From spawning to first-year recruitment: the fate of juvenile sole growth and survival under future climate conditions in the North Sea

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This study shows the effect of climate change on the growth and survival of early life history stages of common sole (*Solea solea*) in different nursery areas of the North Sea, by combining a larval transport model with an individual-based growth model (Dynamic Energy Budget) to assess the fate from egg to young of the year at the end of the first growth season. Three scenarios of climate change, inspired by the 2040 Intergovernmental Panel on Climate Change projections, are tested and results are compared to a reference situation representative of current climate conditions. Under climate change scenarios where wind changes, water temperature increases and earlier spawning are considered, the early arrival of fish larvae in their nurseries results in larger young of the year at the end of summer. However, early arrival leads to higher mortality due to initially slow growth in spring. Future climate scenarios result in higher biomass and reduced first-year survival. How this result translates into changes at population level and stock management needs further investigation. Nonetheless, this study illustrates that processes linking life stages are paramount to understand and predict possible consequences of future climate conditions on population dynamics.

Keywords: climate change scenarios, Dynamic Energy Budget model, growth, larval transport model, life cycle, North Sea, *Solea solea*, survival

Introduction

Many fish species have complex life cycles where different stages of the cycle (egg, larval, juvenile, and adult stage) occur in different habitats with varying conditions. Each stage has its own needs in terms of abiotic conditions, such as temperature and shelter, and food requirements in energetic content and availability. Favourable circumstances for all life stages account for a successful population, and unfavourable conditions for a single life stage may cause population decline despite good conditions elsewhere in life (Petitgas *et al.*, 2013). Eggs and larvae are often pelagic and drift from spawning areas to shallow areas, called nurseries.

Juveniles inhabit such nurseries and adults reside in deeper and often cooler areas (Harden Jones, 1968). For marine fish species, the use of coastal or estuarine nurseries is common and more importantly, most often obligatory (Brown *et al.*, 2018). Connectivity between spawning grounds and nursery areas is a critical step in recruitment of larval fish to the population because if nurseries are not reached the larvae will die. Within a nursery, habitat quality is foremost determined by food availability, predator presence, and temperature (Gibson, 1994). Processes, such as the aforementioned larval drift, but also growth and mortality link the different life stages. These processes are affected by

temperature and hence by climate change. While there are studies relating larval drift and juvenile fish densities to nursery habitat characteristics under current conditions (e.g. Ciotti *et al.*, 2014; Brown *et al.*, 2019), it is necessary to predict future scenarios of larval and juvenile fish performance in nurseries to aid adaptive management of fish stocks by taking life stage performance into account (Teal *et al.*, 2008; van de Wolfshaar *et al.*, 2011, 2015).

Biophysical models have proven useful for assessing the impact of climate change on larval dispersal (e.g. Lett *et al.*, 2010; Andrello *et al.*, 2015), larval survival (e.g. Cetina-Heredia *et al.*, 2015), connectivity (Munday *et al.*, 2009; Kendall *et al.*, 2013), and fish recruitment (e.g. Brochier *et al.*, 2013). However, the complex response of recruitment at nursery grounds to climate change remains to be assessed quantitatively. As a first attempt to address this question for sole in the North Sea, a study on the dispersal of eggs and larvae under combined climate change conditions (temperature increase, wind speed, and direction changes) has recently been published (Lacroix *et al.*, 2018). This study builds upon literature illustrating that under current climate conditions, the dispersal of flatfish eggs and larvae in the North Sea shows high inter-annual variability and is driven by currents (e.g. Bolle *et al.*, 2009; Hufnagl *et al.*, 2013). Current and future climate conditions differ in temperature, wind, and currents; factors impacting this first life stage. Indeed, under future climate conditions, the connectivity between spawning grounds and nurseries, the onset of spawning and the duration of the larval period could differ from current climate conditions (Lacroix *et al.*, 2018). Changes in the onset of spawning can be expected due to its temperature dependence (Fincham *et al.*, 2013). Under future climate change conditions, the distribution and timing of arrival of larvae at nurseries may change in complex, and even contrasting manners between nurseries. Some nurseries may receive more while others receive fewer recruits, based on temperature-driven larval development and patterns in currents (Lacroix *et al.*, 2018).

Differences in connectivity and timing of larval arrival at nurseries *per se* will affect the further development of those juveniles that reach a nursery area (Van der Veer *et al.*, 1994). In addition, changes in climatic conditions will also impact growth and survival of post-settlement juveniles in the nursery. Fish are known to exhibit temperature-dependent growth and development driven by physiological processes (Teal *et al.*, 2012). There is ample evidence of temperature-dependent growth rates in fish (Fonds *et al.*, 1992), often from controlled experimental systems, but also from field studies (Teal *et al.*, 2008; Felix *et al.*, 2011). Especially, the growth rate early in life is faster in warmer conditions, while the maximum attained length is often lower in warmer conditions (Felix *et al.*, 2011; Forster *et al.*, 2012) providing similar feeding conditions. Climate change in terms of increased water temperatures will therefore affect juvenile growth performance in their coastal habitat (Teal *et al.*, 2012). Despite the strong dependence on coastal areas as nurseries, there are not many studies yet considering climate change effects at the nursery level nor linking climate effects of the initial pelagic egg and larval stage and post-settlement development. This is important because the first year often determines recruitment to the population (Rijnsdorp *et al.*, 1992).

Here, we present the case of the flatfish common sole *Solea solea* L. (Soleidae, Teleostei), a key component of the soft-bottom ecosystem (Gibson *et al.*, 2015) and among the most valuable commercial species in the southern North Sea (Pilling *et al.*, 2008). Sole is a batch spawner (Houghton *et al.*, 1985), which

means that one individual lays several batches of eggs during a spawning season. This species spawns in the North Sea in coastal waters in spring (Van der Land, 1991) along a latitudinal gradient (Rijnsdorp and Vingerhoed, 1994). The onset of spawning is temperature-dependent (Fincham *et al.*, 2013). Larval development is temperature-dependent (Fonds, 1979), whereas survival is linked to prey availability, avoidance of predators, and infections. Supply to nursery grounds may be affected by advection and diffusion of the planktonic eggs and larvae (Lacroix *et al.*, 2013). Larvae settle in coastal nurseries and are subject to size-dependent (predation) mortality (Akimova *et al.*, 2016).

The aim of this study was to assess the effects of climate change for spawning, the larval and the post-settlement juvenile life stage addressing the processes of transport, growth, and survival of young of the year (YOY) during this first year (Figure 1). We address impacts on individual growth in terms of length and biomass, and assess survival from egg until the end of the first growth season. We did so by taking the results presented by Lacroix *et al.* (2018) on spawning and larval dispersal and development of the common sole (called hereafter sole) as a starting point to model the growth and development of the predicted arrivals in six nurseries in the North Sea basin. The fate of the post-settlement YOY was projected forward by modelling growth and survival in nurseries using a Dynamic Energy Budget (DEB) approach, validated for North Sea sole (Freitas *et al.*, 2010; Teal *et al.*, 2012). DEB models provide a mechanistic underpinning of physiological rates and therefore individual performance (Kooijman, 2000). Arrival numbers, arrival days, and temperature were taken from Lacroix *et al.* (2018) to model the fate of post-settlement fish in the six North Sea nurseries for historical years (2003–2011) and future years based on the Intergovernmental Panel on Climate Change (IPCC) 2040 climate scenario. We then evaluated the effects of future climate conditions on the first life stages of sole in terms of transport success, growth, and survival (Figure 1).

Methods
Lagrangian larval transport model of sole
The Larvae&Co model is an individual-based model (IBM) resulting from the coupling between a 3D hydrodynamic model with a Lagrangian particle-tracking model. It has been developed for sole to simulate egg and larval dispersal in the eastern English Channel and the North Sea during the period 2003–2011 (Lacroix *et al.*, 2013) (Figure 2).
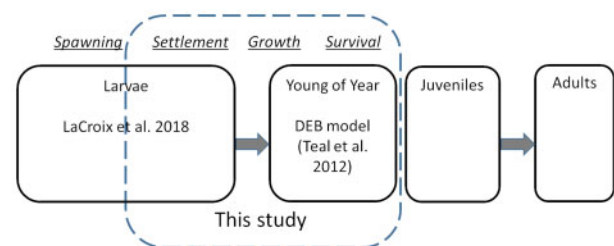

Figure 1. Illustration of the different stages of the life cycle of flat fish and important processes during early life (italic and underlined). The dashed rectangle denotes those stages and processes that are subject of this study. References are given for the two models we combined in this study.
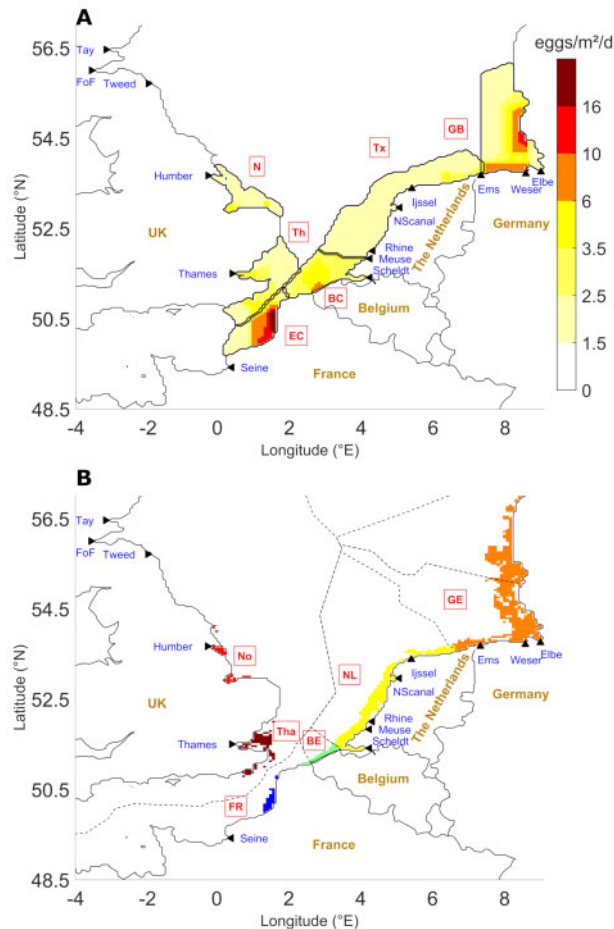
Figure 2. Geographic implementation of the model. (a) Distribution of the main spawning grounds of *Solea solea* in the North Sea and Eastern English Channel (delineated by the black lines) with contour plots of the mean daily egg production [redrawn from ICES-FishMap (2005)]. Eggs are released at six well-known main spawning grounds: the eastern English Channel 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). (b) The six nursery grounds located in shallow muddy to sandy coastal areas of <20 m depth were subdivided following national boundaries: FR (blue), BE (green), NL (yellow), GE (orange) except for the United Kingdom, where a southern (Tha, brown) and a northern nursery (No, red) were distinguished. The dotted black lines represent the national EEZ. Figure with permission from Lacroix *et al.* (2018).

The 3D hydrodynamic model based on the COHERENS code (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. It has a resolution of 5′ in longitude and 2.5′ in latitude (∼5 by 5 km), and 20 sigma-coordinate vertical layers. 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 6-hourly surface wind and atmospheric pressure fields provided by the Royal Meteorological Institute of Belgium based on the analysed/

forecast data of the UK Met Office Global Atmospheric Model (Walters *et al.*, 2017).

Larval trajectories were calculated online using the particle tracking module of COHERENS. The IBM of sole used in this study and the equations and parameters therein have been thoroughly described in Lacroix *et al.* (2013) and are briefly summarized here. The sole IBM includes four stages of development—eggs, yolk-sac larvae up to ∼4 mm, first-feeding larvae (size ∼4–8 mm), and metamorphosing larvae (size ∼8–10 mm); each stage has a specific parameterization and behaviour. Pelagic larval stage duration lasts <2 months and decreases with increasing temperature (T) during the drift as follows: $274.64*T^{-1.5739}$; $137.92*T^{-1.4619}$; $3560.1*T^{-1.9316}$; $1146.1*T^{-1.9316}$, respectively, for eggs, yolk-sac-larvae, first-feeding larvae, and metamorphosis larvae. Mortality is stage and temperature-dependent for eggs and yolk-sac larvae (mortality rate, in day^{-1}, is equal to $0.0004*T^{3.0293}$ for eggs and yolk-sac larvae) (Van der Land, 1991; Rijnsdorp and Vingerhoed, 1994) and stage-dependent for first-feeding larvae and metamorphosis larvae (mortality rate, in day^{-1}, 0.035) (Horwood, 1993).

Vertical migrations are stage-dependent. The eggs and yolk-sac larvae stay in the upper water column due to their positive buoyancy; first-feeding larvae perform diel vertical migrations in the upper water column, and metamorphosing larvae perform tidally synchronized vertical migrations in the lower water column [for more details about the IBM parameterization, see Lacroix *et al.* (2013) and Barbut *et al.* (2019)].

Spawning is temperature-dependent. There is a latitudinal trend in the spawning period, with spawning starting earlier at lower latitudes in the North Sea (Rijnsdorp and Vingerhoed, 1994; Forster *et al.*, 2012) and northeast Atlantic Ocean (Vinagre *et al.*, 2008) as a consequence of a latitudinal gradient in temperature. The spawning period lasts about 3 months (Koutsikopoulos *et al.*, 1991) and the spawning peak occurs at a temperature of about 10°C [Lacroix *et al.* (2013) and references therein]. In the model, the peak spawning date, for each spawning ground, is estimated by computing the average temperature over each spawning ground as described in Savina *et al.* (2010) and by taking the first day where a temperature of 10°C is reached on each of these areas. Then, for each grid cell in a given spawning ground, a parabolic production curve, centred on peak spawning of the spawning ground considered, is computed for the total number of eggs spawned estimated from the egg distribution map (Figure 2a) (ICES-FishMap, 2005), and considering a spawning period of 100 days. The total number of eggs released on each grid cell is equal to the daily egg production from observations (from ICES-FishMap 2005; in eggs per m^2 per day) multiplied by the grid cell surface (27 km^2) and by the spawning period duration. The total number of eggs released in each grid cell does not change with year but the timing of spawning does. Eggs are released at the six well-known main spawning grounds (Figure 2a): the eastern English Channel 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). In total, considering the six spawning grounds, 1.89E6 particles (each of them representing 10E6 eggs) are released each year to represent a total of 1.89E13 eggs, which is in the range of egg production given by Van der Land (1991) for the whole North Sea. The six nursery grounds located in shallow muddy to sandy coastal areas of <20 m depth were subdivided following national boundaries (FR, BE, NL, GE) except for the

United Kingdom, where a southern (Tha) and a northern nursery (No) were distinguished (Figure 2b).

Reference simulation and scenarios

The model was run over a period of 9 years (2003–2011) to take into account inter-annual variability in dispersal and recruitment to the nursery grounds due to environmental year-to-year variability. This simulation, representative of the current conditions, is hereafter called the "reference situation" (REF). The impact of climate change on larval recruitment at nursery grounds was assessed by testing three scenarios of climate change using the "Warm+" mid-term 2040 IPCC scenario at the North Sea scale proposed in Van den Eynde et al. (2011) and described in Lacroix et al. (2018). In the scenario "SST increase" (hereafter called T2), a 2°C increase is applied by adding 2°C to the SST forcing from BSH. In the scenario "SST increase and early spawning" (hereafter called T2S), in addition to the perturbation of scenario T2, an early spawning is considered. The peak date, which is still computed as the first day that a temperature of 10°C is reached (see section above), occurs earlier than in the reference run (42 days on average). The scenario "all perturbations" (hereafter called T2SW) considers, in addition to the previous perturbations, a 4% increase in wind speed, applied by adding 4% to the wind velocity forcing used for the reference run and a change in wind direction by 13° north-eastwards, which is applied by adding 20% to the northern component and 10% to the eastern component of the wind intensity used for the reference simulation. Whatever the scenario, the perturbations are applied at each time step and over the whole domain.

For the purpose of this study, results of the reference simulation and the three scenarios obtained by Lacroix et al.(2018) were adapted to provide time series of the total abundance of larvae arriving at each nursery ground for every year.

Physiology

To model the growth of sole post-settlement juveniles during their first year, we used a DEB model, parameterized for sole in the North Sea (Teal et al., 2012) (all parameters and their values are described in Table 1). A DEB model describes the growth of a post-settlement individual in terms of volume V, based on the energetics of an individual in terms of energy assimilation and energy used for maintenance $[E_m]$ and growth $[E_G]$ (Kooijman, 2000). Assimilation of energy $\{\dot{P}_{Am}\}$ scales with surface area of an individual and is converted to reserves at a constant rate. The energy allocated to growth and somatic maintenance is based on the kappa-rule. This implies that a fixed proportion κ goes to growth and maintenance and 1-κ to is allocated maturity maintenance and reproduction. Somatic maintenance has a priority over growth. When there is little reserve energy growth ceases while soma is maintained as much as possible. Maintenance costs $[P_M]$ are proportional to the structural volume of the organism. Volumetric growth and can be represented as follows:

$$\frac{dV}{dt} = \frac{\left(\kappa f\{\dot{P}_{Am}\}\right)V^{2/3} - [P_M]V}{\kappa f[E_m] + [E_G]}.$$

Physiological rates are temperature-dependent and scale with the Arrhenius function:

Table 1. Estimated parameters of the DEB model for sole [taken from Fonds (1979), Freitas et al. (2010), and Teal et al. (2012)] at 20°C reference temperature.

Symbol	Dimension	Interpretation	Value
$\{\dot{p}_{Am}\}$	J cm^{-2} d^{-1}	Maximum surface area-specific assimilation rate	864
$[\dot{p}_M]$	J cm^{-3} d^{-1}	Volume-specific maintenance costs	54.1
$[E_M]$	J cm^{-3}	Maximum storage density	1 986
$[E_G]$	J cm^{-3}	Volume-specific costs of structure	5 600
κ	–	Fraction of utilized energy spent on maintenance plus growth	0.9
δ_m	–	Shape coefficient	0.192
f	–	Edible proportion scalar	0.17
T_A	K	Arrhenius temperature	8 500
T_L	K	Lower boundary of tolerance range	282
T_H	K	Upper boundary of tolerance range	305
T_{AL}	K	Rate of decrease at lower boundary	50 000
T_{AH}	K	Rate of decrease at upper boundary	100 000
T_{ref}	K	Reference temperature	293
α	d^{-1}	Size-dependent mortality constant	0.0234
β	–	Size-dependent mortality exponent	−0.423
a	g cm^{-1}	Length–weight constant	0.0057
b	–	Length–weight exponent	3.1364

Mortality parameters were fitted to unpublished data made available by A.D. Rijnsdorp. Parameter values for the length–weight relationship were estimated based on 7-year survey data of juveniles age 0, obtained in the autumn Demersal Fish Survey conducted by Wageningen Marine Research.

$$\dot{k} = k_{Tref} \cdot \exp\left(\frac{T_A}{T_{res}} - \frac{T_A}{T}\right),$$

where k_{Tref} is the value of the rate at the reference temperature and $\dot{k}$ is the scaled rate at temperature T. T_A is the species-specific Arrhenius temperature (all temperatures are in Kelvin). The assimilation rate $\{\dot{P}_{Am}\}$ is affected by the species specific temperature tolerance range, bound by an upper and lower limit beyond which the rate decreases rapidly (Kooijman, 2000; Van der Veer et al., 2009; Teal et al., 2012). This is done with the following multiplier (Kooijman, 2000; Teal et al., 2012):

$$\exp\left(\frac{T_A}{T_{res}} - \frac{T_A}{T}\right) \cdot \left(\frac{1 + \exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right)}{1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)}\right).$$

The scalar f sets the edible proportion of the resource, meaning that for $f = 1$ all food is edible and when $f < 1$ only a fixed fraction is edible. We do not model the resource explicitly and have no information on resources for the hindcast, nor for the climate change scenarios. Instead, the scalar was used to scale the attained length of the juveniles at the end of the growth season, set at Julian day 273, for the reference temperature scenario to match observed values from early September surveys of ~11 cm (Teal et al., 2008). By setting the value of f such that the modelled length matches observed length, we implicitly mimic food limitation as has been demonstrated for sole in the field (Le Pape and

Bonhommeau, 2015; Poiesz *et al.*, 2020). For simplicity reasons, we use a fixed value, for adult sole little seasonality in gut fullness was demonstrated (Teal *et al.*, 2012).

A post-settlement individual is described by its structural volume, and the change in volume is modelled on a daily basis given the ambient temperature in a nursery. This daily growth is converted into length using the shape coefficient (Table 1), resulting in length curves of juvenile sole:

$$L = V^{1/3}/\delta_{\mathrm{m}}$$

While volume can shrink fish length cannot. It is asserted in the code that a reduction in volume due to starvation may occur but does not result in shrinkage in length presented in the figures. Biomass attained at the end of the growth season was calculated with the volume reached at the end of the growth season, converted to length. The length–weight relationship derived from survey data (WMR data Demersal Fish Survey, 2003–2011), described by the allometric function $W = a\,L^b$, was used to convert the end of season length to biomass (parameter values are given in Table 1).

Mortality

The hydrodynamic model underlying the transport model provided daily mean temperatures, daily arrival numbers, and the number of larvae that did not reach a nursery, for each nursery and each climate change scenario, for 9 years each. Lacroix *et al.* (2018) calculated the number of viable larvae reaching a nursery based on temperature-dependent mortality losses; viable larvae are the larvae surviving the phase from egg until settlement in a nursery. For each day, for which viable larvae arrived the DEB model was used to calculate the temperature-dependent change in size from the day of arrival until the end of the growth season, set at day 273 corresponding to the end of season in the Dutch nursery early September (Teal *et al.*, 2012). Julian day 1 is set to January first of each calendar year.

Given the obtained daily size information of an individual, we calculated the size-selective mortality during the post-settlement phase in the nursery. Size-based mortality is common and demonstrated for sole (Van der Veer *et al.*, 1994), while there is no evidence for a temperature-dependent component (Zijlstra *et al.*, 1982). Size-based mortality is described by the allometric function:

$$\mu = \alpha\,L^{\beta},$$

where α and β were based fitted to growth data from the Dutch part of the North Sea coast (unpublished data made available by A.D. Rijnsdorp).

We present the contributions of the three sources (transport success, pelagic survival, and post-settlement survival) of survival from spawning until the end of the growth season and the absolute survival for each scenario. Transport success is defined as the number arriving in a nursery divided by the number of eggs released. Of those that were successfully transported to a nursery, a fraction survived based on temperature as described above, defining pelagic survival. Of those survivors that reached nursery, a fraction survived until the end of the growth season, defining post-settlement survival. Total survival, from egg release until

end of growth season, is then the multiplication of transport success, pelagic survival and post-settlement survival.

Because we used mechanistic models, which ignore phenotypic plasticity (Teal *et al.*, 2018) only descriptive statistics are presented. Tests of statistical significance are only useful when taking random samples, which is not the case here.

Results

Larval drift

The variability of temperature, arrival days, and arrival numbers from the larval drift model is shown in Figure 3 for each of the scenarios. The mean temperature of the nurseries France, Belgium, the Netherlands, and UK Thames range between 14.4°C and 14.6°C, while Germany (13.8°C) and UK Norfolk (12.8°C) have a lower mean temperature (values for the reference scenario) (Figure 3a). Figure 3b shows the arrival days of viable larvae in the nurseries (Lacroix *et al.*, 2018). Of the four climate scenarios, the reference scenario has the latest arrivals (mean Julian day =
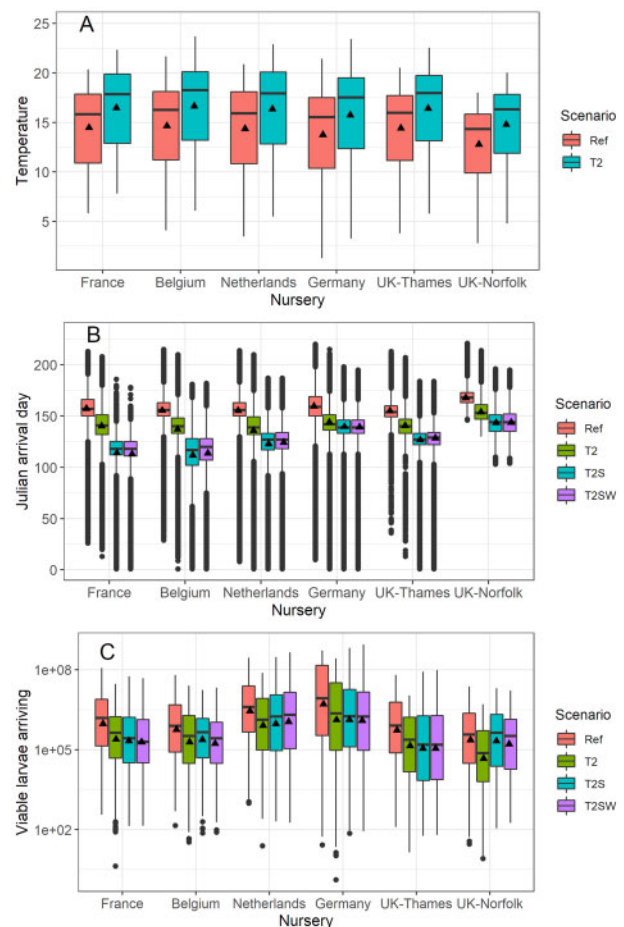

Figure 3. (a) Temperature from January first to day 273 (end of the growth season), (b) arrival times, and (c) Daily arriving numbers as predicted by the larval drift model per nursery and for each scenario (all years combined) [from Lacroix *et al.* (2018)]. Note that there are two temperature scenarios: the reference and a climate scenario (T2). The T2S and T2SW scenarios follow the same temperature profile as the T2 scenario. The boxes in the plot show the median value, bounded by the first and third quantile. The black triangle denotes the mean value.

158, s.e. = 13 days), followed by the T2 scenario (mean Julian day = 142, s.e. = 15 days). The earlier arrival of post-settlement individuals in T2 compared to the reference is due to the increased developmental rate of the eggs and larval stages in response to higher temperatures (Lacroix *et al.*, 2018). The climate scenarios with increased temperature and early spawning (T2S and T2SW) have the earliest arrivals (both a mean of Julian day 133, s.e. 17 days). Any, slight, difference between these scenarios is due to the inclusion of a different wind field in the T2SW scenario. The daily numbers arriving differs between nurseries and scenarios, as was described by Lacroix *et al.* (2018), but there is no clear pattern between the three climate change scenarios across nurseries (Figure 3c). The total numbers arriving are highest for the reference scenario (mean = 8.8E9, s.e. = 1.8E9). The T2 scenario yields least total arrivals (mean = 2.9E9, s.e. =0.8E9), while the T2S (mean = 7.4E9, s.e. = 2.1E9) and T2SW (mean = 8.0D9, s.e. = 2.7E9E7) have intermediate values close to the REF scenario.

Post-settlement growth and survival

Using the DEB model, the growth rate of a post-settlement individual can be calculated based on an arrival day and the accompanying temperature development from the arrival day onwards in a given nursery. Figure 4a shows the length development of a single sole settling in a nursery, until the end of the growth season. Illustrated are the length trajectories of an early, mid, and late arrival day in the Dutch nursery for the reference climate scenario (REF) and the climate scenario with temperature increase, temperature-dependent spawning, and a perturbed wind (T2WS). Late arrival in a nursery results in a steep onset of growth, while with early arrival initial growth is slow. This holds
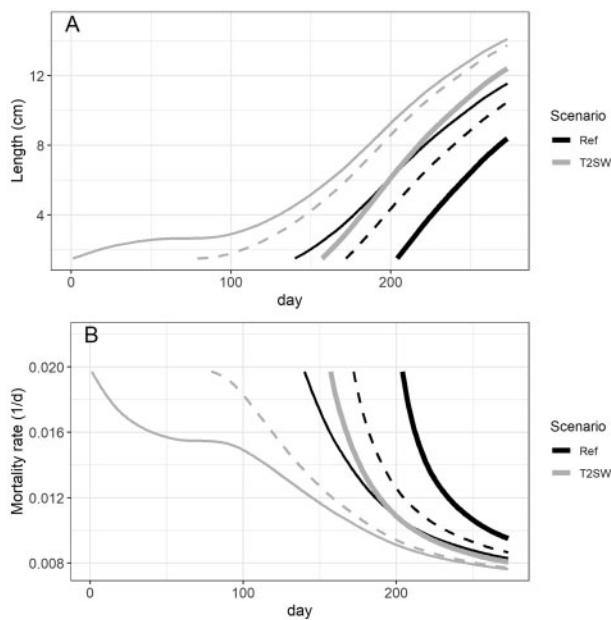

Figure 4. Illustration of length (a) and mortality rate (b) of a single individual at a given Julian day. The solid line represents the growth and mortality trajectories of a post-settlement individual arriving early, the dashed line represents arriving in the middle of the arrival period, and the thick solid line represents late arrival as predicted by the larval drift model for the reference and the T2SW scenario. This example is taken from the Dutch nursery for 2005.

also for the reference and the T2WS climate scenario. The increased temperature does not lead to fast growth early in the season. However, the length a single individual can attain at the end of the growth season is higher than with the reference scenario (REF: mid arrival's end length = 10.3 cm; T2WS mid arrival's end length = 13.7 cm).

For each individual length curve, the daily size-dependent mortality rate can be determined (Figure 4b). The mortality rates follow the inverse pattern of length (Figure 4a), with slow growth resulting in a slow decrease of the mortality rate and fast growth resulting in a steep decrease of the mortality rate. The mortality rate a single individual suffers at the last day of the growth season is lower for the climate change scenario than for the reference scenario based on the length reached (REF: mid arrival's mortality = 0.0086 d^{-1}; T2WS mid arrival's mortality = 0.0077 d^{-1}). The cumulative mortality suffered from day of arrival until the last day of the growth season is of far more importance and determines how many of the arriving numbers survive until the end of the growth season. This result is shown in the following section at nursery level.

Nursery level growth, survival, and biomass

For each year, each nursery, and each arrival day, the individual growth curves and mortality rates are determined considering the mean nursery temperature obtained from the hydrodynamic model. In Figure 5, the lengths attained at the end of the growth season are plotted for each nursery and climate scenario based on the arriving numbers of viable larvae (mean lengths are provided in the Supplementary Appendix). The lengths attained with the reference scenario are smallest (Table 2). The increase in temperature alone, the T2 scenario, causes an increase in mean lengths for all nurseries. The addition of earlier spawning, and hence earlier arrival in the nurseries, increases the mean length even more, but there is no difference in the lengths reached at scenario level between the scenarios with early spawning, despite small differences at nursery level.

Since both arrival day and arrival numbers from the drift model are known, we calculated the survival of post-settlement juveniles for each nursery, year, and climate scenario using the length-based mortality rate function (Figure 6a). This post-settlement survival is determined for each length trajectory; from arrival day until the end of the growth season. Because size determines mortality rate and early arrival is associated with low growth rates, early arrivals stay small for a longer period than late
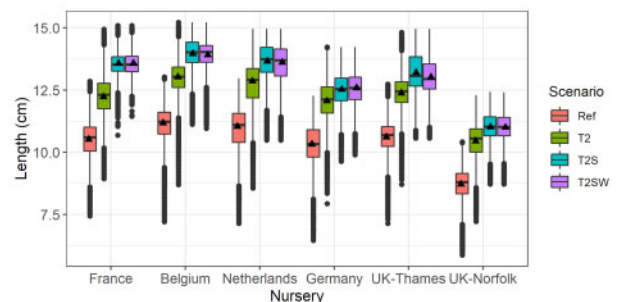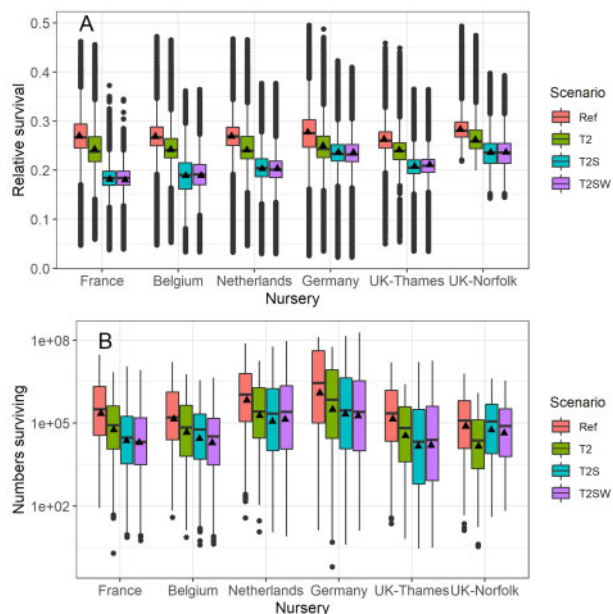

Figure 5. Lengths attained at the end of the growth season for each nursery and climate change scenario. The boxes in the plot show the median value, bounded by the first and third quantile. The black triangle denotes the mean value.

Table 2. Mean and *SD* (between brackets) values, taken over years and nurseries, for six variables addressed in this study, for each climate scenario.
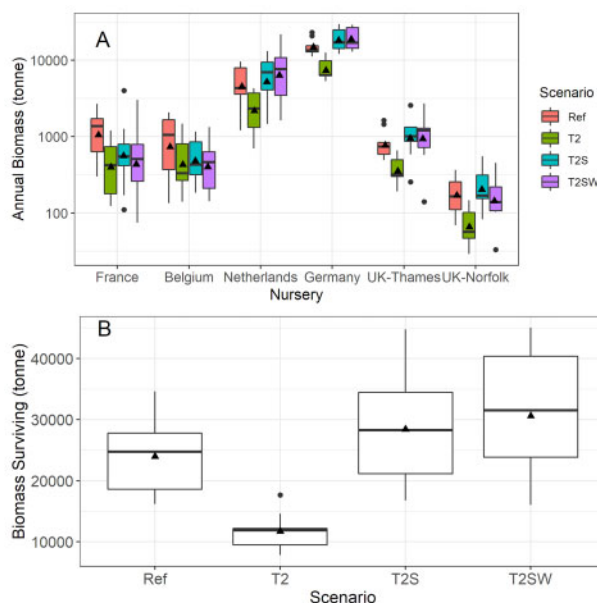
Variable	Ref	T2	T2S	T2SW
Transport success proportion	0.26 (0.049)	0.27 (0.050)	0.27 (0.046)	0.31 (0.059)
Pelagic survival proportion	0.0015 (0.00024)	0.0006 (0.00017)	0.0014 (0.00046)	0.0014 (0.00054)
Post-settlement survival proportion	0.27 (0.036)	0.25 (0.035)	0.23 (0.035)	0.22 (0.036)
Total number surviving	2.4E9 (0.6E9)	0.7E9 (0.2E9)	1.6E9 (0.5E9)	1.8E9 (0.7E9)
Individual length (cm)	10.5 (0.9)	12.3 (0.9)	13.0 (0.9)	13.0 (0.9)
Total biomass (tonne)	24E3 (6.5E3)	12E3 (3.1E3)	28E3 (9.3E3)	31E3 (10.5E3)

For total numbers surviving and total biomass the mean and *SD* were calculated for the sum over all nurseries, providing a North Sea wide value.

Figure 6. (a) Proportion of post-settlement YOY arriving at a nursery and surviving until the end of the growth season, for each nursery and scenario. (b) Absolute daily numbers of post-settlement YOY surviving until the end of the growth season. The boxes in the plot show the median value, bounded by the first and third quantile. The black triangle denotes the mean value.

Figure 7. (a) Total annual biomass of post-settlement individuals at the end of the growth season for each nursery and each climate change scenario. (b) Total biomass for each climate change scenario (mean taken over the years; summed over the nurseries, in tonnes) of post-settlement individuals surviving until the end of the growth season. The boxes in the plot show the median value, bounded by the first and third quantile. The black triangle denotes the mean value.

arrivals (Figure 4), post-settlement survival of late arrivals is therefore higher than for early arrivals. The larger length at the end of the season does not make up for the slow start. As a result of this, post-settlement survival is higher for the scenarios without early spawning than for the scenarios with earlier spawning (Table 2). The French and Belgian nurseries have the lowest survival, the Dutch and UK Thames have intermediate survival, and the German and UK Norfolk have the highest survival (means are provided in the Supplementary Appendix). When considering the absolute numbers that survive from settlement to the end of the growth season (Figure 6b), the pattern resembles the pattern in arrival day (Figure 3). Highest numbers at the end of the growth season are attained with the reference scenario for each nursery (Table 2). The numbers surviving based on the sum over all nurseries are highest for the reference scenario and lowest for the T2, while the scenarios with earlier spawning have intermediate, more similar values (Table 2).

Total nursery biomass at the end of the growth season can be calculated based on attained lengths and the numbers surviving

(Figure 7a). The pattern in average annual biomass differs between nurseries and scenarios. For the French and Belgian nursery, which have the lowest latitudes, the reference scenario has the highest biomass, while for the other nurseries the T2S or the T2WS scenario have the highest biomass. For the UK Norfolk nursery, which has the highest latitude and lowest mean temperature, biomass is not that different between scenarios with exception of the T2 scenario, which results in much less biomass than the others. The T2 scenario provides lowest biomass for all nurseries. Overall, there is little change in the relative contributions of the nurseries to total biomass.

The annual mean biomass at the end of the first growth season, summed over all nurseries, resulting from attained lengths and numbers surviving for each scenario is presented in Figure 7b (means are provided in the Supplementary Appendix). The mean of the annual total North Sea biomass is highest for the climate scenario T2WS (Table 2). This is despite the overall low survival for this scenario compared to the reference scenario. Total

biomass for the T2S scenario is of the same order of magnitude. The reference scenario has despite the high survival and high numbers not the highest mean biomass, which is caused by the small attained length. The T2 scenario, with an increase in temperature but without a shift in spawning period, has the lowest biomass at the end of the growth season, a result of the low overall survival and low numbers predicted by this climate change scenario.

Survival from spawning to the end of the first growth season

The larval drift model provides the fate of all larvae before settlement in a nursery, including those that do not reach a nursery. The number of larvae reaching a nursery is based on transport success and a temperature-dependent survival (Lacroix *et al.,* 2018). We combined the transport success, the pre-settlement (pelagic) survival (Lacroix *et al.,* 2018), and the post-settlement survival result of the current study during the first growth season in a nursery at the North Sea scale.

For each climate scenario, it becomes apparent that the importance of success rate for each process differs. Pelagic survival contributes least to the overall survival, with the lowest value for the T2 scenario (Table 2). Transport success and post-settlement survival are much higher than pelagic survival. The post-settlement survival is lowest for the T2S and T2WS climate scenarios compared to the reference and the T2 scenario. This low contribution of post-settlement survival is due to earlier spawning in these scenarios, which led to increased mortality. The overall survival, from egg to post-settlement, is highest for the reference scenario (Figure 8). Under the modelled climate change conditions the survival of larvae is low. Especially, for the T2 scenario, the overall survival is less than half of that of the reference scenario (4E−5 vs. 1E−4). The overall survival of the T2S and T2WS scenarios is 9E−5 and 9.5E−5, respectively. Including wind in the climate change scenario shows to have a small positive effect on survival.

Discussion

This is one of the first occasions demonstrating the effects of climate change scenarios for pre- and post-settlement fish during their first growth season. We linked the survival of the pelagic stage and the post-settlement stage (first growth season) to determine an overall effect of climate change scenarios on first-year survival and biomass recruitment and found that while transport
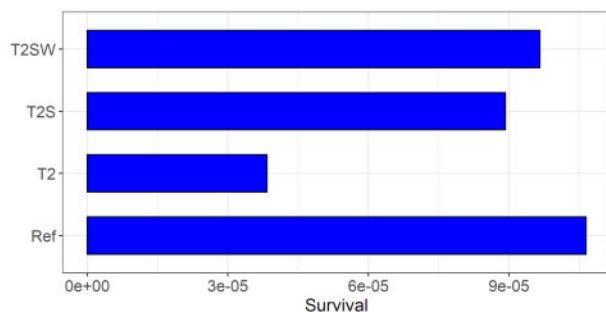

Figure 8. Total survival for each scenario, calculated by multiplying transport success, pelagic survival, and post-settlement survival. Values of the processes are summed over all nurseries, and then the mean over the years is taken for each scenario.

success is higher for future climate conditions, survival in nurseries is lower. Interestingly, the climate change scenarios predict the highest total biomass but the lowest number of surviving individuals. The key to this result is the temperature dependent early spawning and consequently early arrival of larvae resulting in initial slow growth due to the still low temperatures early in the season. These early season temperatures remain low enough to hamper growth, despite a 2 degree rise with the climate scenario, and are keeping the juveniles prone to predation longer. Overall survival from pelagic larvae to post-settlement juvenile is reduced under climate change as represented by the IPCC2040 scenarios.

Increased growth rates and larger lengths at a young age in response to higher temperatures have been demonstrated in both experimental setups as well as in the field (Atkinson, 1994; Van der Veer *et al.,* 1994; Huss *et al.,* 2019). Zijlstra *et al.* (1982) demonstrated temperature dependence of growth for post-settlement plaice during the first growth season, but found no temperature dependence of mortality. Van der Veer *et al.* (1994) also did not find temperature-dependent mortality, but did find size-dependent mortality for the 0-group plaice with the smallest individuals having the highest mortality rates. The DEB model results in increased growth rates and larger end of season lengths and biomass at higher temperatures for post-settlement sole, but these potential benefits for survival are more than nullified by arrival at lower temperatures early in the season resulting in initial slow growth and high mortality rates. Nonetheless, the overall biomass at the end of the season is higher under climate scenarios.

The assumptions made on environmental variables (temperature and wind) in the larval drift model affected the growth and survival of post-settlement sole. However, the largest effect between scenarios was created by the assumption of earlier spawning. This result stresses the importance of taking the full life cycle into consideration even when one aspect of the life cycle is of direct interest. The assumption of temperature driven earlier spawning of sole is based on a latitudinal gradient (Rijnsdorp and Vingerhoed, 1994) in the onset of spawning and corroborated by shifts in timing based on long-term time series locally and at regional scales (Teal *et al.,* 2008; Fincham *et al.,* 2013). To what extent the timing of spawning will change with even further increases of temperature is unknown. Nevertheless, early spawning and early arrival lead to a prolonged growth season for YOY (Teal *et al.,* 2008) and we have shown it may lead to decreased survival but a high biomass. The effect of climate change on species that do not have a temperature response to spawning, as for example other flatfish species like turbot (Munro *et al.,* 1990), might be more similar to the T2 scenario presented here, which could be extended with a scenario including a change in temperature and wind (not done here). The T2 was the worst of the climate scenarios in terms of survival and biomass at the end of the growth season, and also worse than the reference scenario representing current climate conditions. This difference in outcome based on spawning cue assumptions stresses that if one wants to predict growth and survival of marine fishes using coastal nurseries, understanding and predicting changes in phenology of spawning is of paramount importance.

The methodology used can be applied for any species and area but all models should be parameterized for the species and area of interest. The models are deterministic, meaning that no stochasticity is considered in for example temperature profiles or phenotypic plasticity in metabolism or food acquisition. This approach provides knowledge based on process-level assumptions

but does not allow for phenotypic differentiation (Teal *et al.*, 2018). Furthermore, we assume that food is static and availability does not change within season or between climate scenarios. This omission must be acknowledged and at the same time identifies a lack of knowledge on the response of benthic organisms and their availability for sole as food source under climate change conditions.

With the model setup used in this study consequences of climate change on population dynamics or fisheries yield cannot be assessed. In order to do so, all life stages must be included and in a dynamical way. In addition, the effects of climate change must be addressed for all life stages (Rijnsdorp *et al.*, 2009) and size-dependent effects of temperature are expected (van de Wolfshaar *et al.*, 2008). The work presented here can be considered a first step and population dynamical modelling should follow this exercise [see Boyd *et al.* (2020) for a recent example for mackerel (*Scombur scombrus*)]. Also for stock assessment and management the implications of climate change might not be straightforward without links between YOY performance and spawning stock biomass, including climate change effects for all stages. It would be possible to run the stock assessment for sole with juvenile indices adapted to climate effects (Le Pape *et al.*, 2020). However, the growth pattern and therefore reproductive capacity of the stock is also influenced by climate change. Under the Temperature Size Rule, smaller sizes at maturity are predicted at higher temperatures (Forster *et al.*, 2012). So even if less but bigger individuals recruit to the second year, as adult they may be smaller resulting in a lower spawning stock biomass. It could also be possible that survival after the first year is higher due to larger sizes, which may result in more yet small adults, which could cancel out any effects on spawning stock biomass due to size. The effect of climate change on population dynamics and stock to manage could go either way or not change at all, but should be taken into consideration in management advice.

Changes in the environmental conditions in a critical life stage such as pre- and post-settlement juveniles may affect the total population through changes in survival and recruitment to the adult stock (Petitgas *et al.*, 2013). The level of recruitment for sole in the North Sea is largely determined during the first growth season (Rijnsdorp *et al.*, 1992). Akimova *et al.* (2016) found a negative correlation between the pre-recruitment survival index for sole and the temperature in the German Bight, located in the German nursery in this study. The results of our study are in agreement with this negative correlation. A negative correlation between recruitment in terms of abundance to the stock and SST has been found for sole in the North Sea, but for other sole populations neutral or even a positive relationship was found, irrespective of latitude (Horwood, 1993; Brunel and Boucher, 2007; Akimova *et al.*, 2016). This variability in response to climate change is partly due to the fact that not temperature alone affects growth and survival. Predator presence, food availability, shelter, competition for resources all determine the fate of juveniles. Which is the most limiting or driving factor will vary between locations and years. Moreover, the spatial distribution of adults may shift under climate conditions, and this could include a shift in spawning grounds (Perry *et al.*, 2005). The observed overall southward shift of sole may lead to a reduction in connectivity between spawning grounds and nursery areas (Engelhard *et al.*, 2011). A spatial shift in spawning grounds was not considered in this study, but could alter the results for a North Sea case study dramatically, if drift patterns towards coastal areas are negatively

affected. The possible effects of climate, based on mechanistic modelling presented here, underline that understanding and predicting changes in processes contributing to life-cycle connectivity due to climate change is still in its infancy, but it will have major implications on our future use of fish stocks. Anticipating possible changes in early life history stage development and survival due to climate-driven alterations in connectivity and increases in temperature is necessary for sustainable management of fish stocks in the future.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability

Data are available on request.

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