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Growth conditions of 0-group plaice *Pleuronectes platessa* in the western Wadden Sea as revealed by otolith microstructure analysis

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ABSTRACT

Growth studies based on population-based growth estimates are limited by the fact that they do not take into account differences in age/size structure within the population. To overcome these problems, otolith microstructure analysis is often used to estimate individual growth. Here, we analyse growth of 0-group plaice in the western Wadden Sea in two years: a year preceded by a mild winter (1995) and a year preceded by a severe winter (1996). Growth was analysed by combining information on individual growth based on otolith analysis with predictions of maximum growth (= under optimal food conditions) based on a Dynamic Energy Budget model. Otolith analysis revealed that settlement occurred earlier in 1995 than in 1996. In both years, one main cohort was found, followed by a group of late settlers. No differences in mean length-at-age were found between these groups. DEB modelling suggested that growth was not maximal during the whole growing season: realized growth (the fraction of maximum growth realized by 0-group plaice) declined in the summer, although this decline was relatively small. In addition, late settling individuals exhibited lower realized growth than individuals from the main cohort. This study confirms that growth conditions for 0-group plaice are not optimal and that a growth reduction occurs in summer, as suggested in previous studies.

Keywords: 0-group plaice, Dutch Wadden Sea, Dynamic Energy Budget model, Growth, Otolith, Settlement

1. Introduction

Since the late 1960s, shallow coastal areas have been found to be important nurseries for a variety of fish species (Zijlstra, 1972). Hence, the growth dynamics and carrying capacity of these areas have been a research focus for many decades. Crucial for these types of studies has been the development of quantitative sampling devices, especially the development of small demersal trawls (Kuipers et al., 1992). This resulted in a number of classical studies (1960s – 1970s) in European coastal areas focussing on demersal juvenile flatfishes, especially plaice *Pleuronectes platessa* (Edwards & Steele, 1968; Kuipers, 1977; Lockwood, 1980; Macer, 1967; Riley & Corlett, 1966). Advances in methodology led to an increasing knowledge on growth dynamics of this species in shallow coastal areas.

The first approaches to studying flatfish growth dynamics compared potential growth of small fish under experimental conditions with observed shifts in mean size of individuals within populations in the field and these studies led to the conclusion that optimal growth occurred in various European coastal areas (Bergman et al., 1988; van der Veer, 1986; Zijlstra et al., 1982). These findings were subsequently confirmed by a multi-scale spatial survey in the Dutch Wadden Sea and led to the formulation of the 'maximum growth/optimal food condition' hypothesis that proposed that field growth was only determined by prevailing water temperatures (van der Veer & Witte, 1993). However, these studies and conclusions were hampered by the fact that plaice growth estimates were based on shifts in mean population size and that the experimental growth model used was only applicable for small fish and did not take into account fish size (Fonds et al., 1992). Nevertheless, substantial progress has been made since then to try to solve these problems.

Growth studies based on otolith microstructure analysis (Karakiri et al., 1991) and on individual tagged fish (Nash et al., 1994), as well as studies on the effect of temperature on growth (Freitas et al., 2010; Teal et al., 2008), questioned the 'maximum growth/optimal food condition' hypothesis, at least in relation to the summer growth. However, these studies suffered from the same problems; i.e. they were based on growth models defined under a set of experimental conditions that limited their application to a wider size range.

Problems related to the application of growth models to wider size ranges were partially solved with the introduction of the Dynamic Energy Budget (DEB) model (Kooijman, 2000; van der Veer et al., 2001, 2009), a model that can predict maximum possible growth in relation to temperature and fish size. An analysis of population-level growth using this approach rejected the 'maximum growth/optimal food condition' hypothesis and suggested a reduction in growth during summer and autumn (van der Veer et al., 2010). This growth reduction was also observed at a latitudinal scale among various flatfish species (Fonseca et al., 2006; Freitas et al., 2012; Hurst and Abookire, 2006). A completely different approach, using an RNA-based growth index applied on a multi-spatial scale, led recently to the same conclusion: growth is variable among nursery areas and seems to be only maximum immediately after settlement, slowing down during summer (Ciotti et al., 2013a, 2013b). However, these studies are still based on the analysis of average length over time and may suffer from bias due to processes affecting size structure within the population.

Flatfish populations are a built-up of individuals that differ considerably in size since settlement takes place in a time frame of weeks to months, depending on the location and the species. During the first year of life, and especially early in life, size-selective processes might operate affecting the size distribution of the population and hence biasing perceived growth estimates. Size-selective predation may occur as several species of fish predate on small 0-group plaice (Ellis and Gibson, 1995; van der Veer et al., 1997 and references therein). In addition, also size-selective emigration may influence the observed size distribution as larger 0-group plaice tend to move out of the shallow grounds earlier (Geffen et al., 2011; Gibson et al., 1996). To overcome these problems, an analysis based on individual growth is necessary such as by analysing otolith microstructure in terms of daily rings. This approach has already been validated and applied to analyse individual growth in plaice (Al-Hossaini et al., 1989; Bolle et al., 2004; Geffen et al., 2011; Karakiri et al., 1989; Rijnsdorp et al., 1990; van der Veer et al., 2000; among others). Nevertheless, a study combining otolith analysis with DEB modelling, which would provide an unbiased growth analysis of 0-group plaice, has been lacking so far.

Therefore, in the present paper, we combine the analysis of individual growth based on otolith microstructure analysis with predictions of maximum growth based on the Dynamic Energy Budget model (Kooijman, 2000) for 0-group plaice in the western Wadden Sea. Since temperature is an important factor influencing growth in plaice (Al-Hossaini et al., 1989; Geffen et al., 2011; Gunnarsson et al. 2010; Modin and Pihl, 1994; Nash et al., 1994; van der Veer et al., 2000), growth of 0-group plaice was compared between two contrasting years with different temperature patterns (van der Veer et al., 2000): 1995, a year after a mild winter, and 1996 after a severe winter. In addition, intra-annual differences in individual growth were also analysed by following different settling cohorts.

2. Materials and Methods

2.1. Sampling

Juvenile 0-group plaice *Pleuronectes platessa* were sampled at the Balgzand, a large tidal flat area in the western Dutch Wadden Sea (Fig. 1). Flatfish were collected at frequent intervals (2 to 4 weeks) from February to August in 1995 and from March to August in 1996. Fishing was carried out on a grid of 36 stations distributed over the study area at a period of 3 h around high tide, since during this period the population is randomly distributed over the area (Kuipers, 1977). Nine transects each consisting of 4 stations of about 100 m in length were sampled during daytime with a 1.9 m beam trawl (1 ticker chain, net mesh size of 5 x 5 mm) towed by a rubber dinghy with a 25 HP outboard motor at a speed of approximately 35 $m.min^{-1}$. The location of the hauls was established by GPS, and the length of the hauls was assessed with a meter-wheel attached to the trawl. For more information see Zijlstra et al. (1982) and van der Veer (1986). Catches were transported to the laboratory and stored at -20°C for further analysis. Water temperature was measured during each sampling campaign and compared to a daily temperature series collected at the Marsdiep jetty, a fixed sampling station in the Texel inlet just off the southern coast of the island of Texel (van Aken, 2008; Figure 1).

2.2. Processing of samples

In the laboratory, samples were thawed and sorted within a few days of their capture. 0-group plaice were measured to the nearest mm total length and fixed in 96% ethanol. For each sampling date of each year, 16 or 17 individuals of different sizes were selected (in total 104 fishes in 1995 and 114 in 1996, mostly ≥19 mm). From each fish, the sagittal otolith pair was removed and, whenever possible, the left otolith was selected, cleaned and air-dried. In some small otoliths, counting of daily annuli could be done directly; however, most otoliths had to be polished prior to reading. For this, a drop of a liquid thermoplastic adhesive (Crystalbond, Buehler, USA) was placed on the centre of a microscope slide and the otolith was set inside the drop, with the sulcus facing up. Once the adhesive had hardened, grinding was performed under successively finer grit (P1200, P2500 and P4000 silicon carbide abrasive papers; Buehler) and wet-polished (MasterPrep, Buehler) until the sagittal midplane was almost reached. The otolith was then turned so that the sulcus and ground surface were facing downward, and the grinding and polishing steps were repeated on the unground side.

Daily increments (rings) were analysed with a light microscope (Zeiss) coupled to a digital camera (AxioCam ICc3, Zeiss, Germany). The number of increments from the position of the first accessory growth centre, which was assumed to represent settlement (following Geffen et al., 2011), to the otolith edge was counted. Each otolith was counted by two observers (if possible along different radial lines). If the difference between the two counts differed more than 10%, the otolith was read again. If, after a second round of counting, this difference was again more than 10%, the otolith was excluded from further analysis. For counts that were within 10% of one another, the mean was calculated and used as the individual's age, in days post-settlement. Settlement date per individual fish was estimated by subtracting the number of increments after metamorphosis from the sampling date. In addition to the otoliths analysed in this study, previously analysed ones (mostly from fish <20 mm; 1995: 144 otoliths; 1996: 148 otoliths) were also included (van der Veer et al., 2000; van der Veer & Witte, unpublished).

2.3. Growth analysis

A Dynamic Energy Budget (DEB) model (Kooijman, 2010) was used to determine the theoretical maximum growth trajectory of settling fish for comparison with observed lengths. A thorough description of the standard DEB model and relevant equations is given in van der Veer et al. (2010; Eqs. 1-3) and species-specific model parameter values for plaice were taken from van der Veer et al. (2010, 2009, 2001) and Freitas et al. (2010) (Supplementary information Table S1). The forcing variables of the DEB model are food density and water temperature whereby the former is linked to assimilated energy via the scaled functional response (*f*), a dimensionless parameter varying between 0 (representing starvation) and 1 (*ad libitum* food). In the DEB model, food intake is not directly related to growth but "buffered" via a storage compartment. Even under fluctuating food conditions (for instance tidally related), growth will continue as long as there is still energy stored in the reserves. In a rather constant environment (see Kooijman, 2010), the model equations describing the dynamics of the state variables simplify greatly and in case of growth, become mathematically equivalent to the Von Bertalanffy growth model (Kooijman, 2010). Previous work on various flatfish species in different nurseries has confirmed robustness of the DEB parameters (Freitas et al., 2012).

Mean daily temperature data were derived from measurements (every 30 min.) at the Marsdiep jetty (van Aken, 2008) in 1995 and 1996. Simulations of length over time followed individuals from their date of settlement until the end of the year using an initial value of length (and thus structural volume) of 13 mm for 1995 and 15 mm for 1996, based on the modal length of settling individuals observed in each year (Supplementary information Figure S1). Over the period of settlement, various growth curves (in terms of length) were constructed with an interval of 2 weeks (in order to have enough data points to compare with simulations). In each simulation, individuals are assumed to experience constant and maximum food conditions (i.e. f=1) and, hence, resulting growth trajectories correspond to a maximum growth expected at the prevailing water temperatures.

Growth trajectories were obtained for males and females separately because they differ in growth dynamics (van der Veer et al., 2009). For comparison with field growth studies in which sexes were not distinguished, a mean trajectory was calculated by averaging DEB-predicted lengths for females and males, assuming a 1:1 field sex ratio. For each individual plaice, the ratio between observed length at day of catch and DEB-predicted maximum length at the same day (hereafter referred to as realized growth, RG) was calculated and, subsequently plotted against catch date and fish size.

2.4. Statistical analysis

Statistical analyses were carried out in the R package version 3.1.0 programming environment (R Core Team, 2014). Water temperatures at the sampling site (Balgzand) were compared with a long-term temperature series of a nearby area (Marsdiep) using analysis of covariance (ANCOVA), with the lm function in R. Water temperatures at the start of the settlement period were compared between years in the same way. Otolith daily increment counts were compared between observers (including otoliths analysed in previous studies) using Paired Student's t-test. To identify the number of settling cohorts, individuals were grouped into two-week age classes and settlement frequency distributions were analysed, whereby the number of modes was visually identified. 0-group growth was compared among settling cohorts and between years using ANCOVA. Comparison between observed length in the field and maximum length based on DEB model prediction was conducted using analysis of variance (ANOVA). To aid visualizing patterns in RG over time, smoothing curves were added using the Loess function.

Model validation was done following Zuur et al. (2009). For all tests, model assumptions regarding homogeneity, normality, independence, and absence of influential observations were met.

3. Results

3.1. Water temperature

No significant differences in temperatures were found between Balgzand and Marsdiep in 1995 and 1996 (ANCOVA, $p>0.05$) and therefore the daily temperature series from the Marsdiep was used in further analysis. Temperatures during the sampling period increased from April to August in 1995 and from February to August in 1996 (Fig. 2). Mean monthly temperatures in February and March were much lower in 1996 than in 1995 (respectively, 5.8 and 5.6 °C in 1995, and -0.9 and 1.5 °C in 1996). Daily temperatures in February, March and April were significantly different between years (ANCOVA, for all months $p<0.05$).

3.2. Field growth

During the sampling period, larger individuals were found in 1995 than in 1996, which was especially evident after mid-April (Fig. 3). The smallest plaice found in both years were 9 mm total length. In August, 0-group plaice reached a maximum size of 112 mm in 1995 and 98 mm in 1996. In addition, almost all individuals in 1995 were above 60 mm in August whereas in 1996 about 40% of the population was under 60 mm.

Otolith daily increment counts did not differ between observers in this study and in previous studies (Student's t-test, $p>0.05$). Back-calculation of settlement date revealed that settlement occurred earlier in 1995 than in 1996 (Fig. 4). Settlement started in 1995 in mid-February (17 February) while in 1996 settlement started only around mid-March (13 March). The peak in settlement date was also later in 1996 than in 1995, around the 20 March in 1995 and two weeks later, around the 5 April, in 1996. Two cohorts were identified in both years: one main cohort followed by a group of later settlers, which settled in low numbers over a long time period (Fig. 4). In 1995, the main cohort was composed by fish settling between mid-February and mid-April while in 1996 the main cohort settled about 1 month later, between mid-March and the third week of April.

The relationship between age after metamorphosis and fish length suggested a linear relationship (Fig. 5 top panel). During a short period after metamorphosis, no growth is observed. This pattern may be a reflection of the difference in size of metamorphosed individuals (9 – 15 mm). For both years, growth rates between the main cohort and late settlers were not significantly different, as revealed by the non-significance of the interaction term (ANCOVA, $p>0.05$; Fig. 5a and 5c). In 1995, however, late settlers showed in general higher size-at-age values when compared to the main cohort (significant difference in intercept between groups, ANCOVA, $p<0.05$). In relation to sampling date, no differences in growth were found between cohorts in 1995 (Fig. 5b; ANCOVA, $p>0.05$). In 1996, significant differences were found in growth over the course of the year (interaction term significant, ANCOVA, $p<0.001$), with late settlers showing slower growth (Fig. 5d). Nevertheless, it must be kept in mind that the number of observations (otolith readings) from the main cohort in June/July was low (12 from the main cohort vs. 37 from the late settlers), and this difference in growth between groups may not be realistic. Overall, growth was significantly faster in 1995 than in 1996 (ANCOVA, $p<0.001$; not shown).

3.3. Growth

In general, observed length of different groups of settling fish was within the maximum-predicted values for female and male plaice (Fig. 6). Deviations from DEB-predicted maximum length trajectories were found for individuals settling from early and mid-May onwards in 1995 and 1996, respectively. Overall, there was a good fit between observed and predicted length in both years (ANOVA; for both years $p<0.001$; Supplementary Fig. S2). Deviations from DEB-predicted trajectories were significantly larger in 1996 than in 1995 (ANCOVA, $p<0.001$).

Temporal reductions in growth were investigated by plotting realized growth (RG) over time for each year (Fig. 7). Despite a large variation, average RG showed a small decline over the year, more evident in 1996. In both years, the main cohort showed larger RG values (close to 1.0 or slightly higher) compared to late settlers (0.9 and 0.8 in 1995 and 1996, respectively). RG increased with plaice size (Fig. 8) and the smaller the fish the steeper the relationship was. Overall, there was no clear variation in RG with size. This suggests that growth reduction occurs at any fish length.

4. Discussion

4.1. Field growth

An exceptional strong year-class of plaice was observed in 1996 after a severe winter (van der Veer et al., 2000) with much higher densities than in 1995, when a week year-class was observed. Peak abundances of just settled individuals occurred about 2 weeks later in 1996 than in 1995. This delay of larval immigration was mostly caused by a longer larval development period due to exposure to low water temperatures during drift (van der Veer & Witte, 1999). Otolith analysis revealed that settlement occurred earlier in 1995 than in 1996, in respectively mid-February and mid-March. Newly metamorphosed plaice may spend some time in the water column (Geffen et al., 2011); therefore, the time of metamorphosis and settlement may not exactly match. Nevertheless, the settlement patterns described here, resulting from back-calculated settlement dates, do match the patterns based on densities of immigrating individuals (van der Veer et al., 2000).

In February/March, a difference in size range of settled larvae was observed between years, with larvae being slightly larger in 1995 than in 1996. In the beginning of the growing season, there seems to be a time lag of about 1 month in growth between years. This matches approximately the time difference in the beginning of settlement (1995 in mid-February and 1996 in mid-March). This difference was maintained throughout the summer suggesting that the observed differences in size are mainly due to differences in settlement time between years. Nevertheless, growth rates estimated based on otolith analysis were significantly higher in 1995 than in 1996, suggesting that other factors may also play a role. Temperature dependent growth in plaice has been confirmed in several studies (Al-Hossaini et al., 1989; Geffen et al., 2011; Gunnarsson et al. 2010; Modin and Pihl, 1994; Nash et al., 1994; van der Veer et al., 2000). In the western Wadden Sea, temperatures between February and April were significantly lower in 1996 than in 1995, with February and March 1996 being, respectively, 6.7 and 4.1°C lower than in 1995. This difference in temperature at the beginning of the growing period may have been responsible for differences in growth rates between years.

In this study, otolith microstructure analysis was not restricted to settling larvae (small 0-group plaice ≤15 mm) as in previous studies in the area (van der Veer et al., 2000) but comprised the whole size range. This allowed investigating the presence of sub-cohorts due to pulses in settlement, as has been observed in many areas (Geffen et al., 2011 and references therein). Modelling studies have indicated that fish using the Balgzand as nursery ground might, might come from various spawning grounds (Bolle et al., 2009; Hufnagl et al., 2013; Tiessen et al., 2014; van der Veer et al., 1998). However, both in 1995 and in 1996, only one cohort has been observed in the western Wadden Sea, followed by a group of late settlers. Hovenkamp (1991) has observed different cohorts in the area in several years and suggested that, in these years, cohorts originated from different spawning grounds, which could be related to interannual differences in water temperature. However, in 1988 one main cohort has been reported for the same area as well, although early settlers were also observed (Karakiri et al., 1991). Despite the differences in winter water temperature in 1995 and 1996, larvae settled in the western Wadden Sea in these years appear to have originated from the same spawning grounds, in the Southern Bight (van der Veer & Witte, 1999).

No differences in length-at age were found between main cohort and late settlers in both years. In other areas, late settlers were found to be smaller at age than earlier sub-cohorts (Al-Hossaini et al., 1989; Geffen et al., 2011; Modin and Pihl, 1994). In these studies, earlier sub-cohorts showed higher growth rates, which were attributed to higher temperatures. Temperatures in the western

Wadden Sea increased steeply from April onwards and, therefore, late settlers were exposed to higher temperatures, which may have favoured growth. Hovenkamp (1991) reported that late settling plaice could grow up to 3 times as fast as earlier settlers. Mean length per sampling date was, in 1995, smaller for late settlers due to the delayed settlement and start of growth. However, similarly to length-at-age patterns, growth rates along the year did not differ between groups. In 1996, although no difference in length-at-age was found between groups, growth rates along the year appear to differ between main cohort and late settlers. However, this could be an artefact caused by the low number of individuals from the main cohort found from mid-June onwards. In both years, no individuals belonging to the main cohort were found from 15th July onwards, possibly due to emigration of larger juveniles to deeper areas. This is in accordance with the depth distribution patterns of 0-group plaice presently observed in the western Wadden Sea, with large movements towards deeper waters already by mid-summer (Freitas et al., 2015).

4.2. Growth conditions

Challenging the previous assumptions on constant and maximum growth conditions throughout the nursery residence (e.g. van der Veer, 1986; Zijlstra et al., 1982), studies over the last years have revealed a relatively consistent and widespread pattern of reduced growth in the summer along the distributional range of plaice (Ciotti et al., 2013b; Freitas et al., 2012; Geffen et al., 2011; van der Veer et al., 2010) as well as in other flatfish species (Fonseca et al., 2006; Freitas et al., 2012; Hurst and Abookire, 2006). Declines in growth of 0-group plaice were found in this study but, in contrast to previous studies at the Balgzand (van der Veer et al., 2010), reductions were not as strong. Differences may reside in the method used to estimate growth. This study used otolith increment analysis whereas the other used changes in size distribution of the population over time. Otolith microstructure analysis is considered to provide more robust measures as it avoids problems associated with size-selective processes (Ciotti et al., 2014), especially the emigration of larger individuals by the end of summer (Kuipers, 1977) which may result in an underestimation of perceived growth rates when growth estimates are based on population length increments over time. Although the growth reduction is relatively small, it occurs at about the same time in both years irrespectively of fish size.

The comparison of observed field growth with DEB model predictions, suggested variability in realized growth patterns among groups of settling plaice within each year. Late settling individuals exhibited lower growth than maximum predicted for prevailing temperatures when compared to individuals from the main cohort. Despite settling at a time of higher water temperatures, which could have favoured growth, processes resulting in food limitation may have acted, hampering a positive effect on growth. One cannot exclude that different sub-cohorts differ in intrinsic growth rates, for instance by differences in sex ratio (van der Veer et al., 2015) or in ontogenetic background (Kinne, 1962; van der Veer et al., 2000, in press), leading to differences in growth performance. Fox et al. (2014) compared growth rates of 0-group plaice from two nurseries using a common-garden design and concluded that systematic differences in size were not driven by differences in intrinsic growth potential but rather with nursery ground quality.

This study confirms previous results of reduction in growth of juvenile flatfish in summer (Ciotti et al., 2013a, 2013b; Freitas et al., 2012; van der Veer et al., 2010). Nevertheless, this reduction was less strong than that found by analysing shifts in mean population size (van der Veer et al., 2010; Freitas et al., 2012). Although this might suggest some impact of size-selective emigration processes, it falsifies size-selective emigration as the underlying mechanism. Although the underlying mechanisms remain elusive, the fact that this reduction is not related to an internal factor (fish size) suggests the effect of an external factor, such as the recent suggestion of a reduced accessibility of benthos due to a lower activity after the spring phytoplankton bloom (van der Veer et al., in press). However, more research is required to understand the mechanisms behind the observed summer growth reduction.

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Captions to Figures

Figure 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.

Figure 2. Mean daily water temperature (°C) at the Marsdiep jetty from February to September in 1995 and 1996 (NIOZ unpublished data; van Aken, 2008).

Figure 3. Size frequency distributions (-) of 0-group plaice at the Balgzand in 1995 and 1996.

Figure 4. Back-calculated settlement data of 0-group plaice at the Balgzand in 1995 and 1996, based on otolith daily ring counts after settling.

Figure 5. Length-at-age after metamorphosis of 0-group plaice at the Balgzand in 1995 and 1996 (top panels); and mean length of 0-group plaice per sampling date in 1995 and 1996. Open circles (○) indicate individuals belonging to the main cohort and full circles (●) indicate late settlers.

Figure 6. Theoretical growth trajectories predicted by a DEB model (—) and field observations (●). DEB predictions were made assuming *ad libitum* food conditions and using prevailing water temperatures in 1995 and 1996. Each plot refers to a 2-week period of settlement.

Figure 7. Realized growth ratio (RG) estimates for 0-group plaice at Balgzand in 1995 and 1996. Values were averaged for females and males. Open circles (○) indicate estimates for individuals belonging to the main cohort and full circles (●) indicate late settlers. Average RG at each sampling date for each group of settlers are also indicated (red circles for main cohort and blue circles for late settlers). Smoothing curves were also added to capture patterns over time in each year.

Figure 8. Relationship between realized growth ratio (RG) estimates and plaice length at Balgzand in 1995 and 1996. Values of RG were averaged for females

and males. Different symbols correspond to fish caught in different sampling dates [1995: 3 April (●); 2 May (○); 16 May (▼); 31 May (△); 15 June (■); 13 July (□); 14 August (◆); 1996: 9 April (●); 6 May (○); 20 May (▼); 3 June (△); 17 June (■); 4 July (□); 31 July (◆); 28 August (◇)].

Figures

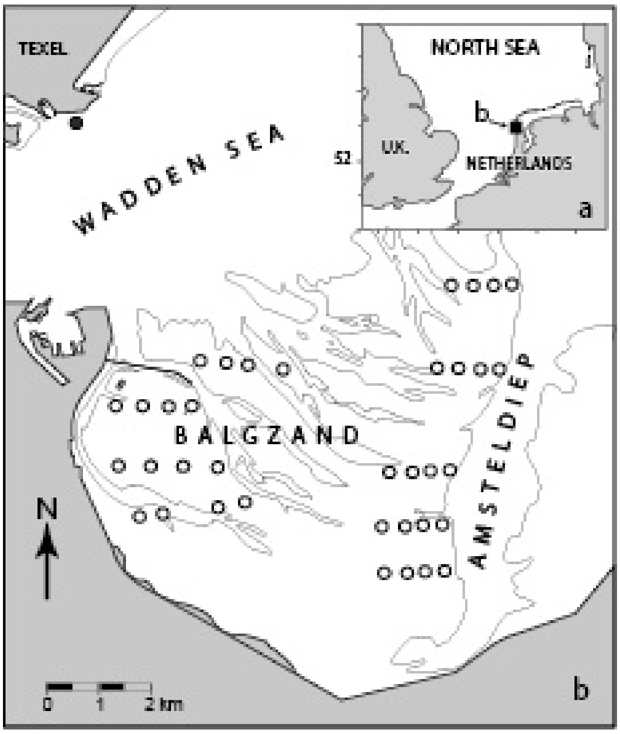

Figure 1

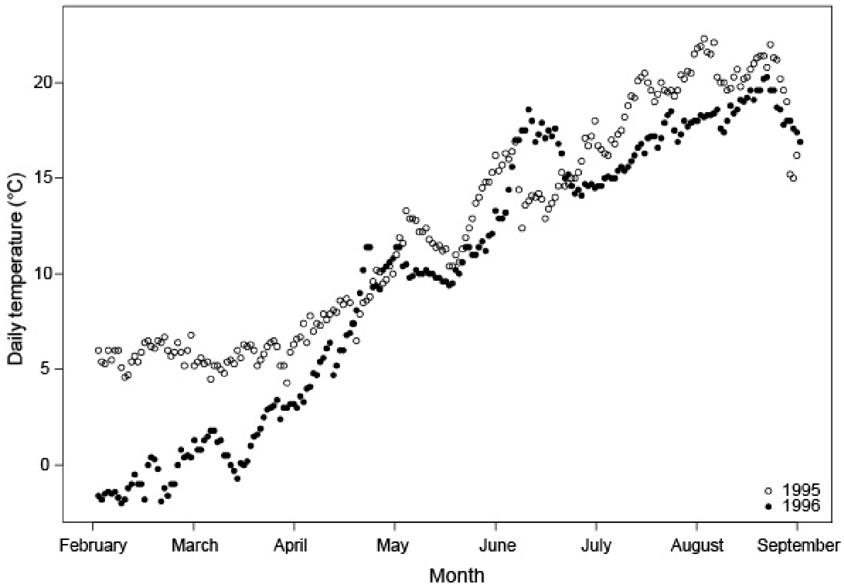

Figure 2

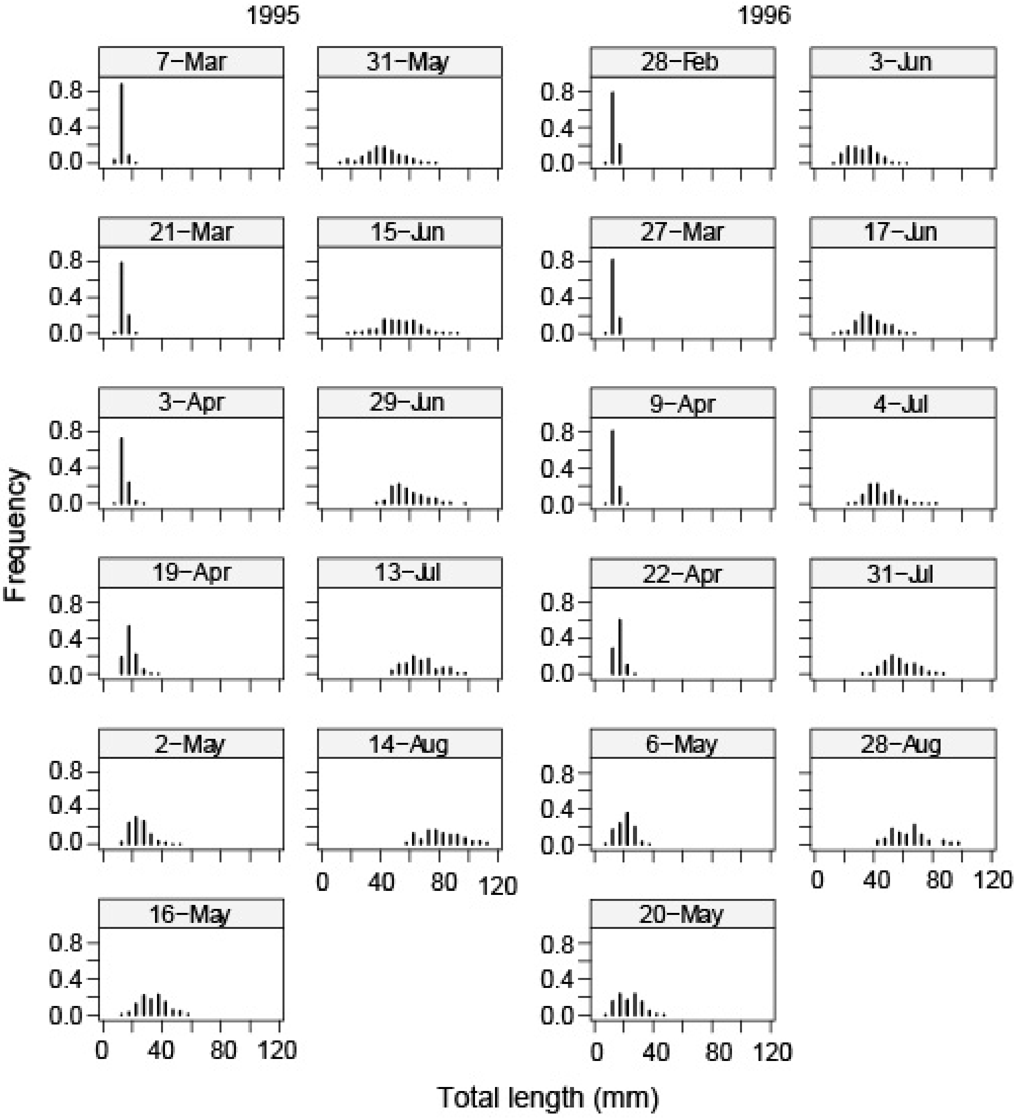
1995
1996
7-Mar
31-May
28-Feb
3-Jun
21-Mar
15-Jun
27-Mar
17-Jun
3-Apr
29-Jun
9-Apr
4-Jul
19-Apr
13-Jul
22-Apr
31-Jul
2-May
14-Aug
6-May
28-Aug
16-May
20-May
Frequency
0.8
0.4
0.0
0
40
80
120
Total length (mm)

Figure 3

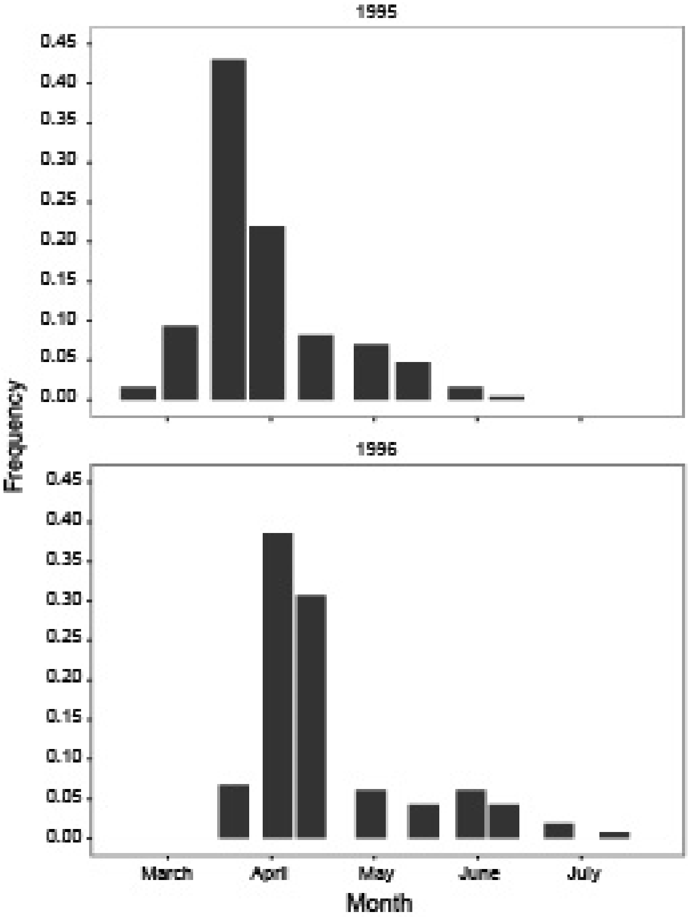
1995
1996
Frequency
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
March
April
May
June
July
Month

Figure 4

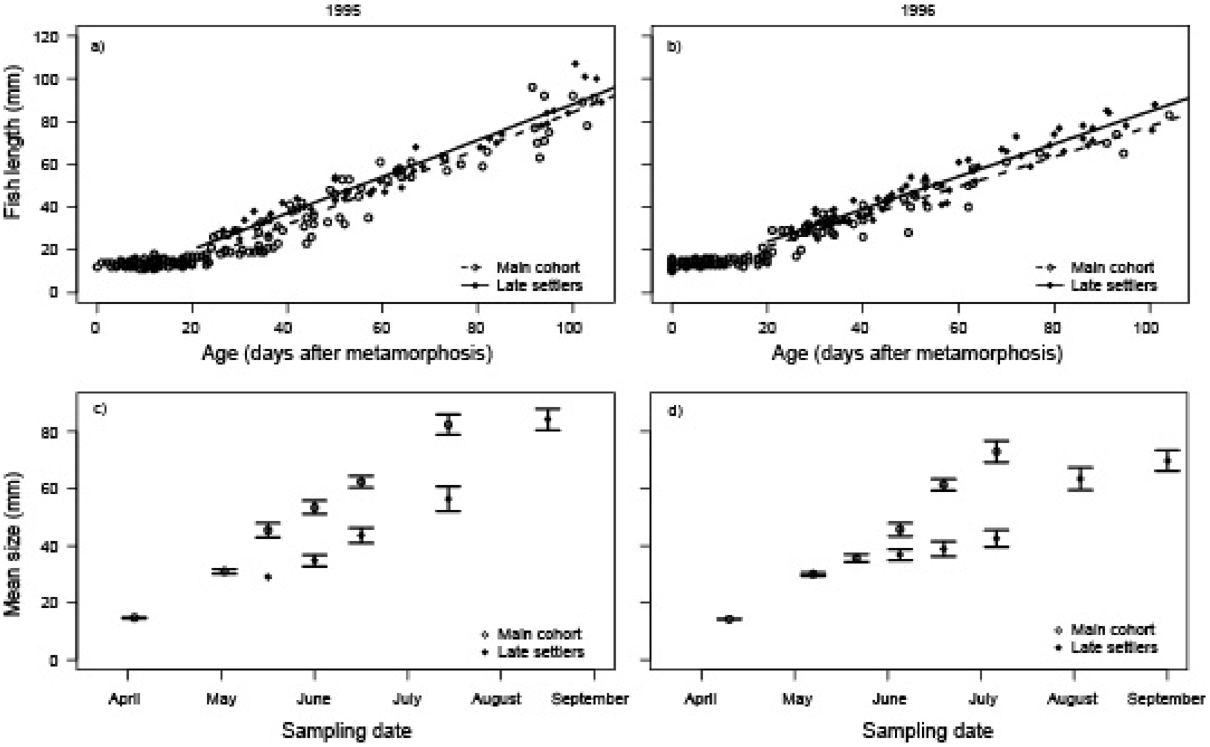
1995
1996
a)
b)
c)
d)
Fish length (mm)
0
20
40
60
80
100
120
Age (days after metamorphosis)
Main cohort
Late settlers
Mean size (mm)
April
May
June
July
August
September
Sampling date

Figure 5

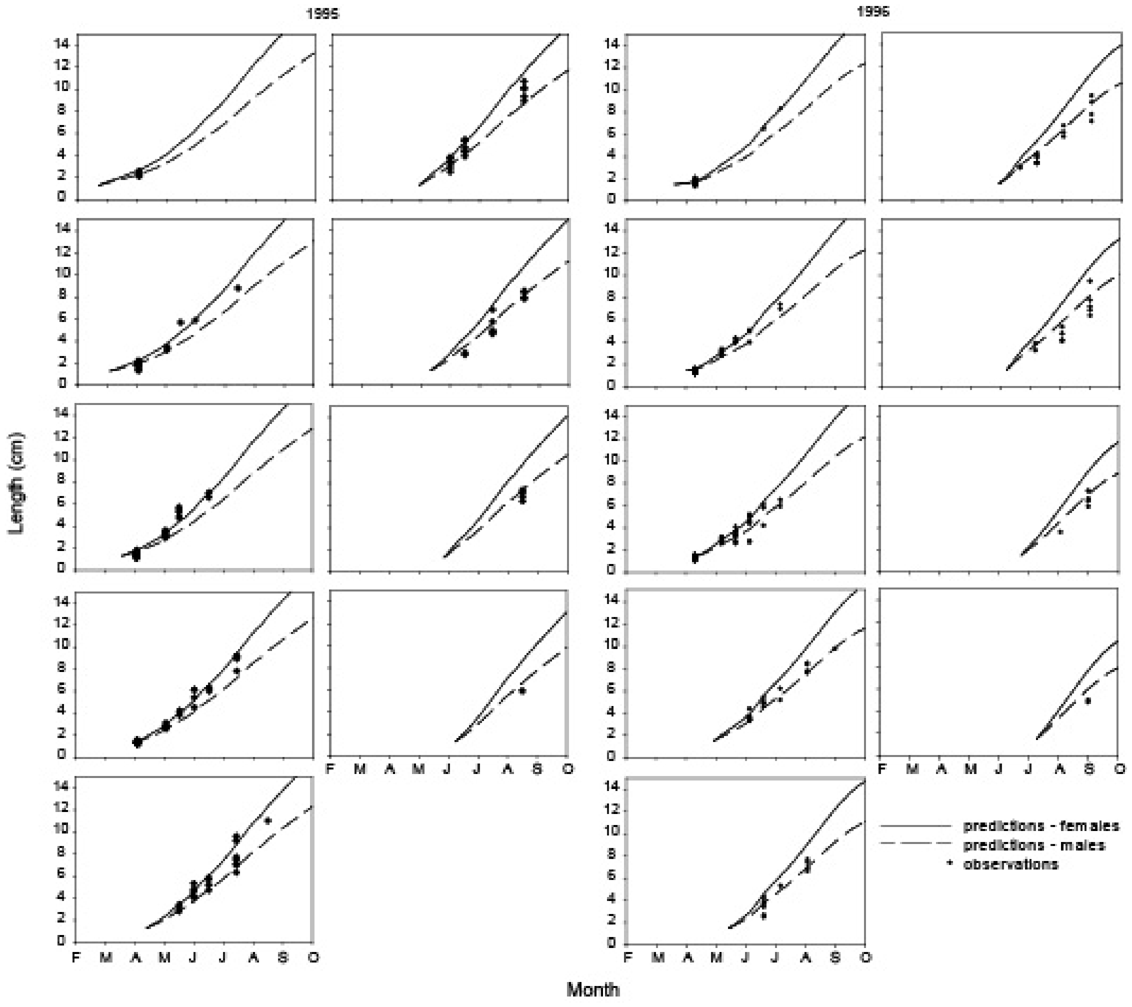

Figure 6

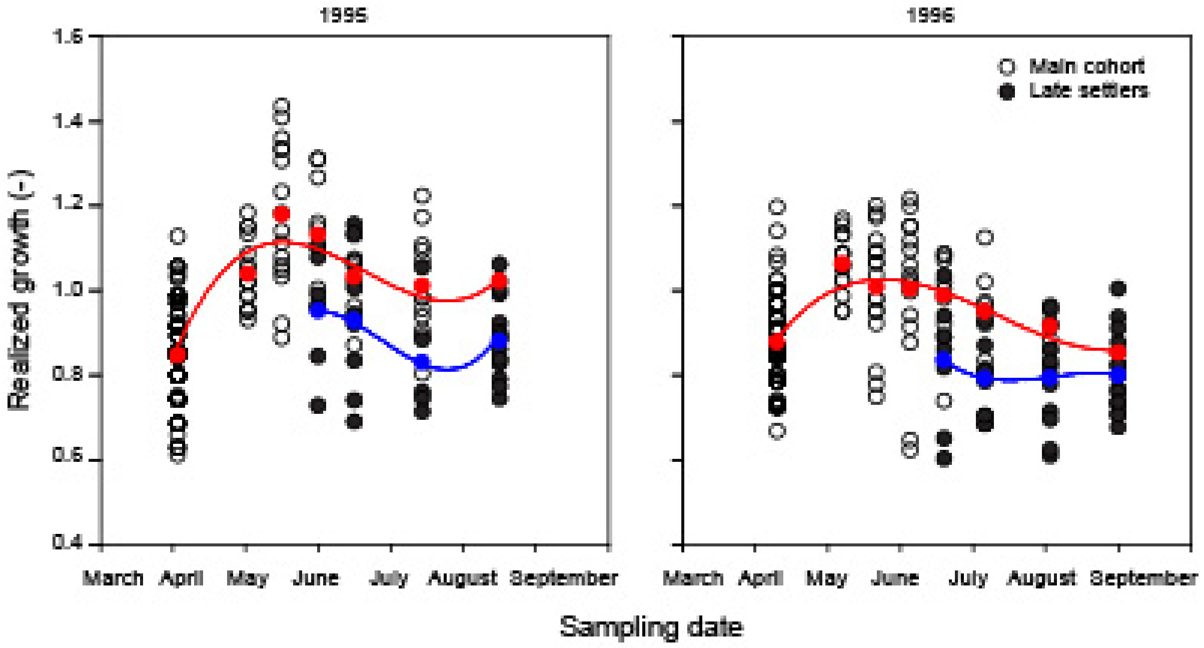

Figure 7

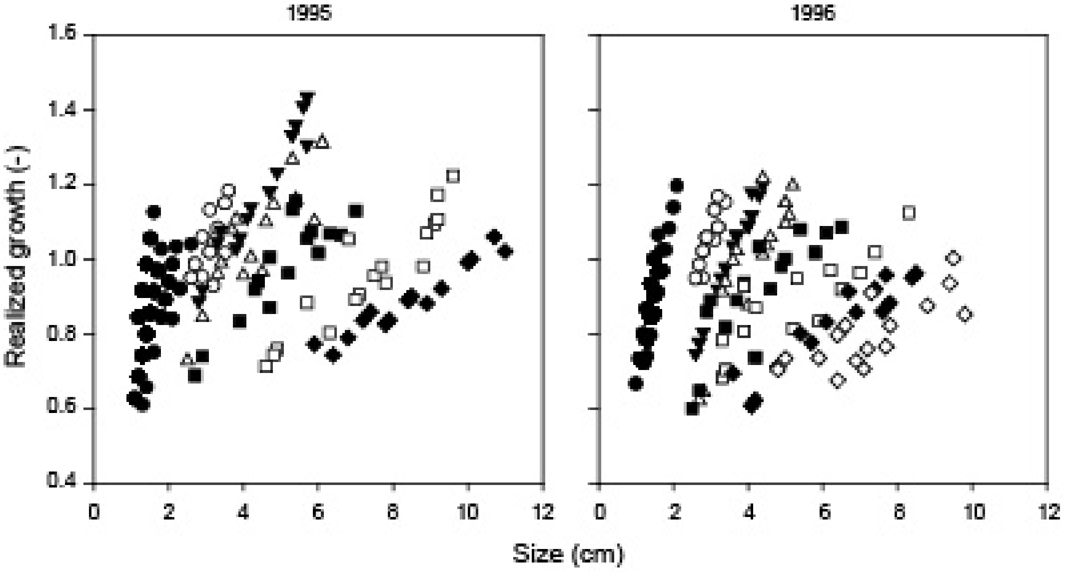
1995
1996
Realized growth (-)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0
2
4
6
8
10
12
Size (cm)

Figure 8

Supplementary information

Table S1. DEB model parameters and temperature dependence parameters for plaice *Pleuronectes platessa*. Whenever parameters differ between sexes, values for males are shown between brackets.

Parameter symbol	Units	Interpretation	Value
v	cm d^{-1}	Energy conductance	0.156
g	–	Energy investment ratio	2.635 (3.930)
k_M	d^{-1}	Maintenance rate coefficient	0.0035
L_w	cm	Maximum physical length	78 (52)
δ_M	–	Shape coefficient	0.219
T_A	K	Arrhenius temperature	7000
T_L	K	Lower boundary of tolerance range	277
T_H	K	Upper boundary of tolerance range	295
T_{AL}	K	Rate of decrease at lower boundary	50000
T_{AH}	K	Rate of decrease at upper boundary	75000

Rates are given at a reference temperature of T_1 = 283 K (=10°C)

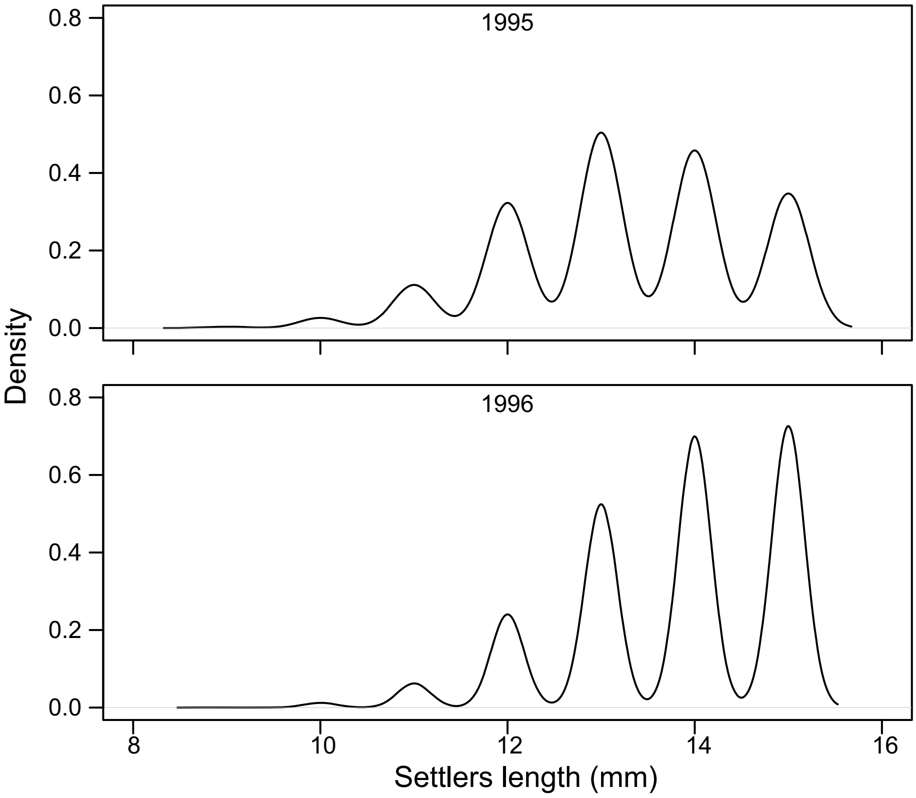

Fig. S1. Density plot of the length frequency distribution of settling larvae (individuals ≤15 mm) of plaice in 1995 and 1996.

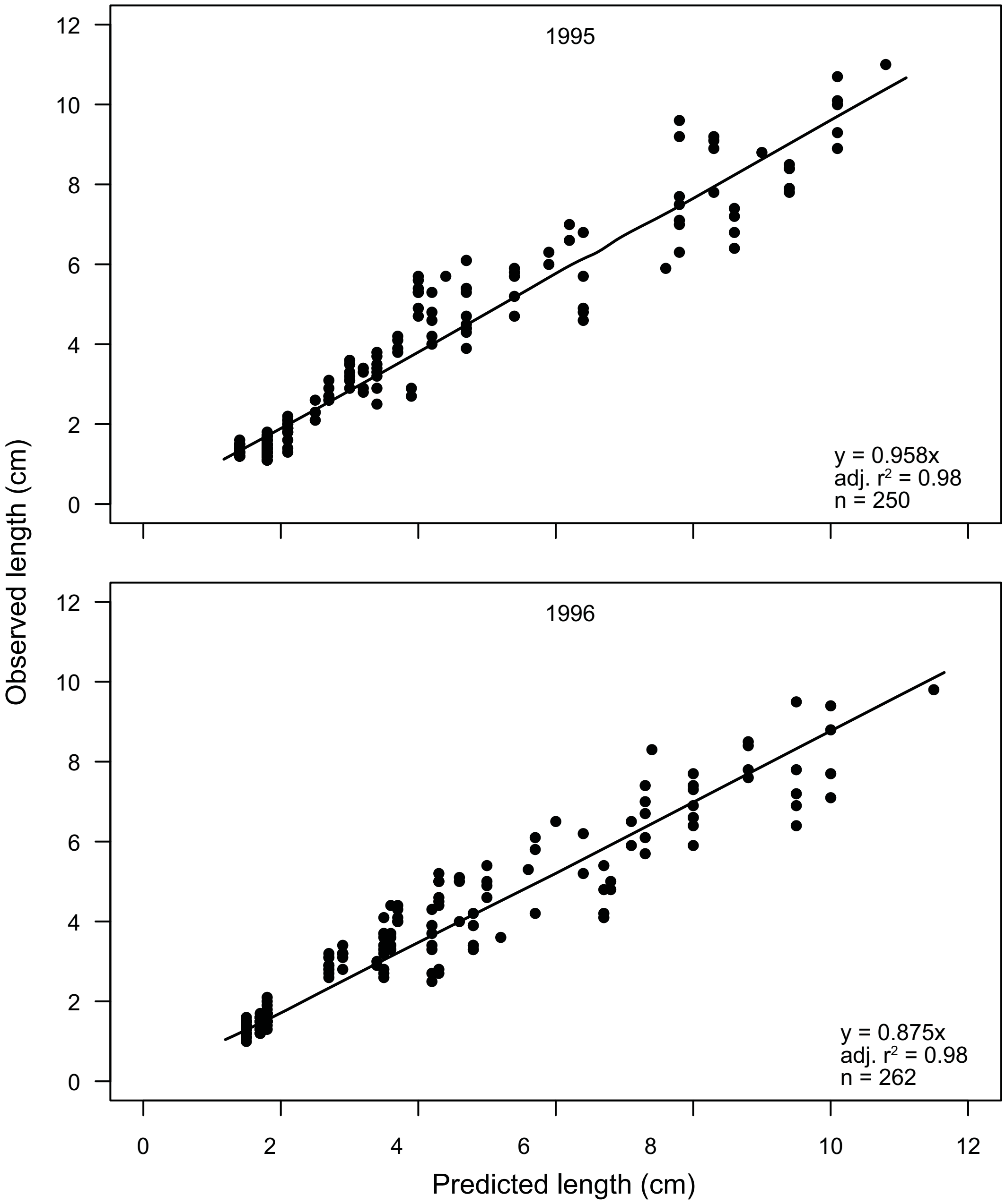

Fig. S2. Plots of observed vs. predicted length (cm) of 0-group plaice in the western Wadden Sea in 1995 and 1996, with respective linear regressions.

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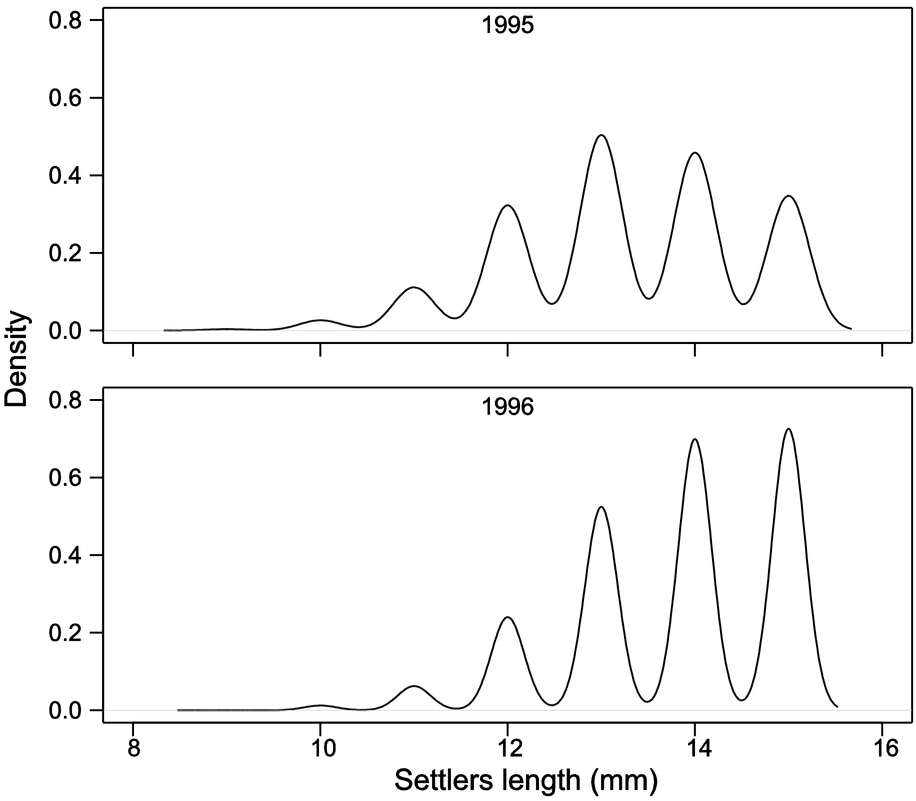

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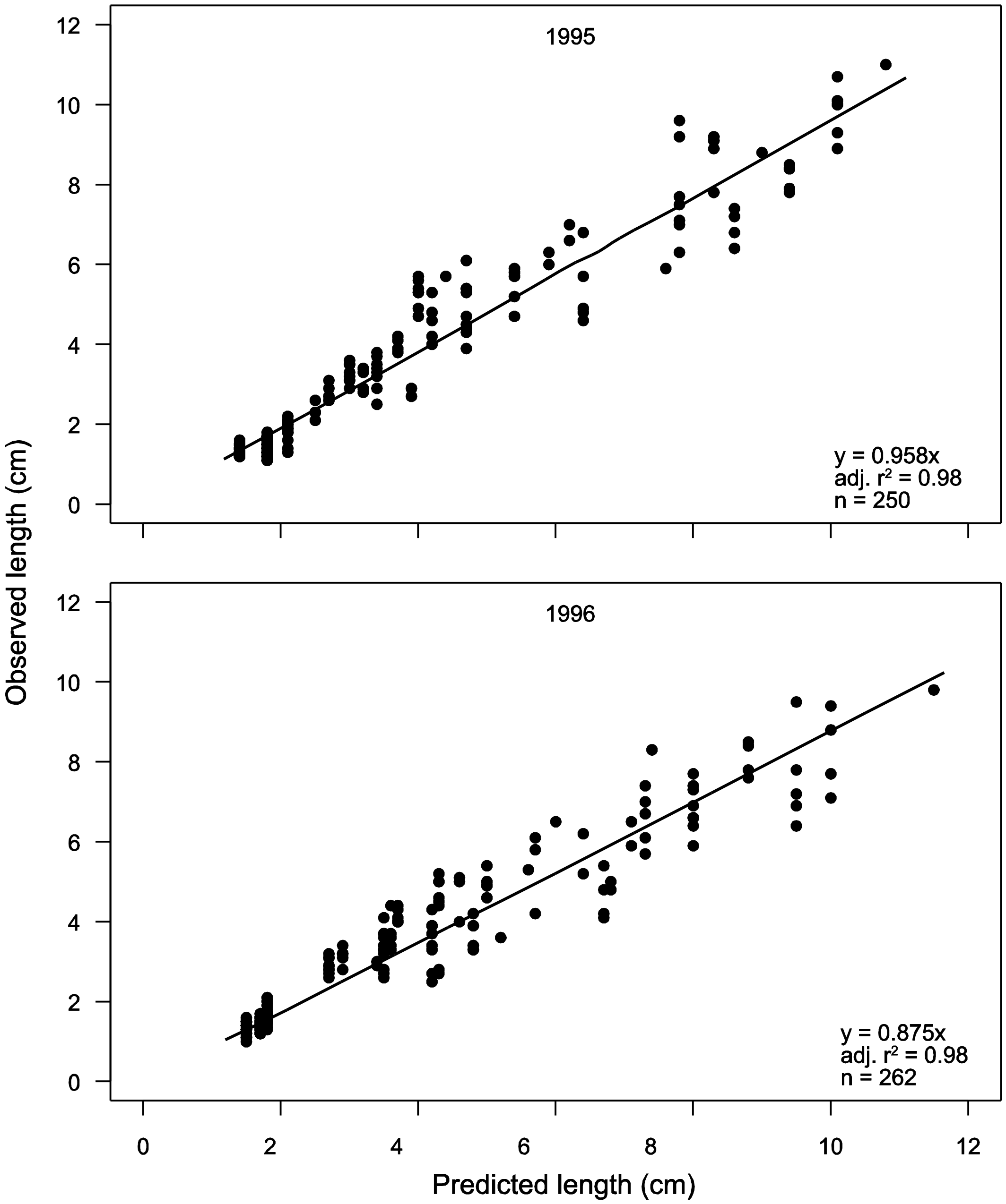

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