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Impact of climate change on temperature-related growth potential of juvenile fish in the western Dutch Wadden Sea

by

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Abstract

Over the last decades, significant changes in the distribution and abundance of fish species are observed in the North Sea region. The ongoing warming trend of the Wadden Sea might drive cold-water species out of the Wadden Sea by exceeding their optimum performance temperature and might give an opportunity for warm-water species to perform well. In the context of the physiology of fish species and temperature conditions of the Wadden Sea, a mechanism is developed to explain changes in the distribution of several fish species. The species of interest are two demersal flatfish species and two contrasting pelagic fish species, respectively, plaice (*Pleuronectes platessa L.*), flounder (*Platichthys flesus L.),* Atlantic herring (*Clupea harengus L.)* and European anchovy (*Engraulis encrasicolus L.*). Projected temperature conditions of a general estuarine transport model (GETM) of the Dutch Wadden Sea were implemented into a dynamic energy budget (DEB) model, resulting in monthly potential growth maps for the years 2009-2011 of two sizes classes of the four fish species. Summer temperatures exceeded several species-specific optimum temperatures in large parts of the Wadden Sea within the study period, whereby high temperatures limit growth. Growth reduction was not projected in every year since there was interannual variability in temperature-related growth. If temperatures keep rising, which is projected, optimum temperatures will be exceeded more frequently and more pronounced in the Wadden Sea. The observed changes in fish species distribution can be temperature driven since several cold-water species live at their upper thermal limit, besides, temperature conditions become more favorable for warm-water species.

1. Introduction

Many marine fish species rely at least during one or more of their life stages on the important nursery function that shallow coastal habitats provide. These coastal habitats support large numbers of especially the juvenile life stage. Juveniles use the general highly productive shallow coastal habitats for the abundance of food and for protection against predators. The Wadden Sea is such a shallow coastal habitat for many North Sea fish species (Elliot et al. 2007; van der Veer et al. 2011; Zijlstra 1972, 1978). Most of them reach the nursery grounds as larvae and spend only their juvenile phase there. Other species use the Wadden Sea as spawning ground, temporarily inhabit the area or pass it on the route to either freshwater or marine open waters (Boddeke and Vingerhoed 1996; Elliot et al. 2007; van der Veer et al. 2011). The quality of the nursery grounds is considered to have an effect on juvenile recruitment to the total fish stocks offshore (Freitas et al. 2016; Gibson 1994).

Over the last decades, significant changes in distribution and abundance of fish species are observed in the North Sea region. Fish species having southern affinities appear to have a northward shift into the North Sea. On the other hand, cold-water species in the North Sea appear to have an offshore drift into deeper waters and/or in northward direction (Alheit et al. 2012; Freitas et al. 2016; Reid and Valdes 2011; Rijnsdorp et al. 2009, 2010). In the Wadden Sea, a decreasing trend in total fish biomass is observed, especially in fish that use the Wadden Sea as a nursery (van der Veer et al. 2015; Tulp et al. 2016). For many of these fish species, maximum catches in the 1980s are followed by an ongoing decrease in abundance, whereby other fish species show an increase. The fish community in the Wadden Sea is slowly shifting from more cold water-adapted species to more warm water-adapted species (van der Veer et al. 2015; van Walraven et al. 2016).

Dynamics in fish species distribution and abundance is mainly determined by the impact of environmental conditions, the variability in spawning success and food availability (Pecquerie, Petitgas, and Kooijman 2009; Reid and Valdes 2011). Environmental conditions can be classified into 5 classes of physiological effects: controlling factors (which set the pace of metabolism), limiting factors (which constrain maximum metabolism), lethal (which completely interdict metabolism), masking factors (which increase obligatory metabolic work) and directive factors (which release and unload metabolism) (Fry 1947, 1971; Neill et al.1994). Variability in temperature has the greatest impact on fish species, since temperature directly control metabolism within the optimal range of a species, but also can act as limiting, masking or even lethal factor (Freitas et al. 2010; Harley et al. 2006; Neill et al. 1994). The ongoing warming of the oceans and seas as a result of climate change is one of the primary factors affecting the change in fish species distribution (Reid and valdes 2011; Rijnsdorp et al. 2009, 2010). Over the past decades, sea surface temperatures of the Dutch coastal waters have increased already by 1 °C (van Aken, 2010).

Temperature affects all physiological rates of an individual fish by modifying the energy available for growth, maintenance and maturation (Freitas et al. 2007; van der Meer 2006; van der Veer et al. 2009). A general framework to understand the impact of variations in temperature conditions on growth of fish species is the Dynamic Energy Budget (DEB) theory (Kooijman 1993, 2010). This theory describes energy flows in a systematic way through an organism depending on its own state (e.g. size) and its environment (e.g. temperature and food

densities). The DEB theory is applicable to all organisms, whereby the required species-specific parameters reflect interspecific physiological differences. Therefore, the DEB theory is an appropriate framework to model and compare the variability in potential growth rates as function of temperature conditions for the several distinct Wadden Sea fish species. The species of interest are two demersal flatfish species and two pelagic fish species, respectively plaice (*Pleuronectes platessa L.*), flounder (*Platichthys flesus L.),* Atlantic herring (*Clupea harengus L.)* and European anchovy (*Engraulis encrasicolus L.*).

Plaice, flounder, herring and anchovy use the Wadden Sea as a major nursery ground, whereby for anchovy the area also acts as a spawning ground (Boddeke and Vingerhoed 1996; Petitgas et al. 2010; van der Veer et al. 2011). Fish species can be categorized in guilds, based on the function an estuary fulfills for these species (Elliott et al. 2007). Plaice and herring are defined as marine juveniles (MJ). Marine juveniles spawn at sea and regularly enter shallow coastal habitats in large numbers as especially larvae/juveniles. Flounder is characterized as an estuarine resident (ER), nevertheless, flounder has characteristics that define it as marine juvenile as well. Anchovy can be considered as a fish species that is a marine seasonal migrant (MS), entering an estuarine for spawning during a particular season (Boddeke & Vingerhoed, 1996; Elliott et al., 2007). The complex life cycle of fish species is not only reflected in the variety of habitats they exploit during different life stages, but as well in ontogenetic changes in thermal tolerance (Petitgas et al. 2013; Pörtner and Peck 2010; Rijnsdorp et al. 2009) (Appendix A).
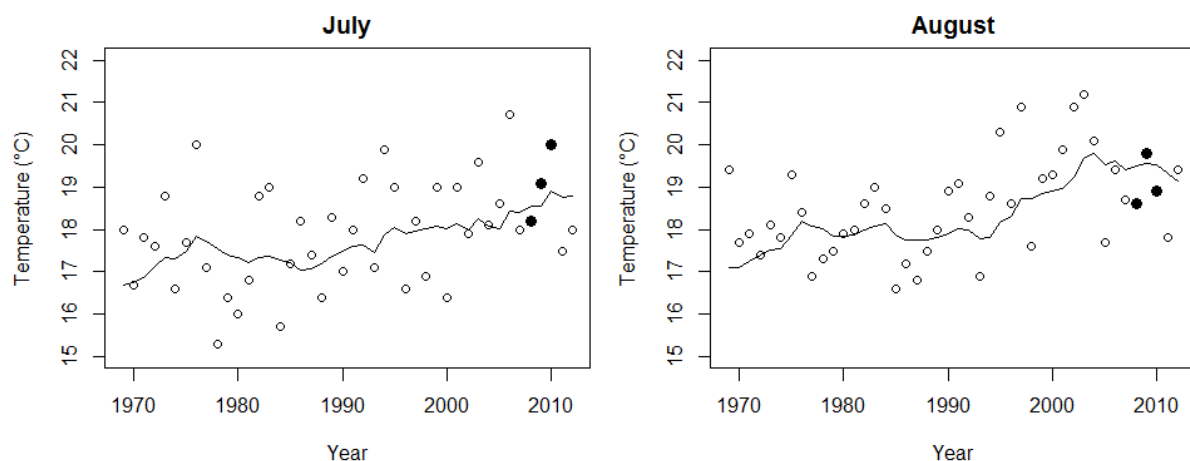

Fig. 1. The monthly mean temperature of July and August for the period 1970 to 2012, measured at the NIOZ jetty (E 4.789166667, N 53.00166667). Black thick dots are the years 2009, 2010 and 2011. A ten year running mean line (Simple Moving Average) is drawn through the temperature observation points.

The ongoing warming trend of the northeast Atlantic region with rising water temperatures of the Wadden Sea, especially summer temperatures (fig 1), might drive cold-water species such as plaice, flounder and herring out of the Wadden Sea by exceeding their optimum performance temperature (Alheit et al. 2012; Freitas et al. 2016; Petitgas et al. 2013; Rijnsdorp et al. 2010; van der Veer et al. 2015). Larger individuals of these species have been proposed as more prone to rising water temperatures because they fail to balance demand and uptake of oxygen for high water temperatures (Baudron et al. 2014; Pörtner and Knust 2007). However, for fish species with southern affinities such as the anchovy, the rising water temperatures in the Wadden sea might give the opportunity to fulfill their life cycle in this area (Petitgas et al. 2012; Raab 2013;

Rijnsdorp et al. 2010). These changes in fish species abundance and composition in the Wadden Sea can have an enormous consequence for the entire Wadden Sea ecosystem and for the commercial fishing in the North Sea, which is of great socio-economic importance (McKenzie et al. 2016; Reid and valdes 2011).

The main focus of this research is to analyze spatial and temporal variability in temperature-related growth potential of the four various contrasting (juvenile) fish species: plaice, flounder, Atlantic herring and European anchovy in relation to climate change in the Dutch Wadden Sea. This will be conducted in the context of the Dynamic Energy Budget (DEB) theory for the summer months of the years 2009-2011. The juvenile life stage of the various fish species is of main interest since this is the life stage during their life cycle they make use of the Wadden Sea (table 1). Predicted temperature conditions will be obtained from the General Estuarine Transport Model (GETM) that is applied on the Wadden Sea for the years 2009-2011 (Duran-Matute et al. 2014). The focus is on the summer period when temperatures are highest and might exceed species-specific optimal temperatures (van der Veer et al. 2015). The GETM temperature conditions of the Dutch Wadden Sea will be used in the DEB theory for modelling the maximum potential growth of plaice, flounder, herring and anchovy (Koojiman 1993, 2010; Teal et al. 2012). By combining the DEB theory with the environmental conditions of the Wadden Sea from the GETM, maximum potential growth maps for the years 2009-2011 can be mapped for two size classes of the species of interest. The two size classes represent lengths of (1) 5 cm (0-group) and (2) 20 cm (plaice and flounder) or 15 cm (herring and anchovy). The impact of temperature on these size classes will be validated with the Demersal Fish Survey (DFS) data, which reflects the actual size distribution of the fish species in the Dutch Wadden Sea (Tulp 2015). This approach will be used as a pilot study to analyze the impact of climate change on the nursery function of the Dutch Wadden Sea. The results of this pilot study might give insight in the spatial and temporal dynamics of plaice, flounder, herring and anchovy in the Dutch Wadden Sea in relation to climate change.

2. Material and method
2.1   Dutch Wadden Sea

The Wadden Sea is located in the south-eastern part of the North Sea along the coast of Denmark, Germany and the Netherlands. The Dutch Wadden Sea is connected with the North Sea via the tidal inlet channels in between the barrier islands (Fig. 2). The tidal amplitude of the Dutch Wadden Sea is between 1.0 and 2.0 m in the western part and can reach a height of about 3.0 m in the eastern part. As a result of the tidal prism, the Wadden Sea area is characterized by large areas of intertidal flats and shallow waters (fig. 2) (Wiersma et al. 2009). The shallow waters of the Wadden Sea make this area more vulnerable to local weather conditions compared to the North Sea (Duran-Matute et al. 2014). The phase lag between atmospheric temperatures and the sea surface temperature of the Marsdiep tidal basin is about 2 days (van Aken 2008). Temperature fluctuations within a day were estimated around 2 to 3 °C during high tide and up to 6 °C during low tide at the tidal flats (van der Veer and Bergman 1987). Averaged monthly mean water temperatures over the period 1861-2006 in the Marsdiep ranged from ± 3 °C in February to ± 18 °C in August (van Aken 2008). Over the last decades, especially summer temperatures show an increasing trend (van der Veer et al. 2015).
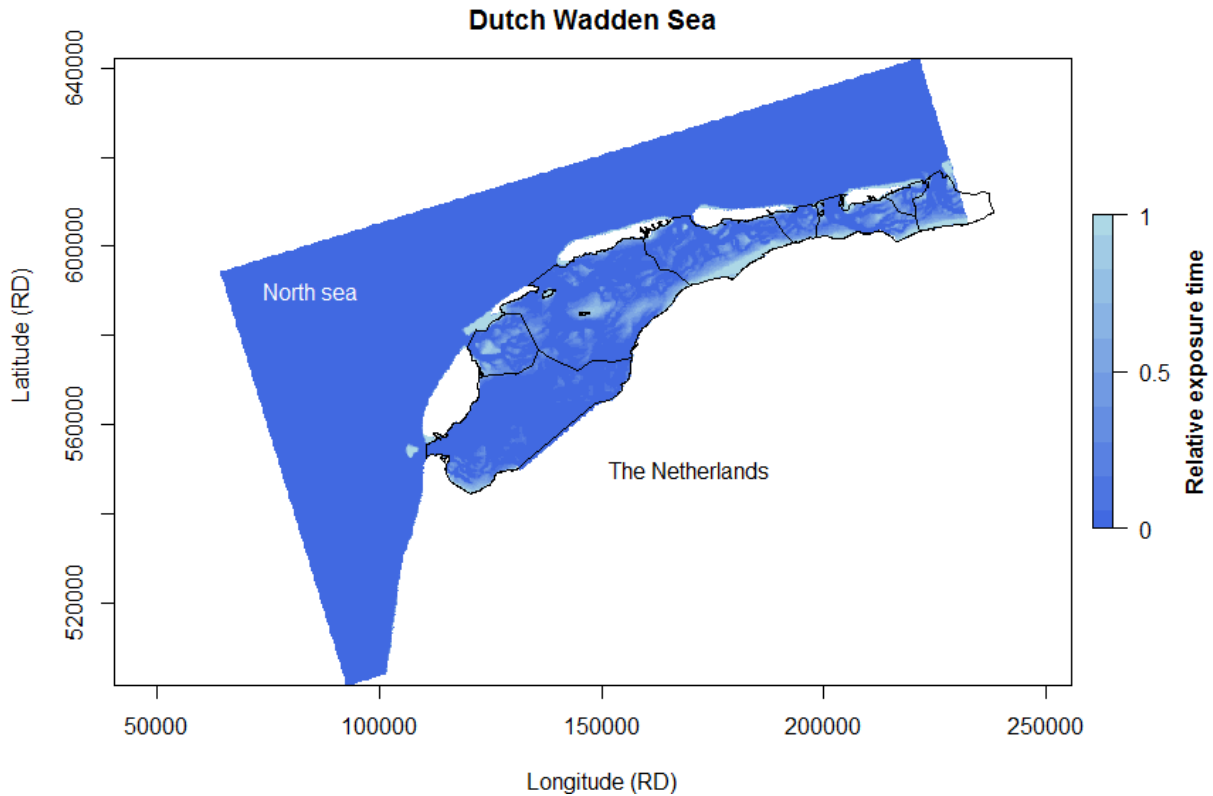
Fig. 2. The Dutch Wadden Sea located in between the mainland and the barrier islands (white) and the tidal basins (Marsdiep, Eijerlandse Gat, Vlie, Borndiep, Pinkegat, Zoutkamperlaag, Eilanderbalg and Lauwers respectively from left to right). The color bar represents a relative exposure time, whereby an exposure time of 1 represents fully exposed to the atmosphere. The entire study area includes a part of the North Sea that borders the Wadden Sea for the use of the boundary conditions for the GETM.

2.2   Fish species

Plaice, flounder and herring spawn offshore, having their spawning grounds either in the North sea or in the English Channel. Currents (e.g. tidal and wind driven) transport the newly hatched larvae into the Wadden Sea which they use as their nursery ground (Dickey-Collas et al. 2009; Freitas et al. 2016; Petitgas et al. 2010). Plaice enter the Dutch Wadden Sea in spring (mid-March-May) and settle with a length of about 1.5 cm. In autumn, most of them migrate out of the Wadden Sea to deeper waters (van der Veer et al. 1990). For two years, plaice return to the Wadden Sea in spring and after their third year they join the North Sea adult population (Kuipers 1977). However, in recent years large juvenile (I- and II-group) plaice have nearly entirely disappeared from the Wadden Sea (Freitas et al. 2016). The arrival time of flounder larvae is slightly later and start from mid-April on and last to may (van der Veer et al., 1991; Martinho et al., 2013). The migration out of the Wadden Sea towards deeper waters take place at the same time as that of plaice (Winter, Griffioen and van Keeken 2010). Herring arrive in early spring (April) when they have reached already a length of about 3 cm and they can remain in their nursery grounds for about two years (Dickey-Collas et al. 2009; Petitgas et al. 2010). Anchovy use the Wadden Sea as spawning ground as well as their nursery ground. Spawning is temperature driven and occurs above a threshold of 14 ° C in the Bay of Biscay. Anchovy migrate out of their nursery ground before winter and return when they are mature to spawn. This can be the next year since anchovy can reach maturity at the end of their first year in southern

waters (Motos, Uriarte, & Valencia, 1996; Petitgas et al., 2013). Species characteristics are summarized in table 1 and a schematic overview of the life cycle of each fish species is shown as a migration triangle in appendix B (Harden Jones, 1968).

Tabel 1. Species characteristics, function of the Wadden Sea, time of entering the Wadden Sea and the period of migrating out of the Wadden Sea. Marine juvenile (MJ), Estuarine resident (ER) and Marine seasonal (MS). Climate change (CC) and Habitat degradation (HD) are the two driving forces. Upstream is defined as the month of migration into the Wadden Sea and downstream is defined as migration out of this area. (1) Bolle et al. 2009 (2) Dickey-Collas et al. 2009 (3) Petitgas et al. 2013 (4) van der Veer 1985 (5) van der Veer, Pihl, and Bergman 1990 (6) Van Der Veer et al. 1991 (7) Van Der Veer et al. 2011 (8) van Walraven et al. 2016 (9) Winter, Griffioen and van Keeken 2014 (10) Zijlstra 1978.

Common name	Scientific name	Guild	Stratification	Spawning ground	Feeding pattern	Sensitivity to driving forces	Habitat use Wadden Sea	Upstream	Downstream	Length at entering/settling	Source
European Plaice	*Pleuronectes platessa*	MJ	Demersel	Southern bight	Zoo benthos	CC; HD	Nursery	March - May	Oct - Nov	1 - 2 cm	1, 4, 5, 7 & 10
European Flounder	*Platichthys flesus*	ER	Demersel	North Sea	Zoo benthos	HD	Nursery + (maturation)	April - May	Oct - Nov	± 1 cm	1, 4, 6, 9 & 10
Atlantic Herring	*Clupea harengus*	MJ	Pelagic	English channel	Plankton	CC; HD	Nursery	Feb - May	Jun-Dec	2 - 3 cm	1, 2, 3 & 10
European Anchovy	*Engraulis encrasicolus*	MS	Pelagic	Wadden Sea	Plankton	CC	Spawning + nursery	May - June	Oct ?	< 1 cm	1, 3 & 8

All of the four fish species use various habitats during their life cycle where they migrate within and between. (Elliott et al. 2007; Gibson 1997; Harden Jones 1968). However, habitat use and migration patterns of fish species may shift as a consequence of climate change (Reid and valdes 2011; Rijsndorp et al. 2010). By moving between and within various habitats during their life cycle, marine fish species experience a variety of temperatures. It is assumed that the earliest life stages, eggs and larvae, have the most narrow thermal tolerance range. Meanwhile, juveniles can exploit the largest range of environmental temperatures. Several studies have evidence that the thermal tolerance window an adult fish can exploit decreases slightly from the juvenile life stage on, especially at the upper thermal limit (Appendix A). However, the underlying mechanism of the decrease in thermal window for adult fish is not clear (Freitas et al. 2010; Pörtner et al. 2008; Pörtner and Farrel 2008; Pörtner and Peck 2010; Rijnsdorp 2009).

2.3 DEB theory

The dynamic energy budget (DEB) theory (Kooijman 1993, 2010) describes the rates at which an organism assimilates and utilizes energy for maintenance, growth and reproduction as a function of its state and its environment. This theory is also known as the κ-rule (kappa) DEB theory, which assumes that the several energetic processes are either body volume and surface area dependent. A fixed fraction (κ) of the energy is allocated to somatic maintenance and growth. No energy is allocated to heating since fish are ectothermic and cannot control their own body temperature. The remaining fraction (1-κ) is allocated, depending on the state of the organism, to maturity maintenance, maturation and/or reproduction. Maintenance has always the priority over growth. Consequently, growth stops if all the energy is used for somatic maintenance. Growth of an organism is volume dependent, whereby the structural volume of the organism is a function of its length and species-specific shape coefficient (Kooijman 1993, 2010; van der Meer, 2006):

$$L = \frac{V^{1/3}}{\delta_M} \qquad (\text{Eq. 1})$$

Species-specific temperature tolerance ranges are incorporated in the DEB theory by assuming that all enzyme rates can be described as a function of temperature. The range of temperatures where body growth is positive is defined as the temperature tolerance range, whereby there is an optimum temperature at which growth is maximal. Temperature has an effect on all physiological rates of an organism and this is incorporated in DEB as the Arrhenius relationship. The Arrhenius relationship as fraction (Fr) to a given species-specific reference temperature is calculated as (Kooijman 1993, 2010; van der Meer et al. 2006; van der Veer 2009):

$$Fr = exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) * \left(\frac{1 + exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right) + exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right)}{1 + exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)}\right) \qquad \text{(Eq. 2)}$$

where T_A is the Arrhenius temperature, T_{ref} the species-specific reference temperature in Kelvin, T_L and T_H are the lower and upper temperature boundaries of the enzymes and T_{AL} and T_{AH} are the Arrhenius temperatures at both boundaries for the rate of decrease. Incorporating the temperature dependent physiological rates as fraction (Fr) and the structural volume of the organism into the growth model results in (Kooijman 1993, 2010; Teal et al., 2012):

$$\frac{dV}{dt} = \frac{(\kappa * f * \{Pam\} * Fr) * V^{2/3} - [p_M] * exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) * V}{\kappa * f * [E_m] + [E_G]} \qquad \text{(Eq. 3)}$$

where {Pam} describes the area-specific maximum assimilation rate, $[P_M]$ the volume-specific maintenance costs, $[E_M]$ the maximum storage density and $[E_G]$ the volume-specific costs of structure. Food density (f) is set to 1 (ad libitum) due to a lack of information on the spatial distribution of food resources for fish in the western Dutch Wadden Sea. The output of the growth model is the volume increase of an organism per day. All the species-specific parameters are listed in table 2. Due to a lack of species-specific parameters for the North Sea, equivalent species-specific parameters are taken from other shallow coastal habitats for the species of relevance (Anchovy).

Tabel 2. Species-specific parameter values used in the dynamic energy budget theory for the various fish species. Square brackets indicate parameters expressed per unit of volume and curly brackets represent parameters that are expressed in units of surface area. Parameters of plaice are obtained from (Freitas, Kooijman and van der Veer 2012; van der Veer et al. 2009), flounder from (Freitas et al. 2010; Freitas, Kooijman and Van Der Veer 2012), herring from (Fässler et al. 2012; Freitas, Kooijman and van der Veer 2012) and anchovy from (Freitas, Kooijman and van der Veer 2012; Pecquerie, Petitgas and Kooijman 2009; Raab et al. 2013).

Symbol	Dimension	Interpretation	Plaice	Flounder	Herring	Anchovy
T_A	K	Arrhenius temperature	7000	7500	8000	9800
T_L	K	Lower boundary of tolerance range	277	277	271	278
T_H	K	Upper boundary of tolerange range	295	296	294	305
T_{AL}	K	Rate of deacrease at lower boundary	50 000	35 000	50 000	50 000
T_{AH}	K	Rate of decrease at upper boundary	75 000	75 000	50 000	100 000
T_{ref}	K	Reference temperature	283	288	288	293
$\{P_{Am}\}$	J cm^{-2} d^{-1}	Maximum surface area-specific assimilation rate	390	576	468	329
$[P_M]$	J cm^{-3} d^{-1}	Volume-specific maintenance costs	19.4	29.8	46	62
$[E_M]$	J cm^{-3}	Maximum storage density	2500	2400	1840	645
$[E_G]$	J cm^{-3}	Volume-specific costs of structure	5600	5600	5600	5600
k	–	Fraction of utilized energy spent on maintenance plus growth	0.85	0.65	0.80	0.65
δ_M	–	Shape coefficient	0.219	0.224	0.190	0.172

DEB predictions of maximum potential growth rates as a function of temperature show increasing potential growth rates to a specific optimum temperature, whereafter potential growth rates rapidly declines (fig. 3). Maintenance increases exponentially as temperature increases, so the required energy available for growth decreases (Kooijman 2010). Temperature related growth reduction is the projected result of this increase in maintenance cost. The temperature tolerance range is assumed as the range of temperatures by which potential growth rates are positive. The species-specific parameters of the DEB model reflect clear differences in temperature tolerance range, optimum temperature and maximum potential growth rate between the four fish species of interest. Anchovy have the highest optimum temperature followed by flounder, plaice and herring. Highest potential growth rates are predicted for (small) anchovy as well, continued by plaice, flounder and herring (fig. 3). The DEB model shows that smaller sized fish have a larger temperature tolerance range than larger individuals do. Furthermore, as fish size increases, a decrease in maximum potential growth rates is predicted as well as a slight shift of the optimum temperature towards lower temperatures. For a temperature of 23 °C (296 K) for instance, maximum potential growth rates are predicted to be zero for plaice of 25 cm, flounder of 30 cm and herring of 12 cm whereby growth rates are still positive for smaller individuals (fig. 3). As a result, lower temperatures become more preferable than higher temperatures as fish size increases.
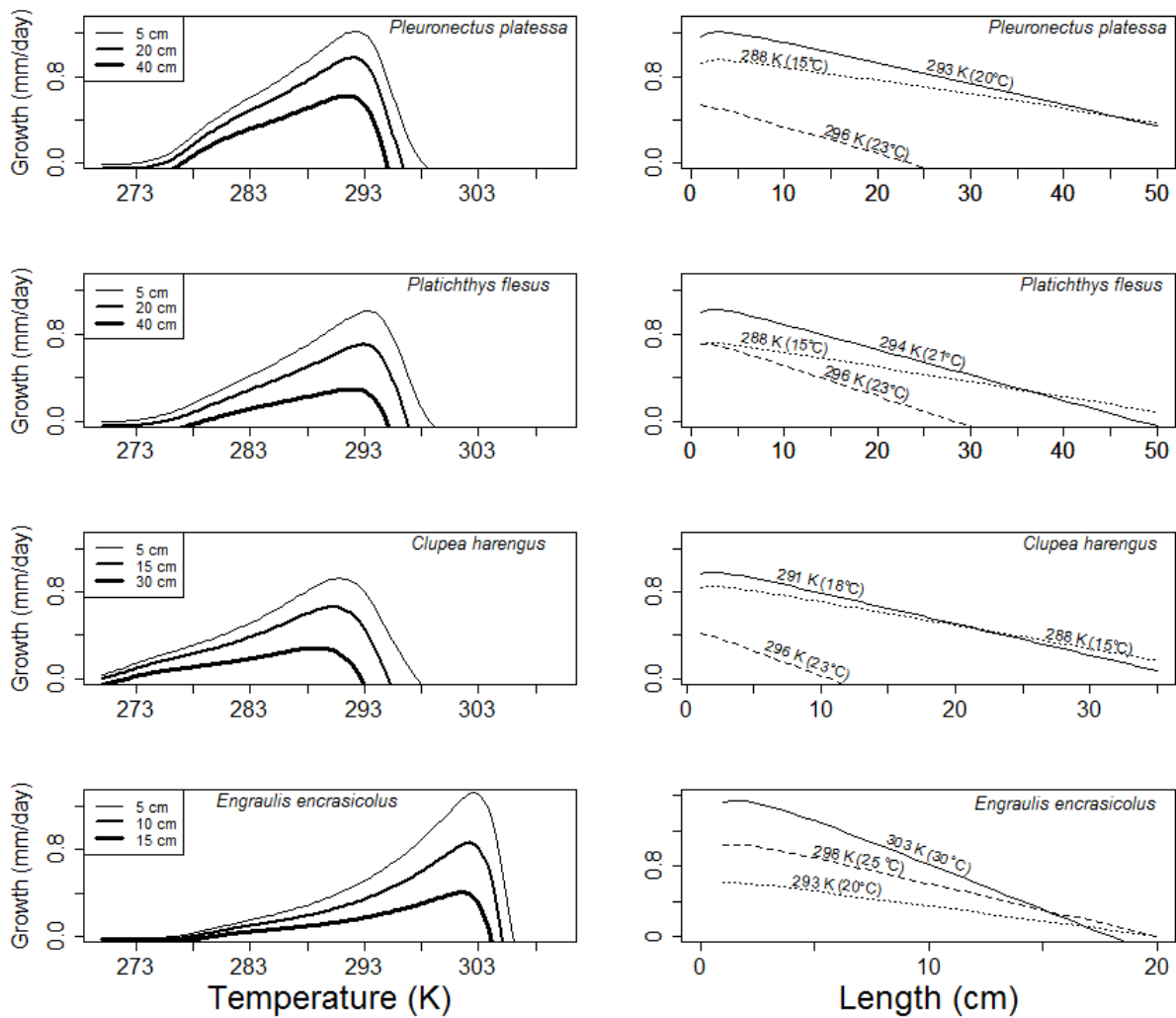
Fig. 3. DEB predicted potential growth rates as a function of temperature (left) and length (right) for plaice, flounder, herring and anchovy.

2.4 General Estuarine Transport Model (GETM)

The environmental conditions (temperature) of the Wadden Sea were obtained from the GETM for the years 2009-2011. At a 200 x 200 m horizontal resolution and with 30 vertical layers, the GETM of the Wadden Sea solves the primitive hydrostatic equations in three dimensions. The GETM includes a realistic bathymetry, fresh water discharge, tides and meteorological forcing as boundary conditions. The entire domain of the GETM includes the Wadden Sea and the surrounding North Sea area up to the 20 m isobath. At the boundary of the model domain, boundary conditions of the North Sea were applied. Every cell has always a water layer of at least 10 cm, otherwise oscillation can occur. A cell is considered as dry when the water depth is lower than 20 cm. Output of the hydrodynamic conditions for the bottom- and surface layer with a temporal resolution of a month were created especially for ecological studies. These monthly averaged temperature conditions were stored as a grid which made the data suitable to implement it in the DEB formulas. The projected environmental conditions were validated with several kinds of observations and showed a great agreement (Duran-Matute et al., 2014).

Monthly mean temperature predictions were used instead of daily mean temperatures, while highest peak temperatures occur at a daily bases. In the current approach, all these peak temperatures are flattened out in the monthly mean temperature predictions. Daily mean temperatures can strongly fluctuate because of the fast thermal response of the Wadden Sea since the time lag between the Den Helder air temperature and the Marsdiep surface temperature is only 2 days (van Aken 2008). The thermal response of the shallower tidal flats is probably even faster and follows the air temperature. Differences between the ebb water temperature and the flood water temperature can be around 3 °C within a day (van Aken 2008). Besides, Wadden Sea temperatures differ between day and night. The combined effect can result in temperature differences up to 6 °C within a day (van der Veer and Bergman 1987). By including mean daily temperatures, more extreme temperature events will be captured. However, temperatures strongly fluctuate within a day as well due to the tides. Moreover, the time scale of the tide mismatches the time scale of one day whereby mean daily temperatures can potentially oscillate for GETM predictions (van Aken 2008, 2010; Duran-Matute et al. 2014) . Therefore, monthly mean temperatures were used to avoid daily temperature fluctuations due to the tide.

2.5 Growth, GETM and validation

The temperature output of GETM was inserted into the DEB equations, whereby potential daily growth rates were calculated. A distinction was made between the demersal flatfish species and the pelagic species. Bottom water temperatures were used for the flatfish species and surface water temperatures for the pelagic species. Growth rates were calculated for every single cell in the GETM grid. By inserting a temperature grid into the DEB equations it was assumed that every grid cell contained at least one individual fish. The hypothetical fish was non migrating, living in one specific cell only, so that growth was a continuous process. Growth was only a function of temperature and size, since, food density was scaled to one (ad libitum). The maximum potential growth rate of an individual fish was calculated by converting the starting length of an individual fish to volume, using the species-specific shape coefficient (Eq. 1). Then, the fraction (Fr) was calculated for the temperature conditions of GETM (Eq. 2), whereafter the fraction (Fr) was used to calculate the volume change after one day (Eq. 3). The newly obtained change in volume was back calculated to a change in length. This change in length between day *n* and day *n+1* represents the potential daily growth in cm per day. Using this method, potential growth rate maps were projected for the four different fish species and two size classes, namely 0-group juveniles of 5 cm and large juveniles of 20 cm (plaice and flounder) or 15 cm (herring and anchovy). The corresponding lengths of the large juvenile size class were based on historical data, which showed that larger individuals were caught commonly in the Wadden sea and former Zuiderzee region (Redeke, 1907)(Appendix D).

For comparing inter-specific differences in maximum potential growth rates, a growth index was created, whereby the species specific optimum temperature for a given length is scaled to 1. This is done by dividing calculated potential growth rates, with the maximum potential growth rate possible (at the optimum temperature) for a given length. The potential growth maps for the summer months were projected using the growth index. A growth index of 1 represents maximum potential growth rates, where a growth index of 0 represent, no growth. Using this growth index it was possible to both compare intra-specific differences in potential growth for different size classes as well as inter-specific differences in potential growth rates. Within the

Wadden Sea, parts were mapped that show a reduction in potential growth due to high temperatures. Growth reduction is defined as the temperatures exceeding the species-specific optimum temperature, whereby these high temperatures limit growth (appendix C). The parts of the Wadden Sea showing growth reduction were assumed to be not suitable to grow optimal. The results were validated with the mean length and length distribution obtained from the Demersal Fish Survey (DFS) (Tulp 2015). However, anchovy is not recorded in the DFS since this pelagic fish is poorly caught during demersal surveys. Therefore, mean length of anchovy was obtained from acoustic surveys in the Marsdiep tidal inlet (Couperus et al. 2016). The DFS is an ongoing survey carried out at the end of the summer with a good spatial resolution whereby the acoustic survey was carried out in October and May for the years 2010 and 2011 only (Couperus et al. 2016; Tulp 2015).

3. Results

Temperatures were modelled to differ strongly between the years 2009-2011. The general pattern shows an increase in temperatures from January towards July and august, whereby in June parts of the Wadden Sea reach already some species-specific optimum temperatures. From August, temperatures decrease rapidly to winter minimum temperatures in December and January. Within the study period, lowest temperatures were modelled in 2010, for the months January and February, with parts of the Wadden Sea reaching temperatures near 0°C. July 2010 is modelled as the month with the highest monthly average temperatures, with large parts of the Wadden Sea reaching temperatures of 21 °C or higher (fig. 4). In contrast to July 2010, August was modelled as the month with the highest temperatures in 2009 and 2011. Monthly mean average temperatures of the Dutch Wadden Sea can be found in appendix E.
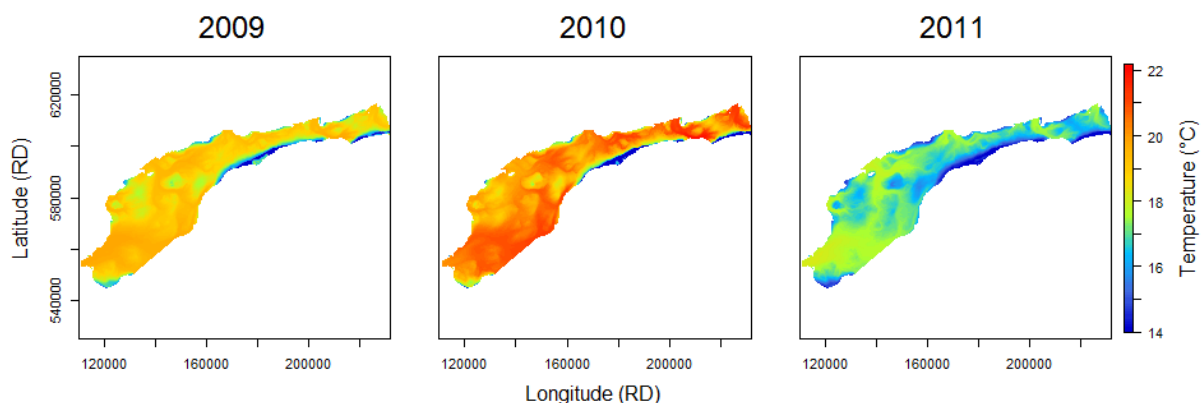

Fig. 4. Projected monthly mean temperatures of July for the entire Wadden Sea for the years 2009-2011.

The spatial patterns of average monthly temperatures in July (summer) for the Wadden Sea are remarkably, with lower temperatures on the tidal flats and higher temperatures in the tidal inlet channels (fig. 4). The diurnal inequality of the tide as a result of the declination of the moon with the earth can be used as an explanation for these spatial patterns. In summer, higher high waters occur at daytime, while in winter, higher high waters occur at nighttime. Which means that the water height is higher during the day than during night. The lunar orbital plane intersects with the northern hemisphere at daytime in summer, generating a higher high water. In winter, the intersection of the lunar orbital plane with the northern hemisphere occurs at night time. In summer, tidal flats warm up quickly during the day, however, at night the tidal flats cool down

just as quickly. Considering the lower high water at nighttime, the cooling effect at night is even stronger since the heat capacity per square meter is lower (Gerkema 2016). The Marsdiep tidal basin is considered as the tidal basin with the highest averaged temperatures over the years. The projected average monthly temperatures in the summer months of 2009-2011 are not outstanding high temperatures within a longer time period (van der Veer et al. 2015), where 2011 is even considered as a relatively cold year (fig. 1).

Potential daily growth rates for the summer months of 2009-2011 were calculated in the context of the DEB model to examine the impact of summer temperatures on the temperature-related growth of plaice, flounder, herring and anchovy for two different juvenile size classes (fig. 5 and 6). However, only the potential growth maps for July are projected since July 2010 is the month with the highest temperatures. Potential growth maps of August can be found in appendix F. The two size classes were respectively 5 cm and 20 cm (plaice and flounder) or 15 cm (herring and anchovy). Another option of presenting the results of the DEB calculations is to look at total length increment at the end of the growing season. However, with total length increment it is assumed that fish are static and not moving out of their cell, so no migration is assumed. Therefore, the option of potential growth rates will be more relevant to examine the impact of temperatures on the habitat suitability of the four fish species. Using this option, every cell presents the maximum potential growth a fish can achieve in this cell for a given moment in time.
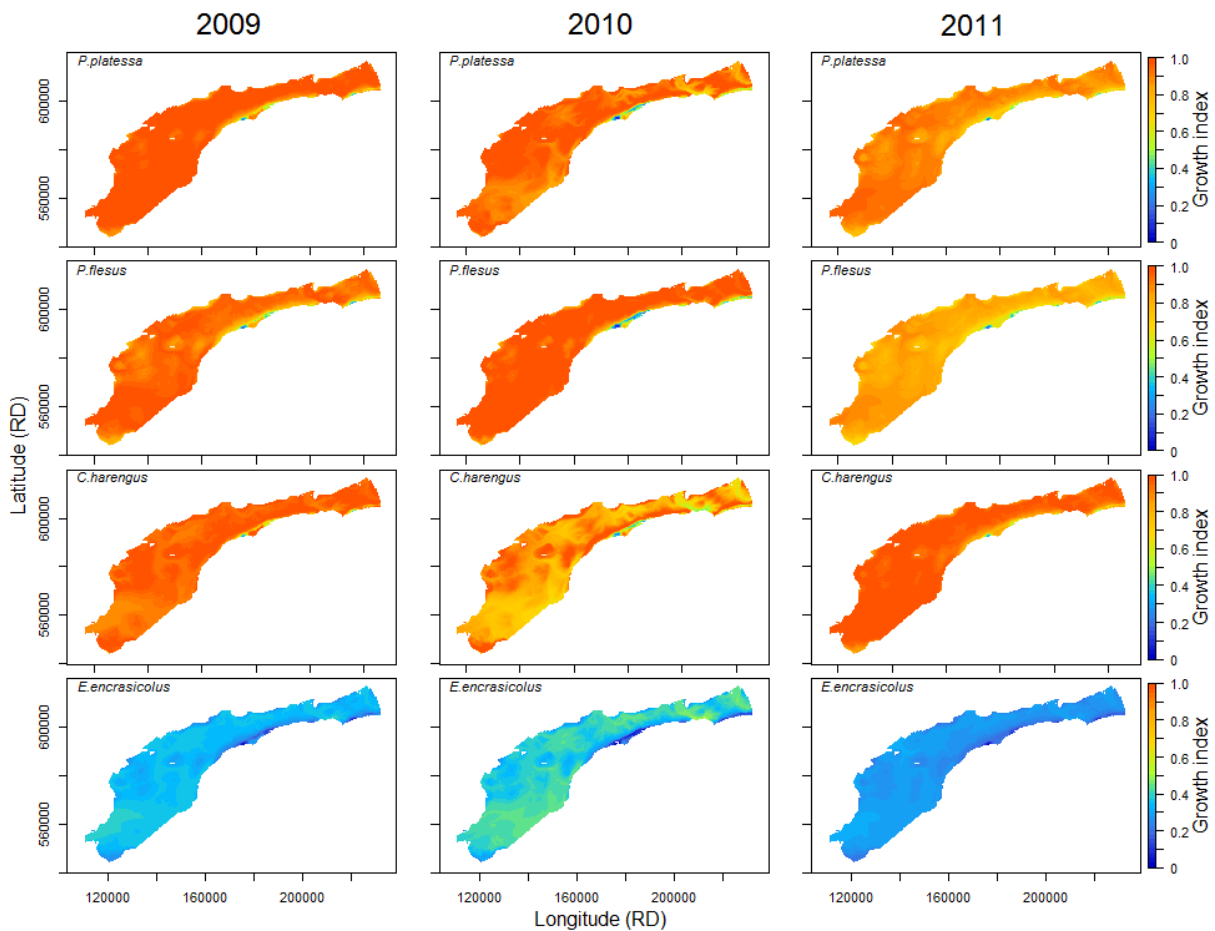

Fig. 5. July. Projected potential daily growth rates for July of the four species of the 5 cm size class and the three different years. A growth index of one represents maximum potential growth rates in cm per day where a growth

index of zero represents no growth. Max potential growth of plaice (1.22 mm day⁻¹), flounder (1.01 mm day⁻¹), herring (0.92 mm day⁻¹) and anchovy (1.32 mm day⁻¹). Projections for August can be found in appendix F.

Plaice. Clear differences in the potential growth maps of July were projected between the years (fig. 5 and 6). In 2009, almost the entire Wadden Sea area was projected to achieve maximum potential growth for plaice of 5 cm, whereas in 2010, parts of the area show lower potential growth rates (fig. 5) due to temperature conditions exceeding the species-specific optimum temperature (fig. 7). In contrast, most of the area is not suitable to achieve maximum potential growth in 2011 (fig. 5), temperature conditions were below optimum in this year because 2011 is considered as a relative cold year (fig. 7). For the larger size class of plaice (20 cm), the spatial distribution of potential growth rates is similar in the years 2009 and 2011 to the that of the smaller size class (fig. 6). However, 2010 shows a larger and more pronounced area of growth reduction for the larger size class of plaice (fig. 8). The larger sized juvenile plaice are more affected by high summer temperatures than the small sized juvenile plaice.
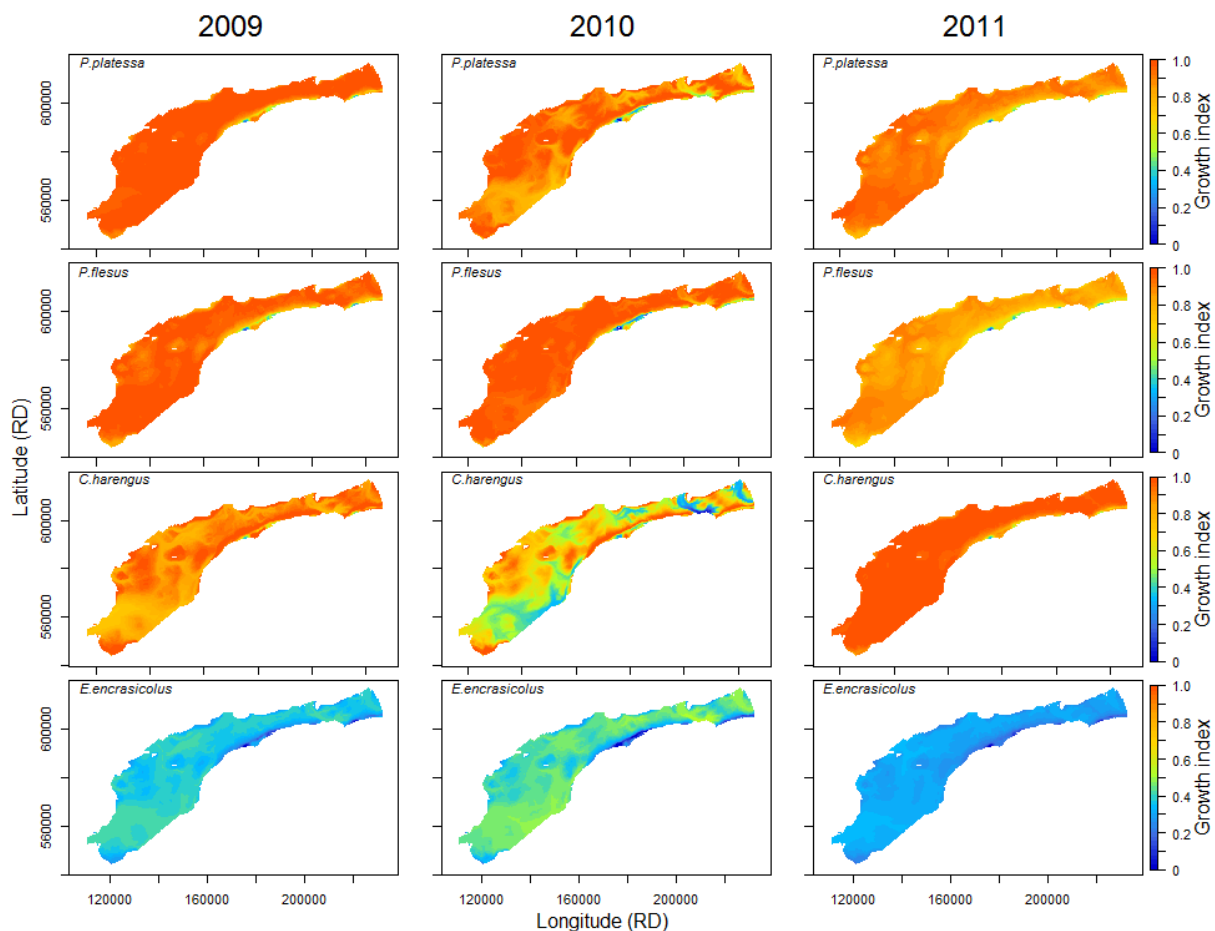

Fig. 6. July. Projected potential daily growth of the four species of the large juvenile size class (20 cm for plaice and flounder and 15 cm for herring and anchovy) and the three different years. A growth index of one represents maximum potential growth rates in cm per day where a growth index of zero represents no growth. Max potential growth of plaice (0.97 mm day⁻¹), flounder (0.70 mm day⁻¹), herring (0.66 mm day⁻¹) and anchovy (0.41 mm day⁻¹) for the corresponding length. Projections for August can be found in appendix F.

Flounder. As with plaice, in 2011 the temperature conditions were not suitable to reach maximum potential growth, whereas in 2009, most of the Wadden Sea area reach temperatures which equal the species-specific optimum temperature (fig. 5 and 6). Highest growth can be

achieved in 2010, where almost the entire Wadden Sea support temperatures for flounder to grow near maximum. However, temperatures are projected to exceed the species-specific optimum of flounder in 2010 (fig. 7) but the effect is very weak (fig. 5). The spatial and yearly patterns are similar for the larger size class of flounder (20 cm), whereas in 2010, a slight reduction in growth is projected for most of the Wadden Sea (fig. 8). Nearly no growth reduction is calculated for both the small and the large size classes of flounder for the different years. It seemed that (juvenile) flounder is weakly affected by high summer temperatures within the study period.

Herring. Herring have the lowest optimum temperature of the four species of interest and show therefore the most dramatic growth reduction. In 2010 and 2009, almost the entire Wadden Sea exceed the optimum temperature of herring (fig. 7), whereas in 2011, most of the area reach temperatures that equal the optimum temperature of herring. The larger size class of herring (15 cm) show growth rates near zero in a small part of the Wadden Sea in 2010, in other parts of the area growth is strongly reduced. In 2009, the growth reduction is less pronounced but temperatures in the entire area exceeded the optimum temperature of herring. The only year of nearly no growth reduction is shown in 2011 (fig. 7 and 8). Both size classes of herring were strongly affected by high summer temperatures, although, the strongest growth reduction is projected for the large juvenile herring.
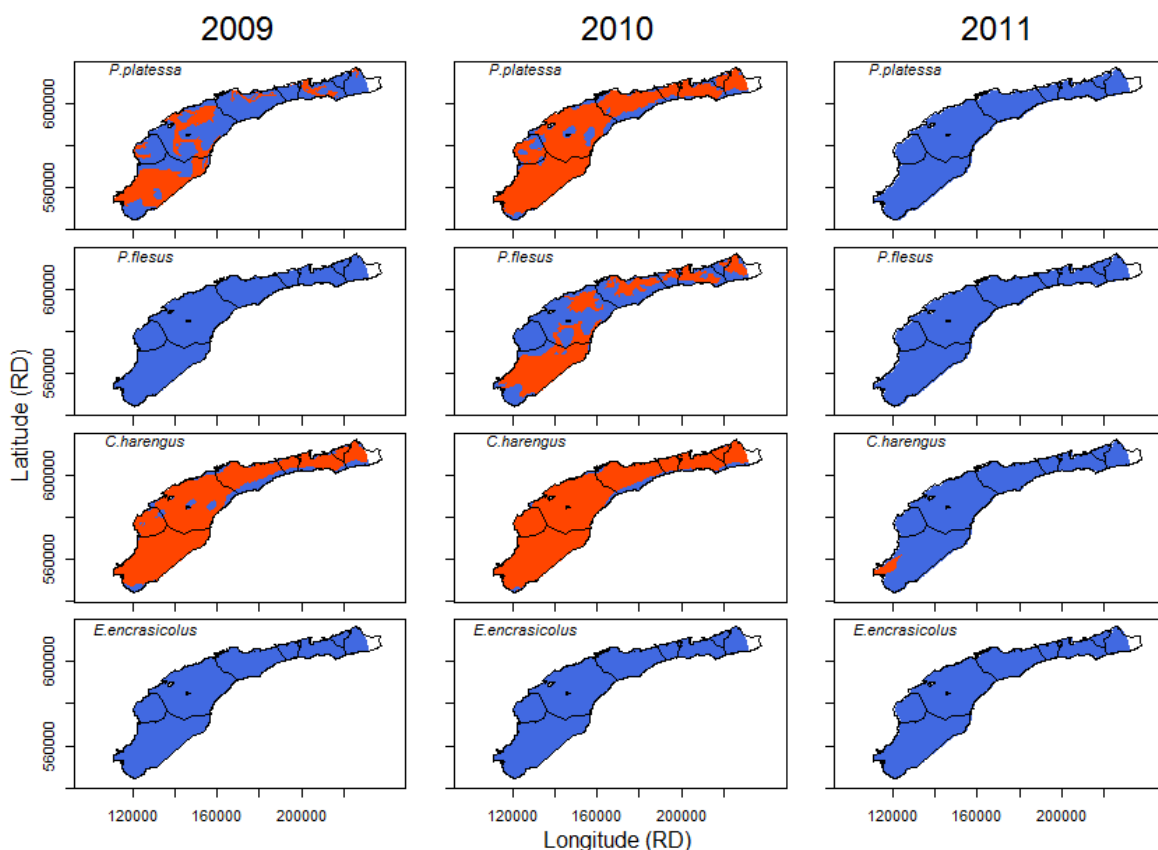

Fig. 7. July. Projected areas of growth reduction of the four species of the 5 cm juvenile size class and the three different years. Blue represents no growth reduction and in red, growth reduction is projected to occur. For August, see appendix G.

Anchovy. In contrast to the other fish species, anchovy is the only fish species having southern affinities. Based on the projected potential growth rate maps of the three different years, the Wadden Sea is not suitable for anchovy to grow optimal. In none of the three years maximum potential growth rates were reached. In 2010, highest potential growth rates were projected, however, these rates were not even close to the maximum potential growth rates anchovy can reach. Similar patterns are projected for the large size class of anchovy (15 cm). It appears to be that the Wadden Sea is not suitable for anchovy to grow optimal because summer temperatures were projected to be below optimum.

Validation. The Demersal fish survey (Tulp 2015) and the acoustic survey (Couperus et al. 2016) showed that particularly small sized individuals were caught for the period of interest. The obtained mean lengths were 9, 10, 8 and 7, for respectively plaice, flounder, herring and anchovy. Size distributions of plaice, flounder and herring confirmed that nearly no large individuals were caught (Tulp 2015). The potential growth maps showed that juveniles of the large size class were more affected by high summer temperatures ,whereby growth is reduced, than the 5 cm juvenile fish.
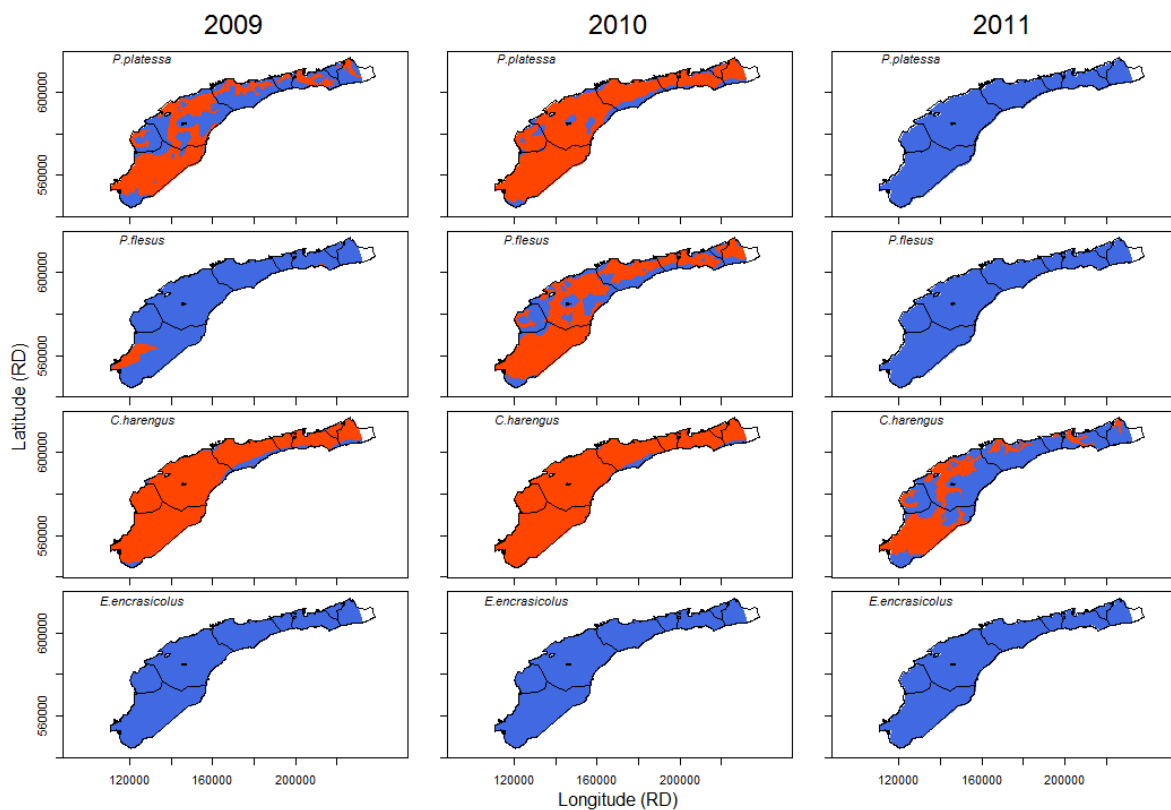

Fig. 8. July. Projected areas of growth reduction of the four species of the large juvenile size class (20 cm for plaice and flounder and 15 cm for herring and anchovy) and the three different years. Blue represents no growth reduction and in red, growth reduction is projected to occur. For August, see appendix G.

4. Discussion

This approach shows that species-specific optimum temperatures were exceeded for several fish species within the study period (2009-2011), whereby growth reduction is projected for

herring, plaice and flounder. Larger juveniles are more prone to high temperatures and show a more pronounced growth reduction compared with the smaller juvenile size class. During the summer months (July and August) within the study period, parts of the Wadden Sea are projected to be not suitable for (large) juveniles to grow optimal, except for anchovy. However, this study only included temperature as an environmental driver to get insight in the observed changes in the fish community of the Dutch Wadden Sea (North Sea), whereby several other environmental and non-environmental drivers can have an effect as well. Other drivers can be e.g. habitat degradation, fishing, spawning success, egg survival, larval drift, predators, food availability and other abiotic factors (e.g. salinity)(Boeuf and Payan 2001; Bolle et al. 2009; Harley et al. 2006; Rijnsdorp et al. 2009; van der Veer et al. 2016). Previous studies argued a better growth of fish in brackish waters having intermediate salinity conditions. The extra obligatory work due to suboptimal salinity conditions is suggested to range from 10% to 50% of the total energy budget. The mechanism behind this is rather unclear (Boeuf and Payan 2001).

Due to a lack of spatial and temporal information of accessible food, food is assumed to be ad libitum and scaled to 1 in this approach. Food availability is one of the most essential variables determining the quality of the habitat for juvenile fish, but, it is rather difficult to quantify the abundance of accessible food (Freitas et al. 2016; Gibson 1994, 1997). Summer growth reduction as projected in this study have been observed in juvenile plaice in the western Dutch Wadden Sea in several other studies as well (Cardoso et al. 2016; Freitas, Kooijman and Van Der Veer 2012; van der Veer et al. 2010, 2016). Nevertheless, the mechanism behind this is neither clear or suggested as a reduced availability in prey items due to less active macrozoobenthos in summer (van der Veer et al. 2016). Furthermore, species-specific optimum temperatures were predicted to be food dependent. Where food is limited, lower temperatures will be more suitable to higher temperatures (Teal et al. 2012). Implementing food conditions of the Wadden Sea in the DEB model would have result in different potential growth projections. It is likely that the potential growth rate projections would have been lower for the two flatfish species because food intake is suggested to be not maximal (van der Veer et al. 2016).

One of the main principles of the Dynamic Energy Budget theory is that all metabolic rates are organized equally between species (Kooijman 1993, 2010). This assumption makes the DEB theory a powerful framework to evaluate interspecific differences of variabilities in environmental conditions (Teal et al. 2012; van der Veer et al. 2009; van der Veer, Cardoso, and van der Meer 2006). Although, a species-specific set of parameters reflect the differences among species. Energetics differ between sexes and can be reflected in different parameter values. In this research only parameter values of female fish were used since most of the parameters sets of male fish are incomplete (Freitas et al. 2010). Parameters for the various fish species were obtained from literature data, and if available, a complete set of parameters was used. However, complete sets of species-specific parameter values were scarce and by a lack of a complete parameter set, parameters were obtained from various data sources. The quality of these composed data sets can be affected because some parameters are temperature dependent via the Arrhenius temperature (van der Veer, Kooijman and van der Meer 2001). Nevertheless, the primary temperature dependent parameters were all obtained from one unique study, so only some temperature independent parameters were obtained from other data sources (Freitas et al. 2010).

Furthermore, for anchovy a set of parameters of the Bay of Biscay was used by a lack of North Sea information of this species. However, a recent study showed hardly no connectivity between

the Bay of Biscay anchovy and the North Sea anchovy. These two populations of anchovy are genetically different from each other, and that the recently increase of anchovy in the North Sea is the result of an increase of the local North Sea population. The thermal performance of the North Sea anchovy might be different from the Bay of Biscay anchovy. A North Sea parameter set of anchovy might give a totally different projection of the potential growth of this species in the North Sea (Petitgas et al. 2012; Raab 2013). Evolutionary response to climate change might take place since species are capable to adapt to changing environmental conditions (Harley et al. 2006; Teal et al. 2015). In this case, species-specific DEB parameters might change as well as fish species adapting to changing environmental conditions (e.g. temperature).

In large parts of the Dutch Wadden Sea, temperatures were projected to exceed the species-specific optimum temperature of plaice, flounder and especially herring. Nevertheless, herring (plaice and flounder) is (are) still present in the Wadden Sea as is shown by the DFS catches and the acoustic survey (Couperus et al. 2016; Tulp 2015). Fish species can respond to high temperatures by avoiding the highest temperatures within the Wadden Sea or migrate out of this area towards the North Sea. Although, spatial and temporal distributions of fish during summer are unknown. For getting a better understanding of fish species distribution during summer, fish surveys need to be conducted frequently in this period. The current model approach supposed that the entire Dutch Wadden Sea is potentially suitable as habitat for fish, whereas parts of the area consist of intertidal flats. These intertidal flats are only accessible during particular time frames within a tidal cycle. Ideally, tidal migration is taken into account, however, this is rather complex (van der Veer and Bergman 1986).

DEB predictions show a shift in their species-specific optimum temperature, however the shift in the optimum performance temperature to lower temperature is weak (Fig. 3). Several studies have substantial evidence in a clear shift in the optimum temperature of a species to lower temperature by an increase in length (Pörtner and Farrel 2008; Pörtner and Peck 2010; Rijnsdorp et al. 2009). Previous studies to the physical performance of plaice incorporated therefore an inverse relationship between fish size and the upper thermal limit (T_H), for each 10 cm of size increment, T_H decreases by 1 °C (Teal et al. 2012; van der Veer et al. 2009). However, the evidence for this is still part of the ongoing discussion and the underlying mechanism is not clear (van der Veer et al. 2009). Implementing the inverse relationship between fish size and T_H would have result in a more pronounced growth reduction for the larger sized juvenile plaice, flounder and herring.

Despite all the considerations of this approach, there is substantial evidence that based on the DEB theory, Wadden Sea temperatures can certainly exceed species-specific optimum temperatures and reduce growth of plaice, flounder and herring juveniles. The larger sized juveniles are projected to be more prone to high summer temperatures than the smaller juveniles. This is in line with the size distribution from the DFS (Tulp 2015), whereby large sized juveniles were hardly caught. This suggest that only 0-group juvenile fish make use of the nursery function of the Wadden Sea and larger sized fish have left this area. This pilot study provided a promising mechanism to analyze trends in fish species distribution in the Dutch Wadden Sea. Daily mean temperatures can be used instead of monthly mean temperature, although, it is unknown if daily temperatures or monthly mean temperatures drive changes in fish species distribution. Nevertheless, if temperatures keep rising, which is projected with several degrees at the end of this century, optimum temperatures will be exceeded more frequently and more pronounced in the Wadden Sea (IPCC 2014). This might drive even the

smallest juveniles of plaice, flounder and herring out of their Wadden Sea nursery grounds in future.

5. Conclusion

Overall, it can be concluded that temperature can have an impact on the distribution of fish species by exceeding species-specific optimum temperatures, whereby high temperatures limit growth. Growth reduction is projected to occur for plaice, flounder and herring in some summer months within the study period. In July 2010, growth reduction is projected to be most pronounced, whereby in July 2011 almost no growth reduction is projected, except for herring. Larger sized juveniles were modelled to be more prone to high summer temperatures. Growth of anchovy is not limited since anchovy is the only fish species having southern affinities. These findings might partly explain the changing fish community and abundances of fish species in the Dutch Wadden Sea since temperatures were projected to be close to several species-specific upper limits of their thermal tolerance range. Although, caution has to be taken by implementing these results since many other environmental and non-environmental drivers can affect the physical performance of fish and their distribution. Concluding, the provided mechanistic approach in this pilot study based on temperature conditions is a promising mechanism to analyze trends in fish species distribution in the Dutch Wadden Sea. Species-specific optimum temperatures will be exceeded more frequently and pronounced in future and might drive plaice, flounder and herring out of the Wadden Sea.

6. Acknowledgement

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Appendix A. Temperature tolerance ranges
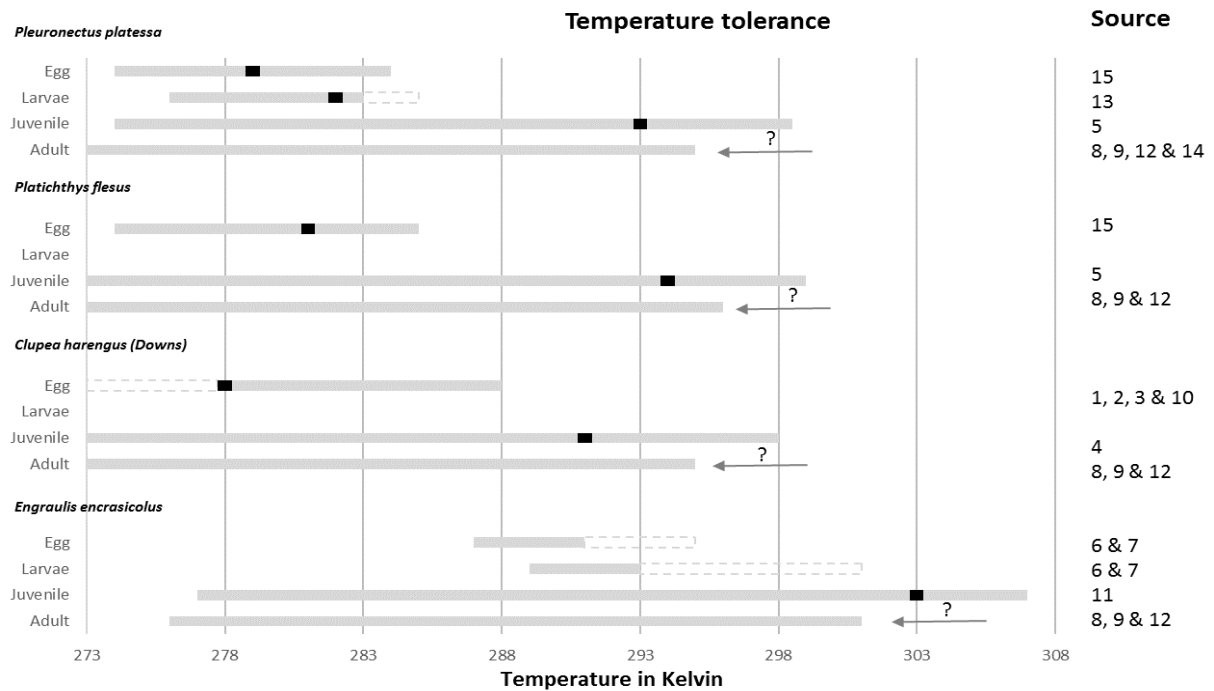
Overview of optimal temperature (black bar) and temperature tolerance range (total light grey bar) of the various fish species and for various life stages. Temperature performance breadth is defined as 69% of the optimal temperature. (1) Blaxter 1956 (2) Burd and Howlett 1974 (3) Dickey-Collas et al. 2009 (4) Fässler et al. 2012 (5) Freitas, Kooijman and van der Veer 2012 (6) Motos et al. 1996 (7) Petitgas et al. 2012 (8) Pörtner and Farrel 2008 (9) Pörtner and Peck 2010 (10) Postuma 1971 (11) Raab et al. 2013 (12) Rijnsdorp et al. 2009 (13) Ryland and Nichols 1967 (14) Teal et al. 2012 (15) von Westernhagen 1970.

B. Schematic overview of life cycles of fish species
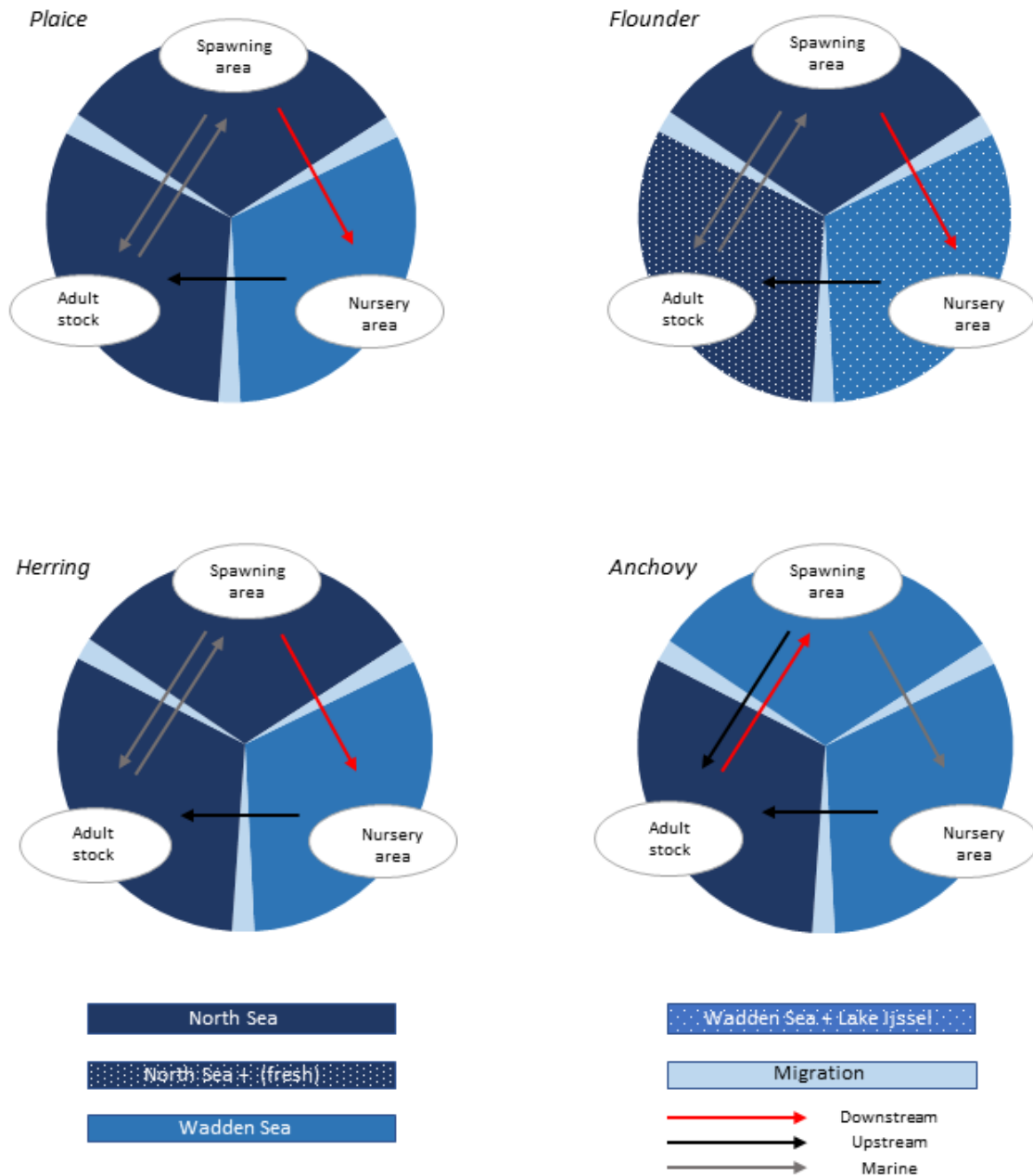
Movements between the various habitats consist from the spawning grounds towards nursery grounds, from nursery grounds towards the offshore adult population and from the adult population towards spawning grounds. This simplified fish migration triangle gives insight in the habitats fish species use during a particular life stage. Downstream means the migration from saline water into more brackish/fresh water, upstream is the migration vice versa. Marine migration is the migration within the marine environment (Elliot et al. 2007; Harden Jones 1968).

C. Growth reduction
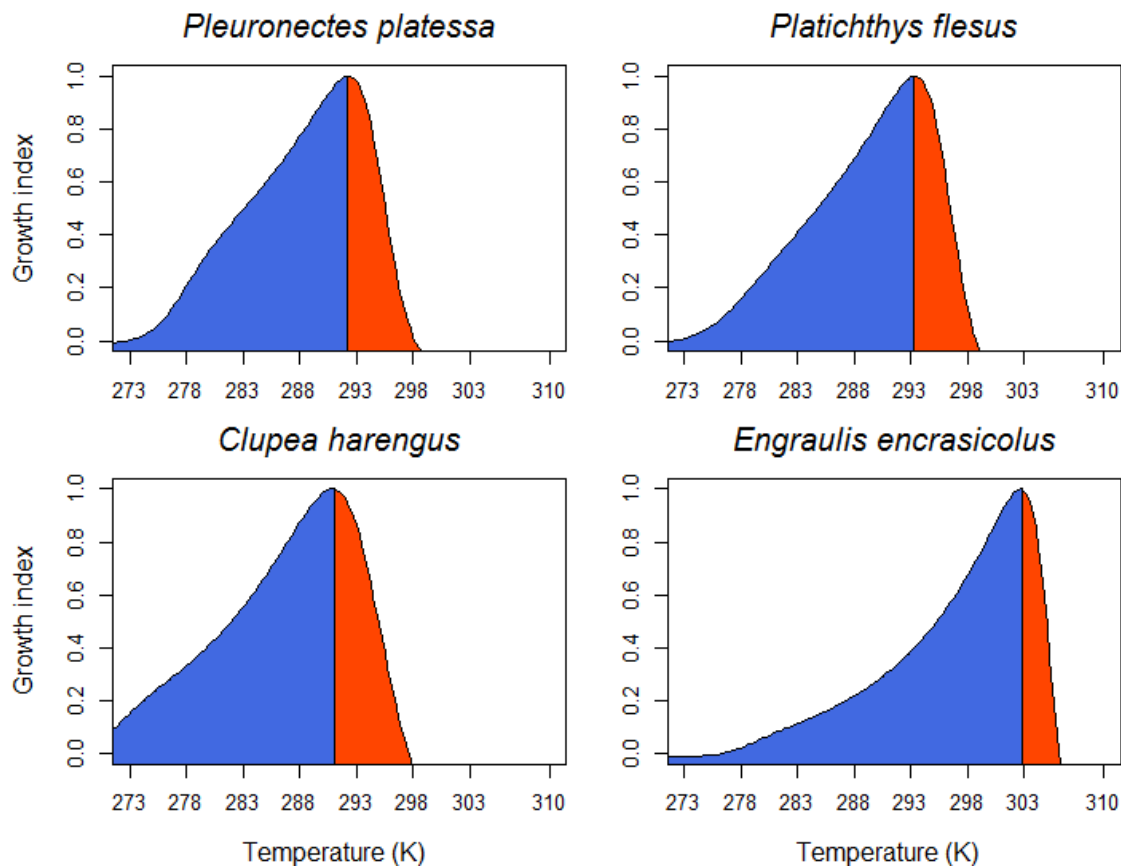
Graphs of the small juvenile size class (5 cm) show the temperature range having no growth reduction (blue) and the temperature range resulting in growth reduction (red). Optimum temperature of plaice (292.25 K), flounder (293.25 K), herring (291 K) and anchovy (302.75 K).

D. Historical data of the former Zuiderzee

Pleuronectes platessa (Plaice)

Plaice use the Zuider zee as a nursery ground. The larvae drift from the North sea, where they mainly hatch in February, towards the Zuider zee. They prefer the areas of the Zuider zee there where the influence of fresh water is not really strong. High numbers of individuals are often found at 'De Meer' and 'het Enkhuizerzand' whereby individuals of the flounder are found rarely (Redeke 1907). Adult plaice is most abundant north of the line Enkhuizen – Stavoren. Juveniles (0-Group) are numerous at 'het Enkhuizerzand' and in autumn at 'wieringer meer'. I-Group and II-Group plaice are mainly been found at the 'Spaanderbank' and along the Frisian coast where they feed on their favorite diet, parts of spiracles from *Mya arenaria* (Redeke 1922).

Platichthys flesus (Flounder)

Similar to plaice, flounder spawn in the North sea and use the Zuider zee as a nursery ground. This is a conclusion based on observations that there haven't been found any flounder eggs in the Zuider

zee. Furthermore, none of the flounders that were caught on the Zuider zee throughout the years of 1905 and 1906 were completely mature and able to spawn. March is mainly the month of spawning for the flounder. The first flounder larvae were caught in the northern part of the Zuider zee at the end of April and May. In July most of the young individuals have a length of about 6 cm and at the end of September and October the individuals have a length of circa 8 – 12 cm. Most of the flounder youngsters (0-Group) clearly prefer the most brackish water in the eastern and southern part of the Zuider zee. The more grown-up individuals can be found throughout the entire Zuider zee. The average length of the 0-Group, I-Group and II-Group individuals is respectively 10 cm, 16 – 21 cm and 20 – 25 cm (size at the end of their first, second and third year of living). At the end of their third or fourth year, the individuals become mature and are able to spawn. The young individuals feed on small crustaceans and shellfish (Redeke 1907).

Clupea harengus (Herring)

Herring use the Zuider zee as a spawning ground, whereby herring spawn in relatively brackish water. The Zuider zee herring differ from the North sea herring in its number of vertebra (<56). The mature individuals enter the Zuider zee during spring, the great migration take place especially in March. The spawning season is from April until July. The eggs hatch in shallow benthic environments between stones, plants, shells and other hard substrates with waters having a salinity between approximately 10 to 15 ‰. The temperature of the water is relatively cold at the beginning of the spawning period but rises rapidly to circa 18 degrees Celsius (Redeke 1907). The larvae are numerous in May and June in waters with a salinity between 5 -10 ‰ (Redeke 1922). The fast growing larvae feed themselves mainly with copepods. They grow until October, thereafter their size do not increase till March. The migration out of the Zuider zee to the North sea of (most of) the juveniles starts when the individuals are 5 or 6 months old. Before the new migration of Herring will enter the Zuider zee in March the grown-ups are almost all left to the North sea to become mature and thereafter return to the Zuider zee for spawning. The average length of the age classes 0-Group, I-Group and II-Group is respectively, 8 – 9 cm, 14 – 15 cm and 21 – 23 cm (size at the end of their first, second and third year of living). The mature adults do not feed themselves in the Zuider zee when they enter this area for spawning (Redeke 1907).

Engraulis encrasicolus (Anchovy)

Like the Herring, the Anchovy use the Zuider zee as a spawning ground during summer time. The migration takes place mainly in May and June. The anchovy prefer to spawn in the northern part of the Zuider zee there where the water is more saline. In contrast to the benthic eggs of the herring, the eggs of the anchovy are pelagic. The duration of the spawning season (May - August) differs from year to year depending on the water condition, especially the temperature of the water is an important driver (Redeke 1907). Favorable years are recognizable for a short spawning period in June. The larvae can be found together with the eggs most of the time north of the line Lemmer – Urk – Marken, mainly in water with a salinity > 15 ‰. After hatching of the eggs, the larvae move in southward direction (Redeke 1922; 1907). The grown-ups with a length of 10 – 12 cm migrate during autumn to the North sea to become mature. The larval stage is a critical period for the survival of larvae during their growth. Temperature seems to be the driver that determines the survival of the larvae. The fact is that the anchovy is a specimen with its living area mainly in southern Europe. The Netherlands is the northern limit of the anchovies distribution area. Therefore, small changes in yearly water conditions can be fatal for the anchovy. This is in contrast with the herring, which is a more hardened organism. There seems to be a moderate correlation between individuals caught during a year and the water temperature in June the year before. It is completely unknown what the reason is for the absence of some large numbers of anchovy during particular years, instead of

spawning in the Zuider zee they prefer to spawn in the North sea during particular years (Redeke 1907).
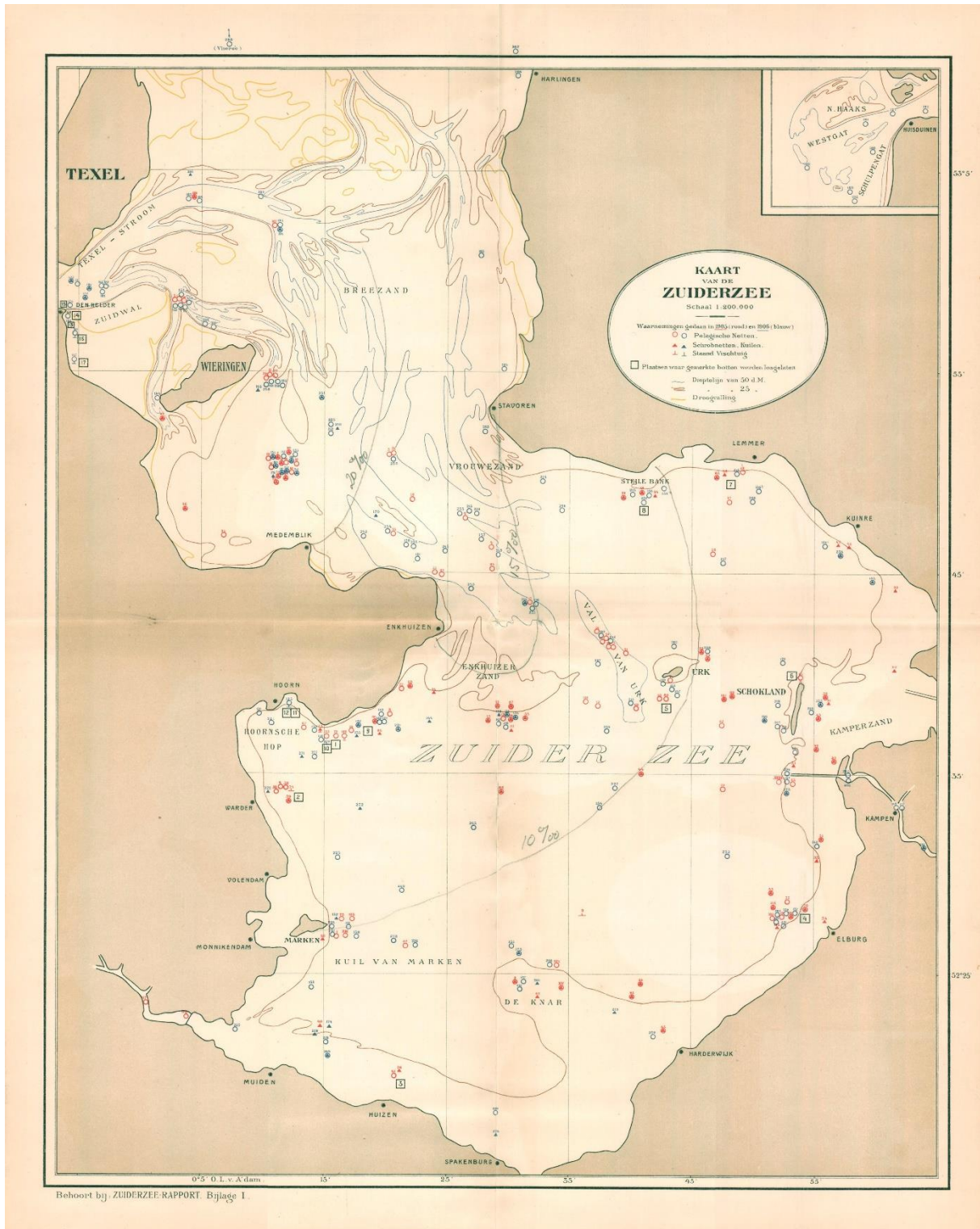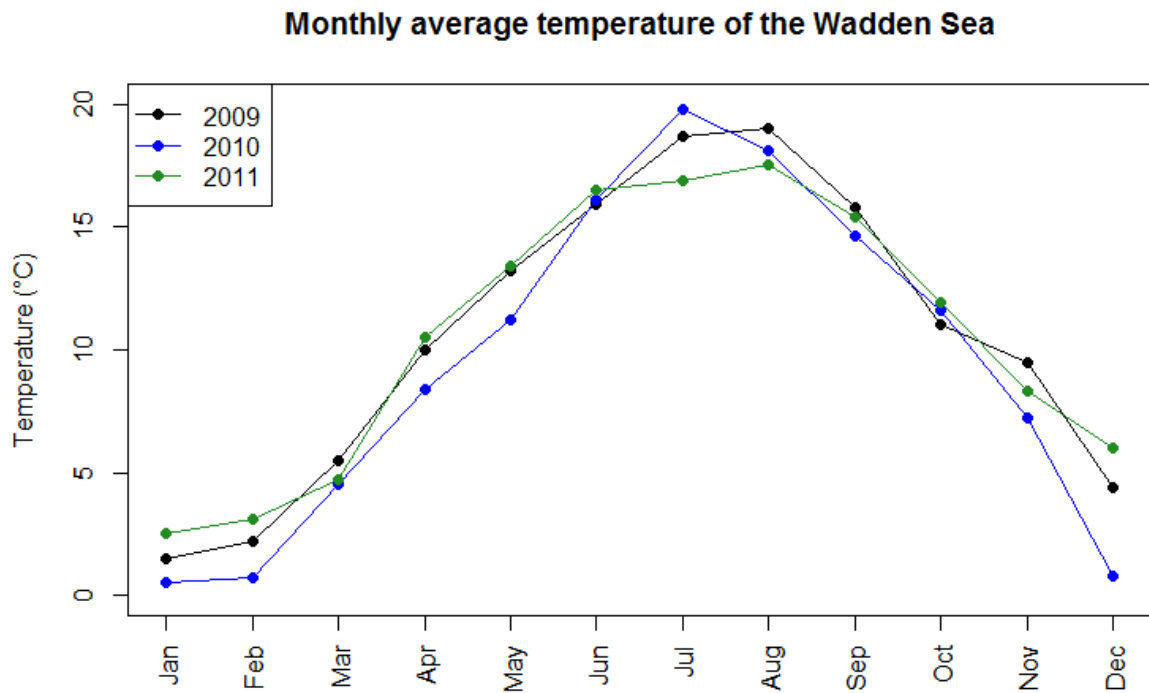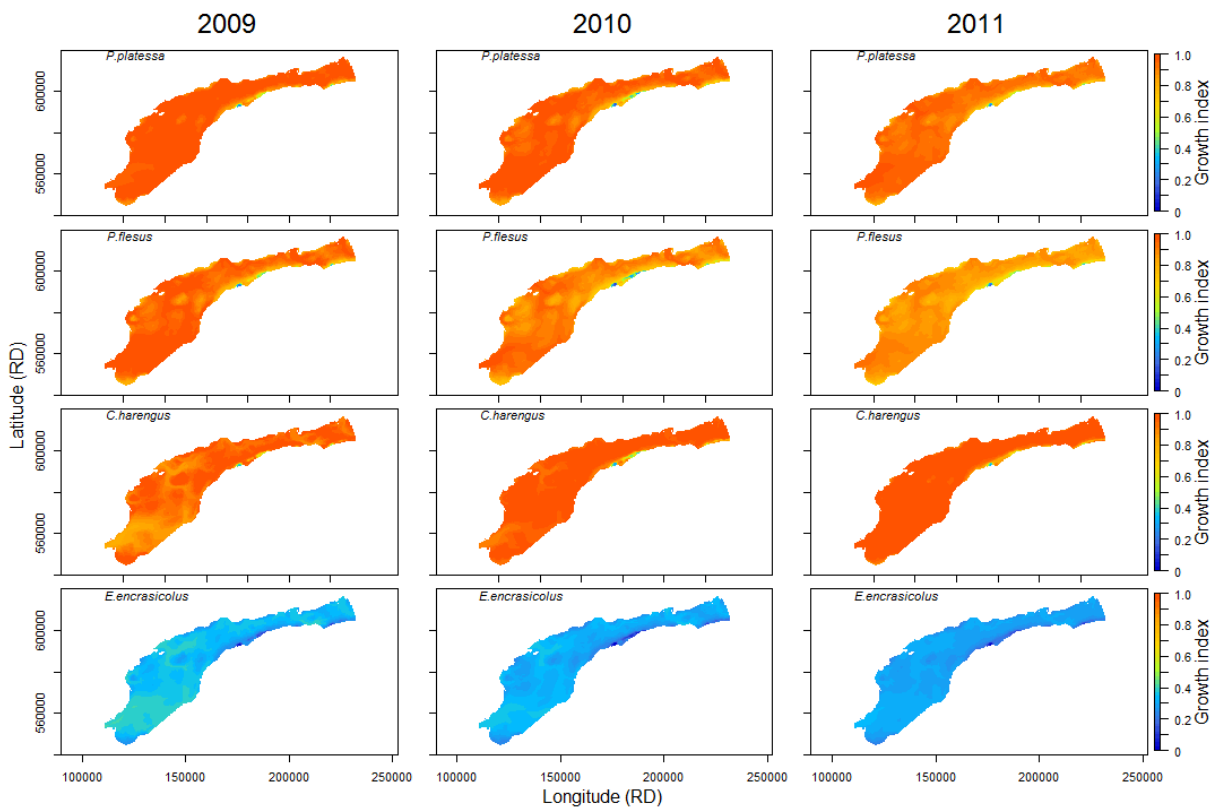

Fig. D. shows the map of the former Zuiderzee. Bathymetry lines are drawn as well as the salinity lines of 10, 15 and 20 pro mile.

## E. Monthly mean temperatures of the Dutch Wadden Sea (2009-2011)

Monthly average temperature of the Wadden Sea

## F. Potential growth rates of plaice, flounder, herring and anchovy for August

Projected potential daily growth rates for August of the four species of the 5 cm size class and the three different years. A growth index of one represents maximum potential growth rates in cm per day where a growth index of zero represents no growth. Max potential growth of plaice (1.22 mm day⁻¹), flounder (1.01 mm day⁻¹), herring (0.92 mm day⁻¹) and anchovy (1.32 mm day⁻¹).
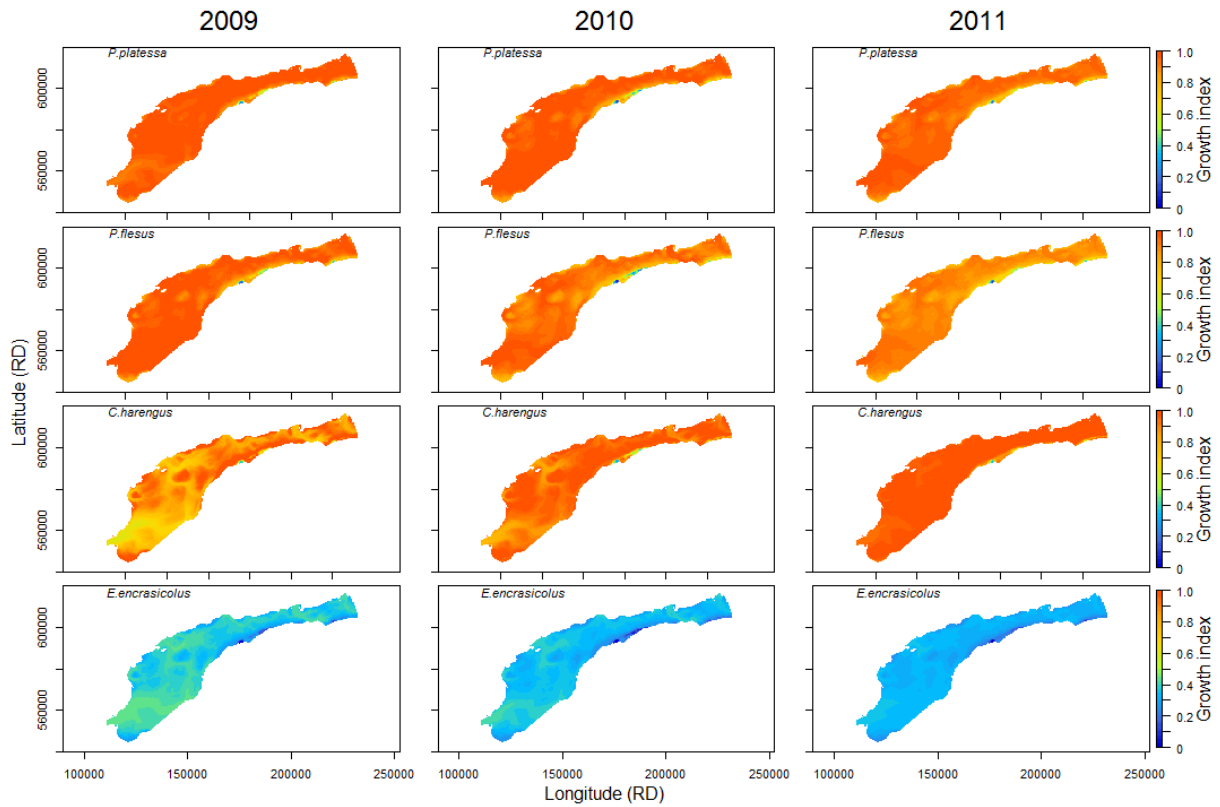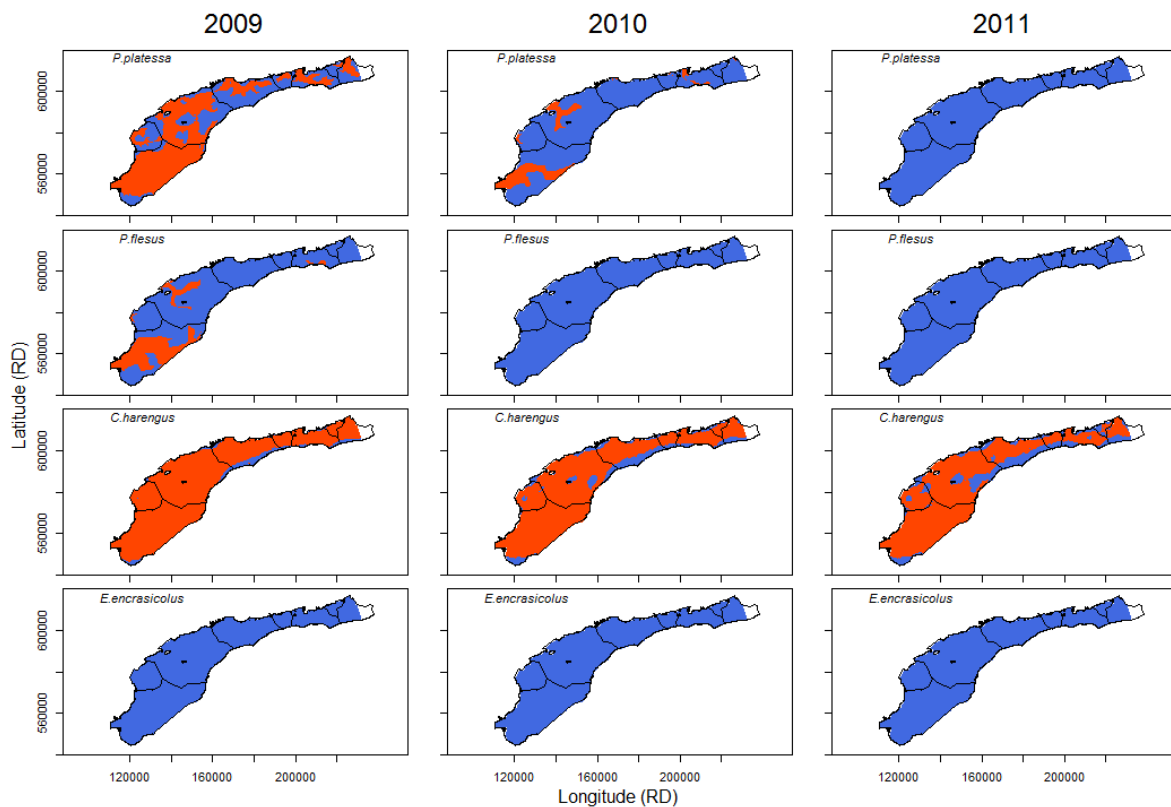

Projected potential daily growth for August of the four species of the large juvenile size class (20 cm for plaice and flounder and 15 cm for herring and anchovy) and the three different years. A growth index of one represents maximum potential growth rates in cm per day where a growth index of zero represents no growth. Max potential growth of plaice (0.97 mm day⁻¹), flounder (0.70 mm day⁻¹), herring (0.66 mm day⁻¹) and anchovy (0.41 mm day⁻¹) for the corresponding length.

G. Growth reduction of plaice, flounder, herring and anchovy in August
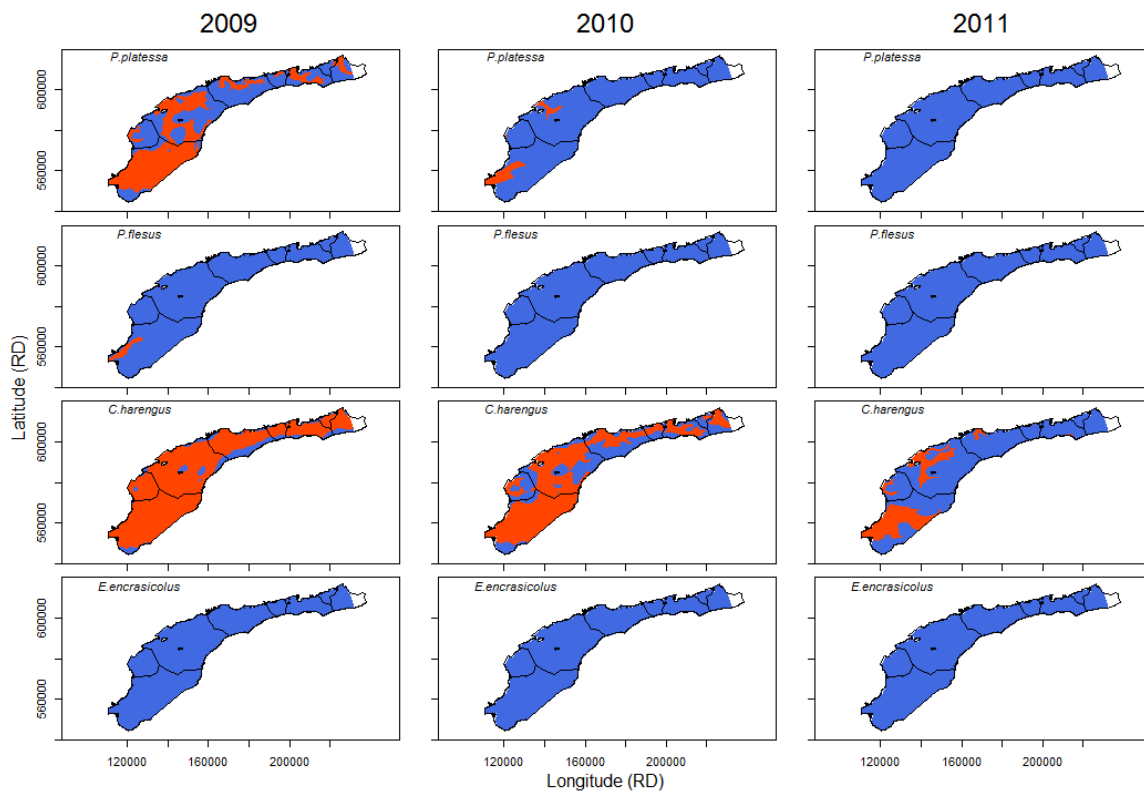
Projected areas of growth reduction of the four species of the 5 cm juvenile size class and the three different years (August). Blue represents no growth reduction and in red, growth reduction is projected to occur.

Projected areas of growth reduction of the four species of the large juvenile size class (20 cm for plaice and flounder and 15 cm for herring and anchovy) and the three different years (August). Blue represents no growth reduction and in red, growth reduction is projected to occur.

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