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Is summer growth reduction related to feeding guild? A test for a benthic juvenile flatfish sole *(Solea solea)* in a temperate coastal area, the western Wadden Sea

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Abstract

Flatfish species are an important target for fisheries. During their juvenile stage they concentrate in coastal nursery areas. Food conditions in these areas are an important factor determining habitat quality and ultimate survival. Recently, growth reduction in summer has been observed in plaice*, Pleuronectes platessa*, feeding on both epibenthic and benthic prey. In the current study, we test the hypothesis that summer growth reduction is a consequence of a reduced availability of benthic prey by analysing summer growth in a fully benthic feeding flatfish, juvenile sole (*Solea solea).* Summer growth was studied for contrasting years with respect to preceding winter water temperature conditions to exclude possible irreversible non-genetic adaptations of growth to water temperature. Individual growth, estimated from otolith daily rings, was compared with predictions of maximum growth at the prevailing temperature. In line with expectations, 0-group sole showed strong summer growth reduction, supporting the notion that summer growth reduction is related to feeding modes. Summer growth reduction underlines the importance of a good definition of how and over what time period growth as indicator of habitat quality is estimated and compared.

1. Introduction

North Sea flatfish species, especially plaice (*Pleuronectes platessa)* and sole (*Solea solea)*, are an important target for fisheries. During their juvenile stage, which can last up to a few years, these flatfishes are concentrated in special areas (Creutzberg & Fonds, 1971; Zijlstra, 1972; Bergman et al., 1988; Beck et al., 2001), and these so-called nursery areas has been the topic of many studies (e.g. Riley & Corlett, 1966; Macer, 1967; Edwards & Steele, 1968; Kuipers, 1975; Kuipers, 1977; Lockwood, 1980; Zijlstra et al., 1982; Berghahn, 1986; van der Veer, 1986; van der Veer et al., 1991, 2001; Kuipers et al., 1992; Pihl & van der Veer, 1992; Nash & Geffen, 2000, 2012; Teal et al., 2012). A main focus dealt with food availability and growth as indicators of the quality of juvenile flatfish habitat (for an overview see Gibson, 1994).

Juvenile flatfish species feed on macrozoobenthic prey-items, including polychaetes and bivalves, and on epibenthic prey items (e.g. Edwards & Steele, 1968; Kuipers, 1977; de Vlas, 1979; Cabral, 2000). The various flatfish species differ in prey choice due to differences in physiology and morphology of the alimentary tract and in feeding behaviour (de Groot, 1969; Braber & de Groot, 1973). It has been thought for a long time that food conditions for juvenile flatfishes in coastal nursery areas were optimal, the so-called 'maximum food-optimal growth conditions' hypothesis (van der Veer & Witte, 1993), suggesting that growth was only determined by prevailing water temperature (Zijlstra et al., 1982; van der Veer 1986; van der Veer et al., 1994). This hypothesis was based on the feeding behaviour of juvenile flatfishes in combination with the presence of high numbers of epibenthic and benthic prey items in coastal nurseries. Furthermore, a considerable part of the diet of juvenile flatfish consisted of regenerating body parts, where flatfishes 'graze' only the protruding body parts of their prey which are used for their locomotion or filter feeding activities (Arndt & Nehls, 1964; Edwards & Steele, 1968; Kuipers, 1977; de Vlas, 1979).

However, more recently, large variability in juvenile flatfish growth was found, both on a spatial scale (in various systems) as well as on a temporal scale (between years) (Amara, 2003; Fonseca et al., 2006; Hurst & Abookire, 2006; van der Veer et al., 2010; Freitas et al., 2012, 2016; Ciotti et al., 2013a,b; Cardoso et al., 2016), pointing to a period of suboptimal growth in late summer (van der Veer et al., 2010; Freitas et al., 2012). This period of reduced growth in summer sheds another light on the nursery function of coastal areas, in that they may not be an optimal area for growth over an entire season for young flatfishes.

Previous research indicated that the biomass of potential food items is not lower in summer, but benthos consumption by flatfishes is (de Vlas, 1979; van der Veer et al., 2016). Several mechanisms have been proposed as explanation for this so-called 'summer growth reduction': [1] reduced benthic activity (such as less frequent presence on top of the sediment) of prey items after the phytoplankton bloom in late summer; [2] increased food demand of flatfishes through a combination of increasing body size and high temperatures whereby prey searching and handling becomes energetically demanding or [3] increased interspecific competition for benthic prey later in summer due to the outburst of young–of–the-year crustaceans (van der Veer et al., 2016).

A first test of the "summer growth reduction" hypothesis compared the growth of two co-occurring species with slightly contrasting feeding behaviour: plaice, a predomiantly benthic feeder, and flounder (*Platichthys flesus)*, a predominantly epibenthic feeder. This study found that growth in plaice declined during summer (Cardoso et al., 2016) in contrast to flounder which did not exhibit growth reduction (Poiesz et al., 2019), supporting the suggestion of the impact of feeding guild (benthic vs epibenthic) on growth performance.

However, plaice and flounder have partly overlapping feeding guilds, feeding on both infaunal benthos and epibenthos, although they have contrasting preferences (de Vlas, 1979).

In this study we extend the test of the summer growth reduction by analysing summer growth in a truly benthic feeding flatfish, juvenile sole (*Solea solea*), which therefore presents a third feeding guild. 0-group sole (with a maximum length of 65 mm) mainly feeds on a variety of benthic macrozoobenthic prey items, primarily polychaetes (*Hediste diversicolor, Marenzelleria ssp.*) and occasionally bivalves (*Ensis leei*) (Kühl & Kuipers, 1983; Cabral, 2000). Summer growth reduction is expected in sole when benthic productivity is reduced or when food demand increases, due to increased metabolic demands. Growth conditions of 0-group sole were evaluated, as in the studies on juvenile plaice and flounder, at the same location (the Balgzand intertidal area in the western Dutch Wadden Sea), and for the same years. Information from otolith microstructure analysis was used to reconstruct individual growth (size-at-post settlement age) at Balgzand and was compared with maximum growth predictions (under optimal feeding conditions) based on a Dynamic Energy Budget (Kooijman, 2000; 2010).

2. Material and methods

2.1. Sampling

0-group sole were sampled at the Balgzand intertidal in the western Dutch Wadden Sea (Fig. 1) during three years: 1995 (after a relatively warm winter), 1996 (after a cold winter) and 2000 (after an average winter) (Fig. 2). These different years were selected because water temperature during early life may affect the growth performance later on in the juvenile phase due to irreversible non-genetic adaptation of growth to temperature (van der Veer & Witte, 1999). Samples were collected at regular intervals of two weeks from March to August in 1995, from February to September in 1996, and from January to October in 2000. During each campaign, nine transects, each consisting of four stations were sampled with a 2m beam trawl (1 tickler chain; mesh size of 5 x 5 mm). For more information see Zijlstra et al. (1982) and van der Veer (1986). During each sampling, water temperature was measured and compared to daily temperature series collected from a long-term monitoring station (Marsdiep jetty) located at the southern tip of Texel (van Aken, 2008; Fig. 1).

All catches were stored at −20°C. Within a week catches were defrosted and sorted for juvenile flatfish. Subsequently, all soles were measured to the nearest mm for total length and width and preserved in 70% alcohol. In line with previous work (van der Veer et al., 1991), all numbers caught were corrected for size-selective mesh efficiency after Dapper (1978) and catch efficiency after Kuipers (1975), using the data for plaice (Supplementary information Fig. S1). For each haul, corrected numbers were expressed as densities per 1000 m^2 (ind. $[10^3 m^2]^{-1}$) and the mean total length (mm) was calculated. The arithmetic mean of all hauls was considered to represent respectively the mean density and mean total length of the population.

2.2. Otolith microstructure analysis

For each year, and each campaign a size stratified subsample of fish were selected in relation to their abundance and size frequency. In total 207 fishes were selected for 1995, 141 for 1996 and 81 for 2000. Both sagittal otoliths were removed from each fish and mounted on a microscope slide, sulcus upwards, in a drop of thermoplastic adhesive (Crystalbond, Buehler, USA). The daily rings from otoliths of smaller fish (<65 mm) was undertaken without any further preparation of the otoliths. Larger otoliths (fish >65 mm) were ground and polished prior to reading. Grinding and polishing were done by several grinding plates from course to fine (P1200, P2500 and P4000 silicon carbide abrasive papers; Buehler) and wet-polished (MasterPrep, Buehler) until the midplane of the otolith was visible. For more information see Cardoso et al. (2016).

Daily rings were counted from the first ring after the spherical growth centre, which was considered as the first daily growth ring after settlement/metamorphosis (Geffen et al., 2011), until the last ring of the otolith. A light microscope (Zeiss) coupled to a digital camera (AxioCam ICc3, Zeiss, Germany) was used for counting the rings. Two observers counted the daily rings independently of each other. When both counts differed more than 10%, counting was repeated. If the counting differed more than 10% for the second time, the otolith was excluded from further analysis. For each otolith, age (in days) after settlement was calculated as the mean of both counts. Settlement date was estimated by subtracting the number of daily rings from the catch date.

2.3. Growth analysis

Individual fish were assigned to a weekly cohort based on back-calculated settlement date. For each of these 'settlement cohorts', the length-age relationship was constructed based on the otolith daily ring counts in combination with the length of the fish.

The theoretical maximum growth trajectories were estimated with a Dynamic Energy Budget (DEB) model (Kooijman, 2010), which predicts growth in relation to prevailing food and water temperature conditions. The impact of food conditions is represented using the scaled functional response (f), a dimensionless quantity ranging from 0 to 1 that relates ingestion to food density in the environment through a Holling type II functional response (van der Veer et al., 2009). Under *ad libitum* food conditions, the functional response variable equals 1, and the dynamics of growth simplifies into the Bertalanffy growth model (Kooijman, 2010):

$$\frac{d}{dt}L = \dot{r}_B(L_\infty - L) \qquad (1)$$

The parameters L_∞ (ultimate size; cm), L (observed length; cm) and $\dot{r}_B$ (von Bertalanffy growth rate constant, d^{-1}) can be written as a combination of DEB parameters as described in the supplementary information Table S1.

Growth rates (assuming a starting length of 10 mm) are affected by prevailing temperature conditions due to thermal dependence of physiological rates, which, in the DEB model, is described using an Arrhenius-type relationship extended to account for the effects of temperature at both lower and upper tolerance boundaries (Kooijman 2010, p. 21; van der Veer et al. 2010, Eq. 4). Water temperatures for 1995, 1996 and 2000 used in the model were derived from measurements taken every 30 minutes from the Marsdiep jetty.

In the DEB model, differences in energy allocation between sexes are reflected in different parameters used (e.g. reproductive investment, energy acquisition and ingestion, assimilation) (Kooijman, 2010). Therefore, maximum growth predictions were made for both males and females separately (van der Veer et al., 2009; Cardoso et al. 2016; Poiesz et al., 2019). The species-specific parameters for sole were taken from van der Veer et al. (2001, 2009, 2010) and Freitas et al. (2010) (Supplementary information Table S1). For more information see van der Veer et al. (2010). For comparison with observed field growth, DEB-predicted maximum growth for males and females were first averaged assuming that the sex ratio was 1:1. The realized growth (RG; -) of each individual sole was estimated as the ratio between observed size at day of catch and the DEB predicted maximum size at the same day. This was calculated separately for all three years. The RG for all three years was compared to catch date and fish size.

2.4. Statistical analysis

Modelling and statistical analysis were carried out within the programming environment R (R Core Team, 2019), and the DEB model was solved using the R-package deSolve (Soetaert et al., 2010). Observed length and calculated maximum predicted growth was compared by using analysis of variance (ANOVA) (Cardoso et al., 2016). Temporal reductions in realized growth (RG) were visually assessed by plotting RG along sampling date and averages were analysed over time. For the various tests, model assumptions with respect to homogeneity, normality, independence, and absence of influential observations were met. For more information see Cardoso et al. (2016) and Poiesz et al. (2019).

3. Results

3.1. Field abundance and growth

For all three years the majority of the settlement occurred over a period of four to five weeks (Fig. 3). In 1995, settlement started in the middle of April and lasted until the end of May, in 1996 from the middle of May to the beginning of July and in 2000 from the beginning of May until the end of June. The peak in settlement occurred later in 1996 than in 1995 and 2000, around the beginning and end of May in 1995 and 2000 and two to four weeks later in 1996.

Juvenile 0-group sole was found for only a short period of time: in 1995 from May until July, and in 1996 and 2000 in June and July (Fig. 4 & 5). Abundances varied between the years and months, with peak densities up to 1400 ind. $[10^3 m^2]^{-1}$ in 1995, compared with 355 ind. $[10^3 m^2]^{-1}$ in 1996 and 222 ind. $[10^3 m^2]^{-1}$ in 2000 (Fig. 5a). Maximum observed densities occurred in 1995 around the end of May and the beginning of June, in 1996 in the beginning of July and in 2000 at the end of July.

In 1995, 0-group sole reached a mean total length of 66 mm in the middle of July, in 1996 33 mm at the end of July and in 2000 65 mm in the beginning of August (Fig. 5b).

3.2. Realized growth

A comparison of the theoretical maximum growth trajectories for the various cohorts predicted by the DEB model with the field observations for 0-group sole showed significant differences in all three years (ANOVA; for all three years, all cohorts together; $p < 0.001$). In all years, field growth of the cohorts was lower than predicted maximum growth (Fig. 6).

In 1995, values ranged from 0.7 to 1.8 in the beginning of May, but ratios declined later in the year to 0.5 to 0.7 from June onwards. Ratios in RG for 1996 and 2000 showed a variation of 0.4 to a maximum of 0.7 for the period June to August (Fig. 7). For all three years, the average RG remained relatively stable from around June onwards. Overall, the mean RG was lower than 1 (the predicted maximum growth), for 1995 RG = 0.7, for 1996 RG = 0.5 and for 2000 RG = 0.5.

4. Discussion

4.1. Growth reduction in sole

In line with the expectations, a growth reduction in 0-group sole was found at Balgzand in summer in all three years of study. Summer growth reduction starts early in 0-group sole, already in mid-May, compared to June in plaice (Cardoso et al., 2016). This implies that it started in relatively small fish of around 20 – 25 mm long, when (benthic) harpacticoid copepods are still an important component of the diet (Amara et al., 2001).

The magnitude of the growth reduction in 0-group sole, down to 50% of the maximum growth, is also stronger than in plaice (Cardoso et al., 2016). Benthic polychaetes are the main food source for 0-group sole (Amara et al., 2001), while 0-group plaice are feeding on a mixture of benthic and epibenthic prey (Kuipers, 1977; de Vlas, 1979; van der Veer et al., 2016). Therefore, a reduced benthic activity of polychaetes will have a larger impact on food intake and hence growth in 0-group sole than in 0-group plaice (van der Veer et al., 2016). It should be noted that maximum growth rates of juvenile sole are 50 – 100% higher than those of 0-group plaice (Fonds et al., 1992; Fonds & Saksena, 1977; Freitas et al., 2010), implying that the food demand of sole is also much higher. Thus the observed stronger growth reduction in 0-group sole compared to plaice is in line with a greater food demand they have. The larger growth reduction in 0-group sole is also reflected in the mean population length of both 0-group plaice and sole at the end of the growing season in the western Dutch Wadden Sea (Creutzberg & Fonds, 1971;

Fonds, 1983), which is almost identical despite the higher growth potential of 0-group sole (Freitas et al., 2010).

The mean population length by the end of July of between 35 - 65 mm (van der Veer et al., 2001; this study), corresponds with the growth and population length in the Dollard (Jager et al., 2001) and in the subtidal and deeper parts of the Wadden Sea (Fonds, 1978). This suggests that habitat quality of Balgzand does not differ from other areas in the Dutch Wadden Sea.

4.2. Is summer growth reduction in juvenile flatfishes related to feeding guild?

A comparison of food demand of the juvenile flatfish population (a few g AFDM m^{-2} per month) with the biomass of available potential benthic food items (10 - 20 g AFDM m^{-2}) (Jung et al., 2017) does not suggest a lack of potential food items. In line with the hypothesis, the 'summer growth reduction' therefore occurs as a consequence of a reduced activity of benthic prey organisms from summer onwards, several months after the spring phytoplankton bloom (van der Veer et al., 2016). The lower food accessibility is thought to cause an increased searching time for benthic feeding juvenile flatfish, which in the end leads to a lower prey intake and thus decreased growth. This implies that summer growth reduction would only occur in demersal benthic feeding species. The growth analyses for the juvenile flatfish community at the Balgzand intertidal are indeed in line with these expectations: no summer growth reduction in mixed epibenthic/benthic feeding 0-group flounder (Poiesz et al., 2019), some summer growth reduction in more benthic/epibenthic feeding 0-group plaice (Cardoso et al., 2016) and significant summer growth reduction in benthic feeding 0-group sole (this study).

The fact that different patterns in summer growth reduction occur between the 0-group flatfish species at Balgzand in relation to feeding guild, suggest that reduced benthic activity or increased food demand is indeed a likely explanation. However, this relationship only provides indirect support for the 'summer growth reduction' hypothesis. Direct evidence would require underwater observations of seasonal activity patterns of the benthic community. In addition to underwater observations, *in situ* valve gape measurements on bivalves might be an approach since it is related to variability in Chl-A (Ballesta-Artero et al., 2017).

An alternative explanation, at least in some areas, might be the development of algal mats which causes oxygen deficiencies for benthic and epibenthic organisms (Norkko & Bonsdorff, 1996; Tallquist, 2001; Auffrey et al., 2004). Flatfishes and other epibenthic predators will use the opportunity of the emerging benthic prey when algal mats develop, but will stagnate in growth when the accessibility of benthic prey decreases again as algal mats are degraded. However, because algal mats and oxygen deficiency were not observed in our study area, we don't consider this a likely explanation for the patterns we present.

Increased competition cannot be ruled out completely either (van der Veer et al., 2016). Intra-specific competition is not likely since, despite large differences in abundance between the three years of study, observed summer growth reduction in 0-group sole did not differ. With respect to interspecific competition, 0-group plaice, flounder and sole have partly different diets (de Vlas, 1979; Amara et al., 2001), so these species only compete partly for resources. Also the co-occurring flatfish species have different feeding tactics, where sole is an olfactory night feeder compared to plaice and flounder which rely more on sight when feeding. Besides flatfish species, other species such as the goby and crustaceans (*Crangon crangon*) also feed on benthic prey. The abundance of gobies and crustaceans in coastal areas, including Balgzand, increases after summer (Hamerlynck & Cattrijsse, 1994; Jung et al., 2017), which might result in a stronger interspecific competition between benthic feeding flatfish and other benthic feeding species. However, in gobies, this competition does not seem to result in reduced summer growth (Freitas et al., 2011). Schram et al. (2006) found that when densities of species increases, sole is affected more by other individuals of other species, as they are predominately chemosensory feeders (de Groot, 1971; Mackie & Mitchell, 1982). Observations on both juvenile and adult sole show that soles need about 1 to 10 seconds to either eat their food or decide to move away. When densities of individuals increase, this type of feeding behaviour is obstructed resulting in potential decrease of benthic food intake for sole.

To further progress an analysis of summer growth reduction there is a need for insights in to the seasonal patterns of epibenthic prey activity, and the impact of increased competition by both crustaceans and gobies for epibenthic prey.

Summer growth reduction alters our perceptions of the nursery function of coastal areas for juvenile flatfish through suggesting that these areas are not yearround optimal feeding grounds for all species as once assumed (van der Veer & Witte, 1993). The implications are that summer growth reduction can also be expected in other (nursery) areas of the Wadden Sea, in line with the findings of Freitas et al. (2012). So far, growth was thought to be determined by factors such as food availability, prey preference, prey size and prey searching and handling time (Gibson, 1994). Summer growth reduction only adds an extra new factor to take into account. Summer growth reduction underlines the importance of a good definition of how and over what time period growth it is estimated and compared.

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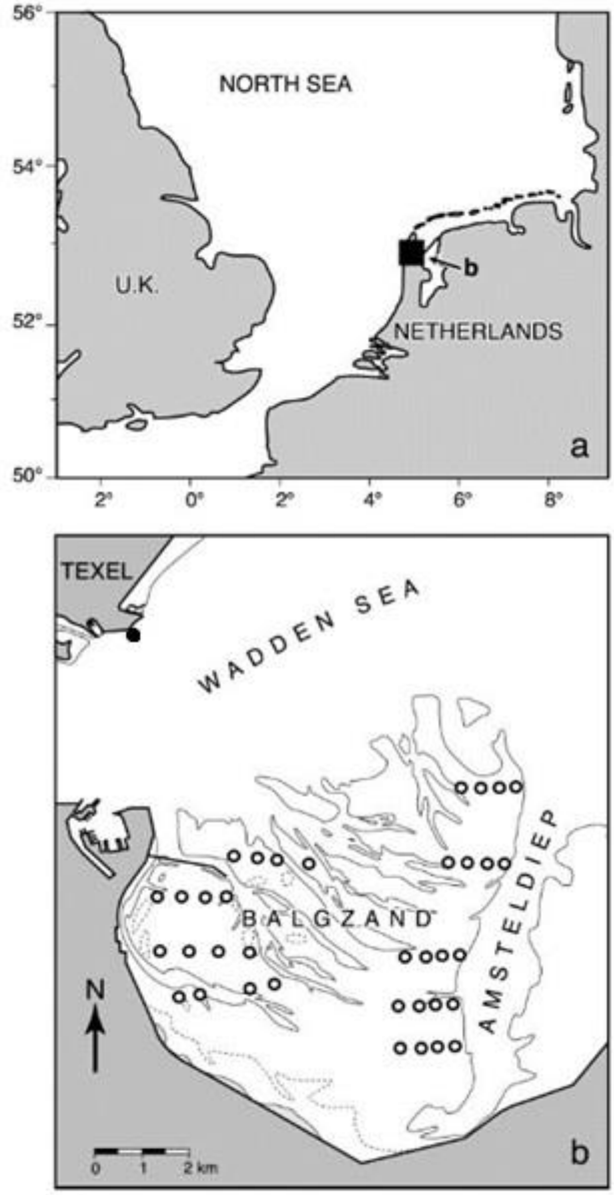


Fig. 1. The Balgzand intertidal area in the western Dutch Wadden Sea with the sampling stations (○). The full circle (●) shows the location of the Marsdiep jetty, where long-term temperature data is measured. Thin lines indicate the low water mark, thick lines indicate the high water mark (Cardoso et al., 2016).

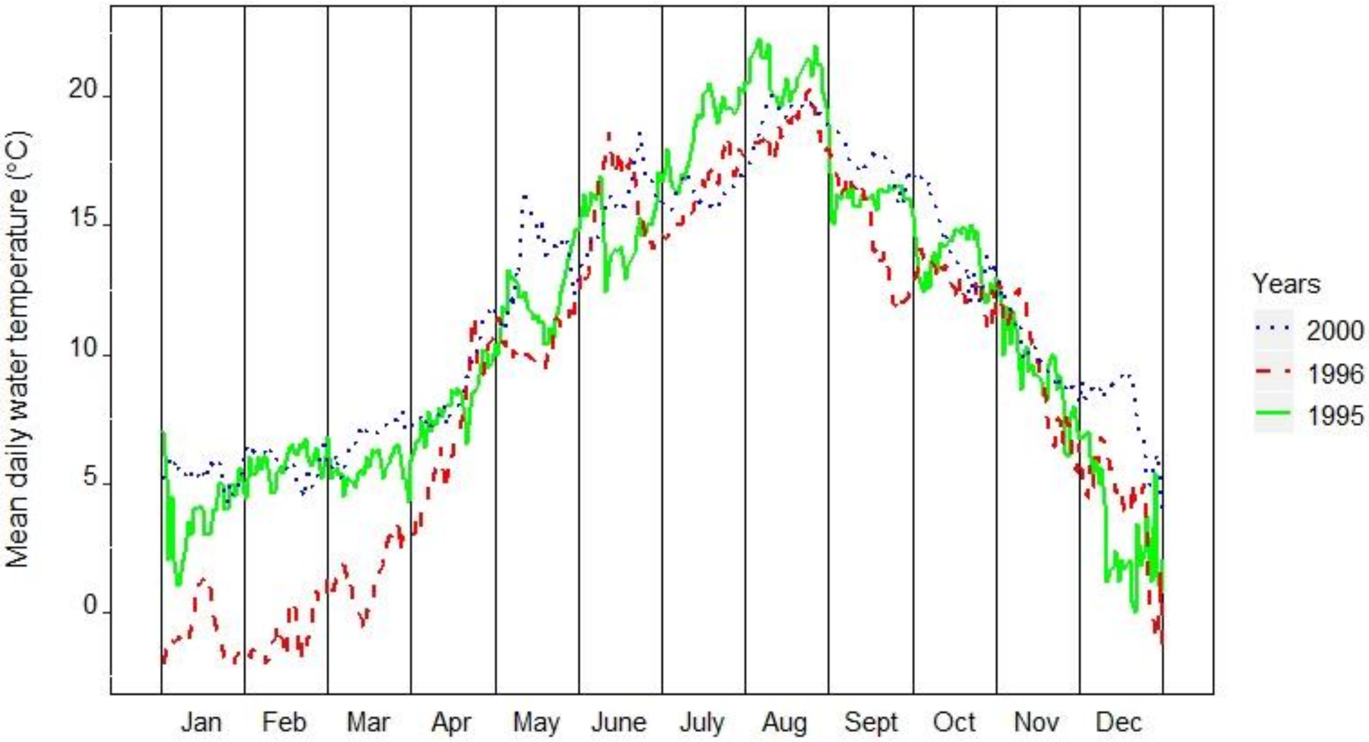


Fig. 2. Mean daily water temperature (°C) at the Marsdiep jetty from January to December in 1995, 1996 and 2000 (NIOZ unpublished data) (Poiesz et al., 2019).

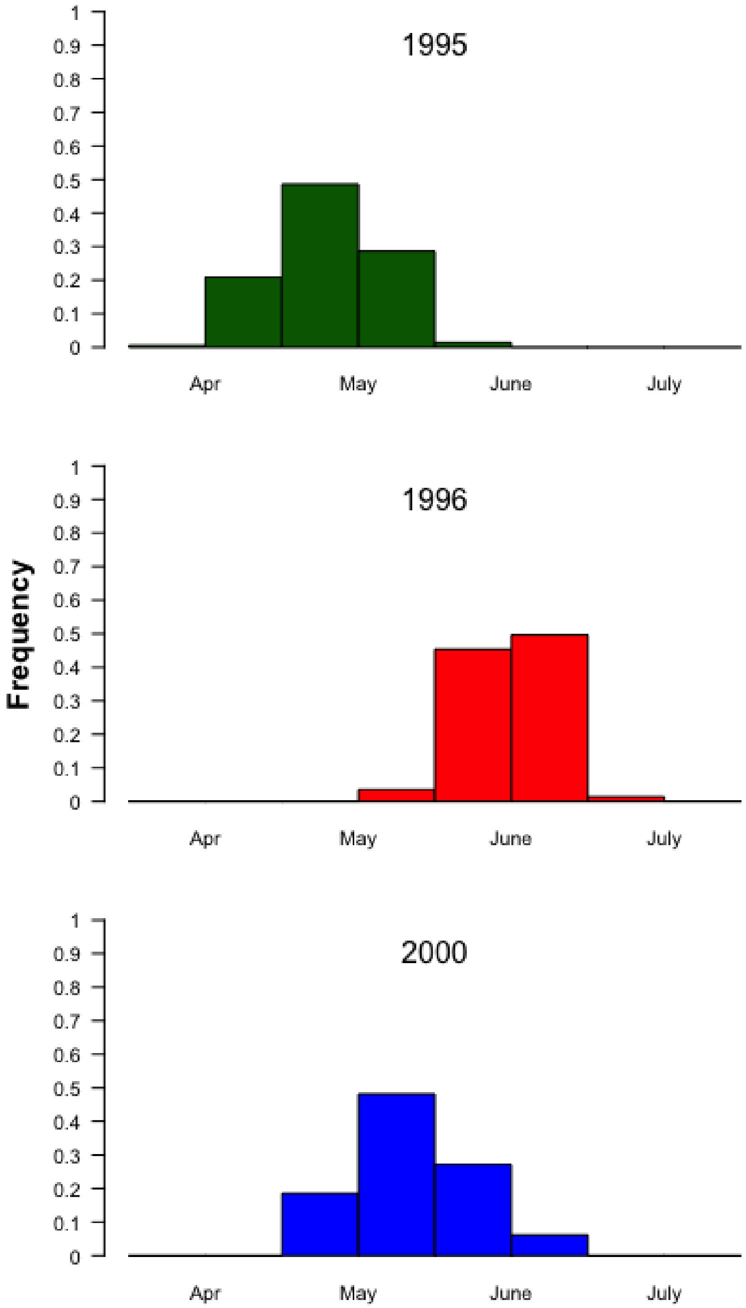


Fig. 3. Back-calculated settlement date per two-weeks periods of 0-group sole at the Balgzand in 1995, 1996 and 2000 based on otolith daily ring counts after settling.

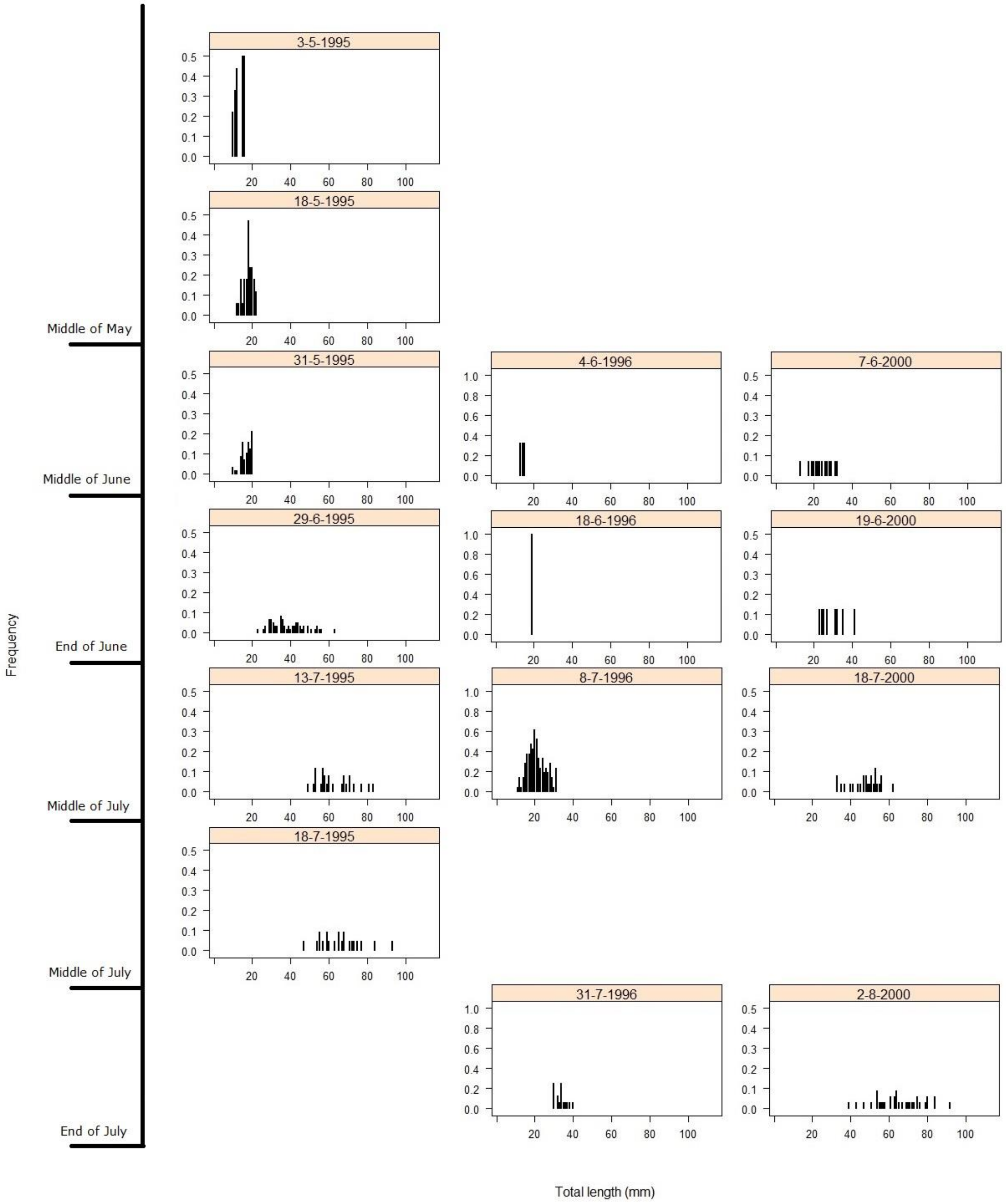


Fig. 4. Size frequency distributions (-) of 0-group sole at the Balgzand in 1995, 1996 and 2000. The different blocks for each year represents a period in time in which all three years could be compared. The lines represents the %-occurrence of a certain size (mm) of a certain date.

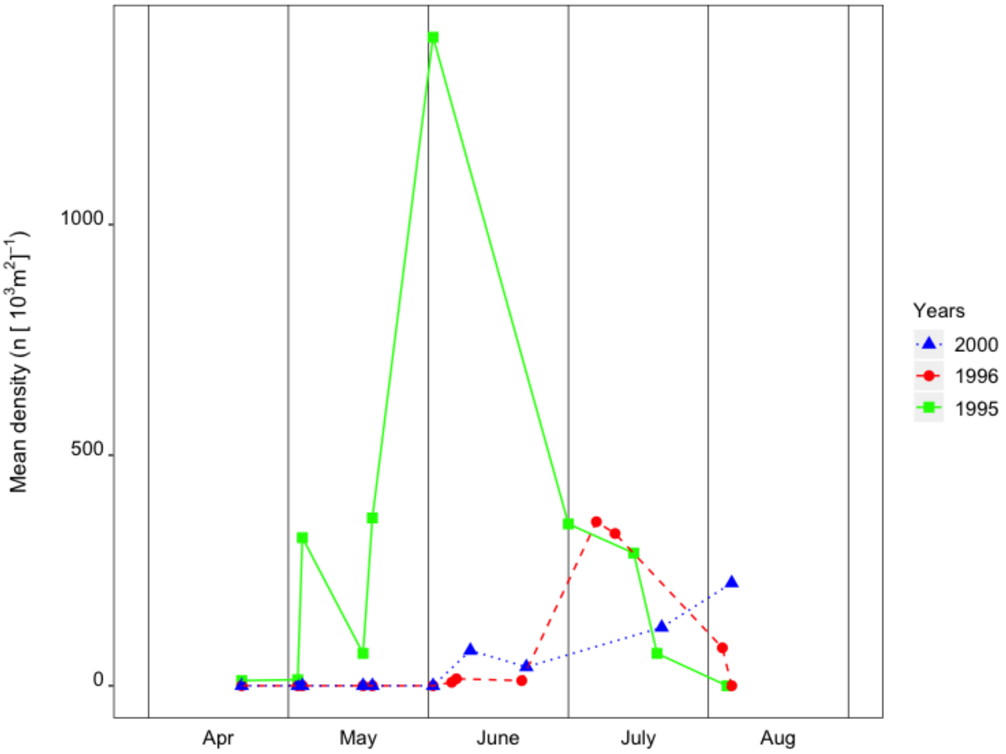


Fig. 5a. Seasonal pattern in mean density of 0-group sole (ind. [$10^3 m^2$]$^{-1}$) at Balgzand intertidal in 1995, 1996 and 2000).

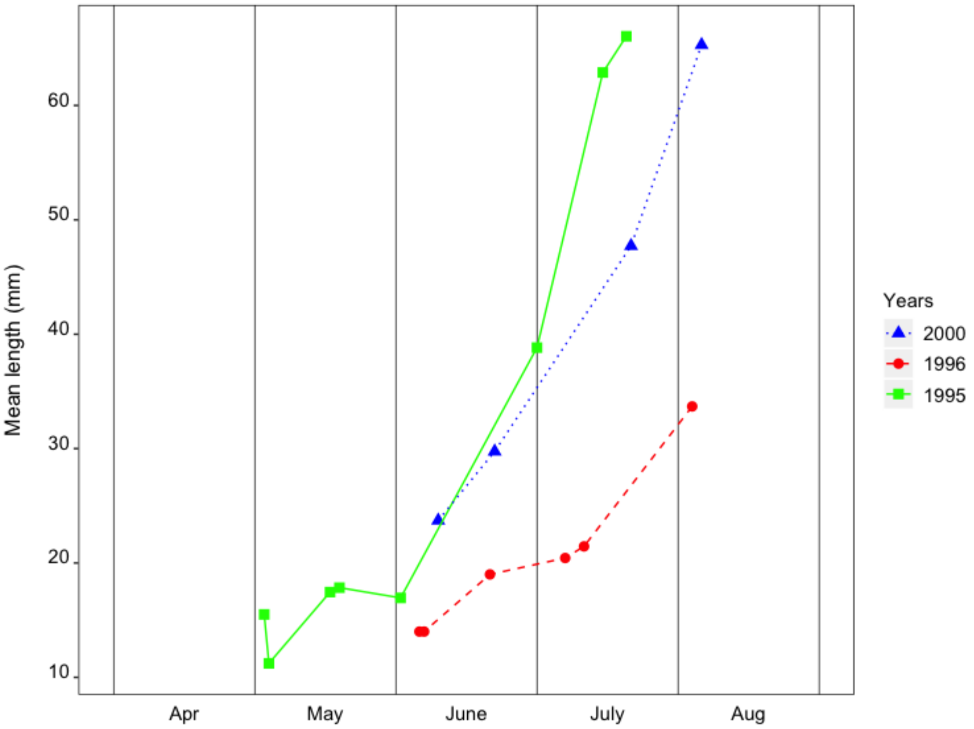
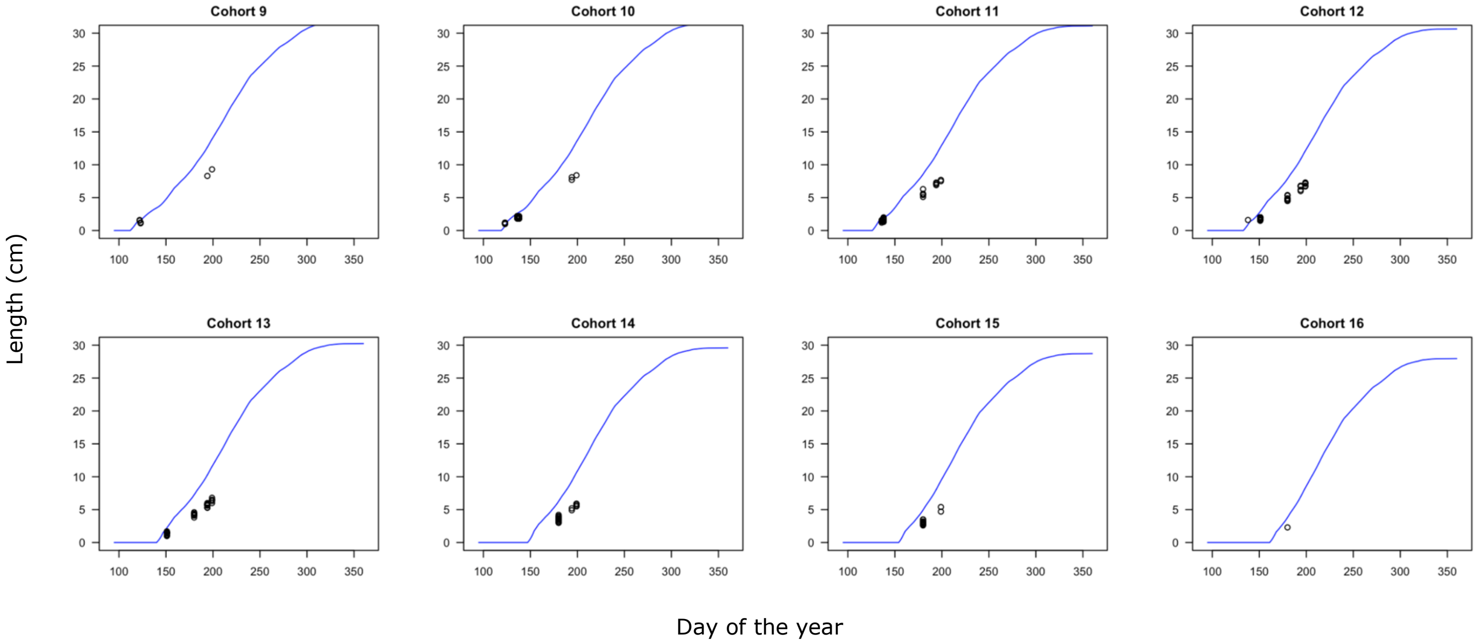
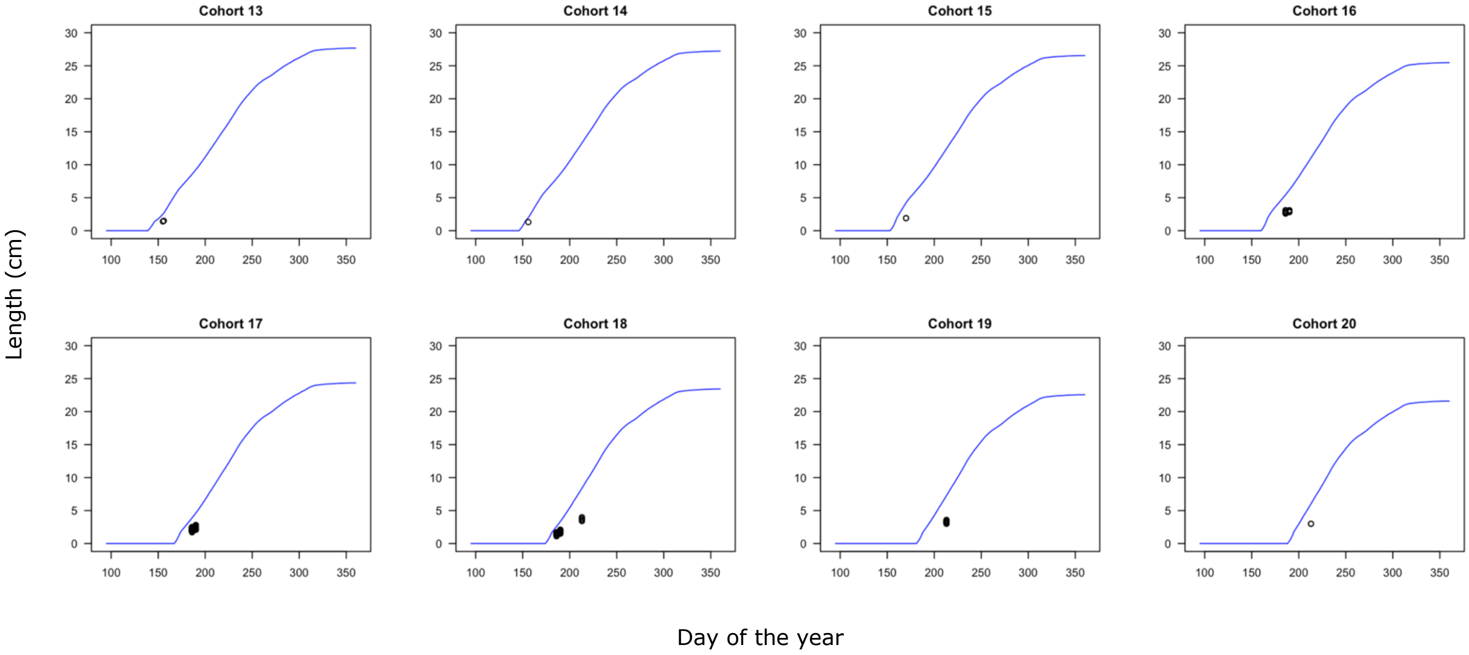


Fig. 5b. Seasonal pattern in mean length (mm) of 0-group sole at Balgzand intertidal in 1995, 1996 and 2000.

1995


Cohort 9
Cohort 10
Cohort 11
Cohort 12
Cohort 13
Cohort 14
Cohort 15
Cohort 16
Length (cm)
Day of the year
0
5
10
15
20
25
30
100
150
200
250
300
350

1996


Cohort 13
Cohort 14
Cohort 15
Cohort 16
Cohort 17
Cohort 18
Cohort 19
Cohort 20
Length (cm)
Day of the year
0
5
10
15
20
25
30
100
150
200
250
300
350

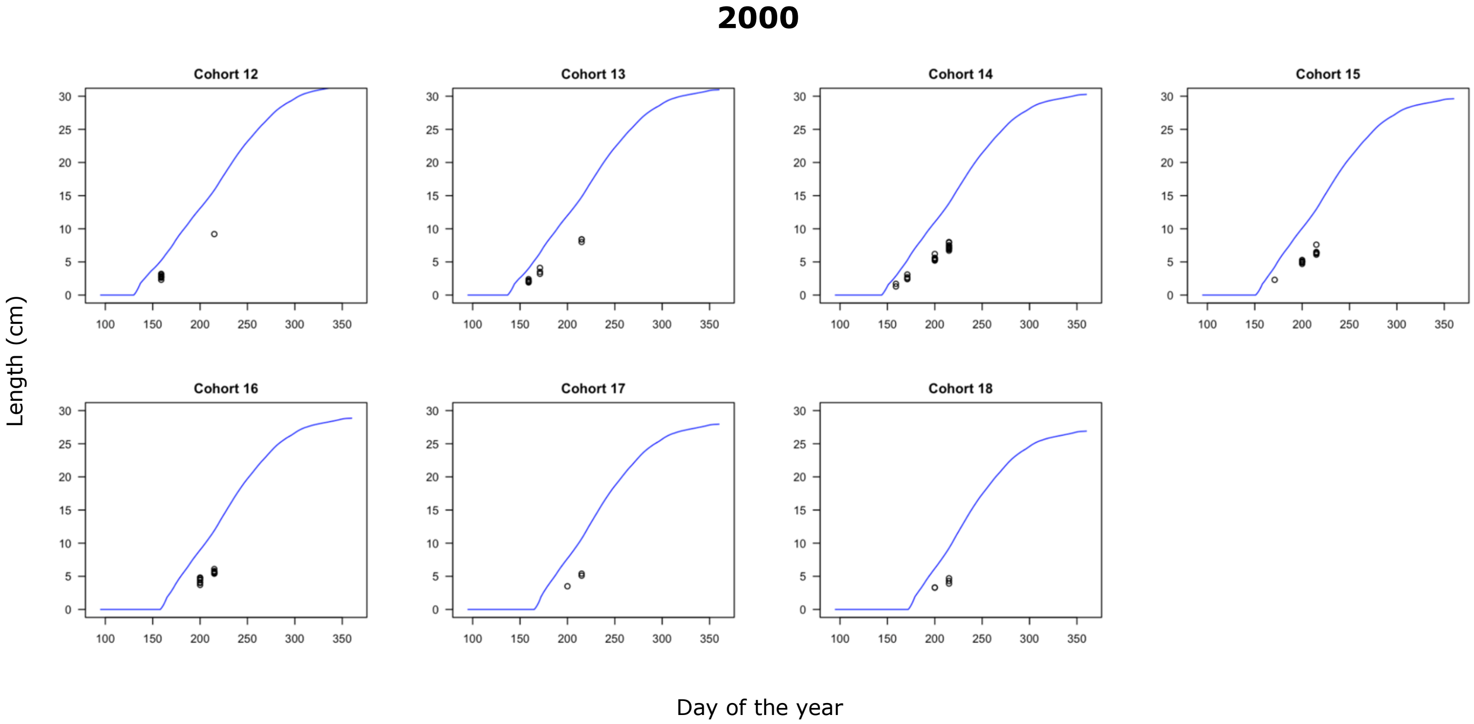


Fig. 6. Theoretical growth trajectories predicted by the DEB model (-) and field observations (o). DEB predictions were made assuming *ad libitum* food conditions and using prevailing water temperatures in 1995, 1996 and 2000. DEB prediction is the average for males and females. Each plot refers to a 1-week period of settlement.

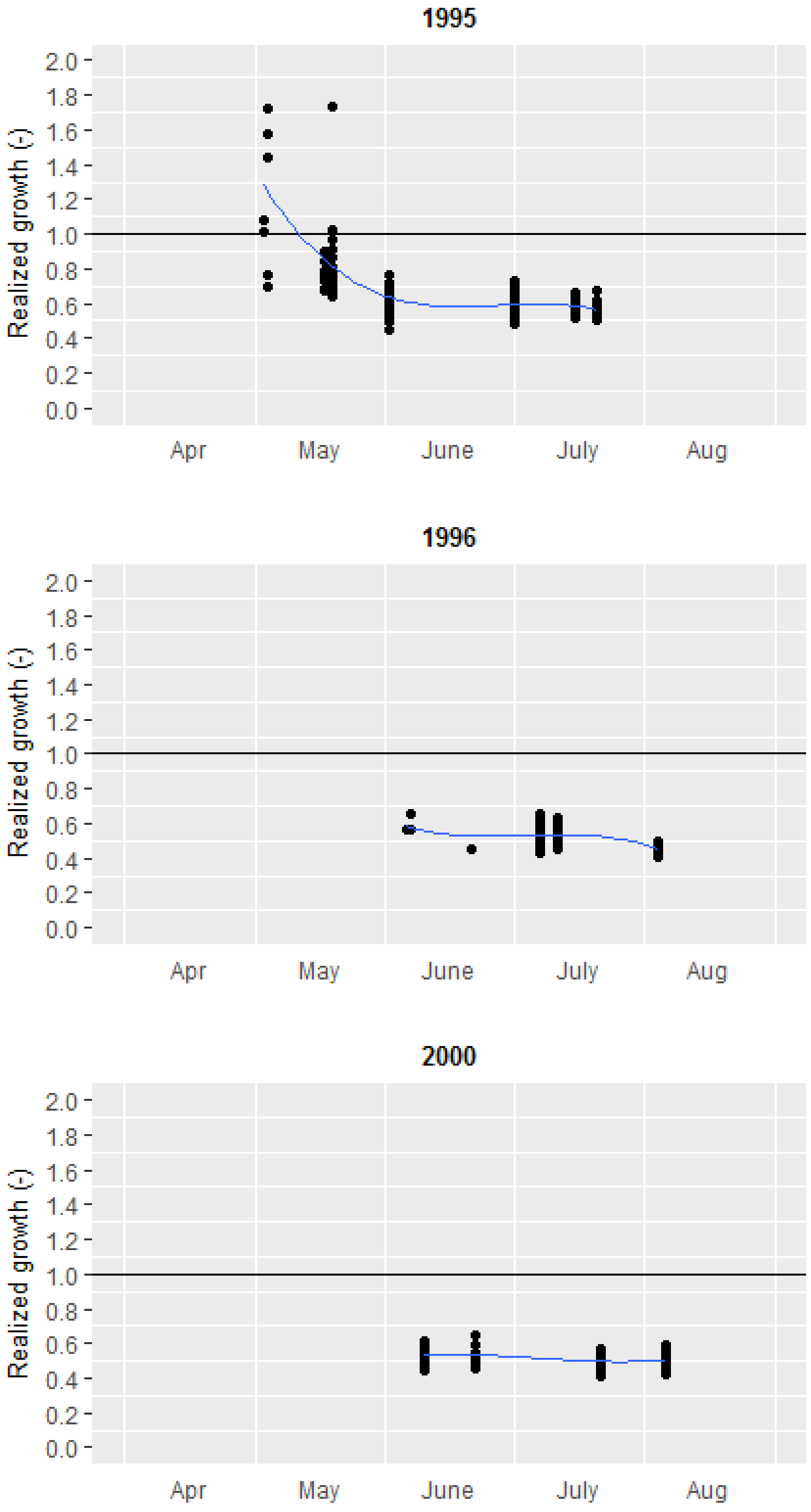


Fig. 7. Realized growth ratio (RG; ●) estimates for 0-group sole at Balgzand in 1995, 1996 and 2000. Values were averaged for females and males. Smoothing curves were added to capture patterns over time in each year (blue).

Supplementary information

Table S1. DEB model parameters and temperature dependence parameters for sole *Solea solea*. Whenever parameters differ between sexes, values for males are shown in parentheses.

Parameter symbol	Units	Interpretation	Value
T_1	K	Reference temperature	293+10
v	cm d^{-1}	Energy conductance	0.435
g	–	Energy investment ratio	3.684
k_M	d^{-1}	Maintenance rate coefficient	0.0097
L_w	cm	Maximum physical length	75
δ_M	–	Shape coefficient	0.192
T_A	K	Arrhenius temperature	6500
T_L	K	Lower boundary of tolerance range	283
T_H	K	Upper boundary of tolerance range	301
T_{AL}	K	Rate of decrease at lower boundary	35000
T_{AH}	K	Rate of decrease at upper boundary	50000

Rates are given at a reference temperature of T1 = 283 K (=10°C)

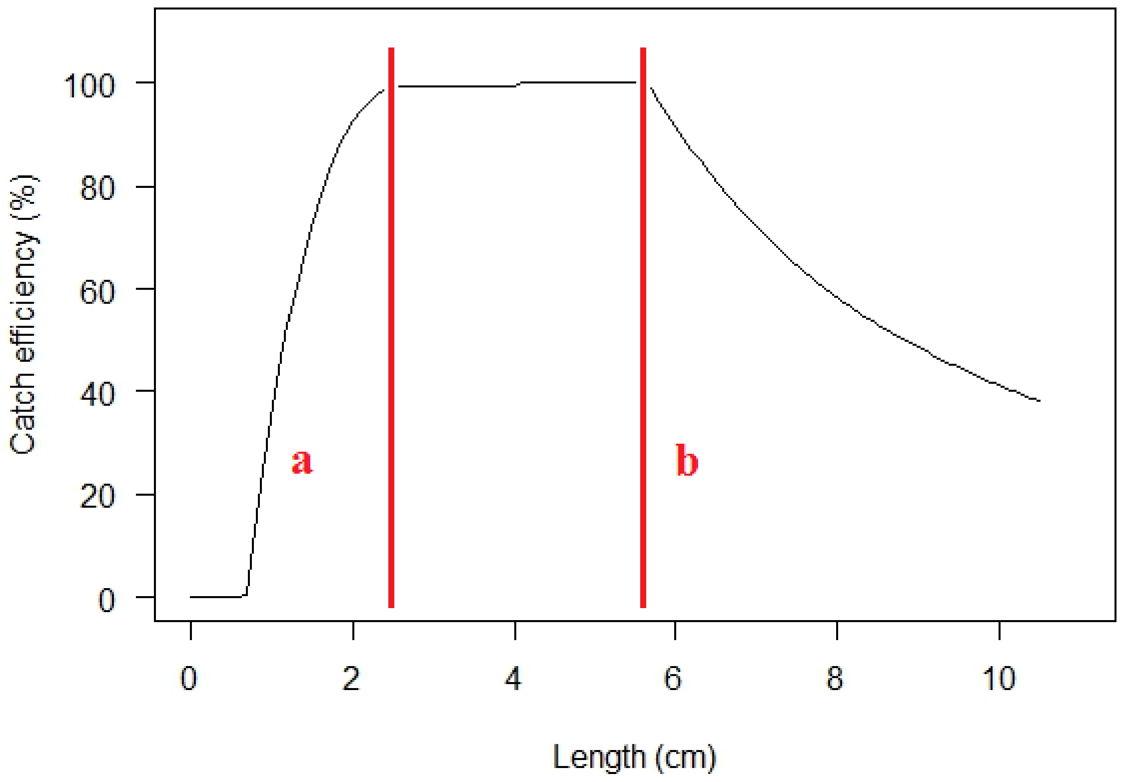


Fig. S1. Combined calculated size-selective mesh efficiency after Dapper (1978) (**a**) and catch efficiency after Kuipers (1975) (**b**) adapted for Sole *(Solea solea)*.