LIMNOLOGY
and
OCEANOGRAPHY

Limnol. Oceanogr. 64, 2019, 1150–1171

doi: 10.1002/lno.11104

How larval traits of six flatfish species impact connectivity

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Abstract

Connectivity and dispersal are important factors for ecosystem dynamics, conservation, and resource management. Dispersal and recruitment success are determined in early life for many marine species. For those larvae that are pelagic, transport from spawning to nursery grounds is driven by hydrodynamic processes. Other environmental factors such as temperature and biological factors such as ecophysiology, behavior, and reproductive strategy (spawning period and spawning grounds) influence the final dispersal pattern and larval survival. We utilized a Lagrangian particle tracking model coupled with a three-dimensional hydrodynamic model (Larvae&Co) to assess the connectivity patterns between spawning and nursery grounds of six commercially exploited flatfish species in the North Sea over a 10-yr period (1997–2006). Standardized analyses have highlighted how spawning and nursery grounds are connected under the combined pressure of environment and life-history traits. Results showed that the six flatfishes can be divided in two groups, each with their specific connectivity patterns. Turbot, common sole, and brill live in two subpopulations in the North Sea; common dab, European flounder, and European plaice represent a single mixed population. In general, the modeled and genetic patterns match, hence showing the strong impact of larval connectivity. The large overlap in connectivity for species that spawn during the same period and the seasonal change in hydrodynamics highlight the strong impact of a summer front in larval dispersal. Our results prove that individual-based modeling is a powerful tool to guide resource management, even in cases of limited biological information.

Understanding and managing ecosystems require sound knowledge of population dynamics in a spatial and temporal context. Many taxa show large displacements early in life due to migration events, which are critical for population connectivity and recruitment success. This is particularly true in the marine environment where the larval stage often involves a planktonic phase (e.g., Hjort 1914, 1926; Cury and Roy 1989; Houde 2008). It is even more important for demersal species, because their recruitment success is dependent on access to suitable nursery grounds after metamorphosis. Survival rate is particularly low and variable during the pelagic stage (in the order of 0.1%, McGurk 1986; Houde 2008; Le Pape and Bonhommeau 2015) and hence affects long-term population size. Connectivity, the realized movement between populations in a seascape, is an important process for marine species. It has been studied at two levels. At an ecological level, connectivity takes place at a contemporary scale and is relevant for (meta)population dynamics whereas at an evolutionary level, connectivity involves a multigenerational time scale (Jones et al. 2009). Most observations of population structure happen at 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).

Despite a largely similar life cycle, large differences in dispersal capacity are observed among marine species. Differences are related to larval traits (López-Duarte et al. 2012) such as behavior (Fox et al. 2006; North et al. 2008; Robins et al. 2013), duration of the larval stage (Shanks 2009*b*), seasonality (Lett et al. 2010), and structure of the water column and currents (Munk et al. 2009). Connectivity is studied with a range of methods such as physical tagging, phenotyping,

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Additional Supporting Information may be found in the online version of this article.

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 of fishes are so tiny that direct observations are rare (Levin 2006). Hence, various alternative indirect methods are used. Egg and larval displacement can be modeled, for example, through a hydrodynamic model, simulating advection and diffusion, coupled to an individual-based model (IBM), simulating behavioral, and life-history traits (e.g., 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). Due to their bentho-pelagic life cycle and commercial importance, flatfish represent an interesting group of fish to study connectivity. The demersal adults spawn planktonic eggs; eggs and larvae are transported by the currents until metamorphosis. 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. 1992*a*; Hunter et al. 2003) and make well-documented seasonal migrations (Hunter et al. 2003; Burt and Millner 2008). Larval dispersal models of European plaice and common sole in the North Sea have pointed to temporal variation of spatial patterns and spatial philopatry linked to suitable nursery grounds (Bolle et al. 2009; Savina et al. 2010; Hufnagl et al. 2013; Lacroix et al. 2013). Population genetic studies of European flounder (*Platichthys flesus* L.) and turbot (*Scophthalmus maximus* L.) (Hemmer-Hansen et al. 2007; Vandamme et al. 2014) have pointed 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 differentiated their life-history traits (following Gause' law of competitive exclusion; Gause 1932, 1934; Hardin 1960). For example, van der Hammen et al. (2013) have pointed out the disjoint spawning periods and slight difference in habitat between turbot and brill (*Scophthalmus rhombus* L.). This should impact the population dynamics and connectivity pattern (Denney et al. 2002), but awaits confirmation.

We focus 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 [PLD]), 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 very abundant; sole and flounder are present at intermediate abundances (Rogers et al. 1998). Exploitation levels differ considerably; sole and plaice are targeted by the bottom trawling fleet, turbot, brill, and flounder are caught as valuable bycatch in a mixed fishery, whereas dab is in most fisheries discarded because of its low-commercial value (ICES 2017). 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, and c), while the North Sea and Skagerrak (IIIa) are considered a single population for plaice. For the management of 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 (ICES management areas are shown on Fig. 1). 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. 2013), knowledge on other flatfish is comparatively 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 similar habitats. This approach facilitates understanding of communities at a regional scale and the measurement of the impact of reproductive strategies and larval traits on dispersal.

The main objective of this study is to compare the impact of life history traits on dispersal during early life in six flatfish species. This contributes to an assessment of spatial variation in connectivity, and to an estimate of the interannual variability of connectivity over a 10-yr period. We answer the following questions: (1) How do life-history traits influence the dispersal pattern at the early life stage? (2) How does the seasonality of the North Sea impact connectivity? (3) What is the impact of life-history traits on population structure? The aim is to investigate how a distinct pattern of larval spatial structure might be linked to regional hydrodynamics and life-history traits.

Materials and methods

Our approach combined a well-established three-dimensional (3D) hydrodynamic model with a particle-tracking model under development. We simulated dispersal of the early life stages of six flatfish species from spawning at the spawning ground to settlement at the nursery ground.

Study area

The study area covers the eastern English Channel (EEC) and the southern North Sea (SNS) and central North Sea (CNS) (the region between 4°W and 9°E, and 48.5°N and 57°N). Currents in these shallow coastal seas are mainly tide- and wind-induced. Average circulation is from south to north (Turrell 1992) (Fig. 2) 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 modeled equal to 0.05×10^6 m^3 s^{-1}, -0.01×10^6 m^3 s^{-1}, 0.02×10^6 m^3 s^{-1}, and

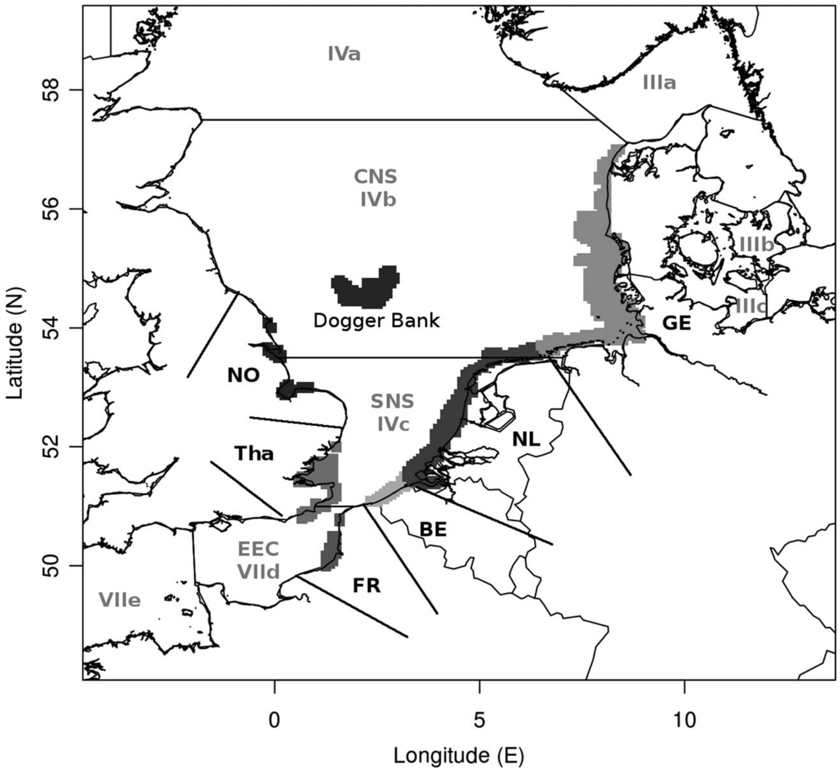

Fig. 1. Location of the spawning zones and nursery grounds of six flatfishes. Spawning grounds are divided in three areas: CNS, SNS, and EEC. The numbers correspond to the ICES management areas (IIIa: Skagerrak and Kattegat, IIIb: Sound, IIIc: Belt Sea, IVa: Northern North Sea, IVb: CNS, IVc: SNS, VIId: EEC, and VIIe: Western English Channel. Nursery sectors codes: France (Fr), Belgium (Be), The Netherlands (Nl), German Bight, including Germany and the SW Danish coast (Ge), Norfolk (No), and Thames estuary (Tha).

0.05×10^6 $m^3 s^{-1}$, respectively, from 1st to 4th quarter on average 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 were equal to 16.9°C (EEC), 17.2°C (SNS), and 15.9°C (CNS) during summer. In winter, the water column is well mixed. In late spring, a thermocline is established over the northern deeper part of the domain, resulting in the formation of oceanic fronts in summer. Two fronts draw our attention: in the north-west across the Dogger Bank and perpendicular to the Dutch coast, in combination with outflow of rivers (Otto et al. 1990) (Fig. 2).

Model

The Larvae&Co model is an IBM that simulates egg and larval dispersal in the EEC and the North Sea. It couples a 3D hydrodynamic model with 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 model, based on the COHERENS code (Luyten et al. 1999), has a resolution of 5′ in longitude and 2.5′ in latitude, and 20 sigma-coordinate vertical layers. The model is forced by 6-hourly wind and atmospheric pressure fields from the analyzed data of the UK Meteorological Office and by weekly sea surface temperature (SST) data (Bundesanmt für Seeschifffahrt und Hydrographie, Loewe 2003). Daily river discharges are included for the main North Sea rivers. Details about the model implementation (equations, forcing, initial and boundary conditions) and its validation are given in Savina et al. (2010).

The individual-based model

Four stages were 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 had a specific parameterization in terms of growth and behavior for each species when sufficient information was available.

Larval trajectories were calculated online using the particle tracking model. The vertical diffusion, which is function of the eddy diffusivity coefficient, was modeled following Visser (1997). Because in the North Sea vertical turbulent diffusion is considered to be the dominant horizontal dispersal

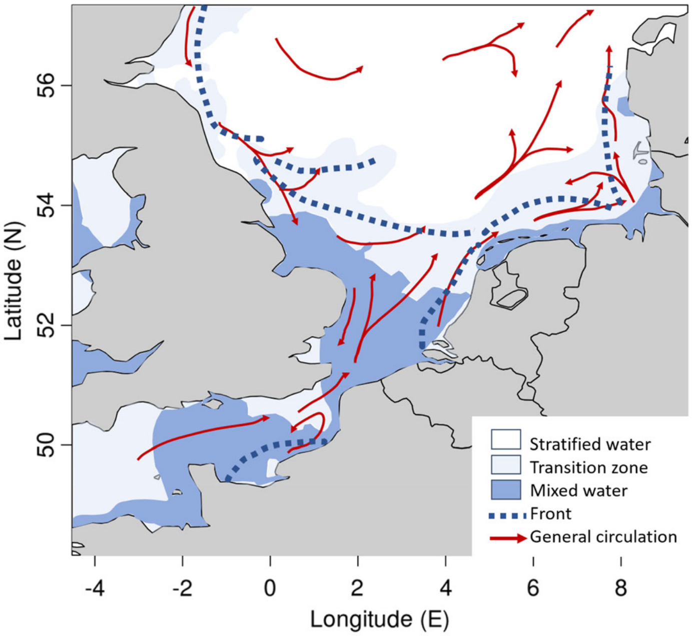

Fig. 2. Schematic representation of the physical oceanography of the North Sea. Arrows represent the general circulation (redrawn from Turrell 1992). Light color represents the transition zones between mixed (dark color) and stratified (white) waters in the North Sea and dotted lines represent the thermal fronts (redrawn from Otto et al. 1990).

mechanism (Christensen et al. 2007), explicit representation of horizontal diffusion was neglected. Specific details on the implementation were presented in Lacroix et al. (2013).

Parameterization for the six species

Particles were parameterized to represent early life stages of different species in order to study connectivity patterns driven by oceanography and biology. Parameters included in the model were spawning (location, distribution function, and period), PLD, mortality, and behavior (vertical migration and settlement condition). Although the reproductive cycle and early life stages were well documented for some of the flatfish species, such as sole and plaice, data were scarce for others.

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 led to a lower spatial resolution.

Spawning grounds and egg densities were estimated from egg distribution for sole, plaice, flounder, dab, and turbot. In addition, to improve spatial coverage in the absence of data on eggs, other sources were also used as a habitat model for dab, preferential spawning habitats and observed fish distribution for turbot or catches during the spawning period for brill. Details on the various sources used to define the spawning grounds are available in Supporting Information Table S1. In the case of different values mentioned in the literature, a mean value was calculated. When the sources were not directly related to egg densities, fish densities were linearly transformed into egg densities to fit with the known egg distribution for some areas (dab and turbot) or used as a proxy of egg distribution in the case of brill. The spawning grounds and egg densities are shown on Fig. 3. References used for the six species are mentioned in the legend caption. Spawning zones have subsequently been spatially divided into three areas based on the ICES divisions: EEC (VIId), SNS (IVc), and CNS (IVb) (Fig. 1) for easier comparison among species.

Spawning period

The spawning period was estimated for every spawning region included in the domain of the present study (EEC, SNS, and CNS) based on published data (Fig. 4). The spawning peak was 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 was a fixed value in the absence of information on a specific cue to trigger spawncing (brill). The spawning duration was set to a fixed period for all species (Fig. 4 and Supporting Information Table S2). A normal distribution centered on the spawning peak was used to model the spawning spread.

Pelagic larval duration

Egg and larval stage duration was 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 °C). 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, either a constant published value was allocated to the different stages (brill) or the duration was estimated on the basis of the spawning peak date and the peak of arrival at the nursery grounds (dab) (Table 1).

Behavior

Three behaviors related to vertical migration have been attributed to the particles. An upward movement due to a positive buoyancy (0.003 m s^{-1}), a nycthemeral migration according to which the larvae swim toward the surface during the night (0.003 m s^{-1}) and toward the bottom during the day (–0.001 m s^{-1}) and a tidal migration synchronous with the tide. The parameterization of the tidal vertical migration process has been upgraded since its documentation in Lacroix et al. (2013). The vertical migration rates changed from positive values (0.001 m s^{-1}) during rising tide (when the sea surface level increases in the grid cell in which the considered particle is located) to negative values (–0.003 m s^{-1}) during falling tide (when the sea surface level decreases in the grid cell considered). Values for vertical migration rates have been defined within the range of the values observed in the

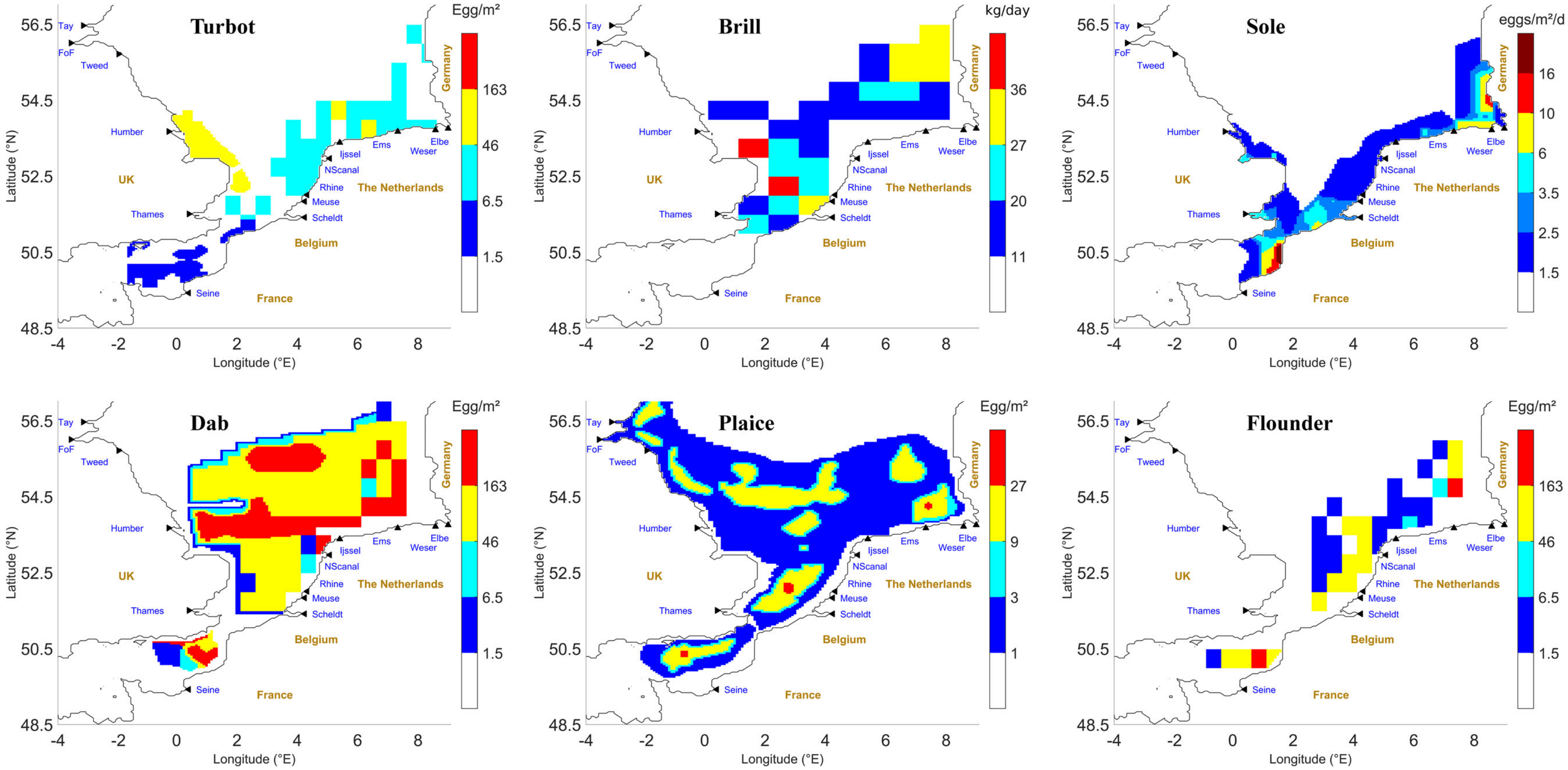

Fig. 3. Spawning distribution of the six flatfishes: Turbot (egg m^{-2}) (Van der Land 1991; Rogers and Millner 1996; Vause and Clark 2011), brill (kg d^{-1}) (van der Hammen et al. 2013), sole (egg m^{-2} d^{-1}) (Lacroix et al. 2013), dab (egg m^{-2}) (Van der Land 1991; Rijnsdorp et al. 1992*b*; Lelièvre et al. 2014), plaice (egg m^{-2}) (Harding et al. 1978; Van der Land 1991; Taylor et al. 2007; Bolle et al. 2009; Ellis et al. 2012), and flounder (egg m^{-2}) (Van der Land 1991; Taylor et al. 2007) in the EEC and North Sea.

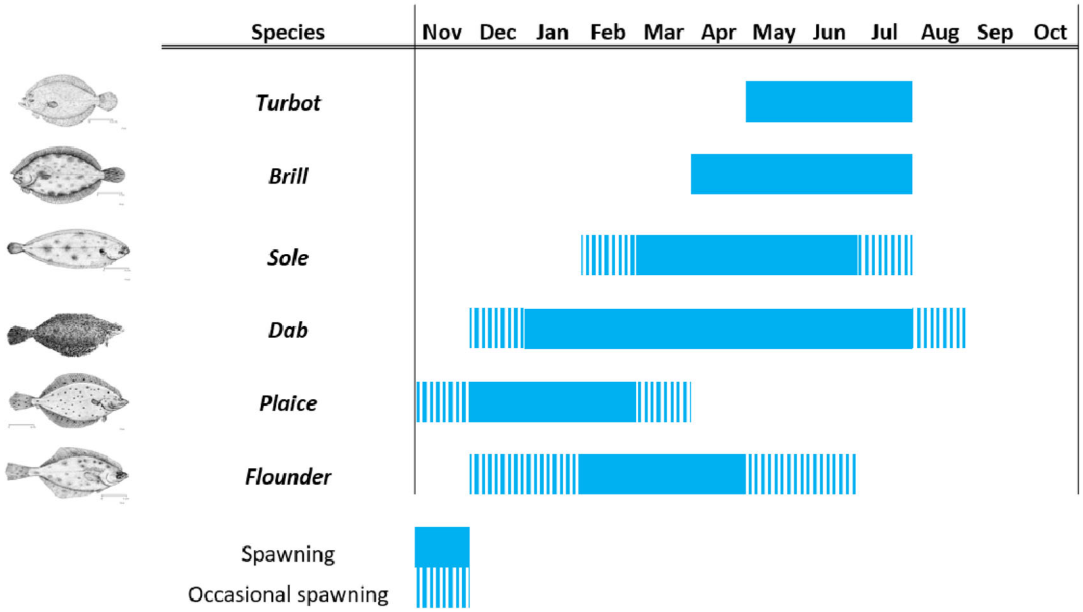

Fig. 4. Spawning period of six flatfishes. The full lines represent a permanent spawning (spawning event occurs each year in all areas) and hatched lines represent an occasional spawning (spawning event occurring only during particular years or specific areas). From top to bottom: Turbot (Jones 1974; 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. 2013), dab (Aurich 1941; Harding and Nichols 1987; 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 2005; Bolle et al. 2009), and flounder (Sims et al. 2004). Details about year-to-year peak day of spawning are listed in Supporting Information Table S2.

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. In the absence of information, larval transport was passive (no vertical migration). Behavior for each species and all life stages are summarized in Table 1.

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) at $0.0004\ T^{3.0293}\ \mathrm{d}^{-1}$ with T the temperature for eggs and yolk-sac-larvae and a constant mortality rate of $0.035\ \mathrm{d}^{-1}$ from first-feeding larvae to metamorphosis. All other flatfish were imposed a constant mortality rate of $0.048\ \mathrm{d}^{-1}$ (Beverton and Iles 1992; Nash 1998) at all stages.

Larval settlement

Settlement occurred at the end of the larval stage. If nurseries are slightly different between species, for example, flounder prefers estuarine habitats associated with a low salinity (Campos et al. 1994; Jager 1999; Amara et al. 2009) whereas dab has a preference for higher salinities (Bolle et al. 1994; Félix et al. 2011), they are all characterized by a shallow bathymetry associated with soft sediments (Gibson 1994; Haynes et al. 2011; van der Hammen et al. 2013). We assumed that larvae attain their preferred habitat if they reach the nursery ground defined on the basis of bathymetry (less than 20 m deep) associated with a muddy or sandy sediment type as described in Lacroix et al. (2013). Areas with these characteristics, which are close to land were considered for all species. In addition to the coastal areas, an offshore nursery, the sandy Dogger Bank (also less than 20 m deep) was considered for plaice and dab (Bolle et al. 1994; Ellis et al. 2012) (Fig. 1). To facilitate comparison among species, the Dogger Bank was joined with the Norfolk area. Nursery grounds were assigned on the basis of national boundaries (Fig. 1). Larvae that ended up outside these nursery grounds after they had reached their PLD did not survive (0% survival rate).

Run specificities

The model has been run over a period of 10 yr (1997–2006) corresponding with the time scale of the NAO (Berglund et al. 2012), in order to represent a broad range of hydrodynamic and environmental conditions.

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. In this study, an exact number of eggs is not known for every species. Therefore, the number of eggs released has been arbitrarily set taking into account the knowledge on the relative distribution for the different species. The number of particles released each year was species-specific (sole: 1.9×10^6; plaice: 48×10^6; turbot: 1.7×10^6; brill: 2.2×10^6; flounder: 1.3×10^6; and dab: 7.4×10^6). Spawning covered the entire spawning area and

Table 1. Summary of the parameters used in the model.

Species	Stage	Larval duration		Vertical migration
		α	β	
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		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		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

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 (1991), 7:Henderson (1998), 8: De Veen (1978), 9: Bolle et al. (2009), 10: Dannevig (1897), 11: Ryland (1966), 12: 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), and 24: Jager (1999).

period. Each particle was associated with a weight according to the spawning distribution of Fig. 3. Particles were released on the bottom at midnight every day during the entire spawning period in the considered spawning ground.

Analysis of the model output

The following metrics were used to compare the modeling results:

Mean temperature experienced by the larvae and mean PLD were calculated based on the individual trajectory of each particle. There was an exception, the PLD of brill and dab has been attributed a constant value. For both metrics, the standard deviation represents the year-to-year variability.

The net displacement between origin and arrival was used to quantify the mean and interannual standard deviation of the distance traveled by eggs and larvae of each species.

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

Connectivity among management areas summarized the dispersal pattern of the six species. Spawning and nursery grounds were 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

Table 2. Mean and standard deviation (year-to-year variability if any) of temperature encountered by the larvae (°C) and total PLD (days) of six flatfishes averaged during the period 1997–2006 and over the whole area.

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

SNS spawning ground), and CNS (Ge nursery ground and CNS spawning ground were grouped).

In addition the impact of life traits and environment on connectivity patterns was investigated:

The connectivity rate among management areas was computed daily (based on the spawning day) and was analyzed separately by destination and origin. Generalized linear models using logit-transformed daily connectivity were used to analyze if there was a significant effect of either the season (month), species, or year on the connectivity among areas.

Results

Life-history traits

The winter spawners plaice and flounder experienced the lowest mean temperature during the PLD (respectively 7.0°C and 9.7°C) (Table 2). Sole, brill, and turbot, which spawned later in the year, experienced higher temperatures (between 12.0°C and 15.4°C). Dab, which spawned over a wide temporal window, experienced a similar mean temperature than sole but was the species with the highest standard deviation owing to interannual variability. As temperature impacted the metabolic rate, and hence larval development, the mean PLD has been computed for each species (Table 2). Late spawning species drifted for a shorter period than early spawners. Turbot had a shorter drift (about 45 d) than the two others late spawners (respectively 49 d for sole and 61 d for brill). Dab presented the longest larval drift (105 d), plaice had a 3-month pelagic phase, and the total PLD was more than 2 months for flounder (68 d). The absence of a standard deviation of larval duration in the case of dab and brill, despite a broad range of temperatures encountered (in particular for dab which spawn from December to August), was due to a lack of knowledge on the temperature-dependent growth rate (Table 1).

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 km and 200 km, but there were strong interspecies differences in realized dispersal (Fig. 5). Despite interannual variability, statistical analysis on dispersal distance (one-way ANOVA, Tukey's test) highlighted two groups of significant difference (Fig. 5). The mean dispersal range was lower for summer spawners: larvae of turbot traveled the shortest distance (102 ± 9 km) whereas sole and brill covered an intermediate distance (respectively 132 ± 27 km and 140 ± 13 km). On the contrary, the mean distance traveled was larger (> 180 km) for species that spawn in winter, where the currents were stronger in the North Sea, and associated with a longer PLD. The average dispersal distance was respectively 184 ± 23 km for dab and 191 ± 23 km for plaice. Flounder traveled the largest distance with a mean of 200 ± 17 km.

Dispersal patterns

Overall, all flatfish dispersed from south to north, following the general circulation pattern of the North Sea (Fig. 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 settled mostly locally. Despite this general pattern, there were some differences among species and years in terms of connections.

Settlement in the French nursery was mainly local. All species exhibited almost 100% of recruitment from the spawning grounds of EEC, 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), few individuals arrived at the French nursery ground due to the absence of (known) local spawning grounds. Regarding the SNS, Thames and Belgian nurseries presented overall a mixed origin of settlers from EEC and SNS whereas in the Dutch nursery, larvae originated from the three spawning grounds (EEC, SNS, and CNS). 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 for turbot, brill, and dab and to a lesser extent for plaice and flounder for which the interannual variability was more pronounced. In contrast, Thames and Belgian nurseries presented an opposite pattern for sole. 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.

At the Dutch nursery ground, the predicted connectivity pattern presented strong differences among species. There was no interannual variability for flounder and brill, which arrived mainly from the SNS. For plaice, dab, and sole, the

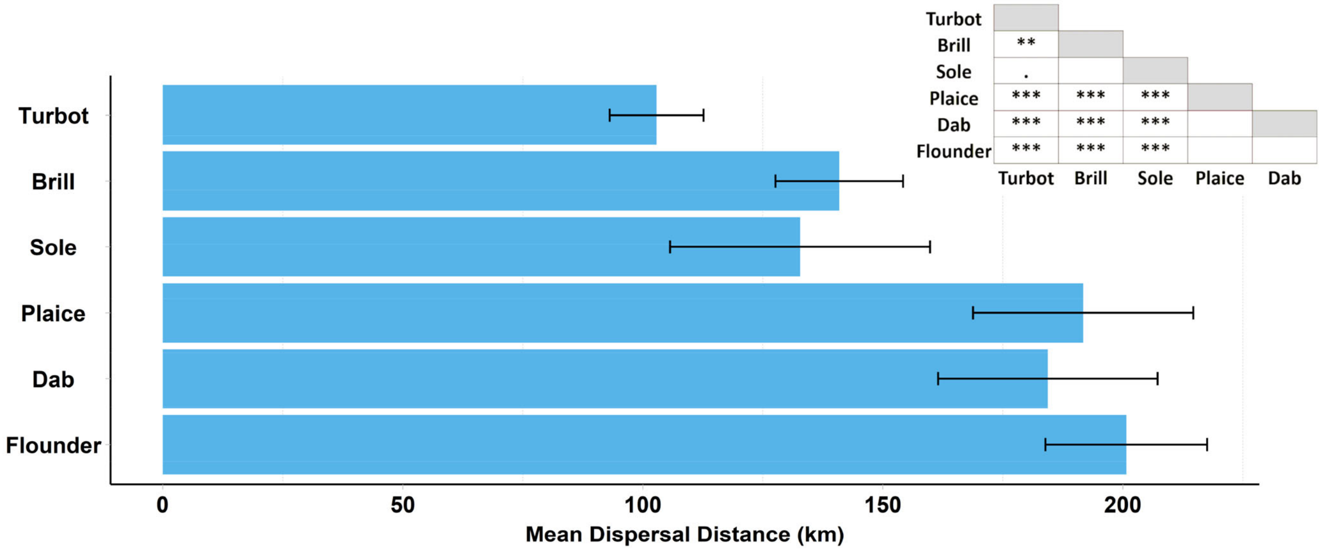

Fig. 5. Mean and standard deviation (interannual variability) of dispersal distance for six flatfishes across the North Sea averaged during the period 1997–2006. Significant effects between each pair of species are presented in the upper right matrix with the following significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

connectivity pattern was more variable, with an important influence of the SNS (up to 100% for plaice in 2004 and 2005 and dab in 2005 and 2006 and 95% for sole in 2001) and a non-negligible input from EEC (up to 70% for plaice in 1997, 72% for dab in 2000, or 53% for sole in 1998). A strong interannual variability was predicted for the origin of settlers.

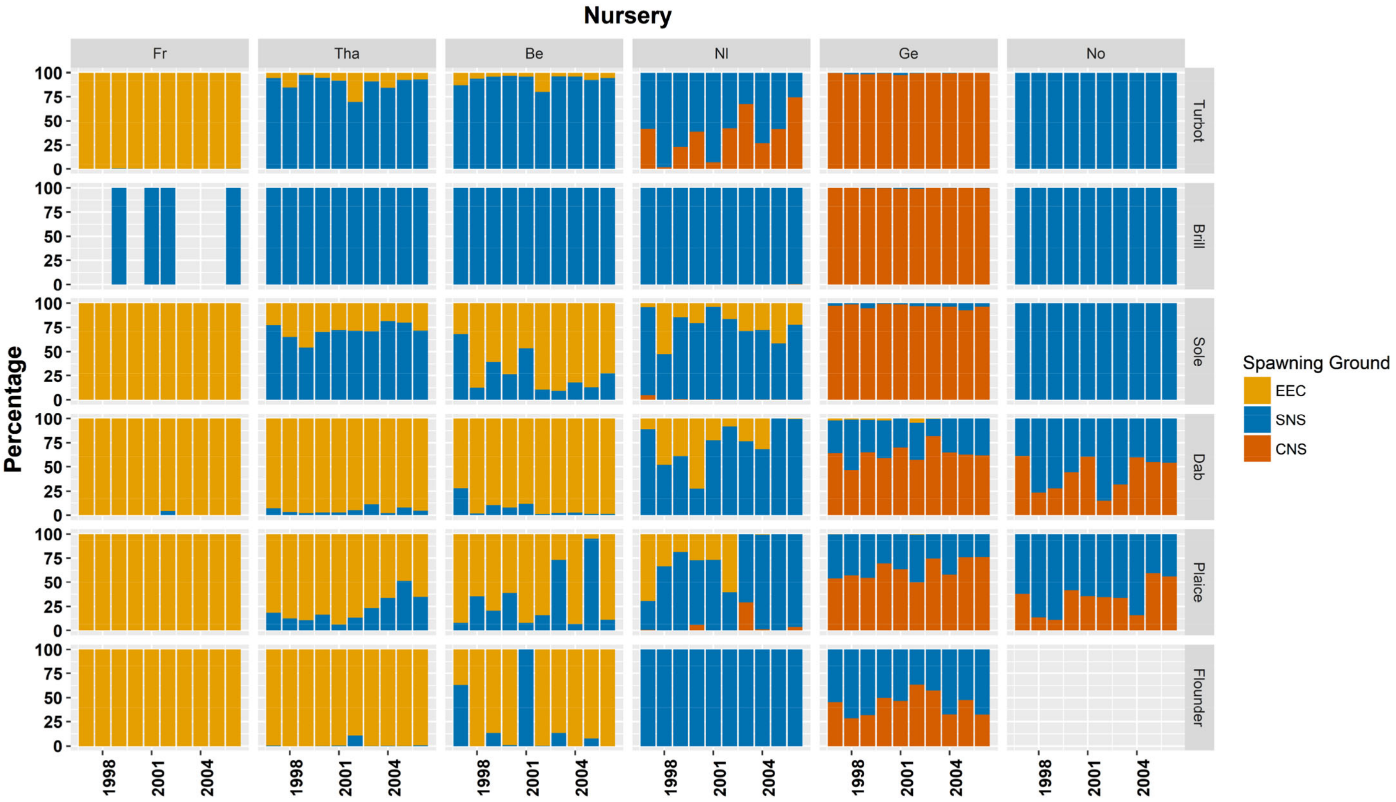

Fig. 6. Proportion of larvae of six flatfishes arriving at a nursery ground in France (Fr), Belgium (Be), The Netherlands (Nl), German Bight (Ge), Norfolk (No), and Thames estuary (Tha) originating from the spawning regions EEC, SNS, and CNS during the period 1997–2006.

For example, for sole, the proportion of larvae native from the EEC varied from 4% in 1997 to 53% in 1998. The same situation was observed for dab (from 72% in 2000 to less than 0.6% in 2005 or 2006), and for plaice, for which most settlers came from the EEC (70%) 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% in 2003). Turbot is the only species for which a large proportion of larvae originated from the CNS (up to 74% in 2006).

The German Bight showed an interesting connectivity pattern. The larvae of three species (dab, plaice, and flounder) originated from the CNS and SNS areas, whereas larvae which settled in this nursery ground for turbot, brill, and sole were mainly spawned in the CNS. In the Norfolk nursery ground, turbot, brill, and sole originated only from local spawning grounds. Plaice and dab showed mixed arrivals from SNS and CNS in this nursery, mainly due to the presence of the Dogger Bank spawning ground.

Connectivity patterns across the North Sea

Connectivity between the three regions of interest showed contrasting patterns among species (Fig. 7). A first group (sole, turbot, and brill) showed limited exchanges between the three areas. There was considerable self-recruitment, 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).

Brill was very different from the other species. It presented a very high level of self-recruitment in SNS and CNS (99.9% and 99.7%, respectively) and almost no exchanges among areas. Turbot favored either self-recruitment or movement to the SNS. Turbot eggs spawned in the EEC remained mostly local and exchanges with the SNS 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%).

For sole, the model predicted a high level of connectivity 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 limited arrivals of larvae along the German coast (Fig. 8). On the other hand, flounder was highly connected between the three areas. The model predicted a low level of self-recruitment in the SNS (4%) and a high number of arrivals from the EEC (96%). The proportion of arrivals in the CNS was mixed from local input (43.4%) and arrivals from SNS (56.6%). Just like sole, flounder presented exclusively northward movement in dispersal pattern.

In contrast to the first group, dab and plaice—members of the second group—had a high level of exchange across the North Sea. In the CNS, arrivals were mixed (63.3% of self-recruitment for dab and 63.2% 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%). 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%). These two species were the only ones exchanging larvae between CNS and SNS in both directions with a large number of eggs

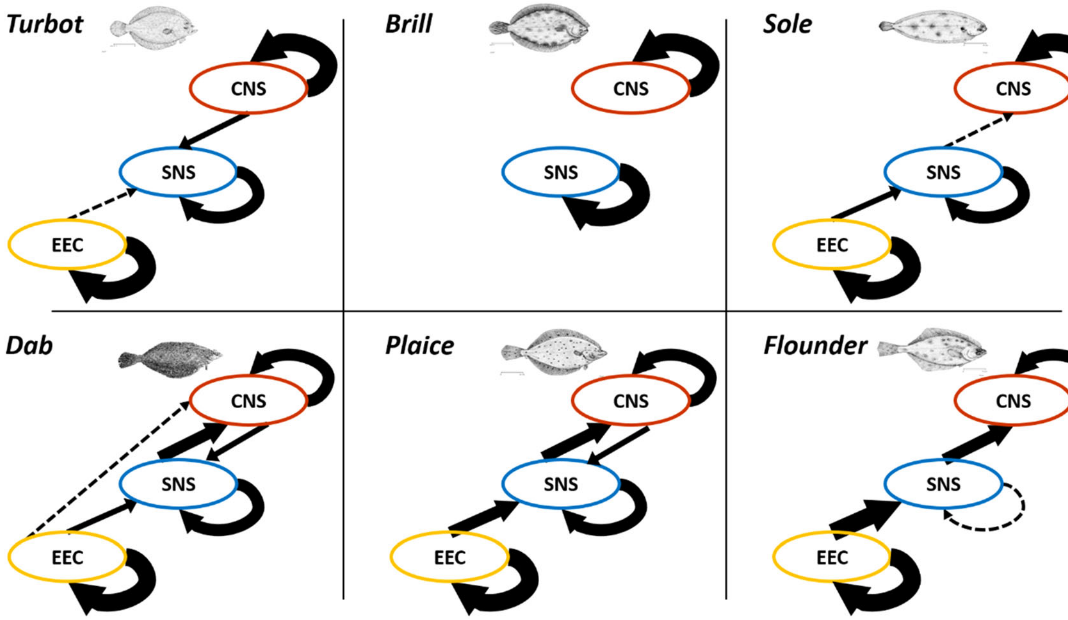

Fig. 7. Scheme of the connectivity pattern between the ICES management units as predicted by the dispersal model. Arrow thickness represents the strength of the connection: Dashed (1–5%), thin (5–35%), medium (35–80%), and large (> 80%). Yellow represents eastern English Channel, blue southern North Sea and red central North Sea.

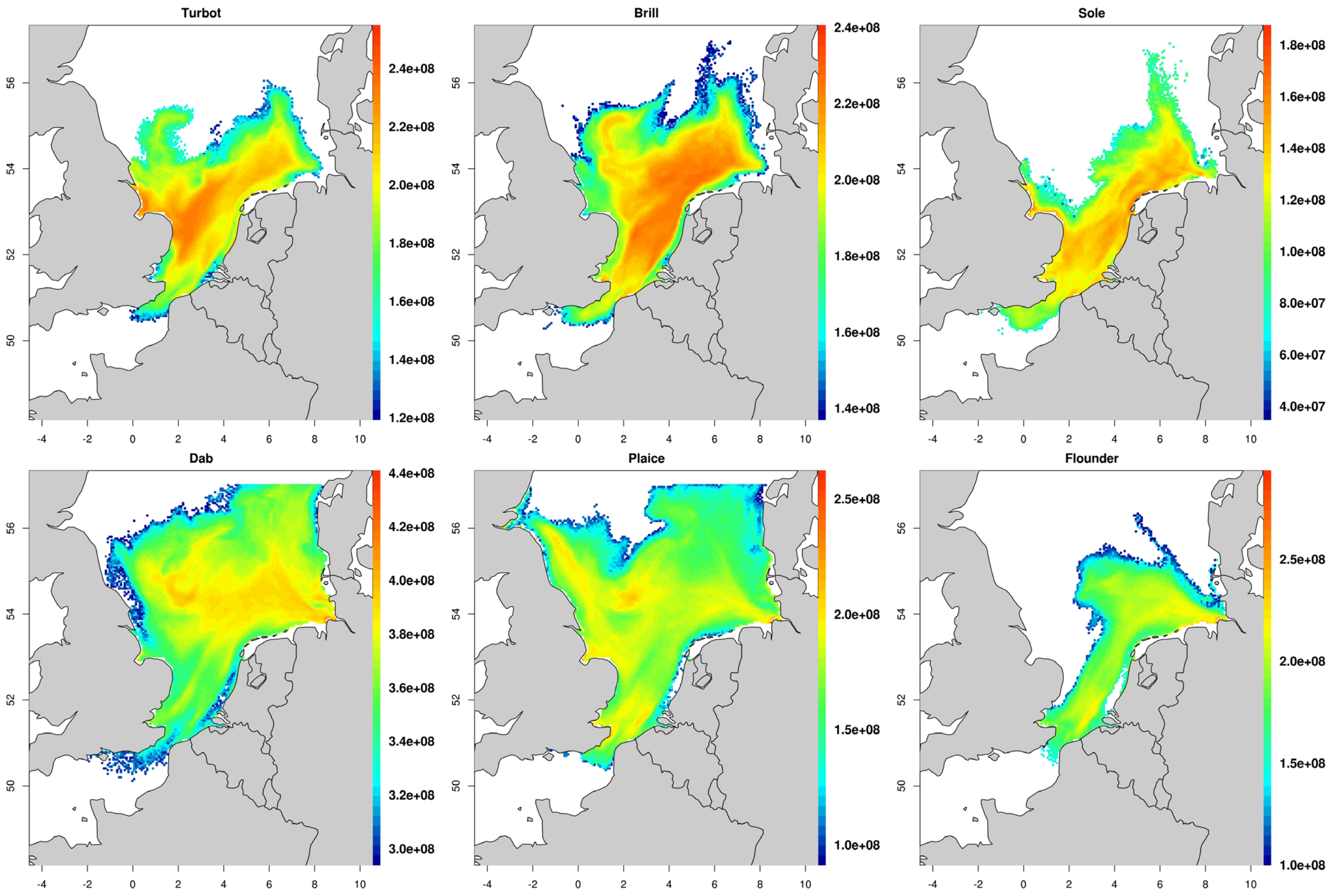

Fig. 8. Larval abundance of six flatfish species at the end of larval transport for eggs spawned in the SNS.

spawned in the CNS settling in the SNS (31% for dab and 14% for plaice).

Impact of season, species, and larval traits on connectivity pattern

Monthly averaged daily connectivity (based on spawning day) between the three areas showed an important seasonal pattern and large differences among species (Fig. 9). A general linear model showed a significant impact of the three parameters (year, month of spawning, and species; $p > 0.01$), but due to the difference in spawning periods, seasonal and species effects remained difficult to distinguish.

Arrivals of larvae from SNS in CNS showed a decreasing pattern from November to August for all species aggregated (Fig. 9, left panel). Eggs spawned from November to March arrived at a large proportion in CNS whereas after May a shift was observed with a drastic reduction in connectivity (less than 25%). For the local recruitment in CNS, the pattern was symmetric (not shown) due to the negligible input from EEC. The seasonal variation of connectivity between SNS and CNS was likely due to the presence of a summer front between the two areas. Overall, the seasonal pattern observed when all species were aggregated can also be observed at the species level. Brill and turbot presented almost no connections due to their late spawning season. Dab, plaice, and sole presented the same pattern with a higher level of connectivity earlier in the season. The temporal lag observed among species might be explained by their different PLD. Only flounder displayed an inverse tendency. Variance analysis of the model showed that species, season, and year explained 39%, 26%, and 4% of the variance, respectively.

The pattern of the seasonal tendency of the proportion of larvae originating from the three areas in SNS presented a contrasted seasonality. A decreasing proportion of settlers originating from EEC was observed during the season when all species were aggregated, and to a lesser extent when all species were accounted individually, except for flounder. This prediction is likely related to the strong currents in winter and to earlier spawning in the southern region. The variance was explained at 38% by the month, 23% by the species, and 8% by the year. Arrivals of larvae from CNS did not present a clear temporal pattern but displayed a strong difference among

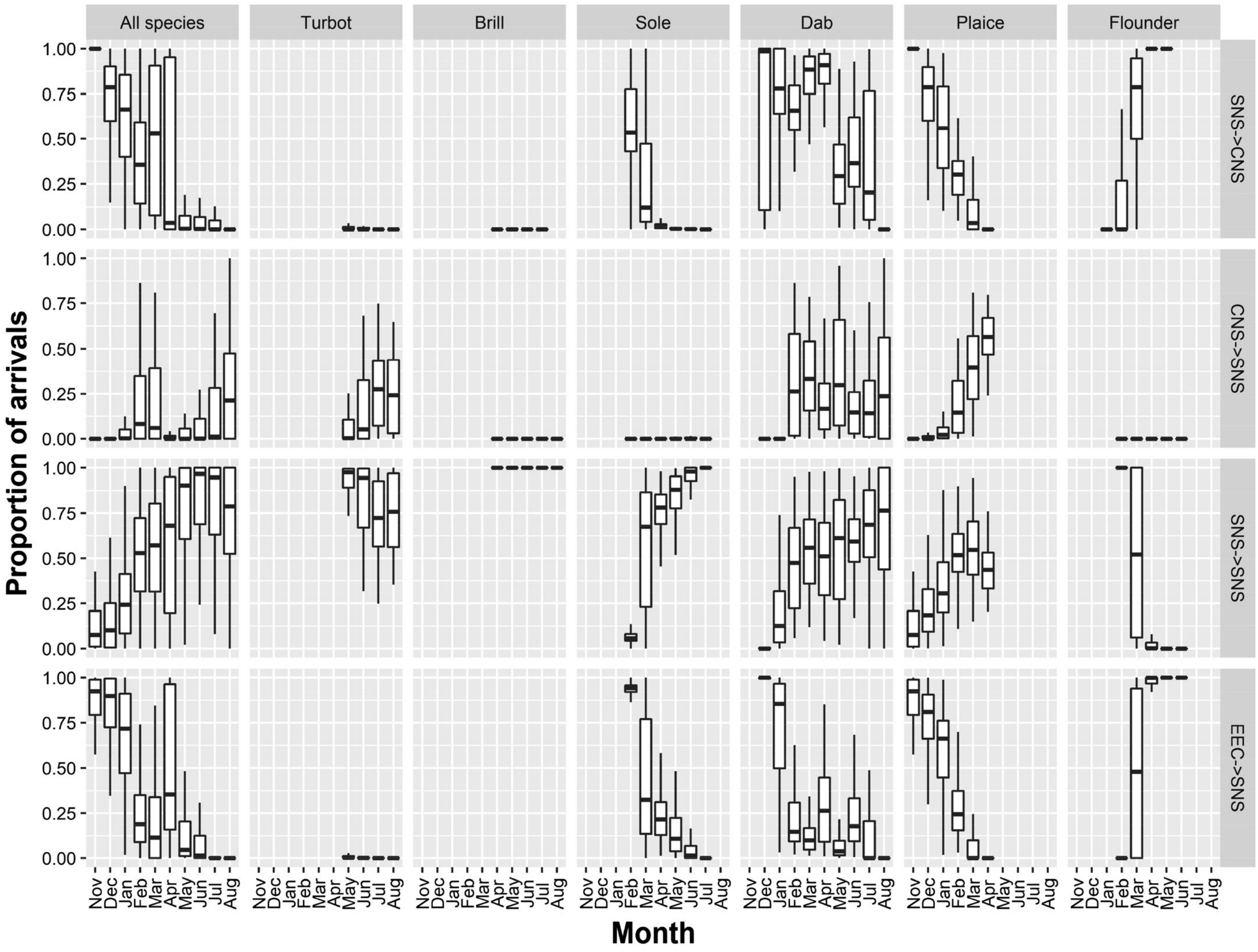

Fig. 9. Monthly boxplots of proportion of arrivals in the CNS from SNS (upper row) and in the SNS from CNS, SNS, and EEC (from second row to lower row, respectively) based on daily connectivity. For each species separately and all species merged (left column).

species in addition to an important interannual variability (Supporting Information Fig. S1). In this case, the variance was explained by the species at 30%, 27% by the year, and 12% by the month. Larval retention (arrivals in SNS from SNS) increased from winter to summer, which is likely associated with a northward limitation of the dispersal owing to the presence of a frontal system at the northern limit of SNS. In the SNS area, the variance of larvae arrivals was explained at 30% by the month, 20% by the species, and 14% by the year.

Discussion

This study demonstrates a large variation in connectivity and spatial distribution among the early life stages of six flatfish species inhabiting the North Sea. Two groups have emerged with similar characteristics in terms of life-history traits and dispersal patterns. Turbot, sole, and brill, which spawned in spring close to the coast, had a shorter PLD and a lower level of connectivity. In contrast, dab, plaice, and flounder were characterized by winter spawning and spawning grounds located further offshore. Their larvae drifted over longer distance and had a higher level of exchange across the region.

A wide range of connectivity

Connectivity between the spawning and nursery grounds of all species was the outcome from the simulated dispersal of particles that followed the south to north general circulation pattern in the North Sea (Turrell 1992). The three management areas of the flatfish stocks are coherent with the dispersal pattern of flatfish. Eggs spawned in the EEC settled locally (French nursery) and dispersed toward the SNS (Thames, Belgian, and Dutch nurseries). Eggs that settled in the SNS originated from the three study areas. The connectivity pattern of the Thames and Belgian nurseries, which are at the same latitude, was similar in all species except for sole.

Sole that settled in Belgium mainly originated from EEC and less from SNS, whereas the reverse pattern was predicted in the Thames nursery. The pattern could be attributed to the high-egg density in the eastern part of EEC. Turbot, brill, and sole showed very high levels of self-recruitment (more than 95%) in the CNS whereas other species were more connected between the SNS and CNS. The latter area is probably not strictly isolated but connected with a northern region not included in the model. This has been shown for plaice (Hufnagl et al. 2013). In addition to variation in space and among species, the model revealed interannual variability. The predicted variation in connectivity was not linear in space and time, which justified the use of a hydrodynamical model to study flatfish settlement.

IBMs require extensive knowledge on 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 beyond our understanding larval connectivity, retention, and successful migration. Also, hypotheses on mortality, spawning ground, and PLD may influence model prediction. The lack of information on some life-history traits (and hence their parameterization) implies uncertainties that might affect the robustness of the model for the species studied. While the biology of some species is well known, uncertainties on life-history traits of other species remain a stumbling block (*see* “Materials and methods” section).

Improving knowledge on the spawning grounds of turbot, brill, and flounder, or on the PLD of brill and dab should improve model prediction. Independent from improving knowledge through extensive field work and experiments, sensitivity analyses, assessing the impact of larval traits parameterization, should also improve model reliability. Assessing model uncertainties is essential when the model is used as a decision-making tool. This issue has been partially addressed in the North East Atlantic Ocean where hydrodynamic models were coupled to a particle model on species-specific traits, such as behavior (Fox et al. 2006; Savina et al. 2010). Model showed an impact of such traits on the prediction. Ideally, sensitivity analyses should consider all parameters together, which is not feasible in complex models requiring important computing resources. An alternative approach proposed by Lehuta et al. (2013), which consists in first assessing the most critical parameters, then estimating uncertainties and processing to calibration, would be worth considering in larval transport models.

Comparison with other modeling and empirical studies

Irrespective of the aforementioned assumptions on parameters and processes, the connectivity patterns estimated by the model are coherent with other modeling studies. Hufnagl et al. (2013) and 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. 2010; Lacroix et al. 2013) and was consistent with the modeling study of Bolle et al. (2009). However, Savina et al. (2016) predicted, unlike this study, an important input (up to 41%) from the North Sea into the EEC for sole. In this study, the only significant movement predicted from north to south was found for dab, in 1 yr (2002). Although the residual current flows NE through the Strait of Dover (between EEC and SNS), in some periods, a reverse current has been observed (Bailly du Bois and Dumas 2005). Hence, under peculiar conditions, dispersal in a SW direction might be possible. Differences in the dispersal pattern of sole predicted in this study and by Savina et al. (2016) might also be explained by differences in hydrodynamic models as illustrated in a comparative study of 11 larval transport models of the North Sea (Hufnagl et al. 2017). Their study, which included the model used here and the model of Savina et al. (2016), showed that dispersal patterns of sole, plaice, and herring were different according to the hydrodynamic model considered. They concluded that modeled hydrodynamics is a critical factor to study larval dispersal and that empirical data are needed to assess accuracy.

Independent information such as 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 the distribution range (Hoarau et al. 2002, 2004; Hemmer-Hansen et al. 2007). Seascape genetic studies, which incorporate various structural and environmental features, are more promising to identify genetic patterns and levels of dispersal (Pita et al. 2011; Selkoe et al. 2016). For example, similar low levels of migration rate were observed in sole, turbot, and brill, and a subtle population structure between the SNS and German Bight in sole and turbot (Vandamme et al. 2014; Vandamme et al. unpubl.). Results for brill were less clear. Population genetic analyses illustrated no difference between the SNS and CNS whereas seascape genetics predicted some scale of differentiation (Vandamme et al. unpubl.). Dispersal patterns linked to adaptation 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).

Although our biophysical model predicted that the Norfolk spawning ground would be isolated for turbot, brill, and sole, no such genetic differentiation was observed in any empirical study. This might be explained by either incompleteness of the model, important adult and juvenile movements, the absence of evolutionary processes to maintain population structure under a regime of a low level of exchange or by insufficient sampling coverage in genetic studies. Due to agreement between the simulated and the genetically measured connectivity patterns on the eastern side of the North Sea, the general consistency of both approaches seems to be a cue for the efficiency of the model. In the specific case of the

Norfolk coast (NE England), the populations might be ecologically separated regardless the absence of genetic differentiation observed, as shown is the case of turbot (Kerby et al. 2013).

Impact of seasonality on dispersal

Seasons impact larval drift (Huret et al. 2010; Robins et al. 2013). The oceanography of the North Sea experiences strong seasonal forcing (Otto et al. 1990). Winter is associated with stronger currents (Holt and Proctor 2008) and colder temperatures, whereas in summer, water temperature is higher and a front occurs between the SNS and CNS (Fig. 1). Analysis of daily connectivity showed an important impact of seasonality on the predicted connectivity (Fig. 9). Sole and flounder, which have similar life-history traits (similar spawning area, both species perform a tidal migration), presented a similar connectivity pattern (Fig. 7). However, in the case of sole, which spawns during spring, local exchange was limited whereas it was more important for flounder. Results are consistent with observations in other species, such as in Northern rock sole in relation to the Bering Sea current (Lanksbury et al. 2007; Cooper et al. 2013).

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 km and 200 km but there were strong differences among species. Differences in terms of PLD (i.e., time spent in the water column) induced differences in dispersal distance. However, PLD is not the only important parameter inducing differences in dispersal distance as illustrated in the case of flounder and brill. Larvae of both species spent similar time in the water column (68 d and 61 d, respectively) but showed a large difference in distance traveled (200 km and 140 km, respectively). In addition to differences in spawning distribution, differences in current strength (Holt and Proctor 2008) and the presence of a barrier to dispersal might explain the difference in distance traveled by both species. Brill, which spawned later in the year than flounder, met weaker currents and might also have traveled less because of the presence of the summer front.

Oceanic fronts represent barriers to dispersal and determine stock structure (Galarza et al. 2009; Schunter et al. 2011). If the water column is well mixed throughout the year in the SNS owing to the shallow depth and tidal mixing, it is not the case in 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). 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 2005; Vandamme et al. 2014). The front might have an important impact on the dispersal pattern. Early spawning species whose eggs and larvae drifted before establishment of the front were most likely not affected (plaice, flounder, and dab), whereas late spawners (sole, turbot, and brill) might have encountered a dispersal barrier. This structuring in two species groups by a hydrodynamical front is clearly visible on our modeled map (Fig. 8). Flounder had a specific dispersal pattern which fits with a spawning period at the end of winter/early spring. Final distribution of larvae showed the setting up of a 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.

In addition to the seasonal pattern, the model predicted a less important but significant impact of year-to-year variability on larval dispersal. Analysis of daily connectivity shown that months explained 20–38% of variance whereas years much less (4–14%). Short-term environmental conditions indeed affect the transport of eggs and larvae in the North Sea. Bolle et al. (2009) have shown how meteorological variability in the SNS influences the transport of plaice eggs and larvae. Winter temperature and residual currents play also an important role in recruitment variability in the North Sea (van der Veer 1986; van der Veer and Witte 1999). The correlation between juvenile abundance and environmental conditions has also been demonstrated in relation with wind intensity, for example, in southern flounder in North Carolina (Taylor et al. 2010) and with river discharge for sole in the Bay of Biscay (Le Pape et al. 2003). The statistical analysis conducted in this study allowed to highlight the significant role of the season and interannual variability on connectivity pattern. Long-term analyses to determine the precise effect of wind, temperature, NAO, or front position could be insightful, in particular in the context of impact assessment of climate change on flatfish connectivity. Such research has been initiated through the assessment of the impact of climate change on sole recruitment and connectivity (Lacroix et al. 2018). Ideally it should be extended to other species.

Biological implication of the reproductive strategy

Life-history traits linked to reproductive strategy experience a high evolutionary pressure from larvae transport or retention in the vicinity of suitable juvenile habitat. Different colonization strategies have been observed among flatfish species (Ramos et al. 2010; Primo et al. 2013). Although the six species studied present a wide range of variation in connectivity, two main strategies emerged. The large overlap in connectivity for species that spawn during the same period (predicted by the model and from independent sources such as genetics) and the seasonal change in hydrodynamic conditions highlighted the strong impact of the summer front on population structure. Turbot, brill, and sole experienced high levels of local retention. These species spawn in spring and summer when current speed is low and the presence of a summer front increases retention and mitigate dispersal. Fronts and eddies are associated with accumulation and production of prey organisms, and so can contribute to larval survival (Nakata 1996; Belkin et al. 2009). In contrast, dab, flounder, and plaice seem to maximize larval dispersal.

The variation in PLD of the six species is temperature-dependent and hence linked to metabolic rate (see "Pelagic larval duration" section). Turbot, sole, and brill, which encountered higher temperatures, had a shorter larval duration (1–2 months) whereas the other species had a longer larval duration (2–3 months). Winter is also the period where larval food (plankton) is less abundant in the North Sea (e.g., Reid et al. 1990), which explains part of the variation in growth rate. Food availability, which was not included in the model, could explain part of the difference in growth rate (i.e., PLD) among different species. The PLD is a proxy of potential dispersal during early life (Shanks 2009*a*). The difference observed here could reflect the species strategy with a high level of connectivity for dab and plaice (longer PLD) and a lower level of connectivity for turbot, brill, and sole (shorter PLD).

Spawning location and behavior are life-history traits experiencing a high selection pressure to maximize recruitment in suitable areas. In systems with strong tidal currents such as in the North Sea, vertical migration synchronized with the tidal frequency is an important factor to reach coastal habitat (Moksnes et al. 2014), especially in flatfish (Lagardère et al. 1999; Fox et al. 2006). The spawning locations are also critical for connectivity. Turbot, brill, sole, and flounder mainly spawn close to the coast, which increases the chances for local retention. Dab and plaice spawn further offshore. To maximize recruitment, plaice spawn either close to the nursery grounds in the Irish Sea, where currents are weak (Nash and Geffen 1999; Fox et al. 2006) or remote from the nursery grounds as in the North Sea, to maximize dispersal. Flounder presents a specific strategy. This species settles preferentially in estuaries, spawns in winter and presents a high level of connectivity between SNS and CNS. A large part of the eggs, which were spawned in SNS and reached CNS, was concentrated close to the coast in the south of the German Bight due to their specific spawning location coupled to tidal migration and a medium PLD. In contrast, plaice and dab eggs dispersed over the whole CNS (Fig. 9). Model predictions are consistent with in situ study on larval distribution of flounder, which also show the high concentrations of larvae in the German Bight (Campos et al. 1994).

Overall, the dispersal strategies of the six species match with the species distributions observed in the area. Turbot, brill, and sole have lower densities in the CNS whereas flounder, dab, and plaice have a larger distribution range up to Iceland, the White Sea, or Baltic Sea (Gibson 2005; Hemmer-Hansen et al. 2007; Kerby et al. 2013; Vandamme et al. 2014).

Consequences for ecosystem knowledge and management

The number of settlers predicted by the model cannot be directly related to recruitment for several reasons. First of all, the spawning stock biomass is unknown in the North Sea for brill, flounder, and dab, resulting in the absence of estimates of the total number of eggs spawned. Furthermore, many processes occurring at the nursery grounds are either density-dependent (e.g., van der Veer et al. 2000; Le Pape and Bonhommeau 2015) or linked to environmental conditions (Rijnsdorp et al. 1992*a*; Fox et al. 2000; Nash and Geffen 2000). Benthic microbial communities produce a specific allelochemical profile that influences the settling of larvae (Woodin et al. 1993; Sebesvari et al. 2013). We assumed that larvae select the preferred habitat at the end of the simulation and that reaching the nursery grounds as defined in this study (*see* "Materials and methods" section) was sufficient as a proxy for settlement. Although our model is based on simple biological assumptions, it successfully explained a significant component of the recruitment variability of sole (Lacroix et al. 2013).

Matches between population units and fisheries management are relevant to determine sustainable exploitation levels of natural resources (Hinrichsen et al. 2011). This study highlights how the combination of life-history traits and environmental conditions affect the migration of the early life stages of flatfish. It clarifies spatial patterning and the position of genetic clines. It also contributes to the understanding and distinction between the historical and adaptive contribution in the genetic structure, and the ecological contribution, especially the migration of early life stages. All organisms in the North Sea show a mosaic of connections (e.g., Jolly et al. 2005; Mariani et al. 2005; Maggs et al. 2008; André et al. 2011).

The considered flatfish species cover a large common geographical area but vary in the way the population is divided in subpopulations. Here, two subpopulations characterize turbot, brill, and sole, whereas dab, plaice, and flounder represent a single mixed population (Fig. 7). The ability to find the source and destination of young fish and the level of spatial structuring of populations is critical for the management of marine protected areas (Planes et al. 2009; Berglund et al. 2012), coastal development (Cicin-Sain and Belfiore 2005), offshore wind farms (Hammar et al. 2016), and fisheries (Fogarty et al. 2007). For example, in the northeast of UK, the local turbot population collapsed in 1970s due to overfishing. The hypothesis is that the population of young turbot was not sufficient to maintain a sustainable number of adults (Kerby et al. 2013). The prediction of the model confirmed this hypothesis with a high level of self-recruitment in the 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 important for fisheries management (Kerr et al. 2010). Knowledge on stock structure impacts exploitation (Kerr et al. 2016).

For example, the presence or absence of distinct subpopulations impacts the sustainable exploitation of sole in EEC (Archambault et al. 2016). In the present study, based on the migration of early life stage, two subpopulations of sole, brill, and turbot (EEC-SNS and CNS) might be considered. In addition, the northeastern English coast has a low level of connectivity with the rest of the area. Whereas based on information of early life-history traits, plaice, dab, and flounder show considerable exchange in the area.

Conclusion

This modeling study highlighted structure in subpopulations of flatfish. Model results showed that individual-based modeling is a useful strategy to guide resource management, even when limited biological information is available for example in the case of brill. Extending the modeled 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 EEC (Archambault et al. 2015).

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Acknowledgments

We kindly thank two anonymous reviewers for their constructive comments. Research was funded by the B-FishConnect research project (G.0702.13N) and the Scientific Research Network "Eco-evolutionary dynamics in natural and anthropogenic communities" (grant W0.037.10N), both funded by the Research Fund–Flanders (Belgium).

Conflict of Interest

None declared.

Submitted 06 February 2018
Revised 07 September 2018
Accepted 19 November 2018

Associate editor: Kelly Benoit-Bird