A relates to live fish, state F relates to fish killed by fishing and state M relates to fish dying of natural causes, all located respectively in areas WC, UK, FrW, FrE, NS (Figure 1). An extra state $\dagger$ is introduced to represent an unobservable dead state which discriminates between the "newly dead" fish from the unobservable "long-time-dead" fish (Lebreton *et al.* 1999; Fernández-Chacón *et al.* 2016). This state is required to estimate the detection rate of fish caught by the fisheries and to distinguish the different causes of mortality. In practice, a fish, that died from fishing or natural causes at time step t, is assigned to the state "long time dead" at the time step $t + 1$ and can not change of state afterwards.

Initialization

Table A1: Matrix I: initial state probabilities (π) are assigned to alive state only, because tagging is performed on alive fish only.

A_{WC}	A_{UK}	A_{FrW}	A_{FrE}	A_{NS}	F_{WC}	F_{UK}	F_{FrW}	F_{FrE}	F_{NS}	M_{WC}	M_{UK}	M_{FrW}	M_{FrE}	M_{NS}	†
*	π	π	π	π	-	-	-	-	-	-	-	-	-	-	-

Dispersal

The first five rows of matrix D corresponds to fish that are alive at time t and move (or not) during the transition to time $t+1$. For instance, $\phi_{WC,UK}$ is the probability for a fish in state A_{WC} at time t to move from the WC area to the UK area and be in state A_{UK} at time step $t+1$. The last 10 rows correspond to fish that are dead and by definition cannot move to another area and hence cannot change state at time $t+1$.

Table A2: Matrix D: migration probabilities ($\Phi_{i,j}$).

	A_{WC}	A_{UK}	A_{FrW}	A_{FrE}	A_{NS}	F_{WC}	F_{UK}	F_{FrW}	F_{FrE}	F_{NS}	M_{WC}	M_{UK}	M_{FrW}	M_{FrE}	M_{NS}	†
A_{WC}	$\star$	$\phi_{WC,UK}$	$\phi_{WC,FrW}$	$\phi_{WC,FrE}$	-	-	-	-	-	-	-	-	-	-	-	-
A_{UK}	$\phi_{UK,WC}$	$\star$	$\phi_{UK,FrW}$	$\phi_{UK,FrE}$	$\phi_{UK,NS}$	-	-	-	-	-	-	-	-	-	-	-
A_{FrW}	$\phi_{FrW,W}$	$\phi_{FrW,U}$	$\star$	$\phi_{FrW,Fr}$	$\phi_{FrW,N}$	-	-	-	-	-	-	-	-	-	-	-
A_{FrE}	$\phi_{FrE,WC}$	$\phi_{FrE,UK}$	$\phi_{FrE,Fr}$	$\star$	$\phi_{FrE,NS}$	-	-	-	-	-	-	-	-	-	-	-
A_{NS}	-	$\phi_{NS,UK}$	$\phi_{NS,FrW}$	$\phi_{NS,FrE}$	$\star$	-	-	-	-	-	-	-	-	-	-	-
F_{WC}	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
F_{UK}	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
F_{FrW}	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
F_{FrE}	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
F_{NS}	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
M_{WC}	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
M_{UK}	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
M_{FrW}	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
M_{FrE}	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
M_{NS}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
†	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Survival

After movement, fish survive (or not) following the survival transition matrix S. r^f is the probability of dying from fishing and r^m fom natural causes. The first five rows of matrix S corresponds to fish that are alive at time t and can survive or not during the transition to time $t+1$. The last 10 rows correspond to fish that are 'long-time-dead'. r^f and r^m are input from external knowledge (see section 2.4.2., ICES 2017) and are not estimated from the tagging data in E-SURGE.

Table A3: Matrix S: calculation of survival probabilities with fishing mortality probabilities (r^f) and natural mortality probabilities (r^m). Survival probabilities are fixed parameters from stock assessment evaluation (ICES 2017).

	A_{WC}	A_{UK}	A_{FrW}	A_{FrE}	A_{NS}	F_{WC}	F_{UK}	F_{FrW}	F_{FrE}	F_{NS}	M_{WC}	M_{UK}	M_{FrW}	M_{FrE}	M_{NS}	†
A_{WC}	⋆	-	-	-	-	r^f	-	-	-	-	r^m	-	-	-	-	-
A_{UK}	-	⋆	-	-	-	-	r^f	-	-	-	-	r^m	-	-	-	-
A_{FrW}	-	-	⋆	-	-	-	-	r^f	-	-	-	-	r^m	-	-	-
A_{FrE}	-	-	-	⋆	-	-	-	-	r^f	-	-	-	-	r^m	-	-
A_{NS}	-	-	-	-	⋆	-	-	-	-	r^f	-	-	-	-	r^m	-
F_{WC}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
F_{UK}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
F_{FrW}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
F_{FrE}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
F_{NS}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
M_{WC}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
M_{UK}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
M_{FrW}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
M_{FrE}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
M_{NS}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
†	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

First encounter event

This matrix is defined differently for the first encounter event (tag-release, $k = 1$) than for the second encounter event (tag-recovery $k = 2$).

Table A4: Matrix B: events and corresponding model states for the first encounter. Fish are captured in their respective area without errors.

	not seen	captured in WC	captured in UK	captured in FrW	captured in FrE	captured in NS
A_{WC}	-	1	-	-	-	-
A_{UK}	-	-	1	-	-	-
A_{FrW}	-	-	-	1	-	-
A_{FrE}	-	-	-	-	1	-
A_{NS}	-	-	-	-	-	1
F_{WC}	1	-	-	-	-	-
F_{UK}	1	-	-	-	-	-
F_{FrW}	1	-	-	-	-	-
F_{FrE}	1	-	-	-	-	-
F_{NS}	1	-	-	-	-	-
M_{WC}	1	-	-	-	-	-
M_{UK}	1	-	-	-	-	-
M_{FrW}	1	-	-	-	-	-
M_{FrE}	1	-	-	-	-	-
M_{NS}	1	-	-	-	-	-
†	1	-	-	-	-	-

Second encounter event

The second elementary matrix presents the probability of each state given the observation for the second and solely encounter ($k = 2$). In the second encounter event, only fish caught by the fishery can be seen. The matrix contains the detection rates ψ:

Table A5: Matrix B: events and corresponding model states for the second and solely encounter. Only fish captured by the fisheries can be recaptured. Detection rate ψ is estimated from the data.

	not seen	captured in WC	captured in UK	captured in FrW	captured in FrE	captured in NS
A_{WC}	1	-	-	-	-	-
A_{UK}	1	-	-	-	-	-
A_{FrW}	1	-	-	-	-	-
A_{FrE}	1	-	-	-	-	-
A_{NS}	1	-	-	-	-	-
F_{WC}	$\star$	ψ	-	-	-	-
F_{UK}	$\star$	-	ψ	-	-	-
F_{FrW}	$\star$	-	-	ψ	-	-
F_{FrE}	$\star$	-	-	-	ψ	-
F_{NS}	$\star$	-	-	-	-	ψ
M_{WC}	1	-	-	-	-	-
M_{UK}	1	-	-	-	-	-
M_{FrW}	1	-	-	-	-	-
M_{FrE}	1	-	-	-	-	-
M_{NS}	1	-	-	-	-	-
†	1	-	-	-	-	-

GOODNESS-OF-FIT TEST

Goodness-of-fit (GOF) tests are an important component of capture-recapture modeling: they are used to assess the accuracy of a model in capturing the variance of the data (Pradel *et al.* 2005). The GOF test is divided into two components the 3G test, which compares the capture histories of newly-tagged and previously-tagged individuals released at the same time, and the M component testing a trap-dependence effect by comparing future capture histories between individuals released on the current occasion versus individuals released on a previous occasion, for all individuals that are seen again. In our case study, the 3G test does not exist, because our datasets only includes dead recoveries (Gauthier & Lebreton 2008). The GOF test then relies on the M component only.

GOF is performed on a reduced model that considers parameters to be state and time-dependent with only six states 'dead' or 'alive' in each area (Pradel *et al.* 2003; Duriez *et al.* 2009; Fernández-Chacón *et al.* 2016). GOF cannot handle multiple unobservable states and models with more than 10 different events. We then pooled together subareas of the EEC and summarized observations in seven types of events (not encountered = 0, encountered alive in WC = 1, recovered dead in WC = 4, encountered alive in EEC = 2, recovered dead in ECC = 5, encountered alive in NS = 3, recovered dead in NS = 6). The GOF test was conducted prior to model selection using the U-CARE software (version 2.2, Choquet *et al.* 2009). The GOF test performed on our data was significant relvealing a lack-of-fit ($\chi^2 = 57.476$, $P = 0.000$ and $df = 24$) to the general Arnason-Schwarz model (Pradel *et al.* 2003). To address this χ^2 of the GOF test divided by the total number of degrees of freedom, to correct for potential lack of fit (Burnham & Anderson 2003; Choquet *et al.* 2009; Fernández-Chacón *et al.* 2016).