Dispersal modelling of the early life stages of flatfish in the Anthropocene

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SUMMARY

Effective fishery management and conservation require the understanding of how spawning grounds and nurseries are connected and what processes influence larval retention, dispersal and population dynamics. In many species, processes early in life are critical for the population dynamics, especially in the marine environment where many taxa have a pelagic larval phase. The transport of larvae from the spawning grounds to the nursery grounds is driven by hydrodynamic processes, but the final dispersal pattern and larval survival is affected by environmental factors, physiology, behaviour and reproductive strategies (spawning period and location). This is especially the case for species with a long pelagic larval phase and where recruitment is strongly constrained by access to nurseries, like flatfish.

My PhD research focuses on six commercially important flatfish species in the North Sea: common sole (*Solea solea*), European plaice (*Pleuronectes platessa*), turbot (*Scophthalmus maximus*), brill (*Scophtalmus rhombus*), European flounder (*Platichthys flesus*) and common dab (*Limanda limanda*). I used a particle-tracking model (LARVAE&CO) coupled to a widely used 3D hydrodynamic model (COHERENS) to determine the role of life history traits on the dispersal pattern of the early life stage of flatfish. Model results show different connectivity patterns: dab, flounder and plaice show a high connectivity level across the North Sea whereas turbot, sole and brill are more isolated. In addition to the impact of life history traits such as pelagic larval duration, those dispersal patterns are strongly linked by spawning period and oceanic circulation, notably the presence of oceanic front during summer.

In this context, anthropogenic pressure might impact processes which occur during early life. Climate change affects ocean physics and hence is expected to impact the dynamics of larval sole. Therefore, it is important to understand the impact of increased temperature and changes in wind speed and direction on larval drift and survival. The impact of five scenarios of climate change inspired by the 2040 projections of the Intergovernmental Panel on Climate Change (IPCC) are discussed and compared with interannual variability. In the case of a climate change scenario including a temperature increase of 2°C, an early spawning and a change of wind speed and direction, the model predicts that, at the North Sea scale, dispersal distance and pelagic larval duration would increase (by 70 % and 22 % respectively). It also predicts that larval recruitment at the nursery grounds would increase in some areas (the Netherlands, Germany and Thames estuary) and decrease in others (France, Belgium and Norfolk), and that connectivity would show contrasting changes between areas. At the regional scale, our model predicts considerable changes in larval recruitment (between -58 % and 36 % according the nursery grounds, with an average of +9 % at the North Sea scale) and connectivity (local retention decreased by 4 % and seeding increased by 37 % at the North Sea scale). All of these factors affect the distribution and productivity of sole and therefore the functioning of the demersal ecosystem and fisheries management.

Understanding the influence of man-made infrastructures such as offshore wind farms on fish population dynamics is an important issue for fisheries management. The six flatfish species are likely to be affected because areas with offshore wind farms, already in place or planned, show a spatial overlap with their spawning grounds. An important overlap between offshore wind farm areas and flatfish spawning grounds was estimated, with a resulting proportion of settlers originating from those areas varying from 2 % to 16 %. Our study suggests that plaice, dab and brill could be the most affected flatfish species, yet with some important local disparities across the North Sea.

Larval transport model requires a good knowledge of the biological processes governing larval dispersal while they may be highly sensitive to some parameters. Various assumptions about larval traits, behaviour and other model parameters can be tested by comparing simulation results with field data to identify the most sensitive parameters and to allow improvement of the model calibration. This thesis showed that biological parameterisation is more important than annual variability to explain larval recruitment variability, whereas for connectivity, year-to-year variability leads to higher variability than changes of the biological parameters. Sensitivity analyses showed that the most influential parameters were growth rate, spawning period, and mortality. Calibration showed that a scenario with a low mortality associated to a long larval duration and with a behaviour involving nycthemeral and tidal migration was the best to reproduce observations.

My thesis helps to understand processes which control the dispersal of early life stages in the marine environment and to assess the potential impact of anthropogenic pressure such as climate change and implementation of offshore wind farms on larval dispersal, with a specific care on methods which can help to assess uncertainties and calibration. Improving knowledge on stock structure and considering the potential changes from a conservation perspective are useful to support fisheries management. Especially in an area like the North Sea where anthropogenic pressures are high, conflicts among sectorial interests are to be expected. The political consequences of fisheries management are particularly meaningful in the context of

the recent departure of the UK from the EU. Management has to make trade-offs among those aspects; knowledge on fish(eries) biology, especially on population structure and connectivity, represents a most valuable contribution.

SAMENVATTING

Effectief visserijbeheer en -behoud vereisen inzicht in de manier waarop paai- en kraamgebieden met elkaar verbonden zijn en welke processen de retentie, verspreiding en populatiedynamiek van larven beïnvloeden. Bij veel soorten zijn processen vroeg in het leven van cruciaal belang voor de populatiedynamiek, vooral in het mariene milieu waar veel taxa bestaan met een pelagische larvale fase. Het transport van larven van de paaigronden naar de kraamgebieden wordt aangedreven door hydrodynamische processen, maar het uiteindelijke verspreidingspatroon en de overleving van de larven worden beïnvloed door omgevingsfactoren, fysiologie, gedrag en reproductiestrategieën (paaiperiode en locatie). Dit is vooral het geval voor soorten met een lange pelagische larvale fase en waar de rekrutering sterk wordt beperkt door toegang tot kraamgebieden, zoals platvis.

Mijn doctoraatsonderzoek richt zich op zes commercieel belangrijke platvissoorten in de Noordzee: tong (*Solea solea*), Europese schol (*Pleuronectes platessa*), tarbot (*Scophthalmus maximus*), griet (*Scophtalmus rhombus*), Europese bot (*Platichthys flesus*) en gewone schar (*Limanda limanda*). Ik gebruikte een deeltjes-volgmodel (LARVAE&CO) gekoppeld aan een veelgebruikt 3D hydrodynamisch model (COHERENS) om de rol van levensgeschiedeniskenmerken op het verspreidingspatroon van platvissen in de vroege levensfase te bepalen. Modelresultaten laten verschillende connectiviteitspatronen zien: schar, bot en schol vertonen een hoog connectiviteitsniveau over de Noordzee, terwijl tarbot, tong en griet meer geïsoleerd zijn. Naast de impact van levensgeschiedeniskenmerken zoals pelagische larvale duur, zijn die verspreidingspatronen sterk verbonden door paaitijd en oceaancirculatie, met name de aanwezigheid van een oceaanfront in de zomer.

In deze context kan antropogene druk processen beïnvloeden die tijdens het vroege leven plaatsvinden. Klimaatverandering beïnvloedt de oceaanfysica en zal daarom naar verwachting de dynamiek van tonglarven beïnvloeden. Daarom is het belangrijk om de impact van verhoogde temperatuur en veranderingen in windsnelheid en -richting op larvale drift en overleving te begrijpen. De impact van vijf scenario's van klimaatverandering geïnspireerd op de prognoses voor 2040 van het Intergouvernementeel Panel over klimaatverandering (IPCC) worden besproken en vergeleken met de jaar-tot-jaarfluctuaties. In het geval van een klimaatveranderingsscenario met een temperatuurstijging van 2°C, een vroege paaitijd en een verandering van windsnelheid en -richting, voorspelt het model dat op Noordzeeschaal de

verspreidingsafstand en pelagische larvale duur zouden toenemen (met respectievelijk 70 % en 22 %). Het voorspelt ook dat de rekrutering van larven in de kraamgebieden in sommige gebieden (Nederland, Duitsland en de monding van de Theems) zou toenemen en in andere (Frankrijk, België en Norfolk) zou afnemen, en dat de connectiviteit contrasterende veranderingen tussen gebieden zou laten zien. Op regionale schaal voorspelt ons model aanzienlijke veranderingen in larvale rekrutering (tussen -58 % en 36 % volgens de kraamgebieden, met een gemiddelde van +9 % op Noordzeeschaal) en connectiviteit (lokale retentie verminderd met 4 % en uitzaaiing op Noordzeeschaal met 37 % gestegen). Al deze factoren zijn van invloed op de verspreiding en productiviteit van tong en daarmee op het functioneren van het demersale ecosysteem en het visserijbeheer.

Het begrijpen van de invloed van kunstmatige infrastructuren zoals buitengaatse windparken op de dynamiek van de vispopulatie is een belangrijke kwestie voor het visserijbeheer. De zes platvissoorten zullen waarschijnlijk getroffen worden omdat gebieden met reeds aanwezige of geplande buitengaatse windparken een ruimtelijke overlap vertonen met hun paaigronden. Er werd een belangrijke overlap geschat tussen buitengaatse windparkgebieden en paaigebieden voor platvissen, waarbij een resulterend aandeel van kolonisten afkomstig uit die gebieden varieerde van 2 % tot 16 %. Onze studie suggereert dat schol, schar en griet de meest getroffen platvissoorten kunnen zijn, maar met enkele belangrijke lokale verschillen in de Noordzee.

Het larvale transportmodel vereist een goede kennis van de biologische processen die aan de basis liggen van de verspreiding van larven, aangezien deze zeer gevoelig kunnen zijn voor sommige parameters. Verschillende veronderstellingen over larvale eigenschappen, gedrag en andere modelparameters kunnen worden getest door simulatieresultaten te vergelijken met veldgegevens om de meest gevoelige parameters te identificeren en om de modelkalibratie te verbeteren. Dit proefschrift toonde aan dat biologische parametrisering belangrijker is dan jaarlijkse variabiliteit om variabiliteit in rekrutering van larven te verklaren, terwijl voor connectiviteit variabiliteit van jaar tot jaar leidt tot hogere variabiliteit dan veranderingen van de biologische parameters. Gevoeligheidsanalyses toonden aan dat groeisnelheid, paaitijd en sterfte de meest invloedrijke parameters waren. Kalibratie toonde aan dat een scenario met een lage mortaliteit geassocieerd met een lange larvale duur en met een gedrag van nyctemerale en getijdenmigratie de waarnemingen het best reproduceerde.

Mijn proefschrift helpt om processen te begrijpen die aan de basis liggen van de verspreiding van vroege levensfasen in het mariene milieu en om de potentiële impact van antropogene druk zoals klimaatverandering en uitvoering van buitengaatse windparken op de verspreiding van larven te beoordelen, met een specifieke aandacht voor methoden die kunnen helpen om onzekerheden en kalibratie te beoordelen. Het verbeteren van de kennis over de bestandsstructuur en het overwegen van mogelijke veranderingen vanuit een standpunt van instandhouding zijn nuttig om het visserijbeheer te ondersteunen. Zeker in een gebied als de Noordzee met een hoge antropogene druk zijn conflicten tussen sectorale belangen te verwachten. De politieke gevolgen van het visserijbeheer zijn bijzonder betekenisvol in de context van het recente vertrek van het VK uit de EU. Het beheer moet deze aspecten afwegen. Kennis over de biologie van vissen en visbestanden, met name over populatiestructuur en connectiviteit, vormt een zeer waardevolle bijdrage.

TABLE OF ABBREVIATIONS

CNS, Central North Sea

EEC, Eastern English Channel

FFL, First-feeding larvae

ICES, International Council for the Exploration of the Sea

LR, Larval recruitment

LTM, Larval transport model

MSY, Maximum sustainable yield

MT, Mean temperature

MTL, Metamorphosing larvae

NAO, North Atlantic Oscillation

NDCM, Mean net dispersal of the centre of mass

NS, North Sea

OWF, Offshore wind farms

PLD, Pelagic larval duration

SNS, Southern North Sea

SR, Stock-recruitment

SSB, Spawning Stock Biomass

SST, Sea surface temperature

TAC, Total Allowable Catch

YSL, Yolk-sac-larvae

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Chapter 1. GENERAL INTRODUCTION

1.1 MARINE ECOLOGY, CONNECTIVITY, RECRUITMENT AND POPULATION DYNAMICS

1.1.1 The ecosystem and marine living resources

1.1.1.1 Interaction between organisms and the marine environment

The bottle gourd (*Lagenaria siceraria*), originally from Africa, was one of the first domesticated plants more than 10 000 years ago, and the only one with a global distribution in pre-Colombian times. The plant was adopted by humans for a wide range of applications from containers to floats for fishing nets, and music instruments. Bottle gourds germinate even after up to one year floating in sea water. A seed released in an African river may drift to the coast of Brazil in less than six months (Kistler *et al.*, 2014). All this evidence supports the hypothesis of a domestication in America in the last 100 000 years BP.

Marine currents are important for the evolution of species and have been studied by Darwin himself. He tested the germination duration of different seeds in seawater and compared his results with marine currents to project distances which seeds could cover and their capacity to colonize new environments (Darwin, 1855, 1856). If marine currents are important to understand continental plant dispersal, it is even more important for marine organisms. In the introduction of my thesis, I highlight that the double knowledge on physical processes and biological traits is essential to understand the distribution and population dynamics of marine organisms.

1.1.1.2 The life cycle of marine species

The life cycle of marine species is complex and depends on a range of processes at different life stages which influence migration and population dynamics. The life cycle shapes the distribution, abundance, population dynamics and evolution of organisms. Marine organisms live in an environment with a high dispersal potential, which is dependent on the life stage. Planktonic larvae and actively swimming adults have a high propensity to disperse while juvenile stages are more likely to frequent a specific nursery ground (Figure 1-1) (Harden Jones, 1968). In nursery-dependent species, access constrains survival. Each stage has a specific phenology and stays in a spatially distinct habitat. I discuss below the biological traits of planktonic eggs and larvae of fish, the juvenile and adult life stages.

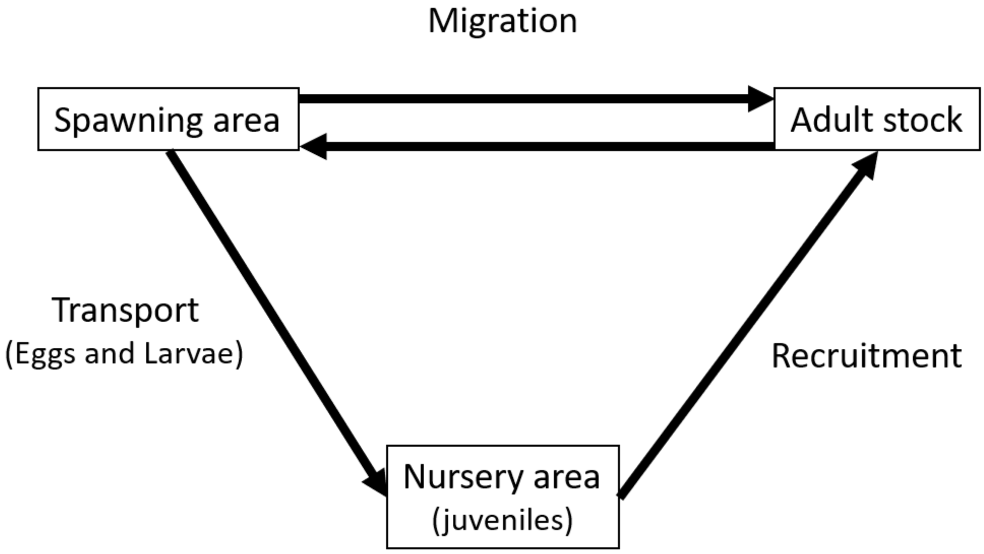


Figure 1-1: Life cycle of marine species (redrawn from Harden Jones, 1968)

The reproductive strategy of many marine species is characterized by a large production of offspring associated with a low survival probability. Eggs and larvae are usually planktonic and drift with the current under influence of wind and tide. The stage is usually short in comparison with the full life span (from a few days to a few months) but may reach more than a year such as in European eel and polar species (Grioche *et al.*, 1997; Shanks, 2009a; Damerau *et al.*, 2014; Miller *et al.*, 2015; Young *et al.*, 2018). Initially, the planktonic stage migrates passively, but evolves to active movement after development of the capacity to swim and feed (i.e Koutsikopoulos *et al.*, 1991; Herbing, 2002). Hydrodynamics and climate associated life history traits are critical to reach the appropriate juvenile habitat, called nursery ground. This stage makes an important contribution to species-specific dispersal.

After metamorphosis to a juvenile, mortality remains high but is nonetheless less variable and less important than during the previous stage (McGurk, 1986; van der Veer *et al.*, 2000a). Despite the importance of the larval stage in cohort strength, mortality processes in the nursery may buffer fluctuations in larval settlement for nursery-dependent species such as flatfish (van der Veer *et al.*, 2000; Fodrie *et al.*, 2009). Mortality during the juvenile stage is due to density-dependent processes and carrying capacity (Sogard, 1997; Iles and Beverton, 2000) in addition to the environmental condition of the nursery ground (i.e: Johnson, 2007; Nash *et al.*, 2007).

Migration is also important during the adult stage and involves seasonal migration between winter and summer grounds, and migration between feeding and spawning grounds (Hunter *et al.*, 2003; Frisk *et al.*, 2014). Mortality during the adult stage is relatively low with the notable exception of fishing mortality in commercially exploited stocks (Helfman, 2007). Moreover, the behaviour and physiology of adults have an influence on the survival of the early life stages through maternal and transgenerational effects (Shama *et al.*, 2016).

In summary, early life stages of fish are key in the dispersal process and in the understanding of the population dynamics. They are the topic of this PhD thesis.

1.1.1.3 Exploitation of marine resources

The last few decades saw a steady increase of seafood consumption, which grew from 9.0 kg per capita in 1961 to 20.2 kg in 2015 (FAO, 2020). The fraction of wild fish stocks that are within biologically sustainable levels has dropped from 90.0 % in 1974 to 66.9 % in 2015. More specifically 31.9 % of fish stock are overexploited while 7 % are underexploited and 59.9 % are fully fished.

To avoid overfishing and maintain living marine resources, a large number of management measures might be considered from the spatial or temporal closure of specific areas, to the establishment of quotas or regulations on fishing gear (Fogarty and Collie, 2009). One of the main questions is to define the spatio-temporal area to apply these measures as well as to define sustainable levels of exploitation. In fisheries sciences several concepts are commonly used to develop those questions:

A first point is the concept of fish stock. A stock could be defined as: “a part of a fish population usually with a particular migration pattern, specific spawning grounds, and subject to a distinct fishery”. In theory, a Unit Stock comprises all the individuals of fish in an area, which are part of the same reproductive process. It is self-contained, with no emigration or immigration of individuals from or to the stock. On practical grounds, a fraction of the unit stock is considered a “stock” for management purposes (or a management unit), as long as the results of the assessments and management remain close enough to what they would be on the unit stock” (ICES, 2012).

Secondly, to define a sustainable level of exploitation the maximum sustainable yield (MSY) is theoretically the largest yield (or catch) that can be taken from a stock over an indefinite period (ICES, 2012). Two sub-indicators are derived from MSY. To determine the full reproductive capacity of population, the B_{MSY} is the biomass that enables a fish stock to deliver the maximum sustainable yield. To define a sustainable level of harvest, the F_{MSY} is used. F_{MSY} is the maximum rate of fishing mortality (the proportion of a fish stock caught and removed by fishing) resulting eventually, usually over a very long-time frame, in a population size of B_{MSY}.

Understanding dispersal and population connectivity is an important issue for fisheries management (Kerr *et al.*, 2010). The level of knowledge on stock structure impacts the exploitation (Kerr *et al.*, 2016), especially the match between population structure and management area (Hinrichsen *et al.*, 2011). For example, the presence or absence of distinct subpopulations impacts the sustainable exploitation of sole in the Eastern English Channel (Archambault *et al.*, 2016). Even though the ocean looks like a continuum, the physical oceanography coupled to the life cycle implies a metapopulation context for many species. Metapopulation is an important concept for fisheries, as suggested by Levin (1969). A metapopulation consists of a group of spatially separated populations of the same species, whose groups could exchange individuals (called migration). A group might also be identified as a sink or source population, which plays an important role in population regulation (Pulliam, 1988) and whose identification is important for marine conservation (Crowder *et al.*, 2000). One of the aims of this PhD thesis is to improve knowledge on population structure and dynamics, especially processes related to the early pelagic stage of fish. This aspect will be investigated by the specific questions 2 and 5 (see below).

1.1.2 Recruitment

1.1.2.1 What is recruitment?

Understanding population dynamics is essential in a context of the exploitation of marine resources. A key concept in population dynamics is recruitment, the addition of new individuals to a population (Gaillard *et al.*, 2008). Recruitment depends on a wide range of biotic and abiotic factors, and can make an important contribution to population dynamics variability, especially for species associated to a pelagic life stage. The relationship between spawning abundance and the number of offspring, called stock-recruitment (SR) relationship, is commonly used as conservation measure of exploited fish species (Walters and Martell, 2004).

However, Spawning Stock Biomass (SSB) explains only a small proportion of recruitment variability (Szuwalski *et al.*, 2015). In a meta-analysis of 211 fish stocks, Cury et al. (2014) show that this relation explains less than 15 % of recruitment variance. This is especially the case for demersal populations, including flatfish, where SSB explains only 5 % of the recruitment variance. A better understanding of processes leading to recruitment variability could improve the evaluation of population dynamics and improve the sustainable management of stocks (Brunel and Boucher, 2007; Houde, 2008). One of the aims of this thesis is to improve knowledge on the factors influencing recruitment variability. This specific aspect of the thesis will be investigated by question 1 (see below).

1.1.2.2 Hypothesis to explain recruitment variability /Influencing factors

Survival rate is particularly low during the pelagic stage (in the order of 10^{-3} %, McGurk 1986; Houde 2008; Le Pape and Bonhommeau 2015) and hence affects long-term population size and evolutionary rate (Portnoy *et al.*, 2009). Especially for demersal species recruitment success is highly dependent on access to suitable nursery grounds after metamorphosis (Houde, 2008; van der Veer *et al.*, 2015).

Predicting recruitment fluctuation of fish populations is often considered the Holy Grail of fisheries sciences (i.e Houde, 2008; Fontes *et al.*, 2016). During the early 20th century, the Norwegian scientist Johan Hjort proposed a thesis to explain fluctuations in fish stock abundance. At first the “Critical period hypothesis” (Hjort, 1914) suggests that the strength of a year class is determined at the early life stage. During this stage, mortality among first feeding larvae is particularly high, individuals are highly sensitive to environmental conditions and dependent on food access (Houde, 2008). The hypothesis was completed by the “Aberrant drift hypothesis” (Hjort, 1926) which suggests that pelagic larvae are affected by ocean circulation, hence determining the arrival of juveniles in suitable habitat. These hypotheses are complemented by Cushing (1974, 1990), who proposed the “Match mismatch hypothesis”. The hypothesis suggests that recruitment is linked to temporal alignment between larvae and prey. Curry et al. (1989) propose the “Optimal window hypothesis“, which suggests that several factors have to be combined to assure survival and successful transport of a cohort.

Other phenomena might affect recruitment, especially processes in the nursery grounds (Iles and Beverton, 2000; van der Veer *et al.*, 2000a; Le Pape *et al.*, 2003b; Juanes, 2007), but processes associated with lower mortality rates than during the pelagic stage won’t be evaluated in the frame of this PhD thesis.

In the context of my PhD thesis an interesting question is:

Question 1: Which environmental factors influence the recruitment of flatfish?

1.1.3 Connectivity

1.1.3.1 What is connectivity?

Population connectivity has been defined as the exchange of individuals among geographically separated subpopulations (Cowen and Sponaugle, 2009). Connectivity, the realized movement between populations in a seascape, is an important process for marine species. It is studied at two levels. At an ecological level, connectivity deals with the contemporary scale and is relevant for (meta)population dynamics. At an evolutionary level, connectivity involves a multi-generational time scale (Jones *et al.*, 2009). Most of the observations of population structure happen on a contemporary time scale. When genetic structure is observed at an evolutionary time scale, historical processes (connectivity over the last millions of years) and contemporary gene exchange are intertwined. Connectivity plays an essential role in the persistence and productivity of (meta)populations, in population structure, genetic diversity and population resilience (Cowen *et al.*, 2007). Understanding connectivity is essential in fisheries management to define stock structure and spatial scale for management (Fogarty *et al.*, 2007).

1.1.3.2 The role of larval dispersal

The pelagic stage is crucial to understand the origin and trajectory of dispersing eggs and larvae among subpopulations. Indeed, a description of connectivity in a metapopulation context has to focus on the process between spawning and reproduction. This process could be separated into several stages. Figure 1-2 gives an overview of the process for a sessile species. Larval transport, which describes egg and larval movement, is a function of behaviour and physical transport. Larval dispersal includes survival, spawning and settlement in addition to larval transport. Finally, connectivity is a function of larval dispersal, post larval survival and eventually any other movement and survival before reproduction.

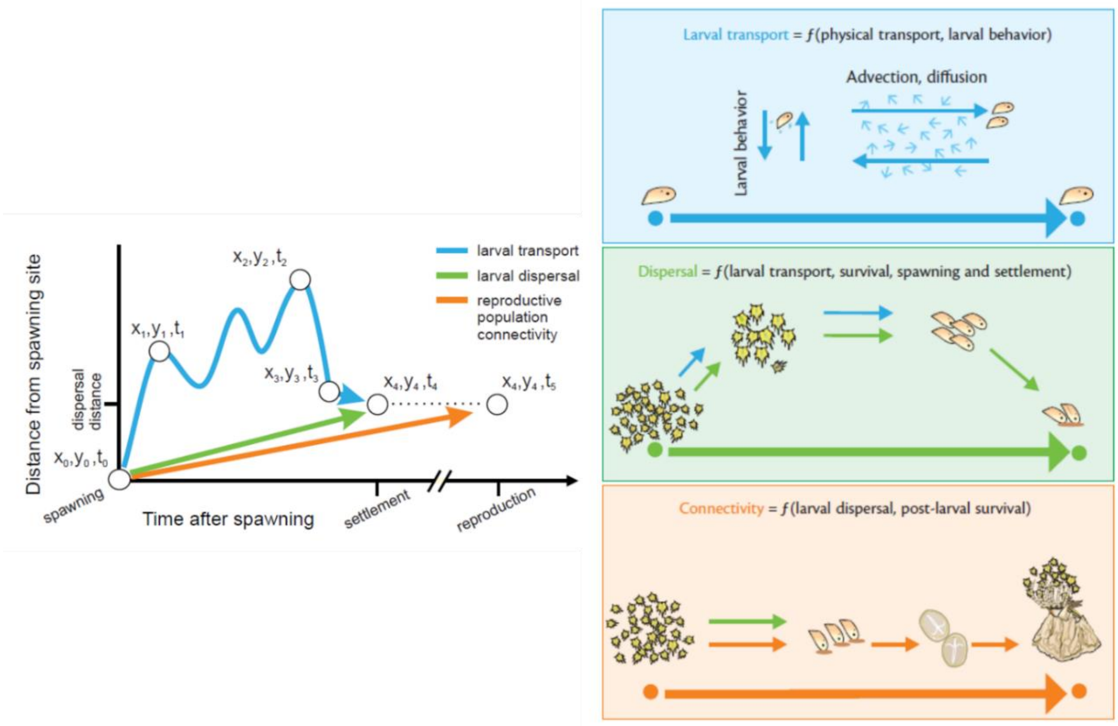


Figure 1-2: Left: Relationship between the spatial and temporal components of larval transport, larval dispersal, and reproductive population connectivity for a sessile species. Right: The concepts of larval transport, larval dispersal, and reproductive population (Pineda et al., 2007).

My PhD thesis will focus on the larval dispersal process to improve knowledge on connectivity in the marine environment.

1.1.3.3 Influencing factors

Recruitment dispersal of the early life stage is influenced by biophysical interaction, while the larval capabilities grow with development (Leis, 2006). Despite a similar life cycle, large differences in dispersal capacity characterize marine species. The differences are related to larval traits (López-Duarte *et al.*, 2012) such as behaviour (Fox *et al.*, 2006b; North *et al.*, 2008; Robins *et al.*, 2013), duration of the larval stage (Shanks, 2009b), seasonality (Lett *et al.*, 2010) or structure of the water column and currents (Munk *et al.*, 2009). For example, oceanic fronts are a barrier to dispersal and determine stock structure (Galarza *et al.*, 2009; Schunter *et al.*, 2011). In the context of my PhD thesis I focus on larval dispersal and in particular on the following question:

Question 2: Which factors impact dispersal during the early life stage of flatfish?

1.1.4 Tools to study connectivity and recruitment

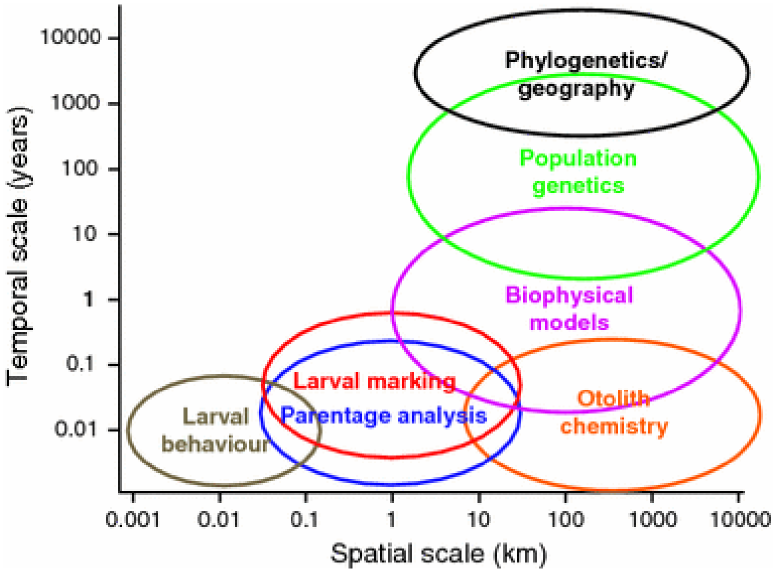


Figure 1-3: Scheme of the spatial and temporal scales over which different approaches and techniques can provide information on larval retention and dispersal in organisms with pelagic larva (source: Jones et al. 2009).

The early life stages of fishes are so tiny that direct observations are rare (Levin, 2006). An abundant literature already exists on the methods to characterize connectivity and recruitment (Cowen *et al.*, 2007; Cowen and Sponaugle, 2009; Jones *et al.*, 2009; Selkoe *et al.*, 2016a; Swearer *et al.*, 2019). Connectivity is studied with various indirect methods to infer the natal sources of larvae. Several historical or environmental processes could affect population structure and could be studied with the help of different methods adapted to the process studied. The methods may be indirect such as genetic markers (Underwood *et al.*, 2012), microbial and parasite communities (Taillebois *et al.*, 2017), morphological features (Morat *et al.*, 2012), microchemical signatures in calcified structures such as in otoliths or shells (i.e Shima and Swearer, 2010; Kool *et al.*, 2013; Gibb *et al.*, 2017), acoustic signatures as observed in whale populations (Balcazar *et al.*, 2015) or more rarely directly, such as physical tags, which remain complex to apply in an open ocean (i.e. Thorrold *et al.*, 2006; Cuif *et al.*, 2015). A modelling approach has also proven to be useful (Miller, 2007). Two main types of models are commonly used in fisheries sciences, population dynamic models which infer population dynamics on the basis of observation on stock and recruitment to describe and predict population dynamics, and models which describe processes and interactions between physical oceanography and biology. The different approaches, linked to spatial and temporal scales, are summarized in 3 in regard to connectivity. This PhD thesis will focus on the second type of model called “Biophysical model”. More complex models including several sources of information as population dynamics and genetics to infer, as example, interspecific competition, local adaptation, coevolution can also be used but will not be investigated in the frame of this thesis.

1.1.4.1 *Biophysical modelling, a tool to study marine dispersal*

The main idea of biophysical models is to couple biological and physical information to predict movement and survival of early life stage. From the time of Darwin, where the knowledge of current and seed potential of germination duration were used to estimate potential dispersal range (see section 1.1.1.1), advances in physical oceanography and fish ecology have facilitated the development of biophysical models based on 2D- or 3D-modelling to simulate dispersal of early life stages (Miller, 2007). Egg and larval dispersal are modelled through a larval transport model (LTM), which results from the combination of (1) a Lagrangian particle module coupled to an hydrodynamic model simulating advection and diffusion and (2) an individual based model (IBM), simulating behaviour and life-history traits (e.g. Cowen et al. 2007; Miller 2007; Pineda et al. 2007; Cowen and Sponaugle 2009). Such biophysical models are useful for understanding the dynamics and critical drivers of ecosystems and facilitate management at specific spatio-temporal scales (Allain *et al.*, 2007; Hinrichsen *et al.*, 2011).

This type of models are influenced by numerous species-specific biotic and abiotic parameters, such as area and period of particle (egg/larvae) release (Ayata *et al.*, 2010), behaviour related to the position in the water column (Fox *et al.*, 2006b; North *et al.*, 2008; Peck and Hufnagl, 2012; Monroy *et al.*, 2017), and estimation of pelagic larval duration or mortality (Cowen *et al.*, 2000). Some models go a step further by including complex processes such as the modelling of the interaction between larval prey and predator or directional active swimming (Fiksen *et al.*, 1998). The numerical model itself may also become more complex, for example through the physical parameters and the spatio-temporal resolution or density and number of particles released (Huret *et al.*, 2007b; Simons *et al.*, 2013; Savina *et al.*, 2016; Monroy *et al.*, 2017; Kvile *et al.*, 2018). The modelling of the early life stages is complex by involving numerous parameters and hypotheses. Predictions are dependent on the access to and quality of information. All this raises the following question:

Question 3: How does one calibrate and evaluate a LTM?

1.1.4.2 *Sensitivity and validation of biophysical models*

Models are widely used in fisheries sciences in support of management. The models have a wide range of applications, ranging from the dynamics of one species to the functioning of a full ecosystem, including fishing and management practices (e.g. Travers *et al.*, 2007; Rose *et al.*, 2015; Grüss *et al.*, 2017). In this context, assessing the validity of a model is essential (Stow *et al.*, 2009). However, it is a complex exercise and often subjective. Especially in the case of complex models, which involve a large number of parameters and for which comparative observations are scarce.

A first challenge is the identification of important parameters and their influence on model output. To study this aspect, sensitivity analysis – which is the study of how uncertainty in the output of a mathematical model or system (numerical or otherwise) can be allocated to different sources of uncertainty in its inputs – is commonly used. Sensitivity analyses allow a classification of parameters into a hierarchy according to the model output sensitivity to their changes. In a model with many parameters or requiring an important computation time, exploring the complete parameter space is impossible. Experimental design is needed to make this type of analysis possible. Many methods exist for a sensitivity analysis and might be chosen based on the objectives of the analysis, the costs of model run, the number of parameters and the nature of their uncertainty domains (Saltelli *et al.*, 2000). A classic procedure in order to assess the impact of parameters on model predictions is to build sensitivity indices, based on variance decomposition (Saltelli, 2008).

A second challenge is the difficulty to have enough observations or to obtain a matching of the spatio-temporal scale between a biophysical model and the observations. Observations themselves, such as eggs and larvae in the open ocean, are already sufficiently challenging. An alternative approach might consist of using other data sources to improve the model parameterisation such as otoliths, biological field data and larval arrival dates in the nurseries. This type of approach was used for example to assess body growth, movement and mortality of European eel based on larval information (Melià *et al.*, 2014). Whenever possible genetic data are useful for the validation of a dispersal model, especially by using parentage data (Bode *et al.*, 2019; Bernard *et al.*, 2020). Lehuta et al (2013) have suggested a procedure for the selection and validation of complex models in a fishery context. I will take this approach in the frame of my PhD thesis to assess the reliability of the biophysical model used to assess connectivity and recruitment.

1.2 THE NORTH SEA, FISHERIES AND FLATFISH

Due to their historical and commercial importance, flatfish in the Northeast Atlantic Ocean make an interesting and well documented group to illustrate the role of the early life stage in population dynamics and connectivity. This is what my PhD thesis aims at by focusing on six commercial flatfishes living in the North Sea and Eastern English Channel.

1.2.1 The physical oceanography and the ecosystem of the North Sea and English Channel

The North Sea (NS) is part of the European continental shelf. It is surrounded by Belgium, the Netherlands, Germany, Denmark, Norway, United Kingdom and France. The North Sea is connected to the Atlantic Ocean in the North and in the South to the English Channel (EC) beyond the Straits of Dover. I focus on the region between 4° W and 9° E and 48.5° N and 57° N, which includes the Exclusive Economic Zones of France, Belgium, the Netherlands, Germany, Denmark and UK and covers the Central North Sea (CNS, corresponding to ICES area IV.b, Figure 1-4), Southern North Sea (SNS, corresponding to ICES area IV.c, Figure 1-4) and Eastern English Channel (EEC, corresponding to ICES area VII.d, Figure 1-4).

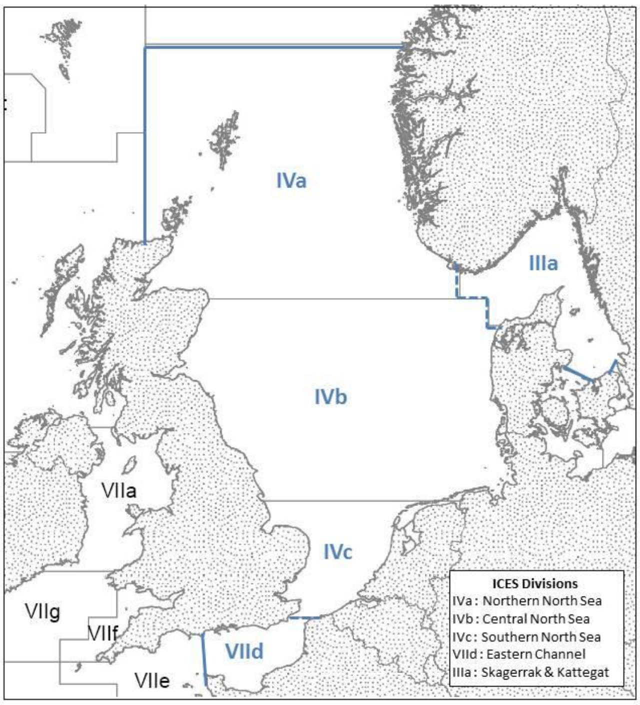


Figure 1-4: ICES Divisions in the North Sea (source: European Commission, 2016).

The NS is a shallow coastal sea whose depth is about 30 m in the Dover Strait, which gradually deepens up to 100 m in the north-western part (Figure 1-5). The seabed is mainly associated with soft sediment (Figure 1-5). Along the coast of England cliffs alternate with pebble beaches intersected by river valleys, large estuaries (as the Humber or Thames, location of the main river could be found in Appendix 1 in the Figure Appendix1-1) and sand and mud flats. On the eastern side of the North Sea, sandy beaches intersected by estuaries (as Scheldt, Rhine, Meuse, Weser or Elbe) prevail associated to tidal inlets and islands as in the Wadden Sea. The North Sea is a temperate coastal shelf sea with a deep channel in the northwest, characterised by a permanently thermally mixed water column in the south and east, and seasonal stratification in the north (Figure 1-6). During winter months the whole area is vertically well mixed whereas stratification is observed in summer in the northern part of the domain.

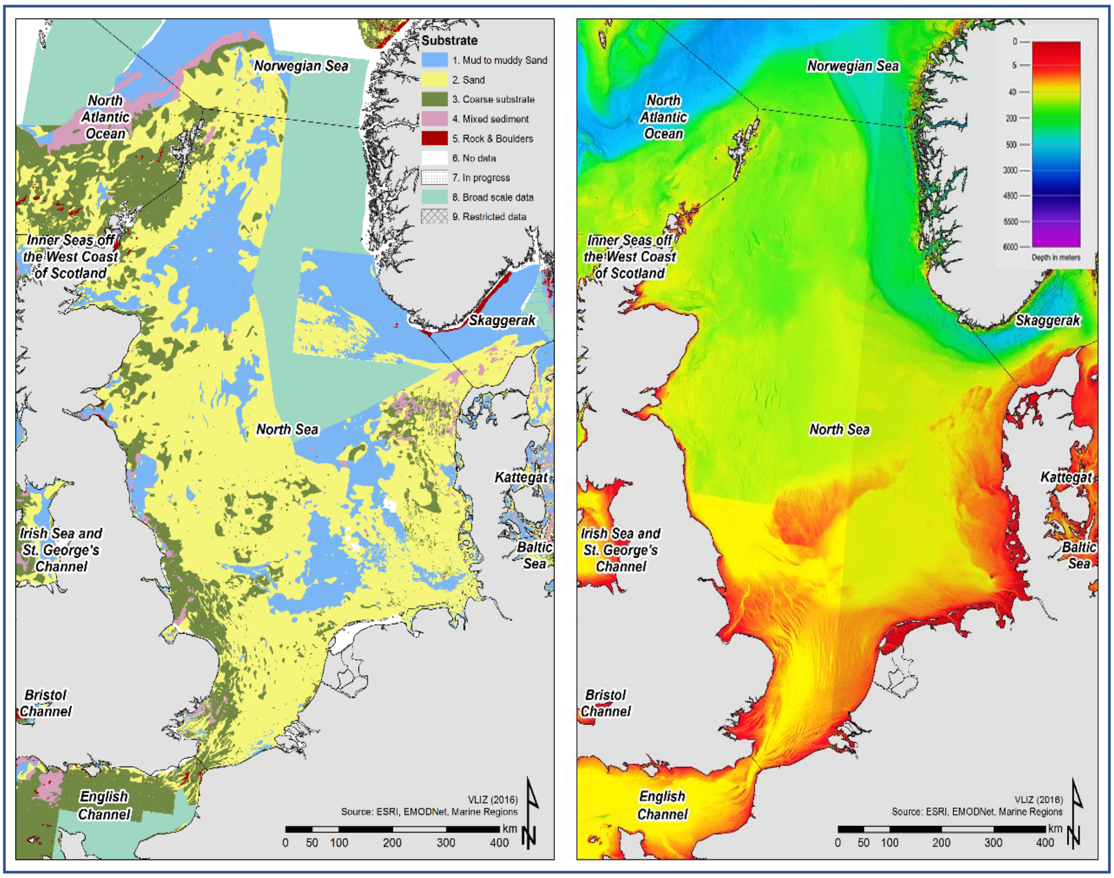


Figure 1-5: Seabed substrate of the North Sea (Left panel) and bathymetry of the North Sea (right panel) (Source: VLIZ 2016)

River systems that discharge into the North Sea represent an important input of fresh water from the Elbe and the Weser which discharge important volumes of fresh water into German Bight and into the Wadden Sea. The Elbe and the Weser have a strong and stable vertical salinity stratification although tidal and wave activity can be very strong. In south of German Bight small freshwater input and strong tidal currents suppress the development of stratification. In contrast with the shallower parts of the North Sea, which are well-mixed from surface to bottom throughout the year, northern part becomes statically stratified in Spring, after a period of sufficient insolation and the stratification generally lasts through the Summer.

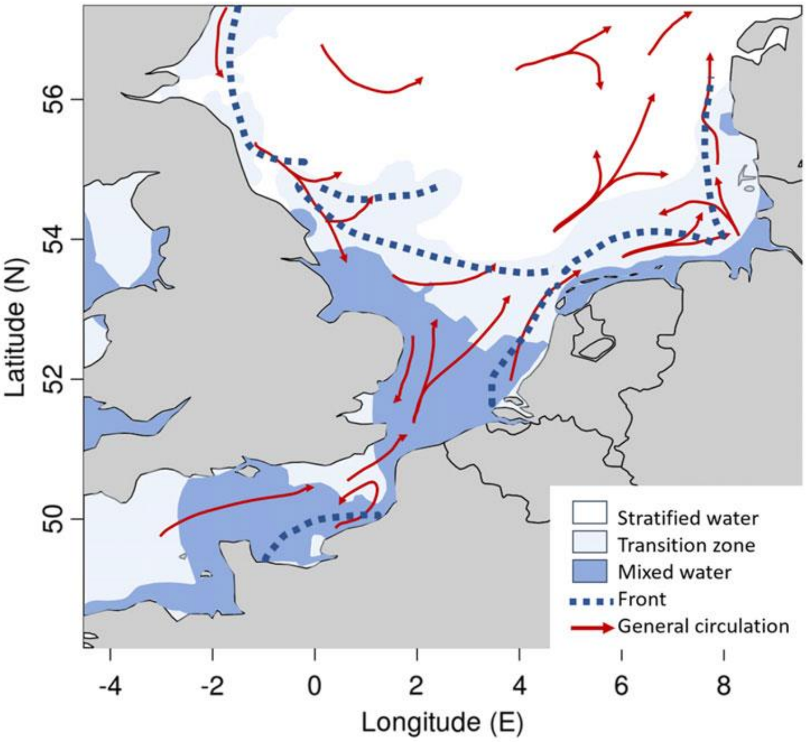


Figure 1-6: Schematic representation of the physical oceanography of the North Sea. Arrows represent the general circulation (redrawn from Turrell 1992). Light color represents the transition zones between mixed (dark color) and stratified (white) waters in the North Sea and dotted lines rep resent the thermal fronts (redrawn from Otto et al., 1990).

Currents in these shallow coastal seas are mainly tide- and wind-induced. Average circulation is from south to north (Turrell, 1992) (Figure 1-6) with strong seasonal variability and some interannual variability in the flow field linked to the North Atlantic Oscillation (NAO). As an example of the seasonal variability, the net water inflow from the EEC to the SNS was modelled equal to 0.05, -0.01, 0.02 and 0.05 10^6 m^3-s^{-1} respectively from the first to the fourth quarter over the period 1955-1998 (OSPAR, 2000). Mean local temperatures (1997-2006) were equal to 12.8°C (EEC), 11.7°C (SNS) and 10.7°C (CNS) with an important seasonal variation. While in winter the mean temperatures were equal to 9.8°C (EEC), 7.3°C (SNS) and 6.9°C (CNS), they reached 16.9°C (EEC), 17.2°C (SNS) and 15.9°C (CNS) in summer. In late spring, as solar input increases, a thermocline is established over the northern deeper part of the domain. The strength of the thermocline depends on the heat input and the turbulence generated by the tides and the wind. In autumn, the increasing number and severity of storms and seasonal cooling at the surface destroy the thermocline and mix the surface and bottom layer, In winter, the water column is well mixed due to wind forcing. Shallow parts of the domains remain well mixed throughout the year, resulting in the formation of oceanic fronts in summer (Figure 1-6). Tidal fronts mark the offshore limit of regions where tide induced mixing is sufficient to keep the water column mixed in competition with the heating of the surface layer. These fronts develop in summer in the western and southern parts of the North Sea where tidal currents are sufficiently strong. Fronts are important because they may restrict horizontal dispersion and because there is enhanced biological activity in these regions, physical processes that have a direct influence on the ecology of the area.

Oceanic fronts represent important barriers to dispersal for marine organisms and hence determine stock structure (Galarza *et al.*, 2009; Schunter *et al.*, 2011). In the North Sea, the frontal system structures the hyperbenthic and benthic communities (Dewicke *et al.*, 2002; De Nooijer *et al.*, 2008) and flatfish, whose population densities are higher south of the front (Gibson, 2005a; Vandamme *et al.*, 2014). In this context, an interesting question is:

Question 4: What is the impact of frontal systems on the larval dispersal of flatfish?

The area is characterized by high current speeds and high levels of turbidity as well as an important primary production (mean net primary production of the North Sea is 145 g C m^{-2} y^{-1}) (Moll, 1998). Primary production is highest in the coastal regions due to nutrient input from the rivers and mixed water columns. Production varies seasonally with the lowest abundance of plankton in winter (Reid *et al.*, 1990). These shallow tidal areas have a naturally high level of productivity that supports richness of the benthic communities. Due to this productivity, these areas are also important as nurseries for juvenile fish. Flatfish represent an important link in the food web, as predator of macrobenthos (common dab, European flounder, European plaice and common sole) and small fish (brill and turbot). They are an important source of food for top predators such as harbour seals (van der Veer *et al.*, 2011).

1.2.2 The North Sea fishery

The fishery of the North Sea has a long tradition and represents an important economic sector. Hence intensive monitoring has resulted in abundant data on fish biology and the impact of fisheries (Thurstan *et al.*, 2010). In the North Sea, the demersal fishery is very important. It represents the majority of the landings, which reached a maximum in 80's but have been declining since 2000 (Lescrauwaet et al. 2013; ICES, 2018). The decline has been attributed to overfishing and the decreased productivity of important stocks, but also to the successful reduction of fishing mortality to sustainable levels (ICES, 2018).

The North Sea is divided into subareas by ICES for management considerations (Figure 1-4). The long-standing question arises whether the stock structure used for management purposes and the biological population structure match (Reiss *et al.*, 2009). My PhD thesis investigates the match in flatfish between the population structure of early life stages and management areas IVb, IVc and VIId.

Regarding management, an interesting question is:

Question 5: Does the spatial structure of management match with the population structure induced by larval dispersal?

1.2.3 Of fish and flatfish, and their exploitation

1.2.3.1 Flatfish represent a rich source of information

Due to their bentho-pelagic life cycle and commercial importance, flatfish represent an interesting group to study connectivity. The demersal adults spawn planktonic eggs; eggs and larvae are transported by the currents until metamorphosis. Juveniles settle in shallow coastal waters before joining the feeding grounds where adults reside. Some species exhibit also specific movements for reproduction. For example, adults of common sole (*Solea solea* L.) and European plaice (*Pleuronectes platessa* L.) are philopatric to the spawning ground (Rijnsdorp *et al.*, 1992c; Hunter *et al.*, 2003) and make well documented seasonal migrations (Hunter *et al.*, 2003; Burt and Millner, 2008).

Flatfish have been caught for a long time in the Northeast Atlantic Ocean and played an important role in fisheries science. Early studies have been guided by the need for information on the biology of seafood, the state of the fishery and the need to understand fluctuations in catches (Holt, 1895; Peterson and Wroblewski, 1984). Based on the numerous studies on flatfish in the North Sea Beverton and Holt (1957) developed methods to study the dynamics of exploited fish. They showed that fishing could have an impact on fish populations, which brought out the need for management measures (Harden Jones, 1968).

This PhD thesis is dedicated to six flatfish species of the North Sea and Eastern English Channel (Figure 1-7). All are commonly exploited, cover different families and genus, and represent a broad range of history traits. Flatfish are grouped in the order of the Pleuronectiformes and its 14 families, among which this study covers three families. First there is the Soleidae with the genus *Solea* which is represented by the common sole (*Solea solea* (Linnaeus, 1758)). Two species represent the genus *Scophthalmus*, namely turbot (*Scophthalmus maximus* (Linnaeus, 1758)) and brill (*S. rhombus* (Linnaeus, 1758)). In addition, three species are member of the Pleuronectidae family, including European plaice (*Pleuronectes platessa* (Linnaeus, 1758)), European flounder (*Platichthys flesus* (Linnaeus, 1758)) and common dab (*Limanda limanda* (Linnaeus, 1758)). Hereafter, common sole, common dab, European flounder and European plaice will be referred to as sole, dab, flounder and plaice respectively. These species are supported by a wide range of biological knowledge. If some are well studied such as sole and plaice, others are relatively less well known. While dispersal of the early life stages of sole and plaice has been well characterized (Bolle *et al.*, 2009; Erftemeijer *et al.*, 2009; Hufnagl *et al.*, 2013; Lacroix *et al.*, 2013; Savina *et al.,* 2016), knowledge on other flatfish is comparatively scant.

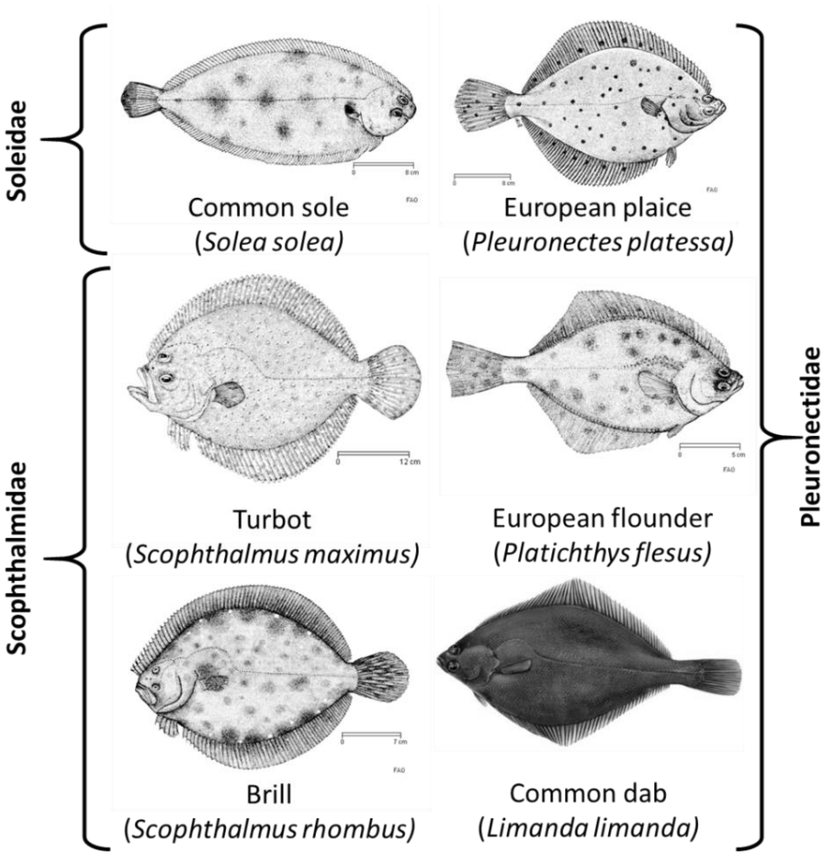


Figure 1-7: Drawings of the six flatfish species studied in this thesis, including their family assignment.

Exploitation levels differ considerably; sole and plaice are targeted in the demersal trawl fishery; turbot, brill and flounder are caught as valuable bycatch in a mixed fishery, whereas dab is mostly discarded because of its low commercial value (ICES, 2017a). Currently, all six species are managed by the International Council for the Exploration of the Sea (ICES) in species-specific geopolitical units. The populations of turbot and sole coincide with the three ICES Divisions of the North Sea (IVa,b,c), while the North Sea and Skagerrak (IIIa) are considered a single population for plaice. For brill, dab and flounder on the other hand, divisions such as Skagerrak, Kattegat (IIIb,c) and English Channel (VIId and/or VIIe) have been merged with the North Sea ICES Divisions (ICES management areas are shown in Figure 1-4).

1.2.3.2 Common sole and European plaice, two well-known species

Unlike the other four flatfish species, which are mainly bycatch species, plaice and sole are main target species whose biology is well known.

1.2.3.2.1 Common sole

Sole lives in the Northeast Atlantic Ocean from Senegal to the South of Norway, and in the Mediterranean Sea at depths usually of 10 to 60 m. They reach sexual maturity at around three years old at an average size of 30 to 40 cm. The spawning season takes place in spring-summer and the larval phase is usually shorter than 2 months (more details on specific life history traits are given in Chapter 2.

In the Northeast Atlantic Ocean, genetic structure is composed of at least three populations, namely the Kattegat/Skagerrak region, the North Sea and the Bay of Biscay, and with indications for a fourth population, namely the Irish/Celtic Sea associated to isolation-by-distance (Cuveliers *et al.*, 2012). The population genetic structure of sole is relatively homogenous in the area considered here with a dispersal pattern linked to adaptation which may be detected at a finer scale using outlier markers among Southern and Central North Sea (Diopere *et al.*, 2018). More recently, study based on genotypes and otolith shape revealed metapopulation structure at the fine spatial scale of the EEC (Randon *et al.*, 2020).

In the study area, the beam trawl fishery is managed in two separate units: Eastern English Channel (Division VIId) and North Sea (Subarea IV). The stocks have a good status. Landings in Division VIId are between 2,000 and 8,000 tonnes and in Division IV between 10,000 and 40,000 tonnes. Fishing mortality is above the MSY in the North Sea and below in the EEC.

Both stocks have their full reproductive capacity to ensure an optimal use in the long term. Recruitment variability is large (Figure 1-8).

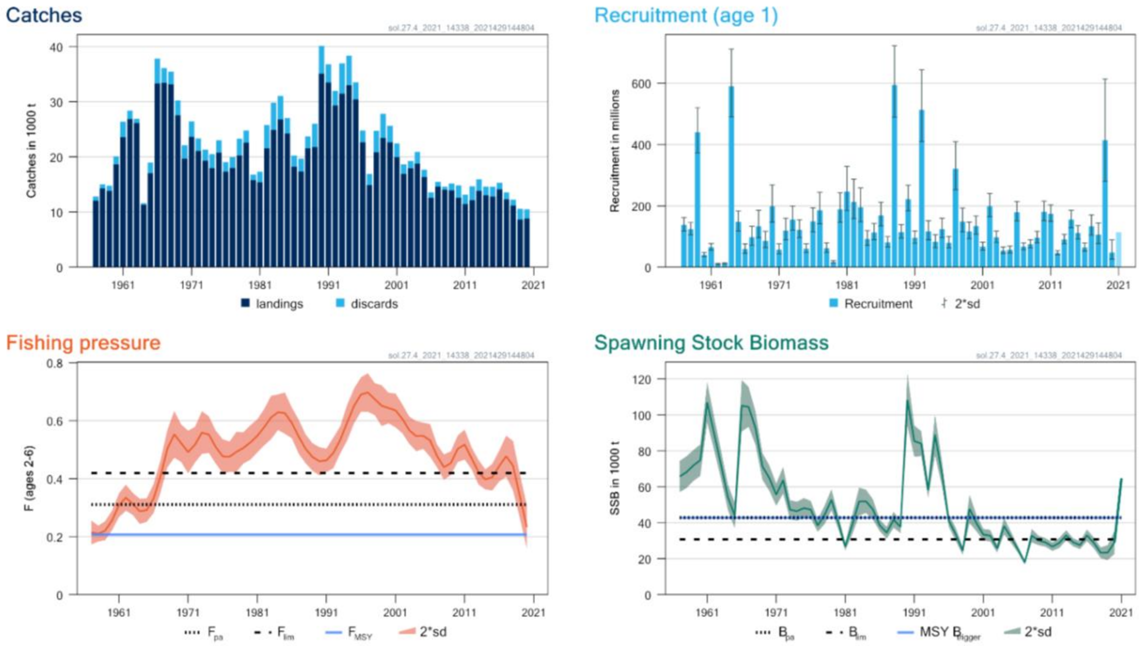


Figure 1-8: Sole in Subarea IV. Summary of the stock assessment. Estimates of discards are only available from 2002. The assumed recruitment value in 2021 is shaded in a lighter colour. (Source: ICES, 2020a).

Since the 1980s, a southward shift in the distribution was reported (Perry *et al.*, 2005; Engelhard *et al.*, 2011).

1.2.3.2.2 European plaice

Plaice lives in the Northeast Atlantic Ocean from Morocco to Norway and in the Mediterranean Sea at depth usually of 10 to 60 m. They reach sexual maturity at about 3 years of age at an average size of 40 cm. Spawning season takes place during winter and the larval phase usually lasts around 3 months (more details on specific life history traits are given in Chapter 2.).

Different biophysical models have been used to study dispersal of early life stage of plaice (Bolle *et al.*, 2009; Hufnagl *et al.*, 2013). In addition to the high level of connectivity among the studied areas in the North Sea, those models have pointed out the temporal variation of the spatial pattern and migration success (Bolle *et al.*, 2009) and identified the potential long term change in North Sea spawning grounds of plaice (Hufnagl *et al.*, 2013). Classical population genetic studies on plaice showed a high level of connectivity across the distribution range (Hoarau *et al.*, 2002b, 2004).

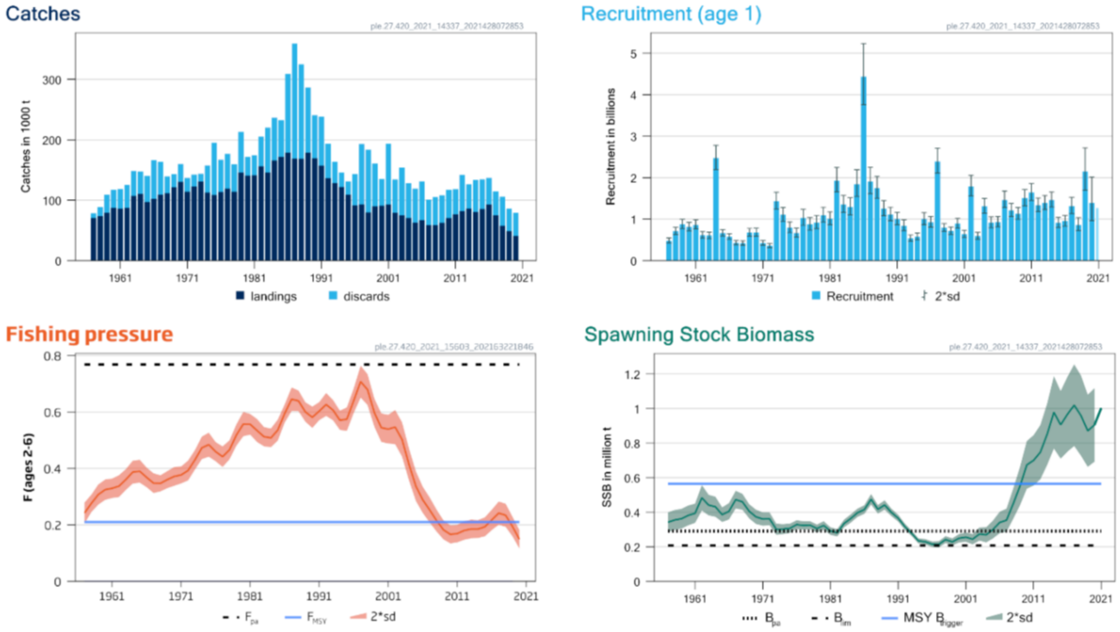


Figure 1-9 : Plaice in Subarea IV and Subdivision III.a.20. Summary of the stock assessment. The assumed recruitment value for 2021 is shaded in a lighter colour. (source: ICES, 2019b)

Plaice is the most commonly caught flatfish in the North Sea and its landings represent by weight eight times the sole landings, but due to the lower value of this fish, the two species represent almost an equal economical value (Pilling *et al.*, 2008). In the study area, plaice is managed in two entities: in the Eastern English Channel (VIId) and in the North Sea (IVa,b,c) and Skagerrak (IIIa,b,c), which are together considered one unit. Both stocks are healthy with a SSB above threshold and a fishing mortality below MSY in the two areas. An important part of the catches are discards (Figure 1-9).

Unlike sole, a shift in distribution is also observed since 1980s for plaice, but northward, on average to deeper water (van Keeken *et al.*, 2007; Engelhard *et al.*, 2011).

1.2.3.3 Common dab, an abundant species

Dab is a very abundant flatfish species. Its distribution area ranges from the Bay of Biscay to Iceland, Norway, the Barents and White Seas as well as the Baltic sea at depth of 20 to 150 m. They reach sexual maturity at about 2 years of age for males and 3 years for females at an average size of 27 cm (Félix *et al.*, 2011). Dab spawn from December to September and have a larval phase which usually lasts more than 3 months (more details on specific life history traits are given in Chapter 1).

Despite being the most abundant, information on dab population structure and connectivity remains unavailable, whether it be modelling of larval dispersal or genetic structure. Potential microsatellites makers have been identified but not used yet to study population structure (Tysklind *et al.*, 2009).

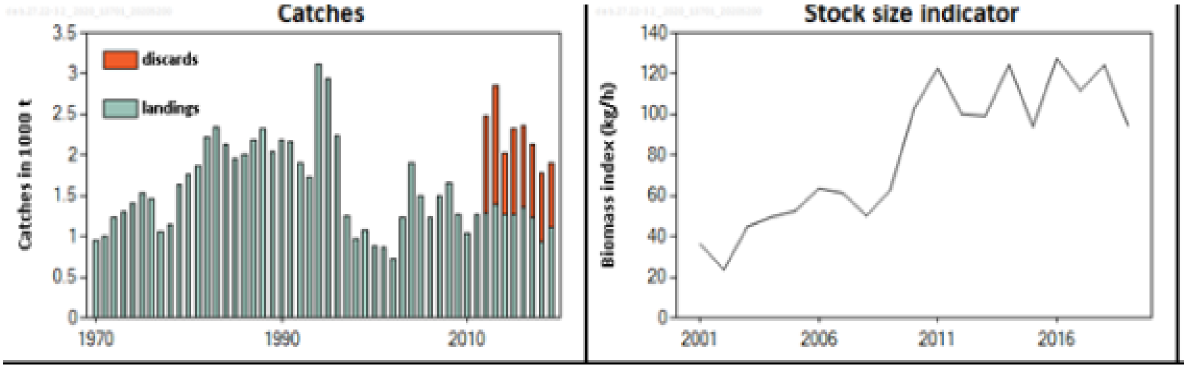


Figure 1-10 Dab in Subarea IV and Division III.a. Left: ICES landings and ICES estimates of discards (in thousand tonnes). Discard data have only been included since 2012. Right: Combined biomass index (kg h−1) of dab larger than 15 cm, from the Baltic International Trawl Survey (BITS – Q1 and Q4) in subdivisions 22, 23, and 24. (source: ICES, 2020).

Dab is not managed by Total Allowable Catch (TAC) and only limited information is available. Stock assessment is indicative of trends only (Figure 1-10) for Subarea IV and Division IIIa. The stock is considered healthy with a fishing pressure below F_{MSY} and SSB above B_{MSY}. It is striking that most catches are discards.

1.2.3.4 European flounder, a species adapted to low salinity levels

Flounder has colonized coastal waters of the Northeast Atlantic Ocean from the White Sea to the Mediterranean Sea and Black Sea at depths of 1 to 100 m. It is one of the few Pleuronectiformes adapted to low salinity levels, which can be found in estuaries up to fresh water. They reach sexual maturity at about 3 years of age for male and 5 years of age for female at an average size of 31 cm. Spawning season takes place during spring and the larval phase usually lasts more than 2 months (more details on specific life history traits are given in Chapter 2.).

If fine scale modelling can help to explain the tidal impact on larval dispersal in the EEC (Sentchev and Korotenko, 2007) or in the Baltic Sea (Corell and Nissling, 2019) the main dispersal pattern remains unknown in the North Sea. Population genetic studies on flounder showed a high level of connectivity across their distribution range (Hemmer-Hansen *et al.*, 2007b). Flounder is managed as a unique stock on area IV and area IIIa. This species is mainly a bycatch species with a high discard rate (Figure 1-11). Fishing pressure is considered below F_{MSY} but the stock status remains undefined (Figure 1-11).

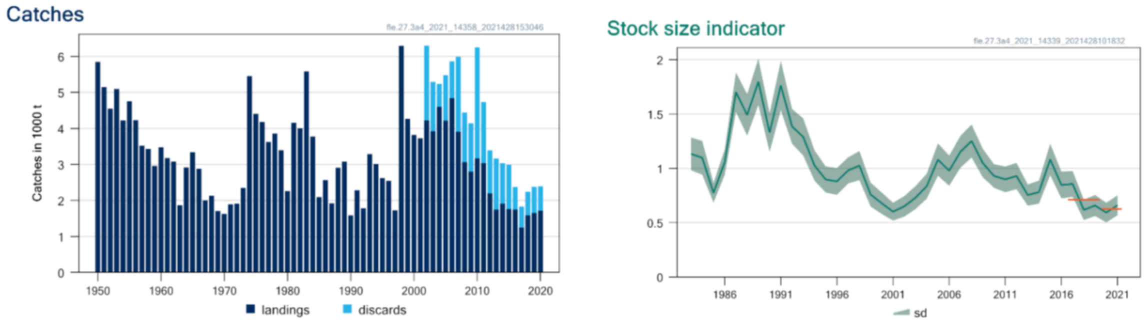


Figure 1-11 : Flounder in Subarea IV and Division III.a. Summary of the stock assessment. Between 1984 and 1997, Dutch landings were not recorded. Discard data are only available from 2002. Stock size indicator (in relative biomass) from the North Sea International Bottom Trawl Survey Q1 (NS-IBTS). The horizontal orange lines indicate the average of the most recent two years and the previous three years. (source: ICES, 2020c).

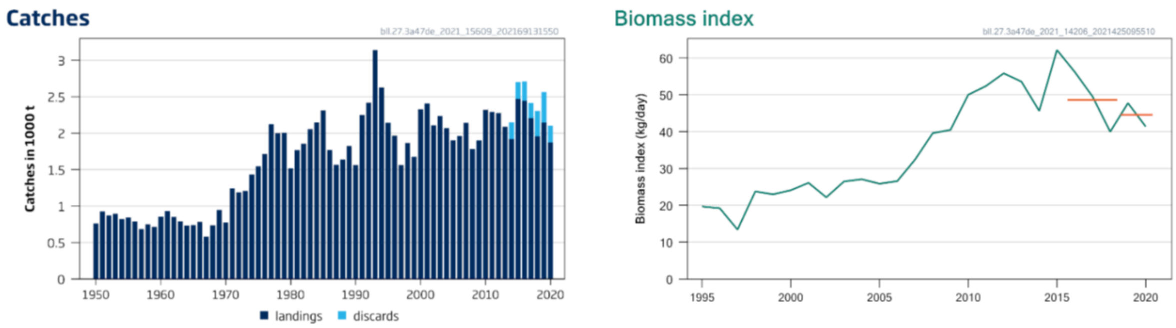
1.2.3.5 Brill and turbot, two rare flatfish species

Brill and turbot are two highly valuable species in commercial fisheries, which are largely distributed in the North Sea but occur at lower densities than the other flatfish species studied (Whitehead *et al.*, 1986; Gibson, 2005a; Hemmer-Hansen *et al.*, 2007b).

1.2.3.5.1 Brill

Brill is present in the Northeast Atlantic Ocean from North Africa to Norway including the Mediterranean Sea, the Black Sea and the Baltic Sea at depths of 5 to 80 m. They reach sexual maturity at about 3 years of age for males and 4 years for females at an average size of 37 cm. Brill spawn in summer and have a larval phase which usually lasts about two months (more details on specific life history traits are given in Chapter 1). Modelling of larval dispersal and connectivity of this species is not available, but genetic data show an homogeneity of the population at the North Sea scale (Vandamme *et al.*, 2020).

From a management perspective brill is evaluated in the North Sea (IVa,b,c), Skagerrak and Kattegat (IIIa) and English Channel (VIId,e). Fisheries mortality is considered below F_{MSY} whereas stock size is above B_{MSY}. Catches are relatively constant since 1980s with a low rate of discards. Biomass has been slightly increasing over the period 1995-2015 and has then decreased (Figure 1-12).



Catches

Biomass index

Figure 1-12: Brill in Subarea IV and divisions III.a and VII.d–e. Summary of the stock assessment. Prior to 2014, landings are as officially reported. Discards are available since 2014. Biomass index is the standardized landings per unit effort (LPUE) from the Dutch beam trawl fleet for vessels > 221 kW. The orange horizontal lines indicate the average of the biomass index for 2019–2020 and for 2016–2018. (source: ICES, 2020d)

Brill show a stable distribution in the North Sea since 1970 with a slow expansion into the North (Kerby *et al.*, 2013).

1.2.3.5.2 Turbot

The distribution area of turbot is from Norway to Iceland up to Morocco and the Black Sea at depths usually from 20 to 150 m. They reach sexual maturity at about 4-5 years of age for males and 3 years for females at an average size of 49 cm. Spawning takes place during summer and the larval phase is usually shorter than 2 months (more details on specific life history traits are given in Chapter 2.).

Although a dispersal model of the larvae is not available, the genetic structure presents an interesting pattern. Populations within the Northeast Atlantic/North Sea area and the Baltic Sea are genetically homogeneous but are different between the two entities (Nielsen *et al.*, 2004). In addition the North Sea population shows a weak division along the Frisian and Sylt front (Vandamme *et al.*, 2020).

Turbot is managed separately in the North Sea (IV) and in Skagerrak and Kattegat (IIIa). Stock has a good status in the North Sea with reasonable fishing pressure and is above the threshold where the full reproductive capacity is reached (Figure 1-13).

Despite this status, the North Sea stock, which is managed as a unique unit, has shown spatial variation in the past. For example, off the northeast coast of Scotland, the local turbot population collapsed in 1970s due to overfishing. The hypothesis to explain this decline is that the population of young turbot was not sufficient to maintain a sustainable number of adults, which implied a relative isolation of this area (Kerby *et al.*, 2013).

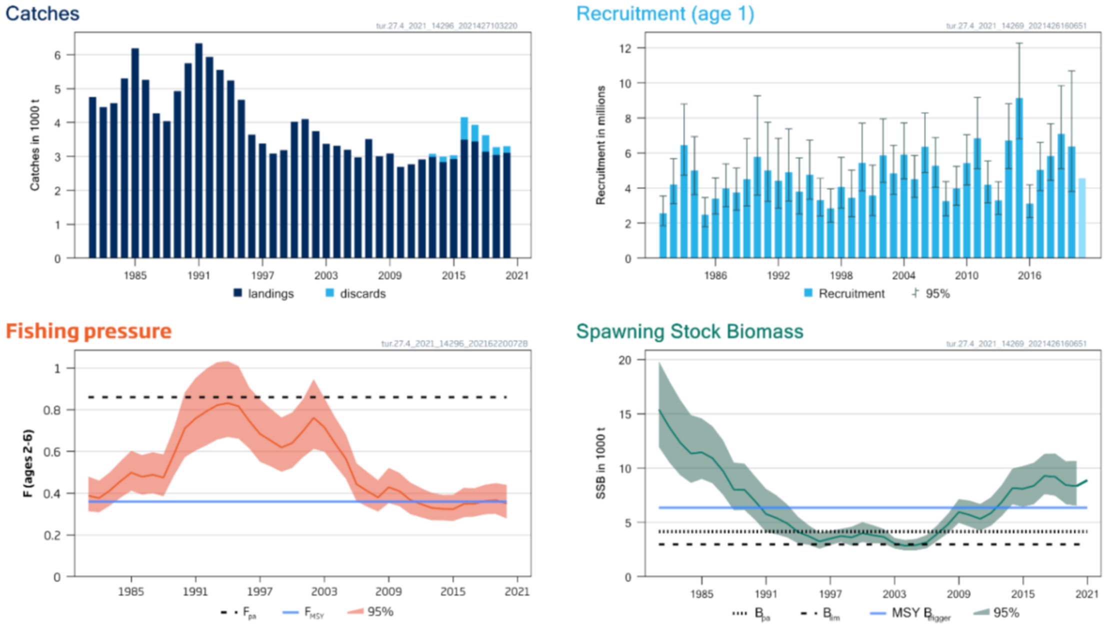


Figure 1-13: Turbot in Subarea IV Summary of the stock assessment (weights in thousand tonnes). Discards are only available from 2013. The assumed recruitment value for 2021 is shaded in a lighter colour. (source: ICES, 2020e)

1.2.3.6 *Life history traits of flatfish*

To avoid interspecific competition, flatfish have developed a wide range of life-history traits, following Gause's law of competitive exclusion (Gause, 1932, 1934; Hardin, 1960). They present a broad range of life-history traits regarding growth (pelagic larval duration), behaviour (predation and vertical migration) and reproduction (spawning period and spawning grounds). In terms of abundance, turbot and brill are rare while plaice and dab are very abundant and sole and flounder are present at intermediate abundances (Rogers *et al.*, 1998). For example, Van der Hammen et al. (2013) pointed out the disjoint spawning periods and slight difference in habitat between turbot and brill. This should impact the population dynamics and connectivity pattern (Denney *et al.*, 2002). Hence, I formulated the following question:

Question 6: How do life history traits influence dispersal during early life?

1.2.4 Other anthropogenic pressures

The Northeast Atlantic Ocean borders a heavily populated area. As a consequence, its coastal areas are used for a broad range of human activities. In addition to fishing (see above), traditional uses involve aquaculture, shipping, national defence, mineral extraction, hydrocarbon exploitation, pipelines and tourism. This has led to the need to manage habitat loss, pollution, eutrophication and the arrival of non-indigenous species. More recent anthropogenic pressures originate from installations for renewable energy, mostly wind farms, and indirect effects from the release of greenhouse gases such as CO_2 and CH_4 leading to climate change. All pressures impact the ocean, although to varying degrees, partially linked to mitigation strategies. The North Sea and the English Channel feature worldwide among the most impacted regions (Halpern *et al.*, 2019) with an unprecedented development of ocean sprawl (Heery *et al.*, 2017).

1.2.4.1 The development of hard structures

Driven by the growing demand for renewable energy, the number of offshore wind farms (OWFs) is increasing, and many more are either being built and/or planned (Ramírez *et al.*, 2020). The recent extension of OWFs in the Southern North Sea is of particular significance (Kalaydjian and Girard, 2017). However, the installation of thousands of turbines in the near future across the entire North Sea raises questions about environmental impacts and the effects on the marine ecosystem (Petersen and Malm, 2006; Bergström *et al.*, 2013). One of the major effects of the artificial introduction of hard substrates into sandy or muddy areas is the increased habitat heterogeneity and substrate provision for fouling organisms. The phenomenon is known as the ‘reef effect’ (Petersen and Malm, 2006; Langhamer, 2012; De Mesel *et al.*, 2015). OWFs may limit the impact of fishing; the reduction in towed fishing gear decreases the disturbance of benthic communities and improves the recovery of previously disturbed communities (Lindeboom *et al.*, 2011; Van Deurs *et al.*, 2012; Wilhelmsson and Langhamer, 2014). The introduction of hard substrates, together with the possible exclusion of fisheries, raises the following question**:**

Question 7: How does expansion of OWFs across the North Sea impact demersal fish?

1.2.4.2 Climate change

Climate impacts connectivity and recruitment through changes in oceanic circulation and temperature. The dependence of larval dispersal on physical and biotic factors leads to a significant footprint of climate variability and climate cycling on population dynamics (Lo-Yat *et al.*, 2011). Lately climate change has a significant impact on marine organisms with species losses and invasions, community changes, regime shifts and tipping points (Van Nes and

Scheffer, 2005; Beaugrand *et al.*, 2019; Swingedouw *et al.*, 2020), phenological and biogeographical shifts (Barton *et al.*, 2016) and the adaptive fate of living organisms (Calosi *et al.*, 2016). Fish populations are no exception (Rijnsdorp *et al.*, 2009); they are particularly affected in their larval dispersal patterns, recruitment and connectivity through changes in oceanic circulation and temperature (Munday *et al.*, 2009).

The impact of temperature rise on larval dispersal is difficult to predict *a priori*, owing to non-linearity and complexity (e.g. cumulative or contrasting effects acting on larval, juvenile or adult stages). Nevertheless, some first projections can be made. Assessing the impact of climate change through *in situ* observation is difficult, but biophysical models represent a solid alternative to investigate potential effect of climate change (Lett *et al.*, 2010). We address the following question:

Question 8: What is the impact of climate change on the early life stages of flatfish?

To answer to this question, the "Warm+" IPCC (Intergovernmental Panel on Climate Change) scenario, which considers an increase of 2°C in temperature associated to a change in wind speed and direction at the horizon 2040, as described in Van den Eynde et al. (2011) was applied at the whole North Sea scale This scenario, although less spatially detailed than a full regional downscaling of the ARC5 would have been, was possible to be implemented in the timeframe of the thesis, and allowed to assess the impact of climate change on flatfish eggs and larvae. This scenario itself and its limits will be discussed in the general discussion of this thesis.

1.3 THE HYDRODYNAMIC MODEL *COHERENS* AND THE BIOPHYSICAL MODEL *LARVAE&CO*

The 3D hydrodynamic model used in this PhD thesis to simulate the oceanic circulation of the North Sea and English Channel is based on the well-established COHERENS V1 code (Luyten *et al.*, 1999; http://odnature.naturalsciences.be/coherens) this code is write in FORTRAN and publicly available on the website. The model has a resolution of 5′ (~5 km) in longitude and 2.5′ (~5 km) in latitude, and 20 sigma-coordinate vertical layers. The model is forced by wind, atmospheric pressure fields and sea surface temperature in addition of river discharges for the main North Sea rivers. Details about model implementation (equations, forcing, initial and boundary conditions) and validation are given in Savina *et al.* (2010a). More details on the hydrodynamic model and its validation can be found in annex 1.

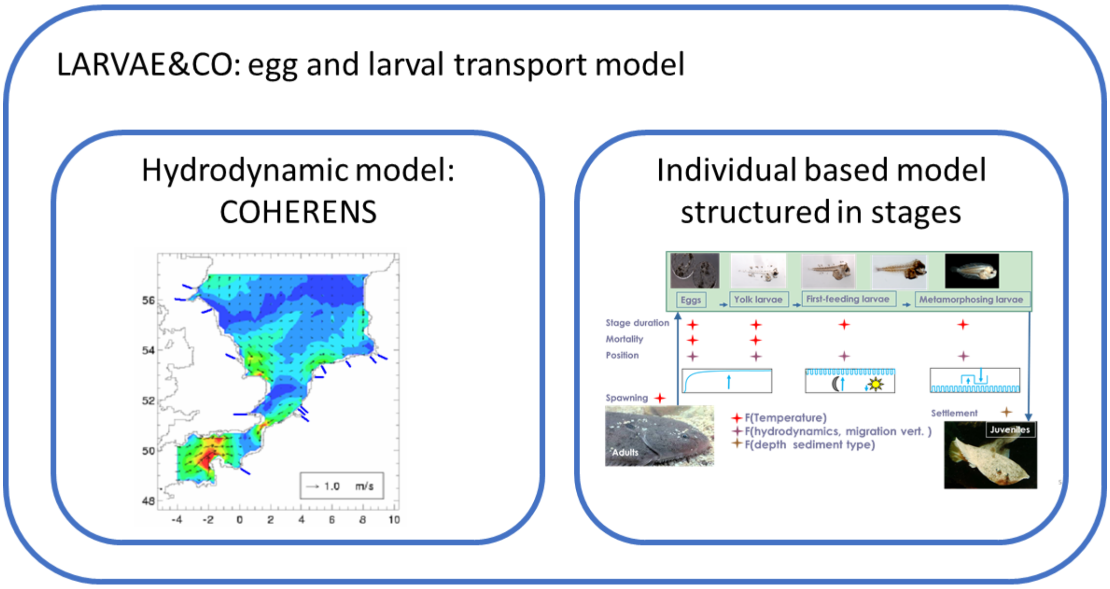


Figure 1-14: The larval transport model of this thesis is made by coupling the hydrodynamic model COHERENS *to an individual-based model to simulate egg and larval dispersal.*

Regarding larval dispersal, the hydrodynamic model (detailed in Annex 1) is coupled online with the Lagrangian particle-tracking model LARVAE&CO (Figure 1-14), which results itself from the coupling between a particle tracking module and an individual-based model detailed below.

1.3.1 Particle-tracking model

Larvae trajectories were calculated online using the particle tracking module of COHERENS, called SEDLAG and described in Luyten et al. (1999) after a correction of the random walk scheme as described in Savina et al (2010) and detailed below.

Originally in Luyten et al. (1999), random motion was simply calculated in the following way: a “maximum velocity” is defined based on eddy diffusivity, which is then multiplied by a randomly generated number between −1 and 1. Thus, for a particle, the change in position from z_n (depth at the grid cell n) to z_{n+1} (depth at the grid cell n+1) over a finite time step δt is given by:

$$Z_{n+1} = Z_n + R\frac{\sqrt{2K\,\delta\,t}}{r} \tag{1}$$

where R is a random number with a uniform distribution between−1 and 1, whose mean is equal to 0 and whose standard deviation is equal to r (r=1/3), and K is the eddy diffusivity (m^2s^{-1}). However, in turbulent marine systems, turbulent diffusivity is commonly spatially non-uniform as illustrated in figure 1-15.

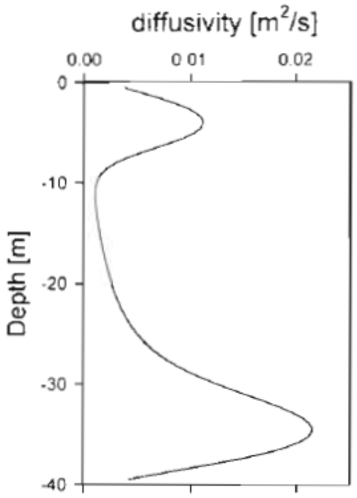


Figure 1-15 : Example of representative diffusivity profiles from Visser (1997). This example includes wind stress, tidal current and pycnocline.

Random walk scheme was corrected following Visser (1997), as described in Savina et al. (2010), by adding a non-random component, which counteracts the erroneous particle accumulation in low-diffusivity areas when only 'naïve' random walk formulation is considered (Eq. 1). In addition, the diffusivity is estimated considering a particle location offset by a distance 1/2 $K'(z_n)\delta t$, rather than at the initial particle location z_n. Thus, for an individual particle, the change in position from z_n to z_{n+1} over a finite time step δt is given by:

$$z_{n+1} = z_n + K'(z_n)\delta t + R\sqrt{\frac{2K\left[z_n + \frac{1}{2}K'(z_n)\,\delta t\right]\delta t}{r}} \tag{2}$$

where $K'(z_n)\delta t$ is the non-random component, with $K'=\partial K/\partial z$ representing the vertical gradient of diffusivity and whose standard deviation is equal to r (r=1/3).

Explicit representation of horizontal diffusion was neglected because in the North Sea, and at the larvae scale, vertical turbulent diffusion coupled to current layer shear is considered as the dominant horizontal dispersal mechanism (Christensen et al., 2007 and ref. therein).

1.3.2 Individual-based model

The individual-based model (IBM), described in Lacroix et al. (2013), is structured into four stages (eggs, yolk-sac larvae, first-feeding larvae, and metamorphosing larvae, see Figure 1-14). Each stage has a specific parameterization in terms of growth and behaviour which are summarized below.

Stage duration is temperature dependant. Available data from literature were interpolated to fit with the following function:

$$\text{Duration of stage}_\text{i} : \text{d}_\text{i} = \alpha_\text{i}\, T^{\beta_i}$$

Where i corresponds to the stage (1: eggs, 2: yolk-sac larvae, 3: first-feeding larvae, 4: metamorphosing larvae). In the absence of specific information on the relation between growth rate and temperature, β is set to 0.

The stage duration is computed at each time step (t_j) from the instantaneous temperature by adding reciprocal fractions of the development according to the following method (same for each larval stage):

```
$Stage_i(t_0) = 0$
Where $t_0$ is the time at the beginning of stage i.
$t_j = t_{j-1} + \delta t$
where j corresponds to the time step number ($\delta t$: 10 min)
While stage $\leq 1$
    $Stage_i(t_j) = Stage_i(t_{j-1}) + 1 / \frac{\alpha_i T^{-\beta_i}}{Ndt}$ with $Ndt$ : number of time step by day
End
```

When stage_i reaches the value of one, $\text{stage}_{\text{i+1}}$ begins. αi and βi are stage-related parameters

Mortality rate is a function of temperature and is expressed in the model under the form:

$$\text{mortality rate: } \text{m}^{-1} = \text{aT}^\text{b} \text{ (with T instntaneous temperature)}$$

In the absence of knowledge on specific effect of temperature, value of b is equal to 0.

Vertical migration, in the model several behaviours can be considered depending on stage, species and knowledge available on this process. The response of fish larvae to environmental cues changes along ontogeny (i.e., due to the progressive development of sensory and swimming capabilities), with endogenous rhythm behaviours (daily, tidal and lunar in periodicity) (Boehlert and Mundy, 1988). Rather than a simple stimulus-response mechanism related to a single environmental factor, but in a suite of cues, different hypothesis and mechanism related are developed in an interesting review by Teodósio et al. (2016). In the model, for each stage, several behaviours can be considered: 1) passive, 2) positive buoyancy (floating), 3) nycthemeral vertical migration according to which the larvae swim toward the surface during the night and toward the bottom during the day or 4) vertical tidal migration in which the vertical migration rates changed from positive value during rising tide to negative value during falling tide. Values for vertical migration rates have been defined within the range of the values observed in the literature (e.g. Berntsen et al., 1994; van der Molen et al., 2007—values not limited to flatfish), in order to obtain an average position of the larvae in the appropriate part of the water column, and to obtain diel vertical migrations and tidally associated vertical migration in the appropriate part of the water column (see more details in Savina et l. 2010, Lacroix et al., 2013 and Barbut et al., 2019 for the parameter values).

In view of this PhD thesis, I implemented the parameterization for five other flatfish species (plaice, turbot, dab, brill and flounder) as detailed in Chapter 2. The thesis provided also an opportunity to make some minor changes to the code, for example in the vertical migration process (details in Chapter 2).

1.4 AIMS OF THE PHD THESIS

Among fish, the early life stages are critical in determining dispersal and recruitment. Key issues are the understanding of how spawning and nursery grounds are connected and what processes influence larval retention, dispersal and population dynamics. This is especially the case for species with a long pelagic larval phase and where recruitment is strongly constrained by access to nursery grounds. Flatfish represent an important component of the North Sea ecosystem, many populations experience a high fishing pressure and show high interannual recruitment variability, which does not seem to be correlated to stock size. The transport of flatfish larvae from the spawning grounds to the nurseries is driven by hydrodynamic processes, but the final dispersal pattern and larval survival is affected by environmental factors, physiology, behaviour and reproductive strategies (spawning period and spawning grounds).

An option to study the hard to observe egg and larval stage is to use a hydrodynamic model coupled to an individual-based model to simulate larval dispersal.

The main objective is to improve knowledge on the role of the larval stage on flatfish recruitment and connectivity and answering to the following questions:

Question 1: Which environmental factors influence the recruitment of flatfish?

Question 2: Which factors impact dispersal during the early life stage of flatfish?

Question 3: How does one calibrate and evaluate a LTM?

Question 4: What is the impact of frontal systems on the larval dispersal of flatfish?

Question 5: Does the spatial structure of management match with the population structure induced by larval dispersal?

Question 6: How do life history traits influence dispersal during early life?

Question 7: How does expansion of OWFs across the North Sea impact demersal fish?

Question 8: What is the impact of climate change on the early life stages of flatfish?

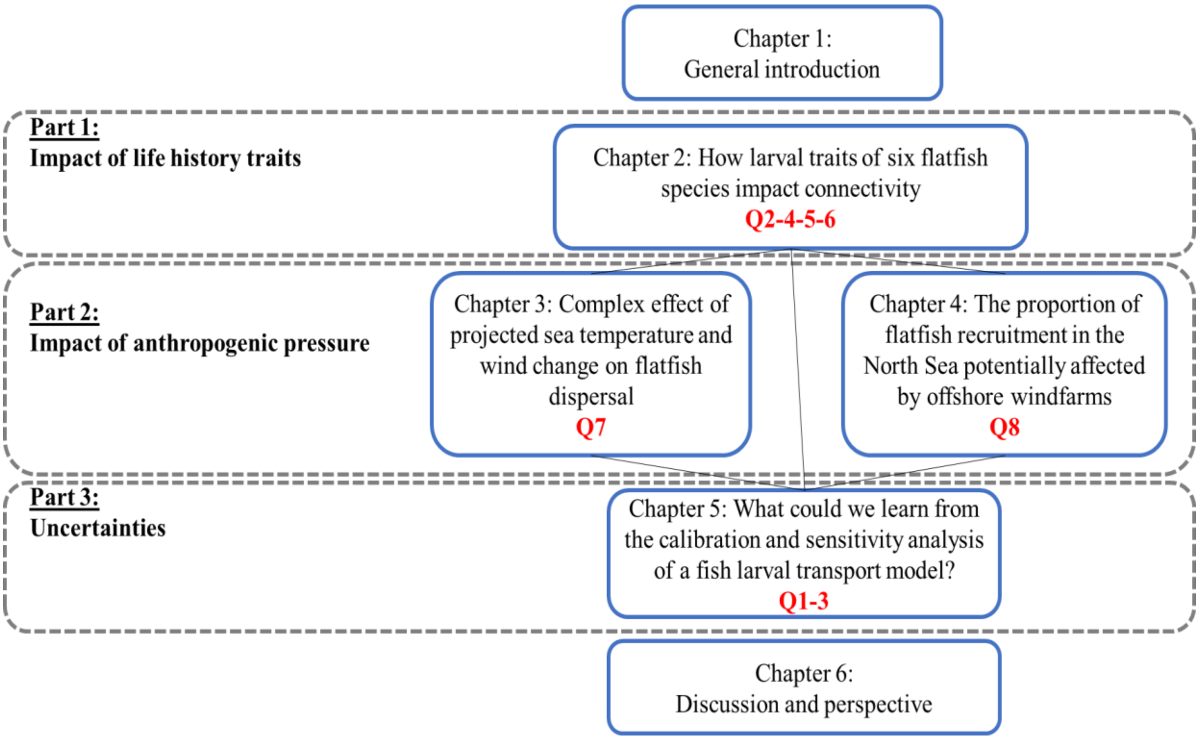


Figure 1-16 : Structure of the thesis, Specific questions are represented in red.

After a general introduction, the first part investigates how the combination of life history traits and environmental conditions impact connectivity (Figure 1-16). Chapter 2 focuses on the dispersal pattern of six flatfish species. The aim is to investigate how a distinct pattern of larval spatial structure might be linked to regional hydrodynamics and life-history traits. The North Sea experiences anthropogenic pressures such as greenhouse gas emissions that lead to climate change or the massive construction of marine wind farms. The second part focuses on these anthropogenic pressures on flatfish population. Chapter 4 is dedicated to the potential impact of offshore wind farms on the dispersal of the larval stages of six flatfishes. Whereas Chapter 3 is dedicated to the impact of climate change on the early dispersal of sole. My contribution to Chapter 3 is mainly related to the statistical rigour of the dispersal modelling. Calibration and validation of complex biophysical models is most challenging when uncertainties on data are large. The third part investigates sensitivity analyses of a larval transport model and evaluates the likelihood of model prediction in the case of sole in Chapter 5. In a final part I discuss the implications of my research and provide a perspective on future research.

Chapter 2. HOW LARVAL TRAITS OF SIX FLATFISH SPECIES IMPACT CONNECTIVITY

Barbut, L., Groot Crego, C., Delerue-Ricard, S., Vandamme, S., Volckaert, F.A.M., and Lacroix, G. This chapter has been published in Limnology and Oceanography 64: 1150–1171 (2019) and slightly adapted.

2.1 INTRODUCTION

Understanding and managing ecosystems requires sound knowledge of population dynamics, both spatially and temporally. Many taxa show long movement episodes early in life, which are critical for recruitment. This is particularly true in the marine environment where the larval stage often involves a pelagic phase (e.g. Hjort 1914, 1926; Cury and Roy 1989; Cushing 1990; Houde 2008). It is even more important for demersal species, as their recruitment success is highly dependent on access to suitable nursery grounds after metamorphosis. Survival rate is particularly low during this period (in the order of 10^{-3} % , McGurk 1986; Houde 2008; Le Pape and Bonhommeau 2015) and hence affects long-term population size.

Dispersal is an important process in marine populations, which might be studied at an ecological level, which deals with the contemporary scale and is relevant for (meta)population dynamics, and at an evolutionary level, which involves a multi-generational time scale (Jones *et al.*, 2009). Most observations of population structure happen on a contemporary time scale. When observed at an evolutionary time scale, historical processes and connectivity are intertwined. Connectivity, the realized movement between populations in a seascape, plays an essential role in the persistence and productivity of (meta)populations, in population structure, genetic diversity and population resilience (Cowen *et al.*, 2007). Despite a largely similar life cycle, large differences in dispersal capacity are observed among marine species. The differences are related to larval traits (López-Duarte *et al.*, 2012) such as behavior (Fox *et al.*, 2006b; North *et al.*, 2008; Robins *et al.*, 2013) and duration of the larval stage (Shanks, 2009b) or to seasonality (Lett *et al.*, 2010) or structure of the water column and currents (Munk *et al.*, 2009).

Connectivity is studied with various methods such as physical tagging, phenotyping, genetic markers and otolith microchemical signatures (Shima and Swearer, 2010; Kool *et al.*, 2013; Gagnaire *et al.*, 2015; Gibb *et al.*, 2017). However, the early life stages are too tiny for direct observation (Levin, 2006). Hence various alternative indirect methods are used. Egg and larval dispersal can be modelled, for example through a hydrodynamic model, simulating advection and diffusion, coupled to an individual-based model, simulating behavioral and life-history traits (e.g. Cowen et al. 2007; Miller 2007; Pineda et al. 2007; Cowen and Sponaugle 2009). Such biophysical models are useful for understanding the dynamics and critical drivers of ecosystems and management at the specific level (Allain *et al.*, 2007; Hinrichsen *et al.*, 2011).

Flatfish are an interesting group of fish to study connectivity. The demersal adults spawn planktonic eggs; eggs and larvae are transported by the currents until they metamorphose, and the juveniles settle in shallow coastal waters. Adults of common sole (*Solea solea* L.) and European plaice (*Pleuronectes platessa* L.) are philopatric to the spawning ground (Rijnsdorp *et al.*, 1992c; Hunter *et al.*, 2003) and make well known seasonal migrations (Hunter *et al.*, 2003; Burt and Millner, 2008). The modelled larval dispersal patterns of European plaice and common sole in the North Sea point to temporal variation and spatial philopatry linked to suitable nursery grounds (Bolle *et al.*, 2009; Savina *et al.*, 2010a; Hufnagl *et al.*, 2013; Lacroix *et al.*, 2013a). For other flatfish species of the North Sea, biological knowledge is sparser. Population genetic studies of European flounder (*Platichthys flesus* L.) and turbot (*Scophthalmus maximus* L.) (Hemmer-Hansen *et al.*, 2007a; Vandamme *et al.*, 2014) point to the influence of either water column stratification or current dynamics. However, processes affecting the adult and larval phase remain to be dissociated.

To avoid interspecific competition, flatfish have developed a wide range of life-history traits (following Gause' law of competitive exclusion (Gause, 1932, 1934; Hardin, 1960)). For example, Van der Hammen et al. (2013) point to the disjoint spawning periods and slight difference in habitat between turbot and brill (*Scophtalmus rhombus* L.). This should impact the population dynamics and connectivity pattern (Denney *et al.*, 2002), but awaits confirmation. This study focuses on the six most exploited flatfish species in the North Sea: turbot, brill, common sole, common dab (*Limanda limanda* L.), European plaice and European flounder. Hereafter in the manuscript, common sole, common dab, European flounder and European plaice will be referred to as sole, dab, flounder and plaice respectively. They present a broad range of life-history traits in regard to growth (pelagic larval duration), behavior (predation and vertical migration) and reproduction (spawning period and spawning grounds).

In terms of abundance, turbot and brill are rare while plaice and dab are highly abundant and sole and flounder are present at intermediate abundances (Rogers *et al.*, 1998). Exploitation levels differ considerably; sole and plaice are targeted in the demersal trawl fishery, turbot, brill and flounder are caught as valuable bycatch in a mixed fishery, whereas dab is mostly discarded because of its low commercial value (ICES, 2017b). Currently, all six species are managed by the International Council for the Exploration of the Sea (ICES) in species-specific geopolitical units. The populations of turbot and sole coincide with the three ICES divisions of the North Sea (IVa,b,c), while the North Sea and Skagerrak (IIIa) are considered a single population for plaice. For brill, dab and flounder on the other hand, divisions such as Skagerrak, Kattegat (IIIb,c) and English Channel (VIId and/or VIIe) have been merged with the North Sea divisions.

While the dispersal of the early life stages of sole and plaice has been well characterized in the North Sea (Bolle *et al.*, 2009; Erftemeijer *et al.*, 2009; Hufnagl *et al.*, 2013; Lacroix *et al.*, 2013a), knowledge on other flatfishes is more scant. Moreover, most studies target a single species, which leaves a shortage of standardized comparisons of dispersal patterns. In view of ecosystem-specific knowledge and ecosystem-based management it is most valuable to assess the ecological features of a larger group of species with a similar habitat for a better understanding of communities, at a regional scale and to measure the impact of reproductive strategies and larval traits on dispersal.

The main objectives of this study are to determine comparatively the impact of larval traits on dispersal and larval settlement at the nursery grounds, to assess the spatial variation of larval dispersal and connectivity of six flatfish species, and to estimate the interannual variability of connectivity over a 10-year period. We answer the following questions: (1) how do life-history traits influence the dispersal pattern at early life stage and (2) what is the impact of life-history traits on population structure? Our findings point to a distinct pattern of larval spatial structure linked to regional hydrodynamics and life-history traits.

2.2 MATERIALS AND METHODS

The approach taken involved the combination of a well-established 3D hydrodynamic model with a particle-tracking model under development. We simulate dispersal of the early life stages of six flatfish species from spawning at the spawning ground to settlement at the nursery ground.

2.2.1 Model

The LARVAE&CO model is an individual-based model (IBM) that simulates egg and larval dispersal in the Eastern English Channel and the North Sea. It results from the coupling between a 3D hydrodynamic model and a Lagrangian particle-tracking model. The model, initially developed for sole and described in Lacroix et al. (2013), has been adapted for the six species of interest, brill, sole, dab, flounder, plaice and turbot, as described below.

The hydrodynamic model

The 3D hydrodynamic COHERENS model (Luyten *et al.*, 1999), has been implemented in the Eastern English Channel and the southern and central part of the North Sea, between 48.5°N and 57°N and 4°W and 9°E in latitude and longitude respectively. The model domain contains a 157 x 205 horizontal grid with a resolution of 5’ in longitude and 2.5’ in latitude and 20 σ-coordinate vertical layers. The boundaries are formed by the northern and western open boundaries (at 4°W and 57°N) and included daily river discharges of 14 rivers. The model is forced by weekly sea surface temperature (SST) data on a 20×20 km grid interpolated in space and time according to the model resolution (*Bundesamt für Seeschifffahrt und Hydrographie, BSH, Germany*) (Loewe, 2003) and by six-hourly surface wind and atmospheric pressure fields provided by the Royal Meteorological Institute of Belgium based on the analyzed/forecast data of the UK Met Office Global Atmospheric Model (Hi Res; Walters *et al.*, 2017). Details about the model implementation (equations, forcing, initial and boundary conditions) and its validation are detailed in Savina et al. (2010) and Lacroix *et al.* (Lacroix *et al.*, 2013a).

Individual-based model

The Lagrangian larval transport model LARVAE&CO (Lacroix et al., 2013) was structured in four different stages representing flatfish life stages from eggs to metamorphosis (eggs, yolk-sac larvae, first-feeding larvae and metamorphosis larvae). Each stage has a species-specific parameterisation in terms of larval duration and behaviour (*in casu* vertical migration). Spawning grounds and periods are also species-specific. Larval trajectories were calculated online using the particle tracking model. The vertical diffusion was modelled by the random walk technique following Visser (1997). Because in the North Sea vertical turbulent diffusion is considered to be the dominant horizontal dispersal mechanism (Christensen *et al.*, 2007), explicit representation of horizontal diffusion was neglected. Specific details on the implementation can be found in Lacroix et al. (2013).

Four stages are considered in the model: (1) eggs, (2) yolk-sac larvae corresponding to larval stage 1 according to the classification of Lagardère et al. (1999) adapted from Al-Maghazachi and Gibson (1984), (3) first-feeding larvae corresponding to larval stages 2 to 4a and (4) metamorphosing larvae, roughly representing larval stages 4b–5a. Each stage has a specific parameterization when sufficient information was available.

Parameterization for the six species

Good knowledge of the processes and parameters involved is required in IBMs. Although the reproductive cycle and early life stages are well documented for some of the flatfish species, such as sole and plaice, data are scarce for others.

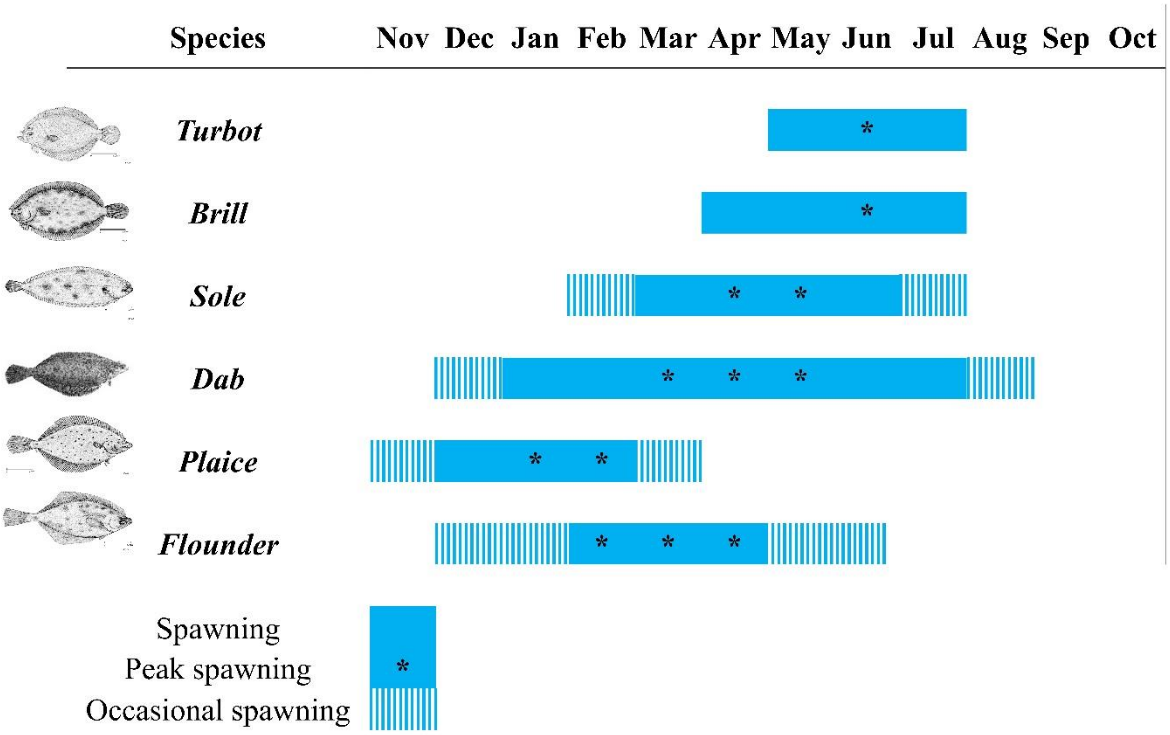


*Figure 2-1: Spawning period of six flatfish. The * represent the spawning peaks and hatched lines represent an occasional spawning. From top to bottom: turbot (Jones, 1974; Munro et al., 1990; van der Land, 1991; van der Hammen et al., 2013), brill (van der Land, 1991; van der Hammen et al., 2013), sole (Lacroix et al., 2013b), dab (Aurich, 1941; Harding et al., 1978; Daan et al., 1990; Henderson, 1998), plaice (Simpson, 1959; Cushing, 1969; Harding and Nichols, 1987; Campos et al., 1994; Rijnsdorp and Vethaak, 1997; Bromley, 2000; Gibson, 2005a; Bolle et al., 2009) and flounder (Sims et al., 2004). Details about year-to-year peak day of spawning are listed in the Table 2-1.*

Spawning period

The spawning period has been estimated on the basis of published data (Figure 2-1). The spawning peak is either related to SST (sole, Lacroix et al., 2013), mean annual temperature (flounder, Sims et al., 2004), latitude (plaice and dab, Aurich, 1941), photoperiod (turbot, Munro et al. 1990) or is a fixed value because of a lack of data (brill). The spawning duration is set to a fixed period for all species (Figure 2-1 and Table 2-1). A normal distribution centred on the spawning peak is used to model the spawning spread.

Spawning grounds

Published data on the adult distribution at spawning and the egg distribution were used to estimate the spawning areas. Unlike the well documented spawning grounds of some species (sole and plaice), the limited knowledge in other species leads to a lower spatial resolution.

Spawning grounds and egg densities have been estimated from egg distribution for the sole, plaice, flounder, dab and turbot. In addition, a habitat model was also used for dab, preferential spawning habitats and observed fish distribution for turbot or catches during the spawning period for brill.

The spawning grounds and egg densities are shown on Figure 2-2. References used for the six species are mentioned in the legend caption. Spawning zones are spatially divided into three areas based on the ICES divisions: Eastern English Channel (EEC, VIId), Southern North Sea (SNS, IVc) and Central North Sea (CNS, IVb) (Figure 2-3).

Behaviour

Vertical migration is a function of life stage and environmental conditions (night and day or tide). Nycthemeral migration means that the larvae swim towards the surface during the night and towards the bottom during the day. Tidal migration means a vertical migration synchronous with the tide. The parameterization of tidal vertical migration process has been improved since its documentation in Lacroix et al. (2013). The vertical migration rates switch from positive values during rising tide (when the sea surface level increases in the grid cell considered) to negative values during falling tide (when the sea surface level decreases in the grid cell considered). Available information was implemented in the model. In the absence of information, larval advection was passive (Table 2-1 Table 2-2).

Pelagic larval duration

Egg and larval stage duration is a function of temperature according to the equation $D = \alpha T^{-\beta}$ where D is the stage duration (in days) and T the temperature (in degree Celsius). Published data on the duration of egg and/or larval stages, obtained from laboratory experiments, larval daily rings from otolith analyses and peak densities were used to estimate α and β parameters. For some species, published information allowed to estimate α and β for the different stages (turbot, sole, plaice and flounder). For others, a constant value was allocated between different stages from a literature value (brill) or the duration was estimated on the basis of the spawning peak date and the peak of arrival on the nursery grounds (dab) (Figure 2-1). Details on the parameterization used are in Table 2-2.

*Table 2-1: Spawning peak (**Julian** day) of six flatfish species by year and ICES area in the North Sea and total duration of the spawning period considered in the model (in day) for each species.*

Species	Year	Eastern Channel	Southern North Sea	Central North Sea	Duration of the spawning period
Turbot	1997-2006	171	171	171	91
Brill	1997-2006	152	152	152	121
Sole	1997-2006	Function of sea temperature (details in section 3.5 in table 3.1)			101
Dab	1997-2006	91	105	120	211
Plaice	1997-2006	10	20	32	101
Flounder	1995	87	51	23	61
	1996	90	59	46	61
	1997	104	83	51	61
	1998	105	79	51	61
	1999	97	72	49	61
	2000	97	73	46	61
	2001	107	86	64	61
	2002	104	81	60	61
	2003	104	78	59	61
	2004	101	72	49	61
	2005	99	78	61	61
	2006	117	100	71	61

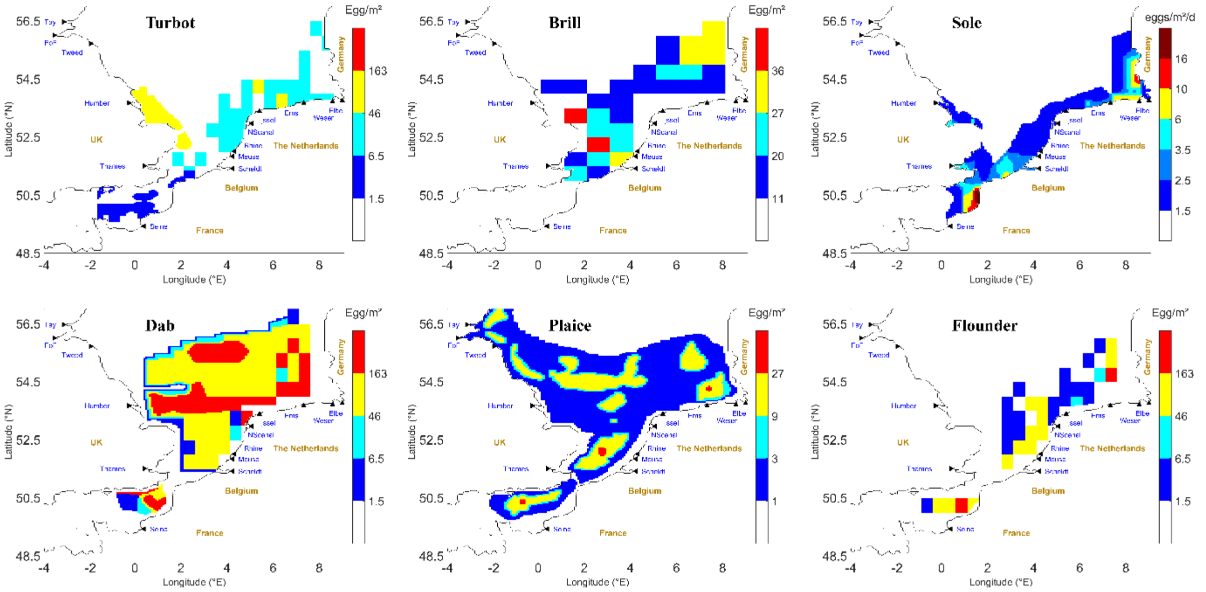


Figure 2-2 : Spawning distribution of the six flatfish: turbot (van der Land, 1991; Rogers and Millner, 1996; Vause and Clark, 2011), brill (van der Hammen et al., 2013), sole (Lacroix et al., 2013a), dab (van der Land, 1991; Rijnsdorp et al., 1992a; Lelièvre et al., 2014), plaice (Harding et al., 1978; van der Land, 1991; Taylor et al., 2007; Bolle et al., 2009; Ellis et al., 2012) and flounder (van der Land, 1991; Taylor et al., 2007) in the Eastern English Channel and North Sea.

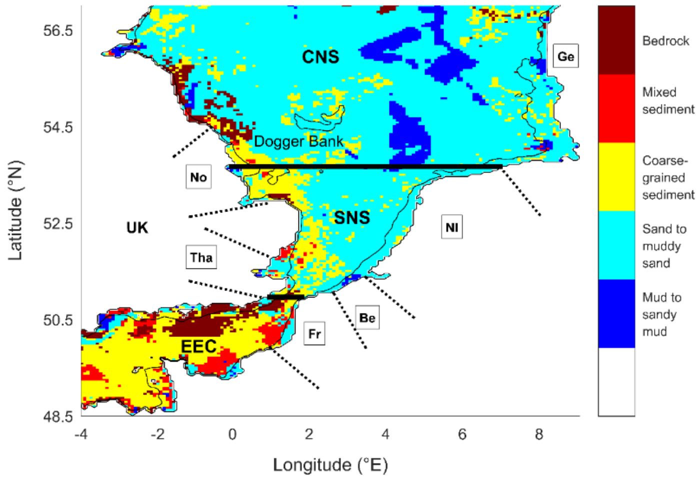


Figure 2-3: Location of the spawning zones and nursery grounds of six flatfish. Spawning grounds are divided in three areas: Central North Sea (CNS), Southern North Sea (SNS) and Eastern English Channel (EEC), corresponding respectively to the ICES management areas (IVb, IVc, and VIId). Nursery sectors are based on national boundaries (Fr, Be, Nl, Ge), except for the UK, where we distinguished a southern (Tha) and a northern nursery (No). Area codes: France (Fr), Belgium (Be), the Netherlands (Nl), Germany, including the SW Danish coast (Ge), Norfolk (No) and Thames estuary (Tha). The Dogger Bank is included in the No nursery ground.

Table 2-2: Summary of the parameters used in the model. The number refers to the following references: 1 : Ayala et al. (2015), 2 : Gibson and Johnston (1995), 3 : Jones (1972), 4 : Lacroix et al. (2013), 5 : Campos et al (1994) , 6 : Van der Land (van der Land, 1991), 7 :Henderson (1998), , 8 : De Veen (1978), 9 : Bolle et al. (2009), 10 : Dannevig (1897), 11 : Ryland (1966), 12 : Talbot (Talbot, 1976), 13 : Harding et al. (1978), 14 : Hovenkamp (1991), 15 : Coombs et al. (1990), 16 : Sundby, (1983), 17 : Creutzberg et al. (1978), 18 : Rijnsdorp et al. (1985), 19 : Sahin (2000), 20 : Engell-Sørensen et al. (2004), 21 : Hutchinson and Hawkins (2004), 22 : Grioche et al. (1997), 23 : Bos et al. (1995) , 24 : Jager (1999).

Species	stage	Larval duration α	β	Vertical migration
Turbot	Eggs	29.12	-0.66	Upward movement
	Yolk-sac larvae	68.85	-1.01	No migration
	First-feeding larvae	1925.5	-1.6	No migration
	Metamorphosing Larvae	39.65	-0.48	No migration
references			1,2,3	
Brill	Eggs	10	0	Upward movement
	Yolk-sac larvae	10	0	No migration
	First-feeding larvae	10	0	No migration
	Metamorphosing Larvae	31	0	No migration
references			3	
Sole	Eggs	274.64	-1.5739	Upward movement
	Yolk-sac larvae	137.92	-1.4619	Nycthemeral migration
	First-feeding larvae	3560.1	-1.9316	Nycthemeral migration
	Metamorphosing Larvae	1146.1	-1.9316	Tidal migration
references			4	4
Dab	Eggs	30	0	Upward movement
	Yolk-sac larvae	25	0	No migration
	First-feeding larvae	30	0	No migration
	Metamorphosing Larvae	25	0	Tidal migration
references			5,6	5,7,8
Plaice	Eggs	114.18	-0.95	No migration
	Yolk-sac larvae	/	/	/
	First-feeding larvae	469.6	-1.14	Tidal migration
	Metamorphosing Larvae	223.5	-1.25	Tidal migration

references	9,10,11,12,13,14			12,15,16,17,18
Flounder	Eggs	12.65	-0.33	No migration
	Yolk-sac larvae	516.5	-1.83	No migration
	First-feeding larvae	20	0	Tidal migration
	Metamorphosing Larvae	300	-1	Tidal migration
references	19,20,21			5,22,23,24

Larval mortality

To penalize long larval durations and increase the realism of the simulations, a survival rate was computed during the full larval stage until metamorphosis. The mortality rate for sole has been described in Lacroix et al. (2013) (0.0004.$T^{3.0293}$ d^{-1} with T the temperature for eggs and yolk-sac-larvae, a constant mortality rate of 0.035 d^{-1} from first-feeding larvae to metamorphosis). All other flatfish were imposed a constant mortality rate of 0.048 d^{-1} (Beverton and Iles, 1992; Nash, 1998) at all stages.

Larval settlement

Settlement occurs at the end of the larval stage at a habitat that is species-specific. It is based on several cues and may involve active swimming, which is not included in the model. In this study, we assume that larvae are able to reach their preferred habitat if they reach the nursery ground defined on the basis of bathymetry and sediment type as described in Lacroix et al. (2013). In addition to the coastal areas, the Dogger Bank was also considered for plaice and dab (Figure 2-3). To compare easily among species, the Dogger Bank was included in the Norfolk area. Nursery grounds were assigned on the basis of national boundaries (Figure 2-3). Larvae that end up outside of these nursery grounds don’t survive (0 % survival rate).

2.2.2 Run specificities

The model has been run over a period of 10 years (1997–2006) corresponding with the time scale of the North-Atlantic Oscillation, in order to represent a broad range of hydrodynamic and environmental conditions.

The use of super-individuals (Scheffer *et al.*, 1995) allows for realistic egg numbers while keeping the number of particles released limited. Each super-individual represents a number of individuals (*Nind*). A weight was associated with each particle according to the spawning distribution on Figure 2-2. The number of particles released each year is species-specific (sole: $1.9\times10^{6;}$ plaice: 48×10^{6}; turbot: 1.7×10^{6}; brill: 2.2×10^{6}; flounder: 1.3×10^{6}; dab: 7.4×10^{6}). This number has been chosen to ensure good model properties in terms of convergence. The main idea is to be sure that the number of particles is large enough to cover all the possible trajectories. This approach has been conducted empirically by doubling the number of particles until the results of simulation were similar as recommended by North *et al.* (2009).

2.2.3 Analysis of the model output

The following metrics were used to compare the modelling results:

Mean temperature experienced by the larvae and mean (and standard deviation) pelagic larval duration are calculated based on individual trajectory of each particle.

The net dispersal between origin and arrival was used to quantify the mean distance travelled by eggs and larvae of each species.

Relative recruitment across the North Sea. In the absence of a precise estimation of spawning stock biomass, it is impossible to establish a prediction on recruitment at the different nursery grounds. Nevertheless, the relative arrival of larvae at the nursery grounds was analysed.

Connectivity matrices among spawning and nursery grounds indicated for each nursery ground and each year the proportion of larvae coming from the different spawning areas that reached a certain nursery.

Connectivity among management areas summarizes the dispersal pattern of the six species. Spawning and nursery grounds are pooled to assess the connectivity between the different ICES management divisions: EEC (the EEC spawning ground was grouped with the French nursery ground), SNS (Be, Nl, Tha and No nursery grounds were grouped with the SNS spawning ground) and CNS (Ge nursery ground and CNS spawning ground are grouped).

2.3 RESULTS

Life-history traits

The winter spawners plaice and flounder experienced the lowest mean temperature during the pelagic larval duration (respectively 7.0 °C and 9.7 °C) (Table 2-3). Sole, brill and turbot, which spawn later in the year, experienced higher temperatures (between 12.0 °C and 15.4 °C). Dab, which spawns over a wide temporal window, experienced a similar mean temperature than sole but was the species with the highest standard deviation. As temperature impacts the metabolic rate, and hence larval development, the mean pelagic larval duration has been computed for each species (Table 2-3). Late spawning species had shorter drift than early spawners. Turbot had a shorter drift (about 45 days) than the two other late spawners (respectively 49 days for sole and 61 days for brill). Dab presented the longest larval drift (105 days), plaice had a 3-month pelagic phase and the total pelagic larval duration was more than two months for flounder (67 days).

Table 2-3: Mean and standard deviation of temperature (°C) and total pelagic larval duration (days) of six flatfish averaged during the period 1997-2006.

Species	Mean temperature encountered by the larvae	Mean larval duration
Turbot	15.4 ± 1.5	44.7 ± 5.3
Brill	14.3 ± 2.5	61.0 ± 0.0
Sole	12.0 ± 1.7	48.7 ± 12.4
Dab	12.8 ± 3.0	105.0 ± 0.0
Plaice	7.0 ± 1.1	90.4 ± 13.7
Flounder	9.7 ± 2.4	67.7 ± 13.4

Dispersal distance

Dispersal distance shows the ability of a species to disperse and to link the nursery with the spawning ground. The potential dispersal range is directly related to the time spent in the water column and to the hydrodynamical conditions. All species studied showed a potential to disperse between 100 and 200 km, but there were strong interspecific differences in the realized dispersal (Figure 2-4). The mean dispersal range was lower for summer spawners: larvae of turbot travelled the shortest distance (102 km) whereas sole and brill covered an intermediate distance (respectively 132 and 140 km). On the contrary, the mean distance travelled by winter spawners was higher (> 170 km): the average dispersal distance was respectively 184 km for dab and 191 km for plaice. Flounder showed the largest distance travelled with a mean of 200 km.

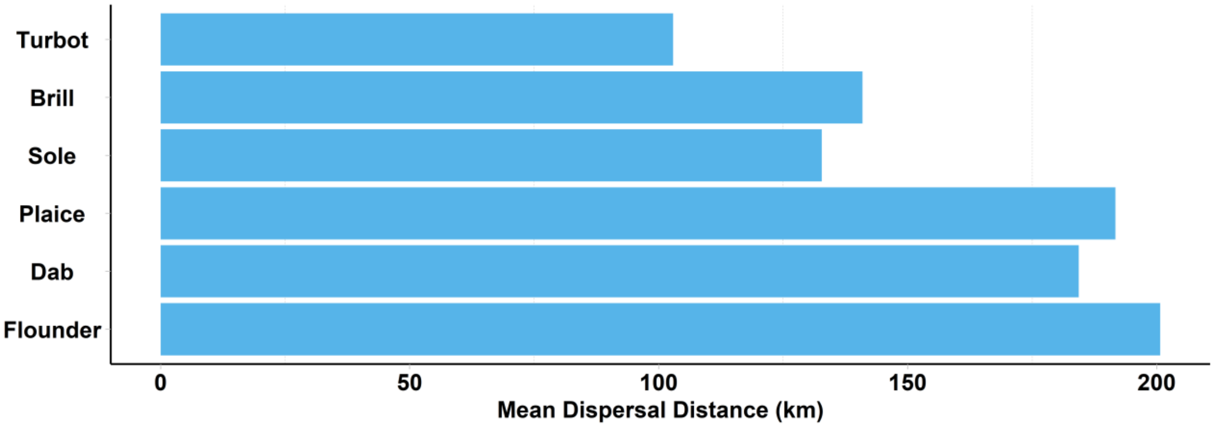


Figure 2-4 : Mean dispersal distance for six flatfish across the North Sea averaged during the period 1997-2006.

Arrival of settlers at the nursery grounds

All six species showed strong differences in their relative recruitment at the nursery grounds (Figure 2-5). The settlement of post larvae, concentrated in the German Bight, reflected the general circulation pattern of the North Sea. Norfolk was an important nursery ground for turbot, dab and plaice but not for the other species. Not any flounder larva arrived in Norfolk due to the absence of any known spawning ground on the west coast of the North Sea. The Thames estuary was the second most important nursery ground for plaice and flounder and the third for dab. The Dutch coast was an important nursery ground for sole, turbot and brill. Overall, the predicted recruitment at the French nursery ground was low, especially for brill, for which little spawning information is available in the EEC.

High inter-annual variations were predicted by the model regarding the number of individuals arriving at the different nursery grounds. For example, the model predicted a relative number of flounder larvae that settled at the Belgian nursery ground between 49 (minimum) and 8500 (maximum), a ratio of 1:173. It varied from 5 to 850 (1:18) for plaice at the Dutch nursery ground and even from 10 to 1500 (1:150) for dab at the French nursery ground according to the year considered.

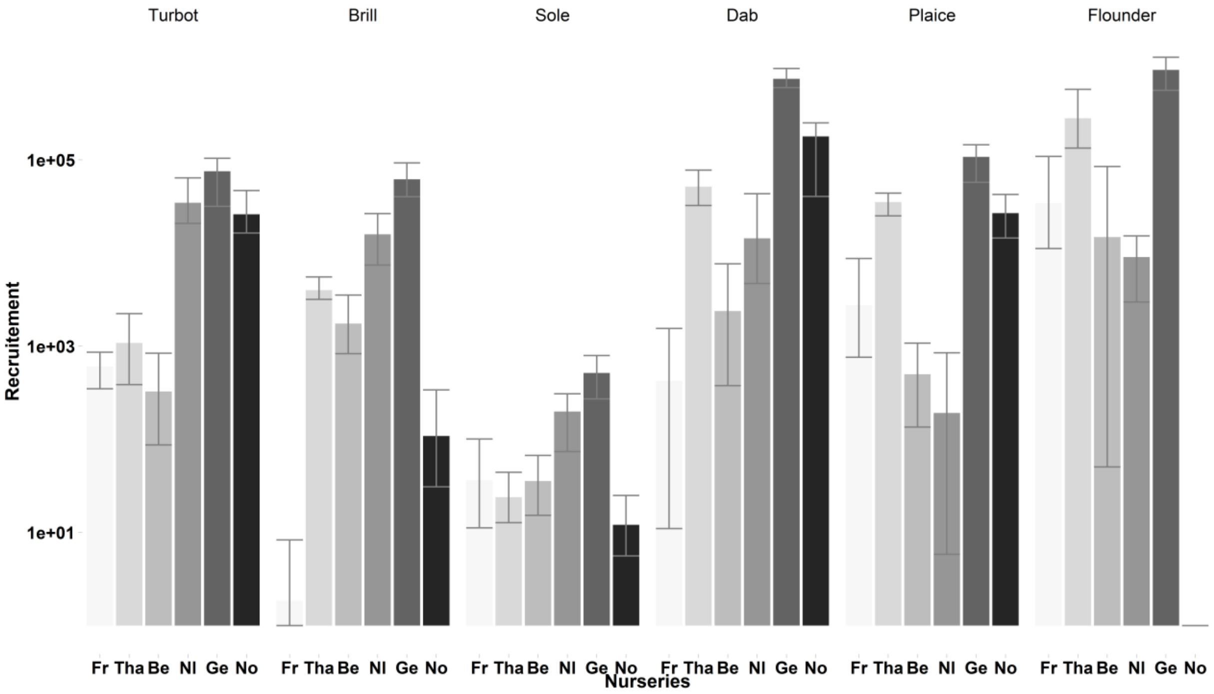


Figure 2-5 : Relative recruitment (±minimum and maximum values computed during the period 1997-2006) for the nursery sectors France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge), Norfolk (No) and Thames estuary (Tha) for six flatfish species.

Dispersal patterns

Overall, all flatfish dispersed from south to north (Figure 2-6). Eggs spawned in the EEC reached the French, Thames, Belgian and Dutch nursery grounds whereas eggs released in the SNS settled mainly in the SNS (Belgian, Dutch, Thames and Norfolk nursery grounds). Larvae born in the CNS mostly settled locally. Despite this general pattern, there are some differences between species and years in terms of connections.

The French nursery ground was isolated for all species, except dab, in 2002 when 4.4 % of the migrants arrived from the SNS. Despite a connectivity of 100 % predicted for brill in some years (1999, 2001, 2002 and 2006) only few individuals arrived at the French nursery ground due to the absence of (known) local spawning grounds. The model predicted fewer arrivals from the EEC for turbot and sole than for dab, plaice and flounder at the Thames nursery ground. The same kind of pattern was observed at the Belgian nursery ground but the interannual variability was more pronounced, due to the strong impact of hydrodynamic conditions. Most of the larvae that arrived at the Belgian nursery ground originated from the SNS area for turbot and brill, whereas for the other species, this nursery received mainly larvae from the EEC. In some years a strong influence from the south was predicted; up to 73 % and 95 % for plaice in

2003 and 2005, and 68 % for sole in 1997. The input of the EEC spawning ground was even negligible for flounder in 2001.

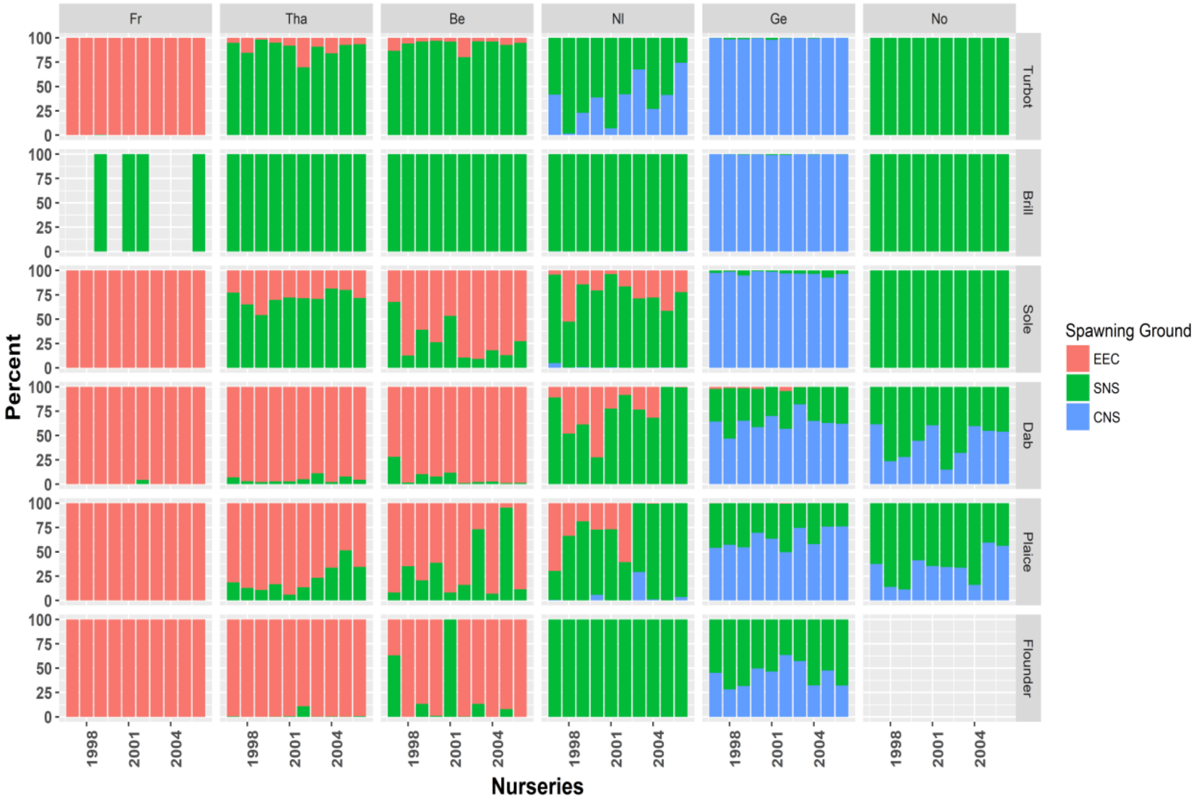


Figure 2-6: Proportion of larvae of six flatfish arriving at a nursery ground in France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge), Norfolk (No), and Thames estuary (Tha) originating from the spawning regions Eastern English Channel (EEC), Southern North Sea (SNS) and Central North Sea (CNS) during the period 1997-2006.

At the Dutch nursery ground, the predicted connectivity pattern presented strong differences between species. There was no interannual variability for flounder and brill, which arrived mainly from the SNS. For plaice, dab and sole, the connectivity pattern was more variable, with an important influence of the SNS and a non-negligible input from EEC. A strong interannual variability was predicted for the origin of settlers. For example, for sole the proportion of larvae native from the EEC varied from 4.2 % in 1997 to 52.0 % in 1998. The same situation was observed for dab (from 72.5 % in 2000 to 0.6 % 2004), and for plaice, for which the majority of settlers came from the EEC (69.7 %) in 1997 to a negligible number of arrivals during the period 2003-2006. In addition, in the case of plaice, the Dutch nursery ground was strongly influenced by the CNS during an exceptional event (29.0 % in 2003). Turbot is the only species for which a large proportion of larvae originated from the CNS and not from the EEC.

The German Bight showed an interesting connectivity pattern. The larvae of three species (dab, plaice and flounder) originated from the Central and Southern North Sea areas, whereas this nursery ground was isolated for turbot, brill and sole, whose larvae were mainly spawned in the CNS. The Norfolk nursery ground was isolated for turbot, brill and sole. Plaice and dab showed a variable arrival from SNS and CNS in this nursery, mainly due to the presence of the Dogger Bank.

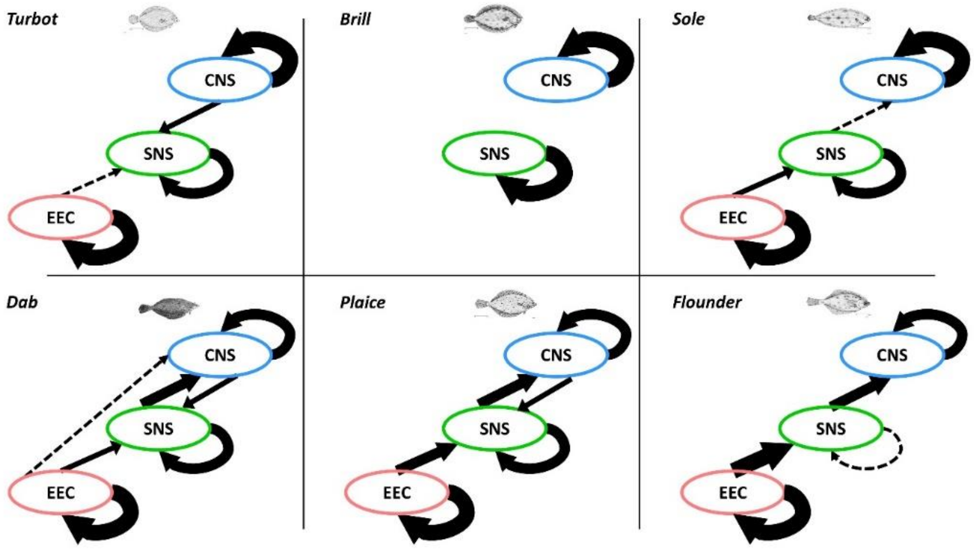


Figure 2-7: Scheme of the connectivity pattern between the ICES management units as predicted by the dispersal model. Arrow thickness represents the strength of the connection: dashed (1 to 5 %), thin (5 to 35%), medium (35 to 80 %) and large (>80 %).

Connectivity patterns across the North Sea

Connectivity between the three regions of the North Sea showed contrasting patterns (Figure 2-7). The EEC presented a high level of self-recruitment for all species and was a source population for the SNS, and to a lesser extent, the CNS. A first group of species (sole, turbot and brill) showed limited exchanges, especially in the CNS where most of the settlers were locally spawned (99. 3% for turbot, 99.7 % for brill and 96.8 % for sole).

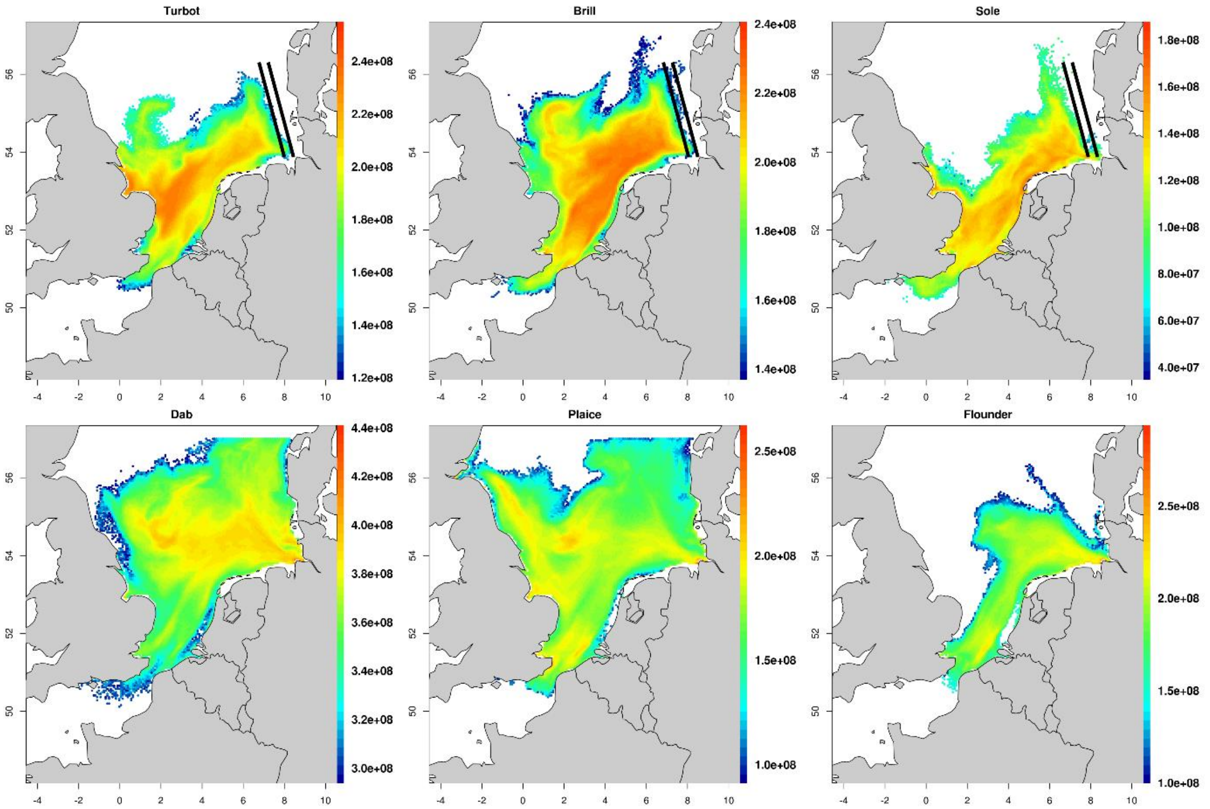


Figure 2-8 : Larval abundance of six flatfish species at the end of larval transport for eggs spawned in the central part of North Sea. The black line indicates the presence of a hydrodynamic front.

Turbot eggs spawned in the EEC remained local whereas exchanges with the southern region were limited (1.7 % from the EEC to the SNS). Turbot is the only species in this first group for which the model predicted a non-negligible input of arrivals in the SNS from the CNS (21%). Both areas are strictly isolated for brill. The model predicted a high level of connectivity for sole from the EEC to the SNS area (29.8%) but a restricted exchange of individuals from the SNS area to the CNS area (3.2%), due to the limited arrival of larvae in the German coast from SNS (Figure 2-8). In contrast, flounder, dab and plaice, representing the second group, had a high level of exchange across the North Sea. In the CNS, arrivals were mixed (63 % of self-recruitment for dab, 43 % for flounder and 63.3 % for plaice). All three areas were well connected for dab (25 % from the EEC to the SNS and 35 % from the SNS to the CNS area). Dab is the only species for which the input from the EEC into the CNS was non-negligible (1.2 %). Flounder was highly connected between all three areas. The model predicted a low level of self-recruitment in the SNS (4.2 %) due to a high number of arrivals from the EEC. In the case of plaice, the SNS was mainly influenced by the EEC (44 %), and the CNS received a large number of individuals spawned in the SNS (36.7 %). In the case of dab and plaice a large number of eggs spawned in the CNS settled in the SNS (31 % for dab and 14 % for plaice).

2.4 DISCUSSION

This study shows a large variation in connectivity and spatial distribution among the early life stages of six flatfish species inhabiting the North Sea. Two groups emerge with similar characteristics in terms of life-history traits and dispersal patterns. Turbot, sole and brill, which spawn in spring and in proximity of the coast, have a shorter pelagic larval duration and a lower level of connectivity. In contrast dab, plaice and flounder are characterized by winter spawning and spawning grounds located further offshore. Their larvae drift longer and have a higher level of exchange across the region.

Advantages and limitations of the biophysical model

Individual based models require a sound knowledge of the biological processes governing larval dispersal. Their output most often provides novel insights and generates new hypotheses, although they may be sensitive to some parameters that influence larval connectivity, retention and successful migration. Also hypotheses on mortality, spawning ground and pelagic larval duration may influence the model prediction. This is particularly important for species with limited knowledge. While some species are well studied (plaice and sole were cited 127 and 183 times respectively between 2006-2016 on Web of Science) it is more challenging for other species where uncertainties on life-history traits remain important (see Materials and Methods). The lack of information about some life-history traits (and hence their parameterization), implies uncertainties which might affect the robustness of the model for the various species studied.

The number of settlers predicted by the model could not be directly related to recruitment. There are several reasons why this is the case. First of all, the spawning stock biomass is unknown for brill, flounder and dab in the North Sea, resulting in the absence of knowledge on the total number of eggs spawned. Furthermore, many processes occurring at the nursery grounds are either density-dependent (e.g. van der Veer 1986; Rijnsdorp and Van Leeuwen 1992; van der Veer et al. 2000; Le Pape and Bonhommeau 2015) or linked to environmental conditions (Rijnsdorp *et al.*, 1992c; Fox *et al.*, 2000; Nash and Geffen, 2000). In addition, habitat settlement is species-specific and implies active swimming based on specific cues, which are not included in the model. It is increasingly understood that benthic microbial communities produce a specific allelochemical profile that influences the settling larvae (Woodin *et al.*, 1993; Sebesvari *et al.*, 2013). We assume that habitat selection occurs at the end of the simulation and that reaching the coastal area is sufficient as a proxy for settlement. Although the model used was based on simple biological assumptions, it successfully explained a significant component of the recruitment variability of sole (about 30%, Lacroix et al. 2013).

Comparison to other modelling and empirical studies

Irrespective of these assumptions, the connectivity patterns estimated by the model are coherent with other modelling studies. Hufnagl et al. (2013) and Bolle et al. (Bolle *et al.*, 2009) using different biophysical models, found the same dispersal pattern and a high connectivity level across the North Sea for plaice. In the case of sole, model prediction resembled previous studies based on the same model (Savina *et al.*, 2010a; Lacroix *et al.*, 2013a) and was consistent with other modelling studies (Bolle *et al.*, 2009). However, Savina et al. (2016) predicted, unlike this study, an important input from the North Sea into the EEC for sole. The only significant movement predicted from north to south was found for dab and during only one year (in 2002). Although the residual current generally flows NE through the Strait of Dover, in some periods a reverse current has been documented (Bailly du Bois and Dumas 2005). Under proper conditions, settlement in a SW direction might be possible. We showed how important hydrodynamics and temperature are for the spatio-temporal dispersal pattern of larvae.

Pelagic larval duration is temperature-dependent because it is linked to metabolic rate (see paragraph “Pelagic larval duration” in Materials and Methods). Model results are consistent with a longer pelagic larval duration of winter spawners (plaice, flounder and dab). Winter is also the period where larval food (plankton) is less abundant in the North Sea (e.g. Colebrook 1969), which explains part of the variation in growth rate. Turbot, sole and brill, which encounter higher temperatures, have a shorter larval duration (1-2 months) whereas the other species have a longer larval duration (2-3 months). In addition, model prediction showed a large variability depending on the spawning area, the moment of spawning in the season and the year.

Dispersal distance parameterizes the ability of species to disperse and colonize non-native areas. Dispersal is correlated with the duration of the planktonic stage (Bradbury and Snelgrove, 2001; Shanks *et al.*, 2003; Siegel *et al.*, 2003) and temperature (O’Connor *et al.*, 2007). Indeed, dispersal range is directly related to the time spent in the water column, the hydrodynamical conditions and the starting point of the drift. All species showed a potential to disperse between

100 and 200 km but there were strong differences between species. Indeed, differences in terms of pelagic larval duration (i.e. time spent in the water column) induced differences in dispersal distance. However, pelagic larval duration is not the only important parameter. Flounder and brill are representative cases. Larvae of both species spent similar times in the water column (67 and 61 days respectively) but showed a strong difference in distance travelled (140 km and 200 km respectively). Reason is the seasonal difference in hydrodynamics with stronger currents in winter (Holt and Proctor, 2008).

The distribution of settlers at the nursery grounds and their origins differed between species and presented an important interannual variability. Larval settlement into the different nursery grounds is an important factor to understand population dynamics and how species with similar habitat are separated temporally and spatially.

In addition to the distribution of young fish, the model predicted connectivity between the spawning and nursery grounds. Particles followed the general circulation pattern in the North Sea from south to north for all species (Turrell, 1992). The interannual variability in larval origin was high, mainly for the Thames estuary, Belgian and Dutch nursery grounds where larvae came from EEC, SNS and CNS in function of the environmental conditions. The predicted variation in connectivity is not linear in space and time, which justifies the use of a hydrodynamical model to predict recruitment. For example, in the Belgian nursery, despite a stable overall connectivity pattern over the years for flounder with larvae coming mostly from EEC, in 2001, most of their larvae originated from the south. Plaice showed an inverted connectivity pattern between 2005 and 2006, switching between larvae coming mostly from the SNS to larvae mostly coming from the EEC.

For example, despite a similar overall connectivity pattern for flounder and plaice, 2001 and 2005 showed opposite dynamics in terms of connectivity. During the year 2001 much of the success transport to the Belgian nursery came from the SNS for flounder whereas it was mainly influenced by EEC for plaice. It was the opposite pattern for the year 2005. Turbot, brill and sole showed very high levels of self-recruitment (more than 95 %) in the CNS whereas other species were more connected between Southern and Central North Sea. The latter area is probably not strictly isolated but connected with a northern region not included in the model as shown for plaice by Hufnagl et al. (2013).

Oceanic fronts are a barrier to dispersal and determine stock structure (Galarza *et al.*, 2009; Schunter *et al.*, 2011). If the water column is well mixed at the SNS, this is not the case at the

CNS. In summer, the oceanic front divides the North Sea latitudinally between tidally well-mixed southern waters and stratified northern waters (Otto et al. 1990, OSPAR Comission 2001). This frontal system structures hyperbenthic and benthic communities (Dewicke *et al.*, 2002; De Nooijer *et al.*, 2008), and flatfish species, whose population densities are higher south of the front (Gibson, 2005a; Vandamme *et al.*, 2014). The front has an important impact on the dispersal pattern. Early spawning species whose eggs and larvae drifted before establishment of the front were not affected (plaice, flounder and dab), whereas late spawners (sole, turbot and brill) encountered a dispersal barrier. This structuring of the two species groups by a hydrodynamical front is clearly visible on our modelled map. Flounder has a specific dispersal pattern which fits with a spawning period at the end of winter/early spring. Final distribution of larvae showed the start of creation of barrier to dispersal, without affecting the south of the German Bight. Due to the presence of seasonal frontal system the spawning period played a major role in the connectivity of the early life stages.

Genetic insights can be used to test the reliability of the model. We focused on studies using microsatellite markers to standardize the comparisons. Classical population genetic studies on plaice and flounder showed similar high levels of connectivity across their distribution range (Hoarau et al., 2002, 2004; Hemmer-Hansen et al. 2007). Seascape genetic studies, which include various structural and environmental features, are more promising to identify genetic patterns and levels of dispersal (Pita *et al.*, 2011; Selkoe *et al.*, 2016b). A seascape genetic analysis showed similar low levels of migration rate in sole, turbot and brill, and a subtle population structure between the SNS and German Bight in sole and turbot (Vandamme et al, personal communication). Results for brill were less clear. Classic population genetic analyses illustrated no difference between the Southern and Central North Sea whereas seascape genetics predicted some scale of differentiation. All these genetic studies used neutral genetic markers. Dispersal patterns may be detected at a finer scale using outlier markers, as was the case for sole (Diopere *et al.*, 2018) and turbot (Vandamme *et al.*, 2014).

There is an interesting case of mismatch in spatial structuring. Although our biophysical model predicted that the Norfolk spawning ground would be isolated for all six flatfish no genetic differentiation was observed in any empirical study. This might be explained by either incompleteness of the model, important adult and juvenile movements or the absence of evolutionary processes to maintain population structure under a regime of a low level of exchange. Due to similarities between the simulated and the genetically measured connectivity patterns, the general consistency of both approaches is a cue for the efficiency of the model. Mismatches between population units and fisheries management are relevant for exploitation of natural resources (Hinrichsen *et al.*, 2011).

Implications for ecosystem knowledge and management

This study highlights how the combination of life-history traits and environmental conditions affect the migration of the early life stage of flatfish. It helps to understand spatial patterning and the position of the genetic cline. It helps to understand and distinguish which component of the genetic structure has a historical and adaptive contribution and which part has an ecological contribution, more specifically the migration of early life stages. Other fish and invertebrates in the North Sea show also a mosaic of connections (e.g. Mariani et al.; Jolly et al. 2005; Maggs et al. 2008; André et al. 2011).

Distribution of these species covers a large common geographical area but presents variation in the way the entire population is divided in subpopulations. Here, two subpopulations are found for turbot, brill and sole, whereas dab, plaice and brill exhibit one mixed population. The ability to find the source and destination of young fish and the level of spatial structuring of populations is critical in many management decisions involving marine protected areas (Planes *et al.*, 2009; Berglund *et al.*, 2012), coastal development (Cicin-Sain and Belfiore, 2005), implementation of offshore wind farms (Hammar *et al.*, 2016) or fisheries (Fogarty *et al.*, 2007). For example, in the northeast of UK, the local turbot population collapsed in 1970s due to overfishing. The main hypothesis is that the stock of young turbots would not be sufficient to maintain a sustainable number of adult fish (Kerby *et al.*, 2013). The prediction of the model confirmed this hypothesis with a high level of auto-recruitment for Norfolk nursery. In addition, dispersal models are also relevant to assess which species are affected by currents, especially in areas with strong seasonal dynamics, such as the North Sea. The distribution of settlers is also relevant to understand the impact of anthropogenic activity (linked to pollution, habitat degradation and coastal engineering) on flatfish at a regional scale.

Understanding dispersal and population connectivity is an important issue for fisheries management (Kerr *et al.*, 2010). The level of knowledge on stock structure impacts the exploitation (Kerr *et al.*, 2016), especially the match between population structure and management area. For example, the presence or absence of distinct subpopulations impacts the sustainable exploitation of sole in EEC (Archambault *et al.*, 2016). The presence of two potential subpopulations of sole, brill and turbot should be considered in management.

Perspectives

This study presented modelled results highlighting structure in subpopulations of flatfish. They show that individual-based modelling is a useful strategy to guide resource management, even when limited biological information is available such as in the case of brill. Extending the modelled migration to juvenile and adult life stages should provide additional conceptual insights and help with the establishment of optimized management measures. The quantification of the exchange by dispersal between areas represents a first step to build a full life cycle model to improve fisheries management. An example of such development is the full life-cycle model of flatfish in the Eastern English Channel (Archambault *et al.*, 2015).

Chapter 3. COMPLEX EFFECT OF PROJECTED SEA TEMPERATURE AND WIND CHANGE ON FLATFISH DISPERSAL

Lacroix, G., Barbut, L., and Volckaert, F.A.M. 2018. This chapter has been published in Global Change Biology, 24: 85–100 (2019) and slightly adapted.

3.1 INTRODUCTION

A typical feature of many marine organisms is the bipartite life cycle, which is divided into a dispersive early life stage and a relatively sedentary juvenile and (sub)adult stage. Dispersal, a key driver of population connectivity, is crucial for the persistence of demes and metapopulations (Orsini *et al.*, 2008) and for the colonisation of new habitats (Herrera *et al.*, 2015). It is a multi-causal process with a strong physical component in the ocean, modulated by individual characteristics and including a major fitness component (Baguette *et al.*, 2013). The dispersal distance covered is shorter than initially thought, adding to the importance of local recruitment, a measure of survival (Almany *et al.*, 2007; Saenz-Agudelo *et al.*, 2011). Mortality rates of the early life-stages of most marine organisms are high, which has led to highly variable survival rates across cohorts and demes (D'Aloia *et al.*, 2015). Hence, population demography, metapopulation dynamics, community resilience and ecosystem dynamics are shaped by connectivity and dispersal (Marleau *et al.*, 2014). More recently, global climate change has measurably changed the physical and biological functioning of the oceans (Beaugrand *et al.*, 2014a; Kendall *et al.*, 2016). Dispersal variability has consequences for the conservation of fish, stock management, the design of marine reserves, the management of non-indigenous invasive species and the prediction of climate-change effects (Levin, 2006).

Larval dispersal is dependent on physical factors (diffusion and advection) and biotic factors (population and community dynamics, life-history traits, swimming and sensory capabilities), leading to a considerable impact of climate variability and climate cycling on population dynamics (Lo-Yat *et al.*, 2011). Recently, human-induced climate change has played an increasingly important role in this background variability, greatly affecting marine organisms and leading to species losses and invasions, community changes, regime shifts (Van Nes and Scheffer, 2005), phenological and biogeographical shifts (Barton et al., 2016) and changes in the adaptive capabilities of organisms (Calosi *et al.*, 2016). Fish populations are no exception (Rijnsdorp *et al.*, 2009); they are particularly affected in their larval dispersal patterns, recruitment and connectivity through changes in oceanic circulation and temperature (Munday *et al.*, 2009). According to the "Warm+" IPCC scenario at the North Sea scale, wind speed would increase by 4% and wind direction would shift from 20° to 33° (north-eastwards) by 2040 (Van den Eynde *et al.*, 2011). The impact of increased temperature on larval dispersal is difficult to predict a priori due to its non-linearity and complexity (e.g., cumulative or contrasting effects acting on larval, juvenile or adult stages). A rise in temperature is expected (i) to decrease larval duration (O'Connor *et al.*, 2007), which might result in an increase (through larval retention, also called self-recruitment) or decrease (through fewer opportunities to reach remote nursery grounds) in local settlement success; (ii) to increase larval mortality, which might decrease settlement success (Madeira *et al.*, 2016); (iii) to advance the spawning period (Teal *et al.*, 2008; Fincham and Engelhard, 2013); (iv) to change the spawning pattern through a shift in abundance and distributions (Rijnsdorp *et al.*, 2009; Engelhard *et al.*, 2011); (v) to change reproductive output (Shama, 2015); and (vi) to alter the overlap with the prey populations (Edwards and Richardson, 2004). Modifications in wind speed and direction might potentially affect egg and larval retention and dispersal through changes in hydrodynamics. An increase in wind strength is expected either to shorten the travel duration of larvae to the nursery grounds or to provide the opportunity for more larvae to reach nursery grounds that might not have been accessible under the current conditions. A modification of wind direction would affect the larval trajectories differently according to the area considered. An increase in larval recruitment is expected where currents would be strengthened towards nurseries and *vice versa*.

Biophysical models have proven useful for assessing the impact of climate change on larval dispersal (Lett *et al.*, 2010 and references therein), larval survival (Cetina-Heredia *et al.*, 2015), connectivity (Kendall *et al.*, 2013) and fish recruitment (Brochier *et al.*, 2013). It is only recently that the IPCC scenarios have been used to evaluate the impact of climate change on living marine resources (Kimura *et al.*, 2010; Stock *et al.*, 2011; Change, 2014). However, the complex response of recruitment at nursery grounds remains to be assessed quantitatively (but see Lett *et al*. 2010).

Here, we present a case with the flatfish (common) sole *Solea solea* L. (Soleidae, Teleostei), a key component of the soft-bottom ecosystem and among the most valuable commercial species in the southern North Sea. Management of the North Sea sole stock is approaching its precautionary reference points following recovery from unsustainable exploitation (ICES, 2016). Sole is a batch spawner (Rijnsdorp and Witthames, 2007), spawning in the North Sea in coastal waters in spring (van der Land, 1991) along a latitudinal gradient (Vinagre *et al.*, 2008). Larval development is temperature dependent (Fonds, 1979), while survival is linked to prey availability, avoidance of predators and infections. Supply of nursery grounds may be affected by advection and diffusion of the planktonic eggs and larvae. Recruitment variability is high; larval survival is food limited at the nursery grounds (Le Pape and Bonhommeau, 2015), and low recruitment follows a cold winter (Horwood, 1993).

LARVAE&CO, the model used in this study, is a particle-tracking model of sole larvae implemented at the North Sea scale. This model has been used to study the relative contribution of hydrodynamics, environmental factors and behaviour on recruitment dynamics and to investigate the interannual variability of sole larval recruitment at nursery grounds over the period 1995-2006 (Lacroix *et al.*, 2013a). Year-to-year variability in larval supply to the nursery grounds was high (coefficient of variation 29%). The model explained 30.7% of the recruitment variability over the 12-year period based on a comparison of estimated abundances of sole larvae at the nursery grounds with virtual population analysis (VPA) estimates of recruitment (ICES, 2011).

This study aims to further test the robustness of the LARVAE&CO model to explain interannual variability of sole larval recruitment at the North Sea scale by considering a longer period (1995-2011 instead of 1995-2006 in Lacroix *et al.*, 2013). We also assess the interannual variability in larval dispersal over this 17-year period. Then, using a subset of years representative of a broad range of hydrodynamic and temperature conditions (2003-2011), we assess the impact of climate change scenarios using theoretical perturbations inspired by IPCC predictions in the North Sea by 2040 on (i) sole dispersal, (ii) connectivity and (iii) regional recruitment at the nursery grounds (eastern English Channel and North Sea). The results of the scenarios are discussed with regard to interannual variability and their consequences.

3.2 MATERIALS AND METHODS

3.2.1 The LARVAE&CO model

The model used in this chapter is the same than in the previous chapter for sole. Spawning is temperature dependent, spawning peak date is defined as the average over each spawning ground of the first day where a temperature of 10°C is reached (Lacroix et al., 2013 and references therein), date of the peak are in supplementary material (Table 2-1Table 3-1).

3.2.2 Computational runs

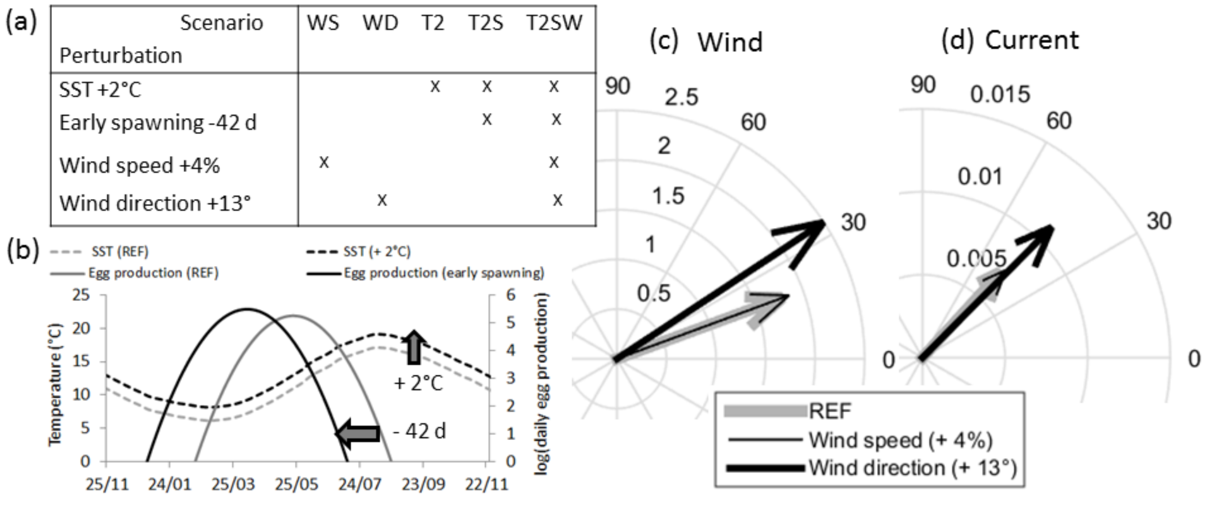
3.2.2.1 Baseline simulation

The model was run over a period of 17 years (1995-2011) to assess model robustness and interannual variability of dispersal and recruitment to the nursery grounds due to hydrodynamic and environmental year-to-year variability.

3.2.2.2 Reference simulation and scenarios

Since the recruitment interannual variability over a shorter period (2003-2011), representative of a broad range of hydrodynamic conditions (contrasted North Atlantic Oscillation (NAO), currents and temperature), is similar to recruitment variability over the full period (see results and discussion), we focused on the shorter period to assess the impact of climate change scenarios. The reference simulation (hereafter REF) used for comparison with the scenarios corresponds to a subset (2003-2011) of the baseline simulation. The sensitivities of larval dispersal, connectivity and recruitment to climate change were assessed by estimating the impact of a hypothetical change in wind speed/direction and SST based on the "Warm+" mid-term 2040 IPCC scenario at the North Sea scale proposed in Van den Eynde et al. (2011). In this scenario, a wind velocity increase of 4%, an increase of south-westerly winds (shift from 20° to 33° north-eastwards) and an increase of water temperature of 1.7°C (rounded to 2°C here) is expected by 2040. In this study, five perturbed simulations (scenarios) are tested and compared to the reference run (Figure 3-1).

In the "wind speed increase" scenario (hereafter called WS), a 4% increase in wind speed is applied by adding 4% to the wind velocity forcing used for the reference run (Figure 3-1c). In the scenario “south-westerly wind increase” (hereafter called WD), an change in wind direction by 13° north-eastwards is applied by adding 20% to the northern component and 10% to the eastern component of the wind intensity used for the reference simulation (c). The wind frequency is not modified. The mean currents resulting from the wind perturbations (-1.3° for WS and -2.3° for WD) are shown in Figure 3-1d. In the scenario “SST increase” (hereafter called T2), a 2°C increase is applied by adding 2°C to the SST forcing from BSH (Figure 3-1 b). In the scenario “SST increase and early spawning” (hereafter called T2S), in addition to the perturbation of scenario T2, an early spawning is considered (Figure 3-1 b). The peak date, which is still computed as the first day that a temperature of 10°C is reached (see section IBM), occurs earlier than in the reference run (42 days on average, Table 3-1). The scenario “all perturbations” (hereafter called T2SW) considers the combination of all previous perturbations. Whatever the scenario, the perturbations are applied at each time step and over the whole domain.



(a)

Scenario Perturbation	WS	WD	T2	T2S	T2SW
SST +2°C			x	x	x
Early spawning -42 d				x	x
Wind speed +4%	x				x
Wind direction +13°		x			x

Figure 3-1: Schematic representation of the perturbations applied in the climate change scenarios. (a) Perturbations considered in each scenario, (b) daily mean SST and spawning season, (c) mean wind (m/s) and (d) mean current speed (m/s) over a six-month period from the start of spawning. Mean over the whole domain (2003-2011).

3.2.3 Analysis of the results

To assess model accuracy in predicting larval recruitment at the nursery grounds, the modelled estimates of recruitment at age-0 (i.e., abundance of larvae just after settlement) were compared to VPA estimates of recruitment at age-1 (ICES, 2015b, 2015a) in the North Sea and the EEC.

The following metrics were used to compare the modelling results.

(1) Mean trajectories: The position of the centre of mass was computed as the average geographical coordinates (longitude, latitude) of all particles released at a given spawning ground; it was recorded every 12 h. The trajectories were then plotted by linking all the positions recorded for each spawning ground separately. In some cases, average positions were located inland. Although confusing, this finding is correct since this is an average position; it does not mean that any of the larvae are physically located inland.

(2) Mean net dispersal of the centre of mass (hereafter NDCM), which quantifies the net distance travelled by the eggs and larvae, was computed as the distance between the initial and final positions of the centre of mass for each spawning ground. For a more complete description of the particle distribution, axis lengths and angle of the kernel statistics (Huret *et al.*, 2010) were also computed.

(3) Mean temperature (hereafter MT): The temperature experienced by the eggs and larvae was archived for each of them separately during the whole pelagic phase, up to settlement at the nursery grounds, and was averaged for all larvae per nursery.

(4) Pelagic larval duration (hereafter PLD): The duration of each stage from spawning up to settlement, which is temperature dependent, was computed and summed for all larvae. The total PLD was then averaged for all larvae per nursery.

(5) Larval recruitment (hereafter LR): LR was calculated as the number of larvae that settled at a given nursery at the end of the larval phase.

(6) Connectivity matrices: Connectivity matrices representing the number and proportion of larvae originating from a given spawning site that have reached a given nursery ground at the end of the simulation were compiled. As there is no quantitative information on larval density that would lead to a successful connection, no threshold was considered. In addition, the connection frequency, representing the number of years where the model predicts a connection, was computed.

(7) Multiple means comparison tests were performed to investigate the effects of site on the trajectories in the baseline simulation and the effect of date (years 2003-2011) and the modified runs on the different factors (NDCM, MT, PLD and LR) for each spawning or nursery ground in the REF simulation and scenarios. In both cases, a paired Student t-test was performed with a Holm-Bonferroni (Holm, 1979) correction with the software R (https://www.r-project.org).

NDCM was computed for the sensitivity analysis at each spawning ground by considering all larvae that originate from a given spawning area. MT, PLD and LR were computed for each nursery ground considering only the larvae arriving at the nursery grounds at the end of the pelagic phase. All factors were computed for all simulations and for each year (2003-2011) and were then averaged over the whole period. The NDCM, MT, PLD and LR values at the end of the larval stage in the perturbed simulations were compared with those in the reference run. In each case, the average was computed over the period 2003-2011 (Mean); the interannual variability over this 9-year period is given by the standard deviation (Stdev), and the relative difference between perturbed and reference simulations (%) and the coefficient of variation (CV) due to year-to-year variability were also computed. The significance of the variability between perturbed and reference runs was also computed for the six spawning or nursery grounds. In each simulation, the contribution from the sites, the scenario (run) and the date were assessed.

3.3 RESULTS

3.3.1 Model accuracy and interannual variability (baseline simulation)

3.3.1.1 Interannual variability of recruitment

The model accuracy was tested for the period 1995-2011 by comparing the computed recruitment with VPA estimates. The correlation was significant ($r = 0.57$, $P < 0.017$); the model explained 33% of the year-to-year recruitment variability at the regional scale (EEC and the North Sea). The predicted interannual variability of LR at the nursery grounds was high (CV equal to 27.2%). At the local scale, the CV due to year-to-year variability varied between 34% (GE nursery) and 78% (BE nursery).

3.3.1.2 Interannual variability of larval dispersal

Particles were transported north-eastwards in the baseline simulation (Figure 3-2), except for the German Bight and the Norfolk spawning grounds, where larvae were transported north-north-westwards and east-south-eastwards, respectively, in accordance with the general circulation in the North Sea. The interannual variability of the trajectories over the period 1995-2011 is important; the standard deviation of the latitude and longitude of the NDCM end position varied from 0.1°N (N spawning ground) to 0.4°N (EC spawning grounds) and from 0.2°E (GB spawning ground) to 0.6°E (BC spawning ground), respectively.

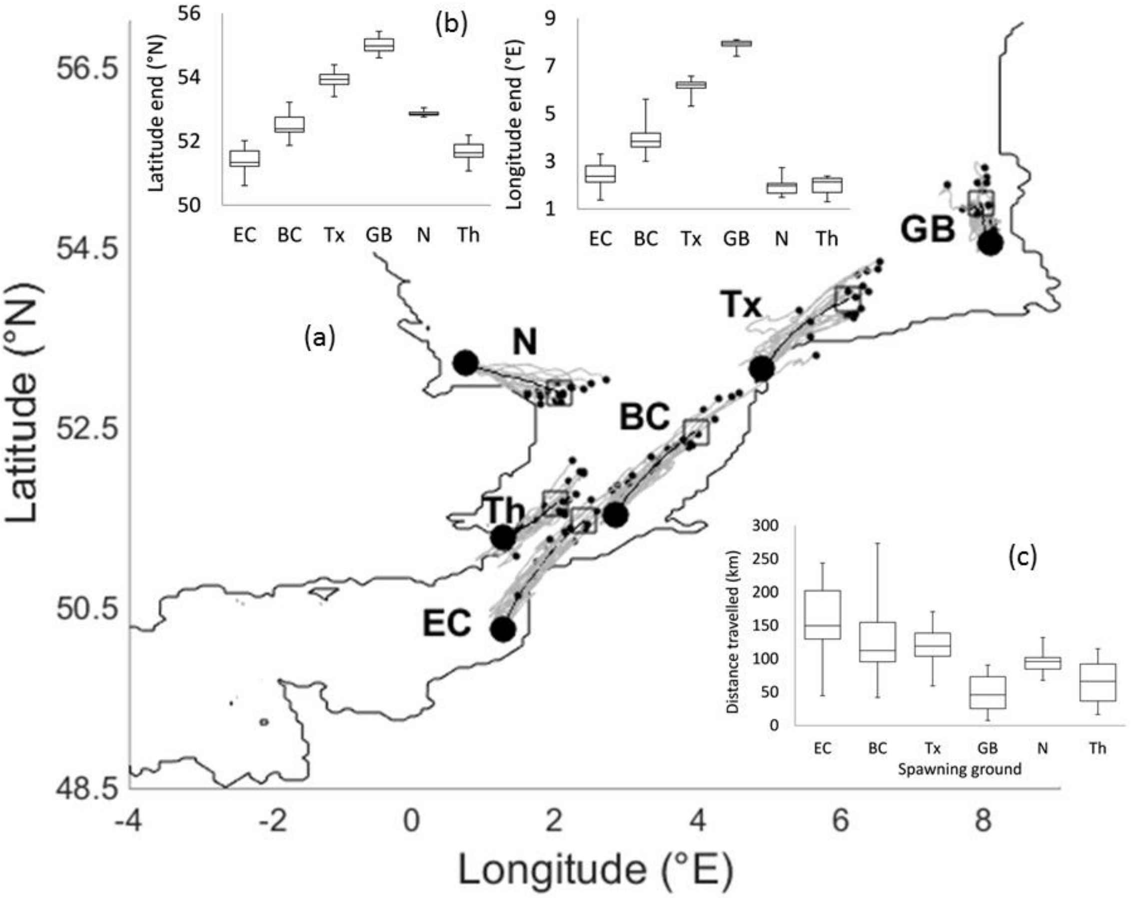


Figure 3-2: (a) Trajectories of the centre of mass at the six spawning grounds over the period 1995-2011 (baseline simulation). Each grey curve represents a different year; the black curve represents the trajectory averaged over 17 years. The black dots represent the origins (large dots) and ends of trajectories (small dots); the black squares represent the end of the mean trajectories. The inset figures show the statistics of latitude and longitude of the NDCM end position (b) and the distance travelled over the 17 years (c). The central line is the median, the edges of the box are the 25th and 75th percentiles, and the whiskers are the minimum and maximum.

There were large and significant ($P < 0.05$) differences in mean distance travelled between the six spawning grounds (Figure 3-2 c) and in the end positions of the centres of mass (Figure 3-2 b). NDCM was the longest for the eggs/larvae released at the EC spawning ground (156.0 km, on average, for the period 1995-2011) as a consequence of the stronger local currents. The eggs/larvae spawned in BC, Tx and N travelled, on average, a comparable distance of 128.0 km, 118.9 km and 95.1 km, respectively. Eggs/larvae covering the shortest distance were released in Th and GB, with distances of 67.9 km and 48.4 km, respectively. The interannual variability of NDCM was high; the difference between the longest and the shortest distances travelled ranged from 64 km to 231 km.

3.3.2 Outcome of the scenarios

3.3.2.1 Larval dispersal

For all spawning grounds, the impact of a 4% increase of wind speed on larval dispersal was limited (relative difference between the average NDCM computed for scenario WS and REF varied between -3.3% and 0.5%, Table 3-1) and was not significantly different than the REF simulation (WS, Figure 3-3 a, b-g). However, the consequence of an increase of south-westerly wind (WD, Figure 3-3) was important (increases of NDCM between 9% and 49%, Table 3-1) and significant for all spawning grounds except for GB compared to the REF simulation (Figure 3-3 a). At all spawning grounds, a temperature increase (T2, Figure 3-3) led to a limited shortening of the trajectories (decrease of NDCM between -10.9% and -1.5%, Table 3-1) but was only significant for GB compared to the REF simulation (a). In contrast, a temperature increase associated with early spawning (T2S) resulted in an increase of NDCM (between 2.2% and 74.5%, Table 3-1) that was not significant compared to the REF run (Figure 3-3a).

The T2SW scenario led to a strong increase of NDCM (from 58% to 138%, Table 3-1) for the EC, BC, Tx and Th spawning grounds and a limited increase for GB and N (10% and 9%, respectively) (Figure 3-3, Table 3-1), but these differences were not significant at the local scale (Figure 3-3 a). Larval trajectories issued from the EC, BC and Tx spawning grounds were extended in their initial direction, whereas those initiated from GB ended up closer to the coast and those originating from N and Th spawning grounds were directed offshore. The angle of the major axis of the dispersal kernel ellipse showed a slight shift towards the east for EC, BC and GB (4, 2 and 1°, respectively) and towards the north for Tx, N and Th (19, 12 and 1°, respectively). At the regional scale, the model predicted a considerable and significant increase ($P < 0.01$) of NDCM by 70% (Figure 3-3 a, right).

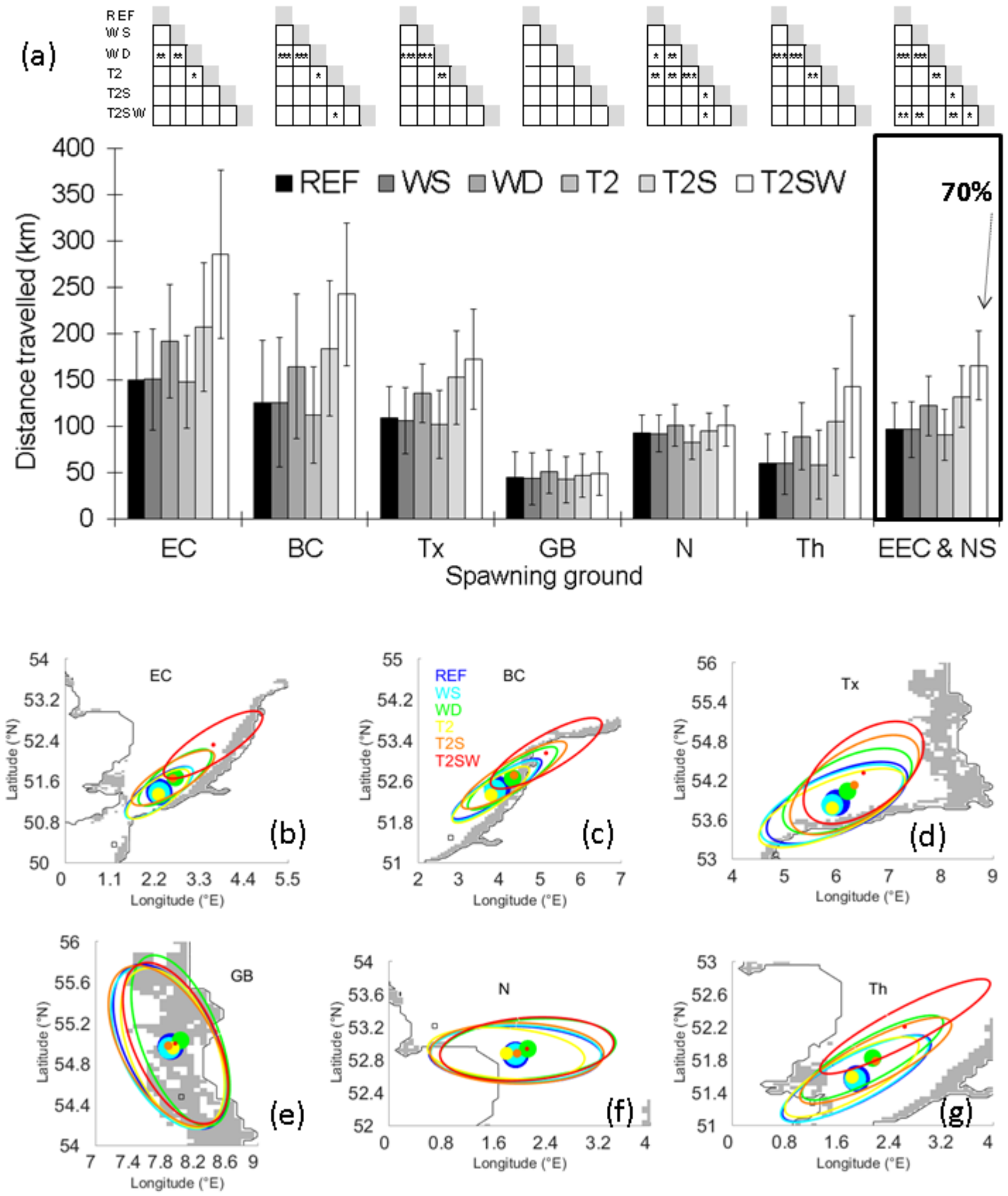
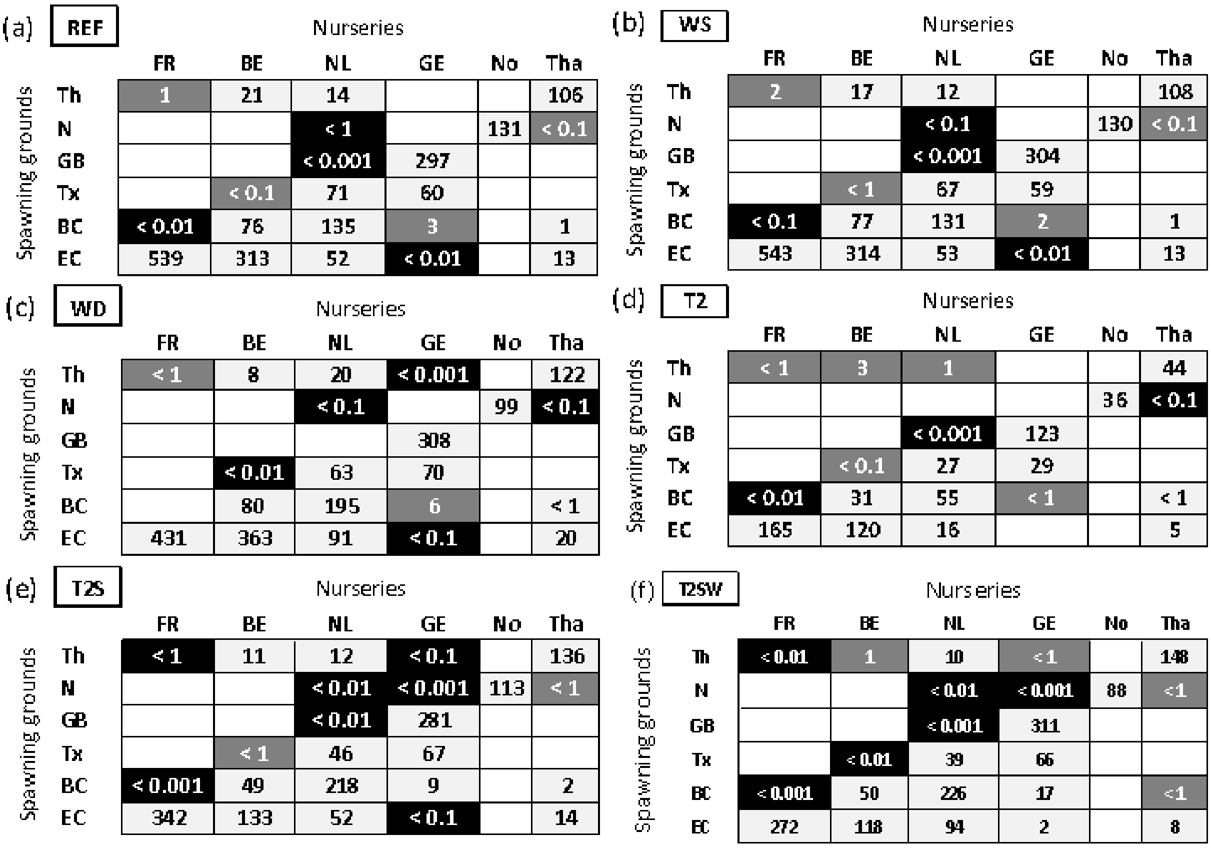


*Figure 3-3: (a) Mean net displacement of the centre of mass (NDCM) over the period 2003-2011 for the reference run and the perturbed simulations. Error bars represent the interannual standard deviation. Significance between each pair of scenarios is presented in the matrices (upper part of the panel) with the following significance levels: '***' (P < 0.001), '**' (P < 0.01), '*' (P < 0.05). (b)-(g) Start (□) and end (•) position of the NDCM and kernel ellipses of the six spawning grounds (mean over the period 2003-2011). Comparison between reference (REF, dark blue) and the five climate change scenarios (WS: cyan; WD: green; T2: yellow; T2S: orange; and T2SW: red). The grey areas represent the nurseries. For details on the scenarios and spawning ground codes, see Materials and Methods.*

3.3.3 Larval connectivity

Connectivity between spawning and nursery grounds over the period 2003-2011 is presented in relation to transport success (Figure 3-6 in Appendix) and the strength and frequency of the connections (Figure 3-4) for all scenarios. In the reference simulation, the model predicted recurrent (9 years over 9) retention (diagonal), eight recurrent connections, four regular (5-8 years over 9) connections, and four connections for which larval exchanges were rare (1-4 years over 9). The strongest connections (> 100.10^3 larvae per km²) were predicted for the cases of retention except for BE and NL, for which connection with the upstream spawning grounds (EC and BC respectively) was the strongest (Figure 3-4 a). All spawning sites supplied larvae to at least one distant nursery ground (although rarely so for GB), and all nursery grounds received larvae at least once from a distant nursery ground, except for No, which was totally isolated.

For the increased wind speed scenario, the classification (recurrent, regular or rare) and strength (weak, medium or strong) of connections remained the same (Figure 3-4 b). When the wind direction was perturbed (Figure 3-4c), due to an increase of the north-eastward current which prevents larval transport in the opposite direction to the general circulation, two weak connections (< 1.10^3 larvae per km²) disappeared and two weak regular connections became rarer. One new weak connection appeared as a result of the enhancement of the north-eastward current, which allowed larvae from the mouth of the Thames to reach German waters. Temperature increase (Figure 3-4 d) had an important impact on connection frequency. Because of PLD shortening, which prevented larvae from travelling very long distances, two weak connections disappeared, one regular weak connection became rarer and two recurrent connections became regular. Overall, transport success (Fig. 3-6) and the strength of connections (Figure 3-4 d) decreased. When the temperature increase was combined with an early spawning (Figure 3-4 e), two new weak connections appeared, from the Th and N spawning grounds to the GE nursery ground, and the regular medium (between $1\text{-}100.10^3$ larvae per km²) connection between the BC spawning ground and the GE nursery ground became recurrent due to the PLD lengthening.



(a) REF

Nurseries / Spawning grounds

	FR	BE	NL	GE	No	Tha
Th	1	21	14			106
N			< 1		131	< 0.1
GB			< 0.001	297		
Tx		< 0.1	71	60		
BC	< 0.01	76	135	3		1
EC	539	313	52	< 0.01		13

(b) WS

Nurseries / Spawning grounds

	FR	BE	NL	GE	No	Tha
Th	2	17	12			108
N			< 0.1		130	< 0.1
GB			< 0.001	304		
Tx		< 1	67	59		
BC	< 0.1	77	131	2		1
EC	543	314	53	< 0.01		13

(c) WD

Nurseries / Spawning grounds

	FR	BE	NL	GE	No	Tha
Th	< 1	8	20	< 0.001		122
N			< 0.1		99	< 0.1
GB				308		
Tx		< 0.01	63	70		
BC		80	195	6		< 1
EC	431	363	91	< 0.1		20

(d) T2

Nurseries / Spawning grounds

	FR	BE	NL	GE	No	Tha
Th	< 1	3	1			44
N					36	< 0.1
GB			< 0.001	123		
Tx		< 0.1	27	29		
BC	< 0.01	31	55	< 1		< 1
EC	165	120	16			5

(e) T2S

Nurseries / Spawning grounds

	FR	BE	NL	GE	No	Tha
Th	< 1	11	12	< 0.1		136
N			< 0.01	< 0.001	113	< 1
GB			< 0.01	281		
Tx		< 1	46	67		
BC	< 0.001	49	218	9		2
EC	342	133	52	< 0.1		14

(f) T2SW

Nurseries / Spawning grounds

	FR	BE	NL	GE	No	Tha
Th	< 0.01	1	10	< 1		148
N			< 0.01	< 0.001	88	<1
GB			< 0.001	311		
Tx		< 0.01	39	66		
BC	< 0.001	50	226	17		<1
EC	272	118	94	2		8

Figure 3-4: Connectivity matrix (larval abundance) between spawning grounds (rows) and nursery grounds (columns) for the reference simulation (a) and the five scenarios (b)-(f). The colour code represents the connection frequency, which is the number of years where a connection is predicted by the model within the period 2003-2011 (light grey: recurrent connection (9 years over 9); dark grey: regular connection (5-8 years over 9); black: rare connection (1-4 years over 9) and white: no connection). The values represent the number of larvae arriving on average at a nursery ground from a spawning ground per km² (10^3) over the years for which the model predicts a connection within the period 2003-2011 (weak connection: < 1.10^3 larvae per km²; medium connection: between $1\text{-}100.10^3$ larvae per km²; strong connection: > 100.10^3 larvae per km²). For an explanation of the scenarios and the spawning and nursery codes, see Materials and Methods.*

Finally, for the T2SW scenario, the transport success (Figure 3-6) and the strength of the connections (Figure 3-4 f) increased for the GE nursery ground and decreased for the FR and BE nurseries. For the NL nursery ground, connections from the EC and BC spawning grounds strengthened and connections from the Th and N spawning grounds decreased. Retention decreased (between -49% and -33%), except for the Tha (+ 39%) and GE (+ 5%) nursery grounds. Seeding decreased (between -99% and -32%), except for the NL (+ 64%) and GE (+ 33%) nursery grounds and for the No nursery ground, which remained isolated. The connection frequency decreased at the southernmost nursery grounds (FR, BE, Tha) and increased at the

GE nursery ground (no change for the Dutch and Norfolk nursery grounds). Over the whole domain, retention decreased by 4% and seeding increased by 37%.

3.3.4 Larval recruitment

Overall, MT and PLD exhibited an inverse relationship for all scenarios (when an impact was negative on MT, it was positive on PLD, and *vice versa*; Figure 3-5 a-b, Table 3.3, Table 3-4) and was consistent in space (either positive or negative) for all nurseries (T2) or for all nurseries except No (WS, T2S and T2SW) and differed according to the nurseries for WD. The impact on LR (Figure 3-5 c, Table 3-5) was only consistent in space for T2. LR was impacted much more by all scenarios (except WS) than MT and PLD (see relative differences in Table 3-3, Table 3-4 and Table 3-5).

An increase of wind speed by 4% (WS) had only a limited impact on LR (between -3.1% and 1.5%, Table 3-5) that was not significant compared to the REF run (Figure 3-5 c), whereas a modification of the wind direction (WD) had a moderate impact (between -24.9% and 35.5%, Table 3.5) that was only significant for the No nursery ($P < 0.01$) and at the regional scale ($P < 0.05$) compared to the REF run (Figure 3-5 c). In the WD scenario, LR decreased in the FR and No nursery grounds (Figure 3-5 c, Table 3.5), while LR increased in the other nursery grounds. For the temperature increase of 2°C scenario (T2 Figure 3-5 a-c), not surprisingly, the MT experienced by larvae increased (Table 3.2) and PLD decreased (Table 3.3), both of which were significant for all nursery grounds ($P < 0.001$ for MT, P < 0.001 or $P < 0.01$ according to the nursery areas for PLD). The LR decreased drastically (-58% to -72%, Table 3.5), which might be explained partly by a higher mortality. It decreased significantly compared to the REF run except for the BE nursery (Figure 3-5 c). A temperature increase combined with early spawning (T2S, Figure 3-5 a-c) resulted in a counterintuitive temperature reduction during the pelagic phase except for the No nursery ground (Table 3.2) and hence to an extension of the pelagic phase (Table 3.3). Recruitment decreased in the FR, BE, and No nursery grounds but increased in the NL and Tha nursery grounds (but not significantly compared to the REF simulation, Figure 3-5 c). For the scenario combining all perturbations (T2SW, Figure 3-5 a-c), the model-predicted LR decreased considerably at the FR (-49.6%), BE (-58.4%) and No (-32.8%) nursery grounds and increased slightly at the GE nursery ground (9.6%) and moderately at the NL (35.6%) and Tha (31.0%) nursery grounds (Table 3.5). At the regional scale, the model predicted an increase of PLD (22%) and LR (+9%) and a decrease of MT (-9%). The former seems counterintuitive considering the temperature increase, but it is an outcome of the complexity and non-linearity of processes. In particular, earlier spawning slows down larval development because the average temperature experienced is lower than in the reference run.

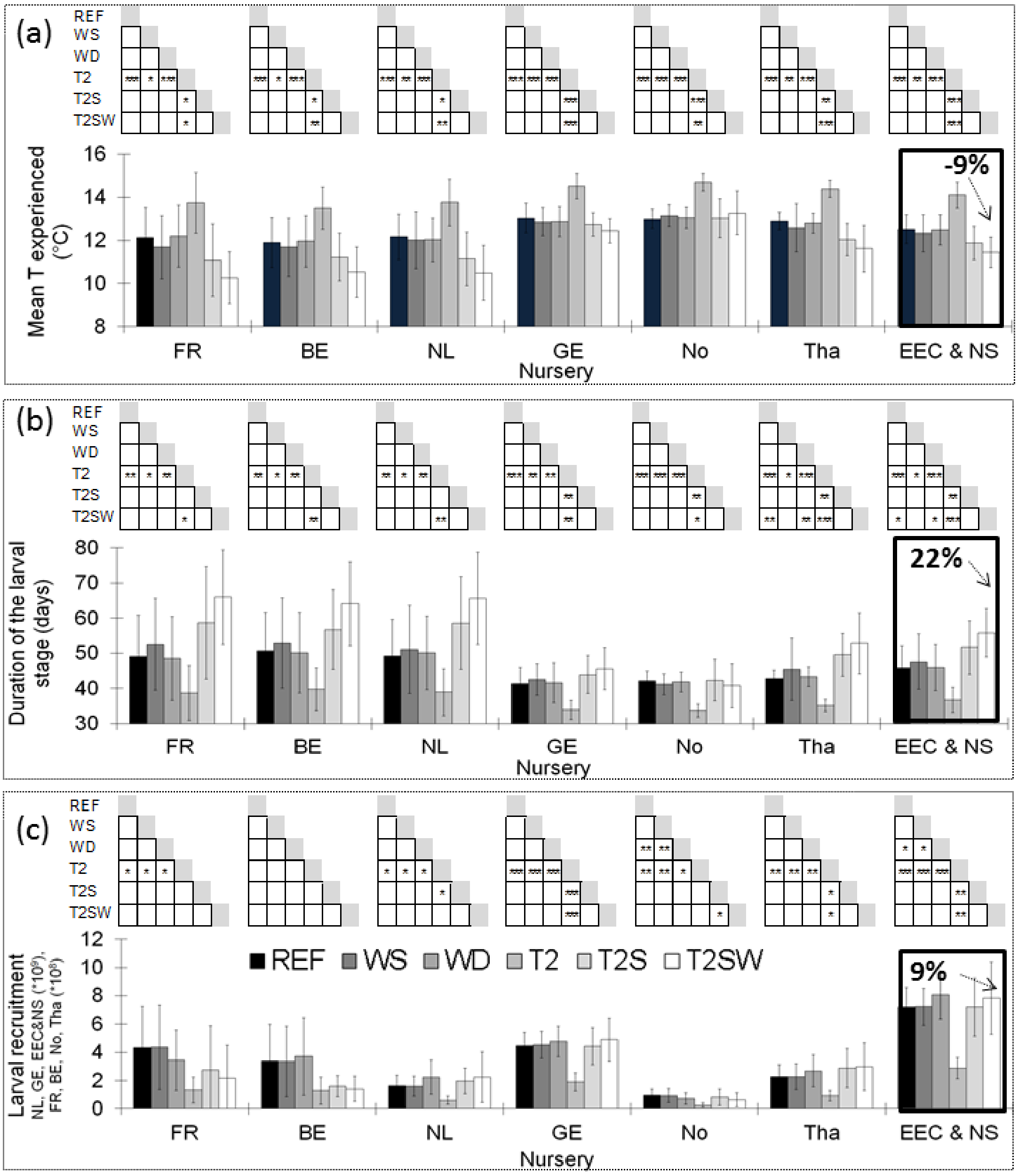


*Figure 3-5: Mean temperature experienced by larvae, MT (a); pelagic larval duration, PLD (b); and larval recruitment at the nursery grounds and at the regional scale, LR (c) for the reference run and the perturbed simulations. The mean covers the period 2003-2011, and the error bars represent the interannual standard deviation. Significant effects between each pair of scenarios are presented in matrices (upper part of the panels) with the following significance levels: '***' (P < 0.001), '**' (P < 0.01), '*' (P < 0.05). For an explanation of the scenarios and nursery codes, see Materials and Methods.*

3.4 DISCUSSION

We used a larval transport model specifically developed for sole and coupled it to a 3D hydrodynamic model of the North Sea to investigate the impact of climate change on larval dispersal, connectivity between spawning and nursery grounds, and nursery recruitment. The model predicts that a climate change scenario involving a temperature increase, earlier spawning and change in wind speed and direction would significantly increase larval recruitment (9%) at the nursery grounds in the year 2040. Retention would decrease by 4%, and seeding would increase by 37%. The model also predicts a large increase in dispersal distance (70%) and PLD (22%).

3.4.1 Model robustness for predicting larval recruitment

There are few options to assess the accuracy of the results except for a test of the correlation with VPA (Lacroix et al., 2013). Here, we compared modelled estimates of recruitment at age-0 and VPA estimates of recruitment at age-1 (ICES, 2015b, 2015a) for the period 1995-2011. Our estimates explained 33% of recruitment variability at the regional scale, which is comparable to the 31% found in Lacroix et al. (2013) over a shorter period (1995-2006). This finding is impressive because the stock-recruitment relationship has poor predictive power, particularly in demersal fish Cury et al. (2014).

3.4.2 Interannual variability

Sole shows considerable recruitment variability (ICES, 2016), which is greater in northern regions and has been linked to winter temperature (Rijnsdorp *et al.*, 1992b). Food limitation, especially at the nursery grounds, determines carrying capacity (Le Pape and Bonhommeau, 2015). However, the recruitment variability of planktonic sole has only been modelled. Here, although a longer period was considered (1995-2011) than in Lacroix et al. (2013) (1995-2006), a comparable high interannual recruitment variability was predicted at the regional (27.2%) and local (between 34% and 78%) scales. We conclude that most of the interannual variability in recruitment is captured within the shorter period of 12 years at the regional and local scales.

A period of 8 to 10 years is representative of the variability in connectivity; it corresponds to the time-scale of the NAO as observed for connectivity patterns in the Baltic Sea (Berglund *et al.*, 2012) and the North Atlantic Ocean (Fox *et al.*, 2006b). A comparison of the connection frequency and the interannual variability of the distance travelled by larvae during the years 2003 to 2011 (REF) and 1995 to 2011 (baseline simulation, results not shown) shows similar values for both periods. The results confirm that a 9-year period suffices to represent the interannual variability of dispersal. Therefore, we focused on a subset of nine years representative of contrasted NAO patterns (2003-2011) to assess the impact of climate change on larval dispersal dynamics.

3.4.3 Dispersal distances and connectivity in the reference simulation

The average NDCM of larval sole is 97 km, which is comparable to juveniles and adults (~95 km) (Burt and Millner, 2008). Larval retention is greater than the arrival of new recruits at most sites; this is a key feature benefiting the long-term persistence of stocks and has been observed in many taxa. Retention depends on local hydrodynamics, larval mortality and the larval precompetency period (Sinclair, 1988; Jones *et al.*, 2005). Additionally, adult migrants and post-larval dispersers contribute to population integrity and shape connectivity patterns and gene flow (Harden Jones, 1968).

Modelling and ecological considerations seem to contradict the homing hypothesis, which states that adult fish tend to be philopatric (Gibson *et al.*, 2015). Some of our modelled populations disperse to adjacent populations over considerable distances (up to 150 km). Two explanations put this in perspective. First, some of the sole spawning grounds are located close to one another and hence have a higher likelihood of exchanging propagules. Second, retention dominates numerically over seeding, such that it is not a question whether philopatry is present or not but to what degree spawners stray between spawning grounds. Empirical measures of population integrity suggest considerable retention. The genetic population patterns of adult sole point to small gradual changes between neighbouring populations, suggesting a dynamic balance between retention and limited dispersal (Cuveliers *et al.*, 2012; Diopere et al., in press). Additionally, the evolutionary distance between population patches of sole has been estimated at 100 km (Kotoulas *et al.*, 1995). This value matches with the modelled ecological dispersal kernel (height of 179 km, width of 68 km) and geographically with the natural distribution of the estuary-linked nursery grounds (Darnaude *et al.*, 2004). This result is not unexpected as it is increasingly accepted that evolutionary and ecological dispersal kernels match (Pinsky *et al.*, 2017). In addition, it supports the idea that the dispersal kernel of marine organisms is species and environment specific, strongly dependent on habitat patch size and generally smaller than initially thought (Pinsky *et al.*, 2012; D'Aloia *et al.*, 2015).

3.4.4 Impact of climate change scenarios

Impact on life-history traits

A modelled temperature increase of 2°C (T2 scenario) shortened PLD by approximately 20%, which is comparable to the ~10-25% shortening in larval duration for reef fish and other organisms (Kendall *et al.*, 2016). Larval fish experience species- and population-specific environmental optima for growth, and temperature has a positive influence on the growth of age-0 sole (Teal *et al.*, 2008). Higher winter temperatures (Becker *et al.*, 1996) and longer seasons have led to increased summer growth in the North Sea.

When extending the modelled growth of sole over the full life cycle, the dynamics of the growth response to temperature and food are, as expected, space and age specific (Teal *et al.*, 2012). Such findings on the effects of temperature on growth and metabolism confirm that climate change may have a considerable impact. Ocean warming substantially affects the aerobic scope and hence growth potential of cold-blooded organisms (Pörtner, 2014; Bozinovic and Pörtner, 2015).

One of the more obvious signs of global change is a shift in larval phenology (Beaugrand *et al.*, 2002; Cetina-Heredia *et al.*, 2015). In our model, spawning of sole occurs an impressive 42 days earlier in 2040. Indeed, four out of seven sole stocks have been shown to spawn considerably earlier over the last four decades (Fincham and Engelhard, 2013), a feature shared by the fish community of the North Sea (Dulvy *et al.*, 2008). The phenomenon is global and has been documented across taxa in continental and aquatic systems (Scheffers *et al.*, 2016; Stephens *et al.*, 2016).

The shift in phenology of sole spawning impacts the match between ichthyoplankton and their food. Planktonic polychaete and mollusc larvae, which feed on algae, represent the core prey of larval sole (Fonds, 1979). Unlike spawning, algal blooms are triggered by wind regimes and light in the North Atlantic Ocean (Wiltshire *et al.*, 2015). The widening rift between spawning and plankton blooms raises considerable concerns for the long-term survival of flatfish (Duffy-Anderson *et al.*, 2015) and roundfish (Beaugrand *et al.*, 2003).

The slower development of larvae in the scenario of an increased temperature regime seems counterintuitive, but it is a direct consequence of warming waters in spring. As adult fish spawn earlier, their progeny experience the lower water temperatures at that time of the year.

Impact on larval dispersal and connectivity

Our biophysical model predicted an average shortening of pelagic larval duration by 20% due to the rising sea water temperature (scenario T2). Empirical evidence points to the speeding up of development in poikilotherms under a regime of higher temperatures (Green and Fisher, 2004; see also Byrne, 2012).

In the scenario combining all perturbations, the model predicted an increase of the north-eastward NDCM and a prolongation of the trajectories for all spawning grounds. At the regional scale, the model predicted a substantial increase of the distance travelled by sole larvae in the T2SW scenario (70%). While the change in larval dispersal distance may be general, the direction and extent of the change was variable. Projected larval dispersal of the dusky grouper Epinephelus marginatus decreased by 10% in the Mediterranean Sea due to warming (Andrello *et al.*, 2015). This value is comparable to a similar decrease (-6%) in sole for the T2 scenario. The supply of eastern rock lobster Sagmariasus verreauxi larvae to the coast dropped (-4%), while the settlement peak shifted considerably poleward (approximately 270 km), largely due to a change in ocean currents (Cetina-Heredia *et al.*, 2015).

An increase of the south-westerly wind (WD scenario) impacted not only larval abundance but also connection frequency, which tended to decline gradually from north to south. The consequence of a T2SW scenario on connectivity was inconsistent among nursery grounds; half of the connections were strengthened and half weakened, while retention decreased for two-thirds of the nursery grounds. At the regional scale, the model predicted a decrease in retention (4%) and an increase in seeding (37%) but a decrease of both (60%) in the case of scenario T2. By comparison, Kendall et al. (2016) predicted a weakening of ~65% in connections due to temperature change and an average domain-wide increase of ~1-3% in retention for coral reef fish and other organisms. Andrello et al. (2015) found a 3% decrease of continental shelf seeding and a 5% increase in larval retention by considering the additive effects of changes in hydrodynamics and warming (larval growth and spawning timing) 100 years in the future. Cetina-Heredia et al. (2015) predicted an ~4% decrease in settlement as a consequence of the counteracting effects of current strengthening and warming. Hence, demographic consequences are typically negative. Changes due to temperature evolve in the same direction, but if changes in phenology are included, the results vary more.

The changing larval dispersal is set within a heterogeneous landscape, a key factor in sustaining metapopulation structure and viability (Hanski, 1998; Kritzer and Sale, 2004). Changing abundances and patterns of retention and seeding of larvae will influence survival and affect the long-term persistence of populations through source-sink dynamics (Duffy-Anderson *et al.*, 2015).

Impact on recruitment

Stage- specific larval mortality of fish larvae depends on the proportion between the instantaneous mortality rate and weight-specific growth as well as body size (Houde, 1997). Therefore, changes in growth will affect condition, survival and recruitment to the nursery grounds. These effects are measurable in our model, which is based on temperature-sensitive growth parameterisation, through a 9% increase in recruitment in the T2SW scenario.

Considering the impact of each perturbation one at a time is useful for assessing and understanding the specific effect; but even then, predicting consequences remains challenging. For instance, in the current study, a water temperature increase led to a considerable decrease in PLD (-20%); theoretically, this should increase retention (Teal *et al.*, 2008; Fincham and Engelhard, 2013). However, SST increase also resulted in higher mortality, which in turn reduced retention dramatically. Moreover, SST increase resulted in advanced spawning (Kristiansen et al., 2014). In the current study, when spawning occurred earlier, the MT experienced by the larvae decreased, even with a 2°C SST increase. When wind perturbations were included in the model, the total impact was far from the sum of each impact. As highlighted by Lett et al. (Lett *et al.*, 2010), interactions between perturbations can be important, and all expected perturbations should be considered (and combined) when biophysical models are used to predict the impact of climate change. In addition, cumulative effects of IBM models are non-linear (Brochier *et al.*, 2013; Andrello *et al.*, 2015). Hence, the impacts of the drivers of overall increased recruitment in the North Sea are strongly dependent on the intensity of climate change and the secondary effects on ocean currents and metabolism.

Consequences for management

Computer-based simulations are a well-accepted tool for predicting global change and developing scenarios (IPCC, 2013), but scenario testing in the marine realm represents a rather recent development (Boyen *et al.*, 2012). This approach is effective for guiding the design of marine protected areas (MPAs) (Berglund *et al.*, 2012; Guizien *et al.*, 2012; Andrello *et al.*, 2015). Patchiness and connectivity are critical elements in population dynamics and hence in the design of MPAs. Flatfish are highly sensitive to climate change as their open life cycle shapes long-term survival (Petrik *et al.*, 2015). MPAs should consider the patchy distribution of nursery grounds of flatfish and the variable dispersal distances of larvae. These factors argue in favour of an integrated seascape approach to understanding population and range dynamics (Razgour, 2015). If done thoughtfully, conservation plans can effectively protect highly vulnerable ecosystems (Queiros *et al.*, 2016).

The climate change scenario considering all perturbations predicts that larval recruitment and connection frequency decrease at some sites but not everywhere, albeit incongruently. This enhanced variability with greater chances for retention (at some sites) fits with observations on plaice in the North Sea (Hufnagl *et al.*, 2013) and on tropical reefs (Kendall *et al.*, 2016). The broad range of factors affecting recruitment success, among which spawner size is crucial in affecting local replenishment, determines the non-linear behaviour of the marine ecosystem (Rijnsdorp and Witthames, 2005; Saenz-Agudelo *et al.*, 2015). However, the relative strengths of these factors and their impacts on the ecosystem remain difficult to predict. Our model is foremost semi-qualitative and could be further developed for key biological traits. For example, SSB determines propagule abundance, settlement success and recruitment. Savina et al. (2016) included SSB information on sole and found population-specific dynamics. The natural mortality rate of sole is poorly studied, but recruitment values vary considerably among years (ICES, 2016). Age-specific energy budgets determine growth and survival (Teal et al., 2008). Finally, multi-generational adaptive evolution due to environmental and anthropogenic drivers reshapes populations (Fronhofer *et al.*, 2015).

The North Sea sole stock has crossed the precautionary reference threshold following recovery from unsustainable exploitation (ICES, 2016). Although the fishery is currently sustainable, assessments do not consider a change in recruitment due to climate change (Pershing *et al.*, 2015). When meeting the 1.5°C global warming target, most fisheries are expected to change

(Cheung *et al.*, 2015). Therefore, connected ecological networks at the regional scale are essential to buffer against growing population isolation (Noss and Daly, 2006).

3.4.5 Conclusions

The strategy of fish to reproduce at selected spawning grounds and to have the progeny develop at spatially distinct nursery grounds is liable to climate-induced impacts on connectivity, the timing of spawning and development. These factors have measured and modelled downstream effects on local distributions (Dulvy *et al.*, 2008), productivity (Engelhard *et al.*, 2011)and cohort strength (ICES, 2016). The modelled changes in fish biology due to climate change are considerable, regardless of the many other factors that affect fish throughout their life cycle, such as changes in community composition (Alvarez-Fernandez *et al.*, 2015), evolutionary adaptation due to truncated age-frequency distributions (Mollet *et al.*, 2013a) and overexploitation (Cheung *et al.*, 2013).

3.5 APPENDIX

Table 3-1 : Date of peak spawning (Julian days from 1st of January) computed as the mean over the spawning area of the first day where a temperature of 10°C is reached for each year within the period 1995-2011 and for the reference simulation and the scenarios where early spawning is considered (SST increase of 2°C) scenario T2S and T2SW. Spawning areas are presented in Fig. 1a. A value of zero means that a temperature of 10°C would already have been reached by the 1st of January. In that case, the peak spawning date is chosen on January 1st.

	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Reference simulation																	
EC	115	141	118	84	110	119	124	105	119	107	99	126	24	98	112	138	105
BC	117	140	119	119	112	116	126	112	119	112	119	124	8	119	112	140	105
Tx	126	149	127	119	119	124	131	117	124	119	126	126	98	124	110	138	122
GB	130	151	135	123	130	122	132	126	124	120	131	127	111	120	115	140	117
N	134	154	133	132	132	133	140	139	126	140	139	133	126	133	130	140	125
Th	119	135	119	115	112	119	132	112	119	112	122	122	105	119	112	134	108
Early spawning (SST + 2°C) – simulations T2S and T2SW																	
EC	6	67	73	0	0	38	0	50	0	24	0	18	0	9	71	37	79
BC	26	119	71	3	9	46	76	35	53	36	22	105	0	26	98	40	92
Tx	110	132	115	82	99	106	113	80	105	95	0	105	0	105	99	109	105
GB	114	135	123	112	109	113	121	107	112	107	112	115	96	112	102	115	104
N	105	130	95	78	110	112	126	98	112	112	119	119	67	119	112	114	105
Th	58	110	77	6	61	75	98	59	63	35	84	100	0	70	95	106	92

*Table 3-2: Mean statistics in net dispersal of the centre of mass (NDCM) for the reference and perturbed simulations (2003-2011). Mean (km) and stdev (km) of NDCM, relative difference (%) of NDCM between perturbed and reference simulations [(NDCM_perturbed-NDCM_REF)/NDCM_REF*100] and interannual coefficient of variation (CV) [Stdev/mean*100] at the six nursery grounds. For details on the spawning grounds and scenario codes see Materials and Methods respectively.*

Simulation	EC	BC	Tx	GB	N	Th
Reference run (REF)						
Mean	150	126	110	45	93	60
Stdev	52.2	66.8	33.1	27.8	19.5	32.1
CV (%)	35	53	30	62	21	53
Wind speed + 4% (WS)						
Mean	151	126	106	44	92	60
Stdev	54.9	69.9	35.6	28.1	19.9	33.6
Relative difference (%)	0.3	-0.2	-3.3	-2.2	-0.4	0.5
CV (%)	36	56	34	64	22	56
Wind direction + SW (WD)						
Mean	192	165	136	51	101	89
Stdev	61.5	77.7	31.9	23.7	22.3	35.9
Relative difference (%)	27.6	30.8	23.8	14.5	9.2	48.5
CV (%)	32	47	23	46	22	40
SST + 2°C (T2)						
Mean	148	112	102	43	83	58
Stdev	50.4	51.8	36.8	24.9	18.6	37.2
Relative difference (%)	-1.5	-10.9	-7.1	-4.7	-10.4	-2.8
CV (%)	34	46	36	58	22	64
SST + 2°C & early spawning (T2S)						
Mean	207	184	153	47	95	105
Stdev	69.4	73.0	50.7	23.3	19.6	57.6
Relative difference (%)	37.9	45.9	39.5	5.2	2.2	74.5
CV (%)	33	40	33	49	21	55
All perturbations (T2SW)						
Mean	286	243	173	49	101	143
Stdev	91.0	77.1	54.5	23.1	22.1	76.4
Relative difference (%)	90.4	92.4	57.5	10.0	9.0	137.6
CV (%)	32	32	32	47	22	53

*Table 3-3: Mean statistics for temperature experienced by the larvae (MT) for the reference and perturbed simulations (2003-2011). Mean (°C) and stdev (°C) of MT, relative difference (%) of MT between perturbed and reference simulations [(MT_perturbed-MT_REF)/MT_REF*100] and interannual coefficient of variation (CV) [Stdev/mean*100] at the six nursery grounds. For details on the nursery grounds and scenario codes see Materials and Methods respectively.*

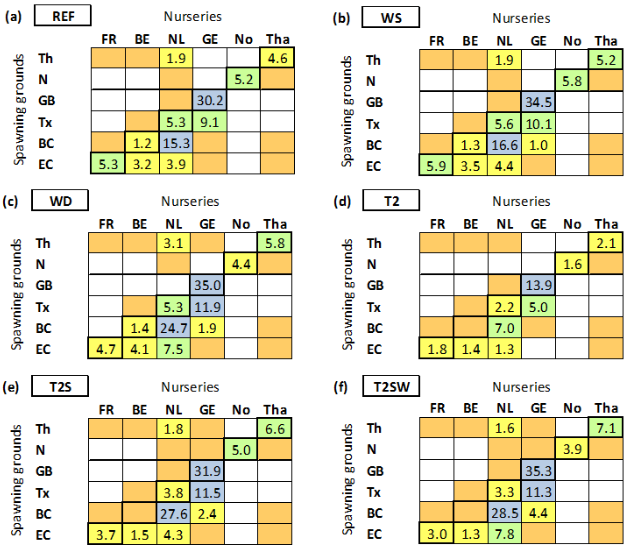
Simulation	FR	BE	NL	GE	No	Tha
Reference run (REF)						
Mean	12.1	11.9	12.2	13.0	13.0	12.9
Stdev	1.4	1.2	1.1	0.7	0.4	0.4
CV (%)	12	10	9	5	3	3
Wind speed + 4% (WS)						
Mean	11.7	11.7	12.0	12.9	13.2	12.6
Stdev	1.5	1.4	1.3	0.6	0.5	1.1
Relative difference (%)	-3.6	-1.9	-1.3	-1.4	1.1	-2.4
CV (%)	13	12	11	5	4	9
Wind direction + SW (WD)						
Mean	12.2	12.0	12.0	12.9	13.1	12.8
Stdev	1.4	1.2	1.0	0.7	0.5	0.5
Relative difference (%)	0.6	0.4	-1.2	-1.3	0.4	-0.8
CV (%)	12	10	8	5	4	4
SST + 2°C (T2)						
Mean	13.7	13.5	13.8	14.5	14.7	14.4
Stdev	1.4	1.0	1.1	0.6	0.4	0.4
Relative difference (%)	13.4	13.3	13.1	11.3	13.0	11.5
CV (%)	10	7	8	4	3	3
SST + 2°C & early spawning (T2S)						
Mean	11.1	11.2	11.1	12.7	13.0	12.0
Stdev	1.7	1.1	1.2	0.5	0.9	0.8
Relative difference (%)	-8.5	-5.8	-8.4	-2.3	0.2	-6.7
CV (%)	15	10	11	4	7	6
All perturbations (T2SW)						
Mean	10.3	10.5	10.5	12.4	13.3	11.6
Stdev	1.2	1.2	1.3	0.6	1.0	1.1
Relative difference (%)	-15.4	-11.6	-13.7	-4.5	2.1	-10.0
CV (%)	12	11	12	5	8	9

*Table 3-4: Mean statistics for pelagic larval duration (PLD) for the reference and perturbed simulations (2003-2011). Mean (day) and stdev (day) of PLD, relative difference (%) of PLD between perturbed and reference simulations [(PLD_perturbed-PLD_REF)/PLD_REF*100] and interannual coefficient of variation (CV) [Stdev/mean*100] at the six nursery grounds. For details on the nursery grounds and scenario codes Materials and Methods respectively.*

Simulation	FR	BE	NL	GE	No	Tha
Reference run (REF)						
Mean	49	51	49	41	42	43
Stdev	12	11	10	5	3	2
CV (%)	24	22	21	11	6	6
Wind speed + 4% (WS)						
Mean	53	53	51	43	41	45
Stdev	13	13	13	4	3	9
Relative difference (%)	7.1	4.7	3.9	2.9	-2.4	6.1
CV (%)	25	24	25	10	7	20
Wind direction + SW (WD)						
Mean	48	50	50	42	42	43
Stdev	12	11	10	6	3	3
Relative difference (%)	-1.1	-0.8	1.9	0.7	-0.9	1.2
CV (%)	25	23	21	14	7	6
SST + 2°C (T2)						
Mean	39	40	39	34	34	35
Stdev	8	6	7	3	2	2
Relative difference (%)	-21.1	-21.3	-20.8	-18.0	-20.2	-18.1
CV (%)	20	15	17	8	5	5
SST + 2°C & early spawning (T2S)						
Mean	59	57	59	44	42	50
Stdev	16	11	13	5	6	6
Relative difference (%)	19.7	12.3	19.3	6.1	0.3	15.7
CV (%)	27	20	23	12	14	12
All perturbations (T2SW)						
Mean	66	64	66	46	41	53
Stdev	13	12	13	6	6	9
Relative difference (%)	34.5	26.7	33.4	10.2	-3.3	23.3
CV (%)	20	19	20	13	15	16

*Table 3-5 Mean statistics for larval abundance at the nursery grounds (larval recruitment, LR) for the reference and perturbed simulations (2003-2011). Mean (# larvae, 10^8) and stdev (# larvae, 10^8) of LR, relative difference (%) of LR between perturbed and reference simulations [(LR_perturbed-LR_REF) /LR_REF*100] and interannual coefficient of variation (CV) [Stdev/mean*100] at the six nursery grounds. For details on the nursery grounds and scenario codes see Materials and Methods respectively.*

Simulation	FR	BE	NL	GE	No	Tha
Reference run (REF)						
Mean	4.32	3.37	16.43	44.64	0.95	2.27
Stdev	2.92	2.62	7.31	9.57	0.46	0.86
CV (%)	68	78	45	21	48	38
Wind speed + 4% (WS)						
Mean	4.35	3.36	15.91	45.30	0.94	2.28
Stdev	2.98	2.49	7.17	9.53	0.50	0.91
Relative difference (%)	0.8	-0.3	-3.1	1.5	-0.8	0.8
CV (%)	68	74	45	21	53	40
Wind direction + SW (WD)						
Mean	3.44	3.72	22.27	47.71	0.71	2.68
Stdev	2.14	2.75	12.16	10.90	0.41	1.13
Relative difference (%)	-20.2	10.1	35.5	6.9	-24.9	18.5
CV (%)	62	74	55	23	58	42
SST + 2°C (T2)						
Mean	1.32	1.28	6.01	18.94	0.26	0.92
Stdev	0.91	0.95	2.76	6.45	0.14	0.36
Relative difference (%)	-69.5	-62.0	-63.4	-57.6	-72.3	-59.3
CV (%)	69	74	46	34	55	39
SST + 2°C & early spawning (T2S)						
Mean	2.74	1.59	19.75	44.21	0.81	2.88
Stdev	3.13	0.75	9.07	13.11	0.57	1.37
Relative difference (%)	-36.6	-52.8	20.2	-1.0	-14.1	27.0
CV (%)	114	47	46	30	70	48
All perturbations (T2SW)						
Mean	2.18	1.40	22.27	48.92	0.64	2.97
Stdev	2.33	0.90	17.82	15.34	0.47	1.69
Relative difference (%)	-49.6	-58.4	35.6	9.6	-32.8	31.0
CV (%)	107	64	80	31	74	57



(a) REF

Spawning grounds	FR	BE	NL	GE	No	Tha
Th	🟧	🟧	1.9			4.6
N			🟧		5.2	🟧
GB			🟧	30.2		
Tx		🟧	5.3	9.1		
BC	🟧	1.2	15.3	🟧		🟧
EC	5.3	3.2	3.9	🟧		🟧

(b) WS

Spawning grounds	FR	BE	NL	GE	No	Tha
Th	🟧	🟧	1.9			5.2
N			🟧		5.8	🟧
GB			🟧	34.5		
Tx		🟧	5.6	10.1		
BC	🟧	1.3	16.6	1.0		🟧
EC	5.9	3.5	4.4	🟧		🟧

(c) WD

Spawning grounds	FR	BE	NL	GE	No	Tha
Th	🟧	🟧	3.1	🟧		5.8
N			🟧		4.4	🟧
GB				35.0		
Tx		🟧	5.3	11.9		
BC		1.4	24.7	1.9		🟧
EC	4.7	4.1	7.5	🟧		🟧

(d) T2

Spawning grounds	FR	BE	NL	GE	No	Tha
Th	🟧	🟧	🟧			2.1
N					1.6	🟧
GB			🟧	13.9		
Tx		🟧	2.2	5.0		
BC	🟧	🟧	7.0	🟧		🟧
EC	1.8	1.4	1.3			🟧

(e) T2S

Spawning grounds	FR	BE	NL	GE	No	Tha
Th	🟧	🟧	1.8	🟧		6.6
N			🟧	🟧	5.0	🟧
GB			🟧	31.9		
Tx		🟧	3.8	11.5		
BC	🟧	🟧	27.6	2.4		🟧
EC	3.7	1.5	4.3	🟧		🟧

(f) T2SW

Spawning grounds	FR	BE	NL	GE	No	Tha
Th	🟧	🟧	1.6	🟧		7.1
N			🟧	🟧	3.9	🟧
GB			🟧	35.3		
Tx		🟧	3.3	11.3		
BC	🟧	🟧	28.5	4.4		🟧
EC	3.0	1.3	7.8	🟧		🟧

*Figure 3-6 Connectivity matrix (transport success) between spawning grounds (rows) and nursery grounds (columns) for the reference simulation (a) and the five scenarios (b)-(f). (a) The numbers represent the transport success, which is the percentage of larvae arriving on average at a nursery ground from a spawning ground (%, *10-3) for the period 2003-2011. Colour code: white: no connection, orange: < 1*10-3%, yellow: 1-5*10-3%, green: 5-10*10-3%, blue: > 10*10-3%. For details on the scenarios, spawning and nursery codes see Materials and Methods.*

Chapter 4. THE PROPORTION OF FLATFISH RECRUITMENT IN THE NORTH SEA POTENTIALLY AFFECTED BY OFFSHORE WIND FARMS

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4.1 INTRODUCTION

The capacity and number of offshore wind farms (OWFs) is increasing in European waters due to the growing demand for renewable energy. Many are either operational, under construction or planned for (Lindeboom *et al.*, 2015; OECD, 2016). The European Union has set the target to have 20% of all energy needs covered by renewables by 2020 (Renewable Energy Directive 2009/28/EC). In this context, the recent widescale extension of OWFs in the southern and central North Sea is of particular significance (Kalaydjian and Girard, 2017). However, the installation of thousands of turbines covering wide areas of the central and southern North Sea (OSPAR Commision, 2014, see Figure 4-1) in the near future across the entire North Sea raises questions about the environmental impact and the effects on the marine ecosystem (Petersen and Malm, 2006; Bergström *et al.*, 2013, 2014).

Several studies have highlighted the effects of OWFs during the construction, operation and decommissioning phases (Petersen and Malm, 2006; Bergström *et al.*, 2014). While impacts relating to the construction phase are significant, they occur over a relatively short time span (Vaissière *et al.*, 2014). Given the short time span involved, Wilhelmsson (2010) suggested that the perturbation is most likely to be of an acceptable level. Other impacts however persist throughout the lifespan of the OWFs. These include underwater sound related to gearbox vibrations and shipping traffic (Nedwell and Howell, 2004; Wahlberg and Westerberg, 2005), electromagnetic fields (Gill *et al.*, 2012) and alterations in the local hydrodynamic conditions (Broström, 2008). Major effects are linked to the introduction of hard substrates in sandy or muddy habitats, increasing the local habitat heterogeneity and providing substrates for fouling organisms. This phenomenon is known as the ‘artificial reef effect’ (Petersen and Malm, 2006; Langhamer, 2012; De Mesel *et al.*, 2015). Additionally, OWFs may limit fisheries related activities. A reduction in the deployment of towed fishing gear decreases the disturbance of benthic communities and may facilitate the recovery of previously disturbed communities (Leonhard *et al.*, 2011; Lindeboom *et al.*, 2011; Wilhelmsson and Langhamer, 2014), creating new opportunities for organisms such as fish.

Both OWFs and other artificial hard substrates have been reported to attract and concentrate fish (Bohnsack, 1989; Pickering and Whitmarsh, 1997; Leitão *et al.*, 2008, 2009), which find shelter against currents, predators, human-induced and natural stressors (e.g: Langhamer, 2012; Reubens *et al.*, 2014; Wilhelmsson and Langhamer, 2014) and an increase in food provision (Pike and Lindquist, 1994; Fabi *et al.*, 2006; Leitão *et al.*, 2007). This behaviour is known to fishermen who increase their fishing effort in the vicinity of artificial hard structures such as oil and gas pipelines in the North Sea (Rouse *et al.*, 2018). Several studies have indicated an increase in abundances of fish close to OWFs, including commercially important species such as Atlantic cod (*Gadus morhua*) and pollock (*Pollachius pollachius*) (Bergström *et al.*, 2013; Stenberg *et al.*, 2015). The concentration of adult fish around wind farm could increase eggs production in OWF areas. OWFs are also known for their positive impact on flatfish biomass as predicted by a modelling study in the Eastern English Channel (Raoux *et al.*, 2017) and illustrated by an apparent size increase of European plaice (*Pleuronectes platessa)* in Belgian OWFs (Vandendriessche *et al.*, 2015). Furthermore, general increases in flatfish density have been observed around artificial structures in the North West Atlantic (Walton, 1982). The closure of fishing grounds, a general practice in OWFs, has had a positive impact on the egg production of turbot (*Scophthalmus maximus*) in the Baltic Sea (Florin *et al.*, 2013).

Fisheries management requires an understanding of the present and prediction of the future state of the environment, including the future state of fish populations after the introduction of OWFs. Many studies have addressed the question of the impact of OWFs on the ecosystem but most of them focus on local scale effects. However, local scale effects may have knock-on effects at the population level. This spill-over effect can be either positive as in the case of marine protected area (Stobart *et al.*, 2009; Abecasis *et al.*, 2014) or negative in the case of nursery habitat degradation (Rochette *et al.*, 2010b). From an ecosystem functioning perspective, these local studies must be extrapolated to the wider environment, e.g. the North Sea at large. One route to achieve such spatial extrapolation is via a modelling approach, which can provide valuable insights into the potential impact of OWFs onto species-specific population dynamics.

In this context, North Sea flatfishes form an interesting group of species to model. In addition to their high economic value, flatfishes have a complex bentho-pelagic life cycle spanning broad geographical scales. There is high potential for interaction with OWFs during their different life stages, each of which involving spatially distinct habitats. During the adult phase, despite differences among species, most migration occurs between feeding and spawning grounds (Gibson, 1997; Hunter *et al.*, 2003), and the effects of OWFs may differ in each of these areas. For some flatfish, such as European plaice, the feeding and spawning grounds are located at different sites. Feeding grounds with increased macrobenthic biomass, for example as a consequence of the presence of OWFs (Coates *et al.*, 2016), could positively impact the fish' condition, while spawning grounds may be strongly impacted by fisheries restrictions, as it has been shown for temporal closure during spawning season (van Overzee and Rijnsdorp, 2014). Indeed, the fishing pressure is higher for target species such as common sole (*Solea solea*) or European plaice due to spawning aggregations. Flatfish produce a large number of eggs, with variable but generally low chances of survival (Juanes, 2007; Le Pape and Bonhommeau, 2015). Large variations in recruitment are at least partially due to the sensitivity of larval survival to environmental conditions and hydrodynamics, which may explain the current lack of stock-recruitment relationships in many exploited fish species (Houde, 2008; Cury *et al.*, 2014). Finally spawning grounds, due to their role in connectivity and recruitment, can be considered a critical habitat for flatfish.

Settlement is not directly related to the number of eggs spawned because of a pelagic larval phase with recruitment constraints at the nursery grounds. In the present study, a model is used to investigate how OWFs throughout the southern and central North Sea, whatever their stage (operational, under construction or planned), may spatially interfere with the population dynamics of flatfish. The study focuses on the ontogenetic phases of the early life cycle because of its important role in the population dynamics. The general aim of this study represents a first step to quantify the potential impact of OWFs on population dynamics. The specific aims are to assess (1) the proportion of overlap between spawning grounds and OWFs, (2) the proportion of settlers originating from (realised and planned) OWFs, (3) the potential connectivity between OWFs and nursery grounds, and (4) how the expansion of OWFs across the North Sea may spatially affect flatfish nursery grounds.

4.2 MATERIALS AND METHODS

4.2.1 Research strategy

The spatial overlap in spawning grounds and the consequent arrival of settlers from (realised and planned) OWFs at the nursery grounds can be used to study the likelihood that an OWF affects flatfish populations. The use of biophysical models is considered a valid methodology to study connectivity and settlement of early pelagic life stages in the open ocean for two reasons (Miller, 2007; Pineda *et al.*, 2007; Cowen and Sponaugle, 2009). First, a direct observation of fish eggs and larvae trajectories is difficult in the open ocean and secondly, direct or indirect tagging such as genetics or otolith microchemistry have a limited power to spatially track fish recruits in a well-mixed sea such as the North Sea. For the present purpose, the Lagrangian larval transport model LARVAE&CO (Lacroix *et al.*, 2013a), resulting from the coupling between a hydrodynamical model and an Individual-Based Model (IBM), was used to simulate the dispersal of early life stages of flatfish. This model has shown to explain a significant part (31%) of recruitment variability of sole in the North Sea (Lacroix *et al.*, 2013a). The simulations were carried out for a 10-year period (1997-2006), in order to span most of the year-to-year variability over the typical timescale of the North Atlantic Oscillation (NAO) cycle (Berglund *et al.*, 2012).

4.2.2 Study area

The Eastern English Channel and the southern and central North Sea are shallow coastal seas, and the currents are mainly generated by tides and wind. The general circulation pattern is oriented from South to North (Turrell, 1992), with some interannual variability in the flow field related to the NAO in addition to strong seasonal variability. For the sake of this study the extent and distribution of existing and planned OWFs were extracted from the OSPAR data base on offshore wind farms (OSPAR Commision, 2014). This study addresses all OWF stages (operational, under construction or planned), distributed over nine geographic sectors of interest (Figure 4-1).

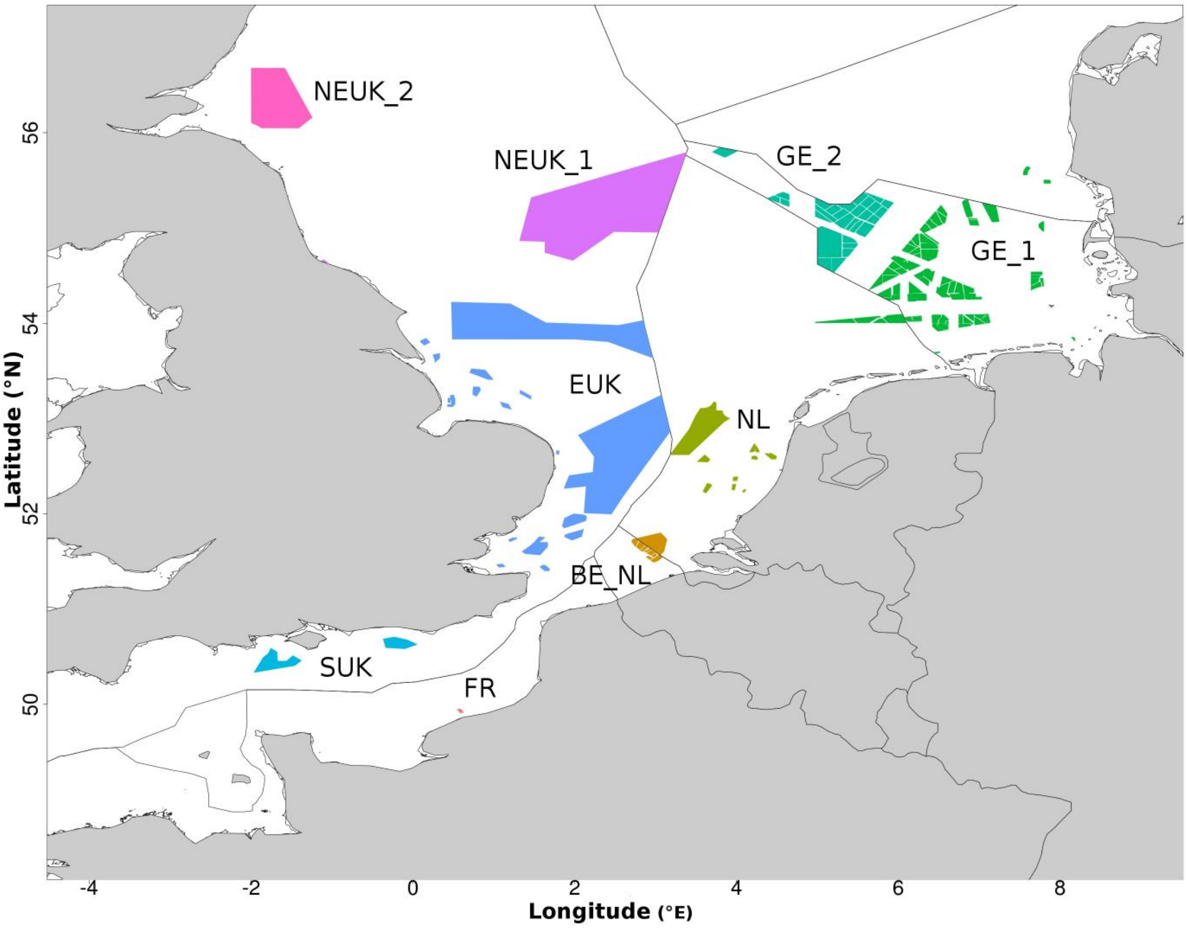

Figure 4-1 Spatial distribution of offshore wind farms (OWFs; all stages) in the southern and central North Sea (from OSPAR 2014). OWFs are grouped by geographic sector: France (FR), Belgium-Netherlands (BE_NL), the Netherlands (NL), Germany 1 (GE_1), Germany 2 (GE_2), South UK (SUK), East UK (EUK), North-East UK 1 (NEUK_1) and North-East UK 2 (NEUK_2).

4.2.3 Species of interest

This study focuses on the six most exploited flatfish species in the North Sea: turbot (*Scophthalmus maximus L.*), brill (*Scophtalmus rhombus L.*), common sole (*Solea solea L.*), common dab (*Limanda limanda L.*), European plaice (*Pleuronectes platessa L.*) and European flounder (*Platichthys flesus L.*). Hereafter, common sole, common dab, European flounder and European plaice will be referred to as sole, dab, flounder and plaice, respectively.

The six flatfish species display a wide range of life history traits related to growth (e.g. pelagic larval duration), behaviour and reproduction strategy (e.g. spawning period and spawning distribution, see Chapter 2), which impact larval drift (Cowen *et al.*, 2007; Pineda *et al.*, 2007).

Nursery grounds are mostly located in shallow coastal waters associated with soft sediments. Nursery grounds are species-specific, based on bathymetry and sediment type (see in supplementary material) and further divided in six areas according to national boundaries (France, Belgium, the Netherlands and German Bight) and two geographically separated nurseries in the United Kingdom (Norfolk and Thames estuary). In addition, the Dogger Bank, which is an important offshore nursery for dab and plaice, was included in the Norfolk nursery ground.

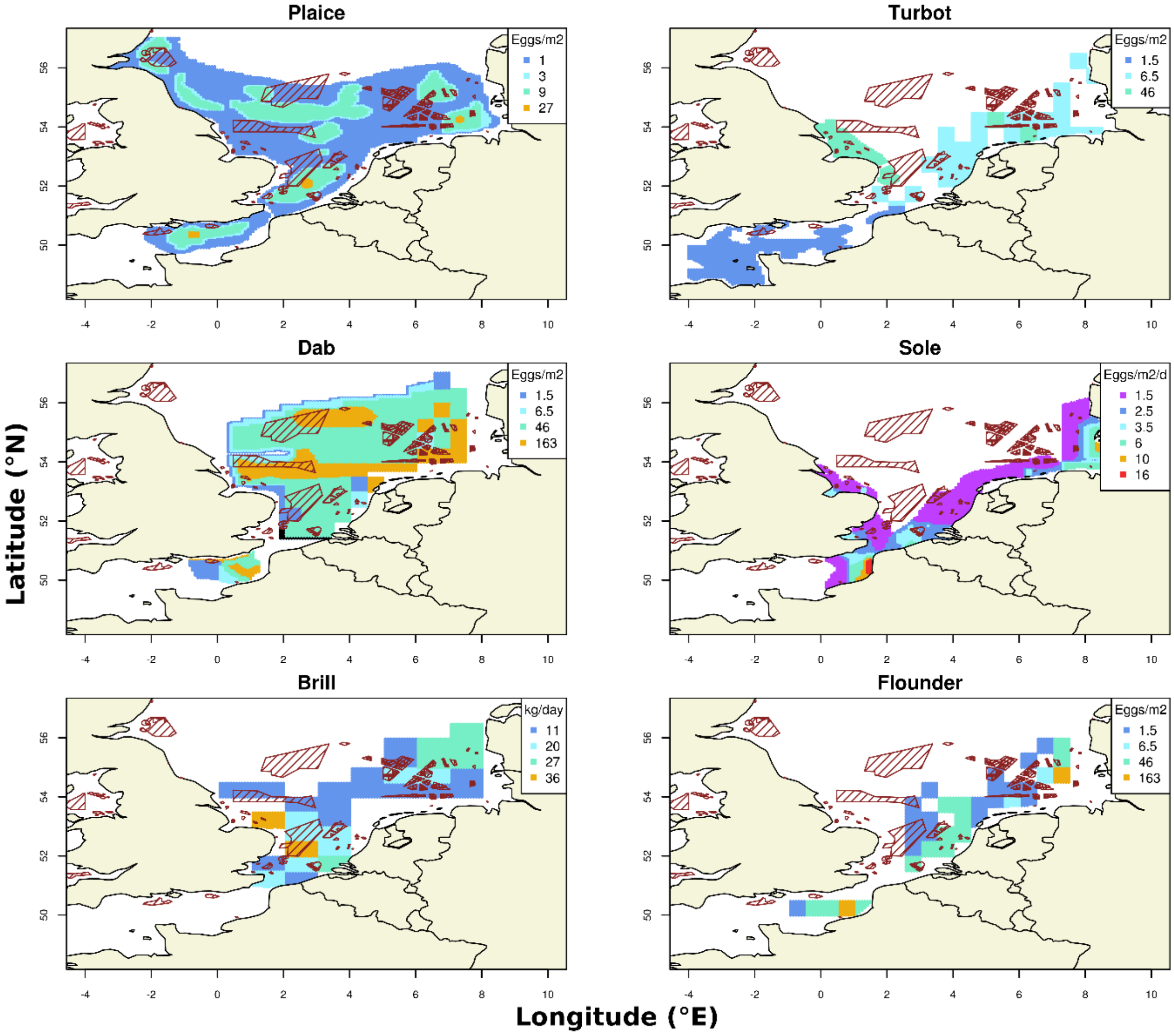

Figure 4-2 Overlap between the distribution of the spawning grounds of the six flatfish (turbot (Egg/m2), brill (kg/day), sole (Egg/m2/day), dab (Egg/m2), plaice (Egg/m2) and flounder (Egg/m2)) species and offshore wind farms (red polygons).

4.2.4 Modelling of the early life stage

The hydrodynamic model and individual-based model

The model used for the 6 species was detailed in Chapter 2. .

Analysis

We assume that the production of eggs has a one to one relationship with the spawning ground surface area and spawning distribution (Figure 4-2). The overlap between the geographic distribution of the spawning grounds and (planned and existing) OWFs is consequently expected to show a one to one relationship with the proportion of eggs spawned in areas with OWFs. The dispersal model was used to assess how much the dispersal and settlement success of flatfish are likely to be affected by OWFs over a 10 years period. The proportion of settlers at a given spawning location originating from OWFs is the relative contribution of settlers originating from OWFs to the total number of settlers in a given spawning ground. Finally, to assess the eventual repercussion of a change in egg production inside OWF areas on settlement, four scenarios were tested. These scenarios consider an hypothetical change of egg production of-20%, +10%, +25% and +50% inside the OWFs and an absence of change outside. No change in the spatial distribution of eggs was considered in these scenarios.

4.3 RESULTS

Contribution of spawning events in offshore wind farms to total egg production and recruitment

The proportion of eggs spawned in the areas with OWFs varies among species (Table 4-1). Dab, which has the largest spawning ground (see Figure 4-2) of the six selected species, present the highest level of overlap: 16.7% of the eggs produced in the model domain by this species will be derived from an area where OWFs are or will be present in the near future. Plaice has a large spawning ground but showed a lower level of overlap with OWFs (about 9%). The spawning distribution of brill showed likewise a 15% of overlap with OWF areas whereas turbot presented a lower level. Flounder and sole, which spawn in more coastal waters, present the lowest level of spatial overlap with OWFs (around 3%).

The six species displayed interannual variation in the mean arrival of settlers from OWFs at the nursery grounds for the period 1997-2006 (Table 4-1 and Figure 4-3). Dab showed the highest proportion of settlers originating from OWFs compared to the other species (16.1%). For brill and plaice this proportion was lower while turbot, flounder and sole showed the lowest level of larval arrivals from OWFs (about 2% of the settlers).

Table 4-1 Proportion of eggs spawned in realised and planned offshore wind farms (OWFs) for the different species and mean, minimum, maximum and standard deviation of the proportion of settlers originating from OWFs during the period 1997-2006.

Species	Proportion of spawning in OWFs (%)	Proportion of settlement from OWFs (%)			
		Mean	Min	Max	Sd
Plaice	9.4	8.9	7.4	10.3	0.97
Turbot	9.5	2.2	1.3	3	0.6
Dab	16.7	16.1	13.3	20.1	2.2
Sole	2.9	1.8	1.1	2.4	0.4
Brill	15.3	6.9	5.5	10.2	1.7
Flounder	3.3	2.3	1.5	3.7	0.7

The inflow of settlers originating from OWFs varied between the years (Table 4-1). The difference between the maximum and minimum proportion of settlers coming from OWFs drew attention (about 30%-60%). In addition to year-to-year variability, the model also predicted spatial heterogeneity (Figure 4-3). For turbot, the Thames nursery was the most affected, with an average of 7.8% of settlers coming from OWFs. The Nl, Ge and No nurseries were also affected (2.6%, 1.4% and 3.9% from OWFs, respectively), while Fr and Be received less than 1% of settlers from OWFs. For brill, Nl, Ge and No were the most impacted nursery grounds. For sole, the most impacted nursery ground was Nl, with about 5% of the settlers coming from OWFs and less than 1.5% for other spawning grounds. For dab, OWF arrivals were important in No, Tha and Ge (30%, 14% and 13%, respectively), while for the French nursery 8% of the settlers on average came from OWFs, with high interannual variability (from 42% in 1999 to low input in 2001 or 2002). For plaice, No and Ge nursery grounds presented the highest number of arrivals from OWFs (12% and 10%, respectively). For Nl and Tha the number of settlers from OWFs was important (5% and 4%, respectively), but limited for Be and Fr (2% and <1%, respectively). Flounder displayed the same interannual variability than dab. While overall, Fr, Tha and Be were the least impacted, a high year-to-year variability was observed, with particularly high values for the Belgian nursery in 1997 and 2001 (13% and 29% from OWFs, respectively). Nl was the most affected nursery ground for this species (on average 6%).

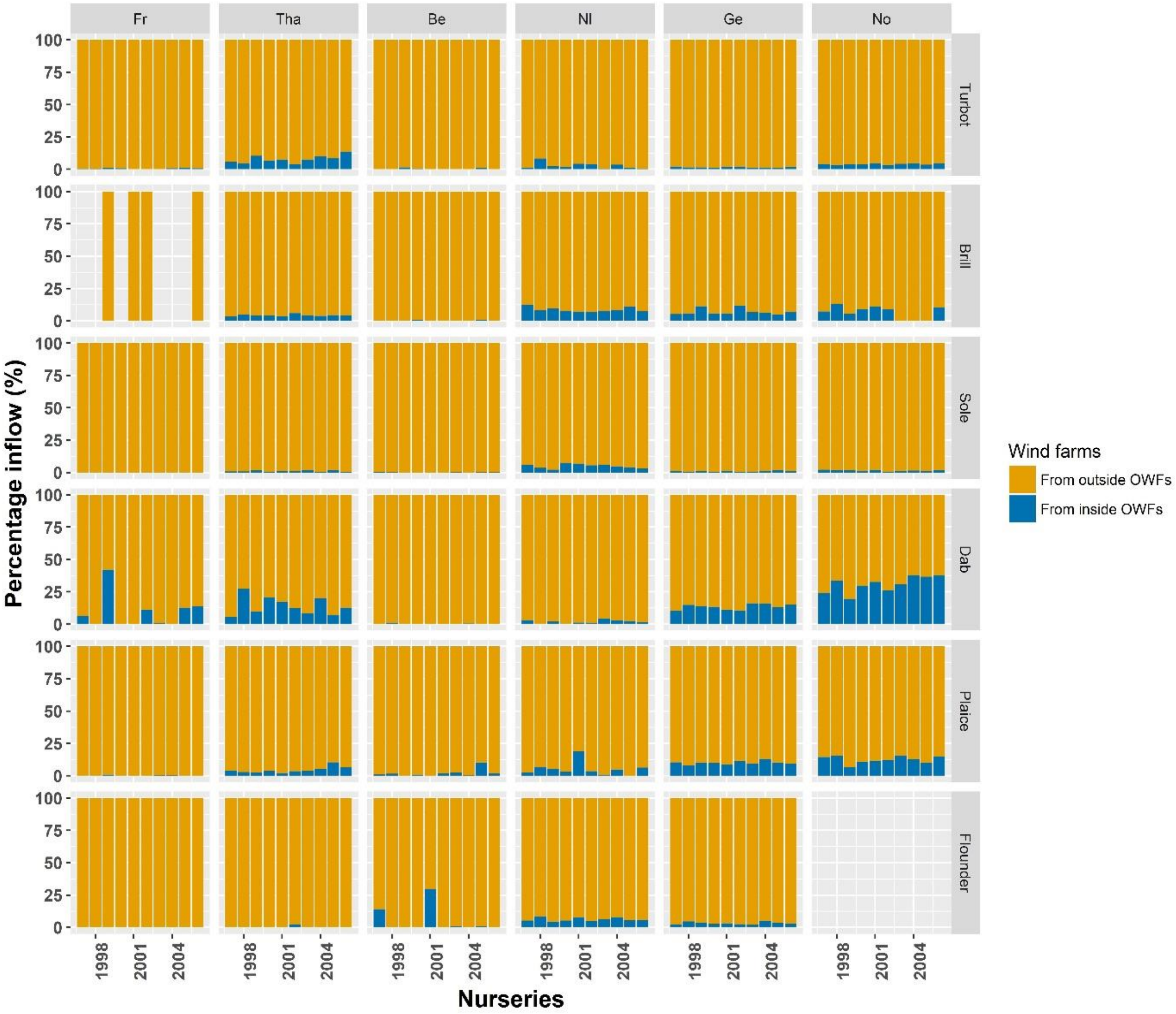

Figure 4-3 Percentage of larval inflow in the nurseries of individuals spawned from areas with and without offshore wind farms (OWFs) for six flatfishes (from top to bottom: turbot, brill, sole, dab, plaice and flounder) at the nursery grounds (France (Fr), the Thames estuary (Tha), Belgium (Be), the Netherlands (Nl), the German Bight (Ge), Norfolk (No)). Empty spaces refer to the absence of settlement.

Specific impact of spawning event in OWF areas on the different nurseries

The inflow of settlers originating from OWFs varied between years (Table 4-1). In addition to the year-to-year variability, the model also predicted spatial heterogeneity (Figure 4-4). All nursery grounds were predicted to be prone to OWFs influences, but the impact is likely to differ among the nursery grounds, the species, and the origin of settlers. For the French nursery ground, two species presented more than 0.5% of arrivals from OWFs: dab from South UK OWFs (8.5%) and turbot from French OWFs (0.5%). The proportion of arrivals from OWFs at the Belgian nursery ground was limited compared to the other nurseries (less than 0.5% for all species, except for flounder and plaice, for which the proportion reached 4.5% and less than 2% respectively) and mainly from local OWFs (BE_NL). In the Dutch nursery ground, brill and flounder are likely to be most prone to OWFs influence, with 8% and 6%, respectively. The settlement of dab was limited. For most species, the main treat of impact comes from the Belgian and Dutch OWFs, except for flounder for which Dutch OWFs imported the majority of larvae originating from an OWF. The German nursery ground displayed a relatively high proportion of settlers from OWFs (more than 5% for brill, dab and plaice). The origin of the settlers also revealed a strong disparity between species in terms of OWFs contribution. Germany 1 OWFs was the major contributor for sole, turbot, brill and dab, and to a lesser extent a contributor for plaice. In the case of dab, there was also more than 1% of input from East UK, NL and Belgium-Netherlands OWFs. For plaice, most of the arrivals was due to East UK, Germany 1 and NL OWFs, with Belgium-Netherlands OWFs playing an important role. In the Thames nursery the origin of settlers predicted by the model indicated that 14% for dab and 8% for turbot were coming from OWFs. South UK OWFs were the major contributors for dab and to a lesser extent for plaice. Brill, sole, turbot and plaice were strongly influenced by East UK OWFs. Finally, the predicted arrivals from OWFs at the Norfolk nursery ground were considerable for dab (more than 30%), and relatively important for plaice (about 10%). East UK OWFs was the main contributor for brill, sole and turbot. North-East UK 1 OWFs played an important role in the case of dab and plaice. OWFs located further offshore or close to the North boundary of the domain (North-East UK 1, North-East UK 2 and Germany 2) had a limited impact in the Southern North Sea at the notable exception of Norfolk for East UK 1.

Table 4-2 : Expected change of settlement (in percent) under different scenarios of altered egg production inside the offshore wind farms.

	- 20%	+ 10%	+ 25%	+ 50%
Plaice	-1.78	-0.89	2.25	4.45
Turbot	-0.4	0.2	0.5	1
Dab	-3.22	1.61	4.03	8.05
Sole	-0.36	0.18	0.45	0.9
Brill	-1.38	0.69	1.73	3.45
Flounder	-0.46	0.23	0.58	1.15

Applying the model to different scenarios of OWF impact onto egg production showed changes in settlement ranging from -3% (-20% egg production scenario) to 8% (+50% egg production scenario) (Table 4-2). Dab was identified as the potentially most impacted species, while the lowest predicted impact goes for sole.

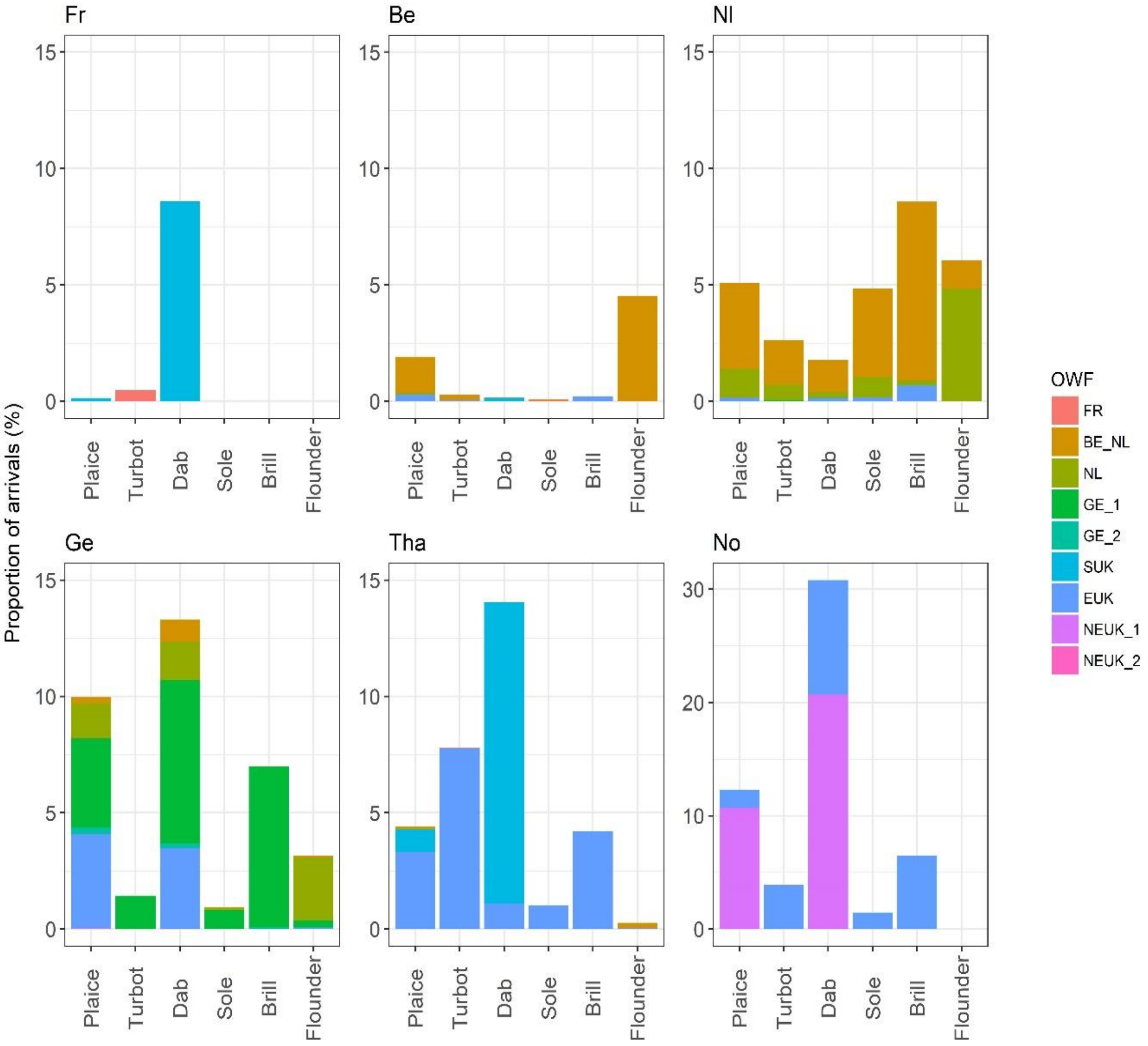

Figure 4-4 Mean proportion of settlers originating from the different offshore wind farms over the period 1997-2006 for the six flatfish species at the French (Fr), Belgian (Be), Dutch (Nl), German (Ge), Thames (Tha) and Norfolk (No) nurseries. The scale to Norflok nursery is different than the other nurseries. For the codes of OWF areas, see in Material and Methods.

4.4 DISCUSSION

This study analysed the level of overlap between spawning grounds and OWFs as well as the proportion of settlers in coastal and estuarine nursery grounds originating from OWFs for the flatfishes plaice, dab, sole, turbot, brill and flounder over a 10-year period (1997-2006). The installation of OWFs in the southern and central North Sea leads to a potential overlap with the spawning grounds of flatfishes, which might impact flatfish settlement and population dynamics. Our results showed that the proportion of settlers arriving at the nursery grounds that might originate from OWFs is not solely related to this overlap. Moreover, the model predicted high variation among species, areas and years.

4.4.1 Spatial overlap between spawning grounds and offshore wind farms

From an ecological and evolutionary perspective the location of spawning areas of marine fish results from a large number of constraints including fertilisation, survival from eggs to juveniles, reduced predation and transport toward suitable nursery (Ciannelli *et al.*, 2015). Also, the spawning grounds show a large variability among the six species due to the wide range of life history traits of the selected species and, hence, different levels of overlap with OWFs. These differences are explained by the species-specific reproductive strategy, spawning ground location, either coastal (e.g. sole) or more offshore (e.g. dab), and the position of spawning hotspots (higher egg densities, Figure 4-2). Three groups emerged: dab and brill which present the highest level of overlap with OWFs of the species studied, sole and flounder which present a lower level of overlap and turbot and plaice that exhibit an intermediate level of overlap.

4.4.2 Settlement of larvae originating from offshore wind farms

The overlap between spawning grounds and OWFs is an important aspect to understand the potential effect of OWFs on the species' population dynamics. Due to the specific life history of flatfish, this overlap is not directly related to recruitment as there is no linear relation between spawning and settlement (Cury *et al.*, 2014). In this context, using hydrodynamic models coupled to individual-based model was useful to understand how spawning grounds and nursery grounds are connected (Pineda *et al.*, 2007). The model predicted three main groups of species in terms of proportion of settlers originating from OWFs, which are slightly different from the three former groups found in the overlap study. Dab had the highest proportion of settlers originating from OWFs, plaice and brill were at an intermediate level and turbot, sole and flounder showed the lower proportion of settlers of OWF origin. The comparison between species presented in this study revealed that the number of eggs spawned in potential OWFs and the number of settlers originating from those areas were different between species.

The proportion of recruits originating from OWFs was lower than the proportion of eggs spawned in OWF areas for all species, particularly for turbot (9.5% of eggs were spawned in OWFs and only 2.2% of the settlers came from OWF areas) and brill (15.3% of eggs were spawned in OWFs and only 6.9% of the settlers originated from OWFs). The higher ratio of overlap than settlement indicates that OWFs will impact mainly areas where the probability of reproductive success is low for the North Sea (i.e area where the probability of settlement is low for eggs and larvae).

4.4.3 Interannual variability and potential impact on the different nurseries

The model predicted high interannual variability in the proportion of settlers originating from OWFs. This variability suggests that the hydrodynamic regime plays an important role in the connectivity between OWFs and nurseries. Environmental conditions affect larval transport and flatfish recruitment in the North Sea (van der Veer, 1986b; van der Veer and Witte, 1999; Bolle *et al.*, 2009). In addition to the interannual variability at the regional scale, the model predicted strong variations at the local scale. The model helps to detect the nursery grounds that will most likely be impacted by the introduction of OWFs. The nursery grounds at the German Bight, Norfolk and Thames estuary might be particularly affected, while the number of settlers originating from OWFs would be more limited at the Belgian nursery. However, there is interannual variability in the connectivity between OWFs and nurseries, which can be substantial in some cases (e.g. flounder in the Belgian nursery, for which the settlement from OWFs is less than 5% on average but could be as high as 30% in some years). Recruitment of flatfish is known to present a high interannual variability at the scale of southern North Sea related to environmental conditions (Bolle *et al.*, 2009; Erftemeijer *et al.*, 2009; Lacroix *et al.*, 2013a), this variability could even be higher when considering recruitment success in small areas, as OWFs, in comparison to the whole North Sea.

4.4.4 Specific effect of different offshore wind farms

Using the dispersal model, it is also possible to assess the impact of a single OWF group onto settlement. Despite their limited coverage, some OWF groups could largely contribute to the larval settlement across the North Sea given their coastal location. Due to the large size and specific position of OWFs located in the Eastern coast of UK, eggs spawned in this area spread throughout the North Sea, as well as to the English coast, where the OWFs had the strongest influence among all species. Due to a more offshore position or location in the north of the study area, some OWFs had a limited impact on populations for which nurseries are mainly coastal. However, they strongly affected species such as plaice and dab that have more offshore nurseries in the central part of North Sea. It must be pointed out that the northern coast of Denmark and the Norwegian and Swedish coasts were not included in our analysis. Other studies on plaice indicate that most eggs spawned in the German Bight arrive in the northern part of the North Sea (e.g. Hufnagl *et al.*, 2013).

4.4.5 Biological implications

The implementation of OWFs could impact flatfish population owing to the expected increase of the number of eggs spawned inside, due to the cue that suggests an increase in size, biomass or density of fish in OWF areas (Walton, 1982; Bergström *et al.*, 2013; Stenberg *et al.*, 2015). For marine fish, the choice of spawning grounds is constrained both by ecological and evolutionary processes (Munk *et al.*, 2009; Ciannelli *et al.*, 2015). In addition to changes in the quantity of eggs produced in OWFs, spawning locations are also susceptible to change in response to environmental changes induced by OWFs.

In the marine environment, maternal effects may affect recruitment, egg quality, the number of batches, the length of the spawning season, fertilisation rate, and (post)larval survival (Chambers and Leggett, 1992; Rijnsdorp and Vingerhoed, 1994; Butts and Litvak, 2007; Donelson *et al.*, 2009; Morais *et al.*, 2014). Adult condition might be influenced by altered environmental quality consecutive to the implementation of OWFs due to the change in species distribution and introduction of hard substrate, which could affect food availability or carrying capacity, and so eggs production and recruitment (Marshall *et al.*, 1999; van der Veer *et al.*, 2003, 2015). Thus, it may be also interesting to focus on the impact of OWFs on the feeding grounds, as they may have an impact on fish condition, and hence fecundity and migration success of fish larvae. Similarly, the behaviour and movement of fish which overlap with OWFs may be another topic of interest.

Nurseries play an important role in population dynamics of flatfish (Nash and Geffen, 2000). After metamorphosis, most larvae settle in shallow coastal nurseries, which most likely limits the direct impact of OWFs on juveniles. However, the interspecific difference in the number of settlers could also affect the juvenile life stage by changing the species composition of the nurseries. Indeed, many processes occurring at the nursery grounds are density-dependent (e.g. van der Veer 1986; Rijnsdorp and Van Leeuwen 1992; van der Veer *et al*. 2000; Le Pape and Bonhommeau 2015). In addition, environmental conditions in nurseries are important for young flatfish (Rijnsdorp *et al.*, 1992c; Cabral *et al.*, 2007). Overlap between OWFs and nurseries could change both the quality and capacity of the nursery grounds (due to a change in species composition, a reduction of surface due to the implementation of hard structures…) and influence the whole population, as in the case of habitat degradation for sole in Western English Channel (Rochette *et al.*, 2010b).

4.4.6 Management implications

Due to their specific life history, flatfish have not been identified as having the potential to benefit from the establishment of marine protected areas (Shipp, 2003). However, some studies showed that spatial restriction of fisheries or implementation of OWFs increase flatfish population size (Walton, 1982; Florin *et al.*, 2013) whereas others reported a limited impact (e.g. Ashley *et al.*, 2014). This study represents a baseline to test the potential impact of planned OWFs. The specific effect on the different species could be dependent of their exploitation level, which means that target species in the North Sea (especially sole and plaice) could be strongly affected by the overlap between OWFs and spawning grounds. This impact can be both positive and negative, depending on the real impact on OWFs on these species. The different scenarios in eggs production effects suggest that dab is the species more prone to OWFs influence. In the North Sea, dab is also the most common species (Rogers *et al.*, 1998). Despite potentially being the most impacted species, dab is not a target species for the fishing industry, so the effect of fishing restrictions could be more limited for this species than for other fished species.

4.4.7 Perspectives

The model excluded several sources of variability in larval survival related to trophodynamics, such as prey abundance and predation (Peck and Hufnagl, 2012). The observed increase in abundance of filter feeders in OWFs could lead to additional uncertainty in larval survival. In addition, a previous study (Lacroix *et al.*, 2018) based on the same model as the one used here, showed how climate change could affect recruitment and the connectivity pattern of sole in the North Sea. Climate change could also affect fish distribution (Perry *et al.*, 2005) and so the overlap between fish and OWFs. The real impact of OWFs on fish density and distribution should be studied *in situ* due to expected knock-on effects in settlement at nurseries and at population level. Once the magnitude of OWF impact on egg production is known, it will be possible to assess the impact on population dynamics from the likelihood of impact by OWFs based on the overlap computed in this study. Offshore wind farms are also know to impact hydrodynamical condition (Merz *et al.*, 2010; Rivier *et al.*, 2016), assessing how this process affect transport of eggs and larvae will be an interesting question for future research.

4.5 CONCLUSIONS

An important overlap between future OWF areas and flatfish spawning grounds was estimated, with a proportion of settlers originating from OWF areas varying from 2 to 16%. This study suggests that European plaice, common dab and brill could be the most affected flatfish species, yet with some important local disparities across the North Sea. Our results predicted interspecific differences resulting from the interaction between life history traits (such as pelagic larval duration, spawning period and distribution) and the environmental conditions (such as temperature and currents). Overall, species seem to be affected differently across the North Sea. Survey to assess the specific effect of OWFs on the different species, especially on eggs production, would help to further understand the potential impact of the presence of OWFs on flatfish population. Overall, our study represents a first step towards the understanding of the effects of OWFs on marine ecosystems. As the effects are many and varied, the results should be integrated into a larger study to assess the cumulative impact of OWFs as proposed by Willsteed *et al*. (2017).

Chapter 5. WHAT DO WE LEARN FROM THE CALIBRATION AND SENSITIVITY ANALYSIS OF A FISH LARVAL TRANSPORT MODEL?

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5.1 INTRODUCTION

Connectivity, i.e. the realised movement between populations in a seascape, has an essential role in the persistence and productivity of (meta)populations, as well as in population structure, genetic diversity and population resilience (i.e Cowen *et al.*, 2007; Selkoe *et al.*, 2016a). The larval phase plays a major role in this process. As described by Szuwalski *et al.* (2015), Spawning Stock Biomass (SSB) is a poor predictor of recruitment variability. Indeed, in many fish taxa, the larval stage, which includes a planktonic phase, is a determining factor for recruitment (e.g. Hjort 1914, 1926; Cury and Roy 1989; Houde 2008). This is especially the case for demersal fishes, including flatfishes, for which SSB explains only five percent of the recruitment variance (Cury *et al.*, 2014). For demersal species, recruitment success depends foremost on access to suitable nursery grounds after metamorphosis. During the pelagic stage, survival is particularly low and variable (McGurk, 1986; Houde, 2008; Le Pape and Bonhommeau, 2015), which directly affects long-term population size. Understanding both connectivity and recruitment dynamics is crucial for fisheries management (Fogarty *et al.*, 2007; Kerr *et al.*, 2010, 2016).

In support of management, models are widely used in fisheries sciences (i.e Royce, 2013; Aeberhard *et al.*, 2018) or to conservation (i.e Ruth and Lindholm, 2002; Marshall *et al.*, 2014) . The models have a wide range of applications, ranging from the dynamics of one species to the functioning of a full ecosystem, including fishing and management practices (e.g. Travers *et al.*, 2007; Rose *et al.*, 2015; Grüss *et al.*, 2017). In this context in regards to conservation, models are used as examples to predict individual exchange and movement in support of marine protected area (MPA) design, especially during larval phase (i.e Baskett *et al.*, 2005; Kaplan *et al.*, 2009; Andrello *et al.*, 2013).

Over the past decades, coupled bio-physical models have become well established (Miller, 2007; Pineda *et al.*, 2007; Cowen and Sponaugle, 2009). Such models, which combine Individual-Based Models (IBMs) and hydrodynamic models, are useful for understanding the dynamics and critical drivers of ecosystems and for facilitating management at specific spatio-temporal scales (Allain *et al.*, 2007; Hinrichsen *et al.*, 2011). However, IBMs require a sound knowledge of the biological processes governing larval dispersal. For example, even for marine species with similar life cycles, large differences in potential and realised dispersal are observed. The differences are related to larval traits (López-Duarte *et al.*, 2012) such as behaviour (Fox *et al.*, 2006b; North *et al.*, 2008; Robins *et al.*, 2013), duration of the larval stage (Shanks, 2009b), seasonality (Lett *et al.*, 2010), spawning period (Ayata *et al.*, 2010) or structure of the water column and currents (Munk *et al.*, 2009). Due to the challenges of direct observation in the marine environment, especially for the poorly documented early life stages (Levin, 2006), life history traits are difficult to assess, and parameterisation remains uncertain. Moreover, the confidence in the models remains incompletely documented. Numerous studies have investigated sensitivity and robustness of Lagrangian transport models, as well for physical parameters as for temporal and spatial resolution or density and number of particles released (Huret *et al.*, 2007b; Simons *et al.*, 2013; Savina *et al.*, 2016; Monroy *et al.*, 2017; Kvile *et al.*, 2018). These insights provide helpful practical recommendations for modellers (North *et al.*, 2009). However, systematic sensitivity analyses to biological parameters are even more limited. Various parameters such as pelagic larval duration, swimming ability, vertical migration behaviour or mortality (Fox *et al.*, 2006b; Peck and Hufnagl, 2012; Monroy *et al.*, 2017) have been highlighted to influence drift patterns and retention. More formal analyses to identify most influential parameters are rarely carried out because the numerous parameters and long simulation times prevent the computation of sensitivity indices on principal effect and interactions. Similarly, the integrated estimation of uncertain parameters through automatic algorithms is often not an option for such models. In the north sea, the model Larvae&Co (Lacroix et al 2013) have been used to study flatfish dispersal (Fournier and Loreau, 2001; Lacroix *et al.*, 2018; Barbut *et al.*, 2019; van de Wolfshaar *et al.*, 2021). In order to improve this bio-physical model for sole and to sort out the many alternative hypotheses on larval drift of this species, we propose to rely on a sequential methodology combining sensitivity analysis and model selection as proposed for example by Lehuta *et al.* (2013).

Such bio-physical models have captured some of the interannual and interregional variation in recruitment of common sole (*Solea solea*) in the North Sea (Bolle *et al.*, 2009; Savina *et al.*, 2010a; Lacroix *et al.*, 2013a). Sole, is one of the most economically valuable flatfish species in the area. Improved knowledge on the population dynamics is required to tailor management. measures to a high inter-annual recruitment variability (Gibson, 1997; van der Veer *et al.*, 2000a). Demersal adults spawn planktonic eggs, eggs and larvae are transported by the currents and following metamorphosis (e.g. Amara *et al.*, 1998) juveniles settle in shallow coastal waters, whose spatial extent impacts year class strength. However, despite an abundant documentation on early life stages (Barbut *et al.*, 2019), the literature shows a broad range of life history traits (such as pelagic larval duration, spawning period and behaviour). For example, vertical nycthemeral migrations of sole larvae are well documented in the Bay of Biscay (Koutsikopoulos *et al.*, 1991) but remain uncertain in the more turbid North Sea waters. Improving the estimation of model parameters related to life history traits can be complex and expensive because it implies empirical field and experimental data. Various assumptions about larval traits, behaviour and other model parameters can be simulated and tested by comparing simulation results with field data to identify the most influential parameters.

The overall aim is to carry out a sensitivity analysis of the larval transport model LARVAE&CO parameterised for North Sea sole in order to quantify the influence of biological parameters and inter-annual variability on recruitment and connectivity, and to improve the model calibration. The specific aims are the following: (1) Is the variability due to uncertainties on parameters is larger than the effect of interannual variability? (2) Which parameters have the most impact? (3) Is there a difference between equally likely parameterisations? (4) Which parameterisation allows fitting recruitment data the best?

5.2 MATERIALS AND METHODS

5.2.1 Research strategy

The Lagrangian transport model called LARVAE&CO (Lacroix *et al.*, 2013a), which combines an hydrodynamics model and an IBM, was used to study the survival of the early life stages of common sole *Solea solea* (Soleidae, Actinopterygii) in the North Sea. The model has shown to explain a significant part of recruitment variability (31%) in the North Sea (Lacroix et al., 2013).

However, parameters remain uncertain and may affect predictions. To improve model performance, three steps were designed. In a first step we perform an ‘exploratory analysis’ on four contrasted years in terms of hydrodynamics, to determine which of biological parameters or inter-annual variability have the strongest influence on connectivity and recruitment. A second step, ’in-depth analysis” aims at further determining which biological parameters have a strong impact on model outputs considering only one specific year. Both steps were realised through “sensitivity analyses” and the computation of sensitivity indices. Finally, in a third step, a ‘calibration’ of the most influential parameters was performed by comparing predicted and observed recruitment over a 12-year period.

5.2.2 Study area

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

5.2.3 Modelling of the early life stage

The hydrodynamic model

The 3D hydrodynamic COHERENS V1 model (Luyten *et al.*, 1999; http://odnature.naturalsciences.be/coherens), has been implemented in the area between 48.5°N and 57°N, and 4°W and 9°E. The model domain contains a 157 x 205 horizontal grid with a resolution of 5’ in longitude and 2.5’ in latitude (approximately 5 x 5 km) and 20 σ-coordinate vertical layers. Two open boundaries are located at the northern and western limit (at 4°W and 57°N) and the model includes daily river discharges of 14 rivers. The model is forced by weekly sea surface temperature (SST) data on a 20 × 20 km² grid interpolated in space and time according to the model resolution (*Bundesamt für Seeschifffahrt und Hydrographie, BSH, Germany*) (Loewe, 2003) and by six-hourly surface wind and atmospheric pressure fields (provided by the Royal Meteorological Institute of Belgium based on the forecast data of the UK Met Office Global Atmospheric Model) (Hi_Res, Walters *et al.*, 2017). Details about the model implementation are available from Savina *et al.* (2010a) and Lacroix *et al.* (Lacroix *et al.*, 2013a), and in the supplementary material.

Individual-based model

In the Lagrangian larval transport model Larvae&Co (Lacroix *et al.*, 2013a), larval trajectories were calculated using a particle tracking model coupled online to the well-documented and intensely used Coherens model. The vertical diffusion was modelled by the random walk technique, following Visser (Visser, 1997). Since vertical turbulent diffusion is considered the dominant horizontal dispersal mechanism in the North Sea (Christensen *et al.*, 2007), explicit representation of horizontal diffusion was neglected. The IBM was structured in four stages, representing flatfish life stages from eggs to metamorphosis (eggs, yolk-sac larvae, first-feeding larvae and metamorphosis larvae). Each stage has a species-specific parameterisation in terms of larval duration, behaviour or mortality.

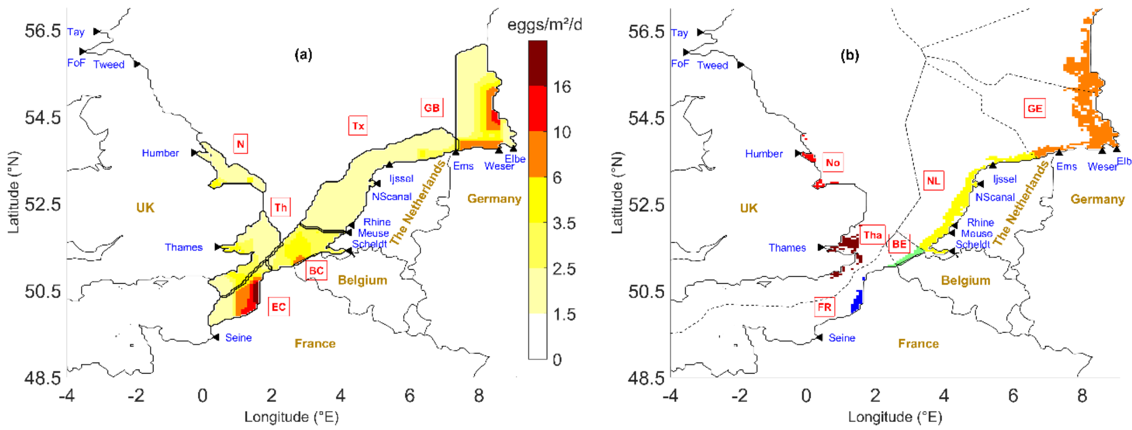


Figure 5-1 Geographic implementation of the model. (a) Distribution of the main spawning grounds of sole in the North Sea and Eastern English Channel (delineated by the black lines) with contour plots of the mean daily egg production (redrawn from ICES-FishMap, 2005). (b) The six nursery grounds of sole defined as the coastal area with a depth of less than 20 m and a substrate of either mud to sand or sand to mud (<5% gravel, following the modified Folk classification of Kaskela et al., 2010). The dotted black lines represent the national EEZ. For details on the spawning grounds and nursery codes, see Materials and Methods. Figure with the permission of Lacroix et al., (2018).

Eggs are released in six main spawning areas (the EEC off the French coast (EC), off the Belgian coast (BC), off Texel (Tx), the inner German Bight (GB), off the mouth of the Thames River (Th) and on the Norfolk Banks (N), ICES-FishMap, 2005). Nursery grounds, located in the coastal area (< 20 m depth) with soft sediment, are divided in six zones on the basis of national boundaries (France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge) and two zones in the UK, Norfolk (No) and Thames estuary (Tha)) (see details on Figure 5-1).

Spawning period

The spawning period was estimated for each spawning region in the domain. For the baseline situation, the spawning peak corresponds to the first day where the local sea surface temperature reaches 10 °C on average. A spawning period of 3 months is considered, centred around the peak. Details about the spawning dates for each year are mentioned in Lacroix et al. (2013). For the sensitivity analysis, early spawning and late spawning are based on the baseline peak ±15 days.

Pelagic larval duration

Egg and larval duration were defined as a function of temperature according to the equation $D = \alpha T^{-\beta}$ where D is the stage duration (in days) and T the temperature (in degree Celsius). In the current study β was fixed and a range was considered for α to allow covering the interval of values found in literature and described in Bolle et al (2009). Parameter values representative for the reference, short and long pelagic larval duration for each stage are given in Table 5-1

Table 5-1 Parameterisation values used for the different larval stages. For short, reference and long pelagic larval duration.

Stage	Larval duration			
	Short α	Standard α	Long α	β
Eggs	164.79	233.44	302.1	-1.5739
Yolk-sac larvae	82.741	117.21	151.69	-1.4619
First-feeding larvae	2136.07	3026.1	3916.1	-1.9316
Metamorphosing Larvae	687.67	974.18	1260.7	-1.9316

Behaviour

Beside passive drift, five behaviours related to vertical migration have been attributed to the particles. An upward movement due to a positive buoyancy for eggs and yolk-sac larvae (0.003 m.s^{-1}) or downward movement for metamorphosing larvae (-0.003 m.s^{-1}), a nycthemeral migration according to which the larvae swim towards the surface at night (0.003 m.s^{-1}) and towards the bottom during the day (-0.001 m.s^{-1}) and a tidal migration synchronous with the tides (-0.003 low tide, 0.001 high tide). For the tidal migration, two cases have been considered:

1) a ‘pressure-based’ vertical migration, in which vertical migration rates switch from positive values when the sea level is higher than the mean sea level to negative values when the sea level is lower than the mean sea level (as described in Lacroix et al 2013) and 2) a ‘current-based’ vertical migration following which vertical migration rates switch from positive values during rising tide (when the sea surface level increases) to negative values during falling tide (when the sea surface level decreases) (as used in Barbut et al. 2019). Values for vertical migration rates have been defined within the range of the values observed in the literature (Berntsen *et al.*, 1994; van der Molen *et al.*, 2007), in order to obtain diel vertical migration and tidally associated vertical migration in the appropriate part of the water column. Table 5-2 shows the eight realistic combinations of the five potential behaviours that were tested. Only the type of behavior was tested and not the value itself. The ‘Mig3’ and ‘Mig7’ test cases correspond to the parameterization used in Lacroix et al. (2013) and in Barbut et al. (2019) respectively.

Table 5-2 Combination of the vertical migration behaviours of the various stages (EEG: eggs, YSL: yolk-sac-larvae, FFL: first-feeding larvae and MTL: metamorphosing larvae).

Stage	EGG	YSL	FFL	MTL
Mig0	passive drift	passive drift	passive drift	passive drift
Mig1	move up	move up	passive drift	move down
Mig2	move up	move up	nycthemeral mig.	passive drift
Mig3	move up	move up	nycthemeral mig.	‘pressure-based’ tidal migration
Mig4	move up	move up	passive drift	passive drift
Mig5	move up	move up	passive drift	‘pressure-based’ tidal migration
Mig6	move up	move up	passive drift	‘current-based’ tidal migration
Mig7	move up	move up	nycthemeral mig.	‘current-based’ tidal migration

Settlement delay

Settlement occurred at the end of the larval stage (Gibson, 1994; Haynes *et al.*, 2011; van der Hammen *et al.*, 2013). For the purpose of the sensitivity analysis, an additional delay of 0, 5 or 10 days was added at the end of pelagic larval duration if the larvae is not in a nursery area, allowing larvae to reach a nursery. Larvae that ended up outside the nursery grounds at the end of their pelagic larval duration did not survive (0 % survival rate).

Larval mortality

To penalise long larval durations and to increase the realism of the simulations, a survival rate was computed during the full larval stage until metamorphosis. The mortality rate used in Lacroix et al. (2013) was set to $0.0004.T^{3.0293}$ d^{-1} with T the temperature for eggs and yolk-sac-larvae and to a constant mortality rate of 0.035 d^{-1} from first-feeding larvae to metamorphosis. A mortality increasing 10 % is considered ‘high and decreasing 10% ‘low’; they were applied separately for each stage with the same temperature dependency.

Model outputs

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

5.2.4 Run specificities

The use of super-individuals (Scheffer *et al.*, 1995) allows to accommodate for large numbers of eggs while keeping the number of particles released limited. The total number of particles released by year is 1.9×10^6 as in Lacroix et al. (2013). Spawning covered the entire spawning area and period. Particles were released on the bottom at midnight every day during the entire spawning period in the spawning ground considered.

5.2.5 Sensitivity analyses

Outcomes of the individual based model can be represented as a function of physical and biological parameters:

$$Y = (y_i, y_{k,l}) = f(X) = f(\theta_{phys}, \theta_{bio})$$

with:

y_i : recruitment predicted in nursery i

$y_{k,l}$: percentage of larvae originating from spawning ground k into nursery l predicted by the model

$X = (X_1, \dots , X_n)$ a set of model parameters which can be subdivided into two categories:

θ_{bio} : biological parameters (such as spawning date, PLD, behaviour …)

θ_{phys} : physical parameters (such as wind, temperature, tide …)

The sensitivity study will focus on assessing the impact of biological parameters on recruitment and connectivity as well as estimating uncertainties associated to these parameters. The impact of hydrodynamic model himself will be assessed through year-to-year variability instead of testing separately the impact of physical parameters. In order to assess the impact of biological parameters on model predictions (recruitment and connectivity), two sensitivity indices, based on variance decomposition (Saltelli, 2008), were computed: **First-order Sensitivity Indices (SI)**, which represent the contribution of a parameter to the variance of an output regardless of interactions (main effect) and **Total-effect Sensitivity Indices (STI),** which sum up the main effect of the parameter and all its contributions to interaction effects. Sensitivity indices sum to one. SI and STI were computed for local larval recruitment and the mean of SI and STI is computed for each nursery to assess impact of parameters on connectivity variability.

Variance of Y can be decomposed into

$$\mathbb{V}\mathrm{ar}(\mathrm{Y}) \ = \ \mathrm{V}_1 + \cdots + \mathrm{V}_\mathrm{n} + \mathrm{V}_{1,2} + \mathrm{V}_{\mathrm{n}-1,\mathrm{n}} + \cdots + \cdots + \mathrm{V}_{1,\ldots,\mathrm{n}}$$

Where V_i is the part of variance from the principal effect of X_i and where each $V_{k,\ldots,1}$ is the part of variance from interaction among parameters $X_k, \ldots, X_l$.

$$\text{Sensitivity index are defined from this decomposition: } \mathrm{SI}_\mathrm{U} = \frac{V_U}{\mathbb{V}\mathrm{ar}(\mathrm{Y})}$$

with U factorial terms which represent effect principal or interaction

In practice, **first order sensitivity indices** will be computed with the equation:

$$SI_j = Var\ (E(Y\ |Xj)/Var(Y)$$

$$\text{Where Var } (E(Y\ |\mathrm{Xj}) \text{ assess the mean variability over the domain } \mathrm{X_j}$$

$$(\text{i. e estimation of the importance of } \mathrm{X_j})$$

Similarly, the sensitivity index of interaction among k factors (i,…,k) is computed with the equation:

$$SI_{i,\ldots,k} = Var\ (E(Y\ |X_i, \ldots, X_k)/Var(Y)$$

Total Effect Sensitivity Indices is computed with the equation:

$$STI_j = \sum_{k\in\#j} S_k = 1 - \sum_{k\in\sim j} S_k$$

with #j all the combination of indices including j

with ~j all the combination of indices excluding j

These indices help to assess how parameters are influential (i.e. how variation in the parameters impact model prediction). The more the sensitivity index approaches 0, the less the factor is influential; the more the index is close to 1, the more the factor is influential.

A specific value of a parameters is hereafter called **modality**.

An **experience** is a set of modalities (one for each parameter which varies).

An **experimental plan** is a collection of different experiences.

An experimental plan which includes all the combinations possible is called a **full factorial design.** The number of experiences in a full factorial design is the number of modalities of each parameter which multiply among themselves and can quickly become important.

Step 1: "Exploratory analyses"

The aim of this step was to explore the property of the numerical model by merging similar parameters (as for example PLD of the different stages) and answer to the following questions: Is there a difference among parameterizations? Is this difference bigger than interannual variability? Which groups of merged parameters are the most influential in model prediction? To explore the influence of biological parameters and inter-annual variability on model output, it was impossible, for computational time reason, to cross all years (environment conditions) with all alternative values of biological parameters (see details in Table 5-3). A first approach using group screening on a subset of biological parameters and years was chosen. The eight migratory behaviours, three pelagic larval durations (PLD) and three mortality levels were selected, and simulations were realised on four contrasted years (1995, 1997, 2003, 2005) in terms of water temperature and NAO, a proxy for the hydrodynamic conditions. The full factorial design, representing then 72 simulations for each year, was evaluated to assess the sensitivity indices (SI and STI) and the range of variation of larval recruitment and connectivity.

Step 2: "Sensitivity analyses"

The aim of this step was to determine which parameters have the strongest influence on model prediction. Assessing the impact of different parameters and test all the combinations (full factorial design) is not possible with many parameters. The interest of the method used in this step is to reduce the number of simulations and keep the number of simulations equilibrated for each modality in regards of the variance analysis. All the parameterisations were evaluated for a specific year (2003, chosen as a 'typical' mean year in terms of water temperature and NAO).

In order to maintain computation time reasonable due to the large number of parameters, an optimised factorial design of the second order was built with the Federov algorithm (Fedorov, 1972) using the *AlgDesign* library on R. Sensitivity indices on connectivity and recruitment were built based on 353 simulations.

Step 3: "Calibration"

The aim of this step was answering to the question "Which is the parameterization enabling the model to best reproduce observation?" To determine the best parameterisation, a calibration was conducted on the most influential parameters identified in step 2, that is duration of eggs and yolk-sac larvae, mortality level, spawning period and the two vertical migration behaviours for sole in the North Sea (with nycthemeral then "current-based" tidal migration and with solely "current-based" tidal migration) as well as a passive behaviour to assess if including complex vertical migration process increases the model fit. A full design (243 simulations for each year) was built and local and regional recruitment predicted by the model were compared with observations.

Observation data

Model outputs are compared to a variety of observations available from different sources and at different scales. For the recruitment at the regional scale, an estimation of the sole recruitment at age 1 provided by scientific surveys for the whole North Sea from 1995 to 2006 was considered (ICES advice 2013 Solea IV). For the local recruitment in the different nursery grounds, a value of juveniles density at age 0 for the east coast nurseries (Belgian, Dutch and German nurseries) is available for the period 1995-1996 and 2000-2006, and a relative recruitment based on fishing effort for the UK nurseries (WGBEAM 2011) were considered from 1995 to 2006.

Recruitment predicted by the model was corrected by the SSB of the previous year to represent a realistic number of eggs spawned ICES advice 2013 Solea IV (the recruitment predicted by the model is the total number of particles multiplicated by SSB). Because of the diversity of local observations, model predictions and data were normalised (by dividing by the mean over the whole period) for each region (Belgian, Dutch, Germany, UK and the whole North Sea) and interannual variations (anomalies) rather than absolute values were compared. Root mean square errors were computed to evaluate model prediction accuracy locally (*RMSEloc* in

French, Belgian, Dutch, German and UK nurseries) as well as at the scale of the whole North Sea (*RMSEtot*) using the following equation:

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

With *Pi* the normalised recruitment predicted by the model for a specific year and nursery *i*, *Oi* the normalised observed recruitment for the same year and nursery and *n* the total number of data. The best parameterisation was estimated by minimising *RMSEloc* and *RMSEtot*. This calibration was conducted on years 1995, 1996 and from 2000 to 2006 for which all data were available. A summary of the parameters tested and the years considered for each step of the analysis is presented in Table 5-3.

Table 5-3 Summary of simulations carried out (parameters, years and experimental design chosen) for the different steps of the study. Each simulation requires 12 h computation time.

Step	Parameter used (number of modalities)	Years	Experimental plan	Number of simulations
Step 1: Exploratory analyses	Duration (3), Mortality (3), Migration (8), Year (4)	1995, 1997, 2003, 2005	full factorial design	72 by year
Step 2: In-depth analyses	Duration of each stage, Mortality of each stage, spawning peak, Migration, settlement delay	2003	Optimised fractional design	353
Step 3: Calibration	Duration of egg and yolk-sac-larvae, Mortality, Spawning period, Migration	1995, 1996, 2000, 2001, 2002, 2003, 2004, 2005, 2006	full factorial design	243 by year

5.3 RESULTS

5.3.1 Step 1: Exploratory analyses

Group screening evidenced a high variance of recruitment at the scale of the whole North Sea as well as in each nursery (Table 5-4). In the North Sea, similar to the local scale, sensitivity indices showed that the main variation is due to pelagic larval duration (STI ≥ 0.4) and to a lesser extent to mortality (0.2 ≥ TSI ≥ 0.1, except for the Dutch nursery where STI is lower than 0.1) (Figure 5-2). Whatever the scale (local or regional), the vertical migration type and year (except for Belgian nursery) were less important in recruitment variability (STI < 0.1) than the other factors. Noticeable local differences appeared with a higher importance of the year effect in the Belgian nursery ground than in the other nursery grounds and a higher importance of the migration type as in the Norfolk and Thames estuary more so than elsewhere. Overall biological parameterisation is more influential than the yearly variability in the case of recruitment.

Table 5-4 Mean settlement (number of larvae in million arriving in the nursery ground) and standard deviation (SD) predicted by the model for the different parameterisations over the year 1995, 1997, 2003 and 2005.

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

Unlike recruitment, connectivity shows a relatively stable pattern regardless of the parameterisation (Figure 5-3). There was no variation in the case of Norfolk where 100 % of the recruitment is local, independently of the year or biological parameterisation. Results are similar in the case of French nurseries where more than 97 % of settlers came from the local spawning ground. In Germany and the Thames nursery grounds, larvae were originating mainly from a local spawning ground (90 % and 87 % respectively on average) and to a lesser extent from a remote spawning ground (10 % from Tx and 13 % from EC respectively). For both nursery grounds, the variability due to biological parameterisation and year-to-year variability was low (± 10-20 %) Belgian and Dutch nursery grounds are the only ones which present a strong variability in the origin of settlers depending on parameter values. In both cases, larvae originated both from local and the closest (upstream of the current) spawning grounds and to a lesser extent from more remote spawning grounds in proportions that varied enormously (± 90 %) depending on the parameters. Larvae arriving in the Belgian nursery ground come from EC and BC, and those arriving in the Dutch nursery originate from BC, Tx and to a much lesser extent from EC.

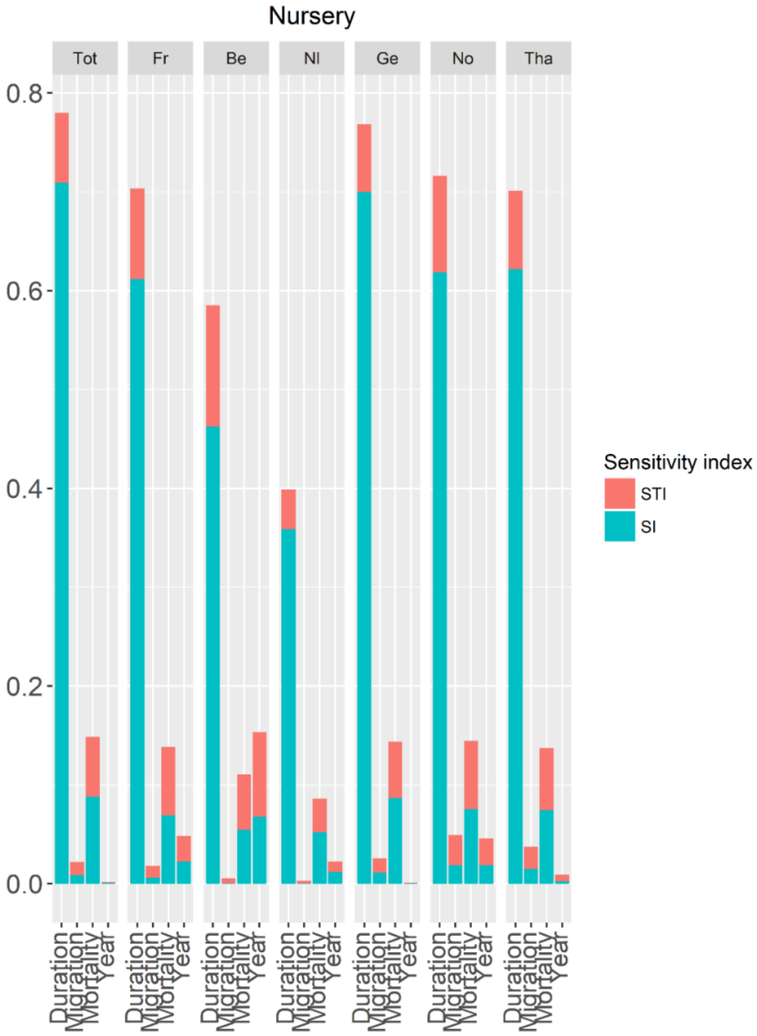


Figure 5-2 Sensitivity indices for the sole larval recruitment in the whole North Sea and in each of the nursery grounds. Blue: First-order Sensitivity Indices (SI), red: Total-effect Sensitivity Indices (STI) computed according to Saltelli (2008).

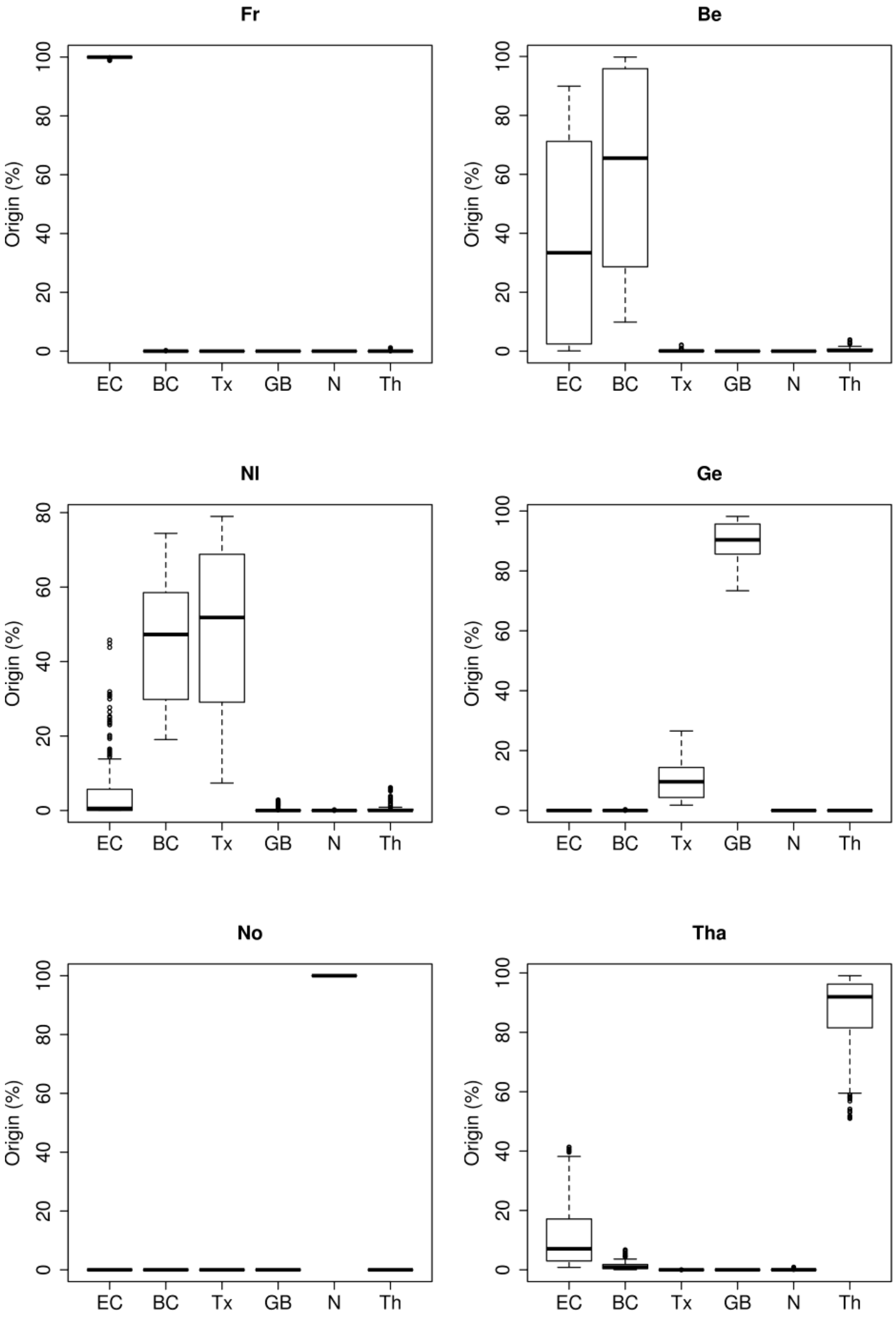


Figure 5-3 Range of variation in larval origin for the six nurseries in France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge); Norfolk (No) and Thames (Tha) for the year 1995,1997, 2003 and 2005 considering the different parameterisations presented at Step 1. For the spawning ground codes, see in Material and methods.

Exploratory analyses (Figure 5-4) related to connectivity showed that the most important factor in all nurseries is the year with the exception of the German nursery for which it is the second most influential parameter. The duration of the pelagic phase is the second most influential parameter in the French, Belgian and Dutch nursery grounds, whereas vertical migration is the second most influential parameter for the Thames nursery and the first for the German nursery. The mortality level had a negligible impact on connectivity (STI ≤ 0.003). The absence of an indicator for the Norfolk nursery ground is due to the fact that the full recruitment originates always from the Norfolk spawning ground independent of biological parameterisation or year. Overall, regarding connectivity, biological parameters are less influential than interannual variability.

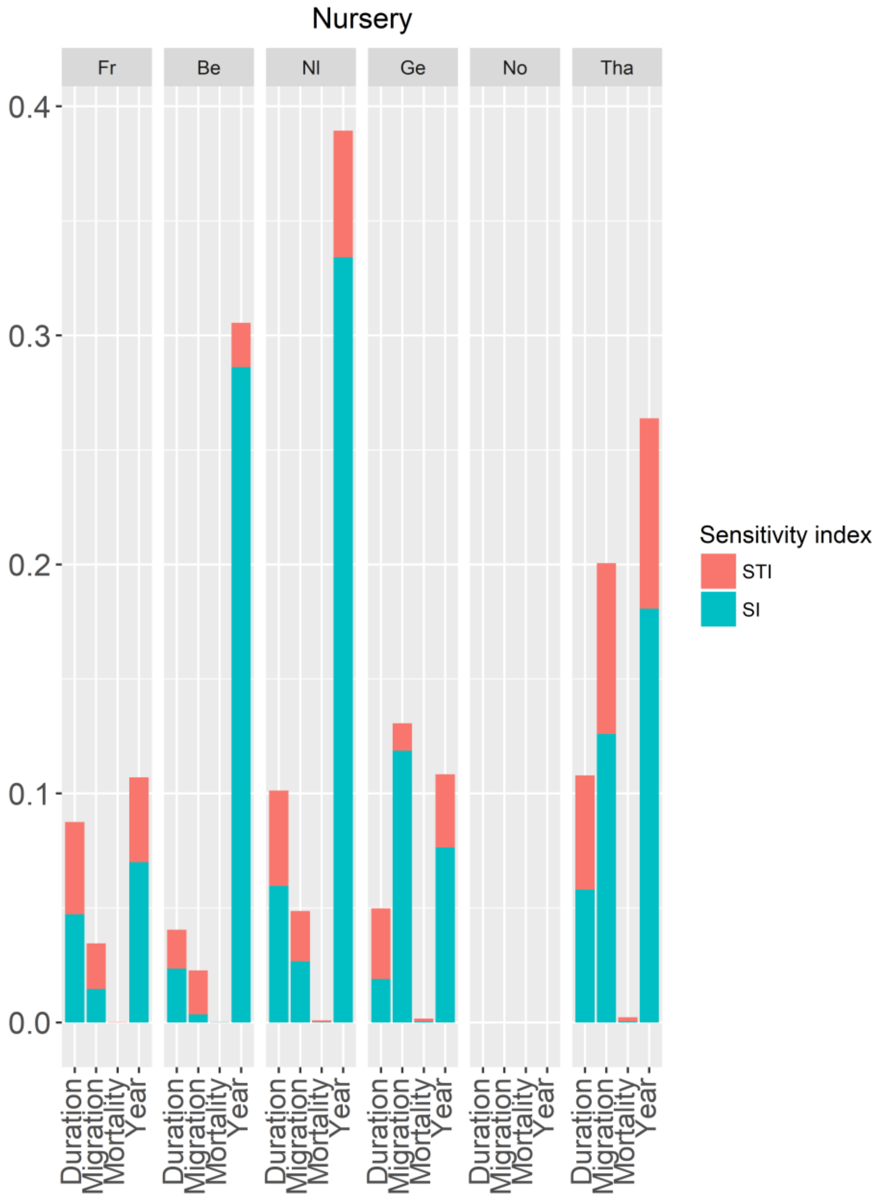


Figure 5-4 Mean sensitivity indices on connectivity for the different parameters tested in Step 1 in the six nurseries in France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge); Norfolk (No) and Thames (Tha). Blue: First-order sensitivity indices (SI), red: total-effect indices (STI) computed according to Saltelli (2008).

5.3.2 Step 2: sensitivity analyses

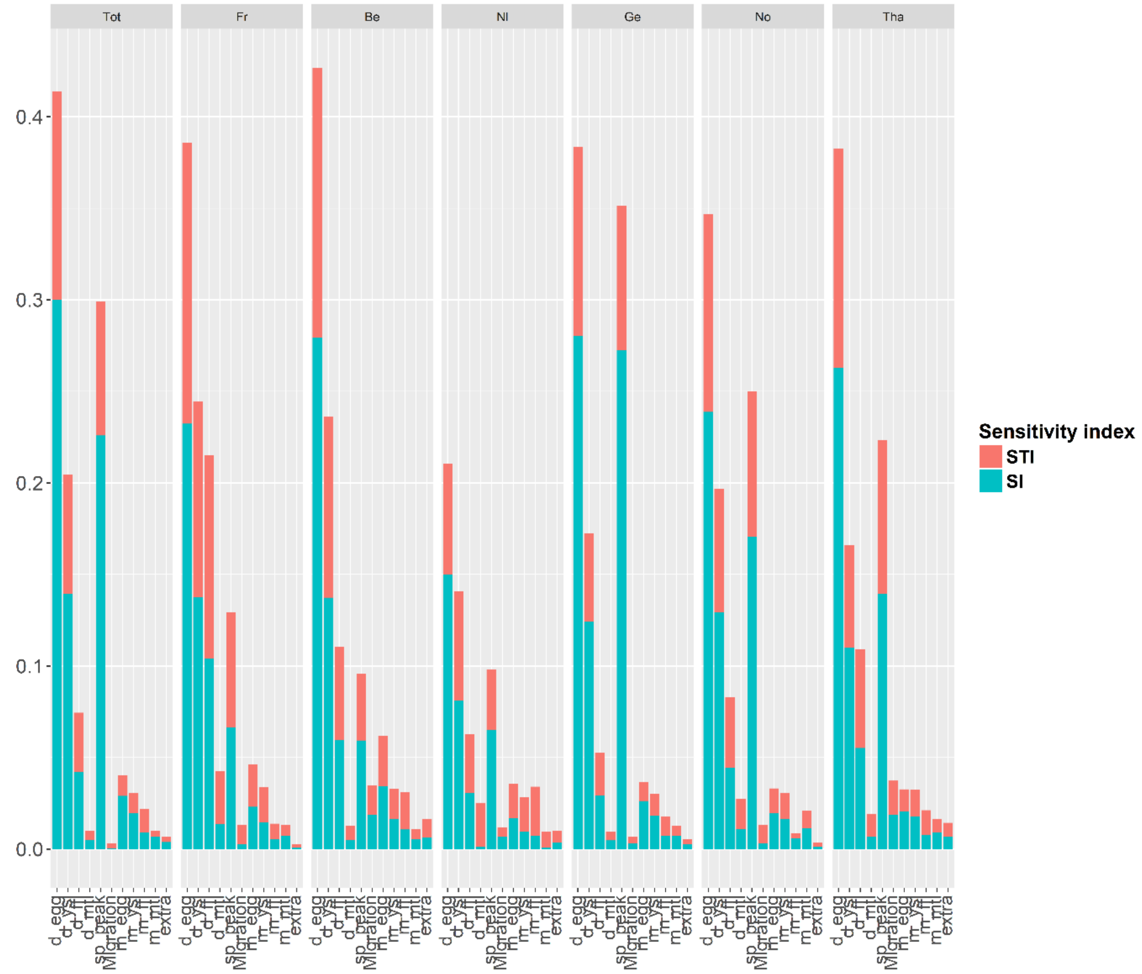


Figure 5-5 Sensitivity indices on recruitment for the biological parameters (duration of egg phase: 'd_egg', duration of yolk-sac larvae: 'd_ysl', duration of first-feeding larvae: 'd_ffl', duration of metamorphosis larvae: 'd_mtl', spawning peak date: 'sp_peak', vertical migration type: 'Migration', mortality of the different stages: 'm_egg', 'm_ysl', 'm_ffl' and 'm_mtl' and settlement delay: 'extra') for the whole North Sea (Tot) and the six nursery grounds: France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge); Norfolk (No) and Thames (Tha). Blue: First-order sensitivity indices (SI), red: total-effect indices (STI) computed according to Saltelli (2008).

The comprehensive sensitivity analyses on recruitment (Figure 5-5) showed that the pelagic larval durations are parameters to which the model is particularly sensitive, especially those related to the first developmental stages. Egg phase duration is the most influential parameter (STI ≥ 0.2) whereas duration of yolk-sac-larvae is the second (in French, Belgian and Dutch nursery grounds) or third parameter (total recruitment and in Germany, Norfolk and the Thames nursery grounds). Whatever the nursery considered, the influence of the duration of the first feeding larvae is lower than the two first stages; the duration of the metamorphosing larvae is even lower. The spawning peak date is also one of the most influential parameters, at the second place for the total recruitment in the Thames, Norfolk and German nursery grounds, at the third place in the Dutch nursery and the fourth place in the French and Belgian nursery grounds. The settlement delay had a limited impact as well as vertical migration and to a lesser extent mortality of the different stages. Regarding connectivity, sensitivity indices showed lower values than for recruitment (most of STI have a value under 0.1, Figure 5-6) showing that the responsibility of variation is more shared across parameters. Spawning period and vertical migration were the most important parameters for the French and Thames nursery grounds. In the case of connectivity, the settlement delay had a considerable importance in the Thames and German nursery grounds (STI are respectively equal to 0.04 and 0.07). Duration of larval stages had a more limited impact than recruitment. Even when the main effects of the parameters are low, they appear to be involved in interactions.

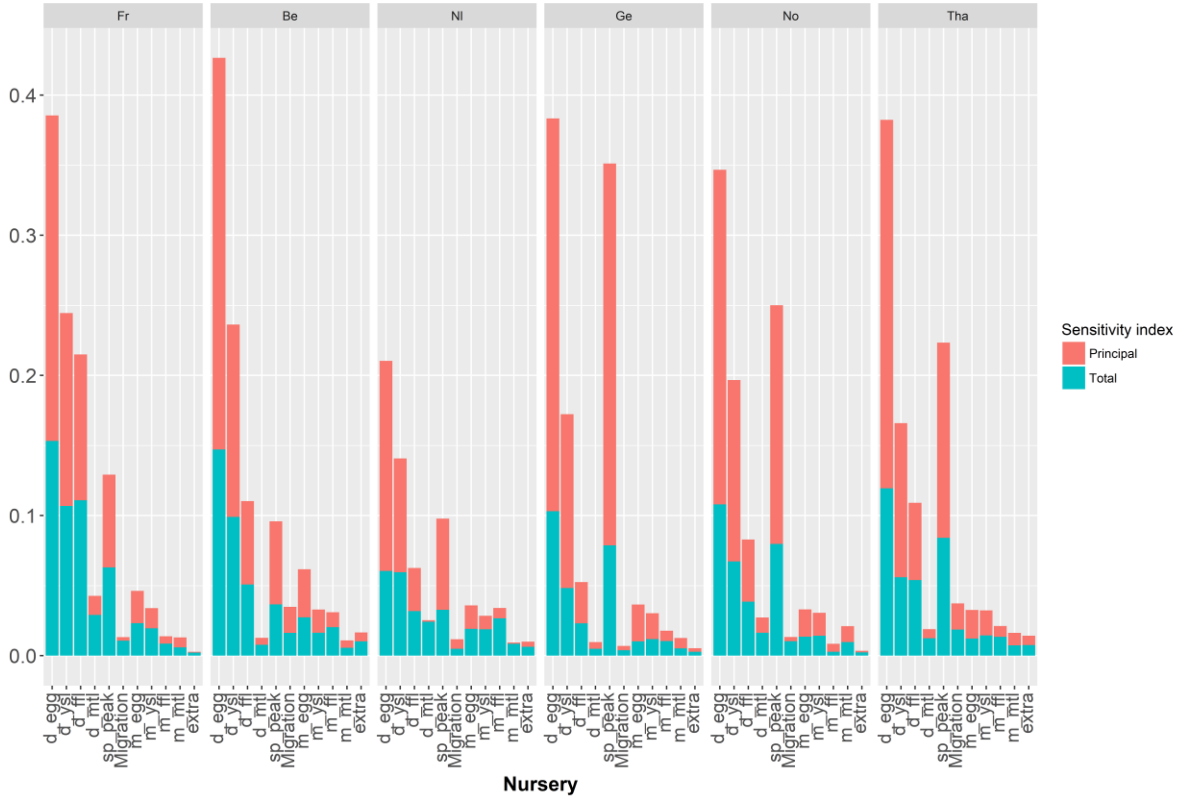


Figure 5-6 Mean sensitivity indices on connectivity for the biological parameters (duration of egg phase: 'd_egg', duration of yolk-sac larvae: 'd_ysl', duration of first-feeding larvae: 'd_ffl', duration of metamorphosis larvae: 'd_mtl', spawning peak date: 'sp_peak', vertical migration type: 'Migration', mortality of the different stages: 'm_egg', 'm_ysl', 'm_ffl' and 'm_mtl' and settlement delay: 'extra') for the six nursery grounds: France (Fr), Belgium (Be), the Netherlands (Nl), Germany (Ge), Norfolk (No) and Thames (Tha). Red: First-order sensitivity indices (SI), blue: total-effect indices (STI) computed according to Saltelli (2008).

5.3.3 Step 3: model fit

Figure 5-7 shows the performance of 243 parameterisations as synthesised by the local (RMSEloc) and total (RMSEtot) indicators. Low values indicate the best fit between model predictions and data. The simulations in which both, nycthemeral and tidal migrations are associated performed better than simulations including the other migration types, both locally and in total. The model considering passive migration presents the worst performance. Regarding the spawning period, the baseline period performs better than an early or late spawning. Overall and in addition to these two parameters, the most performant scenarios are those which associate a low mortality with long larval duration for eggs and yolk-sac-larvae, although the choice of the best model is less clear for those three last parameters.

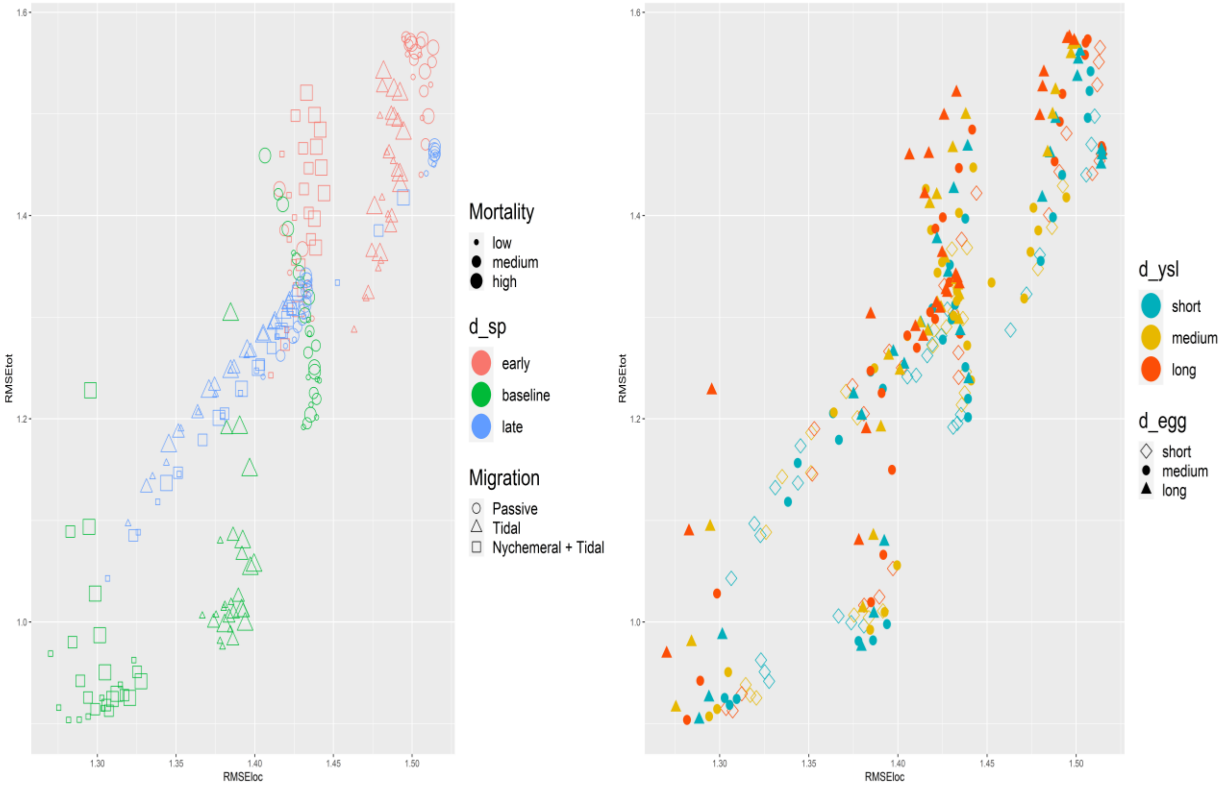


Figure 5-7 Fitting performances of the 243 parameterisations tested (Step 3) on local recruitment RMSEloc (for the UK, Be, Nl and Ge nurseries) and for the whole North Sea RMSEtot. Lower values indicate higher model performance. Left panel: performance for mortality (marker size), spawning peak (d_sp, marker color) and vertical migration type (marker type). Right panel: performance for larval duration of egg stage (d_egg, marker type) and yolk-sac larvae stage (d_ysl, marker color).

5.4 DISCUSSION

Several biophysical models have been used to identify the major factors of recruitment variability during the early life stages (Bolle *et al.*, 2009; Savina *et al.*, 2010b; Peck and Hufnagl, 2012) and variation in dispersal pattern (e.g. Cowen *et al.*, 2007). However sensitivity analyses considering several parameters have been rarely performed (Peck and Hufnagl, 2012). The present study evaluated the impact of the biological parameterisation on model prediction (larval recruitment and connectivity) and compared it with the impact of interannual variation. Focus was on the young stages of a flatfish living in the North Sea and Eastern English Channel. Among the metrics usually considered to characterise kernel dispersal and assess the results of the larval transport models (Huret *et al.*, 2010), this study focused on two metrics which quantify settlement success and dispersal pattern because of their usefulness for fisheries and conservation management: recruitment and connectivity. Overall, this study showed that biological parameterisation is more important than annual variability on larval recruitment, whereas it is the contrary for connectivity. Sensitivity analyses showed that most influential parameters were growth rate, spawning period and mortality. Calibration showed that a scenario with a low mortality associated to a long larval stage, and with a behaviour involving nycthemeral and tidal migration was best at reproducing past observations.

5.4.1 Do biological parameterisation and year-to-year variability have an impact?

A thorough sensitivity analysis of any model is required to assess whether the range of variation induced by parameters impacts the predictions. In the present study, the impact of parameterization is tested in comparison to interannual variability. The hydrodynamic conditions in the North Sea change yearly in relation to the NAO, wind condition and temperature (Bolle *et al.*, 2009; Berglund *et al.*, 2012; Kvile *et al.*, 2018). Sole, just as other flatfish species living in the North Sea, presents a high year-to-year variability of recruitment (Beverton and Iles, 1992; Gibson, 1997; van der Veer *et al.*, 2000a), which might be related to climate (Le Pape *et al.*, 2003b; Henderson and Seaby, 2005b). We find that the variability attributed to the biological parameterisation is higher than the annual variation in hydrodynamics. It highlights the need for a careful model calibration to properly assess larval recruitment.

Regarding connectivity, the LARVAE&CO model predicts less variability due to biological parameterisation than year-to-year variability. The connectivity pattern is quite stable and the main sources of variation are limited to the local spawning ground and adjacent regions. It is for example the case in Germany where the proportion of arrivals from Texel and German Bight varies in function of the chosen parameterization. The larger ranges of variation are predicted in the case of Belgium and the Netherlands; here the variation might be explained by the limited size of the nursery grounds and the possible variation in settlement over those nurseries. Overall, the results show limited variation which is restricted to nurseries and spawning grounds nearby. Sensitivity analyses of the results linked to biological parameters and interannual variability have shown that the most important factor of variability in dispersal and connectivity is the year-to-year variability. Similar results have already highlighted the importance of interannual variability on the connectivity patterns of sole in the North Sea (Bolle *et al.*, 2009; Lacroix *et al.*, 2013a) and in other case studies (Van der Veer *et al.*, 1998; Erftemeijer *et al.*, 2009; Kvile *et al.*, 2018). However, if biological parameters have a lower influence on connectivity than interannual variation, other sources of uncertainties known to influence the results, such as the model resolution or the choice of hydrodynamics models (Hufnagl *et al.*, 2017; Kvile *et al.*, 2018), were not evaluated in this study. They merit further investigation.

Uncertainties of the biological parameters mainly affect recruitment while connectivity is more robust to parameter variation. Hence the model is useful to estimate connectivity, a common output of larval transport models (e.g. Miller, 2007), with a minor focus on parameterisation and proper environmental conditions (such as hydrodynamics and temperature). On the contrary, using the model to predict recruitment would require a thorough calibration. It is an encouraging result because generally data on connectivity are limited while surveys are usually available to assess recruitment reliably on a regular basis.

5.4.2 The influence of parameters on model output

Once the relative impact of interannual variability in comparison to biological parameters is analysed, classifying the importance of model parameters in the prediction process is another important goal. The duration of the larval stage is the most important parameter for recruitment, followed by the date of spawning peak and mortality. Especially the duration that eggs drift in the ocean is crucial, gradually followed by each later development stage in order of importance.

The same is observed regarding mortality with a higher influence of egg mortality than the mortality of metamorphosing larvae due to a higher and temperature dependent mortality rate. This ranking of the importance of parameters from the first to the last development stage seems to match with the empirical knowledge of the larval stage, with a high importance attributed to the early life stages and a decreasing correlation between size and mortality (Houde 2008). The parameters pelagic larval duration and mortality are related to temperature and hence to the date of the spawning peak (Greve *et al.*, 2001; Rijnsdorp and Witthames, 2007). Globally the high degree of interaction in the model illustrates the large correlation among parameters and the necessity of a joined exploration of the parameter space, rather than one at a time analysis.

Other parameters such as settlement delay or migration behaviour have a lower influence on the model output. Previous studies have shown the importance of settling delay to increase recruitment, decrease interannual variability and improve the correlation with recruitment (Lacroix *et al.*, 2013a). In our study this parameter was not considered in the calibration process due to the relatively lower importance in comparison with other parameters. Settling delay has the effect to change drift duration. In our case different larval durations were tested, which might explain the lower importance of this parameter. In the same way, other modelling studies (Rochette *et al.*, 2012; Savina *et al.*, 2016) allow larvae to settle before metamorphosis as soon as they reach a suitable nursery area. Cues to set off larval settlement might be complex (e.g. Dixson and Hay, 2012; Dixson *et al.*, 2014); it would be an improvement if the nature of the settling cue would be known to improve the quality of the model.

Connectivity results are measurably different. If the spawning peak is also an important parameter; migration behaviour is one of the most important parameters whereas mortality and pelagic larval duration have a relatively low importance. An early or late spawning peak changes the hydrodynamic conditions encountered by the larvae and hence changes the dispersal pattern. The strong impact of the release period on the dispersal direction confirms similar modelling results for marine invertebrates (Ayata *et al*. 2010).

Vertical migration has previously been reported to influence the dispersal pattern (e.g. Fox *et al* 2006, North *et al* 2008). The inclusion of vertical behaviour in a biophysical model considerably affected both the mean distance and direction of larval dispersal especially there where tide is important (Sundelof 2012) as is the case in the Thames estuary and German Bight. The lower influence of pelagic duration on the dispersal pattern is typical for species with a long pelagic phase such as sole (Monroy *et al.*, 2017). Mortality is also less important in systems where connections are frequently made; in this case only the density of arrivals changes in contrast to large-scale systems with separated population, such as coral reefs, where mortality impacts connectivity (e.g. Cowen *et al.*, 2000).

5.4.3 Identification of the most optimal parameterisation

The calibration process allows to determine the most efficient parameterization to reproduce recruitment dynamics. The performance of the model considering the ‘baseline’ parameterisation for the spawning peak, is clearly better than alternative hypotheses that consider a late or early spawning, with the latter being the worst. Migration type presents an interesting pattern. In an environment forced by tides, where selective tidal transport might be important for flatfish, including sole (Bailey *et al.*, 2007), it is not surprising that the model had a lower performance with passive than with tidal migration. The vertical migration process may be locally adaptive as is the case for crab larvae (Moksnes *et al.*, 2014). When there is a heritable component, migration mechanisms might evolve rapidly under high selection pressure (Berthold *et al.*, 1992). Also the better performance of the model when nycthemeral migration is included draws attention. Nycthemeral migration has been documented for sole in the Bay of Biscay (Koutsikopoulos *et al.*, 1991) but not in the North Sea. In the latter case waters are more turbid (Fettweis and Van den Eynde, 2003), and hence the difference in day and night illumination limited, which might affect migration cues. In a well-mixed area like the North Sea, we hypothesize that this type of behaviour won’t impact the dispersal pattern. If larvae present this behaviour it might be for another reason not taken into account in the model. However the LARVAE&CO model clearly performs better when including this migration type than with a passive behaviour for first-feeding larvae. The central part of the North Sea is stratified in summer (Otto *et al.*, 1990) which may affect the connectivity of flatfish (Barbut *et al.*, 2019). Stratification of the water column associated with nycthemeral vertical migration might explain the better performance of this parameterisation. In this sensitivity study variable migration speed was not considered, which likewise should impact model prediction (Weinstock *et al.*, 2018).

The calibration showed less clear results regarding the mortality and duration of the larval stage. The lower importance given to the mortality parameterization of the different stages relatively to other parameters would allow to affect the same mortality rate for each stage and to assess performance of the model considering a unique high, medium and lower mortality rate for all stages. The best estimates of the mortality suggested that a low mortality improves model accuracy, but the result is less clear than for migration and spawning peak. Mortality is a complex process which varies in space and time; three main causes of mortality can be distinguished: advection, starvation and predation (Peck and Hufnagl, 2012). In the present study, only abiotic conditions (current and temperature) were considered.

The same conclusion of the lack of a clear impact on the results can be drawn for pelagic larval duration. If the best model estimation is obtained for a long duration of eggs and yolk-sac-larvae, there is no clear pattern which performs better locally and at the scale of the southern North Sea. In the model the temperature is the only parameter influencing directly the PLD, but variation in space and time, linked to food availability should also be investigated. PLD is often estimated from lab studies. There are many reasons why laboratory conditions may differ from the *in situ* environment and lead to wrong estimates of the PLD, where for example settlement does not occur in the same condition *in situ* in comparison to the laboratory (Selkoe and Toonen, 2011). In addition, PLD could be estimated by reading otoliths from field caught fishes, but in such case the link between growth and the environmental conditions is complex as the travel history of the fishes is unknown. Use of genetic and microchemical information could help reducing this source of uncertainty and should improve model prediction.

The parameterisation that reproduces the best recruitment dynamics at the regional scale of the southern North Sea as well as the local dynamics and particle distributions in the nursery grounds, is not guaranteed to reflect the real biological mechanisms. The best simulation is conditional on the other model assumptions, the choice and quality of observation data, and the way the space was explored. However, one might provide leads for model selection, offer the opportunity to direct biological research and propose for improved parameter knowledge, as larval duration or mortality are influential parameters for which calibration does not provide an optimal parameterization.

More complex models could be tested to assess if an increasing level of complexity increases model performance. As example, growth rate and mortality might also be related to environmental conditions, such as hydrodynamics, turbulence, and the match-mismatch between larvae and their food. To assess this aspect several studies have implemented more complex processes in larval dispersal models such as the prey field in metabolic model (Fiksen and MacKenzie, 2002; Huret *et al.*, 2012; Pitois and Armstrong, 2014). It is an option to implement the feeding performance of larvae related to hydrodynamic conditions and individual growth (China and Holzman, 2014; China *et al.*, 2017) in dispersal models (Fiksen *et al.*, 1998). Model complexification could have an added value on model prediction but would increase the number of parameters, which would in turn complicate the assessment of the sensitivity to parameterisation.

An alternative approach might consist of using other data sources to improve model parameterisation such as otoliths, biological field data and arrival dates in the nurseries. This type of approach was used for example to assess body growth, movement and mortality of European eel based on larval information (Melià *et al.*, 2013).

From this study, it seems that a thorough calibration of biological parameters is not needed to assess connectivity but is rather needed for a proper assessment of year-to-year variability of recruitment. However connectivity could also be affected by other parameters not tested in the present study, such as in the physical and hydrodynamic model. Hufnagl *et al.* (Hufnagl *et al.*, 2017) compared 11 larval transport models in the North Sea and concluded that major differences in dispersal patterns characterized the models. Therefore a test of the impact of different hydrodynamic models on the LARVAE&CO model would provide an additional insightful test of interannual variability.

5.4.4 Conclusions

From a fisheries management perspective, it is important not only to quantify model output uncertainties but also to identify the most influential parameters for which an improvement of the precision would contribute to an increase in model reliability. Overall, this study showed the limited variation of connectivity due to biological parameters. Hence the LARVAE&CO model prediction of the early stage of fish is ready for integration in complex models, especially the migration in models including spatial stock dynamics (Archambault *et al.*, 2015) and larval mortality during the larval phase. Both factors have been identified as important and sensitive parameters for fisheries management, especially for sole (Gasche *et al.*, 2013).

Chapter 6. GENERAL DISCUSSION AND PERSPECTIVES

The aim of my PhD thesis was to improve knowledge on the dispersal and recruitment of (flat)fish and to quantify the impact of natural constraints and abiotic pressures. I addressed the following questions:

Question 1: Which environmental factors influence the recruitment of flatfish?

Question 2: Which factors impact dispersal during the early life stage of flatfish?

Question 3: How does one calibrate and evaluate a LTM?

Question 4: What is the impact of frontal systems on the larval dispersal of flatfish?

Question 5: Does the spatial structure of management match with the population structure induced by larval dispersal?

Question 6: How do life history traits influence dispersal during early life?

Question 7: How does expansion of OWFs across the North Sea impact demersal fish?

Question 8: What is the impact of climate change on the early life stages of flatfish?

To answer these eight questions, I developed a case study on flatfish living on the continental shelves of the northeaster Atlantic Ocean, more specifically the North Sea and English Channel. I modelled the dispersal of the early life stage of several species with an individual based model (LARVAE&CO) coupled to a well-proven 3D hydrodynamic model (COHERENS). First, I assessed the dispersal patterns in the North Sea; second, I assess the potential impact of anthropogenic pressure and finally I assessed the likelihood of the prediction. After an analysis of the methods, the general discussion focuses on the lessons learned in regard to management, the potential impact of anthropogenic pressure on the flatfish of the North Sea and finally presents the main perspectives on the extension of the research.

1.1 METHODOLOGICAL ANALYSIS: LARVAL TRANSPORT MODELS FOR FISHERIES SCIENCE

The main objective of this PhD thesis is to test the impact of the environment and anthropogenic pressure on the early life stages of flatfish in the North Sea and Eastern English Channel. Investigating early life stage dispersal and survival is challenging but feasible, because it is a complex process with numerous interactions during larval drift (environmental and phenological at small spatial and temporal scales) and requires the use of models due to the challenges of empirical observation. To realise this objective, an approach based on a biophysical larval transport model was chosen. In this context, assessing the validity of a model is essential for its credibility, especially in a management context. Hence, Chapter 5 is dedicated to the analysis of the uncertainties of the results and compares prediction to data with the aim to calibrate the model to answer to the following question:

Question 3: How does one calibrate and evaluate a LTM?

6.1.1 Coping with uncertainty

Dispersal and survival early in the life of a fish is a complex process related to many interactions among environmental and biological processes. A larval transport model is a simplified representation of those processes, which involves nevertheless a large number of parameters. Numerous studies have investigated the sensitivity and robustness of Lagrangian transport models, as well in the case of physical parameters as the temporal and spatial resolution or density and number of particles released (Huret *et al.*, 2007a; Simons *et al.*, 2013; Savina *et al.*, 2016; Kvile *et al.*, 2018) or the structure of the water column and currents (Munk *et al.*, 2009). Among those parameters, biological parameters are the most uncertain due to the difficulty of direct observation in the marine environment. Life history traits are especially difficult to assess during the poorly documented early life stages (Levin, 2006) and hence parametrization remains uncertain.

Many studies have highlighted the role of biological parameters on dispersal patterns, whose differences are related to larval traits (López-Duarte *et al.*, 2012) such as behaviour (Fox *et al.*, 2006b; North *et al.*, 2008; Robins *et al.*, 2013), duration of the larval stage (Shanks, 2009a), seasonality (Lett *et al.*, 2010) and spawning period (Ayata *et al.*, 2010). The analyses help to understand model behaviour and provide guidelines to modelers. However, systematic sensitivity analyses of the biological parameters are even more limited. More formal analyses to identify most influential parameters are rarely carried out because the numerous parameters and long duration of simulations prevent the computation of sensitivity indices linked to the principal effects and interactions. Similarly, the integrated estimation of uncertain parameters through automatic algorithms is often not an option for these kinds of models. In order to improve the current biophysical model of sole and to sort out the many alternative hypotheses on its larval drift, we propose to rely on a sequential methodology combining sensitivity analysis and model selection as proposed for example by Lehuta *et al*. (2013).

A thorough sensitivity analysis of the model results is needed to assess whether the range of variation induced by parameters impacts the model predictions. I tested the impact of parameterization in comparison to interannual variability. The hydrodynamic conditions in the North Sea change yearly in relation to the NAO, wind condition and temperature (Bolle *et al.*, 2009; Berglund *et al.*, 2012; Kvile *et al.*, 2018). Sole, similar to other flatfish species in the North Sea, experience a high year-to-year variability in recruitment (Beverton and Iles, 1992; Gibson, 1997; Van Der Veer *et al.*, 2000), which might be related to climate (Le Pape *et al.*, 2003a; Henderson and Seaby, 2005a). I observed that, for the recruitment, the variability attributed to biological parameterization is higher than the interannual variation due to hydrodynamics. It also highlights the need for a careful model calibration to properly assess larval recruitment. Regarding connectivity, the model predicts less variability due to biological parameterization than year-to-year variability. Unlike recruitment, sensitivity analyses of the results linked to biological parameters and interannual variability have shown that the most important factor of variability in dispersal and connectivity is the year-to-year variability. Similar results have already highlighted the importance of interannual variability on the connectivity patterns of sole in the North Sea (Bolle *et al.*, 2009; Lacroix *et al.*, 2013b) and elsewhere (e.g. Kvile *et al.*, 2018). However, if biological parameters have less influence on connectivity than interannual variation, other sources of uncertainty known to influence the results, such as the model resolution or the choice of hydrodynamic models (Hufnagl *et al.*, 2017; Kvile *et al.*, 2018), were not evaluated in this study. They merit further investigation. Recruitment suffers from uncertainties of biological parameters while connectivity is more robust to parameter variation. Hence models provide useful estimates of connectivity, a common output of larval transport models (e.g. Miller, 2007), with a minor focus on biological parameterization than on proper environmental conditions (such as hydrodynamics and temperature). In contrast, using the model to predict recruitment would require a thorough calibration. This is an encouraging result because there is generally a limited amount of data available on connectivity, while surveys are usually available to assess recruitment on a regular basis.

Vertical migration has previously been reported to influence the dispersal pattern (Fox *et al.*, 2006a; North *et al.*, 2008). The inclusion of vertical behaviour in a biophysical model considerably affected both the mean distance and direction of larval dispersal, especially there where the tide is important (Sundelöf and Jonsson, 2012), such as in the Thames estuary and German Bight. The sensitivity analyses highlight the local impact of some parameters and the need to take them into account before generalizing the results of Chapter 5 for influential parameters.

Sensitivity analysis requires a lot of computational time (CPU), which increases exponentially, to explore parameter space. Testing all combinations is impossible, hence sensitivity analysis involves a trade-off among computation time and extensive parameter space exploration. The methods I chose to assess sensitivity analyses present some important limitations. At first the group screening approach in particular may have over-weighted the importance of biological parameters in comparison to years. Second, the optimised design reduces the number of simulations but only computes a sensitivity index and doesn't allow to perform a fine exploration of effects and direction of effects as in the case of a full design.

Recent progress in big data analysis and the development of machine learning might represent an interesting solution. Particle dispersal models could be summarized as a large data base where the predicted destination is a function of model parameters (such as larval traits, starting point, and date of release related to environmental conditions). It might be interesting to develop a meta-model in complement to simulations and predict with supervised learning algorithms a set of non-simulated parameters.

In conclusion, methods exist to explore big models with numerous parameters, and I used them to assess the impact of a set of parametrizations in a larval dispersal model. They represent proper approaches to assess models as advocated by Lehuta et al. (2016).

6.1.2 Calibration and validation

Larval transport models could be made more complex to better represent processes which affect the early life stages of fish. One such variable is the prey field. Bioenergetic models have been coupled to dispersal models (Pecquerie *et al.*, 2009) with incorporation of a size-structured prey field (Huebert and Peck, 2014). Other models go a step further by including physical parameters like turbulence and light to estimate mortality (Fiksen and MacKenzie, 2002; Vikebø *et al.*, 2007). One of the major issues is to assess whether adding parameters and complex processes really improve model prediction. Do the new parameters improve the reliability of the model? To investigate this particular aspect, especially when models are used in a management context, data are needed to assess model performance. Data useful to calibrate early life stage models are scarce. In the frame of this thesis, I used recruitment data on different nursery grounds in the North Sea to determine the most efficient parameterization allowing to reproduce the observed recruitment dynamics.

Such approach determines the most probable parameterization of the spawning peak period and vertical behaviour. The performance of my model considering the 'baseline' parameterisation for the spawning peak, is clearly better than alternative hypotheses that consider a late or early spawning, with the latter being the worse.

The incorporation of vertical migration leads to interesting spatial patterns. In an environment forced by tides, where selective tidal transport may be important for flatfish (Duffy-Anderson *et al.*, 2015), it is not surprising that the model showed lower performance with passive than with tidal migration. The vertical migration process might be locally adaptive, as is the case for crab larvae (Moksnes *et al.*, 2014b). When heritable, migration mechanisms might evolve rapidly under high selection pressure (Berthold *et al.*, 1992). Also the better performance of the model when nycthemeral migration is included draws attention. Nycthemeral migration has been documented for sole in the Bay of Biscay (Koutsikopoulos et al., 1991) but not in the North Sea. Here the turbid waters (Fettweis and Van den Eynde, 2003) constrain day and night illumination and affect vertical migration cues. In a well-mixed area like the North Sea, we hypothesize that this type of behaviour will not impact the dispersal pattern. If larvae present this behaviour it might be for another reason not considered in the model.

Calibration showed less clear results regarding the mortality and duration of the larval stage. Mortality is a complex process which varies in space and time. Four main sources of mortality can be distinguished: advection, starvation, infection and predation (Peck and Hufnagl, 2012; Gustavsen *et al.*, 2014; Penczykowski *et al.*, 2014). Including a more complex process to simulate mortality is an interesting perspective. In the model the temperature is the only parameter influencing directly pelagic larval duration (PLD), but variation in space and time, linked to food availability should also be investigated. PLD is often estimated from lab studies, but there are many reasons why laboratory conditions may differ from the *in situ* environment and lead to wrong estimates of the PLD. For example settlement does not occur under the same conditions *in situ* in comparison to the laboratory (Selkoe and Toonen, 2011). In addition, PLD could be estimated by reading otoliths from field caught fishes, but in that case the link between growth and the environmental conditions is complex as the travel history of the fishes is unknown. Genetic and microchemical information might help to reduce this source of uncertainty and should improve model prediction.

The parameterisation that reproduces the best recruitment dynamics at the regional scale of the southern North Sea as well as the local dynamics is not guaranteed to reflect the true biological mechanisms at play. It is conditional on the other model assumptions, the choice and quality of observation data, and the way the space was explored. However, one might provide leads for model selection, offer the opportunity to direct biological research and propose for improved parameter knowledge: pelagic larval duration and mortality are influential parameters for which calibration does not provide a clear optimal parameterization. More complex models could be tested to assess if an increasing level of complexity increases model performance. Model complexification could have an added value on model prediction but would increase the number of parameters, which would in turn complicate the assessment of the sensitivity to parameterisation.

A clear objective is needed to implement a calibration based on the right data. Here the calibration is based on recruitment, which does not contribute to the evaluation of the dispersal reliability of the model. The problem of assessing a question on a substitution criterion is well known and has led to famous examples of poor medical care (e.g. Riggs *et al.*, 1990; D'Agostino, 2000; Nissen and Wolski, 2007). However, from this study it seems that a thorough calibration of biological parameters is not needed to assess connectivity but is rather needed for the proper assessment of year-to-year variability of recruitment.

In absence of the direct observation of the dispersal of early life stage to evaluate the biophysical model, an alternative approach might consist in using other data sources to improve model parameterisation such as otoliths, larval field data and arrival dates in the nurseries (Paoletti et al. submitted). This type of approach was used for example to assess growth, movement and mortality of European eel based on larval information (Melià *et al.*, 2013).

However, connectivity might also be affected by other parameters not tested in the present study, such as in the hydrodynamic model (including model resolution or waves effect on drift) . Hufnagl et al. (Hufnagl *et al.*, 2017) compared 11 larval transport models in the North Sea and concluded that there were major differences in dispersal patterns. Therefore, a test of the impact of different hydrodynamic models on the LARVAE&CO model would provide a complementary insightful test of interannual variability.

6.2 WHAT CAN WE LEARN FOR FISHERIES MANAGEMENT?

Fisheries management is founded on knowledge of population structure and dynamics (Kerr *et al.*, 2010). This thesis focuses on improving knowledge on the early life stages of six flatfish species, including four species (brill, turbot, flounder and dab) for whom knowledge on the early life stages is data limited. Brill, turbot, flounder and dab are not so much target species of the fishery in the North Sea but knowledge on them is important in a "co-management" fishery (Worm *et al.*, 2009). Populations are part of communities and ecosystems and have to be considered in ecosystem-based management, which includes ecosystem connection, appropriate spatial and temporal scales, ecological integrity and biodiversity (Long *et al.*, 2015). Ecosystem-based management aims at sustaining the marine ecosystem and the fisheries they support (Pikitch *et al.*, 2004).

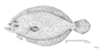
6.2.1 The dispersal patterns of six flatfish species

If sole and plaice have been well studied in the North Sea, the dispersal of the early life stages of other flatfish remains poorly known. The lack of information about some life-history traits (and hence their parameterization) implies uncertainties which might affect the robustness of the model prediction.

Table 6-1 shows the current confidence in model prediction and parameters. Improving the parameters would further enforce model prediction. Such analysis helps to answer to the following question:

Question 2: Which factors impact dispersal during the early life stage of flatfish?

Table 6-1 List of the most uncertain parameters and the level of confidence in model predictions of six flatfish species.

		Uncertain parameters	Confidence
	**Plaice**	Pld	High
	**Turbot**	Spawning ground	Medium
	**Dab**	PLD, spawning distribution, nurseries	Low
	**Sole**	Spawning period	High
	**Brill**	Spawning ground	Very low
	**Flounder**	Spawning ground	Medium

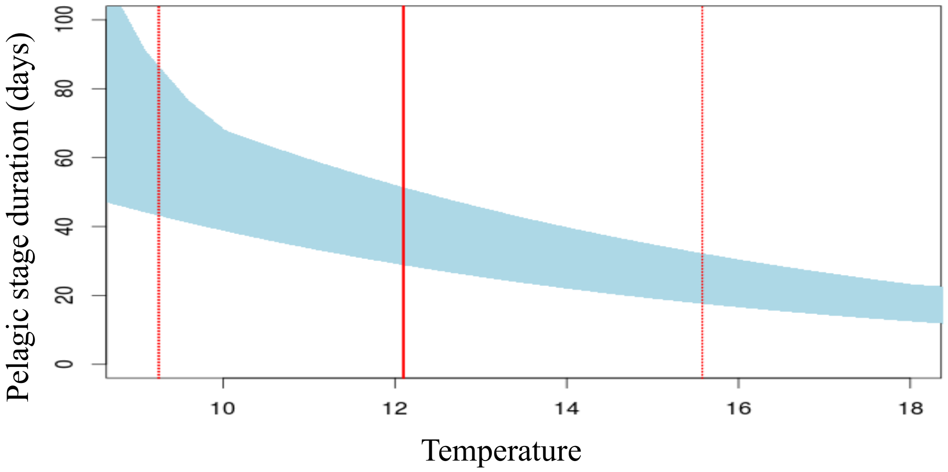


Figure 6-1 Range of variation of sole PLD; the red vertical line illustrates the minimum, mean and maximum temperature experienced by sole larvae in the North Sea.

Sole. Confidence in the model output is high for sole and plaice because they have been well studied in the North Sea and English Channel, and many life history traits have been documented in several independent studies (Chapter 2). Predictions on dispersal are coherent with other studies (Bolle *et al.*, 2009; Hufnagl *et al.*, 2013; Savina *et al.*, 2016) and fit with the genetic population structure (Hoarau *et al.*, 2002a, 2004; Vandamme *et al.*, 2020; Le Moan *et al.*, 2021). However, the parameterization of our model could be better. The pelagic larval duration of sole is a sensitive parameter as shown in Chapter 5. Calibration of the sole model did not allow a clear choice of the best parameters among the important intervals of pelagic larval duration present in the literature following compilation of various sources (Figure 6-1). The difference in pelagic duration is about 20 days in drifting at a mean temperature of 12°C experienced by sole larvae in the North Sea. The source of the estimates are the various studies and methods (Bolle *et al.*, 2005, 2009; Rochette *et al.*, 2012; Lacroix *et al.*, 2013a) as well modelling choices to interpolate the values (interpolation function of empirical data chosen or definition of stages).

Plaice. Similar uncertainties on the life history of sole apply to plaice. The parameterization chosen here for PLD (3 months on average) seems slightly longer in comparison with other studies based on otolith analyses (Bolle *et al.*, 2009). But, unlike sole, the spawning period of plaice is stable. For example, the spawning peak, which is easily estimated, occurs on average on 19 January with a standard deviation of 7 days in the Southern North Sea (Simpson, 1959). This is not so for sole which makes this parameter highly sensitive in the model for sole.

Turbot and flounder. The confidence in modelling the dispersal of turbot and flounder is moderate. The predicted population structure is coherent with the empirical dispersal pattern. Uncertainties on PLD as for plaice or sole remain important but are not critical. Indeed, recent data are available from different sources for those species (see Chapter 2). However, the knowledge on the location of the spawning grounds is limited and data in this study have a low level of resolution.

Dab. The predictive value of dab might be considered low. Indeed, there is limited modelled and empirical information on dispersal to compare with our model prediction (Tysklind *et al.*, 2013). In addition, PLD remains uncertain; the method based on the difference between the observed spawning peak and peak of arrival in the nurseries did not consider variability attributed to the environment. In the model nurseries are considered similar to plaice but in the literature, nurseries have been reported elsewhere (Bolle *et al.*, 1994). Improving and extending the definition of nurseries might change the dispersal estimates (and increase connectivity). The spawning period extends over a long period, hence changes in the function to simulate egg distribution, could also change dispersal pattern (i.e., increase the peak at certain periods could change the pattern due to effect of seasonality). However due to the high density in the North Sea and the association with a long PLD and a large spawning period, a high level of connectivity is likely.

Brill. Brill is the flatfish with the lowest confidence in the model. In addition to uncertain life history traits (I assume a constant PLD), low resolution of spawning grounds and absence of spatial information in the EEC make the modelling power limited (for details see Chapter 2). The dispersal pattern doesn't match with population genetic studies, which observed a well-mixed population structure (Blanquer *et al.*, 1992; Vandamme *et al.*, 2020), whereas the model predicts low exchange among the southern and central part of the North Sea. The mismatch between genetic structure and predicted early life stage dispersal does not mean that prediction is wrong. Genetic structure is a complex process which involves the whole life cycle in addition to historical processes, which are not incorporated in the model prediction.

There are three options to improve the model parameterization of flatfish dispersal in the North Sea. First lab experiments capture information in a controlled environment (e.g. metabolism) and determine the specific effect of parameters (e.g. Teal *et al.*, 2008). This approach might be limited to capture the complexity of interactions in the natural environment and results might be constrained by lab conditions. A second approach is the statistical analysis of distribution patterns, either population-specific (Sakuma *et al.*, 2020), species-specific (Andrews *et al.*, 2020) or as a community (Ovaskainen *et al.*, 2017). A third approach is the *in situ* measurement based on field experiments. To assess variation on a large scale while considering seasonal and interannual variability is complex and challenging. In addition, the estimation of some parameters, such as PLD, remain challenging especially for the early stages (eggs and yolk-sac-larvae). Other *in situ* approaches such as larval tagging or parental analyses (Bravington and Ward, 2004; Cuif *et al.*, 2015) remain complex in the case of flatfish in the North Sea. An integrated approach combining various sources of information such as otolith analyses (microchemistry and shape) and population genetics might improve knowledge on dispersal dynamics.

6.2.2 Life history traits and their impact on dispersal

One of the aims of this PhD thesis was to improve the assessment of the factors influencing the dispersal of flatfish. In Chapter 5, I determined which processes (parameters) have an important impact on the dispersal model of the early life stage of sole. I hypothesise that the results for sole could be extrapolated to other flatfish species in case of similar life history traits. Such assumption does not prove that biological mechanisms included in the model are correct. The model results must be carefully considered, but the modelling approach allows to make hypotheses and answer to the following questions:

Question 4: What is the impact of frontal systems on the larval dispersal of flatfish?

Question 6: How do life history traits influence dispersal during early life?

The parameters which influence most the dispersal of early life stages are the date of spawning peak, the PLD and to a lesser extent vertical migration type. As highlighted in Chapter 2, the dispersal distance is correlated with the duration of the planktonic stage. PLD is not the only important parameter seasonal differences in current strength (Holt and Proctor, 2008) and the presence of a physical barrier to dispersal might explain the difference in distance.

The frontal system structures hyperbenthic and benthic communities (Dewicke *et al.*, 2002; De Nooijer *et al.*, 2008) and flatfish species (Gibson, 2005b; Vandamme, 2014).

The six flatfish species studied might be classified into two categories. Brill, sole and turbot, which present a lower level of connectivity and similar life history traits (spawning mainly inshore during spring/summer and a short PLD), belong to the first category. Plaice, dab and flounder, which present a higher level of connectivity, spawn further offshore (dab and plaice) in autumn/winter and a long pelagic larval duration, are in the second category. The association of these traits can be interesting for a study in itself to assess the optimal reproductive strategy in the North Sea. Spawning season and PLD might be linked. A warmer season is usually associated with a faster growth rate due to easier access to food and a higher metabolism, and hence a decrease in dispersal distance. However, this is not sufficient to explain the association between spawning season and PLD. The optimal strategy to disperse and increase recruitment may be tested through implication of different larval traits or extended to other species which are dependent on coastal nurseries.

6.2.3 The estimation of recruitment and the link to environmental conditions

One aim of this PhD thesis is to improve knowledge on population dynamics, especially processes related to the early pelagic stage of fish. In Chapter 2, it was shown that in addition to life history traits and interannual variability, environmental conditions affect larval transport and flatfish recruitment in the North Sea, which is consistent with literature (van der Veer, 1986; van der Veer and Witte, 1999; Bolle et al., 2009). However, Chapter 5 highlights that parameter uncertainties have a strong impact on model prediction, especially on PLD, mortality rate and spawning peak timing. Such conclusions highlight the importance of a proper model calibration to quantify settlement in nurseries. Unfortunately, calibration data are quite limited with the notable exception of sole and plaice. For most of the species studied, no data on stock biomass or recruitment are available to allow model calibration. However, our model provides trends which are interesting to consider. We assess which environmental factor(s) might have an impact on recruitment.

In addition to interannual variability at the regional scale, the model predicted strong variation of larval recruitment at the local scale. The question of spatialization of larval arrival is very important in the case of nursery-dependent species such as flatfish to understand population dynamics and especially the contribution of the juvenile stage (Le Pape et al 2003, Rochette et al 2010). Larval recruitment estimated by the model is strongly dependent on parameter uncertainties, especially egg densities, which may change the abundance of larvae arriving at the nursery grounds predicted by the model.

The model predicts important recruitment in the German Bight. This prediction might be slightly overestimated in the German Bight and underestimated in the Dutch nursery grounds in comparison with the recruitment data of sole and plaice from demersal young fish survey campaign (WGBEAM, 2019). The result might be explained by the implementation of the model itself, which does not include a proper representation of the shallow Wadden Sea. The Wadden Sea is a well-known area for the larval settlement of sole and plaice. Some larvae, which should have entered the Wadden Sea, continue their drift up to the German Bight. One way to improve the model prediction of recruitment in these two nursery grounds, would be to properly include the Wadden Sea in the model domain.

To move one step further in assessing the role played by environmental conditions on larval recruitment, it might be interesting to realise a long duration simulation (covering more than two full NAO cycles) for all flatfish species and to assess how environmental conditions (such as wind regime, NAO index, river discharge and temperature) impact recruitment prediction, similar to Pacariz et al. (2014) on cod in the Baltic Sea and Bolle et al. (2009) on plaice in the North Sea.

6.2.4 The role of larval food in recruitment processes

In 1914, the Norwegian Johan Hjort was one of the first to hypothesise that the variation in year-class strength of cod resulted from a change in the availability of plankton (Hjort, 1914). David Cushing developed this idea further and proposed the idea of "match/mismatch" (Cushing, 1990). During the "critical period" for larvae, which is the first few days after the yolk sac is resorbed, food is key to survival (Cushing 1990; Houde 2008). Starvation or bad feeding may also limit larval growth (and hence extend the larval phase), decrease the physiological condition and finally increase predation and mortality (Pepin, 1991, 2016; Cowan *et al.*, 1996; Garrido *et al.*, 2015). The presence of larvae and their food is a dynamic process changing in space and time in function of environmental factors (temperature, current, light, nutrients, phytoplankton and zooplankton abundance). Understanding the spatial dynamics of prey availability is important to understand processes related to recruitment.

In the frame of this PhD, spatio-temporal overlap between the occurrence of sole larvae and chlorophyll concentration was assessed with the aim to test if the match/mismatch between sole larvae and food explains the interannual variability of sole recruitment as observed empirically (BOX 1).

BOX 1

Sole larvae prey mainly on zooplankton (Last et al. 1978). Because extensive data on zooplankton are not available, a comparison between larval sole presence and chlorophyll concentration (used as a proxy of larval prey) was made. Indeed, data on zooplankton and patchiness are rare contrarily to chlorophyll observations, which are available from everywhere in the North Sea at a sufficient temporal resolution from remote sensing. The chlorophyll concentration was combined with larval distribution predicted by the model to compare match/mismatch level and sole recruitment observed in the North Sea for the period 2003-2011.

Hypothesis: The spatio-temporal overlap between larval presence and chlorophyll concentration explains partially recruitment variability.

Method

Model dispersal was predicted from the various spawning grounds and the proportion of larvae arriving in the nurseries. For each of the six spawning grounds of sole in the North Sea (see

Chapter 2) we estimated an average chlorophyll concentration from remote sensing and density of larvae from model. We also compared the presence of larvae and chlorophyll concentration for the period 2003-2011 in space and time.

Data: Chlorophyll concentration was obtained from the MERIS sensor in the frame of MARCOAST project (Van Der Zande 2013). Processing details are available from Nechad et al. (2009) and Vanhellemont et al. (Vanhellemont *et al.*, 2011). A time series of the mean chlorophyll concentration over each spawning ground was extracted for each year within the period 2003-2011 (Van Der Zande, pers. Comm.). In addition, some temporal indicators of the phytoplankton bloom such as the start and end date of the bloom, and maximum concentration of the bloom were also computed (Van Der Zande, pers. comm.). Sole recruitment (age 0) calculated from a virtual population analysis (VPA) was estimated from the ICES demersal young fish surveys in the Belgian and Dutch nurseries (WGBEAM 2015).

Model input data: The distribution of larvae is provided by the sole larval transport model described in Chapter 1. Focus was on the first feeding larvae (FFL), which is the most critical stage for starvation (Houde 2008). The selection of the period where the FFL were the most abundant was a three-step process (Figure 6-2). First, we selected the temporal period where FFL were the most abundant (75 %). In a second step, we selected spatially the highest concentration (80 % of larvae) over the period selected and finally we averaged the chlorophyll concentration on this area.

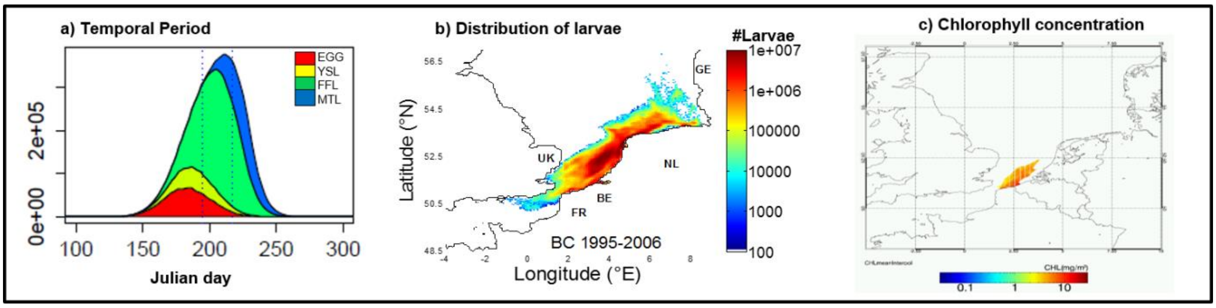


Figure 6-2 Method to estimate the area of the analysis. a) Estimation of the period where the FFL are the most abundant (75 %, dotted lines), (b) selection of area where the highest density of larval fish (80 % of the distribution) is observed during this period and (c) extraction of the time series of chlorophyll concentration averaged over this area.

Match/mismatch criteria: To assess the spatial and temporal correlation between sole larvae and their food, we combined the time series of FFL presence and chlorophyll concentration for each spawning ground and we calculated the common area under the two curves to calculate two overlap metrics.

a) Normalised overlap (NO): we normalised the two times series before computing the common area (intersection between the two curves). This criterion represented the temporal overlap.

b) Not normalised overlap (NNO): computation of the area under the two curves without normalisation. This indicator was mainly driven by the value of chlorophyll concentration and not the temporal overlapping.

Connectivity: To assess the relationship between match/mismatch and recruitment in different areas we used the connectivity matrix predicted by the dispersal model (see Chapter 1), which represents the proportion and origin of migrants. The overlap metrics of all spawning grounds were computed by linear combination on the basis of their relative proportion arriving in nurseries to obtain an annual value for each nursery ground. This was computed for both overlap metrics (NO & NNO).

Statistical analysis: In each of the nurseries, a linear regression was computed between overlapping indicator, recruitment predicted, and recruitment observed to assess correlation.

Results

Overlap between the presence of sole larvae and their prey varies interannually for both indicators. Some years matched considerably between both variables, whereas other years showed a shift (larvae arrived either earlier or later in relation to the phytoplankton bloom) (Figure 6-3).

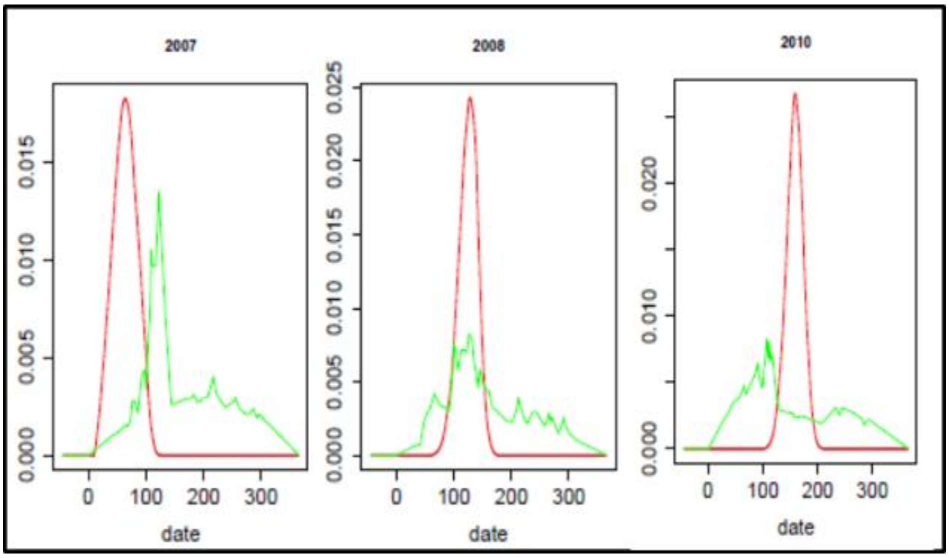


Figure 6-3 Example of a normalised time series for the year 2007, 2008 and 2010 for the larvae spawned in the Belgian spawning ground. Chlorophyll concentration (green) and first-feeding larvae (red).

As an example, the results for the Belgian and Dutch nurseries did not show any correlation between the overlap index and the recruitment, whatever the overlap considered (with or without normalisation) (Figure 6-4). Results were similar for the other nurseries.

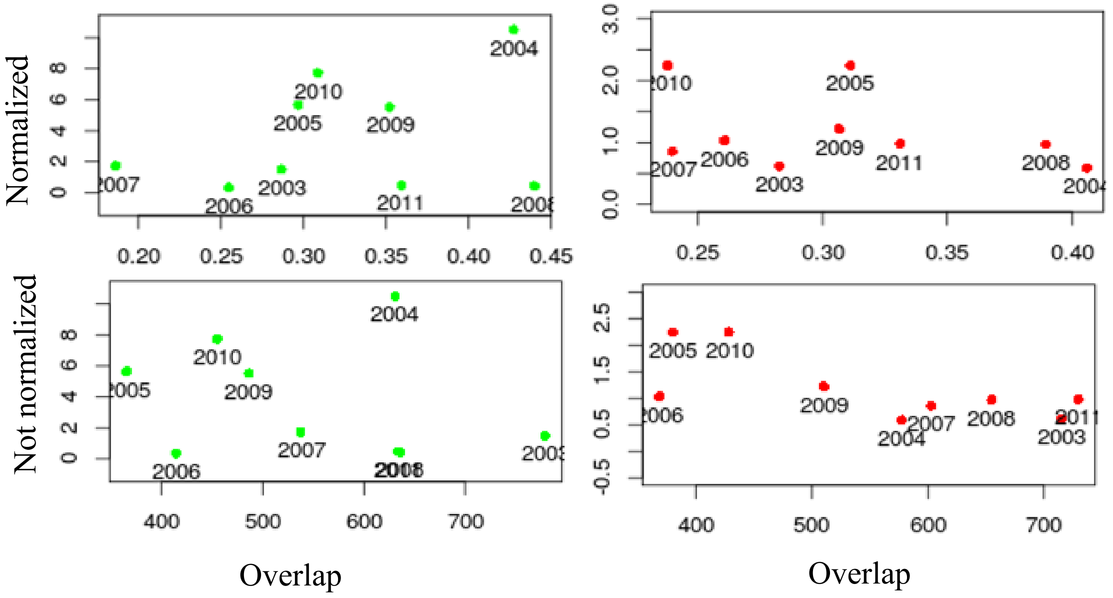


Figure 6-4 Overlap index (upper: normalized, lower: not-normalized) in function of recruitment in the Belgian (left) and Dutch (right) nurseries.

In summary, the analysis did not show a significant correlation between spatial overlap of chlorophyll concentration (used as a proxy of larval food) and larval presence (predicted by the model) and the recruitment observed in the North Sea nurseries (results not shown).

Several hypotheses might explain the absence of a correlation before concluding a lack of impact of food on recruitment of sole larvae. First, the model itself might not be able to accurately represent the spatio-temporal dynamics of larvae in the North Sea. Uncertainties on the estimation of spawning period and pelagic duration may influence the prediction. The model explained 30 % of the recruitment variability (Lacroix et al. 2013) and has been calibrated mainly on recruitment (Chapter 5). It is possible that the best available calibration based on recruitment is not suitable to explain the temporal and spatial dynamics of the larval cloud. A research priority might be the assessment of the model likelihood in comparison with *in situ* data of larval presence. Also, the arrival date in the nursery ground might be important. The construction of a proper proxy of prey might also be most valuable. Second, chlorophyll might not be a suitable proxy of prey for sole larvae. A way to improve the model would be to include the lag between chlorophyll peak and zooplankton peak, estimated from CPR data (Richardson et al. (2006), in the correlations tested. In addition, the high chlorophyll concentration in the southern North Sea is mainly due to *Phaeocystis,* which forms colonies that, above a certain size (400 µm) are not grazed by zooplankton (Lancelot *et al.*, 2009). They largely represent a sink in the food web and can explain the absence of correlation among chlorophyll concentration and recruitment. Third, food might not be limiting. Sole spawn inshore and larvae are present in the water column during summer, which probably prevents sole larvae from food depletion because they live in the presence of high food densities during their pelagic stage (Reid *et al.*, 1990).

Chapter 2 showed the importance of seasonality in dispersal pattern (i.e larval distribution) in the North Sea, seasonality play also an important role in the larval food presence in the North Sea. Investigate this question represents an interesting perspective to improve understanding of recruitment process. In the future, the same study might be repeated with another species such as plaice, which spawns offshore during winter, and for whom food availability might be more critical and for which life traits are well documented and recruitment assessed.

Another perspective is to include prey field (from ecosystem model or direct observation) in the individual based model to improve estimation of larval growth and mortality (Daewel et al., 2008, 2015; Nicolas et al., 2014; Pitois and Armstrong, 2014).

6.2.5 Stock structure and management: a comparison between our findings and flatfish management in the North Sea. The link with ecological and evolutionary connectivity.

Question 5: Does the spatial structure of management match with the population structure induced by larval dispersal?

The Eastern English Channel (EEC) and North Sea are important and complex fishing grounds. The area is bordered by seven countries and divided in several management units, which are mainly inspired geopolitically and do not consider very well oceanographic and spatial features. My thesis has shown that the impact of stock structure on management might be evaluated in regard to the Frisian and German Bight fronts, which are barriers to dispersal. To the north of these fronts populations of flatfish have lower densities (Gibson 2005; Vandamme et al. 2014) and hence the impact of structure might be limited from a fisheries perspective. Uncertainties about prediction, especially for data limited species, have to be used carefully based on the results of this thesis. The prediction of dispersal of early life stage and management area are summarized in Figure 6-5.

Sole is managed as a unique stock in the North Sea (subareas IVa, IVb and IVc), whereas models found a limited dispersal during early life among IVa and IVb. Hence the management area might be a mismatch (Reiss *et al.*, 2009). However sole populations are small in the northern part of the North Sea and this mismatch might not be critical for assessing the population dynamics. Sole is also manage as an unique stock in eastern English Channel, this thesis did not investigate in details this area but recent study (Randon *et al.*, 2020) suggest the presence of subpopulation and a mismatch between population structure and management area.

Plaice shows a high level of modelled connectivity at the larval stage. Management units in the North Sea and English Channel seem coherent with the patterns found in this study. Models predict exchange of larvae from IVc to IVb and *vice versa*. Exchange among the EEC is predicted in a one-way direction from EEC to the North Sea. The species is managed in separate areas in these zones, which seems well adapted.

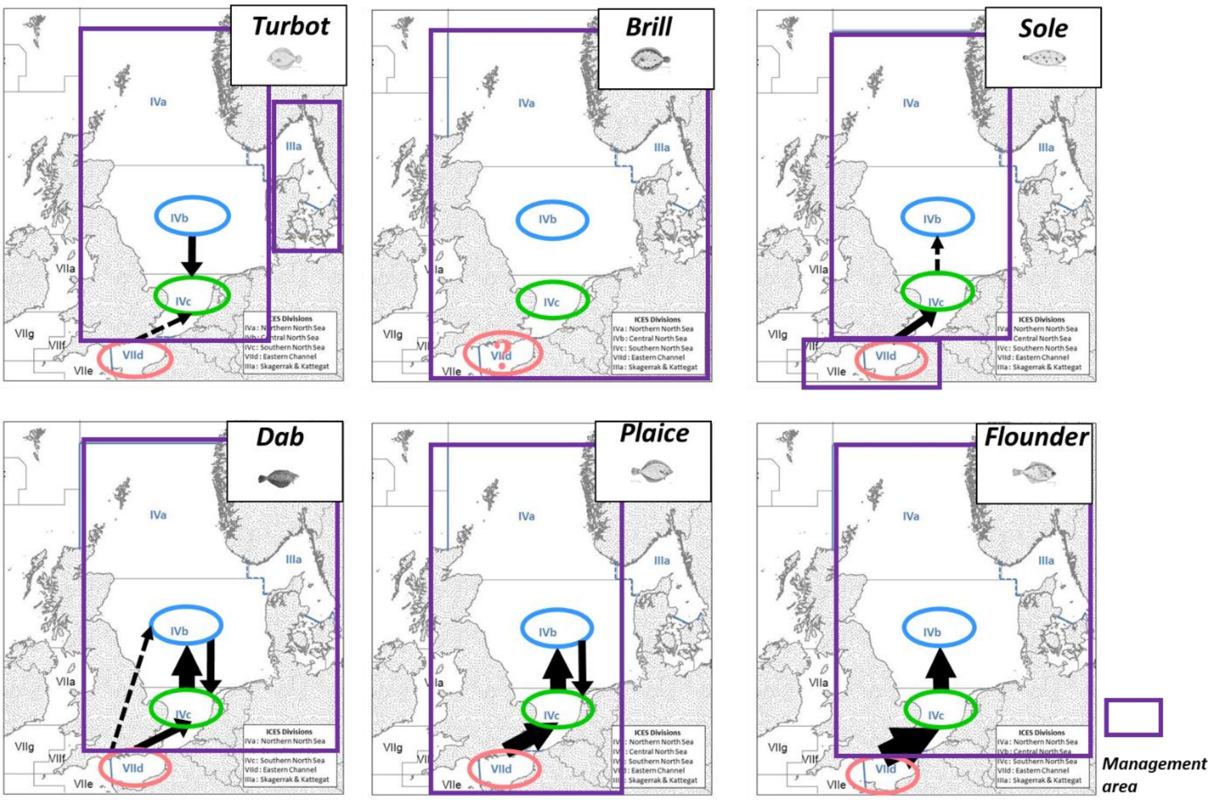


Figure 6-5 Scheme of the connectivity pattern between the ICES management areas as predicted by the dispersal model. Arrow thickness represents the strength of the connection: Dashed (1–5%), thin (5–35%), medium (35–80%), and large (> 80%). Red represents the Eastern English

Channel, green the southern North Sea and blue the central North Sea. Purple rectangle shown the actual management area for six flatfish species.

Dab is not managed by TAC and the stock is managed in subarea IV and IIIa. The high level of dispersal characteristics of the early life stages is reflected in the appropriate management of a unique stock in the North Sea.

The model predicts for **flounder** a high level of connectivity within the North Sea, mainly directed from south to north with a low level of retention in the Southern North Sea. The current approach where management groups subareas IV and IIIa, seems appropriate.

Brill is managed jointly in the English Channel (VIId and VIIe), North Sea (IVa, IVb and IVc) and Skagerrak and Kattegat (IIIa). The approach does not match with the dispersal pattern of the early life stages where the model predicts a lower level of exchange for this species. Brill is also a data limited species. The shift between management unit and dispersal pattern shows that evaluation and management seem not adapted to biological reality. A more local approach might benefit management.

Turbot is managed as a unique entity in the whole North Sea (subarea IV). Early life stages show a low level of connectivity between the southern (IVc) and central North Sea (IVb). Similar to brill, the result shows a pattern in contradiction with the current management unit. Other studies have already highlighted the isolation of local populations in the North Sea, similar to what happened off the northeast coast of the Scotland (Turbot Bank), where turbot collapsed in the 1970s (Kerby *et al.*, 2013). An approach that considers substocks might benefit management.

Since the Skagerrak / Kattegat are included in the management area for many species, an interesting perspective would be to broaden the current model domain to include a proper representation of the Skagerrak / Kattegat in order to assess the potential exchanges of larvae between the North Sea and the Skagerrak / Kattegat. In addition, other life stages than eggs and larvae with an impact on stock structure have to be considered to answer Question 5. Adult fish populations migrate seasonally between feeding and spawning grounds; also juveniles and subadults move around to some extent, all influencing metapopulation structure.

In summary, management units seem relatively adapted for the majority of flatfish species, possibly with the exception of turbot. Stock delimitation is in many cases a geopolitical decision and takes priority over the only scientific knowledge of the considered species (Bosley *et al.*, 2019). In this perspective a change of stock delimitation is not a realistic strategy to improve management (Cadrin, 2010; Kerr *et al.*, 2017). An alternative might be a spatialization of the fishing effort adapted to the local productivity or an adjustment of exploitation level to a small productivity when it is the case when spatial structure of stock is unknown (Fu and Fanning, 2004; Gilchrist *et al.*, 2006; Cadrin and Secor, 2009; Ying *et al.*, 2011; Berger *et al.*, 2016). However this should be analysed from a social and economic point of view and requires the collection of specific data (Punt, 2019).

6.3 ANTHROPOGENIC PRESSURES

Oceans are quickly responding to climate change, habitat loss, and fishing pressure. Quantifying the changes would be most useful to guide local and global management. The North Sea is no exception, and because of its proximity to densely populated coastal areas, experiences considerable anthropogenic pressure. My thesis assesses the potential impact of the main pressures on the flatfish populations of the North, namely offshore wind farms (OWF) and climate.

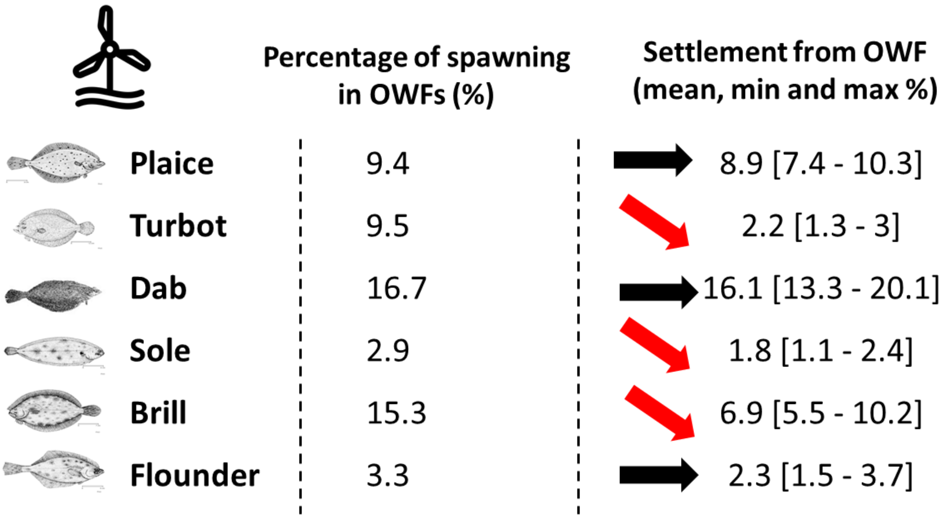
6.3.1 Impact of offshore wind farms

Question 7: How does expansion of OWFs across the North Sea impact demersal fish?

The abundance of OWFs represents an important change of the North Sea environment from open ocean to artificial archipelago. In Europe in 2019, 5047 turbines were installed which represents a capacity of 22 GW (WindEurop, 2020), a capacity which will continue to increase in the coming years. The European Commission expects the EU to produce between 240 and 450 GW of global offshore wind power capacity by 2050 (Wilson, 2020). The main effects of OWFs on fish populations mentioned in the literature are the closure of fisheries and the reef effect (Peterson and Malm 2006, Langhamer 2012, De Mesel et al 2015). Implementation of these artificial structures is likely to affect the dynamics of flatfish populations.

Chapter 4 showed an important overlap between present and future OWF areas and flatfish spawning grounds was estimated, under the assumption of a constant spawning biomass. My research suggests that European plaice, common dab, and brill might be the most affected flatfish species, yet with some important local disparities across the North Sea. Results predicted interspecific differences resulting from the interaction between life history traits and the environmental conditions. As shown in table 6-2, the proportion of settlers originating from OWF areas varied among species, this proportion is notably lower than the overlap of spawning ground suggesting a lower transport success for OWF areas.

Table 6-2 Proportion of eggs spawned in realized and planned offshore wind farms (OWFs) for the different species and mean, minimum and maximum, of the proportion of settlers originating from OWFs based on the period 1997–2006.



	Percentage of spawning in OWFs (%)		Settlement from OWF (mean, min and max %)
Plaice	9.4	→	8.9 [7.4 - 10.3]
Turbot	9.5	↘	2.2 [1.3 - 3]
Dab	16.7	→	16.1 [13.3 - 20.1]
Sole	2.9	↘	1.8 [1.1 - 2.4]
Brill	15.3	↘	6.9 [5.5 - 10.2]
Flounder	3.3	→	2.3 [1.5 - 3.7]

The model excluded several sources of variability in larval survival related to trophodynamics, such as prey abundance and predation (Peck and Hufnagl, 2012). The increase in abundance of filter feeders in OWFs might lead to additional uncertainty in larval survival.

OWFs are also known to impact wind intensity (Akhtar *et al.*, 2021) and hydrodynamical conditions (Merz *et al.*, 2010; Rivier *et al.*, 2016). Assessing how this process might affect transport of eggs and larvae is an interesting question for future research. Wind turbine monopiles are associated to suspended particulate matter plumes, which can also affect ecosystem and flatfish larvae as well as their settlement (Baeye and Fettweis, 2015).

In addition, the choice of spawning grounds is constrained both by ecological and evolutionary processes (Munk *et al.*, 2009; Ciannelli *et al.*, 2015). Not only changes in the quantity of eggs produced in OWFs, but also spawning locations are also susceptible to change in response to environmental changes induced by OWFs. Probably the biggest impact is due to the decreased fishing pressure within the no-go OWFs, which is likely to lead to a higher spawning biomass on the spawning grounds, and hence higher egg biomass (Gill *et al.*, 2020). Other stages are also likely to be impacted. Real impact of OWFs on flatfish is likely to be dependant of the design of the wind farms (size, distance among wind turbines, density…) and makes difficult to assess potential impact. Numerous others questions remain especially the management of conflict among sectorial interests, such as the exploitation of natural resources, natural environment and energy production, and the path to sustainable management. Passive fisheries and aquaculture appear as possible solutions to this conflict (Stelzenmüller *et al.*, 2016). Overall, monitoring is needed to gasp the impact on the natural communities, including flatfish, especially on eggs production, would help to further understand the potential impact of the presence of OWFs on flatfish population.

In summary, our study represents a first step towards the understanding of the effects of OWFs on marine ecosystems, several specific effect of OWFs on fisheries are detailed in a recent special issue of *Oceanography* (Volume 33 (4) 2020) entitled "Special Issue on Understanding the Effects of Offshore Wind Energy Development on Fisheries". As the effects are many and varied, the results should be integrated into a larger study considering the full life cycle to assess the cumulative impact of OWFs as proposed by Willsteed et al. (Willsteed *et al.*, 2017).

6.3.2 What to expect from climate change?

Question 8: What is the impact of climate change on the early life stages of flatfish?

Global climate change is changing measurably the physical and biological functioning of the oceans (Beaugrand *et al.*, 2014b; Kendall *et al.*, 2016). Larval dispersal being dependent on life-history traits and physical factors makes that in the long term climate variability and climate cycling leave a significant footprint on cohorts (Lo-Yat *et al.*, 2011). Chapter 3 predicts that, at the North Sea scale, dispersal distance, pelagic larval duration and recruitment would increase but that at the local scale, recruitment would increase in some areas (the Netherlands, Germany and Thames estuary) and decrease in others (France, Belgium and Norfolk). For connectivity, it has been shown that local retention would decrease by 4 % and seeding would increase by 37 % at the North Sea scale, as illustrated in table 6-3.

The scenarios assessed in this study are not exhaustive. For instance, changes of the rainfall patterns and freshwater runoff might affect larval transport close to the river mouths while projected sea-level rise might affect circulation. In the CLIMAR mid-term (2040) “warm+” scenario, a river runoff increase of 14 % in winter and a decrease of 20 % in summer, as well as a mean sea-level rise of 40 cm are expected (Van den Eynde *et al.*, 2011) at the regional scale. These perturbations have not been tested in the current study although they have been documented empirically. For example, the river plume influences the supply of sole larvae (Le Pape *et al.*, 2003b), river runoff is important to explain recruitment variability (Martinho *et al.*, 2009; Morat *et al.*, 2014a, 2014b) and benthic production is crucial in determining cohort strength (Darnaude *et al.*, 2004). Freshwater input controls the accumulation zones of flounder larvae (Sentchev and Korotenko, 2007). Moreover, the perturbations considered in the current study were extrapolated over the full model domain and assumed constant in time. For a more thorough study of the impact of climate change on sole larval dispersal, recruitment and connectivity in the North Sea, all expected perturbations should be considered, including those not tested yet (e.g., river runoff, storm frequency, and sea-level rise). It is also important to consider spatio-temporal forcing from realistic climate change scenarios (Lett et al., 2010) at the scale of the English Channel and North Sea.

Despite these hypotheses, this scenario represents a baseline to study potential impact of climate change on larval dispersal. From this baseline it is possible to develop future research and management plan based on the methods of Chapter 3 with an updating forcing. In this way assess a panel of climate trajectory is mandatory to assess potential impact.

As example, the choice of an increase of temperature of 2°C was a symbolic choice used in a political context as defined in the COP21. Model outputs from the EURO-CORDEX model (http://www.euro-cordex.net/) could be used in the future and might serve as input for climate change impact studies within the timeline of the Sixth Assessment Report (AR6) of the IPCC expected in 2022.

Impact of temperature appears to have the major effect, sensitivity analysis to temperature with the methods of Chapter 5 is an interesting perspective, especially when model showed that pelagic larval duration is one of the most sensitive parameters and when water temperature is expected to increase in the coming years.

In addition, there are two issues requiring further attention to model correctly scenarios. First, the impact of climate change on the spawning grounds through a shift in the distribution of adult sole (Engelhard *et al.*, 2011) has not been addressed. Hufnagl et al. (2013) used a model to assess the changes in potential spawning grounds of plaice in the North Sea and found that changes in water circulation and temperature affect some nursery grounds by decreasing connectivity. This has consequences for stock distribution and productivity. Secondly, the earlier spawning peak is a consequence of an increase in SST. Since final dispersal is extremely sensitive to the spawning period, an optimized parameterization of the latter should be developed based on Fincham et al. (2013). They determined a gradual shift in peak spawning time with the years in some stocks and a correlation between SST during winter and the date of peak spawning.

In summary, our findings show that climate-driven changes in connectivity will measurably affect the distribution and productivity of sole (and by extension other demersal fish and organisms) in the North Sea. Some effects have already been documented, such as distribution shifts in response to warming and fishing (Engelhard *et al.*, 2011). Also, cohort strength is affected through enhanced recruitment in some years and regions, and reduction in others (ICES, 2016). Under influence of truncated age-frequency distributions and the ensuing evolutionary changes (Mollet *et al.*, 2013b), chances for suboptimal recruitment have increased. These changes in the biology of sole have to be added to numerous other factors that affect fish throughout their life cycle, including changed community composition in response to regime shifts and shifting biogeographic zones (Alvarez-Fernandez *et al.*, 2015), reshaped benthic communities and changed prey fields due to chronic intensive bottom trawling and discarding of bycatch (Hinz *et al.*, 2009), enhanced parasite transmission (Macnab and Barber, 2012; Shama, 2015), food limitation (Le Pape and Bonhommeau, 2015), pollution (OSPAR, 2010) and fishing pressure (Cheung *et al.*, 2013).

An interesting perspective to assess the impact of climate change on the various stages of flatfish is to extend the model to juveniles as made by van de Wolfshaar et al. (2021). The authors coupled the LARVAE&CO model to a DEB model to assess the fate of juvenile sole growth and survival from spawning to first-year recruitment under future climate conditions in the North Sea (Figure 6-6).

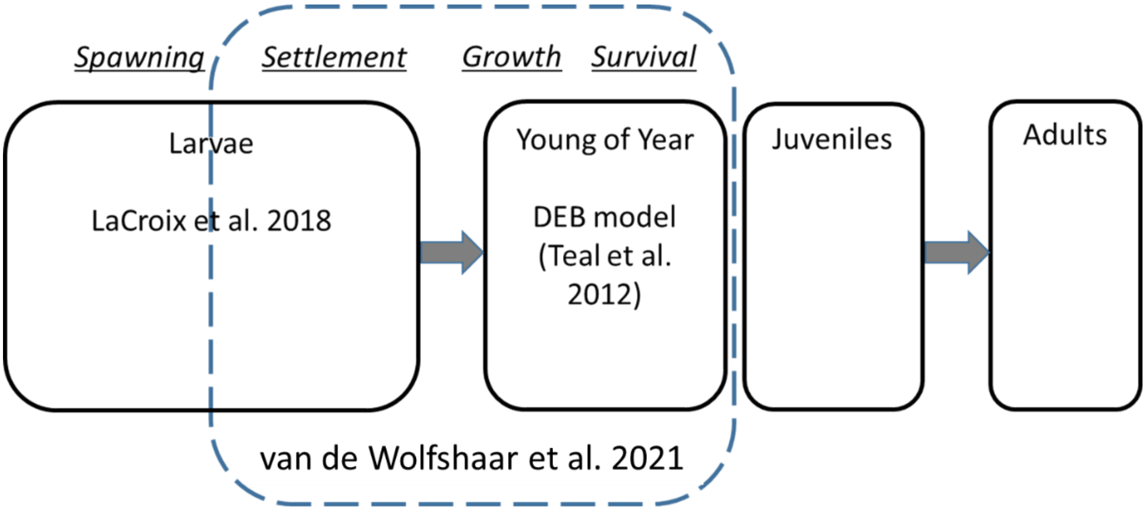
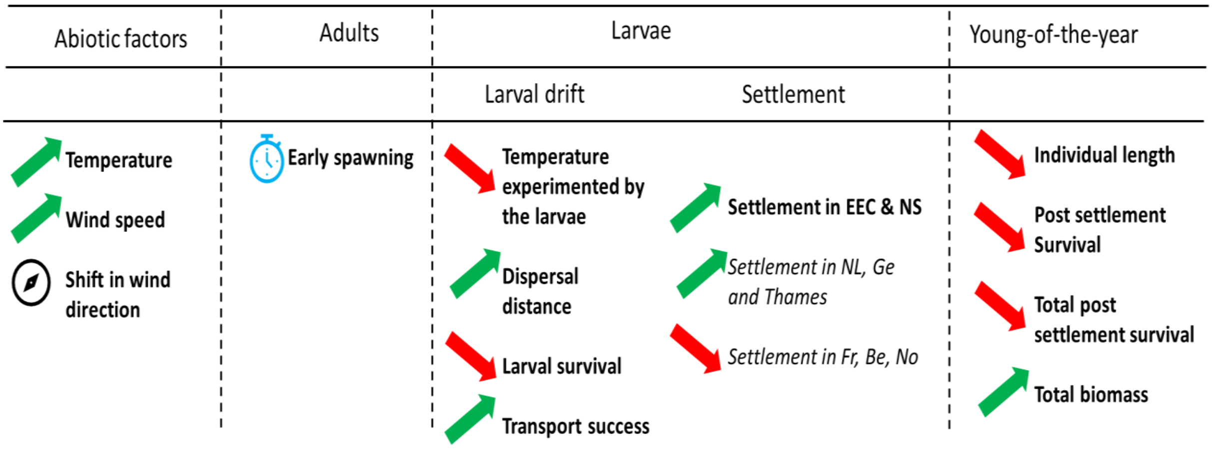


Figure 6-6 The different stages of the life cycle of flatfish are indicated in the rectangles. On top, in underlined italics, are the processes that are addressed (from van de Wolfshaar et al. 2021)

Indeed, a change in arrival period or larval number in the nursery ground is likely to affect *in situ* survival and growth rate. This study shows that under this condition a reduced first year survival is expected but an increase of individual size and finally a higher biomass are also expected (Table 6-3) and highlight a non-linear effect of climate change on young stage of flatfish.

Table 6-3 Effect of climate change on early life stages of sole as described in van de Wolfshaar et al. (2021). Arrows indicate the effect (red for a decrease and green for an increase).



Abiotic factors	Adults	Larvae		Young-of-the-year
		Larval drift	Settlement	
↗ Temperature ↗ Wind speed Shift in wind direction	Early spawning	↘ Temperature experimented by the larvae ↗ Dispersal distance ↘ Larval survival ↗ Transport success	↗ Settlement in EEC & NS ↗ *Settlement in NL, Ge and Thames* ↘ *Settlement in Fr, Be, No*	↘ Individual length ↘ Post settlement Survival ↘ Total post settlement survival ↗ Total biomass

6.3.3 Challenges to predict the future and to build scenarios

It is a major challenge to estimate the relative importance of the various factors which influence survival and dispersal, especially under anthropogenic pressure. Building future scenarios is a complex process. In addition to the uncertainties inherent to the model itself, additional sources of error may arise from the design of the prospective scenarios which are based on assumptions.

Building scenarios is complex; sources of interaction are numerous and difficult to take into account globally; in addition, scenarios might evolve quickly, especially in the case of anthropogenic pressure.

For example, in Chapter 3. , a scenario based on an increase of the temperature of 2 °C was considered as an extreme test case in the beginning of this study. In view of recent projections

(Ribes *et al.*, 2021), it could be considered as the least credible or conservative. In addition, scenarios test hypotheses, where it is difficult to take into account all changes implied by anthropogenic pressure in a complex ecosystem. Marine ecosystems have to do with interactions leading to trophic cascades, bottom-up and top-down control, and regime shifts (Rocha *et al.*, 2018). In the case of flatfish, the impact is not limited to the physico-chemical condition of the ocean, but includes biological and ecological factors such as the life cycle (with for example a change in spawning period or distribution, in feeding and so on). All those potential changes are complex to estimate.

I like to cite a quote of statistician George E.P. Box (1976)*: All models are wrong but some are useful*. In the present case, scenarios might be useful to study locally potential effects of what might happen. It especially illustrates the non-linearity of interactions as in the case of the potential impact of OWFs or highlight the differential impact at a local scale as in the case of climate change. The interest of scenarios is also their potential for reuse in meta-analyses on impact, as is the case for dispersal and climate change in Lett et al (2010). This thesis highlights the need to maintain monitoring to collect data in the way to refine model and improve likely.

Nurseries play also an important role in the population dynamics of flatfish (Nash and Geffen, 2000). After metamorphosis, most larvae settle in shallow coastal nurseries, which most likely limits the direct impact of OWFs on juveniles. However, interspecific differences in the number of settlers might affect the juvenile life stage by changing the species composition of the nurseries. Indeed, many processes occurring at the nursery grounds are density dependent (van der Veer, 1986a; Rijnsdorp and Van Leeuwen, 1992; Le Pape and Bonhommeau, 2015). In addition, environmental conditions in the nurseries are important for young flatfish (Rijnsdorp and Van Leeuwen, 1992; Cabral *et al.*, 2007). Overlap between OWFs and nurseries or climate change could change both the quality and capacity of the nursery grounds (due to a change in species composition, a reduction of surface linked to coastal defence and hard structures, and so on) and influence the whole population, as in the case of habitat degradation for sole in Western English Channel (Rochette *et al.*, 2010a). Therefore, a direct consequence of this thesis is the need for combining the processes which occur during the early pelagic stage and juvenile stage to access potential impact on populations.

Overall, our study represents a first step towards the understanding of anthropogenic pressure on marine ecosystems. As the effects are many and varied, the results should be integrated into a larger context to assess the cumulative impact. Several approaches to assess cumulative impact are suggest by Willsteed et al. (2017), who identify different approaches and discuss key considerations and challenges to assessing the cumulative effects of marine renewable energy developments and other activities on marine ecosystems.

6.4 GENERAL PERSPECTIVES

My thesis determines and distinguishes the main environmental factors and life history traits, which influence the dispersal of the early life stages of flatfish, with a biophysical larval dispersal model. Uncertainties remain but can be at least quantified and calibrated with complementary data. The model makes it feasible to build scenarios to assess the future state of flatfish in the human-impacted North Sea. The thesis focuses on the planktonic stage and represents a step to study connectivity throughout the full life cycle and even over multiple generations. In such perspective, genetic data is an important source of information to improve knowledge on the populations. Such type of data can be used to calibrate/validate larval dispersal model and can, in complement of larval drift model, improve knowledge on population structure and dynamics. Several studies suggest to compare the prediction of larval drift model with genetic data (Kettle and Haines, 2006; Kool *et al.*, 2011) or to combine both in a multigeneration model (Kool *et al.*, 2013). More complex models are also developed to simulate population structure for large size populations as exploited fish. They include demographic parameters, age structure, adults and early life stage movement in addition to genetic parameters (including adaptation process as example) (Andrello *et al.*, 2021). In general multi-disciplinarity is an interesting perspective to help improving knowledge on connectivity. In complement with biophysical modelling (Leis *et al.*, 2011), a broad range of methods can be used to assess connectivity as parentage analysis (Jones *et al.*, 2010; Berumen *et al.*, 2012) or tagging (Roy *et al.*, 2013) which remain difficult to apply for larvae, otolith elemental fingerprinting (Cuveliers *et al.*, 2010; Tanner *et al.*, 2013), isotope analysis (Guelinckx *et al.*, 2008; Darnaude *et al.*, 2014) and genetic traceability (Cuveliers *et al.*, 2012; Nielsen *et al.*, 2012). These methods should help to quantify connectivity and validate model results at the regional scale. Two recent PhD theses have used a multi-method approach to identify to improve identification of population structure of sole at a small scall: In a first thesis Delerue-Ricard (2019) combined genetic and otolith information to study the small-scale connectivity pattern in the North Sea. The otolith-based results discriminated between subpopulations off the Belgian coast, the Netherlands and the Thames estuary, similar to Cuveliers et al. (2010). In a second thesis Randon (2020) studied the mismatch between management units (stock) and the biological units (population) in a combination of tagging, otolith, genetics and population model to identify three subpopulations in the Eastern English Channel whereas the management units considered a unique entity. The results suggest that spatial scale is not necessarily an indicator of stock, but that habitat (in case of the Eastern English Channel) and hydrodynamics (in case of the North Sea) could be important to discriminate between flatfish stocks.

Improving knowledge on stock structure, assessing the relative contribution of each life stage (larvae, juveniles and adults) to population dynamics and identifying pressures that might influence flatfish population structure and dynamics remain interesting questions to explore and manage living resources sustainably in the North Sea. Each life stage undergoes specific pressures: the pelagic phase is subjected to drifting and high mortality, juveniles are constrained by density-dependent processes that may regulate the population in the nurseries, and the adult stage is subjected to high fishing pressure and exhibits different migration patterns. If a shift is made from larval dispersal (this study) to population connectivity, juveniles and adult stage should be considered.

Two aspects draw special interest. Ideally a sound model scenario is based on the past to predict the future. Flatfish in the North Sea have a long history of monitoring. A worthwhile study might focus on a baseline set in the last century and assess model performance for future prediction. It should also be worthwhile to build a generic full life-cycle model, based on long term data (over a century), which integrates ecological knowledge and data gathered for nurseries and adults in a Bayesian framework. The full life-cycle model would simulate past conditions in order to quantitatively describe population dynamics and asses the cause of changes observed in the past. The approach would combine early life stages (from a larval dispersal model) with processes in the nurseries and adult stage, including fishing pressure. Such a model has been developed for sole in the English Channel (Rochette *et al.*, 2012) and should be extended at the North Sea scale.

APPENDIX 1: A SHORT INTRODUCTION TO THE HYDRODYNAMIC MODEL COHERENS

Full details on the model I used and its validation are described in Savina et al. (2010) and reproduced here as a background to this thesis. The hydrodynamic model was not improved in the frame of this thesis. Specific sources for the forcing used and the periods simulated are described in the different chapters of this thesis. In this thesis I opted for COHERENS V1 (available at the starting of the thesis and the one for which the particle tracking module was already available). There is also a second version of this hydrodynamic model COHERENS V2, available now and continuously under development.

The model

NOS (NOrth Sea) is a 3D hydrodynamical model based on the COHERENS V1 code (Luyten et al., 1999). It covers the region between 4°W and 9°E, and between 48.5°N and 57°N, using a 157 by 205 horizontal grid with a resolution of 5′ in longitude and 2.5′ in latitude, and 20 sigma coordinate vertical layers. The boundaries of the model area are the western and northern open boundaries at 4°Wand 57°N and 14 rivers. The basic equations for momentum, continuity, temperature and salinity, written in spherical polar coordinates are discretized on an Arakawa-C grid. The currents are advected with an upwind scheme, while scalars (temperature, salinity) are advected with a total variation diminishing (TVD) scheme in order to simulate as far as possible frontal structures with strong horizontal gradients. The vertical exchange processes are represented through the eddy coefficients υT and λT. Horizontal diffusion is not modelled explicitly. Density is related to temperature and salinity via the UNESCO (United Nations Educational Scientific and Cultural Organization) equation of state of seawater (Millero *et al.*, 1980 in Luyten et al., 1999). The equations are integrated in time using the mode-splitting technique with a small time step (30 s) for the 2D barotropic mode and a larger time step (10 min) for the 3D baroclinic mode. Further details about the governing equations, numerical methods and discretization schemes are found in Luyten et al. (1999).

Surface and bottom forcing

The NOS model is forced by 6-hourly wind and atmospheric pressure fields from the analysed data of the UK Meteorological Office. The wind forcing is spatially variable on a grid with resolution varying from1.25° to 5° in longitude and 1.25° to 2.5° in latitude according to available data (4 values on our model domain). Surface stress is calculated as a function of wind speed using the empirical relations of Geernaert et al. (1986 in Luyten et al., 1999). The bottom stress is calculated by a quadratic friction law with a uniform roughness length. The sea surface temperature is forced by using interpolated weekly SST data obtained from the BSH (Bundesamt für Seeschifffahrt und Hydrographie, Loewe, 2003) on a 20×20 km grid (approximately 2 cells latitudinally and 4 cells longitudinally). For temperature at the sea bottom boundary and salinity at the sea bottom and sea surface boundaries, zero fluxes were assumed.

Open boundaries

Time series of depth-integrated currents and sea surface elevation values to force the model at its western and northern boundaries were provided by CSM (Continental Shelf Model), a two-dimensional hydrodynamic model of the entire Northwest European Continental Shelf, also based on the COHERENS code and run with the same meteorological inputs and the same river discharges as NOS. To prevent spurious vertical velocities at open sea boundaries, the 3D horizontal current is computed assuming a zero normal gradient for the velocity deviation. For temperature, a zero horizontal cross boundary gradient was taken. The sea surface temperature is imposed, so it is assumed that the thermal influence of water from outside the model domain is already considered. Salinity is transported inside the domain during inflow using imposed values except in the eastern end of the northern boundary, where a zero horizontal cross boundary gradient is taken to allow the northward flowing of low salinity waters along the German and Danish coast.

River boundaries

Fourteen rivers were considered. They have been selected amongst the main North Sea rivers (Lacroix *et al.*, 2007b; van Leeuwen, pers. comm.) on the basis of their long-term average discharge (1990– 2005). River discharges were supplied at daily intervals and for each river location (see Figure Appendix1-1 for location and see Table 1 in Savina et al. 2010 for data sources). The river input locations in the model are assumed to be upstream of tidal influences, i.e. a uniform discharge and a salinity equal to 0 are assumed at all depths. For temperature, a zero gradient condition is considered for all the rivers. Again, the sea surface temperature being imposed, it is assumed that the thermal influence of rivers is already considered. The model was run for a 2-year spin-up period to allow a realistic structuring of water masses, starting with uniform initial values of temperature (12 °C) and salinity (33 PSU). Initial conditions for 3D and depth-integrated currents and the sea surface elevation were set to 0. Then, the model was run over 2 years, 1995 and 1996.

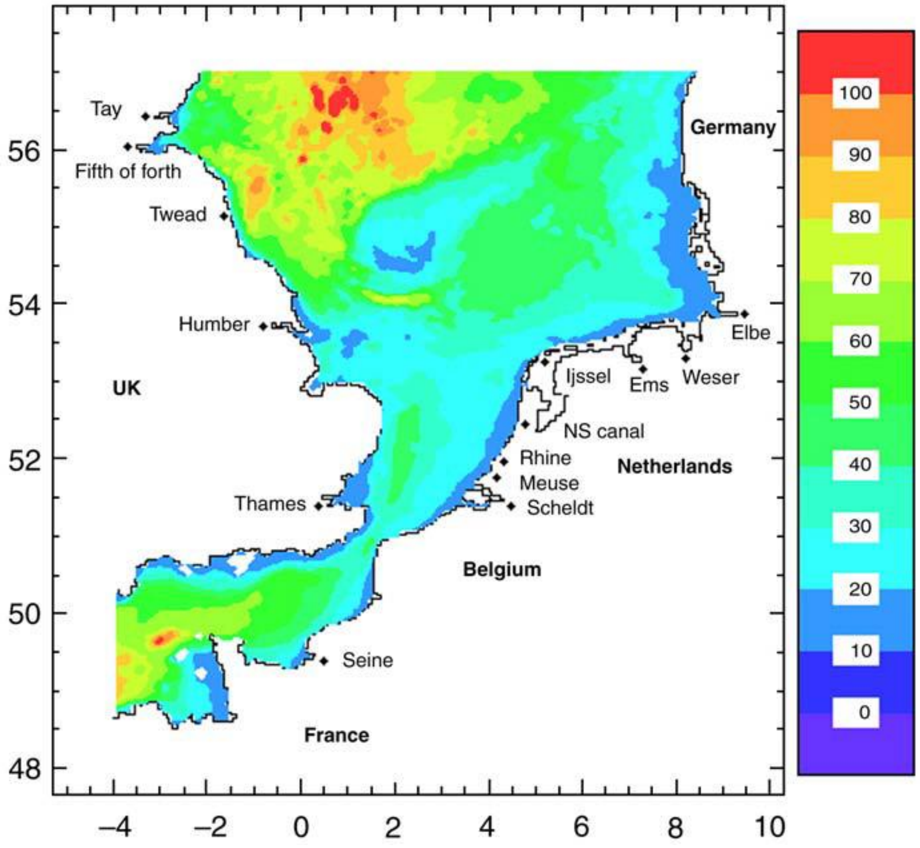


Figure Appendix 1-1 Geographic implementation of the model, with bathymetry (m) and rivers

Validation

A similar implementation (same code, same forcing data, and similar domain but restricted to 52.5°N) has been validated by Lacroix et al. (2004). Comparison between simulated long-term time series (1993–2002) and observations at two stations in the Belgian waters has shown the model ability to simulate the seasonal and interannual variability of salinity for this region under the influence of rivers (Fig. 6 in Lacroix et al., 2004). Comparison between long-term averages (1993–2002) of simulated surface salinity and in situ measurements at 35 stations (BE and NL waters) has demonstrated the model ability to reproduce strong horizontal salinity gradients linked to riverine inputs (Fig. 5 in Lacroix et al., 2004). An additional validation of long-term averages (1993–2003) of surface salinity, considering more stations and covering the whole English Channel and southern North Sea (BE, NL, FR ad UK waters), has been performed for this study. Position of the 42 stations and data sources can be found in Lacroix et al. (2007a, respectively Fig. 6 and Table 5). The use of a selection of objective metrics allows to assess the model skills and confirms the ability of the model to simulate accurately the spatial pattern of salinity, and by extension, its ability to simulate the transport of passive tracers: The correlation between model and observations is highly significant and very good (R=0.92, pb0.001) and the root mean square error (RMSE=1.21) is far lower than the standard deviation of the observations (stdev=3.01). The model efficiency ME (a measure of the ratio of the model error to the variability of the data) and the percentage model bias PB (the sum of model error normalized by the data) have also been computed. According to the classification found in Allen et al. (2007), the model performance is excellent (ME=0.83, PB=−0.84) for salinity.

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