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Stock assessment in the case of the European eel: Towards an international assessment of a Widely-distributed and fragmented population

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Résumé étendu en Français

L’évaluation de stock dans le cas de l’Anguille Européenne : Vers une évaluation internationale d’une population fragmentée et distribuée à large échelle.

Contexte

L’anguille Européenne (*A. anguilla*) est une espèce amphihaline catadrome réalisant la majeure partie de son cycle de vie en eau douce. En effet, sa phase de croissance, lorsqu’elle atteint le stade Anguille jaune, s’effectue dans les eaux continentales d’Europe et d’Afrique du Nord. Suite à sa maturation sexuelle, l’anguille jaune se transforme en anguille argentée pour entamer sa migration vers la mer des Sargasses afin de se reproduire. Les larves leptocéphales migrent ensuite passivement vers les côtes européennes et Nord africaines atteignant le stade civelle une fois arrivées sur le plateau continental. La phase de recrutement correspond donc à l’entrée des civelles en estuaire où leur exploitation commence. Depuis la fin des années 1970, on observe un déclin prononcé de l’Anguille Européenne à l’échelle de l’Europe atteignant, dans certaines régions, jusqu’à 1% de son abondance des années 70s, de telle sorte que cette espèce a été jugée en danger critique d’extinction par l’IUCN. Dans ce contexte, un règlement Européen a été introduit depuis 2007 dans lequel les Etats Membres doivent créer des « Unités de Gestion Anguille » où des mesures de protection spécifiques sont appliquées, au travers d’un « Plan Gestion Anguille » qui doit poursuivre les objectifs de gestion fixés par l’Union Européenne.

Jusqu’à présent, l’évaluation et la gestion de ce stock s’est fait principalement à l’échelle des rivières puis par l’intermédiaire des « Unités de Gestion Anguille », sans « réelle » coordination et centralisation internationale. Or l’anguille Européenne est considérée être une population panmictique ce qui implique que l’évaluation de ce stock doit se faire à l’échelle de son aire de répartition. D’autre part la phase continentale de ce stock est caractérisée par une distribution hautement fragmentée à l’échelle de l’Europe : l’anguille ne possède pas les mêmes traits d’histoire de vie et ne subit pas les mêmes pressions anthropiques suivant la région et le bassin dans lesquels elle évolue. Cette dualité entre panmixie lors de la phase océanique et répartition fragmentée lors de la phase continentale rend l’évaluation de cette population difficile. Néanmoins, le recrutement paraît être le stade le plus adéquat pour tenter d’évaluer la population à l’échelle de son aire de répartition. Si certains modèles permettent d’évaluer le recrutement à l’échelle du bassin versant, encore aucun modèle n’a été mis en œuvre pour évaluer la tendance du recrutement global.

Objectif

L’objectif de cette étude consiste à estimer l’évolution du recrutement à l’échelle de l’aire de répartition de l’Anguille Européenne afin d’évaluer l’état de la population dans son ensemble. Cet exercice n’a, jusqu’ici, jamais été possible du fait des différentes tendances de recrutement observées à l’échelle de l’Europe et de la dimension fractale apparaissant plus ou moins tôt dans le cycle de vie de cette espèce. Ainsi l’agrégation des différents indices de recrutement à l’échelle de l’Europe pour dériver un index global n’a pas été possible.

Un deuxième objectif consiste à étudier de potentielles corrélations entre les estimations de recrutement à l’échelle de grandes régions européennes et des variables environnementales affectant les caractéristiques atmosphériques et océaniques du bassin Atlantique. Ceci dans l’objectif d’inférer des hypothèses sur les causes du déclin de l’anguille Européenne à l’échelle de l’Europe, sur le temps de migration des larves leptocéphales et sur des routes migratoires potentiellement différentes entre les grandes régions d’Europe.

Matériels et méthodes

Le modèle GEREM pour dériver un indice global de recrutement

Le développement du modèle GEREM à l'échelle de l'Europe est le point central de cette étude. En effet, GEREM (Glass Eel Recruitment Estimation Model) offre un cadre méthodologique pour déterminer le recrutement de civelles à différentes échelles spatiales emboîtées. Dans le cadre de mon stage, le modèle permet d'estimer simultanément le recrutement absolu annuel à l'échelle des bassins versants, à une échelle spatiale intermédiaire (i.e. grandes régions européennes) puis à une échelle plus large (i.e. échelle européenne).

L'ajustement du modèle se base sur des séries chronologiques de recrutement annuel dispersées à l'échelle de l'Europe. De plus, la construction du modèle repose sur deux hypothèses principales qui doivent être vérifiées au préalable par une analyse de données appropriée. Nous faisant notamment l'hypothèse que le recrutement suit une tendance similaire au sein des grandes régions européennes construites dans le modèle.

Une analyse dynamique factorielle : travail préalable et aperçu des différentes tendances de recrutement à l'échelle de l'Europe

L'analyse dynamique factorielle modélise des séries chronologiques non stationnaires en termes de tendances communes, d'effets linéaires de variables explicatives, et d'interactions entre les variables réponses. Dans mon stage, cette technique permet de modéliser les séries chronologiques de recrutement via une combinaison linéaire de tendances communes : en plus d'extraire les tendances communes présentes dans l'ensemble de mes séries temporelles, il est possible de savoir à quelle(s) tendance(s) se rattache chaque série et de pouvoir ainsi comparer les séries entre elles en termes de tendances.

Des analyses de corrélation à large échelle

Des corrélations entre recrutement (estimations issues du modèle GEREM) et variables environnementales (NAO, SST, GSI et Production Primaire) peuvent s'opérer à des échelles temporelles différentes (i.e. court-terme *versus* long-terme). Ainsi deux méthodes sont appliquées pour étudier les deux types de corrélation.

- Les analyses de corrélation à court-terme nécessitent de supprimer les tendances et autocorrélations présentes dans les séries temporelles. Ainsi des modèles ARIMA sont ajustés aux différentes séries temporelles et le bruit blanc (i.e. résidus) est extrait afin de ne garder que les variations à haute fréquence et sans autocorrélation. La fonction de corrélation croisée est ensuite appliquée entre les variables explicatives et les variables réponses.
- Les analyses de corrélation à long-terme nécessitent d'appliquer un filtre aux séries temporelles afin de ne garder que la variabilité à faible fréquence : un modèle de moyenne mobile est appliqué à chaque série. Afin de prendre en compte les autocorrélations présentes dans les séries, le coefficient de corrélation de Pearson entre variable explicative et variable réponse est calculé puis le test statistique de Student est modifié via un degré de liberté corrigé.

Résultats

L'analyse factorielle dynamique n'a pas permis de dégager de structure spatiale précise à l'échelle de l'Europe en termes de tendance de recrutement. Néanmoins, il semble que le recrutement dans le Nord de l'Europe ait décliné beaucoup plus rapidement que dans le sud de l'Europe, ce qui confirmerait les résultats du Working Group on Eel (WGEEL). Ainsi plusieurs zones sont construites dans le modèle GEREM en prenant en compte cette différence potentielle de « pente ». Le modèle GEREM respecte en grande partie les hypothèses de modélisation et illustre un déclin global de la population depuis la fin des années 1970 avec un niveau d'abondance atteignant 6% du niveau de référence (moyenne sur les années 1960-1979).

Aucune corrélation à long-terme n'a permis d'expliquer la différence de pente observée dans le recrutement entre le Nord et le Sud de L'Europe. Néanmoins, les corrélations montrent un effet de la NAO et de la production primaire en mer des Sargasses sur la réussite du recrutement à court-terme. Les résultats suggèrent aussi que les larves dérivant vers la zone Méditerranéenne possèdent un temps de migration plus court ainsi qu'une route migratoire différente par rapport au reste de l'Europe.

Conclusion

Le modèle GEREM est à l'heure actuelle le seul modèle permettant d'estimer l'évolution du recrutement à l'échelle de l'aire de répartition de l'Anguille Européenne. En effet, le seul modèle préexistant et visant à évaluer la population dans son ensemble reposait sur de très fortes hypothèses incorrectes

L'application de GEREM à large échelle repose sur deux hypothèses principales (i.e. mêmes tendances et densités similaires au sein des zones du modèle) qui consistent à prendre en compte la dimension fractale du recrutement de l'Anguille. Dans la majorité des cas, ces hypothèses semblent être vérifiées, mais dans certains cas, il est probable que des effets à des échelles très locales (i.e. bassin versant) soient en jeu.

Ainsi, GEREM permet d'améliorer l'évaluation du stock d'Anguille Européenne à travers l'estimation de son recrutement à large échelle. La mise en place d'un tel modèle semble pertinente dans le cadre des travaux menés par le groupe WGEEL du CIEM, qui s'appuient sur une évaluation de la tendance du recrutement pour évaluer l'état de la population.

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I. Introduction

1. The European eel life cycle

The European eel lives in continental waters from Europe to North Africa. Distributed over the whole North Atlantic Ocean during the migratory larval phase, the post metamorphic distribution of *A.anguilla* extends northwards as far as North Cape and to the east of it as far as the Murmansk coast, in Kola Bay and in Northern Dvina. This species has also been recorded in Morocco and Canary Islands which would be the southernmost point of its distribution area. *A.anguilla* colonizes the whole Mediterranean region and the Black Sea eastwards, and settles as far west as Iceland, Madeira and the Azores islands (Tesch and Thorpe 2003) (Fig.1)

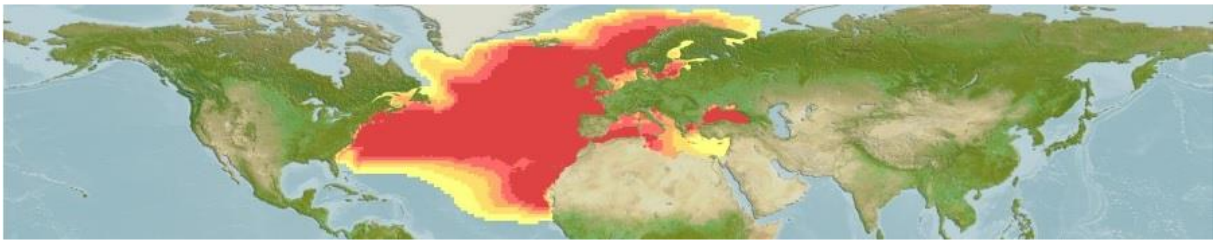

Figure 1: Geographic distribution of A *Anguilla* (Source: Fishbase).

The European eel is catadromous, living in fresh, brackish and coastal waters but migrating to pelagic marine waters to breed. The spawning site lies far out in the Atlantic Ocean in the southwestern Sargasso Sea, 5000 or 6000 km from the European coasts: the center of the area in which larvae of 10 mm and less were found is at 26°N and 60°W (Schmidt, 1925). The breadth of the east-west-oriented spawning area is at least 2200 km (Tesch et al., 1979; Schoth and Tesch, 1982), ensuring a broad distribution along the European and African coasts after the migration process. Abundances of small leptocephali (stage 0) are found in the spawning area in March-June (Tesch and Thorpe 2003).

After hatching, the larvae called leptocephali are transported by currents towards European and North African coasts. Little is known about the oceanic phase of this species and the duration of migration remains highly controversial. Estimates in favor of long migration durations of about two years or more seem however more robust to methodological caveats than methods estimating short durations of migration (Bonhommeau et al., 2010).

The leptocephali drift passively with possibly limited active swimming abilities towards Europe and North Africa. When arriving at the continental shelves, the larvae metamorphose into a transparent larval stage called “glass eel”. They appear on French and Spanish coasts as early as September with the highest densities occurring between late autumn and spring (Gascuel et al.,1995). There are however time delays in recruitment between northern and southern regions over Europe which may be explained by the latitudinal difference and/or differences in seasonal temperature along European coasts.

Then, glass eels enter estuaries using selective tidal transport (Harrison et al., 2014), and start migrating upstream. However, it is known that they can exhibit inter-habitat migration and that a proportion may stay in estuaries, lagoons and coastal waters. In this way, the European eel is often considered as an optionally catadromous fish.

Glass eels metamorphose into young pigmented eels known as elvers. After one year, elvers change into “yellow eel”, which correspond to the growth phase and the life stage resident in continental waters. After 5-20 years in continental environments, eels become sexually mature: in this stage, eels are known as “silver eels” and they migrate back to the Sargasso Sea to spawn (Fig.2)

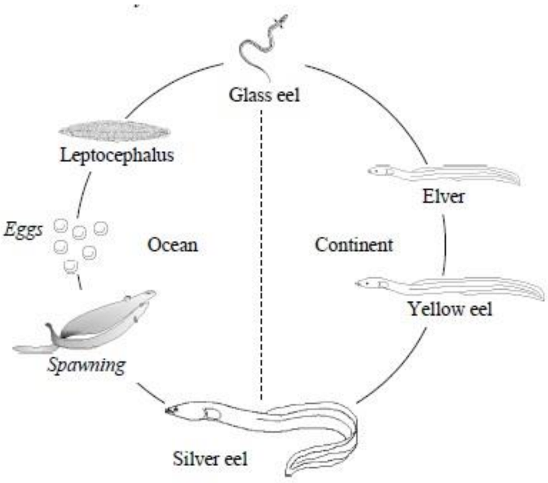

Figure 2: The life cycle of the European eel. The names of the major life stages are indicated. Spawning and eggs have never been observed in the wild (Source: ICES, 2013)

2. A declining population at the European scale: an alarming state

The European eel population has been declining at least since the early 1980s throughout its distribution area and this has been visible at all life stages. The IUCN Red List assessment mentions that the decline in silver eel escapement is estimated to be 50-60% over three generations. A similar pattern is noticeable in the data relating to the yellow eel stage (Jacoby and Gollock, 2014). Because of different trends over Europe, the Working Group on Eel (WGEEL) in charge of the yearly stock assessment, estimated two recruitment indices through a GLM analysis: one for the North Sea area (called North Sea index) and one for the rest of Europe (called Elsewhere Europe index). They concluded that glass eel recruitment indices fell to 1.2% of the 1960-1979 reference level in the "North Sea" series, and to 8.4% in the "Elsewhere" series. In turn, the recruiting yellow eel index has also fallen to 11% of its reference level (ICES, 2016).

Diverse mortality origins have been invoked in the literature to explain this overall decline. Both marine and continental causes are likely to contribute to the collapse of the European eel population. Nevertheless, their relative contribution is still uncertain.

Management actions to restore the European eel stock can only target continental life stages since management actions are not possible on the oceanic phase. In this context, the European Union (EU) enforced measures for the recovery of the stock through the European Eel Regulation (Council Regulation (EC) No. 1100/2007). This regulation sets a management target: immediate actions should be taken to "reduce anthropogenic mortalities so as to permit with high probability the escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock". To achieve this objective, member states were required to implement eel management plans (EMPs) setting measures to reduce all sources of anthropogenic mortalities.

In addition to EMPs in 2007, the European eel is subject to various conservation actions: it was included in the CITES Appendix II, and added to the OSPAR List of Threatened and/or declining Species in the Northeast Atlantic (OSPAR 2010). Moreover *A.anguilla* has been listed as Critically Endangered by the IUCN from 2008 (Jacoby and Gollock 2014).

3. Which framework to evaluate the status of the European eel stock?

To date, European eel fisheries have been mostly managed as if it was a purely freshwater fish, under national responsibility only. The mainly local nature of eel stocks implies that the conservation of European eel is under the responsibility of national governments, with individual river basins as primary management units. However, the oceanic phase is known to limit eel production and the European eel population is considered to be panmictic by most specialists (Als et al., 2011) so that they come from one spawning stock.

The panmixia criterion assumes equal importance of the continental sub-populations. As such, escapement from a specific river, country or region is not equivalent to the subsequent recruitment as this relies on the spawning stock as a whole, irrespective of escapement location. The continental-wide decline observed since the 1980s could be explained by the fact that this population is panmictic and subject to common and/or parallel threats. The actions conducted at the local scale must therefore be coordinated at the European scale in order to compare the trends, and end up with a relevant assessment of the population trends over its distribution area (Dekker, 2002a). In this context, developing the whole-stock assessment process is one of the main priorities set by the WGEEL (ICES, 2016)

Recruitment and spawning stock biomass are two important indices for the assessment of any exploited stocks. For the European eel stock, spawning stock biomass cannot be monitored directly on the spawning ground. Silver eels starting their spawning migration can theoretically be used as a proxy, but data sets are very rare, heterogeneous and not uniformly distributed across the distribution area. The majority of available data relates to glass eels and yellow eels recruitment time-series (Fig.3)

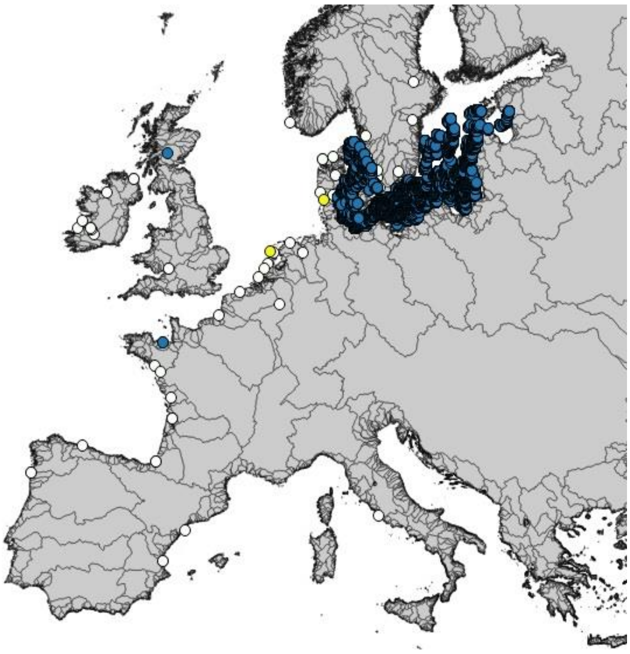

Figure 3: Location of eel monitoring sites in Europe, white circle = recruitment index, yellow circles=yellow eel series, blue circles= silver eel series (data provided by the WGEEL database)

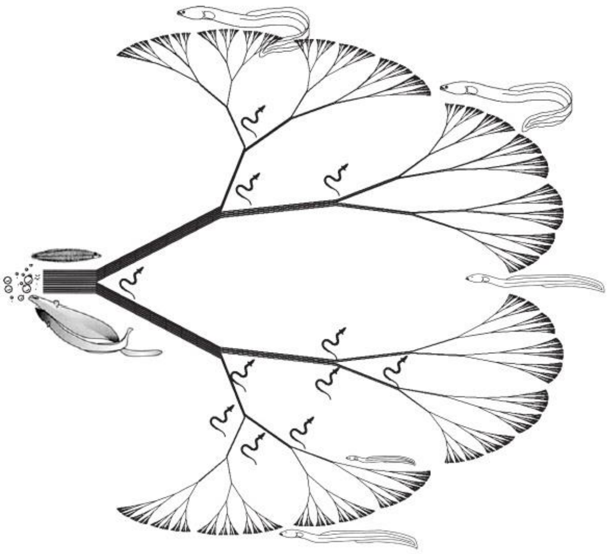

Figure 4: The fractal geometry of the European eel stock (Source: Dekker, 2000a)

Moreover, the European Eel stock is characterized by its fractal geometry (Dekker, 2000a). Indeed, the distribution pattern of the European eel is characterized by a great uniformity during the oceanic phase whereas the stock is fragmented in small units with contrasted environmental conditions and anthropogenic pressures during their continental stages (Fig.4). Moreover, eels display different life-history traits depending on their latitude (skewed sex ratios, growth, age at maturity, length of the continental growth phase). All these heterogeneities make it difficult to assess yellow and silver eel stages at a larger scale.

On the other hand, glass eel represents the youngest exploited stage and is not as influenced by local conditions as subsequent growing stages. Moreover, monitoring projects have taken place throughout Europe and aim at monitoring glass eel recruitment over the distribution area (Dekker, 2002b; Dekker, 2002c).

Along with stock indicators, the current European eel stock assessment consists of a trend analysis and is based upon three recruitment indices: two recruitment indices are derived from North Sea and “Elsewhere Europe” recruitment time series and a last one is derived from yellow eel recruitment time series (ICES, 2016). No attempt to draw a global recruitment index has been carried out so far. Indeed, it seems that recruitment time-series data follow a notable different trend depending on the geographic location throughout Europe, especially between two zones (North Sea and Elsewhere Europe) (ICES, 2010), making the derivation of a global index difficult.

So far, it was therefore impossible to build stock-recruitment relationship for the European eel stock and derive usual reference points such as B_{MSY} and $F_{MSY.}$ Moreover a stock-wide recruitment index could be useful to find a non-detriment finding for European eel (ICES 2015a).

4. A lack in the existing quantitative tools to assess the European eel population

Among the range of available eel models aiming at assessing the population, most of them target yellow eel standing stock and silver eel production at a local scale even though some attempts to derive estimates at the EMU and/or country scales have been undertaken (ICES, 2016). These models are mostly used to derive stock indicators in order to conduct national assessments for EMPs. The main models used for this purpose are DemCam, EDA, Gem and SMEPII which predict absolute escapement (Walker et al., 2011). Regarding glass eel, models such as GEMAC (Beaulaton and Briand, 2007) or a model developed by Bru et al (2009) have been implemented to estimate exploitation rates and recruitment at the catchment scale. While these models enable to assess local eel stocks, very few models have been implemented in order to estimate the status of the European eel stock throughout its distribution area. Although Dekker (2000b) tempted to provide a preliminary assessment of the entire European stock, the analysis was based on very strong assumptions and had therefore scope for improvement.

The assessment of the overall population is a complex issue for eel, given the limited knowledge about the oceanic phase; the considerable diversity in environment, biological, fishery-related factors affecting the continental life stages, the large spatial coverage of the population and data found throughout Europe.

In this context, a model to estimate the state of the European eel population with reliable assumptions was lacking. However, Drouineau et al. (2016) developed an analytical framework that aimed to fill this gap. Indeed, they implemented a model named GEREM (Glass Eel Recruitment Estimation Model) containing basic assumptions, and able to estimate yearly glass eel recruitment at different nested spatial scales. This model can estimate annual recruitment at the river catchment level, at an intermediate spatial scale and at a larger scale. This framework was used by Drouineau et al. (2016) to estimate yearly absolute recruitment in French EMUs and throughout France. Considering the need to estimate the state of the European eel stock as a whole, the model developed by Drouineau et al. (2016) can be used as a starting point to develop a large-scale model allowing to assess the entire population.

5. A population potentially impacted by large scale climatic factors

The cumulative effects of anthropogenic degradations on freshwaters growth habitats have likely contributed to the population decline, but changes in ocean-atmospheric conditions in the ocean may also be key influences (Knights, 2003). In this context, many studies have been carried out to analyze the impact of such changes on the recruitment success. Indeed, recruitment fluctuations may be affected by the spawning location of silver eels, the larval feeding success, or the transport of their leptocephalus larvae by ocean currents (Miller et al., 2009; Knights, 2003; Gutiérrez-Estrada and Pulido-Calvo, 2015; Kettle and Haines, 2006; Friedland et al., 2007; Bonhommeau et al., 2007). However, very few studies have been addressed at the European level whereas it could be worth analyzing such effects at the European scale. While the European Eel population is considered as a panmictic one, uncertainties persist concerning its precise genetic structure (Pujolar et al., 2011; Baltazar-Soares et al., 2014), the different departure points within the Sargasso Sea and the subsequent potential routes taken by the larvae (Pujolar et al., 2007; Kettle and Haines, 2006; Munk et al., 2010), and the migration durations (Kettle and Haines, 2006; Bonhommeau et al., 2009; Bonhommeau et al., 2010). At the same time, climate and atmospheric indices impact the oceanic conditions over the North Atlantic Ocean and are likely to affect marine pelagic communities especially the early life stages. However, the spatial influence of these indices is known to be heterogeneous (Nye et al., 2014; Harris et al., 2014). Therefore, it could be interesting to investigate whether fluctuations in European glass eel recruitment are dependent on ocean-atmospheric conditions (oceanic currents and food availability) and if these effects follow a latitudinal pattern. To this aim, we examined the relationships between glass eel recruitment estimates spread over Europe and global environmental descriptors- with potentially wide ranging geographic effects- on different time scales.

In this context, this study has two main objectives. First, we will explore how we can pass from recruitment time series carried out at a fine scale to an overall eel recruitment estimate by fitting the model GEREM to available recruitment indices from all over Europe.. A second objective is to explore how the European eel population is affected by large scale climatic factors.

II. Materials and Methods

1. Recruitment time series data available at the European level

Glass eel migration process

Various recruitment time series data exist throughout Europe, they are derived from both fishery-dependent sources and fishery-independent surveys (Dekker, 2002b; Dekker, 2002c). Ideally, the strength of the year-class of youngest larvae should be measured annually, but since a monitoring in the Sargasso Sea is not or hardly possible, the nearest surrogate corresponds to glass eel annually recruiting to continental waters. The earliest stage measurable coincides with the recruitment from the sea into a river (estuarine recruitment) contrary to the later migration from the estuary into the upstream river (fluvial recruitment).

The natural migration process provides several opportunities for the development of catching methods and derivation of recruitment time series. Once glass eels arrive on continental shelves, they subsequently migrate towards the coast, using a mechanism known as *selective tidal transport*: during flood tide, glass eel swim in the water column and passively drift towards the coast, while during ebb tide; they hide near the bottom to resist being washed back to the ocean. This phase of selective tidal transport is followed by a resting phase in the estuary: glass eels or elvers cannot progress further upstream until the temperature reaches a certain level (12-15°C) resulting in large concentrations in early spring, especially at the upstream tidal limit. Once temperature has risen further, active migration into the river begins, where eels swim against the river flow (Harrison et al., 2014).

As a consequence, a wide range of fishing gears (Tela, glass eel dipnet, Fykenets) is used by commercial fishermen to filter glass eels during the flood tide. Moreover, the resting phase causes a great concentration of glass eels in time and space allowing active fishing by commercial fisheries at the upstream tidal limit. In some places, the presence of weirs, sluices or ship locks at the marine freshwater interface results in concentration of glass eels providing another opportunity for fishing. Lastly, glass eels or young yellow eels can be collected in traps when they swim actively upstream and encounter obstacles, later in spring (Dekker, 2002a).

Relative recruitment indices

In this study, the different recruitment time series are considered to be indicators of the recruitment produced by the spawning process and the subsequent ocean migration. As such, we seek to avoid the effects of local conditions on recruitment levels. However, the survival of leptocephalus larvae is affected by ocean and atmospheric conditions at their spawning grounds and during their oceanic migration on both large and regional scales (Bonhommeau et al., 2007; Bonhommeau et al., 2009; Bonhommeau et al., 2008). On the other hand, local factors may play a role in determining the migration of glass eels to estuarine habitats after metamorphosis (Arribas et al., 2012). In this way, local conditions may also contribute to the year to year variability in glass eel recruitment to estuaries. To address this issue, we should prioritize the most outward monitoring sites but it remains difficult to distinguish global or regional trends from local ones whatever the monitoring site and method are. Hence, only a network of monitoring stations and an overall analysis are able to disentangle the effects of local conditions.

Moreover, we have to ensure as far as possible that each series has been compiled with maximum possible year-on-year consistency to facilitate the overall assessment of recruitment over Europe as a whole:

- **catches and Catches Per Unit of Effort (CPUE)**

Glass eels are commercially fished in southwestern Europe. A main disadvantage of commercial catches is that they often depend on variations in fishing effort due to changes in absolute level of recruitment and market values. That is why standardization by unit of effort (CPUE) is generally suitable. However in some cases, the use of CPUEs as indices of annual recruitment is not appropriate: when recruitment falls and fishing efforts are intense, the recruitment intensity may not be correlated to the CPUEs but rather to total catches (Gascuel et al., 1995). That is why total commercial catches are thought to be a good indicator of glass eel abundance especially in countries where it is intensively harvested such as Spain (Dekker, 2002a) or in the Bay of Biscay where glass eel was the most important species in landed value in the late 1990s (Castelnaud, 2001). For these reasons most recruitment time series consisted of total commercial catches (Tiber commercial catch, Ebro, Albufera de Valencia, Minho, Nalon, Gironde estuary, Severn, Ems, Vida and Loire) but some of them corresponded to commercial CPUEs. No effort data was found to restore original commercial catches values in the case of the Sèvres Niortaise estuary time series. The total commercial catch time series was too short for the Adour estuary so that both commercial catches and CPUEs were used for this catchment (Fig.5 and appendix I).

- **Glass eel scientific estimates**

Several scientific monitoring programs have been carried out in different sites around the North Sea (Ijzer, Stellendam, Katwijk, Lauwersoog, Rhine, IYFS/IBTS, and Rhingals) (Fig.5 and appendix I). The sampling protocols remain unchanged, except a change of sampling gear for IYFS/IBTS, leading to two separate time series. The sampling takes place at the fresh water/ sea interface in most cases while the IYFS time series are derived from a scientific survey taking place in the open sea. Moreover, no commercial glass eel fishery takes place downstream of the monitoring site and it seems rather unlikely that significant mortality occurs during the passage of the sluices (Dekker, 2002b).

Absolute recruitment indices

We also have different types of absolute recruitment estimates across Europe:

- The series ChGEMAC (Charente), SeGEMAC (Seudre) , GIGEMAC (Gironde) and Tiber are derived from the GEMAC model (Beaulaton and Briand 2007) while AdGERMA (Adour) and LoGERMA (Loire) are estimated with the model implemented by Bru et al. (2009). They were first developed to assess anthropogenic impacts on glass eels in estuaries in order to propose and evaluate management measures. Roughly, these models derive glass eel recruitment at the catchment scale by using catches per unit of sampled volume, which are then multiplied by the total volume of the zone. While the GEMAC model uses either commercial or scientific catches, the Bru et al.'s model requires scientific catches to estimate glass eel daily abundance.

- An absolute estimate has been calculated over a period of 11 years extending from 2003/2004 to 2013/2014 in a South European estuary on the Iberian coast (Oria river, Bay of Biscay) (Aranburu et al., 2016). Glass eel density was predicted using both commercial and experimental glass eel fisheries and a mixed generalized additive model. Current and depth were selected as covariates and date as a random variable then extrapolated to the whole sampling point volume to obtain the daily recruitment. The average seasonal daily recruitment and fishery data were combined to obtain the seasonal recruitment.

- The Vilaine data series represents commercial catches: an important professional fishery operates in the estuary downstream the dam. A trap is located on the dam. The remaining glass eels arriving after the fishing season can thus be caught at the trapping ladder. The relation between glass eel catches and estuarine recruitment is quite well known in the Vilaine estuary where mark recapture experiments were conducted during three years to estimate the escapement from the fishery and also the efficiency of the pass. Therefore, it is possible to estimate the size of estuarine recruitment after the end of the fishery in early spring until summer. Statistical analysis shows that commercial fishery is so efficient (95%) that total catches can be used to estimate total recruitment (Briand et al., 2003)

- In the Somme estuary, commercial fishing takes place downstream from an estuarine dam. On the basis that glass eels were also blocked by this obstacle, an expert-estimated exploitation rate of 75% was used (Drouineau et al., 2016) but no in depth analysis was carried out contrary to the Vilaine estuary. A modulation will be applied to allow for an uncertainty around this estimate.

- Most eel traps are located in Northern Europe (Frémur, Bresle, Viskan, Imsa, Bann, Erne, Shannon, Feale, Inagh, and Maigue), except one in *Vaccares* since commercial glass eel fisheries would not be cost-effective in these areas (Fig.5 and Appendix.1). The trap is generally located upstream an obstacle (dams) to migration. Contrary to glass eel fishery data, those data may be partially impacted by local conditions since traps accessibility are influenced by river flow, water temperature, and eel body conditions. (Edeline et al., 2006; Acou et al., 2009; Crivelli et al., 2008; Piper et al., 2012). However, trapping systems remained unchanged and Dekker (2000a) has shown that long time series can be relatively insensitive to individual aberrant year events, allowing comparisons between data gathered in different ways from different locations. Moreover, an overall analysis would be useful for distinguishing unwanted measurement error from true year-to-year variation in recruitment. The absolute recruitment is then calculated by applying a transfer efficiency that accounts for the average percentage of glass eels going through the obstacle (see part II.2).

However, many trapping sites located in northern Europe especially in the Baltic Sea (Fig.5) collect several age classes composed of young yellow eels. These sites are not suitable since they do not reflect only the year class strength of new recruits from the ocean but several sizes/year classes are recorded simultaneously (ICES, 2016; See Annex 10). For this reason, these data were removed.

Figure 5: Location of the recruitment monitoring sites in Europe, yellow circle = glass eel commercial catches, orange circle = glass eel commercial CPUE, red circle = glass eel scientific estimate, orange star = absolute recruitment estimate derived from trapping sites, red star = other absolute recruitment estimate, black square = recruitment time series removed.

2. Presentation of the model GEREM

The model has been developed and implemented to estimate yearly absolute recruitment at three nested spatial scales, and it has already been applied to the French EMUs (Drouineau et al., 2016). This model runs within a hierarchical Bayesian framework which allows inferring absolute recruitment at larger scales from observations carried out at catchment scales. This approach allows incorporating prior information regarding the different parameters included in the model while accounting for uncertainty in parameters and processes simulated within the model.

State-space model

In the present study, we are applying the model to much of the European eel's range. Hence, the model estimates absolute recruitment at the catchment scale, at an intermediate scale which account for recruitment at regional levels, and finally, the model aims to evaluate the overall recruitment throughout Europe. The three different levels are explained hereafter:

- The European recruitment R(y) corresponds to the absolute recruitment of glass eels over the whole study area during year y. The studied area is composed of N_z zones.
- Zonal recruitment $R_z(y)$ corresponds to the absolute recruitment of glass eels within a zone z. A zone represents a geographical sub-area of the whole study area in which n_z river catchments are present with their own surface area: $S_{1,z},\ldots,S_{nz,z.}$ Catchment surfaces were recorded in the CCM database (Vogt and Foisneau., 2007)
- River catchment recruitment $R_{c,z}(y)$ corresponds to the glass eel recruitment over a river catchment c, which is located in zone z and is characterized by its catchment surface $S_{c,z.}$

We assume that the overall recruitment is divided into recruitment zones according to a multinomial distribution. The multinomial distribution is a generalization of the binomial distribution. We have N_z possible mutually exclusive outcomes with corresponding probabilities p_z (y) and R(y) independent trials. Hence, the random variables $R_z(y)$ indicate the number of leptocephali distributed within a specific zone. However, the multinomial distribution can be approximated by marginal normal distributions (Johnson et al., 1997):

$$R_Z(y) \sim Normal\ (\mathrm{R}(y) * p_z\ (y)) \qquad (1)$$

Similarly, zonal recruitment is divided into river catchments according to a multinomial distribution with proportions equal to a relative surface area within the zone. The multinomial distribution is once again approximated by marginal normal distributions:

$$R_{c,z}\ (y) \sim Normal\ (R_z(y) * w_{c,z}\ , R_z(y) * w_{c,z} * \left(1 - w_{c,z}\right)) \qquad (2)$$

The weight $w_{c,z}$ of each catchment is calculated as a power function of its surface:

$$w_{c,z} = \frac{S_{c,z}^{\beta}}{\sum_{c_i=1}^{n_z} S_{c_i}^{\beta}} \qquad (3)$$

A β value close to 1 would mean that recruitment is proportional to catchment surface, which can be considered as a proxy of available habitat. Tosi et al. (1990) suggested that salinity gradient may be the most important factor guiding glass eels towards river habitats. This should be directly reflected by river discharge and river plume in a given area. If river discharge and salinity gradient are the main factors influencing the proportions in each catchment, then the power is less than one. Indeed, Burgers et al. (2014) demonstrated through a meta-analysis that catchment area was the main factor influencing the river discharge according to a power regression with a power less than 1. A power greater than 1 would imply an over-concentration of glass eels in large catchments. However, this is unlikely due to the occurrence of large commercial catches in small catchments.

Finally, the overall recruitment is assumed to follow a random walk:

$$R(y) = R(y-1) * e^{\epsilon(y)} \text{ with } \in (y) \sim Normal(0, \sigma_R^2) \tag{4}$$

Observation model

Four types of observed time series were available to fit the model contrary to the application to French EMUs where only two types of data were considered. Observed time series are assumed to be log normally distributed, according to ICES (2016).

- The first type of data (1) refers to relative abundance indices i observed in a catchment c:

$$\log(IA_{i,c}(y)) \sim Normal(\mu_{IA_{i,c}}(y), \sigma_{IA_i}^2)$$

With $\mu_{IA_{i,c}}(y) = \log\left(q_i * R_{c,z}(y)\right) - \frac{\sigma_{IA_i}^2}{2}$ (5)

With q_i a scaling factor on which no prior information is available.

- The second type of observed data (2) corresponds to the Somme estuary recruitment time series (commercial fishery total catches) for which an exploitation rate estimate of 0.75 is available with some uncertainties around this estimate. The recruitment has the same properties than relative indices from type 1, but with an informative prior on g based on this expert knowledge:

$$\log(\mathrm{IE}(y)) \sim Normal(\mu_{IE}(y), \sigma_{IE}^2)$$

With $\mu_{IE}(y) = \log\left(g * R_{c,z}(y)\right) - \frac{\sigma_{IE}^2}{2}$ (6)

- Similarly, the third type of data (3) consists of recruitment time series i derived from counting in trapping site c. The index is assumed to be proportional to the absolute recruitment with credible transfer efficiency coefficients on which we were able to build informative prior:

$$\log(IP_{i,c}(y)) \sim Normal(\mu_{IP_{i,c}}(y), \sigma_{IP_i}^2)$$

With $\mu_{IP_{i,c}}(y) = \log\left(a_c * R_{c,z}(y)\right) - \frac{\sigma_{IP_i}^2}{2}$ (7)

- Finally, the last type of data (4) relates to “true” absolute recruitment time series (or even punctual estimates) i observed in a catchment c:

$$\log(U_{i,c}(y)) \sim Normal(\mu_{U_{i,c}}(y), \sigma_{U_i}^2)$$

With $\mu_{U_{i,c}}(y) = \log\left(R_{c,z}(y)\right) - \frac{\sigma_{U_i}^2}{2}$ (8)

Type 4 directly provides an absolute estimate. However, contrary to type 1, types 2 and 3 also inform on absolute recruitment because of the informative priors on their respective scaling factors.

Prior information and expertise

Prior information has been included in the model (Table 1).

The proportion of glass eel recruiting to continental waters within each zone is assumed to vary over time, contrary to the Fench application by Drouineau et al. (2016). The parameters $p_z\ (y)$ are directly dependent on the proportions of the previous year through a dirichlet distribution comporting a dirichlet concentration parameter λ (equal to 80). Indeed, attributing a high value to λ was thought to be a suitable way to smooth inter-annual variations and avoid abrupt changes. However, assigning a very high value to this parameter could have been a problem to estimate low recruitment levels in certain zones of the study area. In this way, a good compromise was to assign a value equal to 80 for this parameter. The overall recruitment during the first year was given a large range of values considering the possible levels of recruitment before the overall decline in the late 1970s. The parameter *g* was assumed to vary between 0.65 and 0.85 given the expert's opinion regarding the level of exploitation rate in the Somme estuary. Global passage efficiency a_c is estimated for each recruitment time series originating from a fish pass monitoring station. This parameter is assumed to be time-invariant, and estimates the average behavior with which glass eels locate the fish way entrance and go through the pass. A meta-analysis carried out by Noonan et al. (2012), demonstrated that global upstream passage efficiency was around 21.1%. Moreover, Briand et al. (2005) found an efficiency of an order of magnitude of 30% in 1999 and 2000 in the Vilaine estuary for glass eels. Similar calculations with Jessop (2000) provide efficiencies of 20% at the downstream site and 40% at the upstream site. Finally Drouineau et al. (2015), estimated a global passage efficiency of 30%. Given the findings presented above and the variations of glass eel passage efficiency across monitoring sites in Europe, we consider that a_c were included between 0.1 and 0.5.

Table 1 : Prior information and estimated parameters used in the model GEREM

Parameters	Priors	Rhat
$\boldsymbol{\beta}$: power parameter of the relation between catchment surface and proportion of recruitment	$\beta \sim \mathrm{Unif}\,(0.01,2)$	1.01
$\mathbf{p_z(1)}$: proportion of recruitment in zone z the first year	$\begin{bmatrix} p_1(1) \\ \vdots \\ p_{N_z}(1) \end{bmatrix} \sim \mathrm{Dirichlet} \begin{bmatrix} \frac{1}{N_z} * \gamma \\ \vdots \\ \frac{1}{N_z} * \gamma \end{bmatrix}$	Min 1.00 Max1.03
$\boldsymbol{\gamma}$: dirichlet concentration parameter for $\boldsymbol{p_z\,(1)}$	$\gamma \sim \mathrm{Unif}(0.5,1)$	
$\boldsymbol{p_z(y)}$: proportion of recruitment in zone z in any given year	$\begin{bmatrix} p_1(y) \\ \vdots \\ p_{N_z}(y) \end{bmatrix} \sim \mathrm{Dirichlet} \begin{bmatrix} p_1(y-1) * \lambda \\ \vdots \\ p_{N_z}(y-1) * \lambda \end{bmatrix}$ With $\lambda = 80$	Min 1.00 Max 1.03
$\mathbf{R(1)}$: recruitment in first year	$\mathrm{Log(R(1))} \sim \mathrm{Unif(14,17)}$	1.01
$\mathbf{q_i}$: catchability of relative index i	$\log(\mathrm{q_i}) \sim \mathrm{Unif}\,(-13,0)$	Min 1.00 Max 1.03
$\mathbf{a_c}$*:* transfer efficiency coefficient through the pass c	$\mathrm{Log(a_c)} \sim \mathrm{Unif}\,(-2.3, -0.7)$	Min 1.00 Max 1.01
$\mathbf{g}$: exploitation rate in the Somme estuary	$\mathrm{Log(g)} \sim \mathrm{Unif}\,(-0.43, -0.16)$	1.00
$\boldsymbol{\sigma_{\mathrm{IA_i}}}$: standard deviation of observation for data(1)	$\tau_{\mathrm{IA_i}} = \frac{1}{\sigma^2_{\mathrm{IA_i}}} \sim \mathrm{Gamma}\,(2,1)\ \mathrm{T}(1,15)$	Min 1.00 Max 1.02
$\boldsymbol{\sigma_{\mathrm{IE}}}$: standard deviation of observation for data (2)	$\tau_{IE_i} = \frac{1}{\sigma^2_{IE_i}} \sim \mathrm{Gamma}\,(2,1)\ \mathrm{T}(1,15)$	1.00
$\boldsymbol{\sigma_{\mathrm{IP_i}}}$: standard deviation of observation for data (3)	$\tau_{IP_i} = \frac{1}{\sigma^2_{IP_i}} \sim \mathrm{Gamma}\,(2,1)\ \mathrm{T}(1,15)$	Min 1.00 Max 1.01
$\boldsymbol{\sigma_{\mathrm{U_i}}}$: standard deviation of observation for data (4)	$\tau_{\mathrm{U_i}} = \frac{1}{\sigma^2_{\mathrm{U_i}}} \sim \mathrm{Gamma}\,(2,1)\ \mathrm{T}(1,15)$	Min 1.00 Max 1.01
$\boldsymbol{\sigma_{\mathrm{R}}}$: recruitment random walk standard deviation	$\tau_{\mathrm{R}} = \frac{1}{\sigma^2_{\mathrm{R}}} \sim \mathrm{Gamma}\,(2,1)\ \mathrm{T}(1,15)$	

Modelling assumptions

In order to estimate the absolute overall recruitment, the model requires at least one index of type 2, 3 or 4 in each zone. Regarding equations (2) and (3), two main underlying assumptions are made. First we consider that recruitment in a catchment river within a specific zone is almost proportional to its surface, so we indirectly assume that similar densities of glass eels are present within a zone. Second, all recruitment index must follow approximately the same trend within the same zone. As such, six geographical zones are established across Europe in which at least one absolute recruitment index or a relative index with sufficient prior information on the scaling factor is provided (observed data of types (2), (3) or (4)) (Fig.5). It is widely recognized that glass eel abundances are maximal along the Bay of Biscay and in the English Channel. This assumption can be deducted from catches and Virtual Population Analysis models (Dekker, 2000b) and can also be inferred from ocean circulation models (Bonhommeau et al., 2009). As a consequence, the Bay of Biscay and the English Channel should not be merged with other parts of Europe.

Finally, we apply a dynamic factor analysis (DFA) (Zuur et al., 2003a) as a preliminary step, in order to study the different trends in recruitment across Europe and to check the assumption that recruitment follows the same trend within a zone. The principles underlying DFA analysis will be detailed below (see II.3)

Bayesian inference

The model was fitted using JAGS (Just Another Gibbs Sampler). The runjags package was used as an interface from R to the JAGS library for Bayesian data analysis (Denwood et al. 2016). The model was fitted to the period 1960-2015 and three chains were run independently in parallel for 40000 iterations after a burn-in period of 40000 iterations. Convergence was checked using Gelman-Rubin diagnostics

Sensitivity analysis

Three analyses were carried out to test the influence of different assumptions on the results of the model.

First, absolute recruitment indices $U_{i,c}$ are considered to be unbiased in the model. To assess the effect of a systematic bias in absolute recruitment indices, we fitted the model successively to altered datasets. For each fit, one absolute recruitment index was multiplied by 1.1 to mimic a systematic bias of 10%. Underestimation was judged more likely than overestimation, since our absolute abundance estimates providing by GEMAC and Bru et al. (2009) models assume that catchability are equal to one.

Then we address the influence of the parameter β by fitting the model with three different values for β (0.5, 1, and 1.5). Indeed, information on β is mainly updated by the model through absolute recruitment indices $U_{i,c}$ present in the same zone (i.e. French Atlantic coast), which represents a small proportion when considering the overall study area (Fig.5). It is then possible that a variation in β does not necessarily impair the goodness of fit and remains credible from an ecological point of view.

Finally, we tested the effect of the value attributed to λ on the main results. The model was thus fitted with three different values: 60, 80 and 100.

3. A Dynamic Factor Analysis (DFA) to investigate the different trends in recruitment over Europe

Dynamic Factor Analysis is a technique used to detect common trends in a set of time series. While other dimension-reduction techniques like PCA are usually applied to treat large data sets, these are not able to take account of time in any way. DFA is a dimension-reduction technique designed for time series data and it can be used to model short and nonstationary time series in terms of common trends, effects of explanatory variables and interactions between the response variables (Zuur et al., 2003b; Zuur et al., 2003a).

Mathematics underlying DFA

The DFA model is given by:

$$Y_t = C + AZ_t + \beta X_t + \varepsilon_t \qquad \varepsilon_t \sim N(0, \sigma^2 V) \qquad (1)$$

Where Y_t is N-by-1 vector containing the values of the N time series at time t, Z_t is M-by-1 vector representing the values of the M common trends at time t, A is the N*M matrix containing factor loadings and determines the exact form of the linear combination of the common trends, ε_t is normally distributed noise (of dimension N-by-1) with expectation 0 and variance $\sigma^2 V$ where V is a covariance matrix. The intercept C is a vector of dimension N-by-1 containing an intercept for each time series. If one wants to include explanatory variables, X_t would be a vector containing the values of the L explanatory variables at time t and β is a N*L matrix containing regression coefficients. Hence, potential effects of explanatory variables are modeled as in linear regression.

If a loading is relatively large and positive, we know that the corresponding time series follows the pattern of the corresponding trend. If a loading is close to zero, we know it doesn't follow this pattern. A loading that is relatively large and negative indicates that the time series follows the trend opposite pattern. By comparing factor loadings, it can be inferred which group of time-series are related to the same common trends. Moreover, each error component ε_t has a different variance and the error components of different time series can be allowed to covary through an unstructured positive definite error covariance matrix V. The trends, which represent the underlying common patterns over time, follow a random walk, which is mathematically defined by:

$$z_t = z_{t-1} + \delta_t \qquad \delta_t \sim N(0, \sigma_\delta^2) \qquad (2)$$

σ_δ^2 is a diagonal error covariance matrix.

Setting up the DFA model

Among the recruitment time series detailed in section II.1, 33 time series out of a total of 41 time series were used in the present analysis. Indeed, some time series (Oria, Vaccares, Tiber, ChGEMAC, SeGEMAC, GIGEMAC, AdGERMA and LoGERMA) were removed because they consisted of few punctual estimates or they were in general too short to be useful in the DFA analysis (Appendix I). Time series were log transformed prior to analysis as they were assumed to be log normally distributed and they were also centered.

Here, we don't model any effect of explanatory variables. Although they represent real variables and are easier to interpret, our goal is not to explain the variations of our response variables but rather identify common patterns shared by the recruitment time series: the common patterns are modeled through hypothetical variables z_t. Moreover, if explanatory variables were included in the model, the trends z_t would only be able to capture the remaining variability not explained by the explanatory variables. As such, the DFA model used is:

$$z_t = z_{t-1} + \delta_t \ \text{ Where } \ \delta_t \sim MVN(0, Q)$$

$$y_t = Az_t + c + \varepsilon_t \ where \ \varepsilon_t \sim MVN(O, R)$$

$$z_0 \sim MVN(\pi, \Delta)$$

The package MARSS (Holmes et al., 2014) within R was used to do dynamic factor analysis. The DFA is a form of state-space model; it is fitted by maximizing the likelihood with Kalman filtering. An Expectation-Maximization (EM) algorithm was used for the optimization. Although some parameters were constrained and set to their default values to make the model identifiable (Q, π, Δ) , most parameters were fixed by the user. Although four different structures for the covariance matrix R can be applied (*diagonal and equal, diagonal and unequal, equalvarcov, unconstrained*), the two most appropriate structures remain the *diagonal and unequal* and *unconstrained* options. However, 33 time series with up to 4 common trends were modelled, and setting R to unconstrained was not possible as the algorithm was not stable with this option. Moreover, time series don't follow trends very different from one another, thus it is unlikely that DFA deliver common trends that are only related to few response variables, even with R fixed to *diagonal and unequal.* Setting R unconstrained makes it difficult to interpret remaining information shared by two response variables which can be geographically remote. For these reasons, we decided to set R diagonal and unequal. Moreover, we decided to test up to four different trends, and the model selection criteria (AICc) was used to determine the number of underlying trends.

4. Correlation analysis

Data used in the correlation analysis

Recruitment data

Since we want to carry out a correlation analysis at the European scale, six recruitment series estimated by GEREM were used to examine dependences between glass eel recruitment and large scale ocean-atmospheric factors. The recruitment estimates are thus equivalent to the $R_z(y)$ provided by the model GEREM. All time series were log-transformed and scaled before analysis. These estimates were thought to be long enough to perform long-term fluctuations analysis. On the other hand, they were able to capture inter-annual variations found in time series within a specific zone while smoothing the aberrant short term fluctuations found in only a few series which may be representative of data bias or local conditions. For these reasons, the $R_z(y)$ time series were considered as reliable recruitment index at a regional scale to assess short term and long term fluctuations.

Large scale ocean-atmospheric factors

All environmental time series were scaled before analysis.

- **Gulf Stream Index**

The Gulf Stream travels eastwards across the North Atlantic Ocean, becoming the North Atlantic current at about 55°W. The northern edge of the current is marked by a sharp fall in temperature called the “north wall”. Monthly charts of the paths of the north wall of the Gulf Stream are available from surface, aircraft and satellite observations since 1966 and these represent its path’s variability. The Gulf Stream is thought to be the main migration path of leptocephali across the Ocean but other successful transatlantic migration for leptocephali shifting towards the southern part of its distribution area seem possible (Kettle and Haines, 2006; Munk et al., 2010). Significant negative correlations have already been determined between glass eel recruitment and the Gulf Stream position index (Knights, 2003) that may be due to unfavorable currents . This effect may not be the same depending on the glass eel arrival location. Annual data from 1966 to 2014 were extracted from the website http://www.pml-gulfstream.org.uk/Data%20Web2014.pdf.

- **North Atlantic oscillation Index (NAO)**

The NAO is known as a large scale atmospheric pressure fluctuation between Northern and Southern Europe. It is defined as the difference of atmospheric pressure at sea level between the Azores and Iceland. The NAO induces changes on different time scales in the ocean circulation, the North Atlantic Oceans’ surface temperatures and the water masses over the North Atlantic Ocean, but with a variety of area-specific mechanisms (Visbeck et al., 2003). As such, it represents an integrative environmental index which can affect the glass eel recruitment success at different temporal and spatial scales. The NAO indices were extracted from the following website:

http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml. Indices were averaged per year and correlations were tested between 1960 and 2015.

- **Sea surface temperature**

Monthly global SST anomalies are available since 1856 and were stored on a 5*5 grid. The area weighted average was computed over the North Atlantic, basically from 0 to 70°N, on a monthly basis from 1856 onwards. North Atlantic SST were extracted from the website http://www.esrl.noaa.gov/psd/data/timeseries/AMO/ and averaged over years from 1960 to 2015. An increase in SST is thought to impact marine productivity and can entail shifts in species distribution according to the region considered (Nye et al., 2014). As such, it has already been suggested that SST in the Sargasso Sea could affect negatively primary production and then glass eel recruitment three years later (Bonhommeau et al.,2007). Moreover, Friedland et al. (2007) showed that a northward shift in the 22.5°C isotherm, which may have caused a displacement of the spawning area towards the north, resulted in a reduction of glass eel recruitment. Hence, the gradual warming trend may also have an impact on glass eel recruitment by affecting both spawning location and transport of leptocephali out of the Sargasso Sea.

- **Primary Production in the Sargasso Sea (PP)**

Dissolved organic matter and particulate organic matter (POM) in the form of zooplankton fecal pellets and larvacean houses are thought to be the main source of food for glass eel larvae (Mochioka and Iwamizu, 1996). Meanwhile, a strong linear relationship between phytoplankton and POM has been described by DuRand et al. (2001) allowing PP to be considered as a good proxy of leptocephali food. We used BATS (Bermuda Atlantic Time Series Study) primary production rates for years 1988-2012 provided by the Bermuda Institute of Ocean Sciences (http://bats.bios.edu/). The sampling procedure takes place at the BATS location (31°40’N 64° 10’W) at different depths from 0 to 140m, several times a month. Different studies and observations point a preferred depth of 160 m during daylight and 60m at night regarding glass eel distribution in the Sargasso Sea (Schoth and Tesch, 1982). Moreover, the hatching process spread over March-June (Tesch and Thorpe 2003). For these reasons we decided to average PP between 0 and 140m and between November and July to account for the time of transfer of PP in the first levels of the food chain as recommended by Bonhommeau et al. (2007)

Correlations analysis at different time scales

Both short-term and long-term correlations were tested at time lags +1, +2, and +3: recruitment estimates from GEREM $Y_{t+\tau}$ were correlated with environmental variables X_t with τ=1, 2 or 3. We also analyzed correlations between recruitment Y_t and $\overline{\overline{X_{t-\tau}^*}}$ where $\overline{\overline{X_{t-\tau}^*}}$ accounts for average conditions over the years t- τ to t. We choose to test correlations between recruitment estimates and environmental data up to a time lag of 3 years to account for processes potentially occurring during the spawning period within the Sargasso Sea and during the subsequent larval migration to the European coasts. Indeed, maximum migration duration is estimated to be not longer than 2-3 years (Bonhommeau et al., 2010). We didn’t take into account the period during which silver eels migrate back to the Sargasso Sea, assuming that this stage was not affected by large-scale oceanic factors due to its capacity to adapt to contrasted environments.

Interannual correlations

We first aimed to analyze correlations between inter-annual variations of recruitment and large scale ocean-atmospheric time series by means of the cross-correlation function (CCF). All environmental data were used in this first analysis except the SST for which we only wanted to test correlations based on its long term evolution. The CCF function (1) enables to investigate time-lagged relationships between environmental time series (NAO, GSI and PP in the Sargasso Sea) and recruitment estimates and should help to identify the nature of the relationship and how they are correlated in time.

$$\rho_{XY}(\tau) = E[(X_t - \mu_X)(Y_{t+\tau} - \mu_Y)]/(\sigma_X\sigma_Y) \quad (1)$$

Here, the influential time series called the input time series is X_t, whereas the output time series is Y_t. However, short-term correlations between the two time series can be masked by overlaying trends in both time-series, and time series models are required to separate autocorrelations within a single time-series from cross-correlations with another. Here, we removed the autocorrelations from each time series of data by fitting an ARIMA model to the data and by using the resulting residuals (procedure called prewhitening) (Appendix VIII). ARIMA models combine autoregressive (AR) and moving average (MA) models into a single statistical model with the option to difference the time series so that it aims to model the various degrees of autocorrelations within time-series. The modelling steps follow the Box-Jenkins methodology (Box and Jenkins, 1976). The CCF function is then applied to the stationary and prewhitened time-series.

Correlations and long-term fluctuations

Prewhitening the time series may hide coinciding long-term trends in the input and output time-series because removing the autocorrelation is equivalent to removing low-frequency variability from data. Therefore, significant correlations on larger time scales may not be visible after prewhitening. Because the environmental descriptors used here such as the SST, GSI and NAO may reflect slowly changing processes over large temporal scales, it would be useful to investigate this second type of correlation between recruitment index and environmental data. As recommended by Pyper and Peterman (1998), a MA model was used to smooth time series data by removing high frequency variation in order to analyze correlations resulting from low-frequency variability. However, smoothing can increase autocorrelations in the time series and Pyper and Peterman (1998) advised to modify the hypothesis testing procedure by computing a corrected degree of freedom for the sample correlation, following this equation:

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N}\sum_j r_{xx}(j) * r_{yy}(j) \quad (2)$$

Where N* is the corrected sample size, N is the initial length of both time series and $r_{xx}(j)/r_{yy}(j)$ are the autocorrelations of X and Y at time lag j. The autocorrelation r is defined by Box and Jenkins (1976) and modified by Chatfield (1989):

$$r_{xx}(j) = \frac{N}{N-j}\frac{\sum_{t=1}^{N-j}(X_t-\bar{X})(X_{t+j}-\bar{X})}{\sum_{t=1}^{N}(X_t-\bar{X})^2} \quad (3)$$

Where $\bar{X}$ is the overall mean. Moreover, autocorrelations were computed over a number of lags equal to N/5 as recommended by Pyper and Peterman (1998). The observed Pearson correlation coefficients were then compared to their theoretical distribution with N*-2 degrees of freedom.

III. Results

1. The different trends in recruitment highlighted by the DFA

A widespread decline over the European continent

Recruitment time series don't seem to be inconsistent between sites (Fig.6). The model containing three common trends was assumed to be the "best model" (AICc equal to 2321.639). Moreover, the normality, independence and homogeneity of residuals assumptions were verified (Appendix .2). The model containing four different trends received an AICc of 2319.366 which was lower than the previous model results, but with only a minor difference (inferior to 5) compared to the one with three common trends. Hence, the model with three common trends was selected to carry out further analysis.

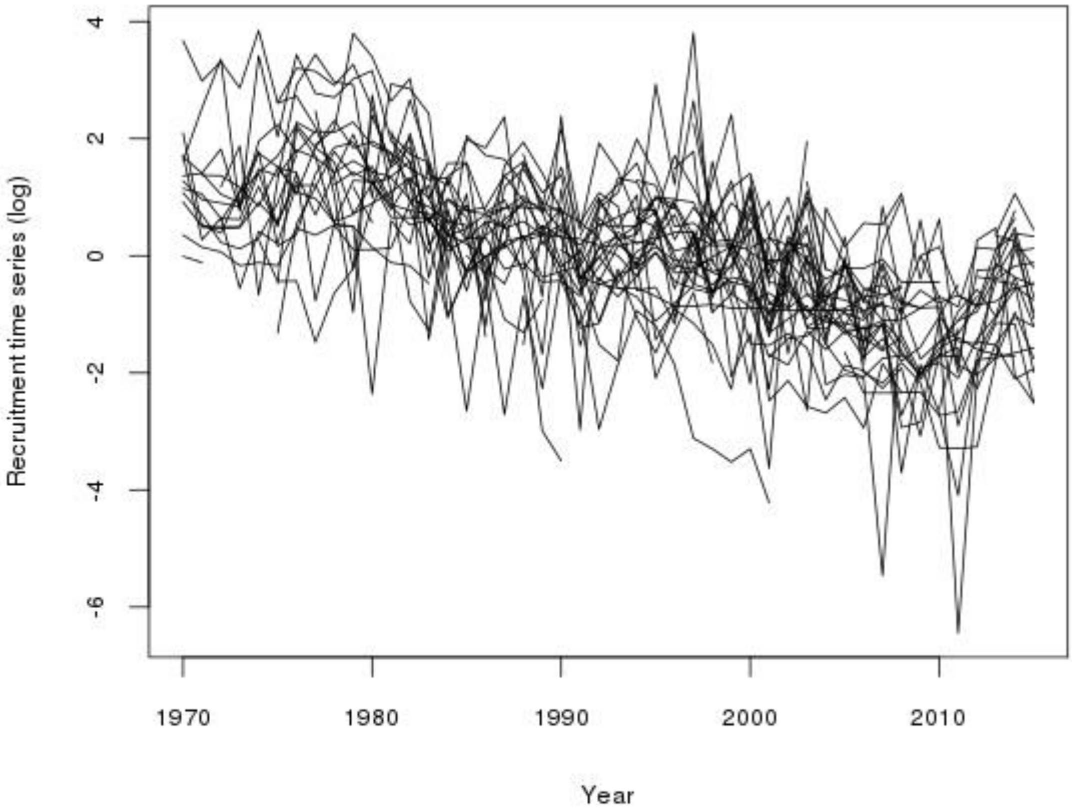

Figure 6: mean-deleted and log-transformed recruitment time series used in the DFA. Each line represents the time series at a site.

All common trends show a more or less pronounced decline differing in their timing. The first common trend (Fig. 7 a) shows a progressive decline with however three punctual and significant increases around 1980, 1995 and 2010 respectively. The present value is however far below the level of the 1970s. The second common trend (Fig7.b) sharply declined in the late 1970s and then stabilized since the early 1990s. Since most factor loadings are negative for the third trend (Fig.8c), we have to analyze its opposite pattern. In fact, this tendency shows a very slight increase from 1970 to the late 1980s followed by a very sharp decrease still ongoing (Fig7.c).

The overall pattern of a time series results from the combination of its three factor loadings and almost all time series have a positive factor loading for the first and second trends and a negative one for the last trend (Fig.8). This confirms that almost all time series show a significant decline more or less pronounced according to the relative importance of their three factor loadings. The first trend describes a general decline since almost all time series are associated to it. The second and third trends reflect a sharper decline and they discriminate early (trend 2) or late (trend3) declines. The IYFS1 and Fremur time series are very short and the model fits these series very poorly (Appendix III), so they shouldn't be taken into account. Moreover, we assumed that a series follows significantly a trend when its factor loading is above 0.2 (Fig.8) because under this threshold, the pattern seems hardly visible, as suggested by (Zuur et al., 2003b). Following this threshold*, Ebro*, *Minho*, *Adour estuary commercial CPUE* and *Adour estuary commercial catch* time series don't seem to have any clear significant trend but the combination of their three factor loadings also results in a drop for these series (Appendix III). Unsurprisingly, the DFA confirmed that we are observing a continent-wide decline of the recruitment of the European eel.

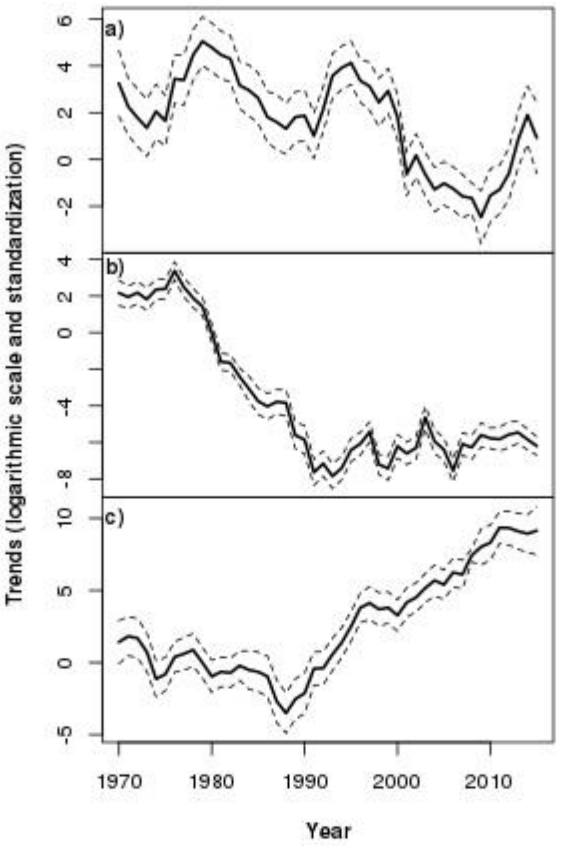

Figure 7: Common trends for the European recruitment time-series obtained by the DFA model containing three common trends (a, b, c).

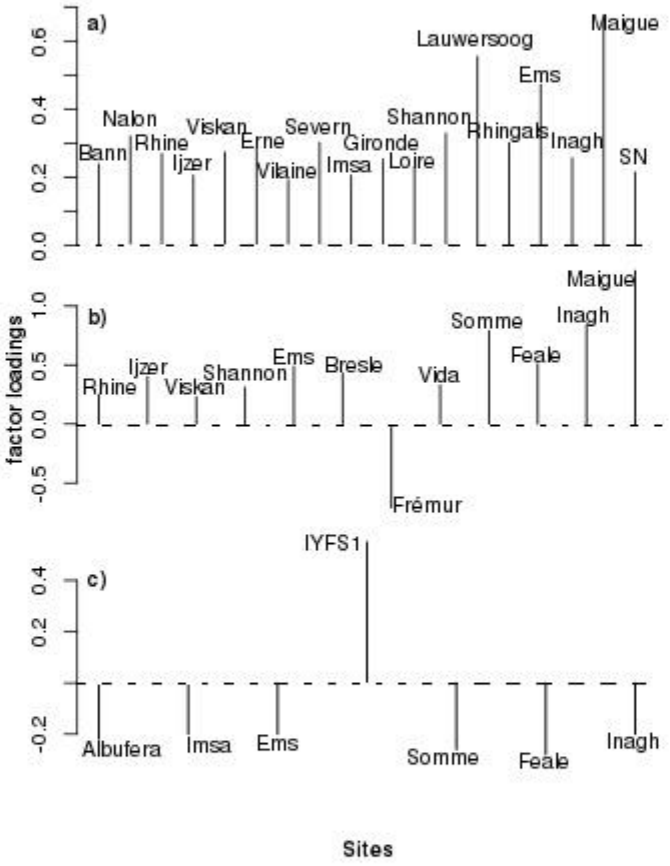

Figure 8: Factor loadings for the European recruitment time-series obtained by the DFA model containing three common trends. Factor loadings smaller than 0.2 were not plotted. Parts a, b and c contain the factor loadings for trends 1, 2 and 3, respectively

Is there any spatial pattern in eel recruitment?

Many series follow the first trend with a factor loading above 0.2 (Fig.8.a). Time series displayed on Fig.8.b and Fig8.c have an effective factor loading for the second or the third trend, and sometimes for both. Trend 2 and trend 3 reflect a sharper decline compared to trend 1, hence time series decreased more abruptly when associated to trend 2 or trend 3. It appears that there is a general latitudinal tendency whereby recruitment time series located in southern Europe (Bay of Biscay, Iberian coast and Mediterranean Sea) seem less impacted by the second and third trends (Tableau 2).

Most series located in southern Europe did not get any factor loadings above 0.2 for the last two trends, contrary to series located further north. We can then assume that northern recruitment time series are potentially subject to a faster decline compared to the overall pattern. To illustrate this, figure 9 shows the contribution of the three common trends on various series. The AdourCP series does not have any meaningful factor loading, and the series remains rather flat. Then, the Lauwersoog time series is dominated by the first trend and is not influenced by trends 2 and 3. Finally, apart from being influenced by the first trend, the Rhine, Imsa and Ems time series are associated with the second, third and both trends respectively. We therefore see that these last three series are more declining than the first two ones, with an intensity depending on their three respective factor loadings (Ems is the sharpest series because it got two significant factor loadings for both the second and third trends). This assumption whereby the time series of Northern Europe have been experiencing a more pronounced decline is similar to the conclusions that ICES drew in its previous reports (ICES 2013, 2014, 2016).

Table 2: Estimated factor loadings and sum of squared measured totals ($\sum_t y_{it}^2$), sum of squared residual totals ($\sum_t e_{it}^2$), and ratio of these two sums of squares for the DFA model with three trends.

	Factor loadings			Sum of squares		
Site	***Trend 1***	***Trend 2***	***Trend 3***	$\sum_t y_{it}^2$	$\sum_t e_{it}^2$	$\sum_t e_{it}^2 / \sum_t y_{it}^2$
Bann	**0.24**	0.11	-0.12	80.84	27.99	0.35
Erne	**0.28**	-0.15	-0.15	57.48	18.08	0.31
Shannon	**0.33**	**0.31**	-0.11	150.22	46.84	0.31
Feale	0.18	**0.51**	**-0.28**	40.92	17.17	0.42
Inagh	**0.26**	**0.85**	**-0.20**	23.12	9.88	0.43
Maigue	**0.67**	**1.31**	-0.07	52.25	5.95	0.11
Rhine	**0.27**	**0.25**	-0.03	80.31	5.29	0.07
Ijzer	**0.21**	**0.40**	-0.16	211.52	26	0.12
Viskan	**0.27**	**0.23**	-0.16	164.28	52.58	0.32
Imsa	**0.21**	0.16	**-0.20**	146.51	68.82	0.47
Lauwersoog	**0.55**	-0.01	0.07	46.03	7.08	0.15
Rhingals	**0.30**	0.03	-0.07	36.52	12.20	0.33
Katwijk	0.13	0.03	-0.08	48.49	37.63	0.78
Ems	**0.47**	**0.49**	**-0.21**	184.30	24.65	0.13
Stellendam	0.10	0.07	-0.17	22.45	5.64	0.25
IYFS1	-0.14	0.07	**0.55**	21.42	11.41	0.53
IYFS2	0.08	-0.01	-0.08	4.56	1.72	0.38
Vida	-0.01	**0.34**	-0.01	42.41	20.5	0.48
Severn	**0.30**	0.12	-0.06	56.97	9.88	0.17
Bresle	0.07	**0.43**	-0.18	8.94	3.22	0.36
Frémur	-0.02	**-0.7**	-0.005	18.6	12	0.65
Somme	0.15	**0.79**	**-0.26**	11.40	0.1	0.009
Vilaine	0.19	0.10	-0.12	42.64	2.44	0.06
Gironde	**0.25**	0.07	-0.04	24.34	4.92	0.20
Loire	**0.23**	0.19	-0.06	47.53	1.49	0.03
AdourCPUE	0.11	0.1	-0.03	11.81	2.30	0.2
Adour	0.13	0.14	-0.07	8.14	3.38	0.42
Sèvres N	**0.21**	0.14	0.09	3.19	2.34^{E}-10	7.36^{E}-11
Nalon	**0.32**	0.13	-0.17	100.83	5.74	0.06
Minho	0.16	0.11	-0.15	40.62	6.8	0.17
Ebro	0.08	0.15	0.01	33.73	16.64	0.49
Albufera	0.02	0.11	**-0.21**	57.95	14.05	0.24
Tiber	-0.03	0.15	-0.19	25.42	3.14	0.12

However, the North/South spatial segregation highlighted by the DFA analysis and ICES works is far from perfect, especially when performing a hierarchical clustering. The hierarchical clustering was carried out on recruitment time series based on the combination of their three factor loadings by using the Ward's minimum variance (Fig.10). Some series were withdrawn in this analysis (*Katwijk, IYFS1, IYFS2, Bresle, Frémur, Somme, Feale, Inagh, Maigue, and Sèvres Niortaise*). Katwijk was very poorly fitted (Table 2; Appendix III) so that the model fitted to this series did not reflect its trend. Moreover, other series were discarded because they were too short. Indeed, the different models fitted well these series but over a very short period and sometimes the overall models were aberrant, as it was the case with IYFS1 and Fremur time-series (Apendix III). At best, there remained an indetermination concerning the relevance of the overall model fitted to these series. Vida was also short extending from 1971 to 1990, but there remained much less ambiguity regarding the model fitted to this series. Indeed this series experienced a very sharp and early decline which was totally coherent with trend 2. (Appendix III)

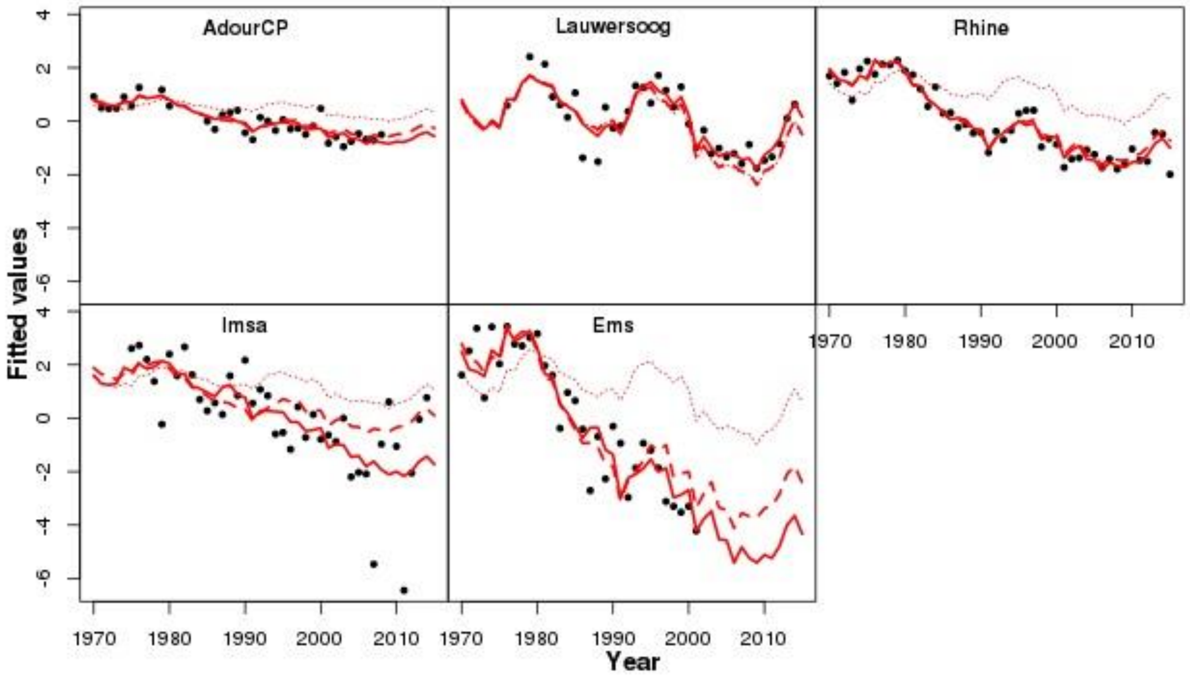

Figure 9: effects of the three common trends on various recruitment time-series in the DFA analysis. The dotted line is the curve obtained by $a_{i1}z_{1t} + c_i$ and illustrates the effects of the first common trend on each recruitment time series i. The dashed line represents the effects of the first two common trends ($a_{i1}z_{1t} + a_{i2}z_{2t} + c_i$), and the solid line is the model fit.

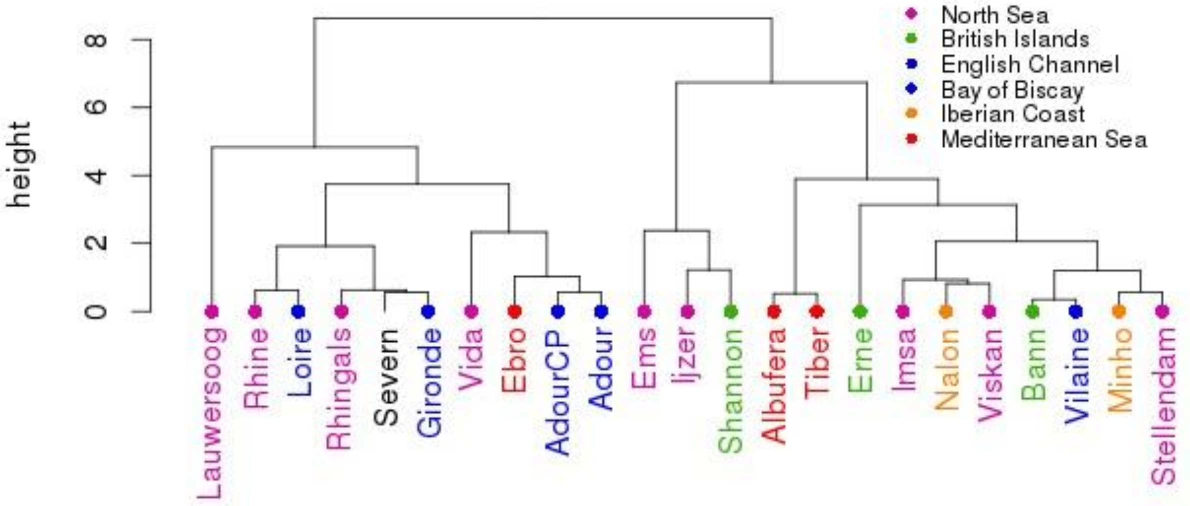

Figure10: Hierarchical clustering of the recruitment time series based on their factor loadings determined by the DFA analysis.

The hierarchical clustering does not reveal any clear spatial pattern but there is rather a mixture of recruitment time series coming from different areas within each group of the cluster. This conclusion was also put forward by ICES (2010) while performing a range of analysis (cluster analyses, PCA, and MDS techniques) on recruitment time series where they did not find any consistent spatial clustering. As such, the European eel population has been experiencing an overall decline but no precise and clear spatial clustering has been found at the European level: some series distant geographically could demonstrate similar trends (e.g. Stellendam and Minho) whereas other series geographically close differed (e.g.

Lauwersoog and Stellendam) (Fig.10). This could be due to variations in local conditions rather than a different trend as suggested by ICES (2010). If a spatial pattern exists, it is more likely to be a latitudinal pattern as shown in Tableau 2 or in the ICES GLM analysis with the series of Northern Europe showing, in average, a more pronounced decline than those coming from southern Europe. Hence, the different zones constructed in the model GEREM (Fig.5) should be appropriate, especially in view of the hypothesis that same densities of glass eels occur in the same zone.

2. The European eel stock situation through the model GEREM

Robustness of the model

Gelman and Rubin diagnostics confirmed that the chain converged after 80000 iterations (40000 burn-in and 40000 samples for inference). $\bar{R}$ Statistics were less than 1.03 for all parameters (Table 1).

The posterior distributions of some $\tau_{IA_i}, \tau_{IE}, \tau_{U_i}, \tau_{IP_i}$ (precision of observed time-series) were influenced by their respective prior distributions (Appendix IV). However, since the precision in a lognormal distribution is nearly equal to the inverse of the squared coefficient of variation, we considered that the precision should be greater than 1 (i.e. a coefficient of variation inferior to 1). Greater values leaded to unlikely dissymmetries with median and modes very distinct from the mean, especially when the mean is low (because of the Laurent correction). Moreover, the parameters log (a_c) and log (g) (scaling parameters for trap series and total catches in the Somme estuary) were also influenced by their respective prior distributions in some cases (Appendix IV) but we thought that prior knowledge was reliable enough to keep them. The discrepancy between prior and posterior distributions for those parameters is probably due the model assumptions of similar trends and densities of glass eels in a same zone. On the other hand, the model fitted quite well available abundance indices (Appendix V). On 41 time series available, only 8 abundance indices were less well fitted by the model (Appendix V and VI). As such, the model with its data, prior distributions, and modeling assumptions, was able to fit 80% of abundance indices, which suggests that the model assumptions were reasonable. The model fitted less well the SeGEMAC, Tiber, Bresle, Somme, Vaccares, Katwijk, Inagh and Erne time series which received a negative R^2 (a negative R^2 is sign of a systematic bias). SeGEMAC, Bresle and Somme abundance indices were poorly fitted because they may reflect recruitment densities slightly higher or lower than the average zonal densities within their respective zones. For the other ones, they were less well fitted by the model because they showed a general trend a bit different from the other series of the same zone. Both Tiber time series displayed a sharper decline than other series from the Mediterranean region, which was not visible during the DFA analysis. This was due to differences in data transformations: data were log transformed by removing null data in the model whereas a log (x+1) transformation was performed in the DFA analysis. This only impacted the trend of the Tiber time series which contained very low values at the end of the series, and consequently smoothed the trend in the last years.

Apart from these particular cases, the model was able to fit most abundance indices. This suggests that the model is likely to be trustworthy and reveal average behaviors and processes that govern recruitment of glass eel. Some time series were less well fitted because they might reveal local specificities in terms of density or temporal trend.

Recruitment estimates at different spatial scales

The overall European glass eel recruitment has been estimated and, unsurprisingly shows a clear decline from 1980 onwards. The recruitment was already decreasing in 1960, showing however a rise in the late 1970s but dropping again in 1980 (Fig 11). It seems that the overall recruitment is increasing since 2010 after a minimum level reached in 2009. The recruitment estimates for 2015 seems to be however lower than 2014. These findings are similar to the recruitment analyses performed by ICES (2016, see annex 8).

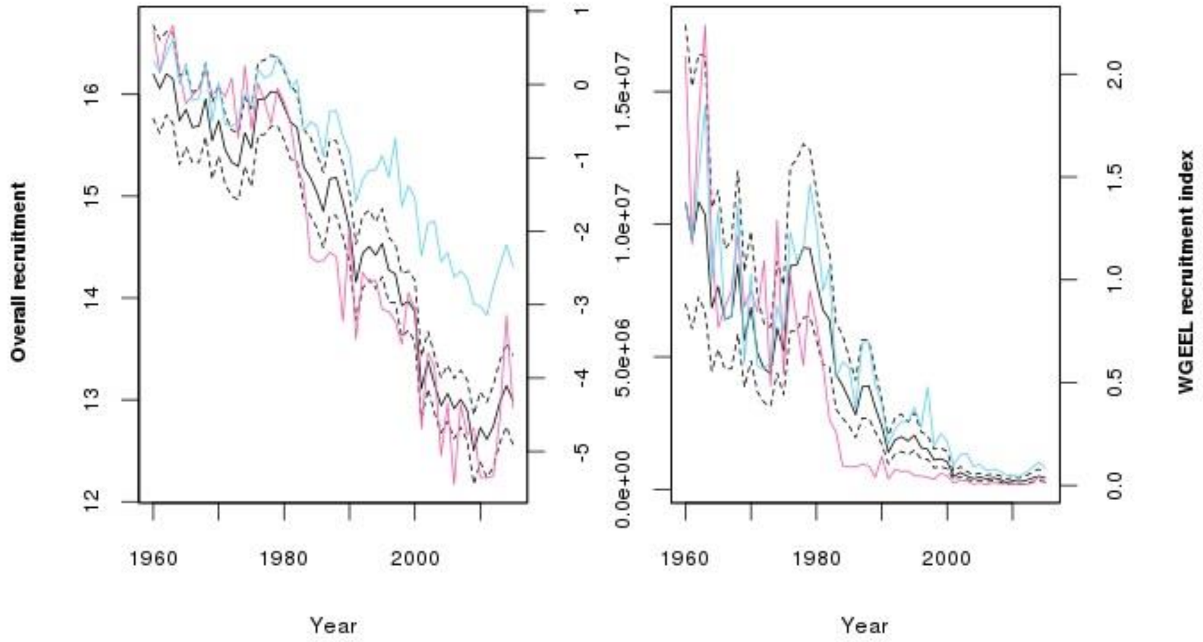

Figure 11: Estimated European glass eel recruitment by GEREM in log-scale (left panel) and in kg (right panel). Solid lines indicate the median whereas dashed lines represent the corresponding credibility intervals (95%). The blue line represents the "Elsewhere" WGEEL recruitment index and the pink line represents the "North Sea" WGEELrecruitment index.

The model estimates an overall recruitment of 10825 t in 1960 against a recruitment of 440 t in 2015 falling to almost 6% of the 1960-1979 average, which is consistent with ICES (2016) estimates (1.2% for the North Sea and 8.4% for elsewhere index). The coefficients of correlation between the European glass eel recruitment and "Elsewhere"/"North Sea" indices are equal to 0.98 and 0.89 respectively (Fig.11 right panel).

The overall study area covers a total surface of 2077693.5 km^2 and the maximum density at the European scale was equal to 5.22 kg/km^2 in 1960 whereas the ratio was equal to 0.13 kg/km^2 in 2009 when the recruitment reached its lowest level.

All $R_z(y)$ decline from the late 1970s or early 1980s onwards, except for the English Channel and the Mediterranean zones (Fig.12). In these two zones, recruitments decreased since the beginning of the period. However, the Albufera recruitment time series is the only series extending back to 1960 in the Mediterranean zone and clearly shows a substantial decline from 1960 onwards. Moreover, no recruitment time series extends back to 1960 in the English Channel. Hence, the earlier decline observed within this zone is not reliable as indicated by the larger credibility intervals from 1960 to 1975 in this zone (Fig.12).

The North Sea recruitment estimate is consistent with existing knowledge and well correlated to the "North Sea" index estimated by WGEEL with a correlation coefficient of 0.86 between the two indices. The recruitment indices from other areas are well correlated to the "Elsewhere" recruitment index calculated by WGEEL. The British Isles, Bay of Biscay, English Channel, Iberian Coast and Mediterranean Sea indices got a correlation coefficient of 0.90, 0.91, 0.65, 0.86 and 0.72 respectively. The English Channel and Mediterranean Sea indices are less well correlated to the "Elsewhere" index than other recruitment indices, but this may be due to the absence of long-term series as discussed above.

The 2015 recruitment level in the North Sea is 0.88% of the recruitment in 1960. For other zones, this ratio fluctuates between 2.77% (British Isles) and 8.58% (Iberian Coast). The slope of the English Channel recruitment index is not interpretable because of large credibility intervals at the beginning of the period due to lack of data in those early years. These trends confirm the conclusions drawn from the DFA analysis.

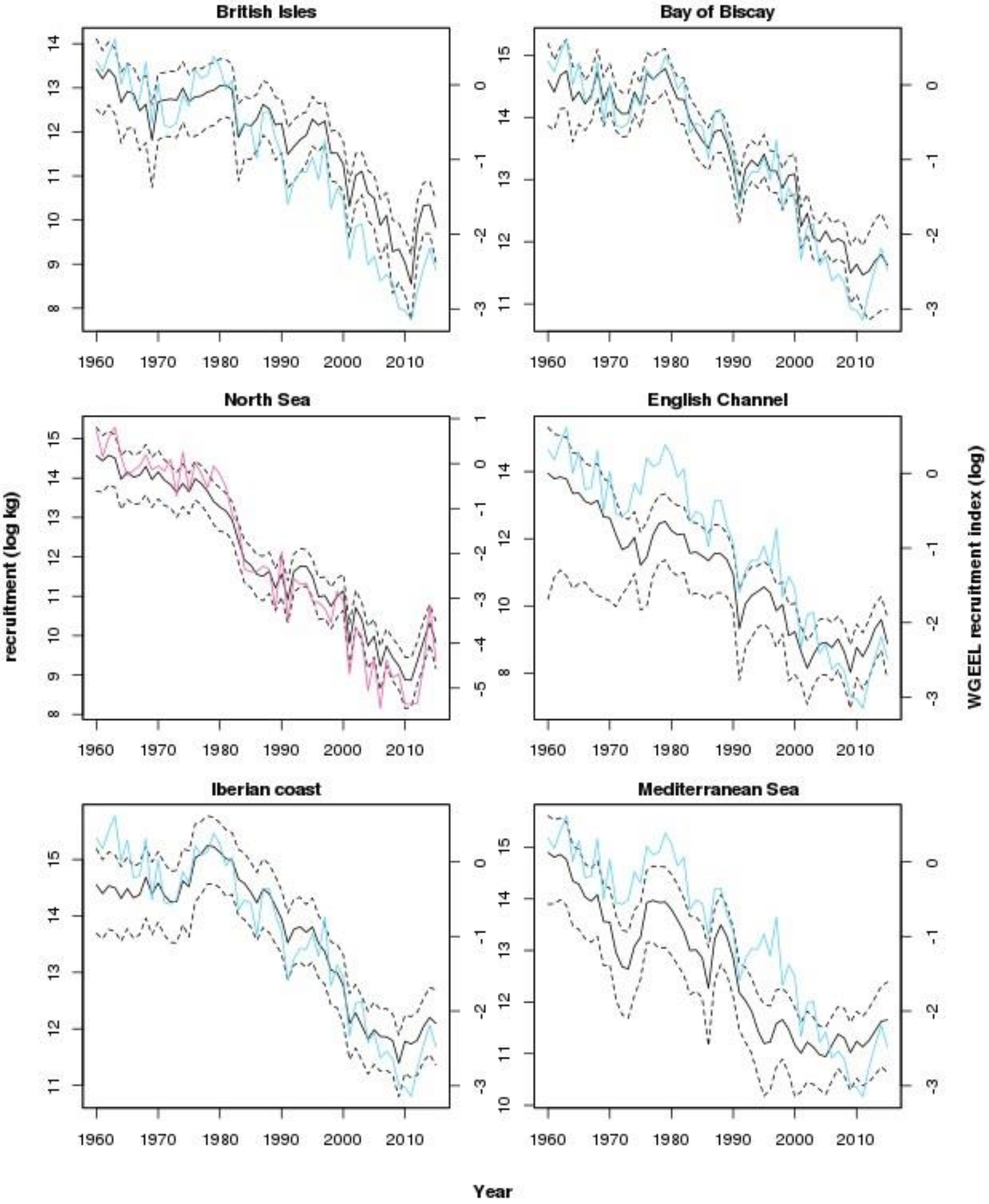

Figure 12: Estimated glass eel recruitment within each zone of the model GEREM in log-scale. Solid lines indicate the median whereas dashed lines represent the corresponding credibility intervals (95%). The blue line represents the “Elsewhere” WGEEL recruitment index and the pink line represents the “North Sea” WGEELrecruitment index.

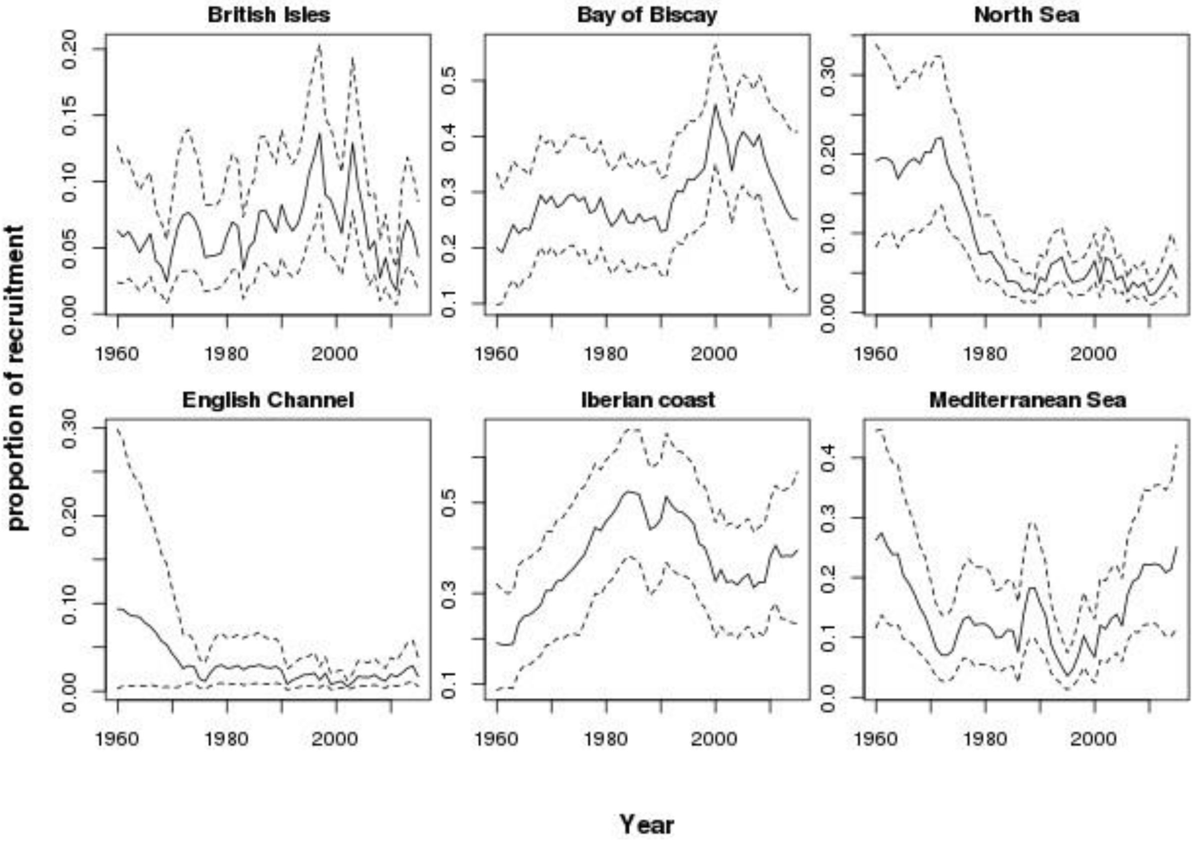

Figure 13: Proportion of glass eels recruiting to each zone of the model GEREM. Solid lines indicate the median whereas dashed lines represent the corresponding credibility intervals (95%)

The North Sea recruitment index has the sharpest decline over the European continent followed by the British Isles. This can be observed by analyzing the proportion of glass eel recruiting to each zone. According to the model, the proportion of recruitment in the North Sea zone drops substantially in the 1970s from 0.20 to stabilize close to 0.05 during the rest of the period (Fig13).

Besides being affected by the overall decline (Fig 11), the North Sea receives proportionally less and less glass eels over time which leads to a sharper decline during the study period. On the other hand, the Bay of Biscay and the Iberian Coast receive more and more recruits over time. In some way, this slightly smooths the decline resulting in a more moderate decrease over the study period for these two regions.

Recruitment is concentrated within two main zones: the Bay of Biscay and the Iberian coast. The Bay of Biscay concentrates between 20% and 45% of total recruitment while the Iberian coast supports between 20% and 50% of total recruitment (Fig.13), which also have the highest minimum and maximum densities (Tableau 3). The maximum level of recruitment appeared in the early 1960 for most series while it occurred in the late 1970s for the Bay of Biscay and Iberian Coast. This maximum explains the first increase occurring in the late 1970 and early 1980 visible in the first common trend of the DFA analysis. On the other hand, the minimum levels of recruitment happened in 2009 or 2011 for most series, except for the Mediterranean region where it occurred in 2005. This suggests that the decrease has slowed down or stopped in recent years.

At a finer scale (i.e. river basin), the power coefficient β had a median value of 0.76 with a 95% credibility interval comprised between 0.69 and 0.79. This parameter is thus significantly lower than 1 demonstrating that river discharge influences the proportion in each catchment.

Table 3: minimum and maximum absolute recruitment and densities estimated by the model GEREM for each zone. Years of minimum and maximum recruitment are presented in italics and in brackets.

	Absolute recruitment (kg)		Density (kg/km^2)	
	min	max	min	max
British Isles	5180 *(2011)*	675070 *(1960)*	0.04	5.38
Bay of Biscay	95190 *(2011)*	2633045 *(1979)*	0.36	10.03
North Sea	7090 *(2011)*	2149210 *(1962)*	0.01	2.97
English Channel	3060 *(2009)*	1139475 *(1960)*	0.02	7.02
Iberian coast	88710 *(2009)*	4191365 *(1978)*	0.23	10.74
Mediterranean sea	56625 *(2005)*	2947380 *(1960)*	0.14	7.14

Sensitivity analysis

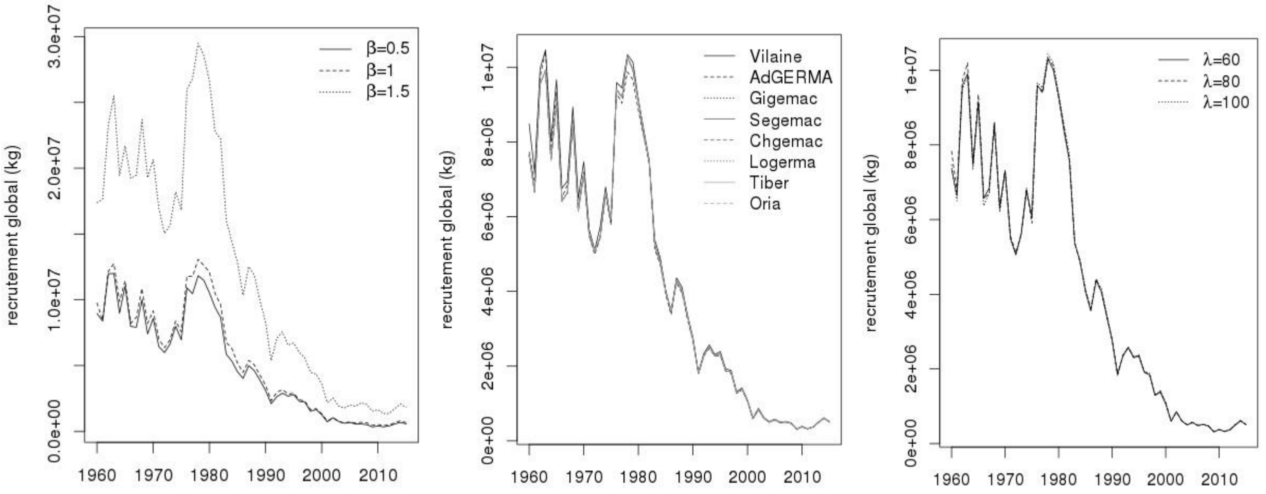

Figure 14: European recruitment (median) estimated by GEREM when fitting the model with different β values (first panel), on altered absolute recruitment datasets (second panel), and with different values for λ (last panel).

Whatever the scenario, the estimated trend for the European recruitment remained unchanged, which was most important aspect to check (Fig.14). The value of λ and the altered values of absolute recruitment indices had no effect on total recruitment. However, the value of β had a larger influence on results. Total recruitment was approximately 10% lower when β was set to 0.5 than when it was set to 1 in 1978 (where the largest difference occurs). However, it was approximately 2.25 times higher when β was set to 1.5 at the same time but this value is unlikely to occur as explained in II.2.

Changes made to absolute recruitment datasets and λ didn't affect the distribution of recruitment among zones (Fig A 7.1, Appendix VII).

As expected, changes to the *GiGEMAC* and *LoGERMA* series caused a very slight increase of the β value compared to other series (Fig A 7.2, Appendix VII). These series are related to the largest catchments (79605 km^2 and 116981 km^2 respectively) so that a relative increase of the recruitment in these catchments forced β to get closer to 1 to predict higher densities in bigger catchments. Interestingly, a change in the *SeGEMAC*, which is the smallest watershed, didn't cause a significant decrease of β compared to other larger catchments. An increase of λ didn't cause any significant modification of β (Fig A 7.2, Appendix VII). In all cases, the changes remained very small when compared to credibility intervals.

β was the parameter with the largest influence. However, we can notice a significant increase of R_z only when β is equal to 1.5 for most regions (Bay of Biscay, North Sea, Iberian Coast, and Mediterranean Sea) while changes were limited between the two most plausible values (0.5 and 1) (Fig A 7.1, Appendix VII).. Only two zones seem to be affected by a variation of β between 0.5 and 1. A decrease of R_z as β increase from 0.5 to 1 is noticeable for the British Isles region while the English Channel recruitment increases significantly at the same time. (Fig A 7.1, Appendix VII) For the British Isles zone, recruitment time-series (3) were collected in many catchments of similar surface ranging from 1075 km^2 (Maigue) to 4450 km^2 (Bann) whereas it was collected in a relatively small catchment for the English Channel zone (the Somme is a 6550 km^2 catchment whereas the Seine estuary in the same zone has a surface area of 78650 km^2).

3. Correlation analysis at the European scale

No correlations between recruitment indices and the GSI or the SST

Neither the GSI nor the SST have shown significant correlations with recruitment estimates whatever the time lag and the type of correlation tested (short-term vs long-term) (Appendix IX). However, we found a significant short-term positive correlation lagged by 6 (for the North Sea) or 7 years (for the Bay of Biscay and Iberian Coast) between the GSI and several recruitment indices (not shown) when performing cross-correlation analysis, which was beyond the maximum time lag originally intended. It is currently not possible to explain such correlations given these time lags, so we assumed that this correlation was due to hazard.

This absence of correlation between recruitment and GSI within an interval of 1-3 years indicates that there is no obvious linear relationship between glass eel recruitment success and the position of the Gulf Stream on both short and long time scales. This finding complements the results of Bonhommeau et al. (2007). Glass eel recruitment was not significantly affected by North Atlantic SST averaged over the different assumed migration periods. However, Bonhommeau et al. (2007) demonstrated a strong and significant negative relationship between variations of temperatures in the Sargasso Sea and recruitment indices, thereby suggesting a link between sea temperatures and subsequent glass eel survival but on finer spatio-temporal scales. The correlations between recruitment estimates at the European scale and Sargasso Sea temperatures were beyond the scope of this study but it would have been interesting to test it in order to complement the correlations results between recruitment and PP in the Sargasso Sea.

Short term correlations between certain recruitment indices and PP in the Sargasso Sea

Short-term correlations between PP in the Sargasso Sea and the North Sea/Mediterranean Sea recruitment estimates have been found. Results obtained with other recruitment estimates (not shown) were not significant according to the confidence threshold. More precisely, we found a significant positive correlation between the North Sea recruitment estimate and PP with a 2 years' time lag while a significant positive correlation was found with a 1 year time lag between PP and the Mediterranean Sea estimate (Fig. 15). This means that PP in the Sargasso Sea from November to July of years t-1/t seem to influence recruitment during winter of year t+2 or t+1 for the North Sea and Mediterranean Sea respectively. The 2 yrs. (North Sea) and 1 yr. (Mediterranean Sea) lagged correlations coefficients were equal to 0.46 and 0.6 respectively (Fig.15). Thus, fluctuations of PP in the Sargasso Sea might partly explain variations of subsequent recruitment. The difference of time lag in the correlations may be explained by a difference of migration duration between the Sargasso Sea and different parts of Europe (North Sea vs Mediterranean Sea in this example).

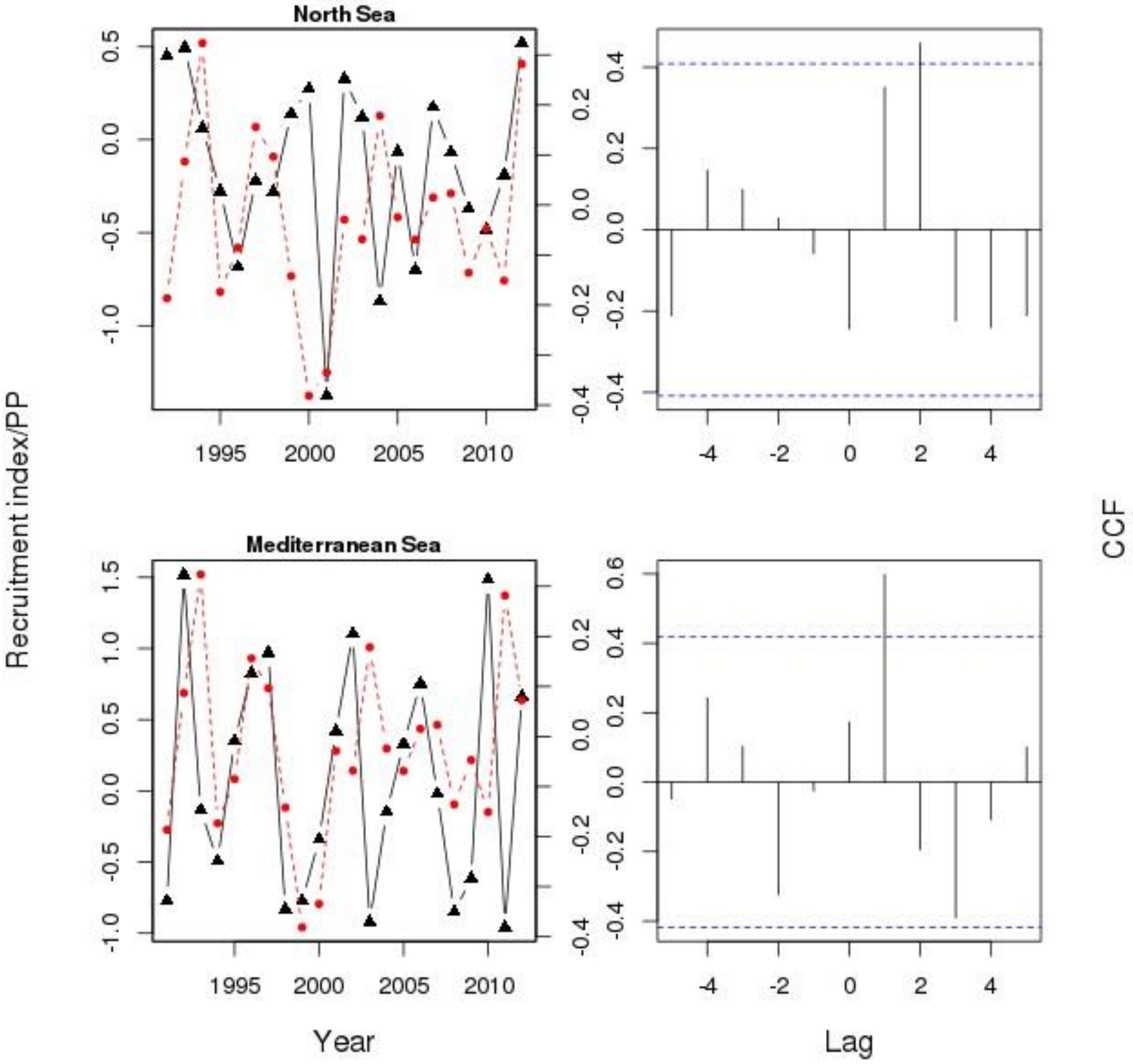

Figure15. Left panels: standardized and pre-whitened time series of GEREM recruitment estimates (black solid line with triangles) and PP in the Sargasso Sea 2 years lagged for the North Sea area and 1 year lagged for the Mediterranean Sea area (red dashed line with circles). Right panels: cross correlations of corresponding pre-whitened time series. Blue dashed lines indicate confidence threshold for α=0.05. This confidence interval relies on assumptions that 1) the processes generating recruitment estimates and PP in the Sargasso Sea are uncorrelated, 2) the processes are not auto-correlated, 3) the populations are normally distributed, and 4) the sample size is large

The NAO index affect the recruitment at a broad scale

Long-term fluctuations between recruitment estimates and NAO were finally not tested as NAO didn't show any trend and autocorrelations over the period 1960-2015. Most recruitment estimates were significantly and negatively affected by the NAO index on a short-time scale. Positive correlations are only found in the British Isles region, which is surprising since leptocephali drifting towards this region follow approximately the same migratory route than those shifting towards the North Sea or the English Channel zones. These positive correlations could be due to statistical coincidence. The correlations are, in most cases, lagged by 3 or 4 years, except for the Mediterranean Sea region where the correlation is lagged by only one year (Fig. 16). Although the strength of these correlations is questionable (correlations coefficients around -0.3), this finding led to the hypothesis that changes in the ocean related to the NAO may be influencing recruitment fluctuations: a high NAO index could contribute to a poor recruitment level after the migration process, as suggested by Knights (2003) and Friedland et al. (2007). Indeed, the NAO has been associated with changes in the physical and biological environment of the northeast Atlantic and the Sargasso Sea. Although no correlation has been found between the NAO and PP in the Sargasso Sea in the present analysis (not shown), changes in the NAO index appear to have the potential to both modify transport patterns of Atlantic eel leptocephali and affect their feeding success during the entire migration process (Miller et al., 2009). Since the NAO can have heterogeneous effects across the North Atlantic Ocean on a variety of temporal scales (Visbeck et al., 2003), it is hardly possible to determine the mechanisms behind the relationships detected in the present analysis. However, if the recruitment in the Mediterranean Sea is truly affected by the NAO and PP in the Sargasso Sea lagged by 1 year, then the migration duration could not exceed one year, contrary to other parts of Europe where correlations are found with more important time lags.

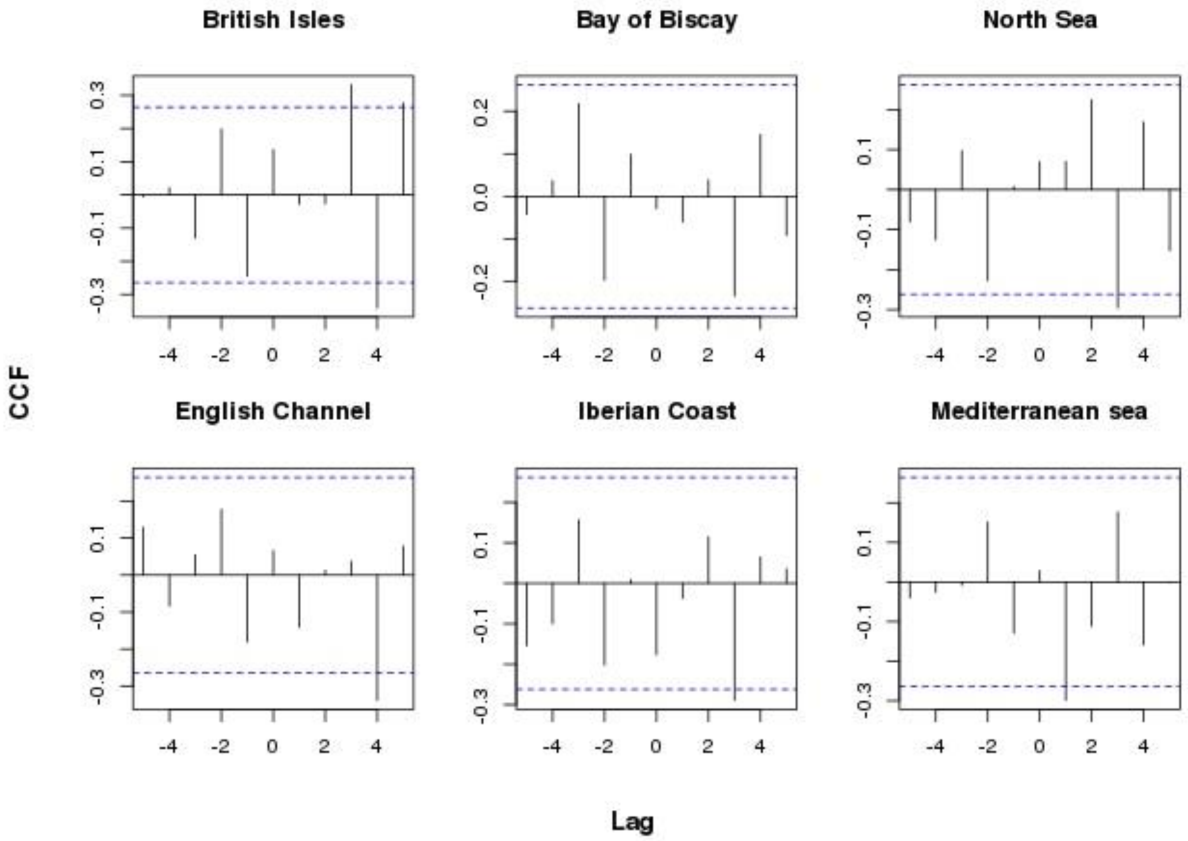

Figure16: Cross-correlations between pre-whitened GEREM recruitment estimates and NAO index. Blue dashed lines indicate confidence threshold for α=0.05. This confidence interval relies on assumptions that 1) the processes generating recruitment estimates and PP in the Sargasso Sea are uncorrelated, 2) the processes are not auto-correlated, 3) the populations are normally distributed, and 4) the sample size is large.

IV. Discussion

1. Modeling methodologies and underlying assumptions

In the present study, the model GEREM aims at estimating glass eel recruitment at the European scale by using individual recruitment time series scattered over Europe to derive an overall recruitment index. This exercise was challenging given data availability, and more importantly because of glass eel ecology. First, there is still a lack of recruitment time series data available across the whole continent. Second, the fractal distribution pattern of the European eel stock and trapping methods made the analysis rather difficult. In this context, Dekker (2000a) affirmed that the acquisition of exact and detailed knowledge of the total continental population was hardly possible.

Recruitment modeling

Besides global and regional effects, there exist local factors potentially affecting recruitment at the catchment scale. This was partly visible in the recruitment time series used in the present study. Moreover, the importance of environmental factors affecting glass eel migration can differ according to location, estuary characteristics and physiological status of the eels (Elie and Rochard, 1994; Zompola et al., 2008). Meanwhile, the model GEREM was conceived to overcome these heterogeneities and was largely designed to estimate estuarine recruitment freed from local conditions. As such, it assumed that recruitment at the catchment scale resulted from two successive multinomial distributions at two different spatial scales.

The recruitment within each zone was derived from a product of the overall recruitment and a proportion p_z, which was allowed to vary over time. This distribution is purely statistical and depicts the random passive distribution of leptocephali generated by oceanic currents among the different zones. At the finest spatial scale, the proportion of recruitment in each river catchment is a function of its surface area raised to a power β.

The model assumes that recruitment trends are similar within a same zone since the weight $w_{c,z}$ is a constant parameter over time. This assumes that no local process acts at a finer spatial scale than a zone to affect recruitment trend within a watershed. This assumption is important since zonal and subsequent overall recruitment trends rely directly on this hypothesis. It was thus necessary to identify regional zones where trends in glass eel recruitment remain similar. As such, the DFA didn't show any clear spatial clustering of recruitment time series based on their relative trends, but potentially a North-South gradient whereby northern recruitment time series illustrate in general a sharper decline than recruitment time series present in southern Europe The model fitted a majority of recruitment indices demonstrating that the two main assumptions of the model (same trends and same densities within a zone) were mostly verified. Some time series were less well fitted (Appendix V) either because they showed a notable different trend compared to series of the same zone (Tiber, Ems, Erne, Shannon, Imsa, Katwijk) or because they reflected higher or lower densities than average (SeGEMAC, Bresle, Somme). Indeed, Arribas et al. (2012) suggested that local phenomenon could sometimes contribute to the year to year variability in glass eel recruitment to estuaries over Europe. For example they showed that rainfall and westerly winds may generate more productive environmental conditions in local shelf waters off the Guadalquivir estuary, benefiting growth, survival and retention of leptocephali during the final step of their oceanic migration. Hence, a part of variability contained in these time series may be produced by local mechanisms not explained by the model. Ideally, local effects should be taken into consideration in the modeling procedure through, for example, a random effect around the weight $w_{c,z}$. However, in this case, the model didn't converge and could not extrapolate recruitment at the regional scale.

The factor β was equal to 0.76 revealing a more constrained credibility interval ([0.69-0.79]) compared to the French application (Drouineau et al., 2016) . The factor β was primarily updated thanks to observed data of type (4) present within a same zone (i.e. Bay of Biscay). However, prior scaling parameters such as g and a_c were very constrained (Appendix IV). As a consequence, the factor β might have been also updated thanks to series (2) or (3) in certain zones. This estimate encompasses the power coefficient of the relationship between average discharge and catchment area estimated by Burgers et al. (2014) [0.71-0.85], suggesting that river discharge play a major role in the orientation of glass eel towards estuarine habitats. Indeed, displacement upstream seems to be governed by salinity gradients in still waters, while the current strength seems to be the most useful cues to find the way upstream in flowing rivers (Aida et al., 2003). The coefficient β increased (compared to the first application) as more absolute recruitment indices were available. Meanwhile the model was shown to be sensitive to the value of β. It is thus important to keep including observed data of type (4) (and potentially (2) and (3)) to improve its estimation and that of glass eel recruitments at different spatial scales. Indeed, even though the general trend remained unchanged (which is the most important aspect in this study), the overall recruitment could be 10% lower when setting β to 0.5 instead of 1. Moreover, recruitment was also sensitive to the value of β in zones such as British Isles and the English Channel regions.

Information included in the model

The British Isles and North Sea regions were made up of recruitment time series of type (1) or (3). As such, absolute recruitment estimates within these zones are directly derived from recruitment time series (3) multiplied by a scaling factor a_c which stands for the average proportion of glass eels going through a fish way annually. Uncertainty intervals regarding estimates a_c were taken from a range of literature that aimed at studying fish way passability in the case of eels (Drouineau et al., 2015; Jessop, 2000; Briand et al., 2005) or migratory fishes more generally (Noonan et al., 2012) in a variety of geographical locations. Ideally, these estimates taken from the literature reflected both attraction efficiency and fishway passability, but didn't take into account the potential proportion of elvers remaining in the estuary. Indeed, past investigations showed that some anguillid eels sampled from coastal environments may spend their whole life in marine waters (Tsukamoto et al. 1998; Tsukamoto and Arai 2001), especially in the Baltic Sea (Tzeng et al., 2000). The mechanisms governing movements and migration behaviors resulting in the colonization of river systems remain poorly described. However, Aida et al. (2003) describes several recruitment mechanisms and movement behaviors, suggesting that some eels migrate upstream whatever the population parameters and environmental conditions (cf "*Pioneers*") while some others display density-dependent migratory movements (cf "*Founders*"). However, density threshold can depend on a variety of parameters, and more generally small elvers are considered to be active migrants (Imbert et al., 2010) and most obstacles were located close to the sea. We thus considered that most glass eels and elvers were likely to migrate downstream the fishway during the year, and that only a minor proportion may stay in the estuary.

Recruitment time series used in the model

There is no absolute recruitment estimate (4) currently available in Northern Europe, mainly due to the absence of glass eel fisheries, which represents a serious lack of information. Moreover, there is also a particular lack of information about recruitment to the east coast of England, thus there is a need to assess recruitment into the western parts of the North Sea. No information is yet available also in the Eastern or Southern Mediterranean Sea. A better spatial coverage through the implementation of new monitoring programs has already been proposed (Dekker, 2002a). These would be valuable data to improve estimates from the model GEREM.

The model was not sensitive to a systematic bias attributed to absolute recruitment time series, making these absolute estimates reliable. The estimated trend in the overall recruitment remained similar and the overall absolute recruitment remained unchanged. Because of the overall decline and high fishing efforts in some areas, we chose to give priority to total commercial catches as glass eel abundance indices (Gascuel et al., 1995). However, it could arise that CPUEs time-series were almost strictly identical to total commercial catch time series from the same catchment (Adour catchment, Fig.10). Meanwhile, some commercial catch time series showed a much sharper decline than the majority of other series across Europe (*Ijzer*, *Ems* and *Tiber*), which could be due to reduced operation intensities after several seasons with extremely poor catches (Dekker 2002b, Dekker 2002c). But this could also be due to true recruitment trends showing much sharper declines caused by regional or local phenomenon. Hence, further work would be required to select the most appropriate indices between catches and CPUE. Moreover, a common situation arising with CPUE and commercial catches is hyperstability. It occurs when CPUE or total catches remain stable while abundance decreases (Hilborn and Walters., 1992). This arises when fishermen change their behaviors as a function of abundance to target fish aggregations that are not representative of the overall status of the stock. However all fishery-based indices showed at least a substantial decline and displayed similar trends to other type of data, including scientific survey which should not be subject to this bias, making the hyperstability hypothesis unlikely.

2. GEREM: a stock assessment model to assess a widely distributed population

Towards an improvement of the trend-based approach

In this study, the model GEREM was developed to estimate European eel recruitment and to provide new insights on the state of the whole stock. Working with absolute estimates was required because the GLM analysis (ICES 2016) pointed out different trends in recruitment indices so that it was not possible to directly aggregate those indices. To do that, an intermediate step in GEREM consists in evaluating absolute recruitment at a regional scale where recruitment time series were assumed to follow the same pattern.

ICES advice on the status of the European eel stock is based on the analysis of the trend in eel recruitment (Category 3 – stocks for which survey-based assessments indicate trends) which is a quite simple approach based on the most reliable series available. However, this advice has been based on two different trends (i.e. North Sea and Elsewhere Europe) and didn't overcome the complex spatial structure of the stock (ICES, 2014). Hence, it was never possible to strictly assess the state of the European eel population as a whole which was not consistent with the panmixia hypothesis. In the present study, the model GEREM aimed to fill this gap by improving the overall glass eel recruitment estimate in order to refine the estimation of the overall trend.

The approach currently used by ICES to assess the state of the European eel population consists of a status-and-trend diagram where the reference value of the recruitment ($R_{reference}$) corresponds to the mean recruitment of the baseline period 1960-1979 and where the trend is calculated over a period of 5 years.

Contrary to previous works which used two different recruitment indices; we carried out the same analysis with the overall glass eel recruitment estimate derived from the model GEREM (Fig.19). It indicates that most recruitment estimates were within the critical zone while the recent years (2013, 2014 and 2015) showed a slight positive linear trend with however a very critical status far from the healthy zone. This explains the reasons why ICES advised to keep mortality levels as close to zero as possible in 2015 (ICES 2016).

Information on recruitment is essential to follow up natural variations and results of management actions over the area of distribution of the European eel. Even though they play a minor role in the national assessments, these are crucial to the overall evaluation of the population and Eel Regulation. Moreover, the model GEREM could provide a coherent methodological framework to meet ICES requirements in view of a Non-Detriment-Finding (NDF) assessment (ICES 2015a). Indeed, the scale to be used to make this assessment should cover the entire stock of the European eel and a positive glass eel recruitment trend over a minimum of one eel generation is thought to be an indication of a recovering stock while glass eel recruitment index fluctuating within the 1960-1979 reference baseline is an indicator of a recovered stock. Finally, the use of GEREM could be helpful in the determination of glass eel quotas over France and Spain since quota levels per EMU are set by taking into consideration recruitment levels within each river basin.

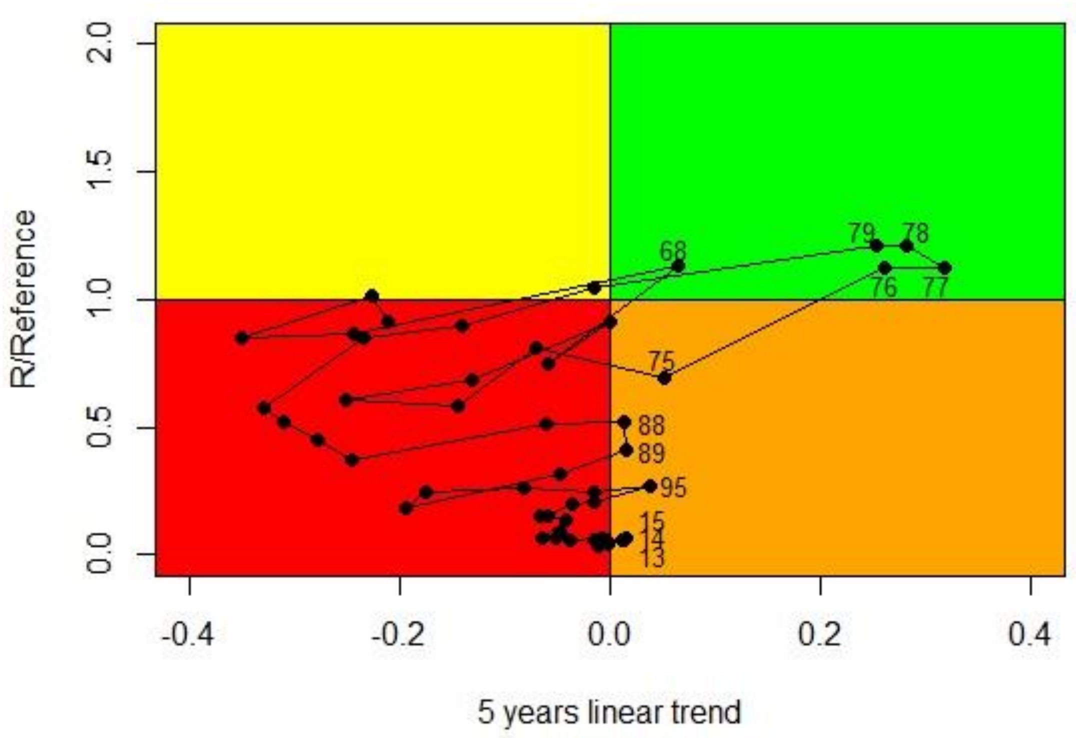

Figure 17: Recruitment status-and-trend with respect to the four zones (green=healthy zone, yellow=cautious zone, orange=other cautious zone, red=critical zone) currently employed by ICES. Application to the overall recruitment estimate from the model GEREM.

GEREM: a starting point for improving stock-recruitment relationships?

Even though the trend-based approach provides a good signal for stock status, it doesn't provide information on the level of management action required and this approach alone does not allow deriving management reference points which are crucial for fisheries management.

Because of the panmictic nature of the stock, biological advice should be based on an assessment of the status of the whole stock. Moreover, it is still not known whether or not all areas contribute to successful spawning. For these reasons, it is obvious that management advice and possible reference points have to be derived from an assessment of the entire population.

In the case of eel, fisheries are scattered throughout the natural distribution in small-scale fisheries targeting the different life stages (i.e. glass eel and/or yellow eel and/or silver eel) (Dekker 2000a; Dekker 2003). Moreover, unlike other marine species, eel is impacted by many other anthropogenic mortality sources (pollution, migration barriers, habitat degradation) which are difficult to estimate at a large scale. For these reasons, and given the current knowledge, it is impossible to determine the production function and thus derive the biomass B_{MSY} and the mortality $F_{MSY.}$

It is also very difficult to derive biological reference points using classical methods such as the examination of the stock-recruitment relationship in the case of eel. While the assessment of glass eel recruitment at the European scale was carried out through a large scale modeling approach in the present study, an equivalent is not possible for the silver eel stage (proxy of the SSB). The most up-to-date attempt to derive a stock-recruitment relationship was carried out by ICES (2013). Even though member states are required to provide estimates of escapement for each EMU, no estimate of historical escapement at the stock scale is available. Landings data and expert knowledge about exploitation rates were used to reconstruct time-series of escapement for the past years. In addition to the gaps and uncertainties, these data don’t cover the entire area, which is truly problematic to derive a consistent stock-recruitment relationship in the case of eel. Since large scale modeling to estimate silver eel escapement is impaired by the fractal geometry of the eel stock, the approach currently used consists of the summing up of stock indicators carried out at the EMU scale, but full coverage of these data has never been achieved and seems unrealistic.

Moreover, a great deal of literature along with the present study have pointed out many processes occurring during the oceanic phase that might impact glass eel recruitment success (Miller et al., 2009; Knights, 2003; Gutiérrez-Estrada and Pulido-Calvo, 2015; Kettle and Haines, 2006; Friedland et al., 2007; Bonhommeau et al., 2007). Indeed, the larval migration is likely to last for a long period (i.e. 2 or 3 years) (Bonhommeau et al., 2010) and could be the limiting stage to explain glass eel recruitment levels. Unreliable data and influence of oceanic conditions on larval transport probably explain why all attempts of fitting stock-recruitment relationships have failed (ICES 2013). However, given that reliable and widely distributed data are available in the future; stock-recruitment relationships may help understand processes determining glass eel recruitment. Although data on recruitment and especially on spawning biomass present weaknesses, ICES (2014) has indicated that the stock recruit relation had demonstrated a recruitment declining faster than the spawner escapement. This could reflect strong depensation (Hilborn and Walters, 1992) and /or overwhelming environmental drivers and/or spawner quality issues. All in all, reference points based on data and the particular case of eel would be probably more appropriate than the standard advice proposed by the European Eel Regulation (Council Regulation (EC) No. 1100/2007). Therefore, stock recruitment relationship in the case of eel has to be adapted taking into account the potential effects of spawner quality and ocean climate indices and may be relevant providing that more data reflecting the whole stock status are available.

3. Application of GEREM to the European eel population

The application to the overall population was particularly relevant given that no global index to assess the European eel population has been derived yet. Data were available for 30 river catchments across Europe and the Kattegat-Skagerrak area was covered by the IYFS scientific survey. Hence, all data put together covered 67% of the whole study area and accounted for about 38% of the overall recruitment according to the model.

By comparison, Moriarty and Dekker (1997) estimated that recruitment in France, Spain, Portugal, and the Bristol Channel area in the United Kingdom was around 538t in 1993 accounting for 76% of total European recruitment. Lambert (2008) led a similar approach to the model of Dekker (2000b) and estimated a recruitment of approximately 1500t in the same area, 74% of total European recruitment. GEREM estimate for the Mediterranean Sea, Iberian coast, Bay of Biscay, and English Channel zones gave similar results: the corresponding recruitment was approximately equal to 1760t in 1993 therefore accounting for 87% of overall recruitment.

An assessment of the state of the European eel stock was carried out by Dekker (2000b) using an extremely simplified cohort-model based on life stage and data from Moriarty and Dekker (1997). Recruitment was estimated at about 2000 million eels annually, corresponding in average to 740000 kg, most of which enter countries around the Bay of Biscay. On the other hand, GEREM estimates an annual recruitment of almost two million kilograms in 1993 which is 63% higher than the overall recruitment estimated by Dekker (2000b). However, several strong assumptions might have led to biased estimates in the study carried out by Dekker (2000b). Indeed, several assertions were stated for the continental stock as a whole (ratio between yellow and silver eel catch, mean weights for each of the life stages, the duration of the pre-exploited and exploited yellow eel stages, the level of natural mortality), for both sexes combined. This model required also incorrect assumptions about the stability of recruitment and fishing activity (fisheries were assumed to be in a stable state) and catches were known without errors. On the other hand, GEREM used the most reliable recruitment time series scattered over Europe and required much fewer assumptions which seem more reasonable.

Unsurprisingly, the overall trend was a compromise between both indices derived by the WGEEL (i.e. North Sea and Elsewhere indices) showing however a greater correlation (0.98) with the “Elsewhere” index (Fig.11). This is not surprising since this index gathers most recruitment time series available across Europe. These time series come from different locations where glass eel are most abundant. Indeed, all zones except North Sea represent 80% of the overall recruitment in 1960 while they represented 95% in 2015, suggesting that the trend deducted from North Sea time series perform a minim weight in the overall trend.

Consistently with the DFA analysis, recruitment in the North Sea area shows a more severe decline compared to other zones, as depicted by the proportion of recruitment allocated to the different zones (Fig 12). It appears that the level of glass eel recruiting to North Sea has been affected by the general decline and additional mortality sources proper to the North Sea region. Few studies have been undertaken to analyze glass eel recruitment fluctuations in conjunction with changes in North Sea circulation. The present study did not display significant correlations between the North Sea estimate and environmental factors which could have explained the difference in slope. However, significant regime shifts in the physical and biological structure of the Northeast Atlantic and North Sea have been observed, affecting a wide range of marine organisms from zooplankton to fishes (Richardson, 2004; Weijerman et al., 2005). In the period 1965 to 1980, both plankton composition in this area and the fish stocks showed long term changes that could all be explained by a sustained reduction of Atlantic inflow. The reduction of the Atlantic inflow is thought to be responsible for the recruitment depression in North Sea herring occurring between 1971 and 1979 (Corten, 2013). Durif et al. (2011) used the Skagerrak coastal time series to explore the impacts of oceanic factors on fluctuations in eel recruitment abundance. In particular, analyses showed that increased inflow from northern North Sea led to high abundance in the Skagerrak and that the drift of larvae to the Skagerrak coast depends on changes in ocean circulation within this area. Hence, poor circulation conditions in the North Sea area could be one of the reasons why glass eel recruitment has been declining further compared to elsewhere in Europe.

4. The use of GEREM estimates to analyze correlations between large-scale environmental factors and glass eel recruitment at the European scale

Impact of large scale SST patterns and transport on eel survival

Glass eel recruitment fluctuations could not be linked to GSI, confirming the results of Bonhommeau et al. (2007). As such, no obvious correlations between the position of the Gulf Stream and subsequent recruitment could be established once again, suggesting that this variable may not be decisive for glass eel recruitment success.

Long-term correlations between North Atlantic SST and glass eel recruitment were not significant. The high degree of autocorrelations present in the original time series reduced considerably the corrected degree of freedom, preventing the establishment of a significant correlation between North Atlantic SST and glass eel recruitment time series (Appendix IX). However, it may have been interesting to correct the resulting degree of freedom by taking into account partial autocorrelations instead of autocorrelations: partial autocorrelations are a representation of the correlations between values of a time series at lag L removing the influences of the values between x_t and x_{t-L}. Partial autocorrelations would have been appropriate to remove redundancies in successive autocorrelations.

By considering the North Atlantic SST, we assumed that global fluctuations of SST over the North Atlantic Ocean were representative of temperature conditions faced by leptocephali during their entire oceanic phase. It would have been relevant to build SST time series of the

Atlantic Ocean covering the possible migration routes of leptocephalous larvae towards different parts of Europe. However, it was not possible to do so because of an imprecision knowledge on this migration route and of a lack of time. This may also explain why no significant linear relationships were found between SST and glass eel recruitment. Indeed, water temperature is known to affect growth, feeding, and reproduction of fishes, as well as changes of suitability of marine habitats, thus leading to changes in the distribution, abundance and migration processes of fish species (Thomas et al., 2004). In view of this, several studies pointed out significant relationships between SST patterns and glass eel recruitment success by averaging SST on restricted spatial scales either in the Sargasso Sea (Bonhommeau et al., 2007) or over possible migration routes taken by larvae during their entire migration (Gutiérrez-Estrada and Pulido-Calvo 2015). Bonhommeau et al. (2007) concluded that sea temperatures impacted glass eel survival mainly via food availability in the Sargasso Sea.

Primary production in the Sargasso Sea affects glass eel recruitment success

We reported two significant correlations between primary production and subsequent glass eel recruitment in both North Sea and Mediterranean zones. Although not very strong, these correlations suggest that trophic conditions in the Sargasso Sea may impact glass eel survival and that bottom-up control may play a significant role at the early stage of the long oceanic migration. This finding suggests that food availability in the Sargasso Sea may affect glass eel recruitment in northern Europe two years later while glass eel recruiting to the Mediterranean zone may be impacted one year later. If these correlations were proved to be true, then we could envisage different migration durations between glass eel recruiting to river catchments in northern Europe and those arriving in the Mediterranean Sea.

Glass eel influenced by the physical and biological structure of the North Atlantic

Our results confirmed findings of other studies carried out over the past years: changes associated with the NAO seem to impact the European eel recruitment (Knights, 2003; Friedland et al., 2007; Kettle et al., 2008) . This is not surprising because of the long migration period of the European eel. All studies pointed out a significant inverse correlation between the NAO and glass eel recruitment at the Den Over monitoring station (ICES 2001; Knights, 2003; Friedland et al., 2007). A variety of mechanisms can lead to this inverse correlation found in most recruitment estimates. For example, Knights (2003) hypothesized that the positive phase of the NAO is associated with elevated sea surface temperature (SST) and shallow wintertime stratification in the Sargasso Sea, reducing food availability to the newly hatched larvae. The NAO also appears to be associated with changes in patterns of branches of the Gulf Stream (Bersch, 2002; Reverdin, 2003): although a strengthening of the Gulf Stream might be expected to facilitate successful recruitment to Europe, the increase flow may have caused an expansion of Gulf Stream recirculation in recent decades (Curry and McCartney, 2001), resulting in increased retention of leptocephali in the western half of the gyre. Since NAO induces changes on different spatio-temporal scales (Visbeck et al., 2003), it remains difficult to determine which mechanisms cause glass eel recruitment fluctuations. A correlation between NAO and glass eel recruitment lagged by three or four years may reflect a change in trophic conditions within the Sargasso Sea (a high NAO may induce poor trophic conditions one or two years later) while a correlation lagged by one year in the case of the Mediterranean Sea could induce other mechanisms during the larval migration. It is currently impossible to conclude on the underlying mechanisms.

Are there different migration durations and migratory routes?

Correlations between glass eel recruitment and environmental factors were lagged differently depending on the arrival location of glass eel. Whether it was primary production or NAO index, glass eel recruitment to the Mediterranean region was always lagged by a shorter time interval compared to other parts of Europe. This may involve a shorter migration and thus a different migratory route taken by larvae shifting towards the Mediterranean Sea. This hypothesis should be considered cautiously but it remains a possibility. Indeed, a Lagrangian model of the current-carried migration of the leptocephali of the European eel has been implemented by Kettle and Haines (2006). Although the model concludes that the Gulf Stream is the main migration path, it suggests that there may be a successful transatlantic migration from the northeast corner of the spawning region toward Morocco and the Mediterranean Sea, as indicated by McCleave (1993). Meanwhile, Munk et al. (2010) assumes that a significant proportion of the more easterly distributed *A. anguilla* larval population could be transported in the easterly frontal currents and advected in the Subtropical Counter Current (SCC) towards Europe, that would lead to a first arrival of larvae in the Southern part of the European continent. Munk et al (2010) indicated that organisms transported in these currents could be conveyed over substantial distances by eastward frontal flows of 0.2-0.3 m.s-1 (approx.6000-9000 km yr-1) which is to be compared with a direct distance to Europe from this area of the order of 5500 km. Other strong frontal currents up to 0.5-1.0 m.s-1 have been found during other studies of the same subtropical fronts (Fernández and Pingree 1996). In this way, the estimates of these frontal currents velocities in the SCC indicate that these current have the potential for advecting larvae to Europe faster than the approximately 2 years estimated by modelling studies of drift in the Gulf Stream current system (Kettle and Haines, 2006; Bonhommeau et al., 2009).

Recruitment estimates from GEREM

Both long-term and short-term correlations were analyzed between large-scale environmental variables and glass eel recruitment using recruitment estimates from GEREM. It appeared interesting to use such estimates given that they aimed at modeling fluctuations in recruitment on a regional scale taking into account the whole ocean phase and leaving out local phenomenon potentially affecting recruitment variations at a finer scale. Hence, such estimates appeared interesting to study correlations between large-scale oceanic and atmospheric factors and glass eel recruitment. While we were expecting to find correlations between primary production in the Sargasso Sea and most recruitment estimates, only the North Sea and Mediterranean areas displayed significant correlations. Several assumptions can be put forward to explain such discrepancies. Even though we kept the most reliable time series to derive recruitment estimates from GEREM, still some bias can persist in the data that could lead to incorrect fluctuations on short-time scales. If most data are biased in a zone, then the resulting regional recruitment estimate can be wrong and lead to incorrect results. The second reason could originate from local conditions that may have more impacted recruitment fluctuations and mask the effect of primary production in the Sargasso Sea. The last reason may arise from the model structure. GEREM estimates regional recruitment through two multinomial distributions, namely a random walk and a Dirichlet distribution. These distributions can sometimes smooth the amplitude of inter-annual variations and mitigate certain short-term fluctuations, misrepresenting subsequent correlations.

V. Conclusion

GEREM is currently the only model that provides a methodological framework to estimate glass eel recruitment at a large scale potentially covering the whole distribution area. Indeed, the only preexisting model that attempted to evaluate the entire European eel population was based on very strong and incorrect assumptions.

The application of GEREM at a large scale supposes that two main assumptions taking into account the fractal dimension of recruitment should be satisfied (i.e. same trends and similar densities within a zone). In most cases, these hypothesis seem to be verified, but for certain series, trends and densities of recruitment may be partially explained by local factors. However, it was not possible to model glass eel recruitment at a fine scale by considering river basin conditions that may have affected glass eel recruitment.

In view of this, GEREM improves substantially the methodological framework currently used by the WGEEL to evaluate the overall population, through the estimation of glass eel recruitment.

The application of GEREM to the European eel population with existing data proves a global decline since the late 1970s with however recruitment in North Sea showing a more severe deterioration. Although continental causes are suspected to be partly responsible for the decline of the European Eel population, environmental conditions during the oceanic migration are likely to play a major role in this decrease. No long-term correlations have been identified to explain the likely difference of trend between Northern and Southern Europe. However, NAO and PP in the Sargasso Sea may affect glass eel recruitment on short-time scales, also suggesting that migration duration may be shorter for larvae drifting towards the Mediterranean Sea.

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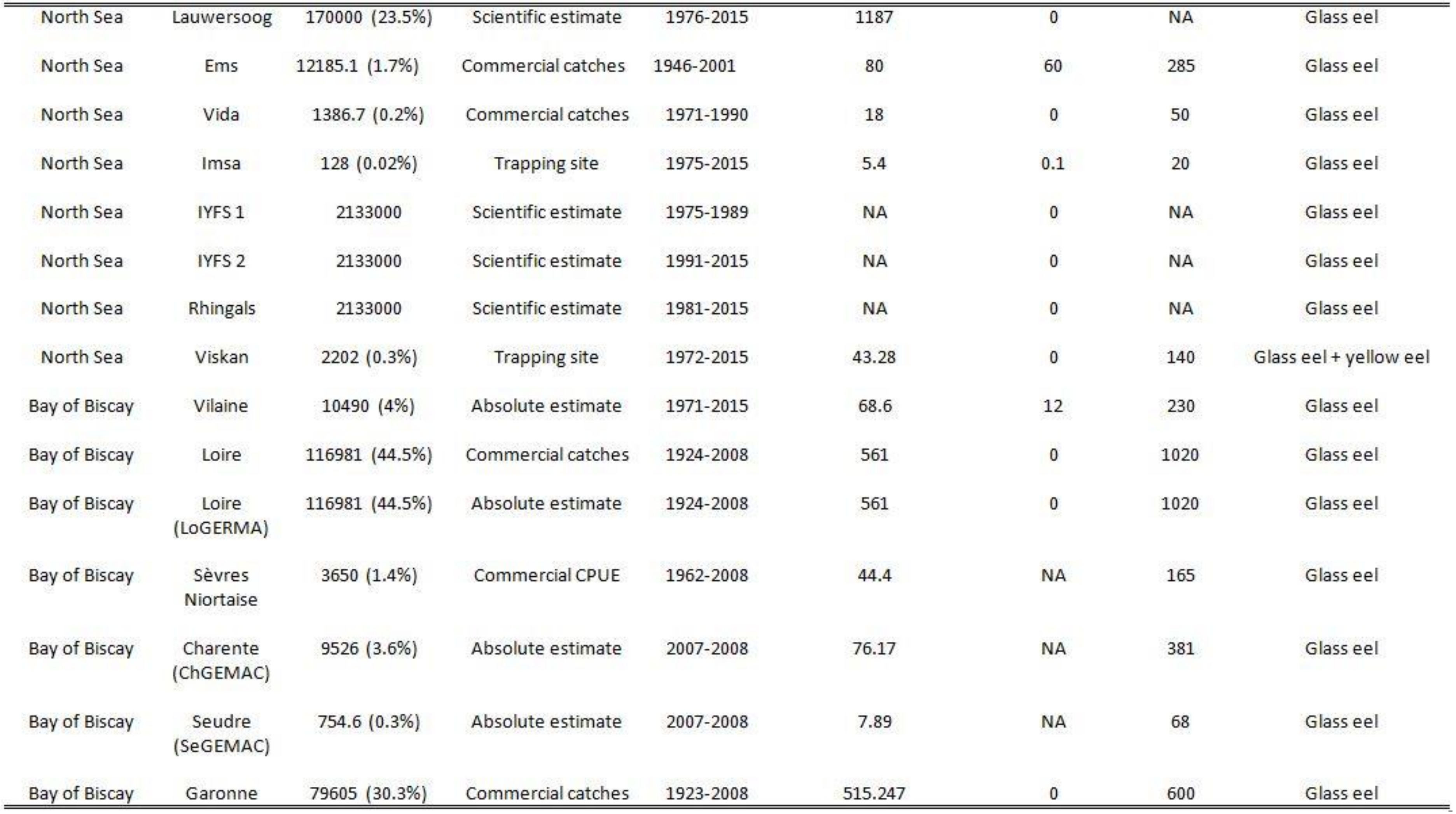
Appendix

Appendix I: Information on recruitment data series and monitoring sites used in the DFA analysis and the model GEREM

Table A.1.1: An overview of glass eel monitoring sites and information relating to recruitment data series

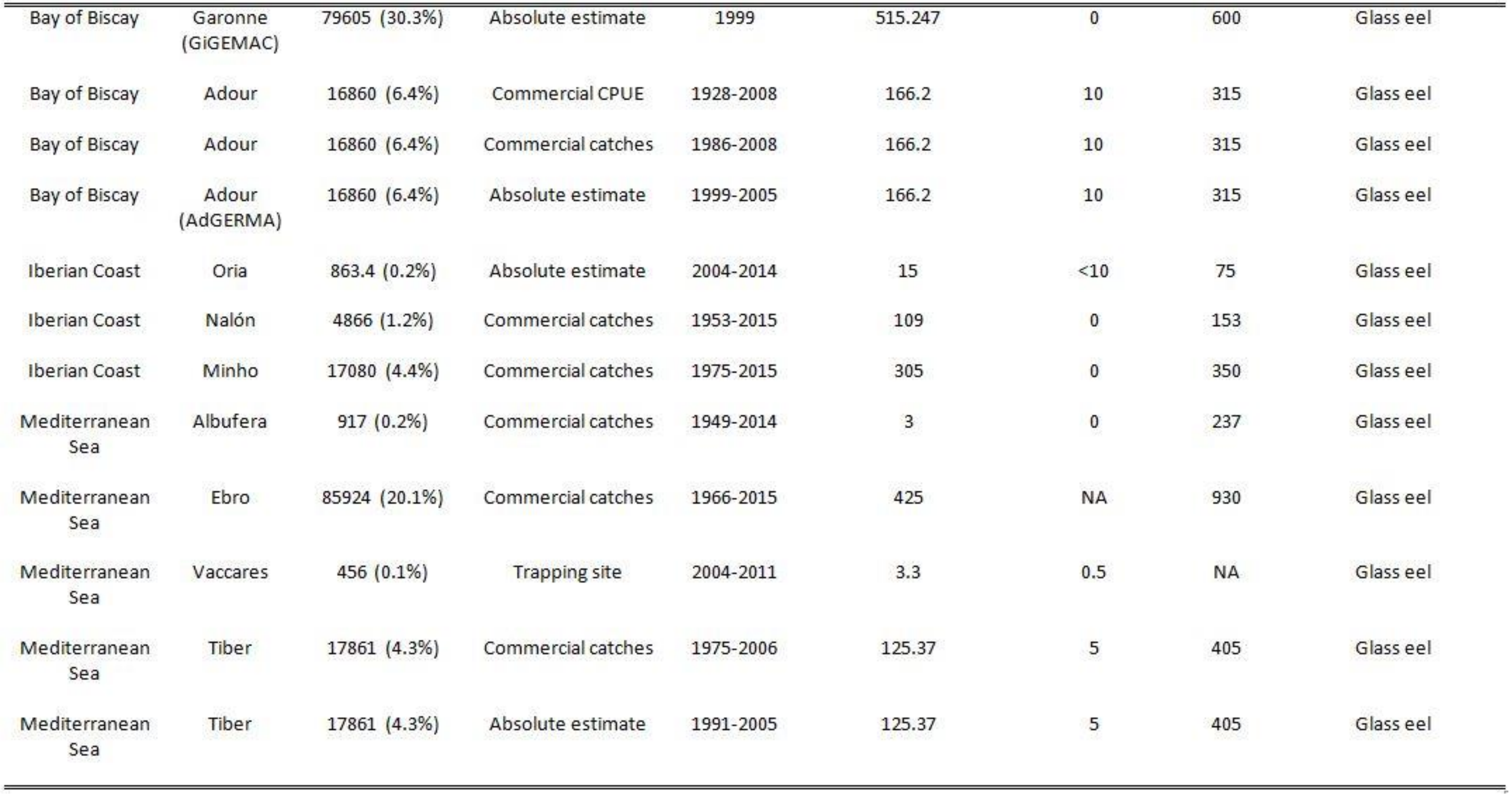
Zone	Catchment	Catchment area (km^2) (%zone)	Type	extent	River discharge ($m^3.s^{-1}$)	Distance from the sea (km)	River length (km)	Life stage
British Isles	Bann	4450 (3.5%)	Trapping site	1960-2015	100	10	40	Glass eel + yellow eel
British Isles	Erne	4000 (3.2%)	Trapping site	1959-2015	100	2	150	Glass eel + yellow eel
British Isles	Maigue	1075 (0.9%)	Trapping site	1994-2015	NA	NA	62	Glass eel
British Isles	Inagh	4550 (3.5%)	Trapping site	1996-2015	1	NA	36.6	Glass eel
British Isles	Feale	1153 (0.9%)	Trapping site	1985-2015	21	NA	74	Glass eel + yellow eel
British Isles	Shannon	11700 (9.3%)	Trapping site	1977-2015	176	83	250	Glass eel + Yellow eel
English Channel	Severn	11381 (7%)	Commercial catches	1972-2015	61	0	354	Glass eel
English Channel	Frémur	60 (0.4%)	Trapping site	1997-2015	0.17	4	17	Glass eel + yellow eel
English Channel	Bresle	743 (0.5%)	Trapping site	1994-2015	7.5	NA	72	Glass eel + yellow eel
English Channel	Somme	6223.4 (3.8%)	Absolute estimate	1992-2012	33.25	NA	245	Glass eel
North Sea	Ijzer	1101 (0.15%)	Scientific estimate	1964-2015	5.5	3	76	Glass eel
North Sea	Stellendam	170000 (23.5%)	Scientific estimate	1971-2015	1187	0	NA	Glass eel
North Sea	Katwijk	170000 (23.5%)	Scientific estimate	1977-2015	1187	0	NA	Glass eel
North Sea	Rhine	170000 (23.5%)	Scientific estimate	1938-2015	1187	0	1230	Glass eel

Table A.2.1: An overview of glass eel monitoring sites and information relating to recruitment data series (continued)



North Sea	Lauwersoog	170000 (23.5%)	Scientific estimate	1976-2015	1187	0	NA	Glass eel
North Sea	Ems	12185.1 (1.7%)	Commercial catches	1946-2001	80	60	285	Glass eel
North Sea	Vida	1386.7 (0.2%)	Commercial catches	1971-1990	18	0	50	Glass eel
North Sea	Imsa	128 (0.02%)	Trapping site	1975-2015	5.4	0.1	20	Glass eel
North Sea	IYFS 1	2133000	Scientific estimate	1975-1989	NA	0	NA	Glass eel
North Sea	IYFS 2	2133000	Scientific estimate	1991-2015	NA	0	NA	Glass eel
North Sea	Rhingals	2133000	Scientific estimate	1981-2015	NA	0	NA	Glass eel
North Sea	Viskan	2202 (0.3%)	Trapping site	1972-2015	43.28	0	140	Glass eel + yellow eel
Bay of Biscay	Vilaine	10490 (4%)	Absolute estimate	1971-2015	68.6	12	230	Glass eel
Bay of Biscay	Loire	116981 (44.5%)	Commercial catches	1924-2008	561	0	1020	Glass eel
Bay of Biscay	Loire (LoGERMA)	116981 (44.5%)	Absolute estimate	1924-2008	561	0	1020	Glass eel
Bay of Biscay	Sèvres Niortaise	3650 (1.4%)	Commercial CPUE	1962-2008	44.4	NA	165	Glass eel
Bay of Biscay	Charente (ChGEMAC)	9526 (3.6%)	Absolute estimate	2007-2008	76.17	NA	381	Glass eel
Bay of Biscay	Seudre (SeGEMAC)	754.6 (0.3%)	Absolute estimate	2007-2008	7.89	NA	68	Glass eel
Bay of Biscay	Garonne	79605 (30.3%)	Commercial catches	1923-2008	515.247	0	600	Glass eel

Table A.3.1: An overview of glass eel monitoring sites and information relating to recruitment data series (continued)



Bay of Biscay	Garonne (GiGEMAC)	79605 (30.3%)	Absolute estimate	1999	515.247	0	600	Glass eel
Bay of Biscay	Adour	16860 (6.4%)	Commercial CPUE	1928-2008	166.2	10	315	Glass eel
Bay of Biscay	Adour	16860 (6.4%)	Commercial catches	1986-2008	166.2	10	315	Glass eel
Bay of Biscay	Adour (AdGERMA)	16860 (6.4%)	Absolute estimate	1999-2005	166.2	10	315	Glass eel
Iberian Coast	Oria	863.4 (0.2%)	Absolute estimate	2004-2014	15	<10	75	Glass eel
Iberian Coast	Nalón	4866 (1.2%)	Commercial catches	1953-2015	109	0	153	Glass eel
Iberian Coast	Minho	17080 (4.4%)	Commercial catches	1975-2015	305	0	350	Glass eel
Mediterranean Sea	Albufera	917 (0.2%)	Commercial catches	1949-2014	3	0	237	Glass eel
Mediterranean Sea	Ebro	85924 (20.1%)	Commercial catches	1966-2015	425	NA	930	Glass eel
Mediterranean Sea	Vaccares	456 (0.1%)	Trapping site	2004-2011	3.3	0.5	NA	Glass eel
Mediterranean Sea	Tiber	17861 (4.3%)	Commercial catches	1975-2006	125.37	5	405	Glass eel
Mediterranean Sea	Tiber	17861 (4.3%)	Absolute estimate	1991-2005	125.37	5	405	Glass eel

Appendix II: Verification of the assumptions underlying the DFA: Normality, independence, and homogeneity of residuals

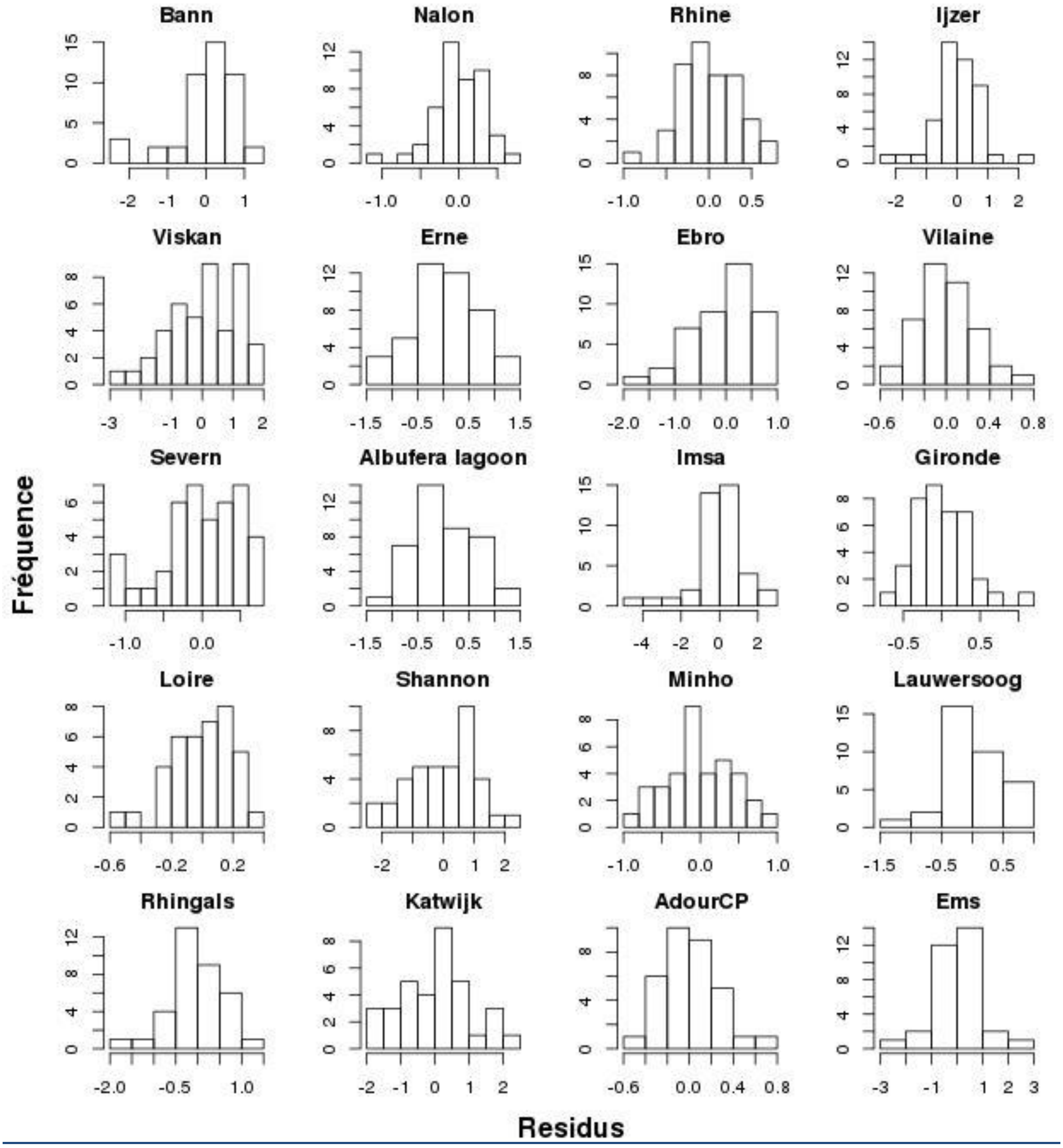


Figure A 2.1: Histogram of residuals: checking normality of residuals

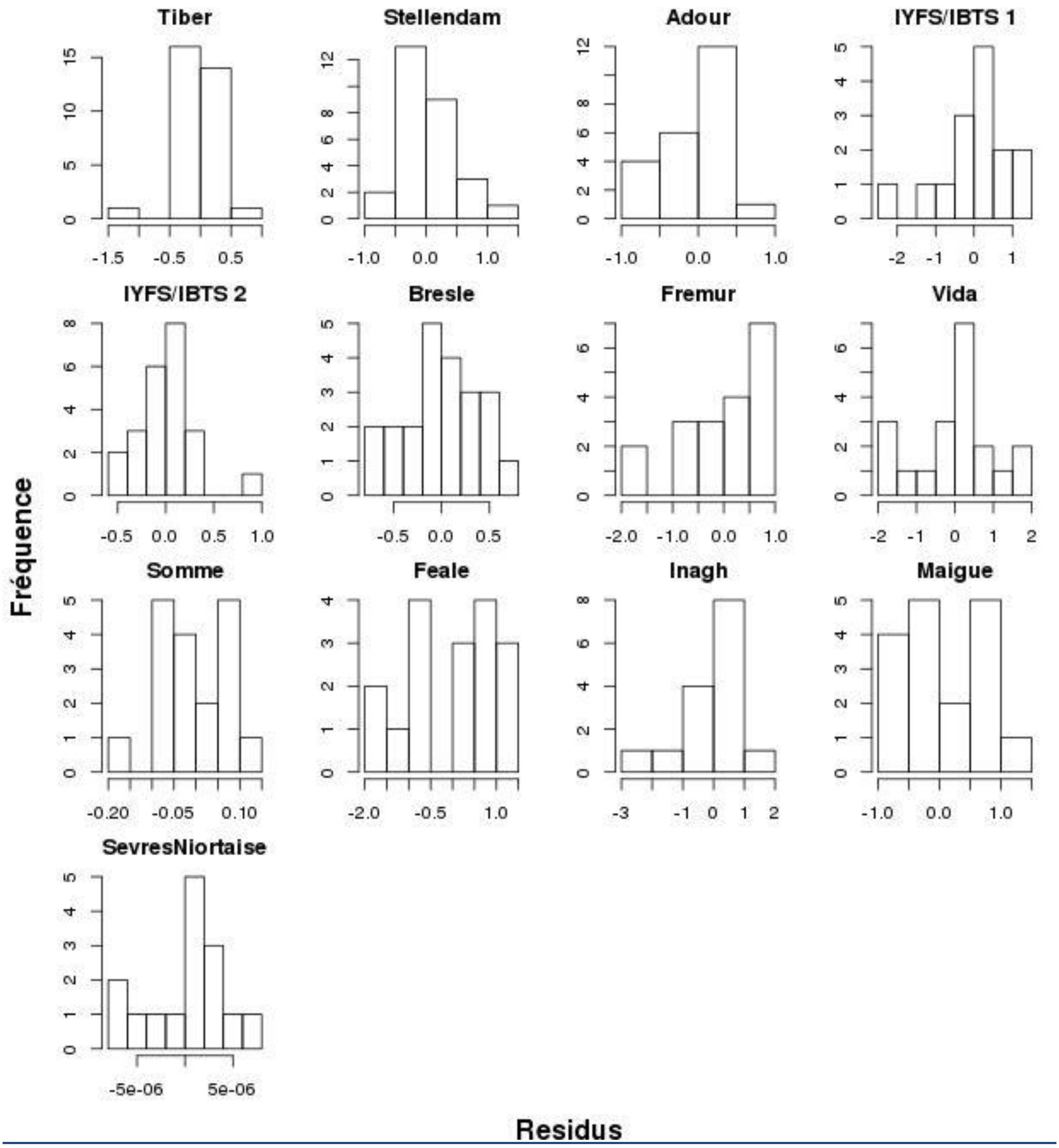


Figure A 2.1: Histogram of residuals: checking normality of residuals (continued)

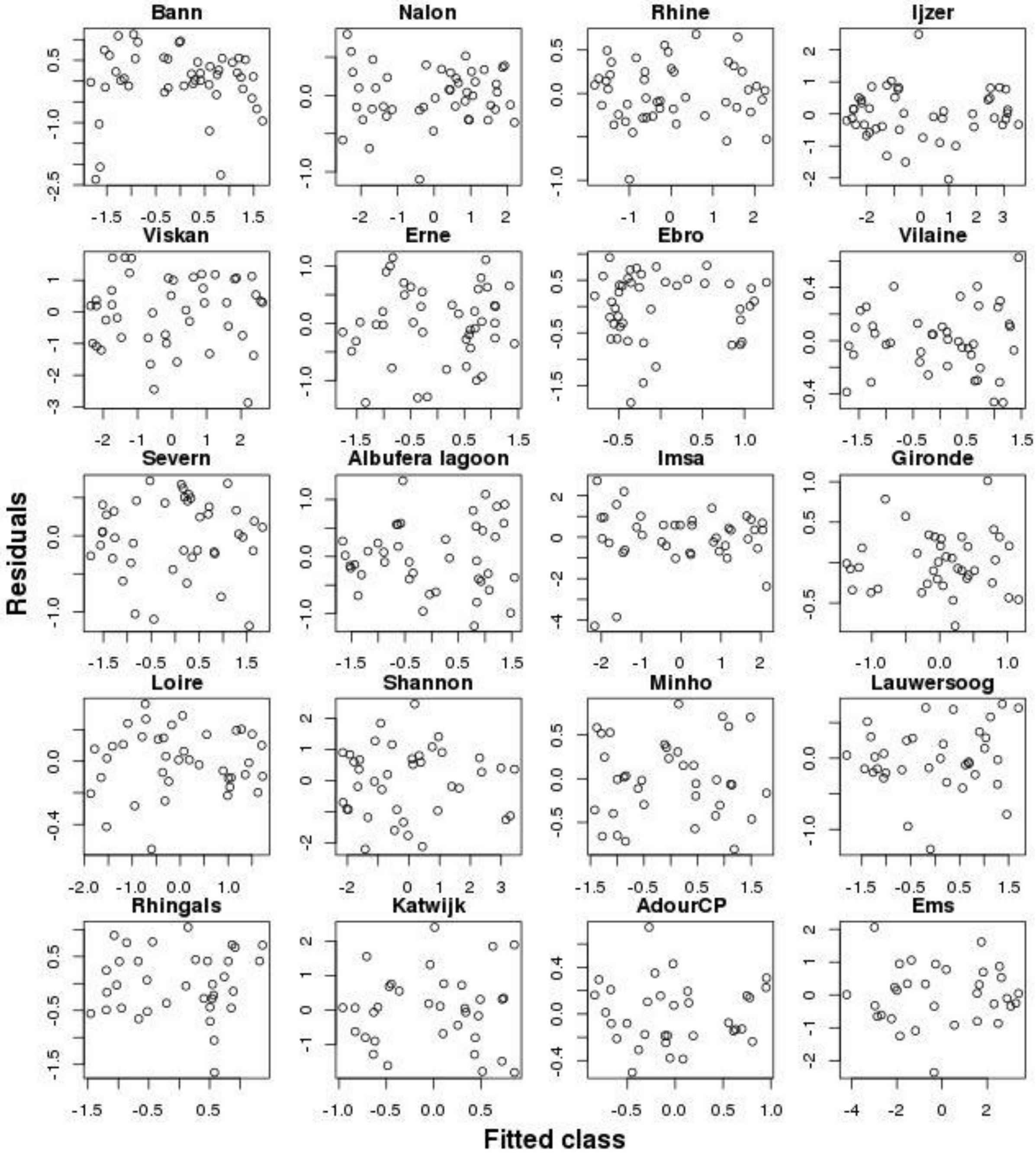


Figure A 2.2: Plot of residuals against fitted values: checking homogeneity of residuals

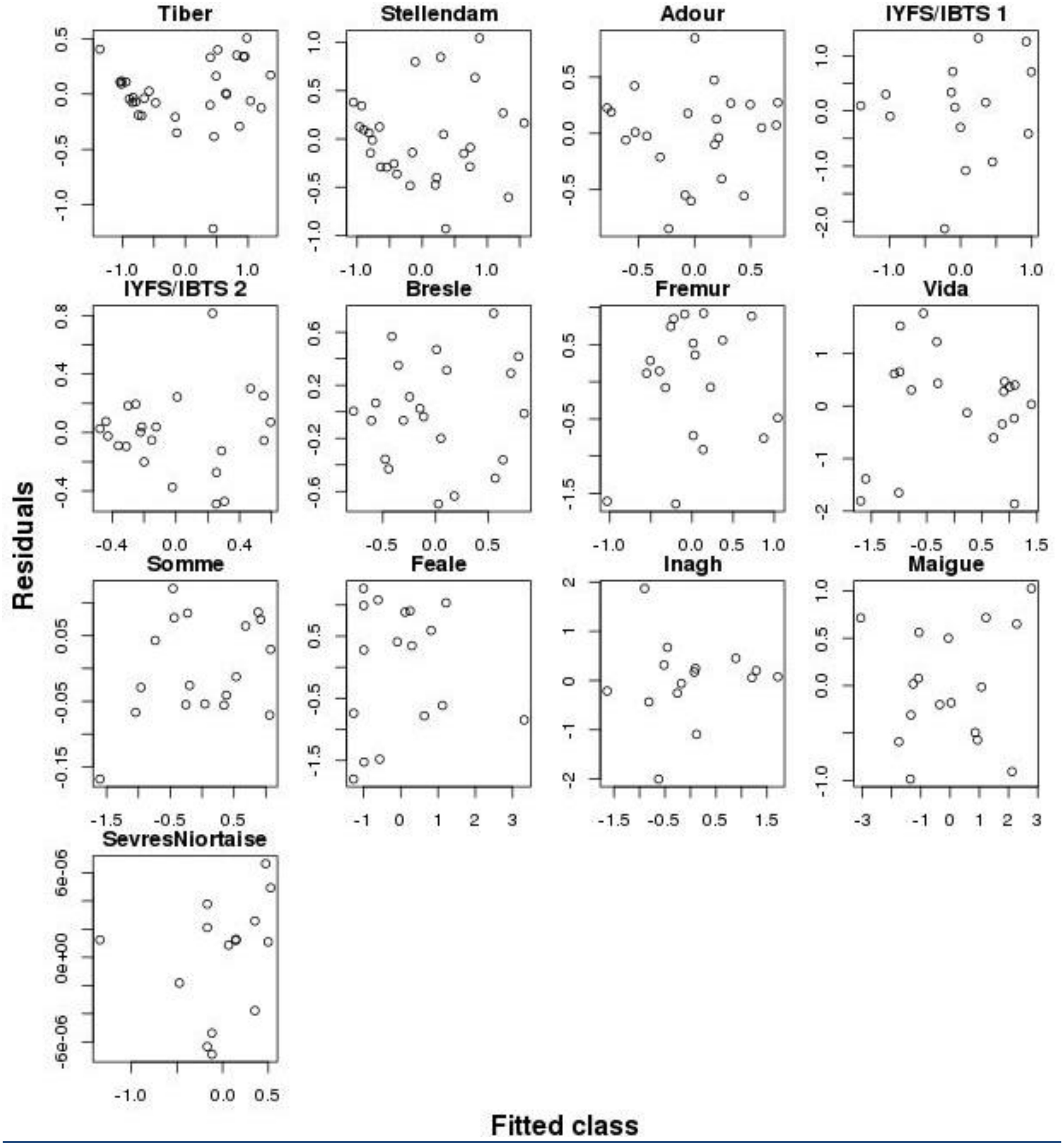


Figure A 2.2: Plot of residuals against fitted values: checking homogeneity of residuals (continued)

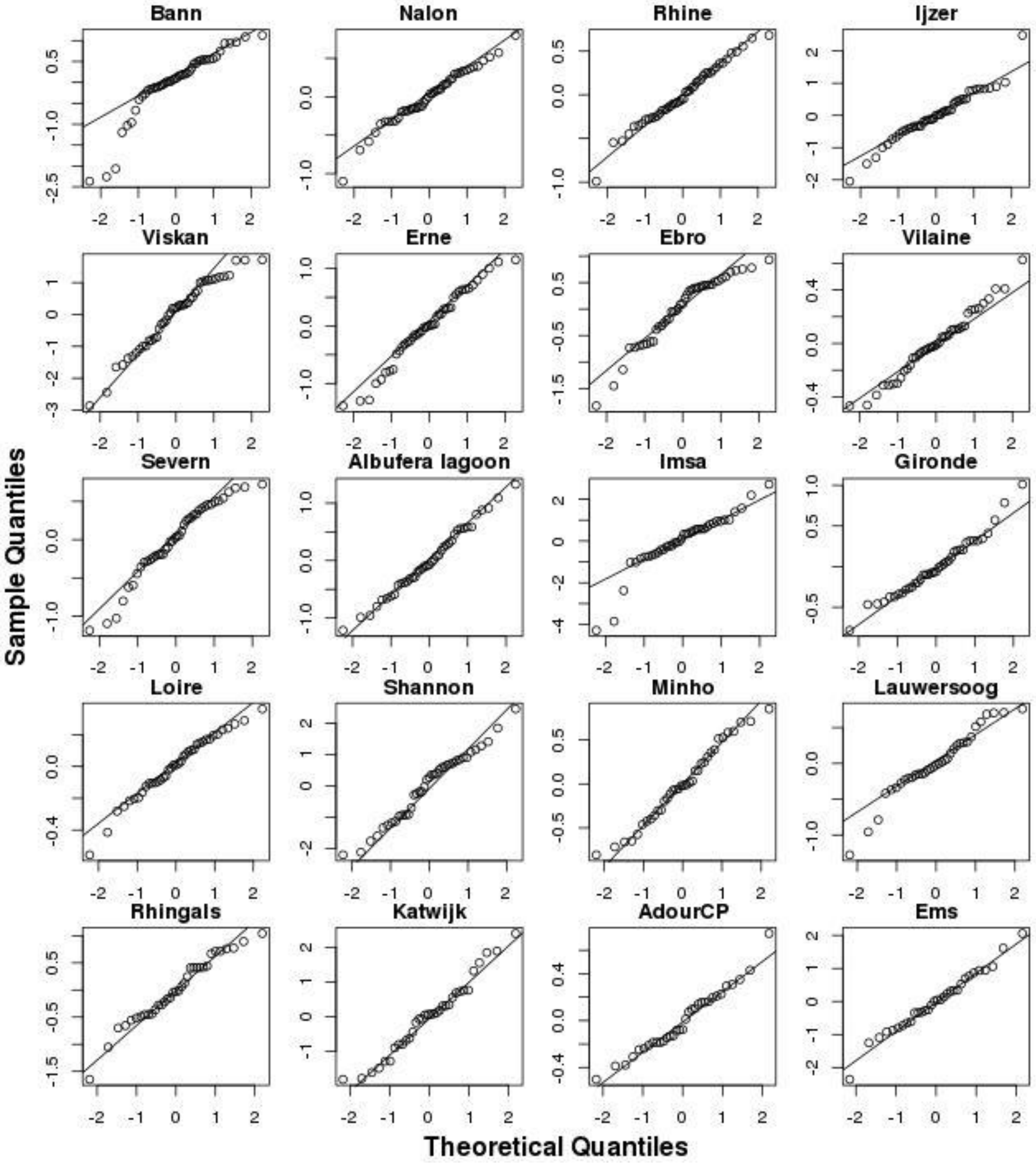


Figure A 2.3: QQplot of residuals: Test of normality

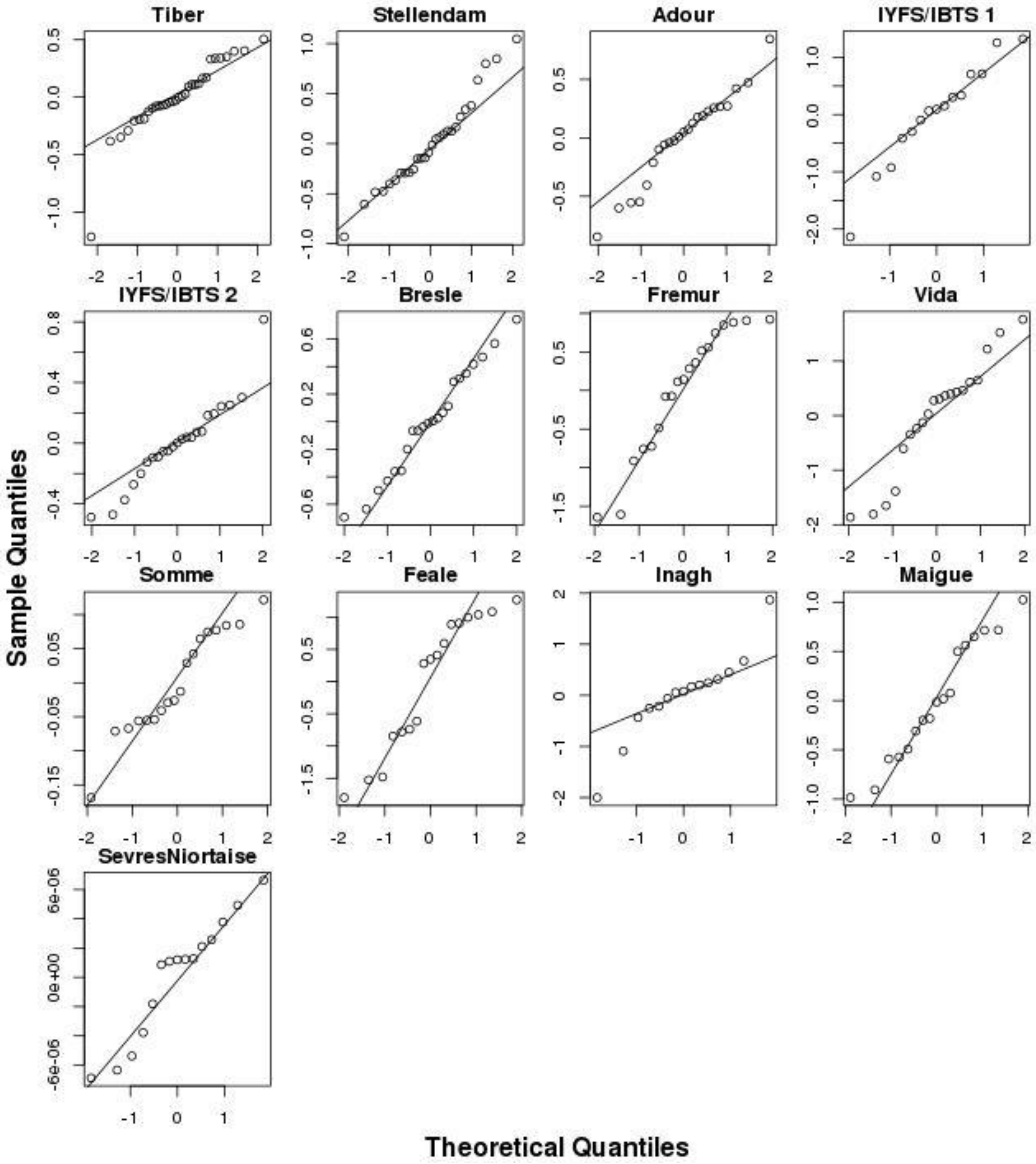
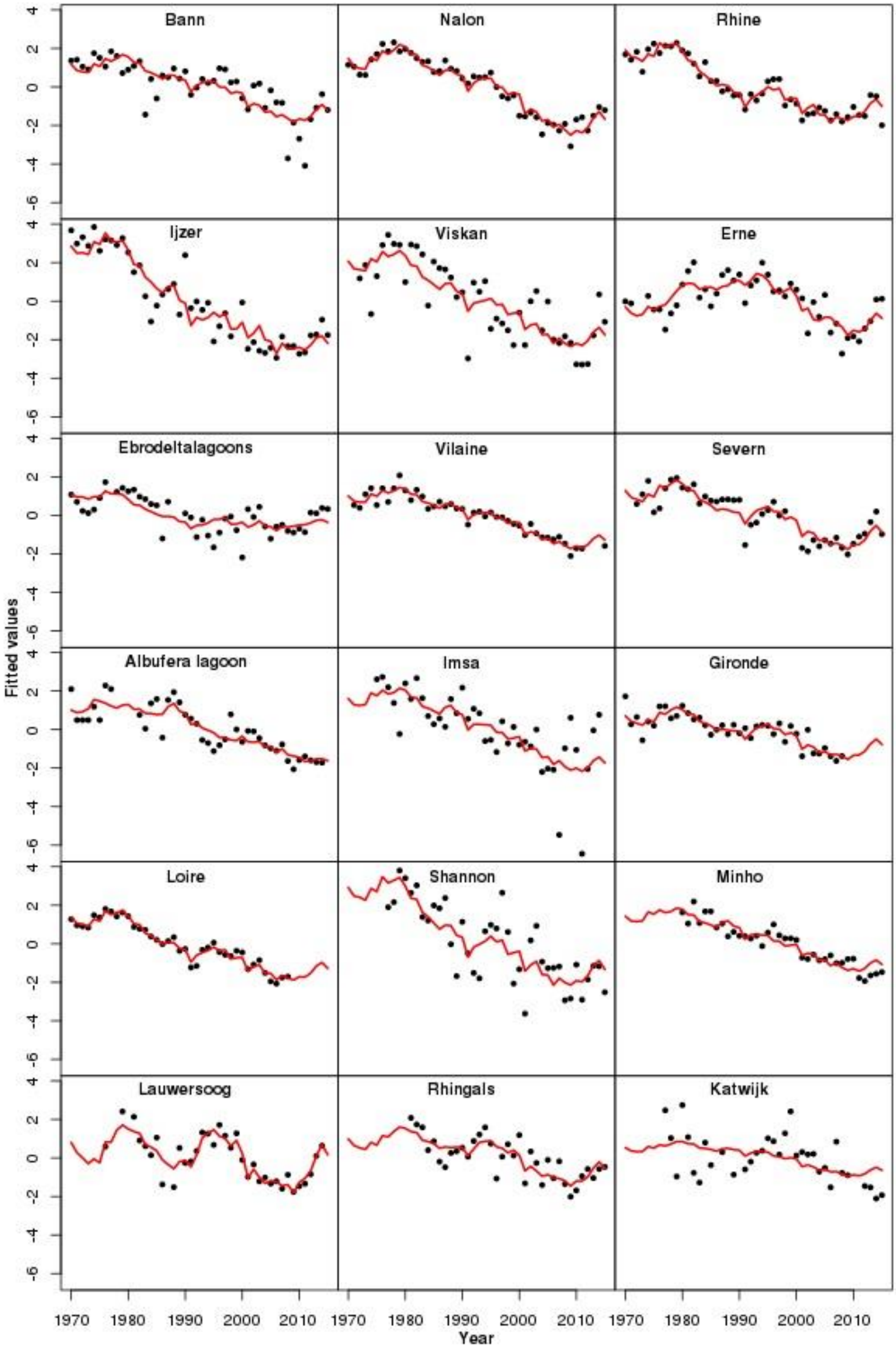
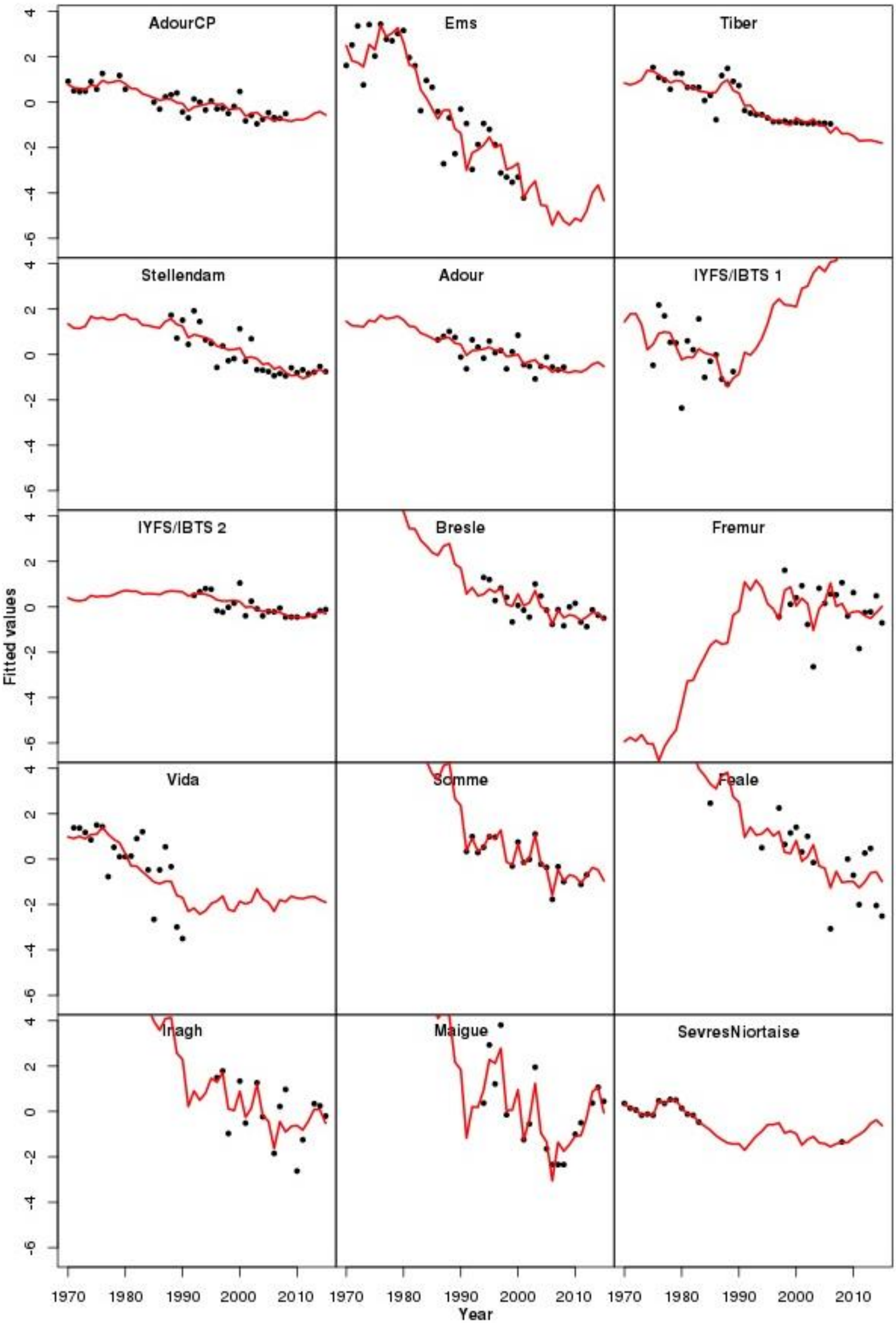


Figure A 2.3: QQplot of residuals: Test of normality (continued)

Appendix III: DFA model fitting to recruitment time series




AdourCP
Ems
Tiber
Stellendam
Adour
IYFS/IBTS 1
IYFS/IBTS 2
Bresle
Fremur
Vida
Somme
Feale
Inagh
Maigue
SevresNiortaise
Fitted values
4
2
0
-2
-4
-6
1970
1980
1990
2000
2010
Year

Appendix IV: Representation of priors and posteriors used in the model GEREM

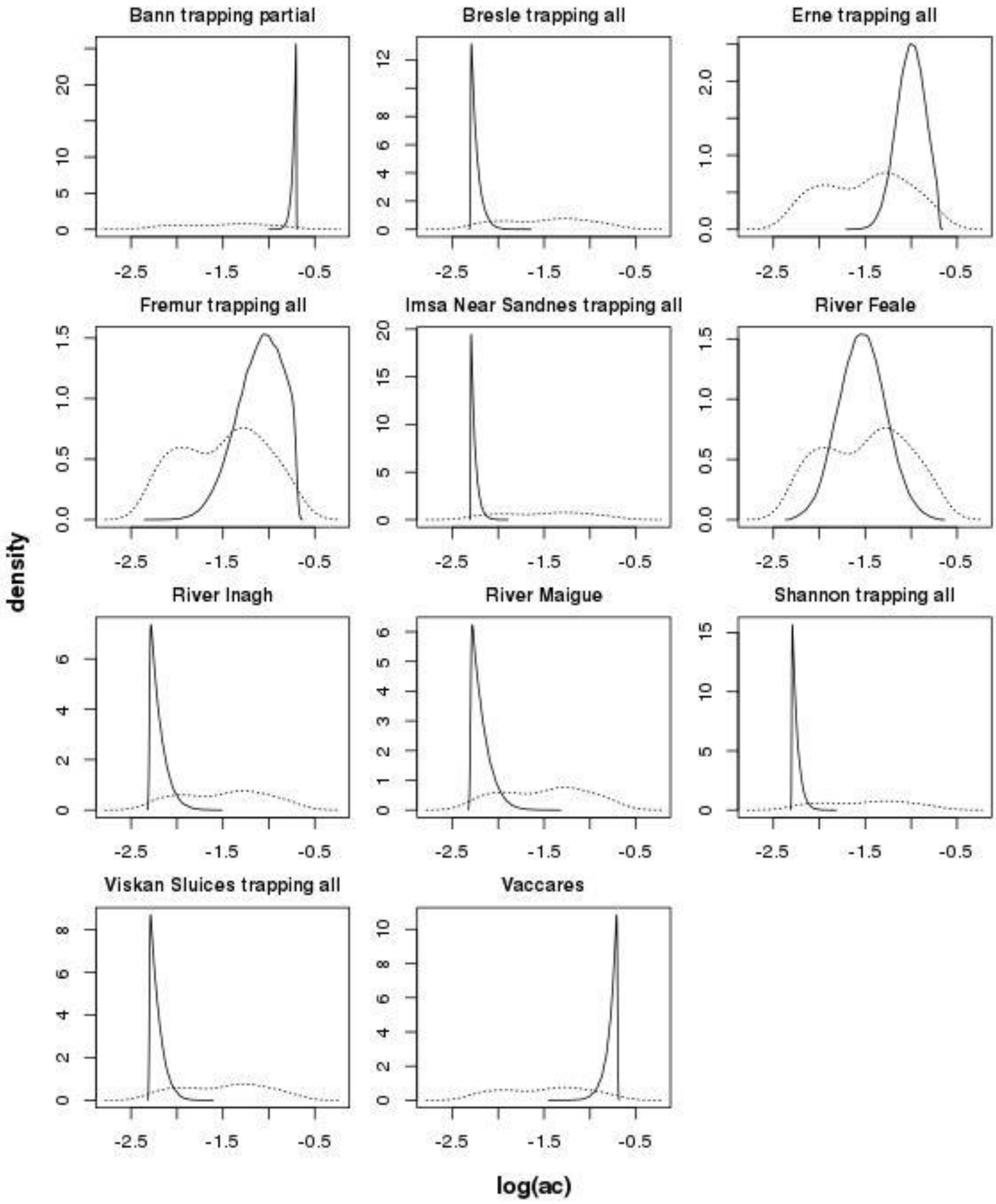


Figure A 4.1: Priors (dotted line) and posteriors (solid line) regarding the transfer efficiency coefficient through the pass c (log (a_c))

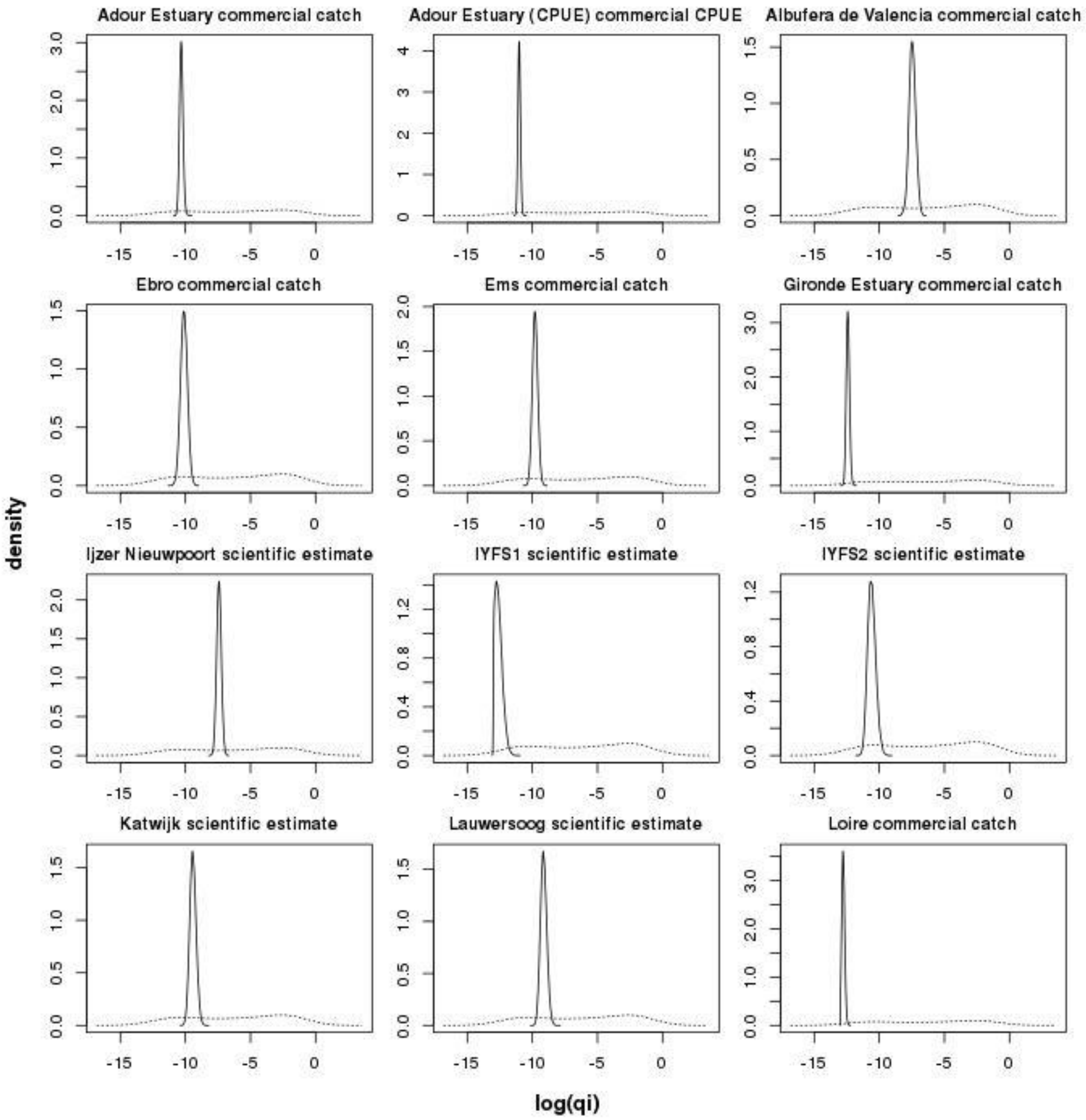


Figure A 4.2: Priors (dotted line) and posteriors (solid line) regarding scaling factors q_i used for relative recruitment indices (1)

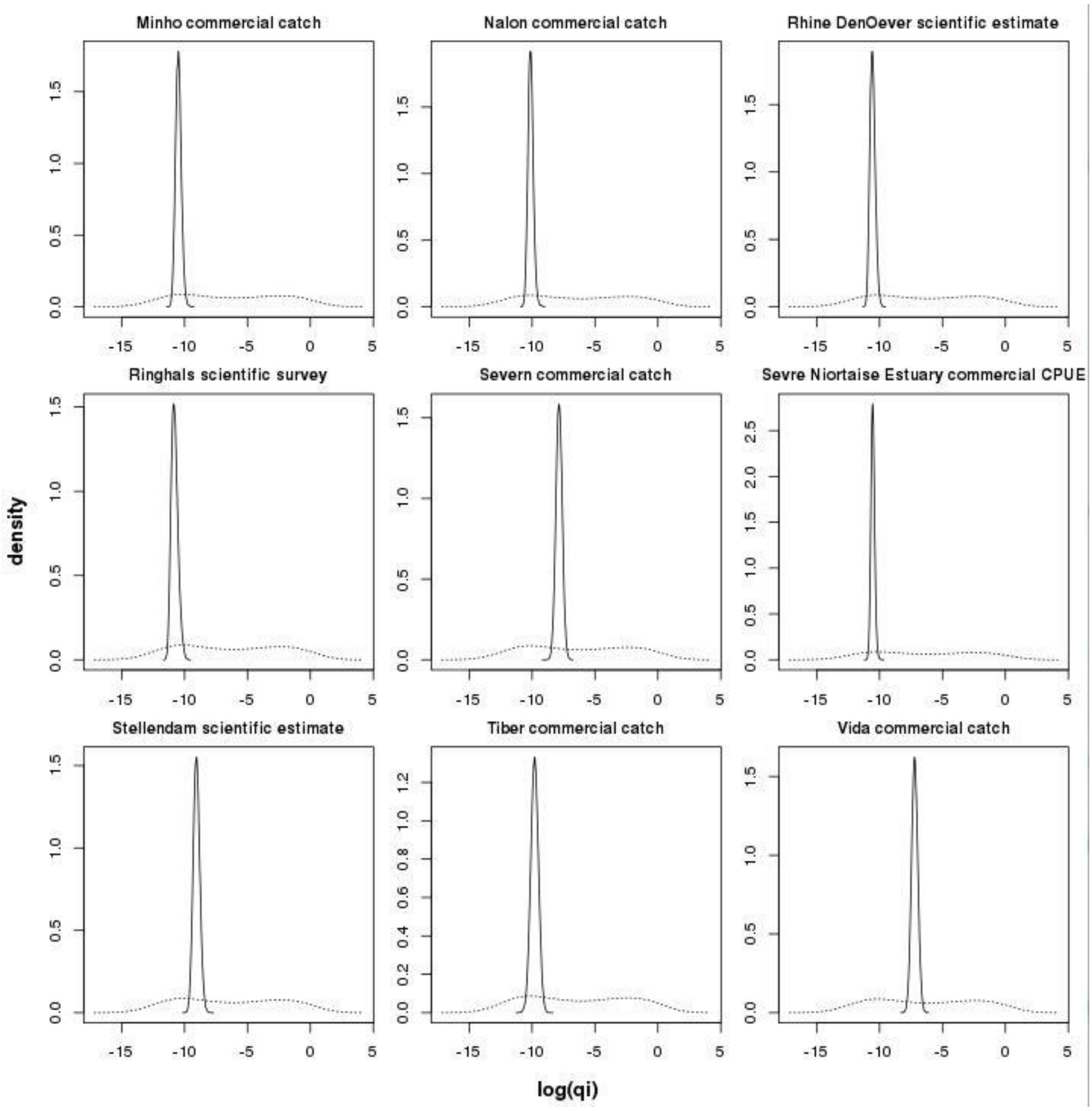


Figure A 4.2: Priors (dotted line) and posteriors (solid line) regarding scaling factors q_i used for relative recruitment indices (1) (continued)

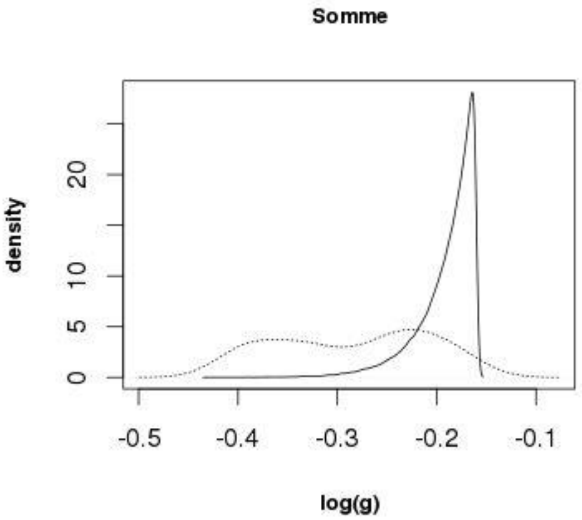


Figure A 4.3: Prior (dotted line) and posterior (solid line) regarding the exploitation rate in the Somme estuary (log (g))

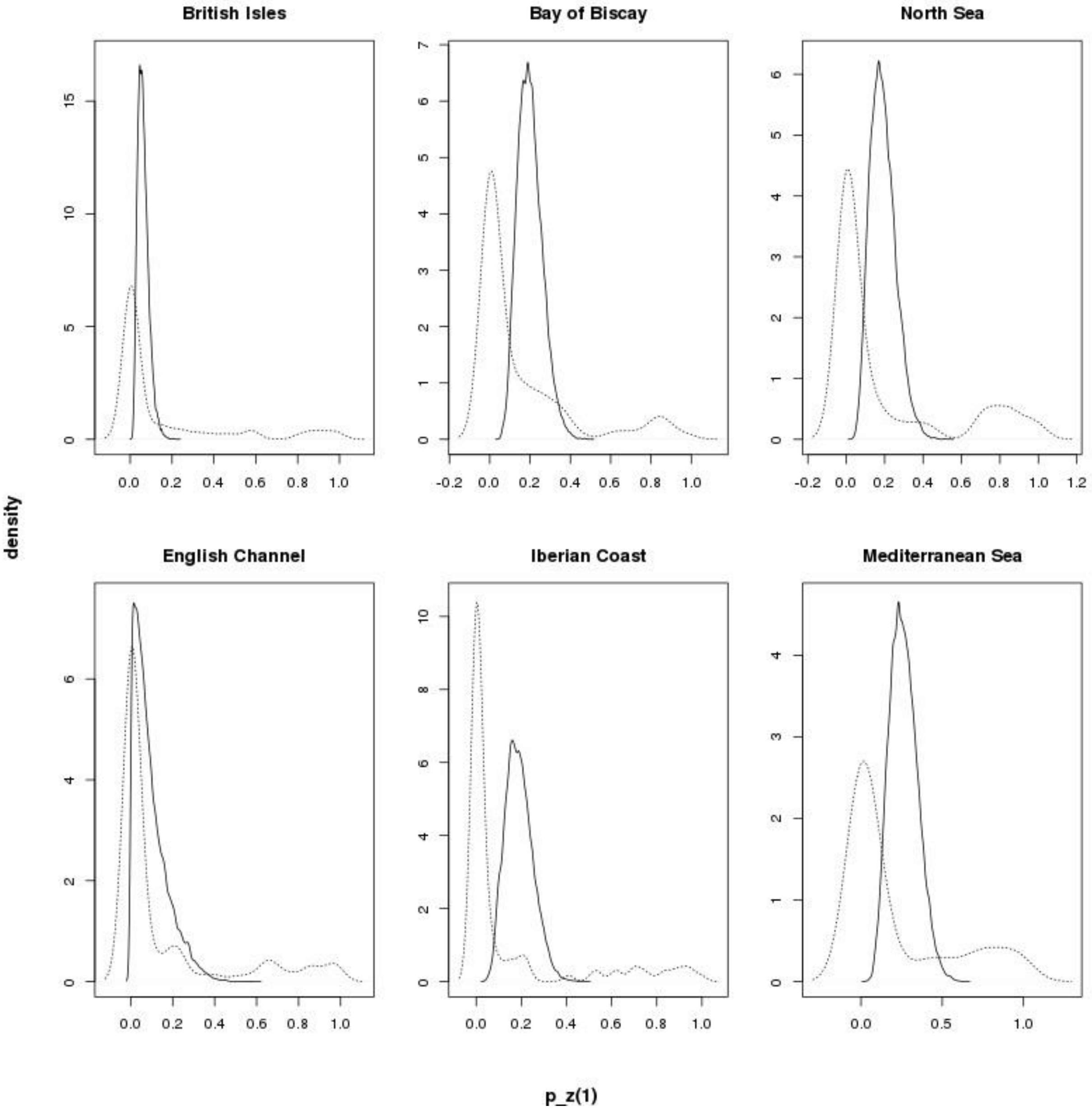


Figure A 4.4: Prior (dotted line) and posterior (solid line) regarding the proportion of recruitment within each zone of the model GEREM occurring the first year (p_z (1))

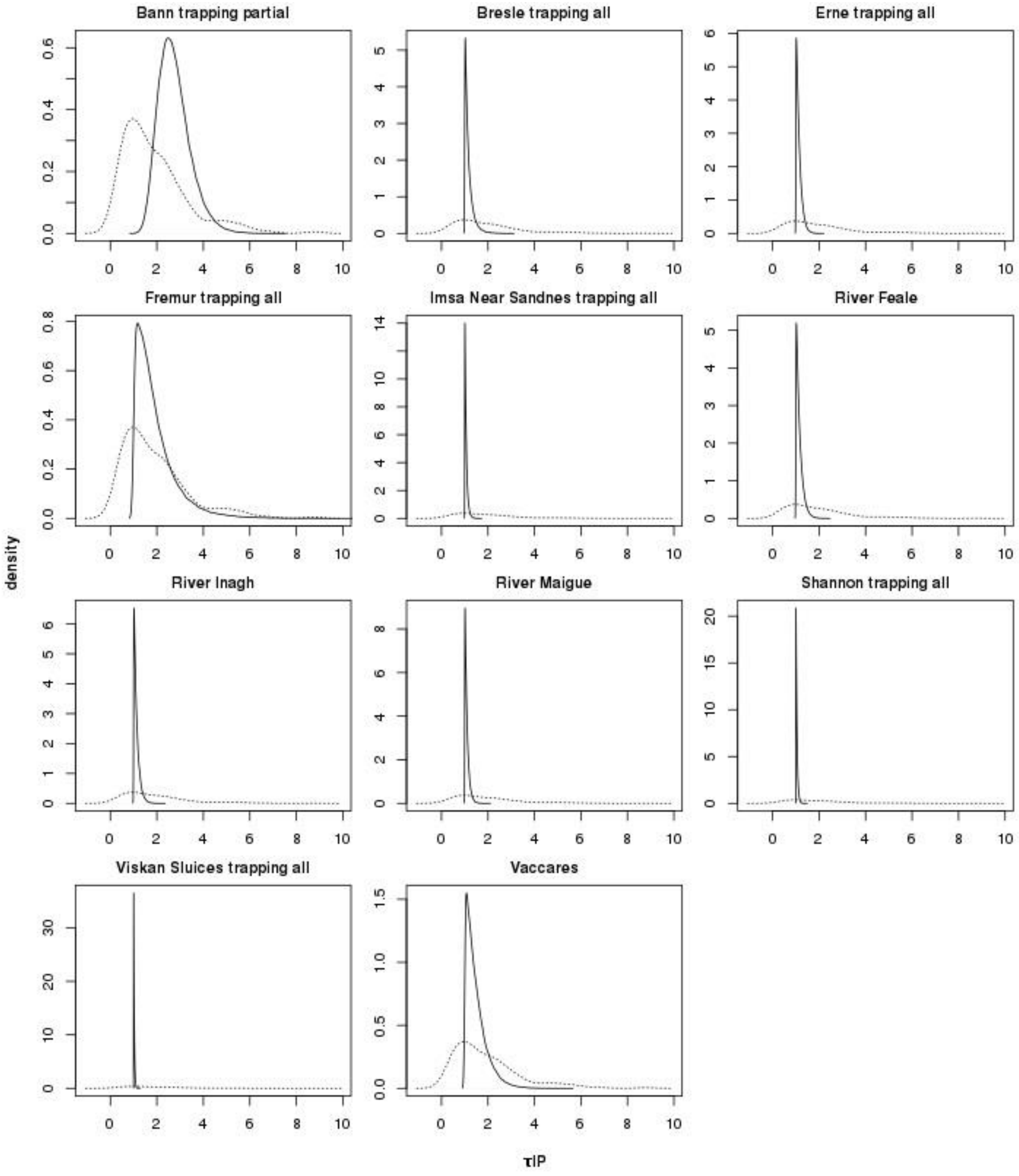


Figure A 4.5: Prior (dotted line) and posterior (solid line) regarding the precision of observed time series (3)

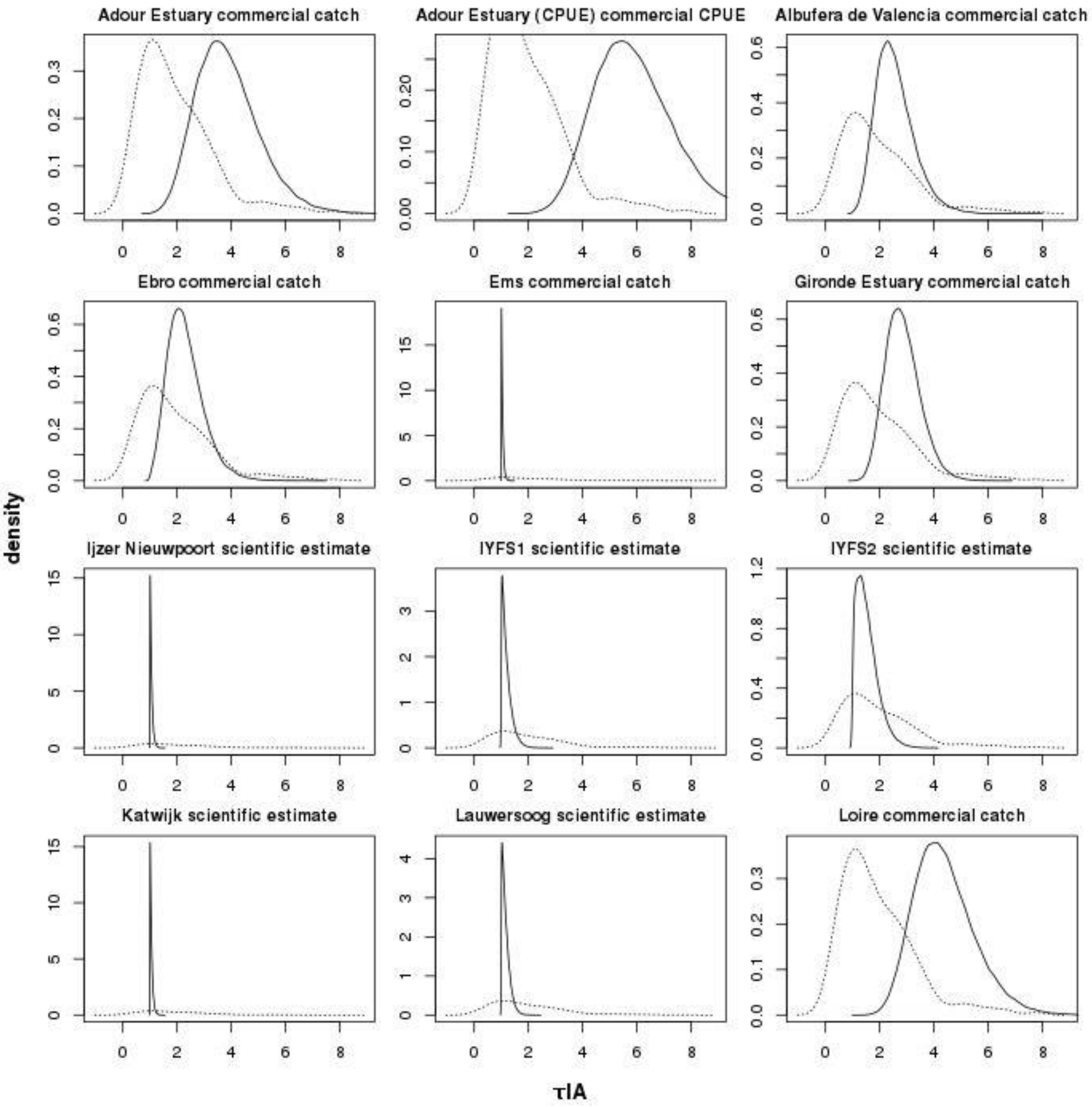


Figure A 4.6: Prior (dotted line) and posterior (solid line) regarding the precision of observed time series (1)

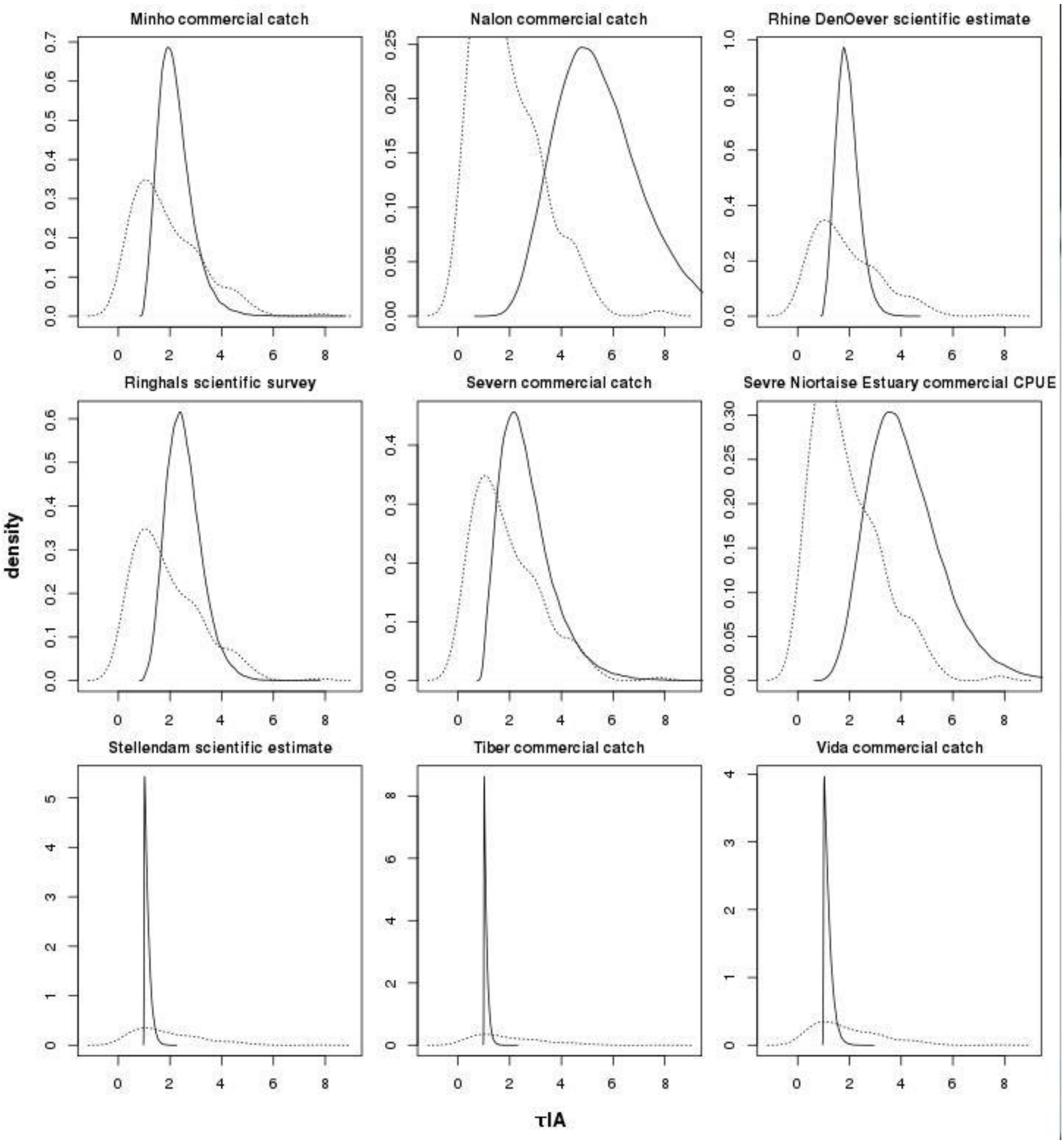


Figure A 4.6: Prior (dotted line) and posterior (solid line) regarding the precision of observed time series (1) (continued)

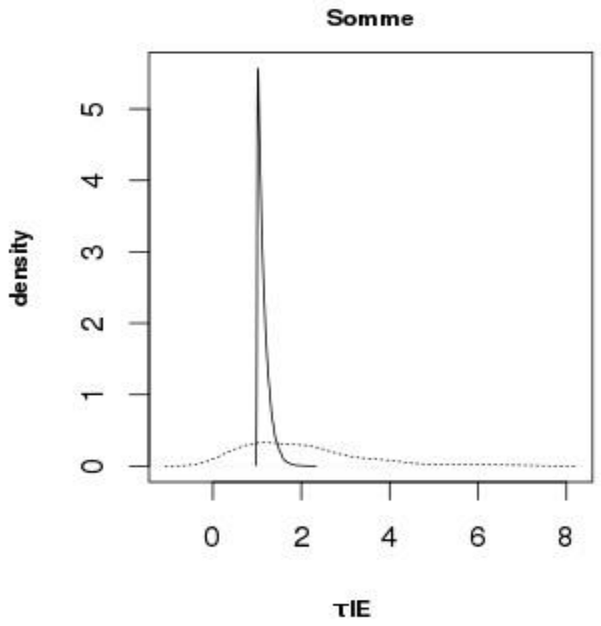


Figure A 4.6: Prior (dotted line) and posterior (solid line) regarding the precision of observed time series (2)

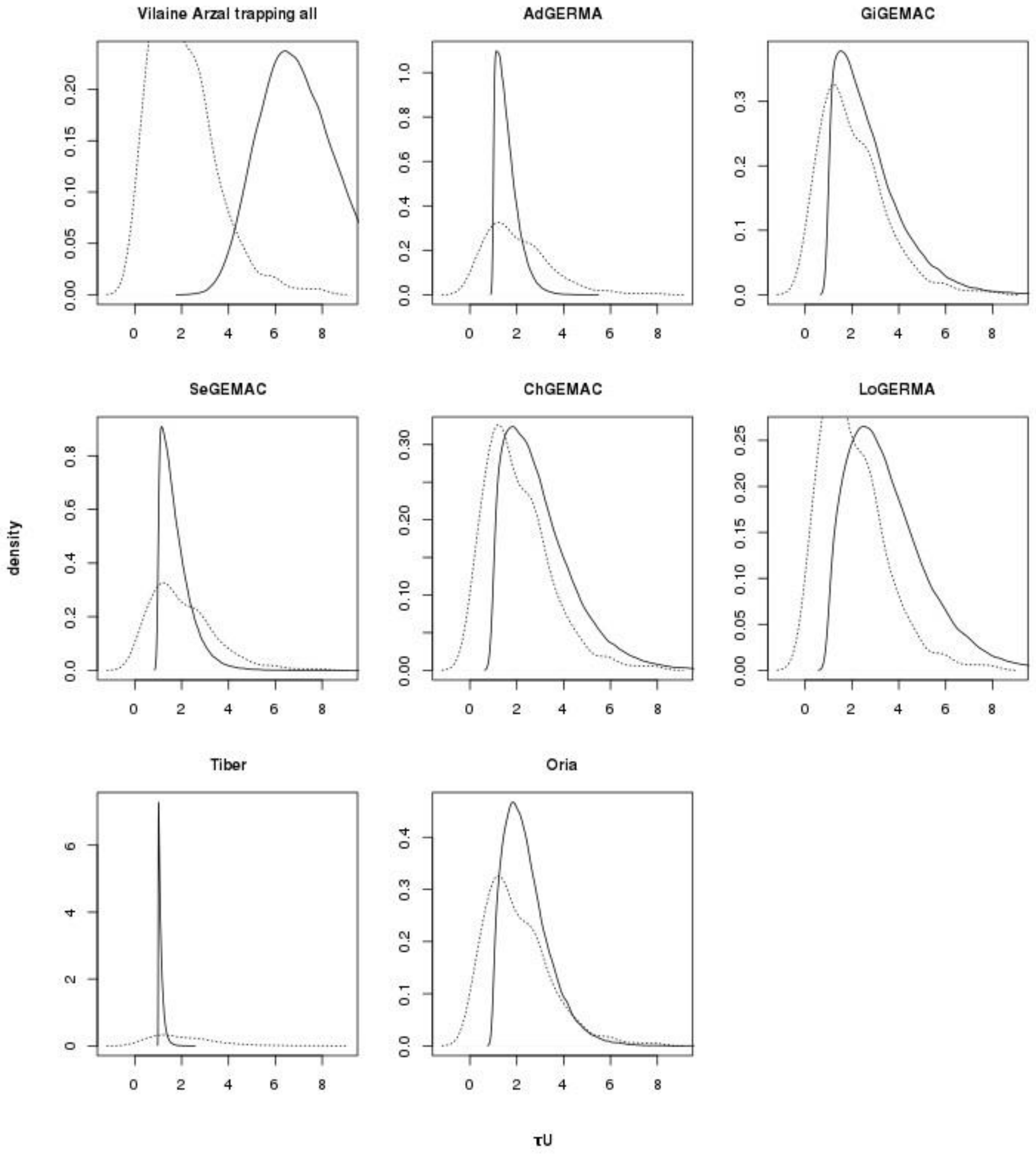


Figure A 4.7: Prior (dotted line) and posterior (solid line) regarding the precision of observed time series (4)

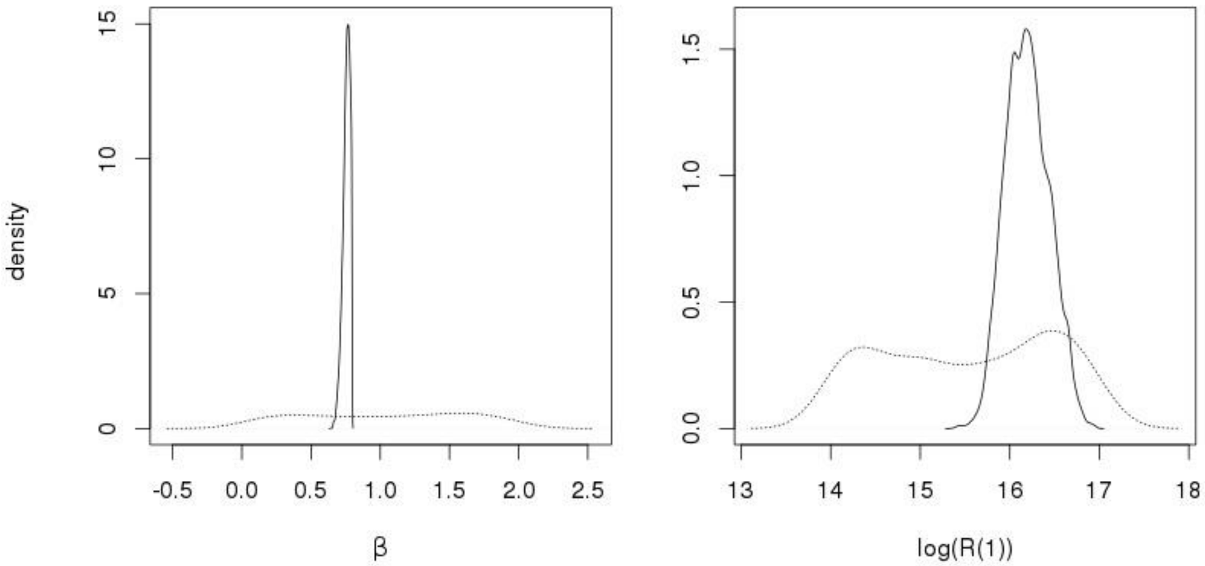


Figure A 4.8: Prior (dotted line) and posterior (solid line) regarding the factor β (left panel) and log(R (1)) (global recruitment the first year) (right panel)

Appendix V: GEREM model fitting to recruitment time-series

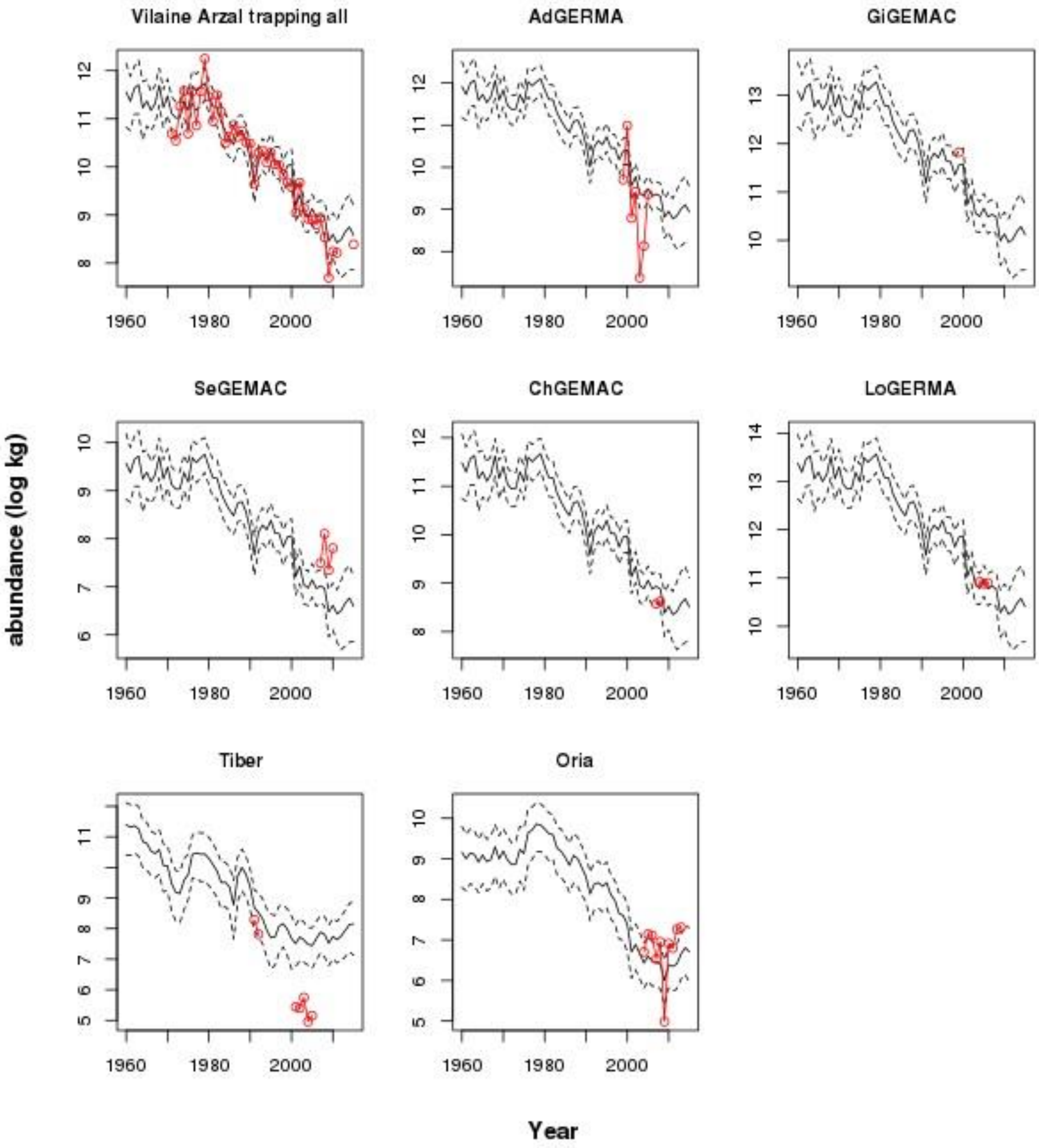


Figure A 5.1: Estimation of recruitment from GEREM at the river basin scale (black solid line) and fit to recruitment time series (4) (red solid line)

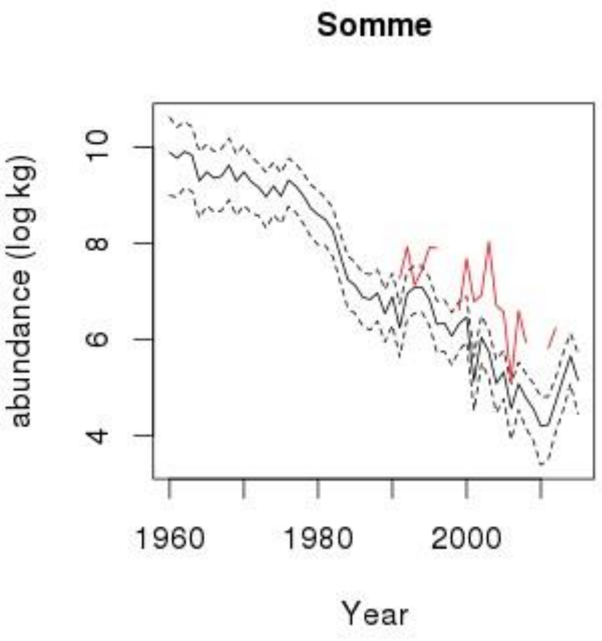


Figure A 5.2: Estimation of recruitment from GEREM at the river basin scale (black solid line) and fit to recruitment time series (2) (red solid line)

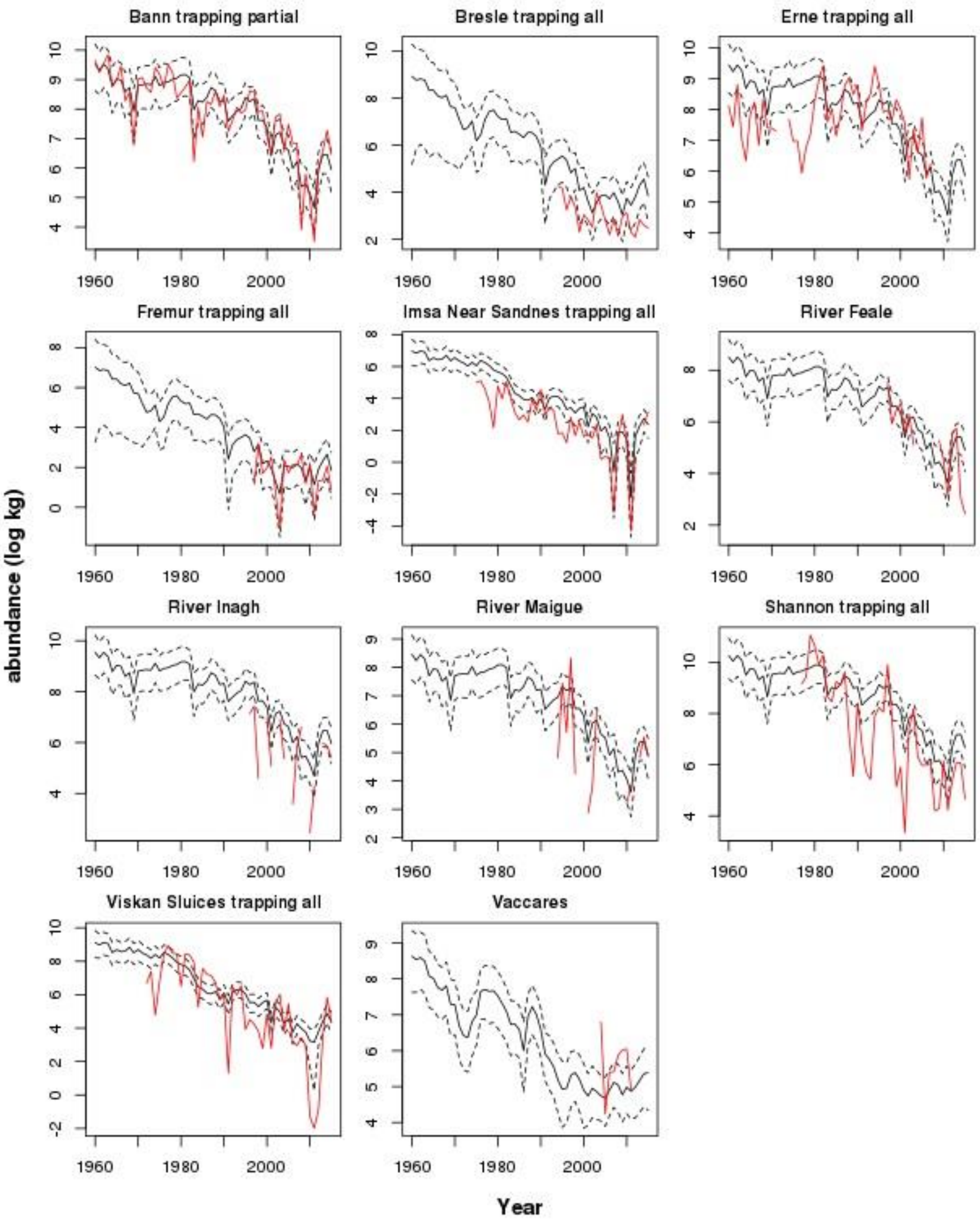


Figure A 5.3: Estimation of recruitment from GEREM at the river basin scale (black solid line) and fit to recruitment time series (3) (red solid line)

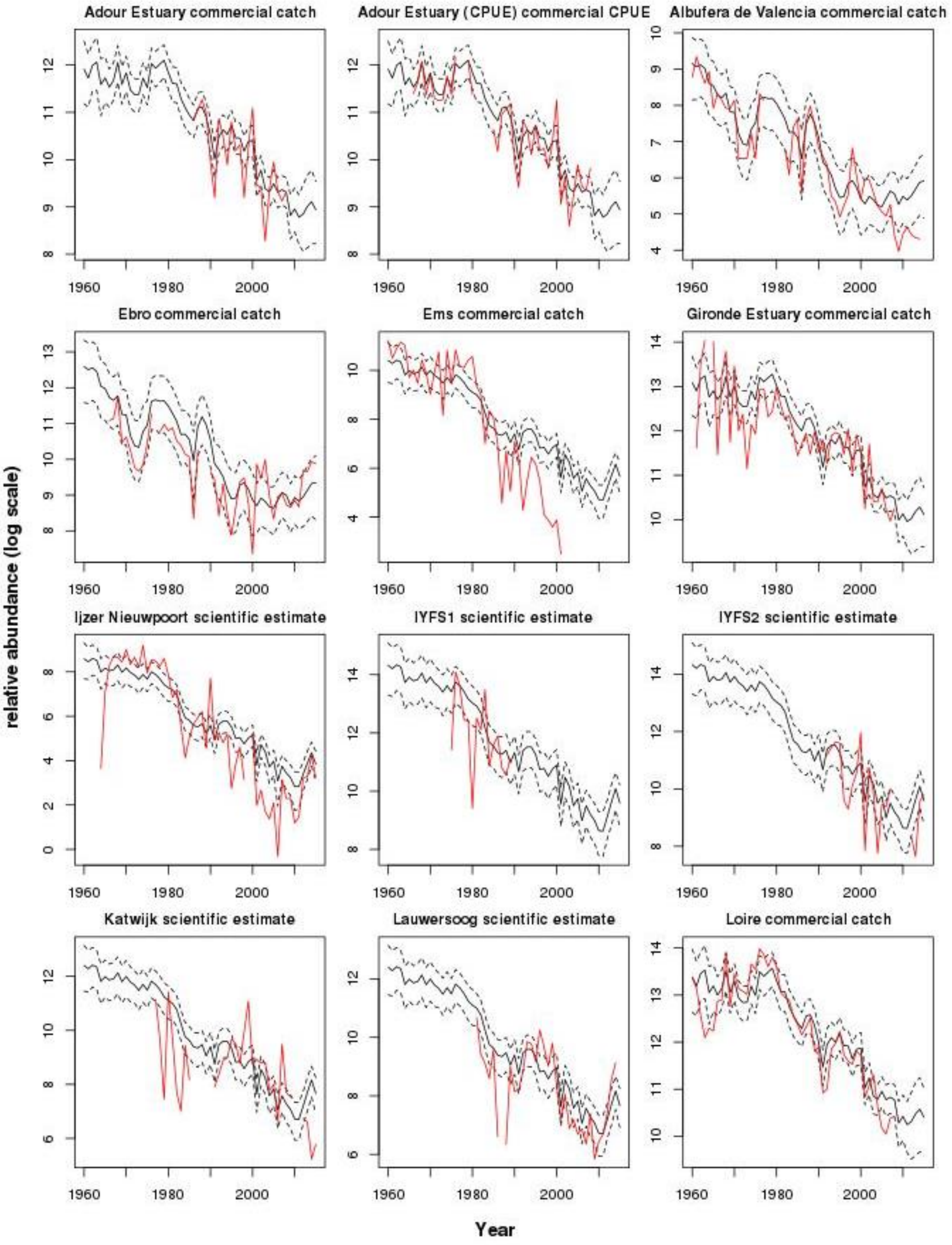


Figure A 5.4: Estimation of recruitment from GEREM at the river basin scale (black solid line) and fit to recruitment time series (1) (red solid line)

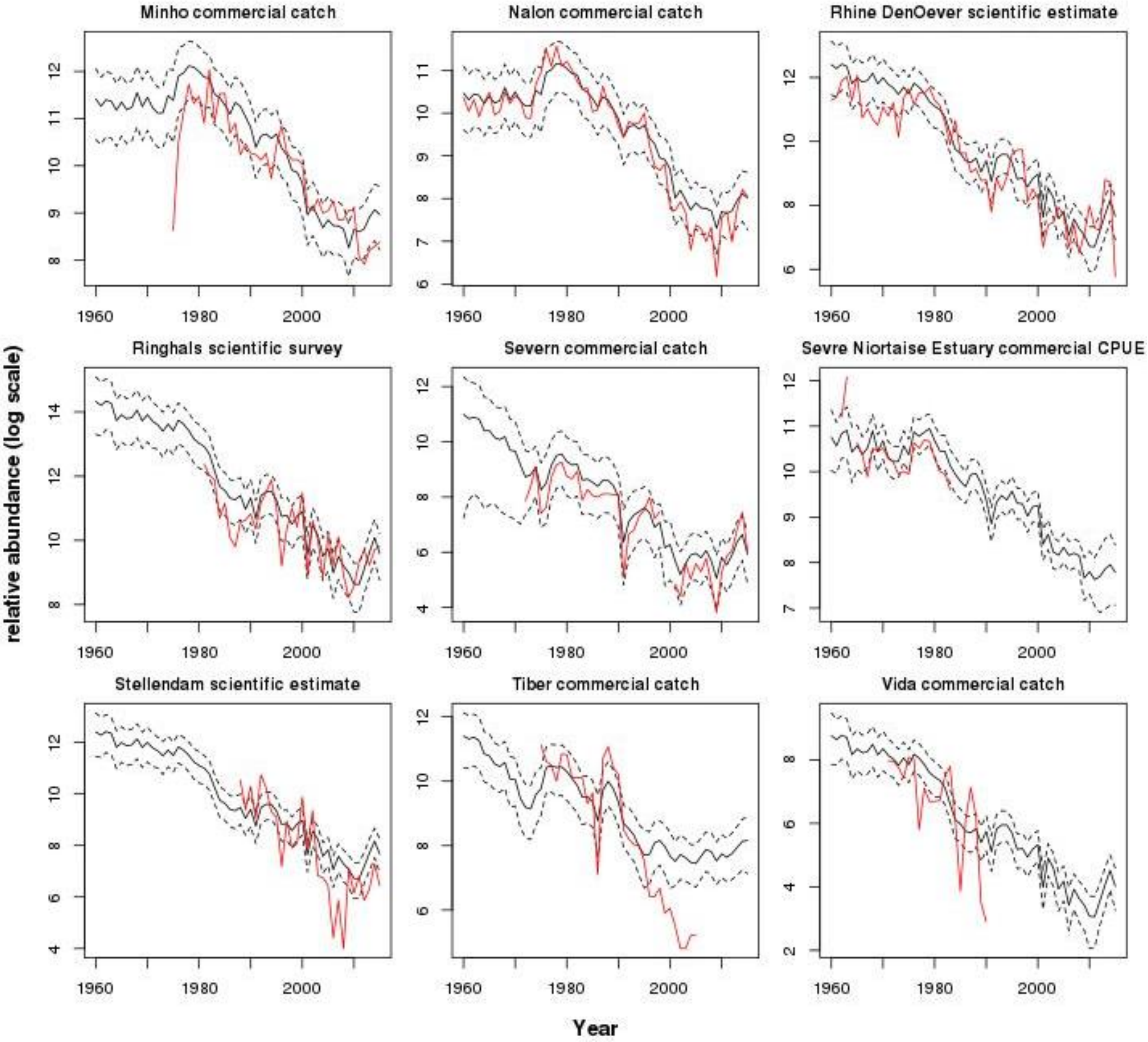


Figure A 5.4: Estimation of recruitment from GEREM at the river basin scale (black solid line) and fit to recruitment time series (1) (red solid line) (continued)

Appendix VI: Coefficient of determination for the different recruitment time-series used in the model GEREM

Recruitment time-series	Coefficient of determination
Vilaine Arzal trapping all	0.929
AdGERMA	0.152
GiGEMAC	-Inf.
SeGEMAC	-10.529
ChGEMAC	-150.985
LoGERMA	-63.673
Tiber	-1.207
Oria	0.0367
Adour estuary commercial catch	0.675
Adour estuary (CPUE) commercial CPUE	0.869
Albufera de Valencia commercial catch	0.837
Ebro commercial catch	0.563
Ems commercial catch	0.670
Gironde estuary commercial catch	0.649
Ijzer Nieuwpoort scientific estimate	0.734
IYFS1 scientific estimate	0.037
IYFS2 scientific estimate	0.524
Katwijk scientific estimate	-0.068
Lauwersoog scientific estimate	0.337
Loire commercial catch	0.832
Minho commercial catch	0.612
Nalon commercial catch	0.937
Rhine Denoever scientific estimate	0.818
Rhingals scientific survey	0.663
Severn commercial catch	0.885
Sèvres Niortaise Estuary commercial CPUE	0.588
Stellendam scientific estimate	0.559
Tiber commercial catch	0.635
Vida commercial catch	0.388
Bann trapping partial	0.843
Bresle trapping all	-2.485
Erne trapping all	-0.545
Fremur trapping all	0.504
Imsa Near Sandnes trapping all	0.511
River Feale	0.430
River Inagh	-0.059
River Maigue	0.102
Shannon trapping all	0.418
Viskan Sluices trapping all	0.527
Vaccares	-0.961
Somme	-1.643

Appendix VII: Results of the sensitivity analysis carried out in the model GEREM

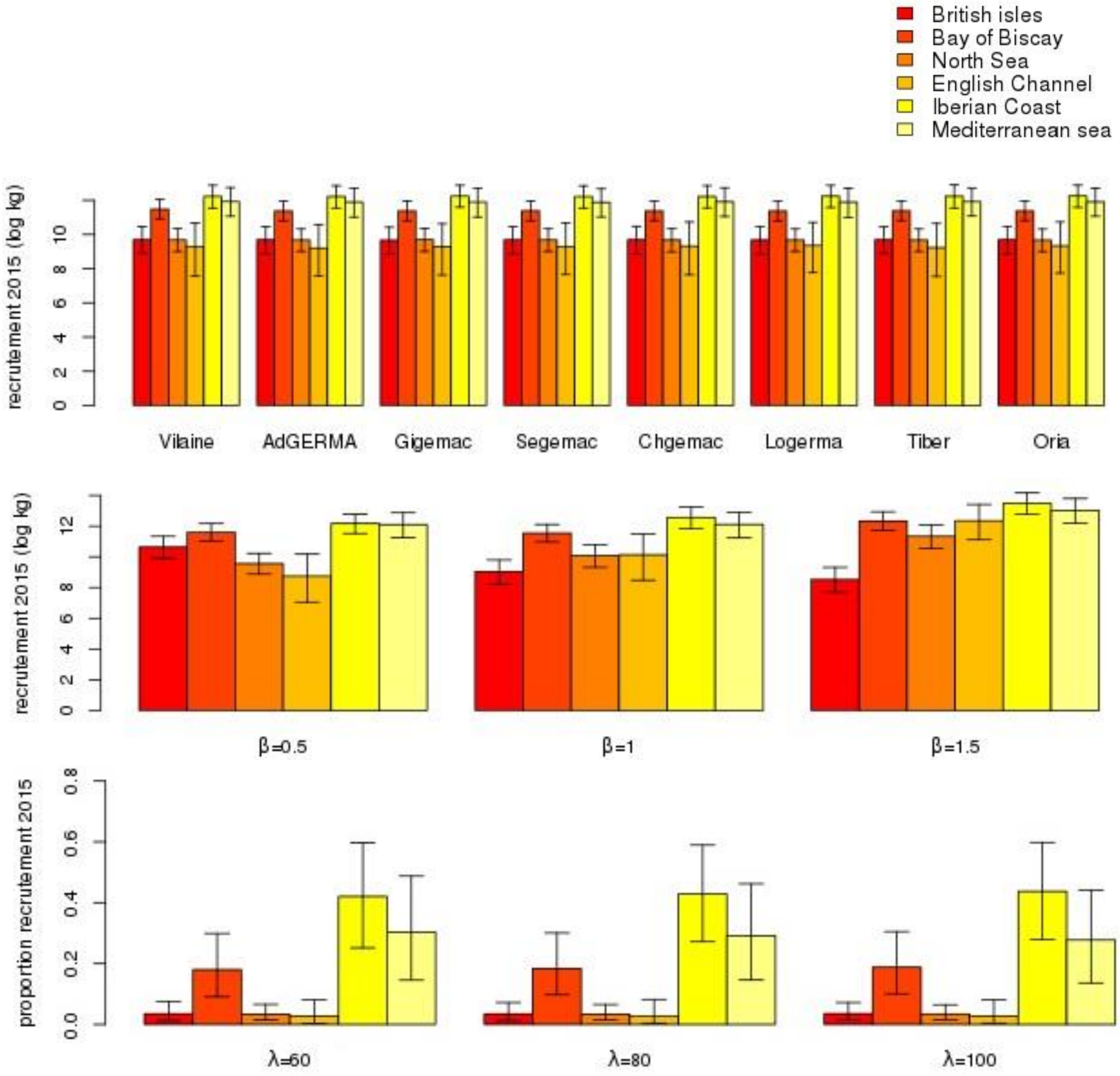


Figure A 7.1: Zone recruitments estimated by the model for the last year when the model is fitted to altered absolute recruitment (top panel), different values of beta (middle panel) and different values of lambda (bottom panel). Bars represent the median while vertical segments represent the 2.5% and 97.5% quantile of the a posteriori distributions

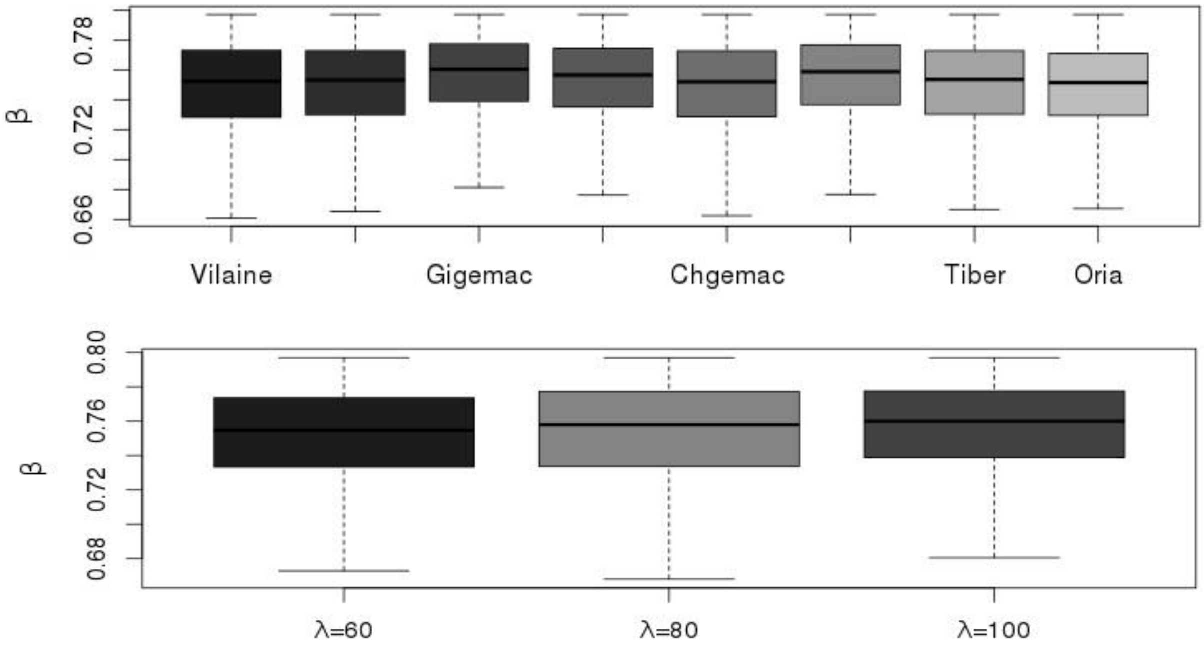


Figure A 7.2: Medians (horizontal bars) and 2.5% and 97.5% quantiles (segments) of β estimated by the model when it is fitted on altered absolute recruitments datasets and different values of λ

Appendix VIII: Summary of fitted ARIMA models to GEREM recruitment estimates and environmental factors

Time-series	p	d	q
Primary Production	0	1	0
R1	0	1	0
R2	0	1	0
R3	1	1	0
R4	0	1	0
R5	0	1	0
R6	0	1	0

Time-series	p	d	q
NAO	0	0	0
R1	0	1	0
R2	2	1	2
R3	1	1	0
R4	0	1	0
R5	1	1	0
R6	0	1	0

Time-series	p	d	q
GSI	0	1	0
R1	0	1	0
R2	0	1	0
R3	1	1	0
R4	0	1	0
R5	0	1	0
R6	0	1	0

These ARIMA models were used to carry out correlation analysis on short-time scales and where fitted to remove autocorrelation in time-series.

p = order of the autoregressive parameters (AR)

d = order of differencing

q = order of the moving average parameters (MA)

R1=Recruitment in the British Isles zone

R2=Recruitment in the Bay of Biscay zone

R3= Recruitment in the North Sea zone

R4= Recruitment in the English Channel zone

R5=Recruitment on the Iberian Coast

R6= Recruitment in the Mediterranean Sea

Appendix IX: Results of the Student test to assess the statistical significance of correlations between recruitment and environmental factors on long-time scales

	SST_1				SST_2				SST_3				$\overline{SST_2}$				$\overline{SST_3}$			
	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}
R1	52	3.14	1.8	3.18	52	3.2	-1.83	3.18	52	3.25	-1.84	3.18	52	3.14	-1.84	3.18	52	3.14	-1.87	3.18
R2	52	2.99	-1.79	3.18	52	3.04	-1.71	3.18	52	3.1	-1.63	3.18	52	2.99	-1.77	3.18	52	2.99	-1.75	3.18
R3	52	2.94	-1.4	3.18	52	2.99	-1.24	3.18	52	3.04	-1.1	3.18	52	2.94	-1.32	3.18	52	2.93	-1.25	3.18
R4	52	3.0	-1.2	3.18	52	3.05	-1.09	3.18	52	3.1	-1	3.18	52	3.00	-1.14	3.18	52	3.0	-1.09	3.18
R5	52	2.89	-2.16	3.18	52	2.94	-2.2	3.18	52	3.00	-2.16	3.18	52	2.89	-2.23	3.18	52	2.89	-2.30	3.18
R6	52	3.06	-1.1	3.18	52	3.12	-1.01	3.18	52	3.17	-0.94	3.18	52	3.06	-1.05	3.18	52	3.06	-1.01	3.18

Figure A 9.1: correlations between SST (Sea Surface Temperature) over the North Atlantic Ocean and recruitment estimates from GEREM.

SST1, SST2, SST3=SST one year, two years, three years before recruitment takes place

$\overline{SST_2}$, $\overline{SST_3}$ = *SST averaged over 2 years and three years respectively before recruitment takes place*

R1=Recruitment in the British Isles zone

R2=Recruitment in the Bay of Biscay zone

R3= Recruitment in the North Sea zone

R4= Recruitment in the English Channel zone

R5=Recruitment on the Iberian Coast

R6= Recruitment in the Mediterranean Sea

N=length of the initial time-series; N*=corrected sample size; when $t_{obs} > t_{th}$ in absolute values, then the hypothesis H0 (no significant correlation) is rejected

No significant correlation have been found between recruitment estimates and SST over the North Atlantic Ocean on long-time scales

	GSI_1				GSI_2				GSI_3				$\overline{GSI_2}$				$\overline{GSI_3}$			
	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}	N	N*	t_{obs}	t_{th}
R1	43	3.18	-0.45	3.18	43	3.08	-0.46	3.18	43	3.06	-0.48	3.18	43	3.06	-0.45	3.18	43	2.94	-0.45	3.18
R2	43	3.11	-0.68	3.18	43	3.01	-0.69	3.18	43	2.98	-0.72	3.18	43	2.98	-0.67	3.18	43	2.87	-0.67	3.18
R3	43	3.16	-0.86	3.18	43	3.06	-0.87	3.18	43	3.03	-0.87	3.18	43	3.03	-0.86	3.18	43	2.92	-0.85	3.18
R4	43	3.00	-0.72	3.18	43	2.90	-0.73	3.18	43	2.88	-0.75	3.18	43	2.88	-0.71	3.18	43	2.77	-0.71	3.18
R5	43	2.98	-0.52	3.18	43	2.88	-0.56	3.18	43	2.86	-0.63	3.18	43	2.86	-0.53	3.18	43	2.75	-0.54	3.18
R6	43	2.97	-0.85	3.18	43	2.88	-0.93	3.18	43	2.86	-1.03	3.18	43	2.86	-0.88	3.18	43	2.74	-0.91	3.18

Figure A 9.2: correlations between the GSI (Gulf Stream Index) and recruitment estimates from GEREM

GSI1, GSI2, GSI3=GSI one year, two years, three years before recruitment takes place

$\overline{GSI_2}$, $\overline{GSI_3}$ = *GSI averaged over 2 years and three years respectively before recruitment takes place*

R1=Recruitment in the British Isles zone

R2=Recruitment in the Bay of Biscay zone

R3= Recruitment in the North Sea zone

R4= Recruitment in the English Channel zone

R5=Recruitment on the Iberian Coast

R6= Recruitment in the Mediterranean Sea

N=length of the initial time-series; N*=corrected sample size; when $t_{obs} > t_{th}$ in absolute values, then the hypothesis H0 (no significant correlation) is rejected

No significant correlation have been found between recruitment estimates and the GSI index on long-time scale

Appendix X : RUNJAGS code

```
# MODEL D'ETAT

model{

for (zone in 1:nbzone){
        weightZone[zone]<-sum(pow(surfaceallbv[zone,],beta))
}

for (bv in 1:nbbv){
        weight[bv]<-pow(surface[bv],beta)/weightZone[zonebv[bv]]
}

logRglobal[1]<-logR1

Rglobal[1]<-exp(logRglobal[1])

for (zone in 1:(nbzone)){
Rzone[1,zone]<-Rglobal[1]*propR[zone,1]
}
for (bv in 1:nbbv){
Rbvpred[1,bv]<-Rzone[1,zonebv[bv]]*weight[bv]
sdRbv[1,bv]<-sqrt((0.000001+Rzone[1,zonebv[bv]])*(0.000001+weight[bv])*(.999999999999-weight[bv]))
Rbv[1,bv]<-max(0.000000001,Rbvpred[1,bv]+epsilonRbv[(1-1)*nbbv+bv]*sdRbv[1,bv]) #troncature pour éviter des log de 0
}

for (annee in 2:nbyear){
mulogRglobal[annee]<-logRglobal[annee-1]
logRglobal[annee]<-mulogRglobal[annee]+epsilonR[annee]*sdRwalk
Rglobal[annee]<-exp(logRglobal[annee])
for (zone in 1:(nbzone)){
Rzone[annee,zone]<-propR[zone,annee]*Rglobal[annee]
}
for (bv in 1:nbbv){
Rbvpred[annee,bv]<-Rzone[annee,zonebv[bv]]*weight[bv]
sdRbv[annee,bv]<-sqrt((0.000001+Rzone[annee,zonebv[bv]])*(0.000001+weight[bv])*(.999999999999-weight[bv]))
Rbv[annee,bv]<-max(0.000000001,Rbvpred[annee,bv]+epsilonRbv[(annee-1)*nbbv+bv]*sdRbv[annee,bv])   #troncature   pour
éviter des log de 0
}
}
for (zone in 1:nbzone){
        Rzone_final[zone]<-Rzone[nbyear,zone]
        alpha[zone]<-initpropR[zone]*precisionpropRwalk+0.01
```

```
}
```

 # MODEL D’OBSERVATION

```
for (annee in 1:nbyear){
for (isurvey in 1:nbsurvey){
#######observation model for data (1)
########
logIApred[annee,isurvey]<-logq[isurvey]+log(Rbv[annee,bvsurvey[isurvey]])-0.5/tauIA[isurvey]
logIAObs[annee,isurvey]~dnorm(logIApred[annee,isurvey],tauIA[isurvey])
}
for (ipiege in 1:nbpiege){
#######observation model for data (3)
########
logIPpred[annee,ipiege]<-loga[ipiege]+log(Rbv[annee,bvpiege[ipiege]])-0.5/tauIP[ipiege]
logIPObs[annee,ipiege]~dnorm(logIPpred[annee,ipiege],tauIP[ipiege])
}

for (iexpert in 1:nbexpert){
#######observation model for data (2)
########
logIEpred[annee,iexpert]<-logg[iexpert]+log(Rbv[annee,bvexpert[iexpert]])-0.5/tauIE[iexpert]
logIEObs[annee,iexpert]~dnorm(logIEpred[annee,iexpert],tauIE[iexpert])
}

for (icomptage in 1:nbcomptage){
#######observation model for data (4)
########
logUpred[annee,icomptage]<-log(Rbv[annee,bvcomptage[icomptage]])-0.5/tauU[icomptage]
logUObs[annee,icomptage]~dnorm(logUpred[annee,icomptage],tauU[icomptage])
}
}
```

 # PARAMETRES

```
beta~dunif(0.01,2)
propR[1:nbzone,1]~ddirich(alpha[1:nbzone])
for (annee in 2:nbyear){
propR[1:nbzone,annee]~ddirich(lambda*propR[1:nbzone,annee-1])
}
lambda<-80

for (y in 1:(nbbv*nbyear)){
        epsilonRbv[y]~dnorm(0,1)
}
```

```
for (y in 1:nbyear){
        epsilonR[y]~dnorm(0,1)
}
logR1~dunif(14,17)
for (survey in 1:nbsurvey){
        logq[survey]~dunif(-13,0)
}
for (piege in 1:nbpiege){
loga[piege]~dunif(-2.3,-0.7)
}
for (expert in 1:nbexpert){
logg[expert]~dunif(-0.43,-0.16)
}

precisionpropRwalk~dunif(0.5,1)


for (isurvey in 1:nbsurvey){
        tauIA[isurvey]~dgamma(2,1)T(1,15)
        sdIA[isurvey]<-1/sqrt(tauIA[isurvey])
}

for (ipiege in 1:nbpiege){
       tauIP[ipiege]~dgamma(2,1)T(1,15)
       sdIP[ipiege]<-1/sqrt(tauIP[ipiege])
}

for (icomptage in 1:nbcomptage){
        tauU[icomptage]~dgamma(2,1)T(1,15)
        sdU[icomptage]<-1/sqrt(tauU[icomptage])
}

for (iexpert in 1:nbexpert){
        tauIE[iexpert]~dgamma(2,1)T(1,15)
        sdIE[iexpert]<-1/sqrt(tauIE[iexpert])
}


tauRwalk~dgamma(2,1)T(1,15)
sdRwalk<-1/sqrt(tauRwalk)
}
```

AGRO CAMPUS OUEST

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Titre français : L'évaluation de stock dans le cas de l'Anguille Européenne : Vers une évaluation internationale d'une population fragmentée et distribuée à large échelle.

Titre anglais: Stock assessment in the case of the European eel: Towards an international assessment of a widely-distributed and fragmented population.

Résumé (1600 caractères maximum) : L'anguille Européenne est une espèce catadrome subissant un déclin important depuis la fin des années 1970, à tel point qu'elle est jugée en danger critique d'extinction par l'IUCN depuis 2008. S'agissant d'une seule population panmictique, l'évaluation de son stock doit se faire à l'échelle de son aire de distribution. Cependant, l'évaluation de la population entière reste difficile du fait de sa distribution à large échelle et de sa dimension fractale, affectant notamment la phase continentale. Ainsi, le recrutement semble être le stade le plus adéquat pour tenter d'évaluer la population à large échelle. Le modèle GEREM (Glass Eel Recruitment Estimation Model) offre un cadre méthodologique pour modéliser le recrutement à différentes échelles spatiales, prenant en compte la dimension fractale du recrutement de l'Anguille dans sa démarche de modélisation. L'objectif principal consistait à développer ce modèle à l'échelle Européenne, afin de dériver un indice global de recrutement afin d'évaluer la population entière. Les résultats indiquent une chute d'abondance depuis la fin des années 1970, atteignant 6% du niveau de référence (1960-1979) en 2015, alors qu'un déclin plus prononcé est observé en mer du Nord. Dans la majorité des cas, les hypothèses de modélisation semblent être respectées, fournissant ainsi une démarche de modélisation utile pour l'évaluation du stock d'Anguille Européenne à l'échelle de son aire de distribution.

Abstract (1600 caractères maximum): The European eel, a catadromous species spread over Europe and North Africa, has been declining significantly since the late 1970s at the scale of its distribution area. As such, it has been listed as critically endangered by the IUCN red list since 2008. Since the European eel is considered to be a single panmictic population, its stock assessment must be conducted throughout its entire range. However, assessing the overall population remains difficult given its widespread distribution and its fractal geometry, especially visible during the continental phase. Hence, glass eel recruitment seems to be the "best" stage to assess the state of the overall population. In this context, a model named GEREM (Glass Eel Recruitment Estimation Model) provides a methodological framework to model recruitment at different spatial scales. This model was implemented to take into account the fractal dimension of glass eel recruitment. The main objective was to develop this model at the European scale in order to estimate the overall glass eel recruitment trend, which had never been done before. Results indicated an overall decline of the population reaching very low levels in 2015 (6% of the 1960-1979 recruitment average), while a more pronounced decline was observed in the North Sea compared to elsewhere in Europe. In most cases, modelling assumptions were satisfied, providing therefore a useful modelling approach to assess the state of the overall population.

Mots-clés : A.*anguilla*, évaluation de stock, panmixie, dimension fractale, modélisation statistique

Key Words: A.*anguilla*, stock assessment, panmixia, fractal dimension, statistical modelling